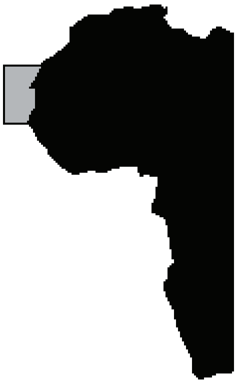

Seasonal dynamics and characterization of coccolithophore export production in two major upwelling regions

Cape Blanc (NW-Africa) & Chile (30°S)

Dissertation
zur Erlangung des Doktorgrades
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vorgelegt von
Meral I. Ikbal Köbrich
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Noch nie ist jemand diesen Weg gegangen,
und niemals wird ein anderer diesen Weg gehen,
denn es ist Dein Weg.

Du siehst Augen, die Dir in die Seele schauen,
da kommen Hände, die geben oder nehmen,
da sind Arme, die halten oder verwehren
da verlauten Stimmen, die dich bereden

Niemand kennt den Weg, den du vor Dir hast,
nur Du,
wenn Du ihn gehst

M.Ikbal K.

Danke …

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... çok teşekkürler

Zusammenfassung

Coccolithophoriden, die eine wichtige Gruppe des Nannoplanktons darstellen, gehören zur Klasse der Prymnesiophyceen. Die Zellen dieser Organismen sind zumeist umhüllt von Karbonatplättchen, den Coccolithen. Bestimmte Coccolithophoriden können definierten Oberflächenwassereigenschaften zugeordnet werden. Daher können einzelne Arten, so wie ganze Gemeinschaften als ozeanografische Indikatoren der Gegenwart, als auch Vergangenheit herangezogen werden.

Aufgrund ihrer ozeanweiten Verbreitung, ihrer Fähigkeit zur Photosynthese und zur Kalzifizierung spielen sie eine gewichtige Rolle im globalen Kohlenstoffkreislauf. Darüber hinaus bilden sie einen großen Anteil des Karbonates der Meeresböden. Im Hinblick auf die zukünftige Entwicklung ist es notwendig Charakteristika einzelner ozeanische Regionen zu erkennen und Zusammenhänge zwischen Coccolithophoriden und Oberflächenwassereigenschaften zu erklären. Um Gemeinschaften über einen längeren Zeitraum zu beobachten ist die Untersuchung mittels Sedimentfallen eine erfolgreiche Methode, wobei die Menge der absinkenden Partikel bestimmt werden können.

In der vorliegenden Untersuchung wurden Sedimentfallenproben aus den Auftriebsgebieten vor NW-Afrika und vor Chile hinsichtlich ihrer Coccolithen Bestandteile untersucht. Diese Gebiete sind als Hochproduktionsgebiete bekannt. Der Küstenauftrieb beeinflusst sogar Gebiete weit außerhalb der Küstenregion Kap Blancs (NW-Afrika). Dort bilden sich so genannte *riesige Filamente*, die in ihrer Ausdehnung und ihrer zeitlichen Fortdauer saisonale und jährliche Schwankungen aufweisen. Der Küstenauftrieb vor Chile ist durch die besondere klimatische Anomalie des El Niño beeinflusst. Beide Gebiete bieten die Möglichkeit Coccolithophoriden-Gemeinschaften aus Auftrieb beeinflussten Regionen zu untersuchen und die Gemeinschaften mit definierten hydrografischen Eigenschaften zu vergleichen.

Die Sedimentfallenzeitserie der Kap Blanc (NW-Afrika) Station umfasst insgesamt vier Jahre (wovon ein Jahr näher an der Küste positioniert war) und jeweils ein Jahr aus den Gebieten vor Chile. Hier wurden die Coccolithenflussraten während des El Niño 1997/98 und eines nicht El Niño Jahres (1993/94) untersucht. Die taxonomische Charakterisierung der beiden Auftriebssysteme hinsichtlich des Coccolithenvorkommens zeigte eine diverse und komplexe Gemeinschaft, deren detaillierte Beschreibung hiermit zum ersten Mal erfolgt. Die Berechnung des Coccolithen-Karbonates, die auf der ausführlichen taxonomischen Identifizierung beruht, zeigte Werte, die in (meso-)eutrophen Regionen zu finden sind.

Durch die Untersuchung einer Sedimentfalle, die näher an dem NW-Afrikanischen Küstenauftrieb ausgesetzt wurde, stellte sich ein definierter jahreszeitlicher Verlauf im Coccolithenexport heraus. Der Vergleich des Exportes mit Umweltparametern wies eine Verknüpfung zwischen der maximalen Coccolithenflussrate und der Windstärke, des Auftriebsgeschehen und der Sonneneinstrahlung auf, als auch die durchschnittliche Oberflächenwassertemperaturen und Nährstoffgehalte des Oberflächenwassers. Hierbei wiesen diese Umweltparameter Werte im mittleren Skalenbereich auf bei gleichzeitiger maximaler Flussrate der Coccolithen. Durch die Untersuchung weiterer Sedimentfallenzeitreihen wurden stark variierende

Coccolithenflussraten sichtbar, die jedoch eine relativ konstante Artengemeinschaft aufwiesen. Vor NW-Afrika ist die Hauptsaison für die maximale jährliche Flussrate der absinkenden Coccolithen Herbst zu Winter, wobei starke jährliche Schwankungen auftreten.

Neben dem allgemeinen saisonalen Verlauf der absinkenden Coccolithen konnte eine signifikante Änderung in der Artengemeinschaft der Coccolithophoriden für den Winter 1990/1991 festgestellt werden. Die gesteigerte Präsenz kleiner Arten wie *Ophiaster spp*. und *Acanthoica spp*. ist durch ein vermehrtes Aufkommen im Oberflächenwasser, als auch ein nachfolgend schneller Transport in die Tiefe erklärbar. Dieses Ereignis spiegelt die starke Dynamik der Kap Blanc Region wieder, ebenso wie die gute Übereinstimmung des Coccolithenexportes mit der sich verändernden Umgebung.

Der Vergleich einer Oberflächensediment-Probe mit der Sedimentfallen-Gemeinschaft vor Kap Blanc, der die Veränderung innerhalb der Artenzusammensetzung ermöglicht, offenbarte eine große Ähnlichkeit zwischen den zwei Gemeinschaften.

Um eine generelle Charakterisierung der Coccolithenflussraten von Auftriebsgebieten zu beschreiben, wurden zusätzlich die Coccolithenflussrate vor Chile untersucht. Bezüglich der Artenzusammensetzung wurde eine ähnliche Gemeinschaft gefunden. Jedoch konnte man eine Phase des vermehrten Exportes gegenüber einer Phase sehr geringen Exportes gegenüberstellen. Diese Phasen wurden in den Proben aus dem El Niño Ereignis nicht dokumentiert. Der Vergleich von Coccolithophoriden und weiteren Planktonorganismen zeigte einen jahreszeitlichen Verlauf der maximale Exportflüsse von nacheinander Diatomeen, Silikoflagellaten, Coccolithophoriden und Foraminiferen. Dieser Verlauf korrespondiert mit dem Nährstoffangebot des von der Küste aufgetriebenen Wassers. Während des El Niño veränderten sich die Eigenschaften des Oberflächenwassers dramatisch, insbesondere in Bezug auf den Nährstoffgehalt. Der beobachtete Exportverlauf des Planktons unterschied sich, spiegelt jedoch wiederum das Oberflächenwasser mit dem reduzierten Nährstoffgehalt wieder.

Der Vergleich der Planktonexporte (Diatomeen, Silikoflagellaten, Foraminiferen und Coccolithophoriden) von dem NW-afrikanischen Auftriebsgebiet legte einen gewissen jahreszeitlichen Ablauf dar: maximale Werte des Phytoplanktons im Winter und der Foraminiferen im Frühjahr. Der Coccolithenfluss zeigte eine ökologische Präferenz der Coccolithophoriden, die hier charakterisiert ist durch Parameter wie z.B. Licht und Nährstoffangebot, Auftrieb und Turbulenz des Oberflächenwassers, die durchschnittliche Werte aufweisen.

Abstract

Coccolithophores, a major group of the nanophytoplankton, belong to the class Prymnesiophyceae. The cells of coccolithophores are typically surrounded by layer(s) of calcium carbonate plates, the coccoliths. Certain coccolithophores can be assigned to particular water masses or to photic zone characteristics and, therefore, single species as well as whole assemblages can be used as oceanographical indicators for the present and the past.

Due to their ocean wide distribution, their large contribution to the fine grained carbonate ooze of the deep sea, their ability to photosynthesize and to calcificate they play an important role in the global carbon cycle. With respect to future development it is necessary to identify characteristics of specific oceanic regions and hence to elucidate the interactions between coccolithophores and water mass properties. To survey communities over a defined period of time, sediment trapping is a successful method which determines the bottomward flux of these particles from the surface waters.

In this study therefore sediment trap samples of the upwelling region off NW-Africa and off Chile were studied in regard to coccolith fluxes. These regions that are associated with equator ward flowing eastern boundary currents have long been recognized for their high productivity. The coastal upwelling influences even areas offshore Cape Blanc (NW-Africa) where giant filaments form fluctuating in extension and duration seasonally and interannually. Off Chile, the coastal upwelling is influenced by the specific climatic anomaly, El Niño. Both areas offer the opportunity to survey coccolithophore assemblages of upwelling influenced regions and to compare the assemblages to distinct different oceanic conditions.

The time-series study of the Cape Blanc (NW-Africa) deployment covered in total four years (one year the sediment trap was deployed closer to the coast) and of Chile one year each. There the coccolith flux of the El Niño event of 1997/98 and during a non El Niño year (1993/4) was studied. The detailed taxonomical characterization of the fluxes of both upwelling systems revealed a complex and diverse community. Its documentation was carried out for the first time. Based on the detailed species identification defined coccolith derived carbonate estimates revealed same fluxes as observed in (meso-)eutrophic regions.

The study of a sediment trap deployed closer to the NW-African coastal upwelling revealed a distinct seasonal cycle of the coccolith flux. The comparison of the coccolith flux pattern with environmental parameters revealed a relationship between maximum coccolith fluxes and average wind, upwelling, irradiance intensities, sea surface temperature, and nutrient content of the surface waters. In general, strongly fluctuating coccolith fluxes were revealed, however, presenting a relatively constant species composition. Off NW-Africa, the season of major coccolith flux seems to be during winter and fall revealing strong interannual variability. Furthermore, a significant change in species assemblage occurred during winter 1990/91. The increased occurrence of small sized species such as *Ophiaster spp.* and *Acanthoica spp.* is explained by the increased occurrence in the surface waters and subsequently fast settling to the deep. This event displays the highly dynamic region of the Cape Blanc region as well as the close correspondence of coccolith flux and the changing environment.

To elucidate the difference of the finally settled and buried assemblage a comparison of the coccolith flux of the sediment trap of Cape Blanc with surface sediment was carried out showing a close similarity between both species compositions.

To generally characterize coccolithophore communities of upwelling regions, the coccolith flux off Chile was additionally studied. With respect to species composition a similar assemblage was present. However a strong seasonal difference of high and low flux periods is documented which was absent during El Niño. The comparison between coccolithophores and fluxes of further plankton species showed a seasonal pattern of subsequently occurring maximum fluxes of diatoms, silicoflagellates, coccolithophores and foraminifers which corresponds to the nutrient availability of the coastal upwelled water. During El Niño a massive change in water properties, especially nutrient load occurred. The observed flux pattern of the plankton was different, but again displaying the surface waters with its decreased nutrient load.

The comparison of the plankton fluxes (diatoms, silicoflagellates, foraminifera, and coccolithophores) for the NW-African upwelling revealed a certain seasonal pattern, with maximum fluxes of phytoplankton in winter and of foraminifera in spring. Here the coccolith fluxes revealed the ecological preferences of the coccolithophores as a niche that is characterized by average ranged parameters such as light and nutrient availability, upwelling and turbulence of the surface water.

Contents

I. Introduction

1.1 Coccolithophores

General Introduction

Coccolithophores are a major group of the phytoplankton. They belong to the class Prymnesiophyceae. Typically, the cells of coccolithophores are surrounded by layer(s) of calcium carbonate plates, the coccoliths. As a result coccolithophores are of major interest in respect of climate. Owing to their great abundance and their capability to carry out photosynthesis and calcification they interact manifold with climate and in the world biogeochemical cycles (Westbroek *et al.*, 1993) (Fig. 1.1.).

Coccolithophores have a widespread oceanic distribution pattern, living in the photic zone and being most diverse at low latitudes. They seem adopted to warm, oligotrophic, stratified, respectively low turbulent, and stable water conditions (Brand, 1994; Kinkel *et al.*, 2000; Kleijne, 1993; McIntyre and Bé, 1967; Mitchell-Innes and Winter, 1987; Winter and Siesser, 1994). However, there standing crops are low reflecting low reproduction rates. On the other hand, some species bloom in highly productivity regions (e.g. *Emiliania huxleyi* and *Gephyrocapsa oceanica* (Broerse, 2000)). Generally highest population growth occurs in regimes with higher nutrient availability, such as upwelling environments (Boeckel, 2003).

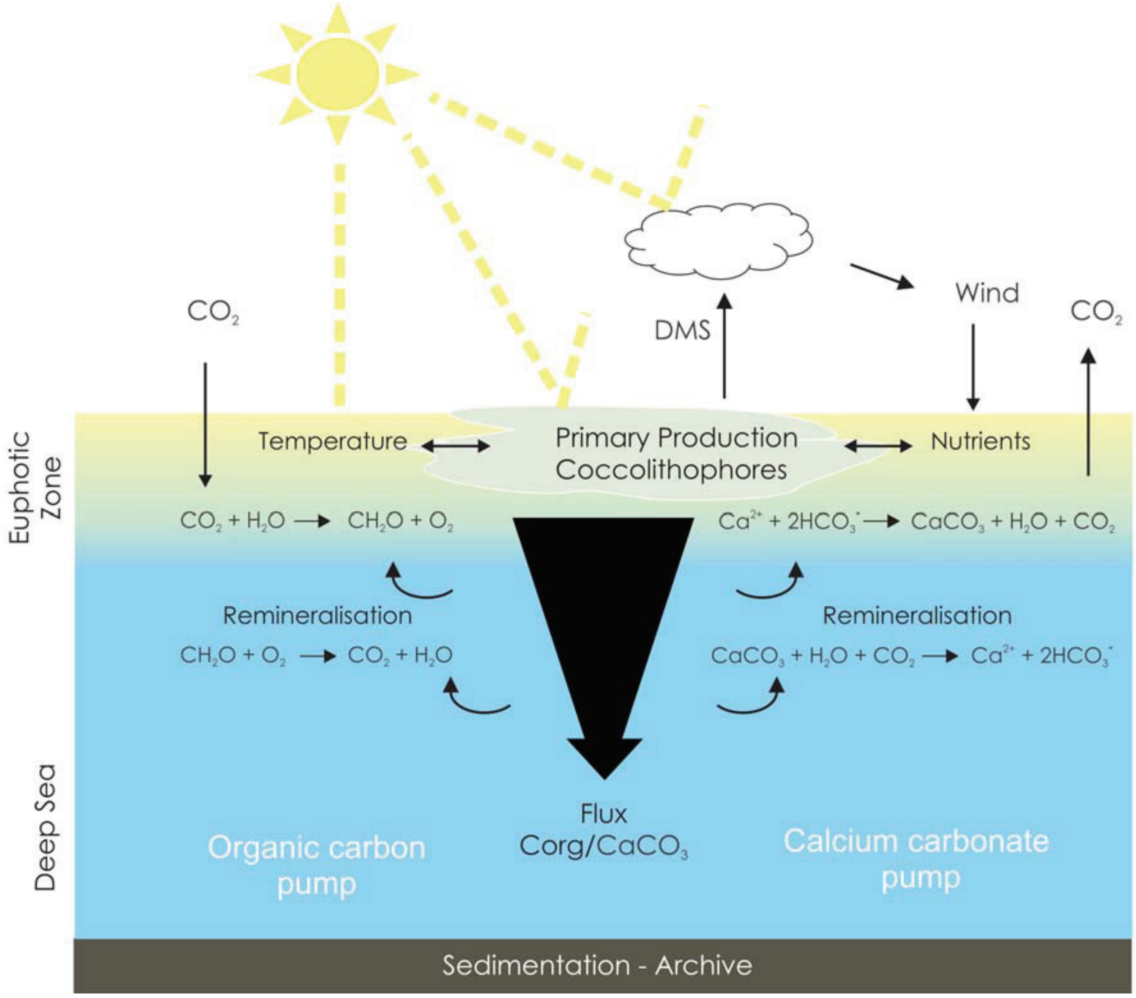

Fig 1.1: Overview of major oceanic and atmospheric processes associated with the primary production of coccolithophores. Bloom forming species increase the albedo effect (substantially reflection of incoming light). Some coccolithophores can emit dimethylsulphoniopropionate that oxidizes to dimethylsulfid (DMS) which in turn acts as a condensation nuclei, thus triggers the formation of clouds. Due to growth (photosynthesis) and death (remineralisation) coccolithophores interact with the global carbon pump and due to the production and loss of coccoliths with the global calcium carbonate pump.

Due to protected and accelerated bottomward transport via faecal pellets (Honjo, 1976) or in mucous bound macroaggregates (marine snow), the sediment coccolith assemblages preserve the general composition of the overlying photic zone communities (Baumann *et al.*, 2000; Kinkel *et al.*, 2000; McIntyre, 1967; Okada and Honjo, 1973). The resulting taphocoenose of the settled coccolithophores show a distinct biogeographic distribution patterns, defining latitudinal belts or zones of coccolithophores assemblages (McIntyre and Bé, 1967). Five zones are recognized (McIntyre and Bé, 1967; Okada and Honjo, 1973; Winter *et al.*, 1994; Winter and Siesser, 1994): subarctic, transitional (temperate), subtropical, tropical and subantarctic. However, this simplistic classification omits effects of coastal currents, gyres, eddies, upwelling (Quinn *et al.*, 2004; Sáez *et al.*, 2004) and rather obscures species specific biogeography.

Recent studies of distinct species (*Coccolithus pelagicus*, *Calcidiscus leptoporus*, *Helicosphaera carteri*, *Syracosphaera pulchra*, *Umbilicosphaera spp.*) and the genus *Gephyrocapsa* expand the knowledge and reveal differences between coccolithophores distribution patterns of northern and southern hemisphere of the Atlantic (e.g. the absence of *C. pelagicus* in the Subantarctic and the presence of *C. leptoporus* in temperate South Atlantic in higher abundances (Boeckel, 2003; Ziveri *et al.*, 2004). In general, these floral zones are characterized by variations in assemblage composition rather than high endemicity. The great majority of coccolithophore species being virtually cosmopolitan displaying broad ecological tolerances (Bown, 1998; McIntyre and Bé, 1967; Young *et al.*, 2005).

Proxy

The production and sedimentation of biogenic particles in the ocean are strongly coupled. Seasonal flux patterns of biogenic material within the water column usually reflect biological production cycles in the surface waters (Deuser *et al.*, 1990; Honjo *et al.*, 1982). Variations in magnitude of biogenic particle fluxes reported from different oceanic sites can be related to different productivity conditions of large-scale surface water biogeochemical provinces (Jickells *et al.*, 1996). Coccolithophores quickly respond to fluctuations in surface condition and are therefore well suited to preserve the longer-term climatic signal (Andruleit *et al.*, 2004; Giraudeau *et al.*, 1993; McIntyre and Bé, 1967; Samtleben and Schroeder, 1992). As a result, the distinct assemblages of coccolithophores can be assigned to particular water masses or to photic zone characteristics and, therefore, single species as well as whole assemblages can be used as oceanographical indicators (Okada and Honjo, 1973; Winter and Siesser, 1994). Coccolithophores in sediments provide good proxy records of the environmental conditions that control the distribution and production of calcareous nannoplankton in surface waters and dissolution of their calcitic remains on the sea floor (Roth, 1994). Thus, the understanding of extant coccolithophore ecology is needed to quantitatively assess the information preserved in the sediment record, and to use it as biotic proxies of climate change.

Sediment trap

To survey the export production of living surface water communities sediment trapping is a successful method. The quantity and composition of sinking matter, as measured with traps, are functions of variable components within the overlying pelagic system (Delesalle *et al.*, 2001; Legendre and Rassoulzadegan, 1996; Peinert *et al.*, 1989) and reflects the seasonality of the production (Deuser *et al.*, 1990). For coccolithophores, the material of sediment traps provide invaluable information on species composition and their seasonal variations in abundance (Broerse, 2000; Samtleben and Bickert, 1990; Ziveri *et al.*, 1995).

Regional time series studies

Recent studies imply regional characteristics regarding coccolithophore distribution, as well as detailed and specified ecological preferences (Andruleit *et al.*, 2000; Chen *et al.*, 2007; De Bernardia *et al.*, 2005; Tanaka, 2003; Triantaphyllou *et al.*, 2005; Ziveri *et al.*, 2000a,b; Ziveri and Thunell, 2000). For example, in the Canary Island region a distinct seasonal pattern of high flux and low flux period was depicted with a coccolithophore assemblage revealing a rather constant relative distribution over time. Nevertheless, interesting findings about the relationship of *Emiliania huxleyi* and *Florisphaera profunda* were made (Sprengel *et al.*, 2000). Even short time events as bloom development and their ecological implications can be observed (Andruleit, 1997; Broerse *et al.*, 2000b), as well as single species bloom like pulses (Beaufort and Heussner, 1999; Knappertsbusch and Brummer, 1995).

$CaCO_3$ - Flux

Due to these detailed studies regarding species composition of the coccolithophore community and the knowledge about species specific carbonate mass (Young and Ziveri, 2000) the contribution of coccolithophore to the overall calcium carbonate export can be estimated broken down according to different oceanic regions (Broerse, 2000; Tanaka and Kawahata, 2001).

Plankton community structure

Interannual variability induced by reoccurring hydrographic/climatic conditions as the El Niño–Southern Oscillation (ENSO) phenomenon gives the opportunity in combination with sediment trapping to study the development and the resulting effects to the existing phytoplankton community and in particular to the coccolithophores (De Bernardia *et al.*, 2005). The seasonal export pattern of different phytoplankton groups and their interaction or relationship to coccolithophores was infrequently a further focus of former studies (Beaufort and Heussner, 1999; Jickells *et al.*, 1996; Romero *et al.*, 2002a). In general, the efficiency of the biological carbon pump is dictated by the composition of the phytoplankton. Consequently, the impact of primary production on marine (geo-)chemistry strongly depends on the species of phytoplankton that photosynthesize (Dandonneau *et al.*, 2004). In upwelling regions the plankton community is dominated by diatoms (Romero, 1998), whereas high numbers of coccolithophores usually occur besides the primary upwelling centres in waters with low silica content (Giraudeau *et al.*, 1993). Within the phytoplankton succession observed in upwelling areas, they often follow blooms of diatoms, when the photic zone becomes depleted in silica and starts to stratify (Giraudeau and Bailey, 1995; Mitchell-Innes and Winter, 1987). Further, these aspects are of importance since they display the basic parameter for modelling future development of phytoplankton communities and their implication for global climate (change) (Gregg and Casey, 2007). First attempts of modelling coccolithophore and further phytoplankton groups have been made for NW-Africa (Giraud, 2006) and the Black Sea (Oguz and Merico, 2006).

Living – settling - accumulation

The study of collected material via sediment trap is a link between the findings of the living community (plankton samples) and of the over time accumulated taphocoenose. In case of plankton samples which are always random records affected by the patchiness of distribution (Martin, 2003; Srokosz *et al.*, 2003) a large number of samples would be needed to provide sufficient information on seasonal or interannual patterns (Andruleit *et al.*, 2004). Despite of this, plankton samples provide information of highly variable coccolithophore communities displaying changing environmental parameters (nutrients and interaction with other phytoplankton) on an almost daily scale (Andruleit *et al.*, 2003).As a result they provide invaluable information on the extant coccolithophore ecology and diversity. The knowledge of intraseasonal and interannual variations increases due to the study of settling assemblages even though alterations take place (e.g. grazing, breakage, and dissolution). Sediment trap samples are reminders of different assemblages within a longer time period. The settling particles are collected from a broader area which is influenced by currents and eddies. Thus, the annually averaged assemblages of the traps can be used to discuss the occurrence of taxa in surface sediments, as well as their ecological preferences (Andruleit *et al.*, 2004; Baumann *et al.*, 2005).

However, despite all alterations processes leading to altered and impoverished fossil assemblages, the coccolithophore record has a much higher preservation capability than many other proxies and thus a unique potential to monitor and reconstruct environmental changes such as overall production pattern (Balch *et al.* 2004; Beaufort *et al.* 1996).

As result of the past studies dealing with the described diverse aspects of coccolithophore ecology and relationships, the knowledge increased steadily. Nevertheless, especially in highly productive areas such as continental margins little is known about the importance of coccolith export and coccolithophore ecology respectively export species assemblage. Although roughly half of the oceanic biogeochemical cycling concentrates on continental margins, processes controlling fluxes in these important areas are far from being fully understood. Various approaches are needed to identify and quantify particulate transport mechanisms at these ocean boundaries (Beaufort and Heussner, 1999).

1.2 Upwelling in Eastern Boundary Current Systems

The regions associated with the Atlantic and Pacific equatorward-flowing Eastern Boundary Currents (EBC), i.e. the California, Humboldt, Canary, and Benguela Currents, have long been recognized for their high productivity (Barber and Smith, 1981). Although their area makes up a small fraction of the world ocean (by most estimates less than 1%), they account for 5% of global marine primary production and 17% of global fish catch (Pauly and Christensen, 1995). High productivity areas such as the eastern boundary current systems take up 15% of the world oceans but still account for almost half of the global export production (Berger, 1989).

Production

Efforts to evaluate the potential production of the world ocean have been made since there were sufficient data to infer a global estimate. Current global values (Berger, 1989) based on in situ data (i.e. C^{14} uptake) range between 20 and 50 Gt C (1 Gt C = 1015 g C): Global satellite-based values range from 27 to 50 Gt C yr^{-1}; with most models exceeding 40 Gt C (Behrenfeld and Falkowski, 1997). Although satellite-based primary production algorithms still contain uncertainties of a factor of two when compared with in situ data (Balch *et al.*, 1992; Balch and Byrne, 1994).

Process

This high biological productivity is fuelled by nutrient laden upwelled water based on equatorward wind along the north-south coastline. The shallow offshore flow maintains the upwelled water in high light conditions for sufficient time to enable biological utilization (Carr, 2002a). Upwelling itself is a mesoscale process that occurs in direct vicinity to the coast. However, the productive band of high phytoplankton biomass is wider and extends to over 100 km. Major Eastern boundary current systems can be subdivided into subregions which extend 500 km offshore due to the influence of filaments developing and moving offshore by the wind forcing, pronounced example is off NW-Africa (Gabric *et al.*, 1996; Kostianoy and Zatsepin, 1996).

Wind stress

The four major eastern boundary current systems are characterized by latitudinally varying seasonal cycles of equatorward coastal wind stress. Further they can be meridionally differentiated by seasonal cycles of wind forcing (Carr, 2002a). In general, occasionally occurring strong winds have a disproportionately large influence on water movement. Upwelling rates fluctuate greatly in response to fairly small changes in wind speed (Colling and Brown, 2001). In this respect, the Canary Current presents the greatest variability, both with latitude and within monthly averages (Carr, 2002a).

Mixed layer

Further, strong winds determine a mixed layer that may extend 50 m or more below the surface (Colling, 2001; Dugdale and Wilkerson, 1985). If the strength of the wind causes the mixed layer to be deeper than the euphotic zone light limitation of the phytoplankton and restriction of primary production may occur (Gabric *et al.*, 1993). In case the advection of the deep water to the surface subsequently stabilizes the nutrient-laden water in the euphotic zone by solar heating the fundamental mechanism will support the high biological productivity of coastal upwelling ecosystems (Huntsman and Barber, 1977; Nykjær and van Camp, 1994).

SST Anomaly

In general, the upwelled nutrient-rich sub-thermocline water derives from 50-200 m depth. As a result, the coastal water is colder than the surrounding water and is used to determine upwelling events (or at least an influence by upwelling impulses) (Colling, 2001). To calculate the difference between sea surface temperature (SST) of the upwelling region and an open ocean area of the same latitude can be used to determine an upwelling index (sea surface temperature anomaly). A difference greater than minus three is defined as upwelling (Speth *et al.*, 1978; Speth and Köhne, 1983).

Summary

In summary, upwelling regions have in common a high productivity and variable wind forcing in time and space. This results in fluctuation of upwelling events that in turn may include alteration in filament development, their offshore movement as well as their expansion. Consequently, nutrient concentration of the surface water undulates. In addition to changing nutrient input, primary production is strongly influenced by turbulent mixing (light limitation) induced by strong wind pulses. The studied areas off NW-Africa and off Chile differ in their dependence and imprints on the mentioned features. Further, they possess peculiar features influencing the hydrography. Therefore, the study areas will be introduced in the following characterizing their peculiarities.

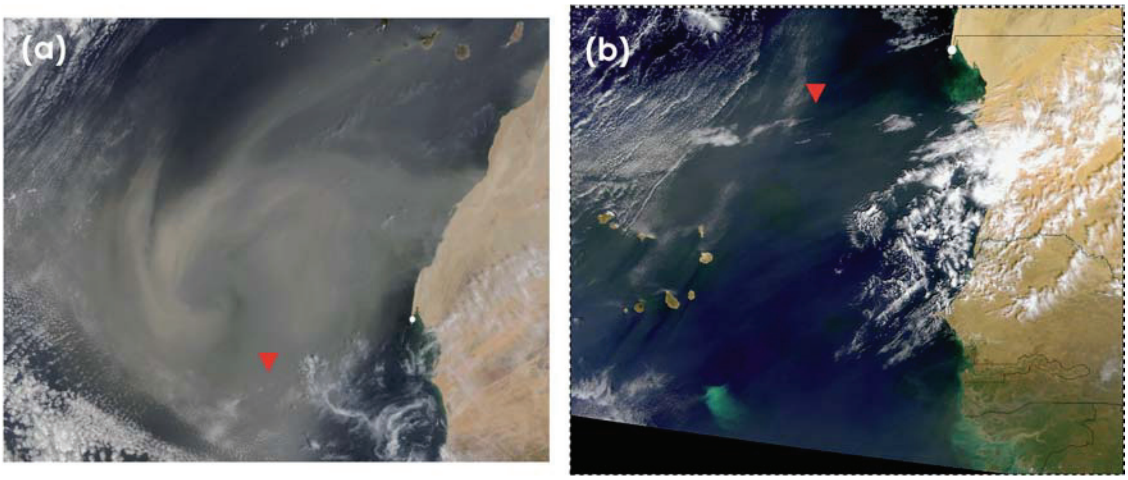

Fig. 1.2:
(a) Iimage of dust blow off the Mauritanian coast
(b) Phytoplankton bloom off Mauritania
white dot: Noudahibou at Cape Blanc
red triangle: Sediment trap

1.2.1 Study area: Cape Blanc, NW-Africa

Wind

The upwelling region along the NW-African coast differs in intensity during the seasons. Off Cape Blanc the upwelling is year-round driven by the trade winds. The wind direction during 1998 to 1991 was mostly from east and northeast. In general, fluctuations in wind speed occurs at 10 to 20 day intervals when an eastward shift takes place and the velocity diminishes for a period of about 3 days (Dugdale and Wilkerson, 1985). Almost immediately the surface offshore flow diminishes and the countercurrent moves in close to the shelf break (Barton *et al.*, 1998; Gabric *et al.*, 1993; Huntsman and Barber, 1977).

Mixed Layer

Besides the upwelling the strong winds produce a mixed layer that extends 50m or more below the surface (Dugdale and Wilkerson, 1985; Huntsman and Barber, 1977). Especially during winter time the continental trades occasionally extend over the sea blowing very dry and warm air offshore loaded with dust from the Sahara (Fig. 1.2a). The lithogen flux of the sediment trap may mirror the dust load. The maximum flux was observed in spring followed by alteration between high fluxes and minimum fluxes throughout the year (Ratmeyer *et al.*, 1999b). The dust load may be an additional source fertilizing the open ocean (Moore and Braucher, 2007), thus influencing the existing phytoplankton community.

Giant filaments

The advection of the deep water to the surface and the subsequent stabilization of the nutrient-laden water in the euphotic zone by solar heating is the fundamental mechanism supporting the high biological productivity of coastal upwelling ecosystems (Huntsman and Barber, 1977; Nykjær and van Camp, 1994). This coastal upwelling is connected with a southward flow over the shelf. As a result off Cape Blanc elevated pigment concentrations are observed on a regular basis (Fig. 1.2b). This filaments develop and move from the coast some hundreds kilometres offshore (Kostianoy and Zatsepin, 1996). The area of elevated pigment concentration is a result of the combined effects of offshore export primary production and upwelled nutrients and in situ growth of phytoplankton in offshore waters (Gabric *et al.*, 1993; Lange *et al.*, 1998). The upwelling centre moves seaward at a speed of 4-5 km d^{-1} during an upwelling event. After 4-6 days of persistent wind forcing the centre reaches the shelf break and remains there until relaxation of the wind (Gabric *et al.*, 1993). The plumes and filaments extend at least 450 km from the adjacent coast (Barton, 1998). Surface water masses between 24°N and 20°N called giant filament persist throughout the year but the intensity varies interannually and seasonally (van Camp *et al.*, 1991). Even though the sediment traps were not moored within the coastal upwelling cell they were influenced by the upwelling events due to the offshore meandering giant filaments (Gabric *et al.*, 1993) (Table 1).

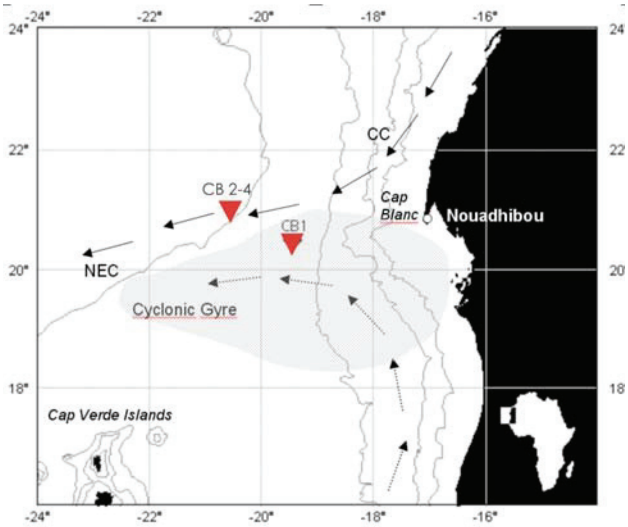

Fig. 1.3: Hydrography of the mooring location of CB; shaded area: affected by a mesoscale gyre

Besides these filaments, the hydrography off Cape Blanc is complex focusing on near surface currents due to a cyclonic gyre. A mesoscale gyre exists south of the area where the CC detaches from the continental slope which occurs throughout the year (between 15° and 22°N). This persistent mesoscale cyclonic gyre varies in position within the seasons, being furthest north in autumn to winter

Mooring	Trap type Opening	Position	Water depth	Trap depth	Sampling duration	Samples x days
CB 1	Mark V (0.5 m^2)	20°45.3'N 19°44,5'W	3646 m	2195 m	Mar 22 88– Mar 08 89	13 x 27
CB 2	Mark VI (1.17 m^2)	21°08.7'N 20°41.2'W	4092 m	3502 m	Mar 15 89– Mar 24 90	22 x 17
CB 3 up CB 3 low	Kiel SMT 230 (0.5 m^2)	21°08.3'N 20°40.3'W	4094 m	730 m 3557 m	Apr 29 90 – Apr 08 91	19 x 21.5 16 x 21.5
CB 4 up CB 4 low	Kiel SMT 230 (0.5 m^2)	21°08.7'N 20°41.2'W	4108 m	733 m 3562 m	May 03 91– Nov 19 91	19 x 10 20 x 10
CB 9	Kiel SMT 230 (0.5 m^2)	21°15,2'N 20°42.2'W	4121 m	3580 m	Jun 11 98 – Nov 07 99	20 x 27.5*

Table 1.1: Mooring location, duration and water depth of the studied sediment traps off Cape Blanc;

*CB 9 1.sample 7.5 days, last 11.5 days
CB4 up Data from Baumann pers. comm.

Mesoscale gyre

and largest in summer (Barton, 1998) (shaded area in Fig. 1.3). It is fuelled by the Canary Current that veers away from the shelf to continue as the North Equatorial Current toward the west. The cyclonic water moves between the Canary Current and Africa south of 20°N with northward advection of warm water in the east (Klein and Tomczak, 1994).

Water masses

This circulation extends through the upper permanent thermocline. As a result the South Atlantic Central Water (SAWC) is advected northward along the African shelf. A frontal zone that extends from 20°N in the east and 10°N in the west separates the North Atlantic Central Water (NACW) and South Atlantic Central Water, the water masses of the North Atlantic thermocline (Klein and Tomczak, 1994). These water masses differ in their characteristic regarding salinity and nutrient load with NACW being saltier and less nutrient–rich (Barton and Hughes, 1982; Mittelstaedt, 1991). Further SACW water is always mixed upward but never downward.

Summary

In summary, the environmental condition of the mooring location varies significantly seasonally and interannually. Based on the variability of the trade winds mesoscale changes in upwelling events occur, which in turn forces the development and movement of the giant filaments. Additionally wind induces turbulent mixing that may result in light limitation, at least in fluctuating light conditions (Dugdale and Wilkerson, 1985). Further the source of the upwelled water – either SACW or NACW – determines the nutrient input via upwelling, thus strongly influencing the phytoplankton production of the euphotic zone.

1.2.2 Study area: Chile (30°S)

Peru-Chile Current

The Peru-Chile Current is a typical representative of an Eastern Boundary Current (EBC) system (Shaffer *et al.*, 1995). Nevertheless, its productivity is outstanding even within the EBC systems. Due to its extension of over 40° of latitude and its persistent coastal upwelling it contributes largely to the organic production of the western Pacific and has substantial importance for fish catches (Escribano *et al.*, 2004; Hebbeln *et al.*, 2000). As a result, the production exceeds 2 g C m^{-2} d^{-1} and is almost twofold higher than the production of other Eastern Boundary Current systems of the eastern Pacific (Carr, 2002b). During the season maximum pigment concentrations are present in austral winter (July to September) whereas in austral summer (December to April) the minima is observed (Thomas *et al.*, 1994). The export flux revealed a high percentage of carbonate (>50%) (Hebbeln *et al.*, 2000). Thus, the question of the proportion of coccolithophores to this high carbonate flux arises. The phytoplankton distribution of the Peru-Chile Current System is often characterised by a high temporal and low spatial variability (Montecino *et al.*, 2002).

Table 2 Mooring location, duration and water depth of the studies sediment traps off Chile

Mooring	Position	Trap depth	Water depth	Sampling duration	Samples x days
CH 3-1	30°01.5'S 73°11.0'W	2333m	4360m	22.07.1993– 18.01.1994	20 x 9
CH 4-1	30°00.3'S 73°10.3'W	2303m	4330m	25.01.1994– 04.07.1994	20 x 8
CH 10-2	29°59.9'S 73°16.8'W	2578m	4500m	14.02.1997– 01.11.1997	20 x 13
CH 11-1	29°58.8'S 73°18.1'W	2526m	4442m	15.11.1997– 01.07.1998	19 x 12

Upwelling process

The process of the primary upwelling off Chile is driven by the trade winds. The northern region of Chile (18-30°S) experiences year-round coastal upwelling and moderate wind speed (5-10m s^{-1}) with maximum winds coming from S-SW during spring-summer (Blanco *et al.*, 2001). The events of upwelling favourable wind off central Chile (27°-37°S) lasts 2-3 days with a periodicity of around one event per week (Rutllant *et al.*, 2004a). Within the season a difference in intensity of the upwelling exists with the maximum favourable winds in spring and winter (Rutllant *et al.*, 2004b). Due to wind relaxation and veering to NW, the nutrient-rich water advects onshore as it downwells against the shelf. These processes increase the stability of the water column, favouring phytoplankton growth (Escribano *et al.*, 2004). As long as the westerly component is dominant (July to October) pigment concentrations are >0.2 mg m^{-3} at the mooring location of the studied sediment traps which lies off the primary coastal upwelling centre (Thomas, 1999; Thomas *et al.*, 2001). Satellite derived images reveal the influence of offshore waters by filaments developing and moving from the coast (Fig. 1.4).

'Normal' condition

The studied sediment traps CH3-1 and CH4-2 (Table 2) were moored within the 1990 to 1995 El Niño Southern Oscillation (ENSO) phenomenon, however, they are regarded as an example of a year displaying 'normal' hydrographic condition (Trenberth and Hoar, 1996). SST as well as the indices Southern Oscillation Index (SOI) and Monthly Multivariate ENSO Index (MEI) exhibit normal conditions, i.e. non El Niño or La Niña condition (Blanco *et al.*, 2002) prevailed off Chile during the study period of 1993 to 1994 (Fig. 1.5).

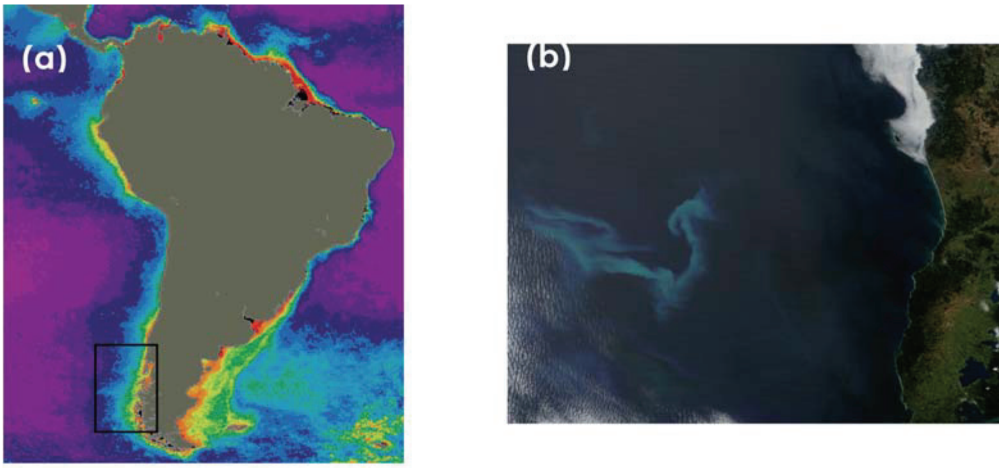

Fig. 1.4: (a) Continent of South America with chlorophyll concentration (yellow to red high concentration, blue to purple low); Image was acquired by the Medium Resolution Imaging Spectrometer (MERIS) aboard the European Space Agency's ENVISAT **(b)** Phytoplankton bloom offshore Chile; image taken by MODIS; visibleearth.nasa.gov

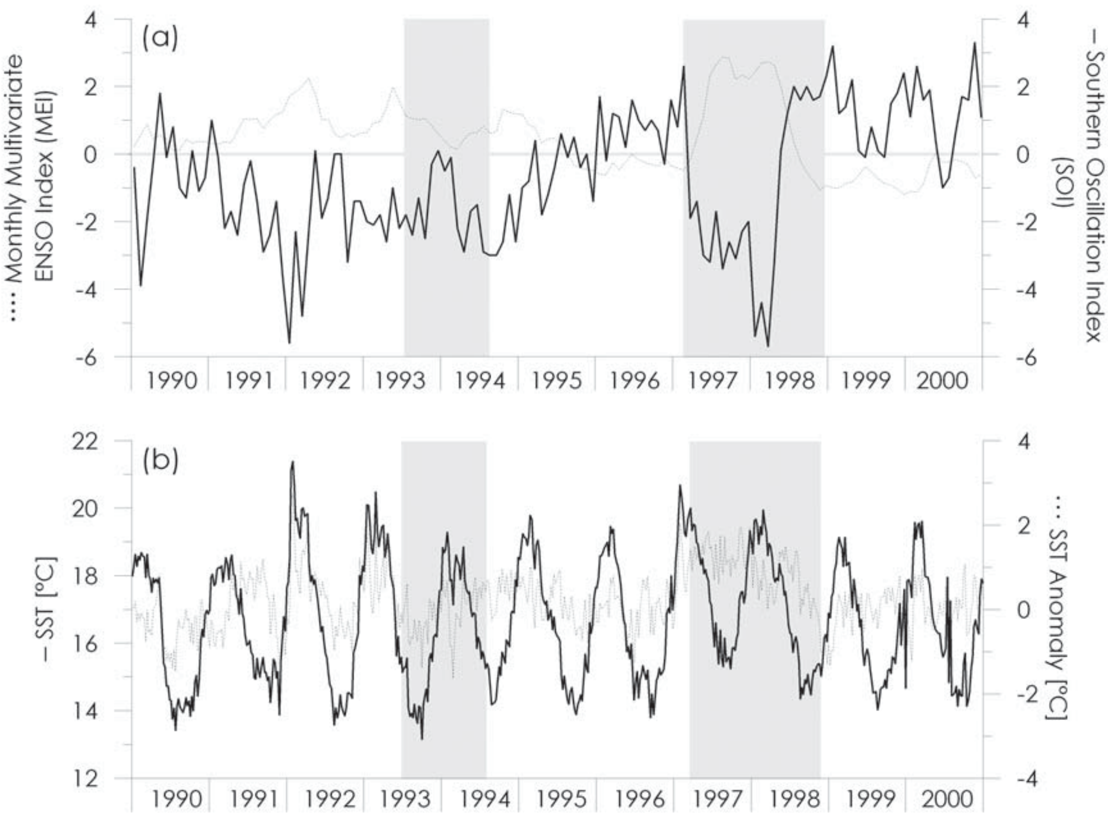

Fig. 1.5:
(a) Monthly Multivariate ENSO Index (MEI, dotted line) Southern Oscillation Index (SOI, drawn through line)
(b) Sea-surface temperature (SST) (drawn through line; data from IGOSS nmc Reyn_SmithOIv2 weekly SST) and SST Anomaly (dotted line) at the mooring site. The shaded areas indicate the study periods: 1993-94 (CH 3/4) and 1997-1998 (CH 10/11).

El Niño - Southern Oscillation

The additional study of two further sediment traps (CH10-2, CH11-1; Table 2) enables the comparison between the coccolith assemblage of 'normal' hydrographic conditions and the coccolith assemblage during drastic changed environmental setting due to El Niño. The El Niño/Southern Oscillation (ENSO) events in the tropics trigger the most dramatic changes in meteorological and hydrographic conditions over the entire Pacific (see references in Goes *et al.*, 2001). They affect the region every five to seven years. During an El Niño event, the pressure gradient over the Pacific changes resulting in a weakening of the South-East trades. Additionally, there are bursts of westerlies in the western Pacific. The sea-surface slope of the Pacific 'collapses', so that the thermocline becomes near-horizontal, enabling a considerable volume of warm mixed-layer water to move eastwards across the ocean. At the east boundary these waves split into northward- and southward travelling coastal waves. Usually the upwelling brings up nutrient-rich waters from below the thermocline. During the El Niño upwelling sometime stops altogether. Even if it does not, the lowering of the thermocline in the eastern tropical Pacific means that any upwelled water comes from within the already depleted nutrient-depleted surface layer (Colling, 2001). Thus, depending on the intensity of the ENSO event, surface water along the entire east coast of Pacific become warmer, marking the beginning of a prolonged period of a shallow mixed layers, reduces intensities of coastal upwelling, greatly reduced nutrient inputs into the euphotic column and extremely low biological productivity (Goes *et al.*, 2001). The consequences of these changes on the region's biogeochemical cycles are still poorly understood.

In 1997/98 the strongest El Niño was recorded. A weakening and reversal of the trade winds in the western and central equatorial Pacific led to the rapid development of unusually warm sea surface temperatures east of the International Date Line in early 1997. The western Pacific warm pool (SST > 29°C) migrated eastward with the collapse of the trade winds, and the equatorial cold tongue–the strip of cool water indicative of equatorial upwelling that normally occupies the eastern and central Pacific between the coast of South America to the

El Niño 1997/98

international date line–failed to develop in boreal summer and fall 1997. The course of the rapidly growing El Niño started in April 1997 with a marked deepening of the thermocline and oxycline. Thereafter, fluctuations of the thermocline and oxycline brought back colder, oxygen-poor and presumable nutrient-rich waters cluster to the surface. These conditions lasted until September/October 1997, but changed dramatically again when a second rapid deepening of the thermocline occurred at the end of November/beginning of December 1997 (McPhaden, 1999; Ulloa *et al.*, 2001). Then, SST anomalies averaged nearly 4°C (Fig. 1.5b). In summary, after May 1997 warm conditions prevailed and positive SST anomalies of 1-3°C (i.e. deviations from the climatologically norms) lasted up to 14 months, reaching maximum intensity in late 1997 and early 1998. Off northern Chile, there were two positive peaks in SST anomalies. The seasonal pattern remained similar to that of previous or succeeding years (Fig. 1.5). Upwelling favourable winds were present even during the El Niño conditions of the spring and summer season (Escribano *et al.*, 2004).

The biological consequences of this El Niño impact was studied revealing a reduction in phytoplankton biomass, but with no clear differences in community structure (Ulloa *et al.*, 2001). The zooplankton biomass fluctuated up to an order of magnitude (Ulloa *et al.*, 2001). The community of pelagic copepods showed no drastic changes in total abundance or structure (Cubillos and Arcos, 2002). In summary, the biological impact of the strong El Niño of 1997/98 was remarkably low (Chavez *et al.*, 2002)

Plankton

The impact of these climatic variations on the sedimentation of particles was already studied by the same sediment trap material (Hebbeln *et al.*, 2000; Marchant *et al.*, 1998). The total fluxes were the same during 'normal' condition and El Niño year. However the composition of it changed. Elevated flux of lithogenic particles points to higher fluvial input due to increased precipitation during the El Niño year. Changes in species composition of the foraminifera export imply higher sea surface temperatures. The export of diatoms and foraminifers reveal remarkably changes. The annual mean export of diatoms was reduced by 75% in comparison to 1993/94 (Romero *et al.*, 2001). Enhanced fluxes of foraminifers were found with maximum numbers in December 1997 to January 1998 (Marchant *et al.*, 2004).

Fluxes

The possible effect of coccolithophores to a great hydrographic change such as the El Niño of 1997/98 induced was the key question of the study of two sediment traps (CH10-2 and CH11-1, Table 2). Further the role of coccolithophores within the plankton community, as well as the overall coccolithophore export during an El Niño condition is looked at.

1.3 Aims

The aims of the present study were to characterize the coccolith flux of sediment trap samples moored in two upwelling regions of important Eastern boundary current systems, off Chile and off NW-Africa. The SEM-studies were conducted by counting and identifying the species. (The methods are described in detail in each manuscript.)

Each study focused on following general aspects:

- detailed taxonomical identification of the coccolithophores
- characterization of seasonal pattern of the coccolith fluxes
- extracting ecological affinities of coccolithophore species
- determining relationships between coccolithophore fluxes and hydrographic conditions
- estimation of coccolith derived carbonate fluxes
- compare coccolithophore flux patterns with supplementary plankton flux dynamics

These aims are documented in the three manuscripts and in the subsequent chapters *Synthesis*, *Future Perspectives*, and *Plates* that have the following content:

1. Publication

Seasonal variation of coccolithophore fluxes and species composition in a sediment trap off NW-Africa focuses on the link of hydrographic conditions and coccolithophore species composition of the export. Based on the species assemblage the coccoliths derived carbonate export was estimated. This is set into relation to surface accumulations rate of underlying Holocene sediment.

2. Publication

Seasonal dynamics of coccolith fluxes and species assemblage off Cape Blanc (NW-Africa) deals with the coccolith flux off Cape Blanc with emphasize on the species composition and their seasonal flux pattern. It spotlights the different possibilities of coccolith fluxes occurring, especially an event in winter 1990/1991 when maximum coccolith fluxes were accompanied with a significant change of the species composition.

3. Publication

The study documented in *Seasonal variations of the coccolithophorid export off Chile (30°S) under ‚normal' and El Niño conditions* aims to reveal the effects of El Niño (1997/1998) on the coccolithophore fluxes and its species composition off Chile.

Synthesis

The chapter *Synthesis* connects the results of coccolith fluxes with flux pattern of further plankton groups such as diatoms, silicoflagellates, and foraminifers. Conclusions about the ecological affinities of coccolithophores are described. Furthermore, the depicted results are summarized in schematic overviews. Finally, the coccolith-carbonate fluxes of the studied upwelling areas are estimated and annotated.

Future Perspectives

The chapter *Future Perspectives* points up further research aspects that arose from the present study.

Plates

Finally, chapter *Plates* documents taxonomically the diverse and detailed studied species composition of the upwelling area of NW-Africa and Chile by given in part additional information (for example on seasonal pattern, relative abundances, and morphometry).

II. Seasonal variation of coccolithophore fluxes and species composition in a sediment trap off Cape Blanc (NW-Africa)

M. I. Köbrich and K.-H. Baumann (Journal of Nannoplankton Research, in Review)

Abstract

Off Cape Blanc – NW-Africa (20°45'N 19°44'W), the flux of coccoliths were studied in a one year moored sediment trap (March 1998 to March 1989). The flux of coccoliths was at minimum during spring und fall. The minimum flux ($51x10^7$coccoliths $m^{-2}d^{-1}$) in fall (September) corresponded to a strong decrease in nutrient content of the surface waters. In winter, coccolith flux reached maximum values ($384x10^7$ coccoliths $m^{-2}d^{-1}$). Then, insolation, wind velocity, and sea surface temperature ranged in average values indicating an average nutrient content and average light penetration into surface waters.

Detailed morphometric measurements were the basis for precise estimations of the coccolith derived carbonate content of the settling particles. Numerically important taxa (*Emiliania huxleyi*, *Florisphaera profunda*, and *Gephyrocapsa oceanica*) as well as few massive taxa, like *Helicosphaera carteri*, *Coccolithus pelagicus*, and *Calcidiscus leptoporus*, mainly form the coccolith carbonate which amounts up to 13.32 mg $m^{-2}d^{-1}$ (mean) with a relative contribution of coccoliths to the total carbonate flux of 7 – 35%. The morphometric measurements further revealed a bimodal distribution of *F. profunda* separating two morphotypes, *F. profunda* var. *profunda* and *F. profunda* var. *elongata*.

The sediment trap assemblage revealed a good correlation in respect of coccolith flux (respectively accumulation), species composition and the coccolith derived carbonate content with the underlying Holocene surface sediment.

Keywords: Cape Blanc; sediment trap; coccolithophores; seasonality; succession; morphometry of species; carbonate flux;

2.1 Introduction

The development of phytoplankton as coccolithophores is influenced by the interaction of nutrients and light. Off NW-Africa the speed and direction of the trade winds determine the upwelling intensity, and consequently the additional nutrient input, as well as the development and extension of filaments from the coast to the open ocean. The wind strength has also an impact on the vertical mixing respectively 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 period due to the caused turbulences (Blasco *et al.*, 1981; Dugdale and Wilkerson, 1985; Huntsman and Barber, 1977).

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

Off Mauritania the fluxes of particles into the deep ocean are well documented (Fischer *et al.*, 1996; Neuer *et al.*, 1997; Ratmeyer *et al.*, 1999a; Ratmeyer *et al.*, 1999b; Wefer and Fischer, 1993). 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 influences even offshore waters through the formation of "*giant filaments*" that are characterized by high pigment concentrations (Estrada, 1974; Gabric *et al.*, 1993; Kostianoy and Zatsepin, 1996; Lange *et al.*, 1998; Thomas *et al.*, 2004). Information on the coccolith fluxes of this high productive region is still not available.

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

2.2 Study area

2.2.1 Oceanographic setting

The mooring station (20°45.3'N, 19°44.5'W) lies within the east boundary current system of NW-Africa, an upwelling region driven by the trade winds. Between 24°N and 20°N 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 characterized by the Canary Current (CC) which is a branch of the subtropical gyre and detaches from the continental slope in south-westerly direction (Fig. 2.1). At the latitude of Cape Vert (15°N) all of the flow has turned westward to supply the North Equatorial Current (NEC) (Barton, 1998). South of the area where the CC detaches from the continental slope a cyclonic gyre exists which persists throughout the year (between 15° and 22°N). This mesoscale cyclonic gyre of surface water varies in position and extension within the seasons, being furthest north in autumn/winter and largest in summer (Barton, 1998).

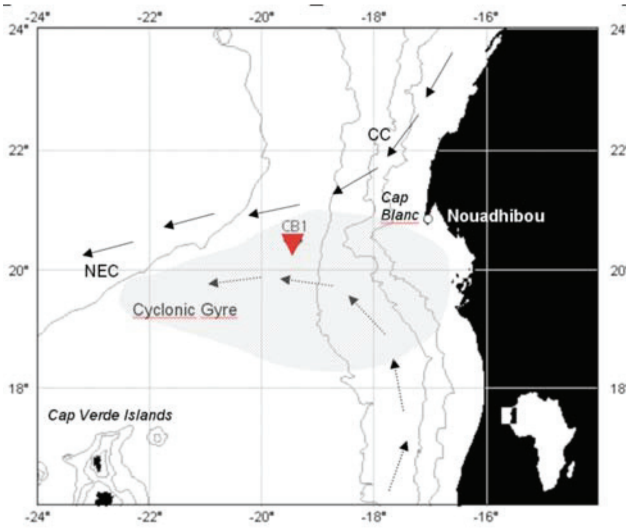

Fig. 2.1: Mooring location/ core location (▼CB1; GeoB 1121), bathymetry, schematic near-surface circultation at Cape Blanc off NW-Africa (CC Canary Current, NEC North Equator Current); shaded area indicates a gyre that changes its position and circulation pattern throughout the year (Gabric *et al.*, 1993)

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

2.2.2 Wind, sea surface temperature and insolation

The average wind speed measured at Nouadhibou airport (Cape Blanc, Mauritania) showed a slight increase in spring that culminated in a June/July maximum (Fig. 2.2). Afterwards the wind speed decreased steadily until reaching its minimum in December/January. Only in September/October the steady decrease was interrupted by a remarkably increase (Fischer *et al.*, 1996). The wind direction was mostly from east and northeast.

The characteristic cold sea surface temperature (SST) of the upwelling region was used to determine upwelling events and strength. Therefore, the difference between SST of the mooring station and the SST of the open ocean (40°W) with same latitude was calculated and defined as SST anomaly (following (Speth and Köhne, 1983) (data from 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 strongest upwelling from April to June followed by a steady decline in intensity 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 not as intense as in the beginning of the year (Fig. 2.2).

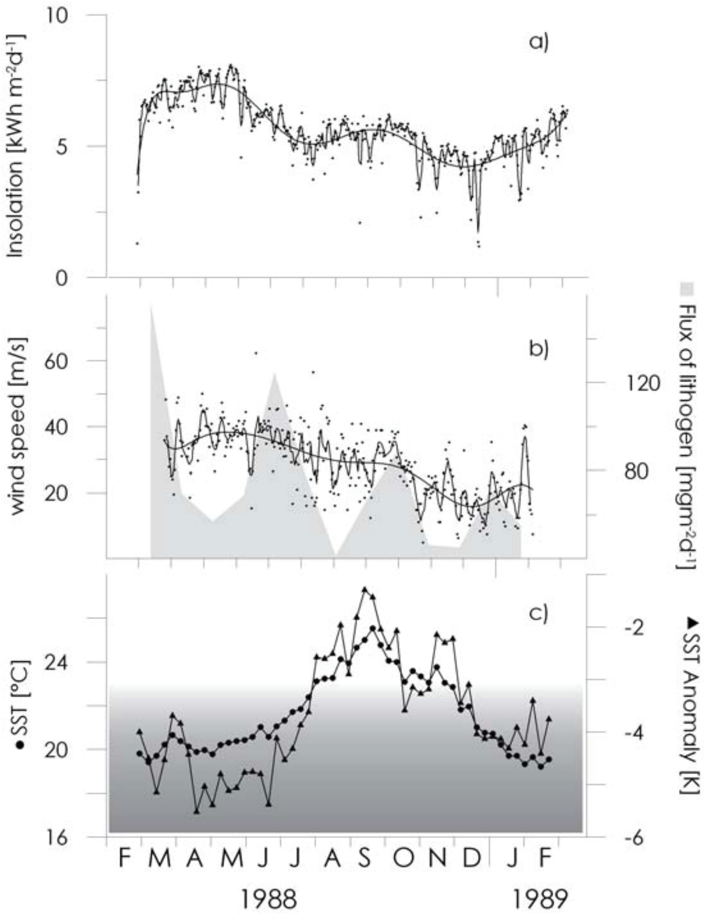

Fig. 2.2: **(a)** Insolation data (●) for the mooring location and study period (running average window width 3; function of polynomial degree 10) **(b)** wind speed (redrawn with running average window width 3; function of polynomial degree 10, data from Ratmeyer *et al.*, 1999b) and lithogenic particle flux (Fischer *et al.*, 1996) **(c)** SST and calculated SST Anomaly. Grey shaded area indication upwelling. All data were corrected for the settling time of 25d (for more detail see Müller and Fischer, 2001)

The stabilization 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 and Barber, 1977; Nykjær and van Camp, 1994). The insolation data (from http://eosweb.larc.nasa.gox/sse/) reveals a steady decrease from April to December followed by a slight increase in spring; during autumn and winter the lowest values were observed (Fig. 2.2).

2.3 Material and Method

The sediment trap was moored off Cape Blanc in a depth of 2195m (water depth 3646 m). From March, 1988 until March 1989 a total of 13 samples were collected, each sample had a collecting 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 followed the method of Andruleit (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 transection 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 concept of Cros (2002) and Young *et al.* (2003).

To gain estimates of daily coccolith fluxes, each coccosphere was converted into coccoliths based on species specific values (Boeckel and Baumann, 2008).

The surface sediment sample (GeoB 1121) was prepared using a similar dilution/filtering technique Andruleit (1996). Due to the assumed accumulation rate of 0.08 g $m^{-2} d^{-1}$ based on Winn *et al.* (1991) coccolith counts were converted in numbers per gram of dry sediment.

Coccolith derived carbonate was calculated using the mass equation of Young and Ziveri (2000) and the results of size measurements carried out in this study (see Table 2.2).

Size measurements were made directly on the TV-screen of the SEM at a magnification of x5,000 or x10,000 by using an internal Zeiss measuring system. The resolution was of 0.1–0.2 µm. For all species distal shield size of at least 20, but often more than 30 randomly selected specimens were measured on six of the 13 samples of the sediment trap. In total, more than 150 coccoliths were measured. Species measured were *C. leptoporus*, *C. leptoporus* small morphotype, *C. quadriperforatus*, *E. huxleyi*, *F. profunda*, *Gephyrocapsa spp.*, *U. sibogae*, and *U. foliosa*.

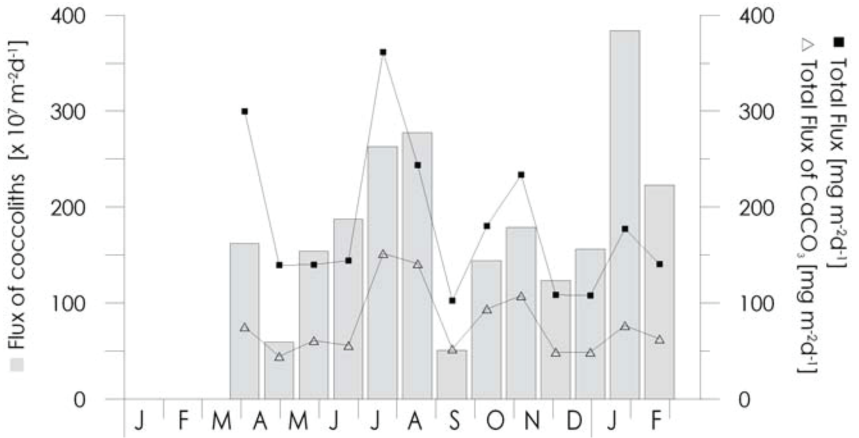

Fig. 2.3: Flux of coccoliths, of total mass and of total carbonate flux

2.4 Results

2.4.1 Seasonal fluxes of coccolithophores

The flux of coccoliths was high during summer (July to August) and winter (January to February) with low values during spring (March to April) and fall (September to December) (Fig. 2.3). The highest coccolith flux was recorded in January 1989 (384 x 10^7 $m^{-2}d^{-1}$) and the lowest in September 1988 (51 x 10^7 liths $m^{-2}d^{-1}$) coinciding with maximum SST. In contrast, high coccolith flux occurred during low SST. The mean coccolith flux was 182 x 10^7 $m^{-2}d^{-1}$.

Fig. 2.4: Seasonal flux of the most common occolithophore species of the settling assemblage of CB1

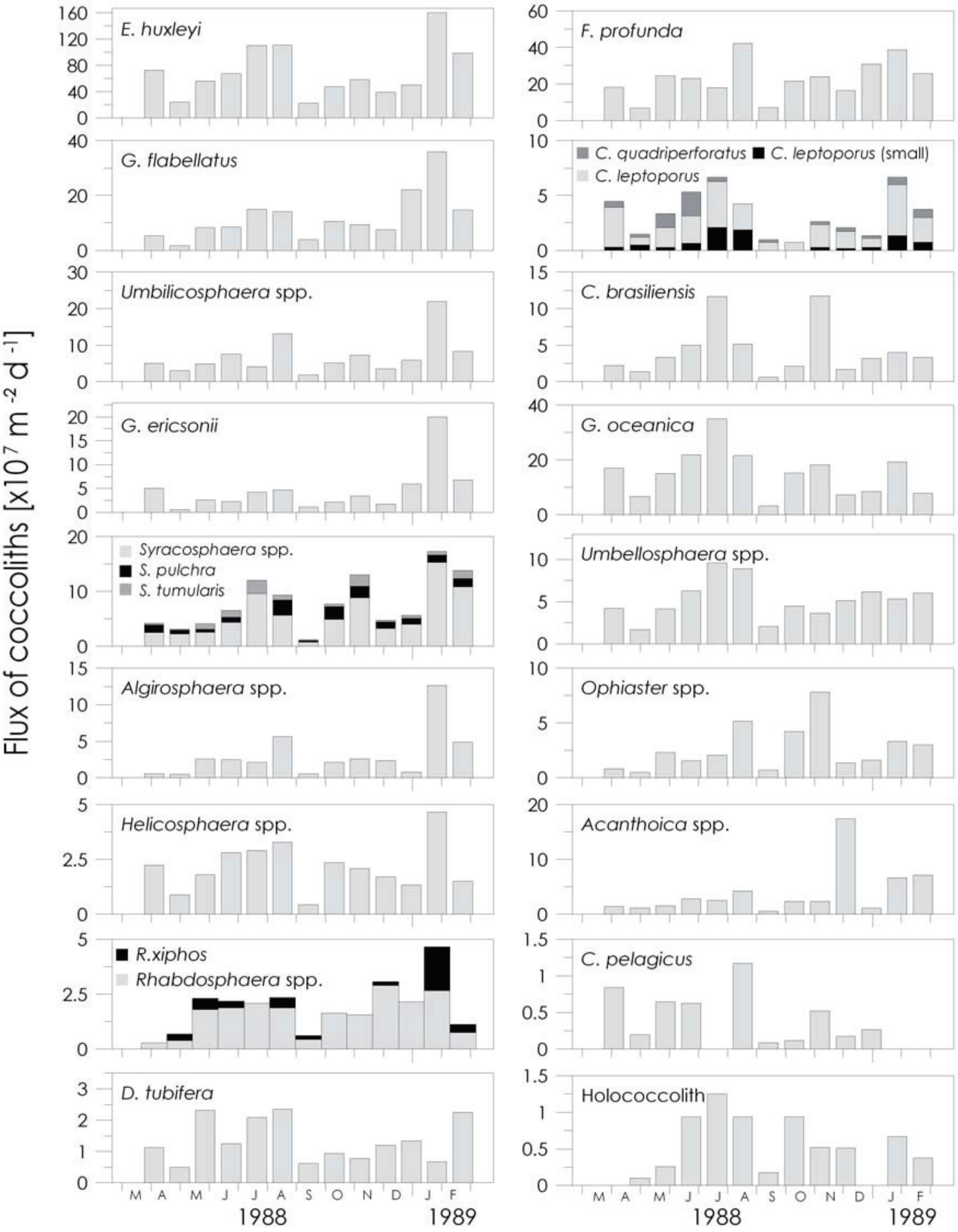

Table 2.1: Identified occolithophore taxa found during the whole sampling period in sediment trap samples off Cape Blanc (CB1) (*max. in two samples absent)

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

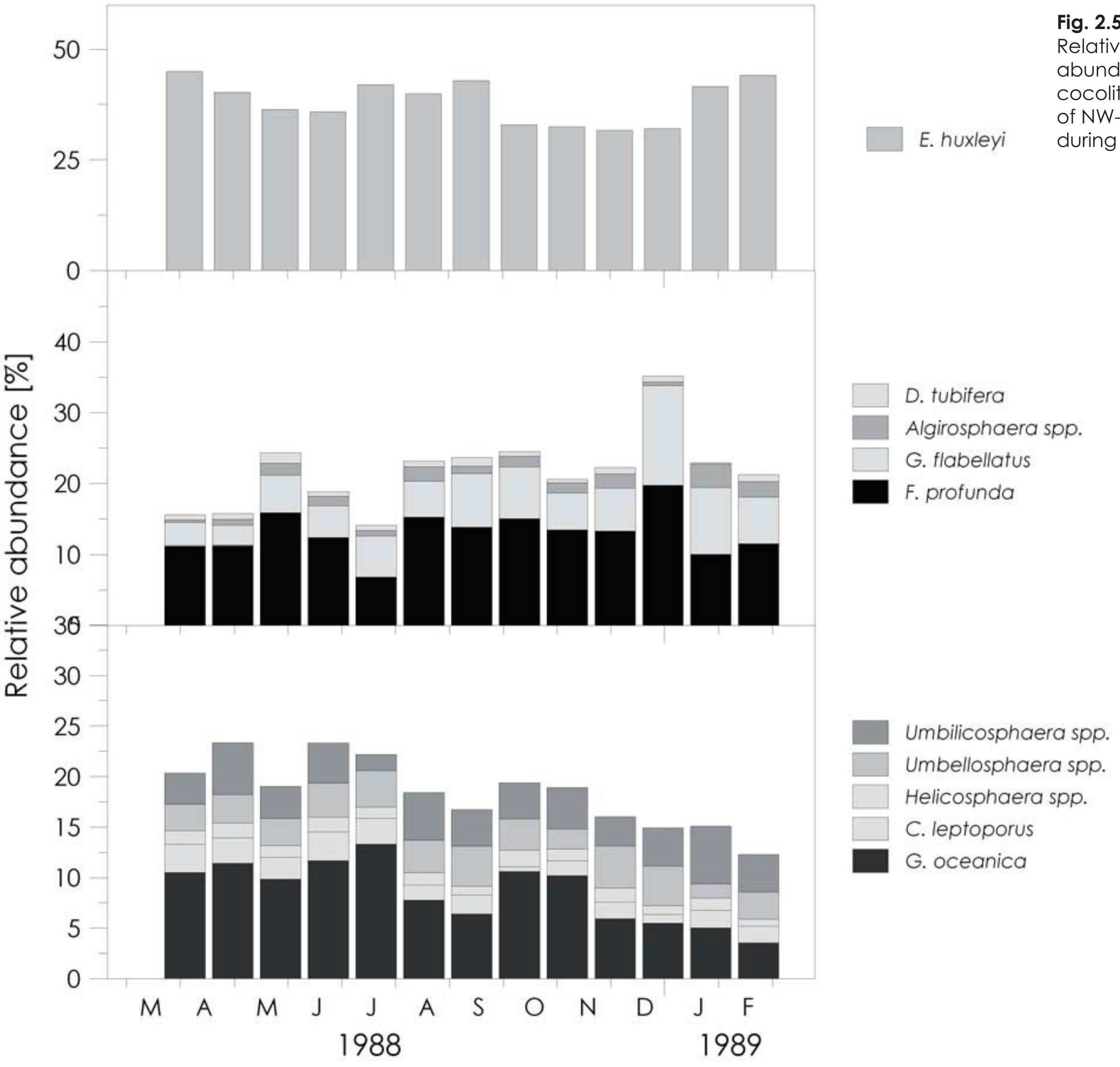

Fig. 2.5: Relative abundance of cocolithophores of NW-Africa during 1988/89

The samples revealed a diverse coccolithophore assemblage. In total 63 heterococcolith-bearing species, one species in its hetero- and holococcolith bearing state (*Syracosphaera pulchra – Calyptrosphaera oblonga*) and one species bearing holococcoliths (*Syracolithus dalmaticus*) were identified. Coccoliths were excellent preserved with no signs of dissolution.

The most abundant species are listed in Table 2.1 (complete lists will be available in the database of PANGEA). For the following interpretation and discussion the species exceeding five percent relative abundance at least once during the study period were considered.

In general, *E. huxleyi*, *G. flabellatus*, *Algirosphaera spp.*, *Umbilicosphaera spp.*, *Helicosphaera spp.* and *Rhabdosphaera spp.* had their maxima in January (1989) and an additional high flux period in August (1988). Also *G. ericsonii* flux was at maximum in winter but without a pronounced peak in summer. *G. oceanica*, *C. leptoporus*, *Umbellosphaera spp.* and *D. tubifera* reached their maxima between May and August and had an additional high flux period in winter (January or February) (Fig. 2.4).

The flux of *C. pelagicus*, *Syracosphaera spp.*, *Ophiaster spp.*, *Acanthoica spp.*, *C. brasiliensis*, and of the holococcolith-bearing species varied throughout the year (Fig. 2.4).

The assemblage of the coccolithophores was dominated by *E. huxleyi* (30–45%), *F. profunda* (6–19%), and *G. oceanica* (3–13%) (Fig. 2.5). *Algirosphaera spp.*, *G. flabellatus*, *F. profunda* and *Umbellosphaera spp.*, had 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.

2.4.2 Morphometric measurements

In general *E. huxleyi* is the most abundant living coccolithophore and dominates the coccolith flux in the study. The morphology of 194 coccoliths of *E. huxleyi* shows a unimodal distribution (Fig. 2.6a). Sizes range from 2.5–4.9 µm with a mean of 3.3 µm. Varieties as given by Young and Westbroek (1991) have not been distinguished in this study. 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 also occur.

F. profunda is the main contributor to the deep-photic zone flora of low- to mid-latitudes (Okada and Honjo, 1973; Okada and McIntyre, 1977). Overall, nannolith lengths in the stud-

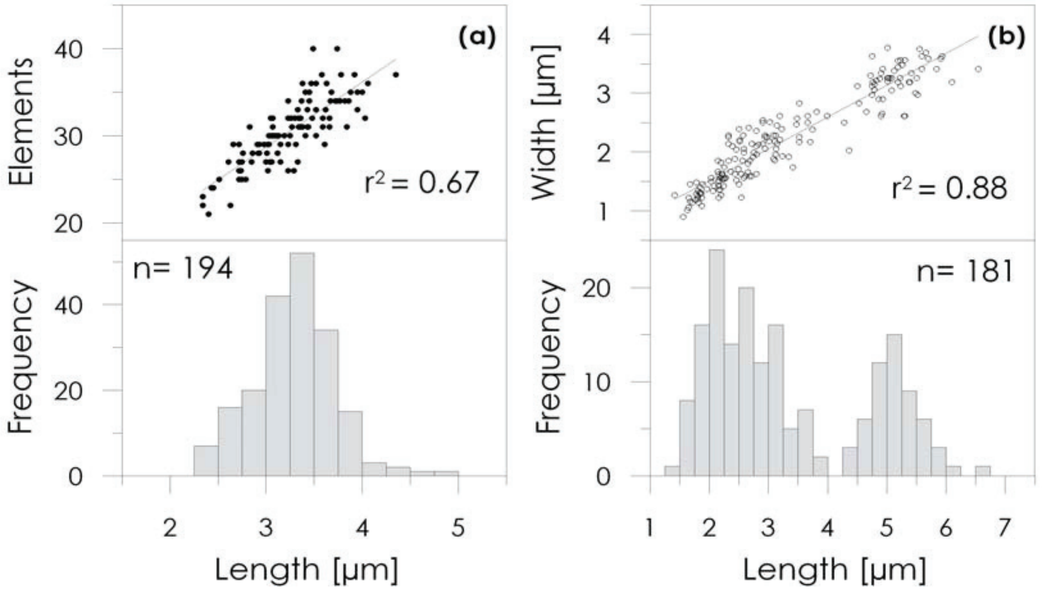

Fig. 2.6: **(a)** Size variation and frequency distribution (at 0.25 µm intervals) of *E. huxleyi* and **(b)** length and width variaiton and frequency distribution (at 0.25 µm intervals) of *F. profunda*

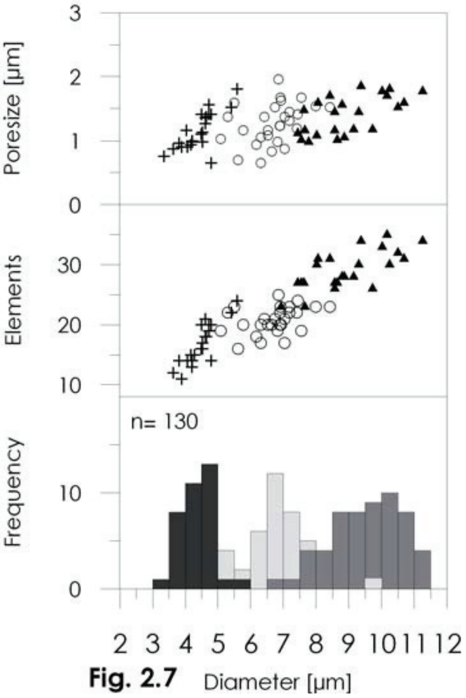

Fig. 2.7

Fig. 2.7: Scatter plot of diameter versus pore size, diameter versus number of elements in the distal shield of the genus *Calcidiscus*, and frequency size distribution (at 0.5 µm intervals) (+ *C. leptoporus* small, ○ *C. leptoporus*, ▲ *C. quadriperforatus*)

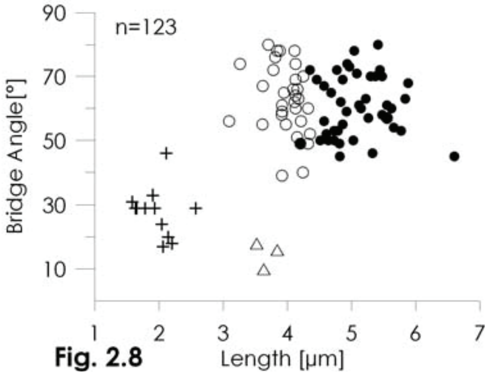

Fig. 2.8

Fig. 2.8: Coccolith size variation data of length versus bridge angle measured in *Gephyrocapsa spp.* (+ *G. ericsonii*, △ *G. muellarae*, ○ *G. oceanica* small, ● *G. oceanica* large)

ied sediment trap samples are 1.4 to 6.4 µm (Fig. 2.6b). In addition, the scatter plot and the frequency distribution clearly document a bimodal distribution pattern indicating that two varieties of *F. profunda* are present in the investigated samples, with var. *prolongata* forming larger nannoliths (Reid, 1980). The latter is between 4.3 µm and 6.5 µm in size, whereas nannoliths of 1.4 µm to 3.9 µm may correspond to *F. profunda* var. *profunda*. Varieties as given by the size data have not been distinguished in the counts and carbonate calculations are made with the total mean size (3.4 µm).

The placoliths of heterococcolith-bearing stage of *C. leptoporus* group into three indistinct clusters – with *C. leptoporus* small type, the intermediate *C. leptoporus* and the large *C. quadriperforatus* as introduced by Geisen *et al.* (2002) – with overall sizes 3.4–5.5 µm, 5.1–8.4 µm, and 6.9–11.4 µm, respectively.

The coccoliths of *Umbilicosphaera sibogae* and *U. foliosa*, which have recently been raised to species rank (Sáez *et al.*, 2003), show distinct variation in diameter, element numbers, and size of the central area. The distal shield size of *U. sibogae* is 3.1 µm to 5.1 µm, with a mean of 4.4 µm, and the larger proximal shields having a mean of 4.9 µm. The distal shield of *U. foliosa* is 5.0–6.8 µm in diameter with a mean of 5.8 µm.

In the present study cocco-liths of the genus *Gephyrocapsa* were distinguished by morphological differences. Overall, lengths and widths of the placoliths are extremely well correlated ($r^2 = 0.97$). *G. ericsonii* coccoliths are 1.6–2.7 µm long. Small *G. oceanica* coccoliths are medium-sized, 3.1–4.4 µm long, whereas lengths of large-sized *G. oceanica* generally range from 4.2 µm to 5.9 µm.

Table 2.2 Used coccolith carbonate weights for individial species and mean coccolith length of selected taxa based on size measurements carried out within this study (+ indicates 'no size measurements on CB trap samples available'; in this case data from Young and Ziveri (2000)was used

Species	Coccolith-CaCO$_3$[pg]	Mean length [μm]
Acanthoica spp.	0.3	+
Algirosphaera spp.	0.9	2.38
Alisphaera spp.	2.6	+
C. brasiliensis	2.6	+
C. quadriperforatus	206.6	9.85
C. leptoporus	70.3	6.88
C. leptoporus (small)	18.5	4.41
C. pelagicus	336.0	12.75
Calciopappus spp.	2.6	+
Calciosolenia spp.	2.6	+
Coronosphaera spp.	12.1	+
D. tubifera	1.5	+
E. huxleyi	1.9	3.28
F. profunda	3.7	3.25
G. ericsonii	1.0	1.98
G. flabellatus	2.6	+
G. muellerae	6.5	3.63
G. oceanica	14.6	4.77
H. hyalina	35.2	6.39
H. carteri	110.0	9.34
M. elegans	2.6	+
Ophiaster spp.	0.1	+
P. discopora	65.9	+
Pontosphaera spp.	70.0	+
R. clavigera	41.0	8.47
R. stylifera	40.5	+
R. xiphos	2.6	+
Rhabdosphaera spp.	8.0	+
S. corona	12.1	+
S. pulchra	16.6	5.90
S. tumularis	12.1	+
Syracosphaera spp.	0.1	+
U. anulus	8.0	+
U. foliosa	32.0	5.82
U. irregularis	5.8	+
U. sibogae	12.7	4.40
U. tenuis	8.7	+
Holococcoliths	2.6	+
Others	2.6	+

2.4.3 Coccolith – carbonate flux

Calculated coccolith carbonate (CaCO$_3$) fluxes based on morphometric measurements and literature data (Table 2.2) varied significantly between 3.9 and 22.8 mg m^{-2}d^{-1} in the studied sediment trap (Fig. 2.6). The mean calculated coccolith–CaCO$_3$ flux was 13.32 mg m^{-2}d^{-1}. In average, coccoliths contributed 18% to the measured total CaCO$_3$ flux. Variation in the relative fraction of coccolith–CaCO$_3$ to the total carbonate was high (7%–35%).

Few species contributed significantly to the coccolith–CaCO$_3$ content either due to their high specific carbonate mass or due to their high numbers. Thus, the rare and subordinate species *Helicosphaera carteri*, *C. leptoporus*, and *C. pelagicus*, were important contributors based on their coccolith weight (Young and Ziveri, 2000). These massive species contributed 35–40% to the coccolith–CaCO$_3$. Due to their high abundance *E. huxleyi*, *G. oceanica*, and *F. profunda* contributed for 35–40% to the coccolith derived carbonate.

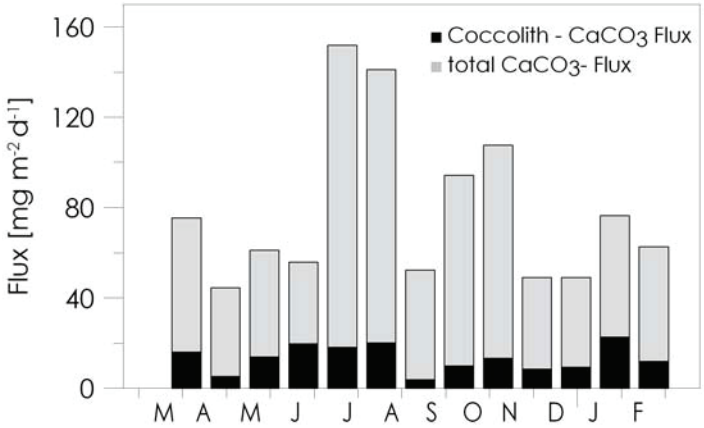

Fig. 2.9 : Comparison of total carbonate flux and calculated coccolith derived carbonate flux of CB 1

2.4.4 Coccolith and coccolith – carbonate accumulation rates

The total coccolith accumulation rate of the Holocene sediment sample (GeoB 1121) was 59x10^7 coccoliths $m^{-2}d^{-1}$. In total 20 heterococcolith-bearing species were identified. *E. huxleyi, F. profunda* and *G. oceanica* were the main species with a relative abundance of 48.5%, 17% and 14.3% respectively. *Umbilicosphaera spp.*, *C. leptoporus* and *Helicosphaera spp.* were common (3.6%, 4.0% and 2.6%).

The calculated coccolith–$CaCO_3$ content accounts for 85.7 mg g^{-1} sediment (8.57 wt%) and an accumulation rate of 6.52 mg $m^{-2}d^{-1}$, (17.86 g $m^{-2}y^{-1}$) which is 14.9% of the total carbonate accumulation rate ($CaCO_3$ content of the sediment is 57.40 wt%).

2.5 Discussion

2.5.1 Seasonality of the coccolith assemblage

To explain the seasonal flux pattern of coccoliths and their species composition during 1988 – 1989, we focused on the interaction of wind, nutrient, and light for the study period and area (Table 2.3), since the dynamic of phytoplankton in upwelling regions are much controlled by forcing factors (Margalef, 1978a). The flux of phytoplankton material in turn, is based to a great extent on the production in the surface waters. Further the comparison of coccolith flux to the flux of siliceous phytoplankton (Romero *et al.*, 2002b) will aid to explain the seasonal flux pattern of the coccoliths.

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

Table 2.3: Summary of the interaction of light, nutrient and wind which determine the flux of coccoliths at CB 1. The upwelling intensity can be described based on SST anomaly and consequently the nutrient input. The mean irradiance experienced by phytoplankton is influenced by the intensity of insolation, upwelling and wind speed, thus by the strength of turbulences and mixing of the water column.

As Margalef already 1978 described in Margalef's Mandala the ecological preferences of living coccolithophores are characterised by medium turbulent and mesotrophic waters, whereas diatoms dominate in nutrient rich and turbulent environments (Margalef, 1978a). Balch (2004) extended this profile with respect to light. Taken this into consideration, the low flux of coccoliths in spring 1988 (Fig. 2.10) can be explained as follows: The upwelling as indicated by SST anomaly was strongest of the study period, as was the wind strength (Fig. 2.2). 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 as well as strong upwelling, causing turbulences and vertical mixing, induce a decrease in favourable light conditions in the surface waters (Fischer *et al.*, 1996; Rost and Riebesell, 2004). Nelson and Conway (1979) concluded that the light regime is more important than nutrient concentration in controlling the use of inorganic nutrients in the northwest African upwelling system by phytoplankton. Strong wind limits the *effective* time period for the light-driven primary production (Dugdale and 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; Huntsman *et al.*, 1980; Sverdrup, 1953). In general, the maximum production rates are achieved only during periods of wind relaxation when vertical mixing is reduced (Gabric *et al.*, 1993). Consequently, the strong upwelling and wind strength seemed to be unfavourable.

From April to July coccolith flux increased until the first seasonal maximum in August 1988. Diatom flux increased as well until their maximum in July was reached (Romero *et al.*, 2002b). Simultaneously upwelling and wind speed decreased. We conclude that the water movement and turbulence have ebbed and light availability in surface water increased influencing positively the primary production, as seen in the peak of diatom flux and high flux of coccoliths. Phytoplankton differs in their ability to cope with variable irradiance. Coccolithophores seem to have a slightly higher light saturation for growth compared to diatoms (Rost and Riebesell, 2004). Diatoms are also commonly the first to bloom when the water column begins to stabilize early in the seasonal cycle (Rost and Riebesell, 2004). The flux pattern of coccoliths and diatoms of CB1 seem to confirm these general concepts of the living phytoplankton.

In September 1988, the overall flux and consequently the flux of the studied coccolitho-

Fig. 2.1
Flux of siliceo
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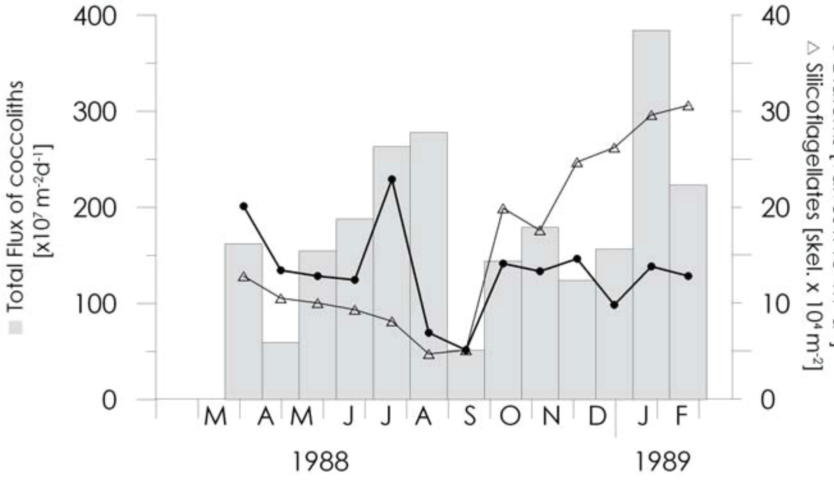
(2002b) and
coccolit



phores had their minimum. The upwelling ceased, and no additional input of nutrients occurred. After the high fluxes of diatoms in March and July and the first peak of coccoliths respectively peak of coccolithophores in June/July the water was probably depleted in nutrients. Dugdale and Wilkerson (1985) showed that the euphotic zone in that area can temporally be depleted in nutrients.

Later on in autumn, the increase of coccoliths corresponded to the onset of increasing upwelling most probably supplying the surface water with additional nutrients. The intense aeolian input represents a further nutrient source for that time (Romero *et al.*, 2003). The light regime seems favourable as well, since upwelling was not strong and wind speed was lowest over the sampling period (Ratmeyer *et al.*, 1999b; Romero *et al.*, 2003).

In January and February, maximum coccolith flux corresponded to average values of the influencing forces such as light availability, nutrients, upwelling intensity, and SST. Thus, Margalef's Mandala – describing living communities – 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 pigment concentration during spring and winter (see SeaWiFS climatology; Thomas *et al.,* 2004) and even far offshore high pigment concentrations have regularly been found (Estrada, 1974; Gabric *et al.*, 1993; Kostianoy and Zatsepin, 1996; Thomas *et al.*, 2004). The seasonal fluxes of coccoliths and diatoms in 1988–1989 implicate a change in the dominating phytoplankton group causing these elevated pigment concentrations. The spring/summer peak seems to be dominated by diatoms whereas the winter peak is dominated by coccolithophores. The change in dominance is supported by modelling findings of Giraud (2006). Off NW-Africa the flux of phytoplankton reveals a progression from diatoms, over coccolithophores to silicoflagellates also in the year 1989-1991 (Köbrich *et al.*, subm.).

Coccolithophore assemblage

E. huxleyi, *F. profunda*, *G. flabellatus*, *Algirosphaera spp.*, species of *Umbilicosphaera spp.*, and *Syracosphaera spp.* reflect the described general pattern by revealing two seasonal maxima, high flux in summer and maximum in winter. These species do not account for the same ecological niches in general: *E. huxleyi* being a bloom forming, placolith-bearing cosmopolitan (Westbroek *et al.*, 1993), *F. profunda* and *G. flabellatus* living in the deeper photic zone with *F. profunda* indicating the vicinity of the nutricline (Winter and Siesser, 1994), and *Umbilicosphaera spp.* being weakly associated with warm, saline, slightly mixed water of rather oligotrophic conditions (Okada and McIntyre, 1979; Ziveri *et al.*, 2004; Ziveri *et al.*, 1995).

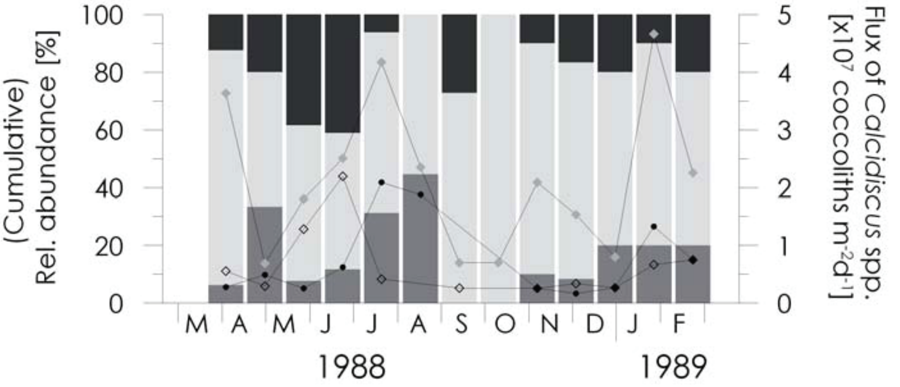


Fig. 2.11: Flux of *C. leptoporus* small (●), *C. leptoporus* (◆), and *C. quadriperforatus* (◊) of CB1 and the relative proportion of ■ *C. quadriperforatus*, ░ *C. leptoporus*, and ▓ *C. leptoporus* small

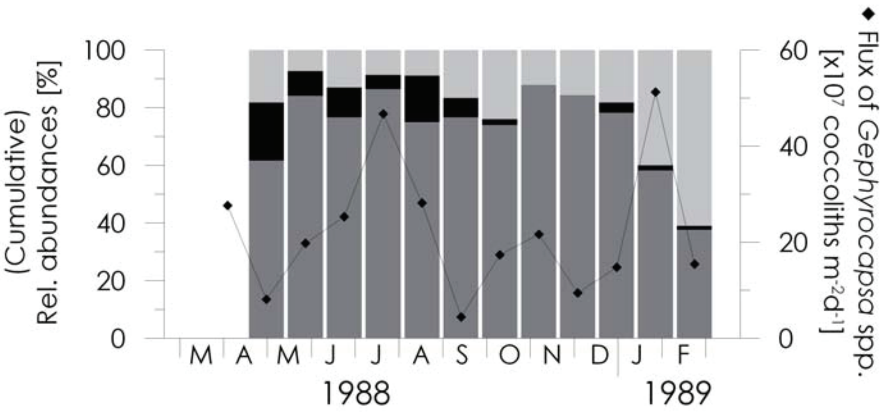


Fig. 2.12: Relative abundances of ▮ *G. oceanica*, ▮ *G. muellerae*, and ▯ *G. ericsonii* (100% equal the flux of Gephyrocapsa *spp.*) Absolute flux of Gephyrocapsa *spp.* of CB1

However, the collected trap material is an average in respect of time and space, thus a whole ecological structure is present at once. The former living phytoplankton community may have be patchy distributed. Already in 1978 Margalef describes the plankton community off NW-Africa as a *mountain range* pattern. Small scale fluctuations develop around a trend that shows large scale fluctuations. This dynamic and not static pattern is linked to processes of decaying movement associated with the systems of the *giant filaments* (Gabric *et al.*, 1993; Margalef, 1978b). Thus finding coccolithophores together that are associated to specific ecological preferences may be explained by the small scale spatial diversity within the upwelling region, and the joint collection within the sediment trap.

As described by Young and Westbroek (1991) the 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 type A and type C in our samples. Type A was the common morphotype, as documented for the world oceans as well. The presence of *E. huxleyi* type C may indicate the influence of the (coastal) upwelled cold water, since type C is associated to cold water conditions (Hagino *et al.*, 2005; McIntyre and Bé, 1967).

Species of the lower photic zone, such as *F. profunda* and *G. flabellatus*, increased in relative abundance in winter (December to January) when the insolation had its minimum and the turbulences due to wind was low. They may benefit from a condition of low irradiance and sufficient nutrient supply due to their adaptation to low light conditions (Quinn *et al.*, 2005). Further their habitat close to the nutricline provides the required nutrients during the 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.

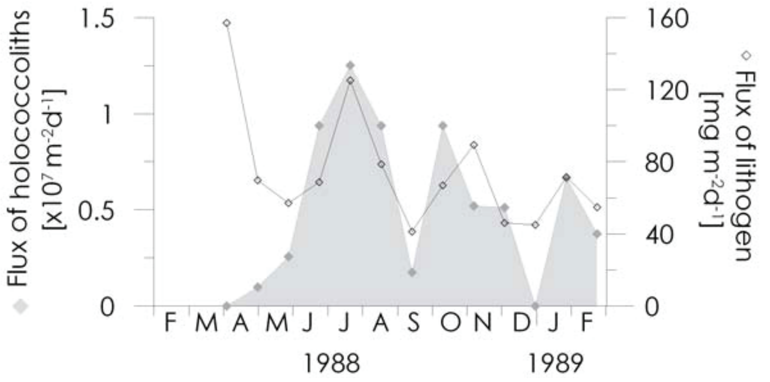


Fig. 2.13: Flux of holococcoliths and lithogenic material of CB 1

The single (morpho-)types of *Calcidiscus* revealed discrete flux pattern of *C. quadriperforatus* and of *C. leptoporus* small with the small type increasing later in summer, but showing similar pattern than *C. quadriperforatus*. The intermediate type *C. leptoporus* covers up these differences by exposing a more fluctuating seasonal pattern (Fig. 2.11). To assign the different morphotypes of *Calcidiscus* to specific single environmental parameter during the study period is rather speculative. The continuous dominance of *C. leptoporus*, thus during significantly altering environmental conditions may indicate its broad tolerance as documented by Boeckel *et al.* (2006)

During spring and summer *G. muellerae* was present indicating cold and nutrient enriched waters based on the assumed strong upwelling. Its steady decrease in relative abundance (Fig. 2.12) corresponds to the steady decrease in influence of the cold upwelled coastal water. Also, the decline in *G. oceanica* relative abundance (Fig. 2.12) supports the reduced influence of turbulent and nutrient enriched waters induced by the steady decrease in wind speed. As surface sediment study revealed, *G. oceanica* seems to be correlated to turbulence (Boeckel *et al.*, 2006), besides its relation to nutrient content of surface waters (Andruleit *et al.*, 2003; De Bernardi *et al.*, 2005).

The flux of holococcoliths corresponded very well to the flux of lithogenic particles (Fig. 2.13). As holococcoliths are composed out 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 the sea. These dust loads can be released into the water during time of wind relaxation. From 1988 – 1989 high sinking velocities of particles in the water column, thus a short settling time were observed (Ratmeyer *et al.*, 1999b). The high lithogen 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 to the organic carbon fluxes as documented by Ratmeyer *et al.* (1999b). The high sinking speeds as a consequence of the high organic matrix loading may oppose the degradation and disintegration of holococcospheres and finally holococcoliths. In spring, the time of strong mixing and upwelling the forces may be unfavourable for the settling (and/or production) of the holococcoliths.

2.5.2 Upwelling regions – a comparison

For different upwelling regions the comparison of yearly mean fluxes of coccolithophores shows similar values. The mean flux off Cape Blanc (CB1) with $65\text{x}10^{10}$ liths $m^{-2}y^{-1}$ lies between the range of the Somalian upwelling with a flux of $17\text{x}10^{10}$ liths $m^{-2}y^{-1}$ (data of trap MST-9 in Broerse *et al.*, 2000) and the Namibian upwelling with $160\text{x}10^{10}$ liths $m^{-2}y^{-1}$ (data of trap NU in Romero *et al.,* 2002a). The mooring stations of CB and MST-9 lay in comparable oceanographic regions. They are influenced by upwelling and/or filaments that develop from the coastal upwelling to the open ocean but they are not moored in the coastal upwelling itself, but the NU trap was moored closer to the coastal upwelling cell. In oligotrophic sites a flux of $14\text{x}10^{10}$ liths $m^{-2}y^{-1}$ (data of trap NABE-48 from Ziveri *et al.,* 2000a) and $19\text{x}10^{10}$ liths $m^{-2}y^{-1}$ (ESTOC, data from Sprengel *et al.,* 2000) were reported (Fig. 2.14a).

Milliman (1993) estimated the carbonate export production to range between 2–5 g $m^{-2}y^{-1}$ in the central ocean gyres and 30–40 g $m^{-2}y^{-1}$ in the eastern upwelling zones. The mooring station of Somalia (MST-9), Namibia (NU) and Mauritania (CB) have a yearly carbonate flux of 22, 21 and 22 g $m^{-2}y^{-1}$ respectively. All mooring stations lay close to the upwelling reveal-

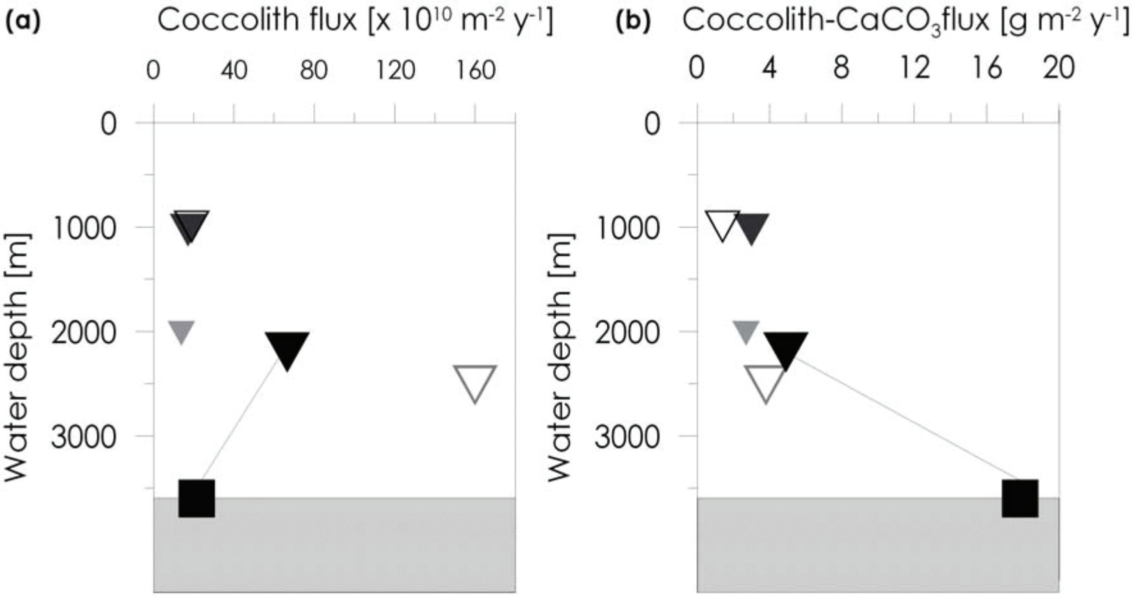


Fig. 2.14 **(a)** Comparison of average coccolith flux/ accumulation **(b)** average coccolith-carbonate flux /accumulation recorded in sediment traps (▼CB1, ▼NABE, ▽NU ▽ ESCTOC, ▼MST) and surface sediment at the mooring station CB1(■ GeoB 1121)

ing high carbonate fluxes due to the influence of the upwelling. The mooring station of NABE-48 with a yearly carbonate flux of 11 g m^{-2} resembles an oligotrophic site, as sediment traps at the Canary Islands (ESTOC) with 8.7 g m^{-2}.

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

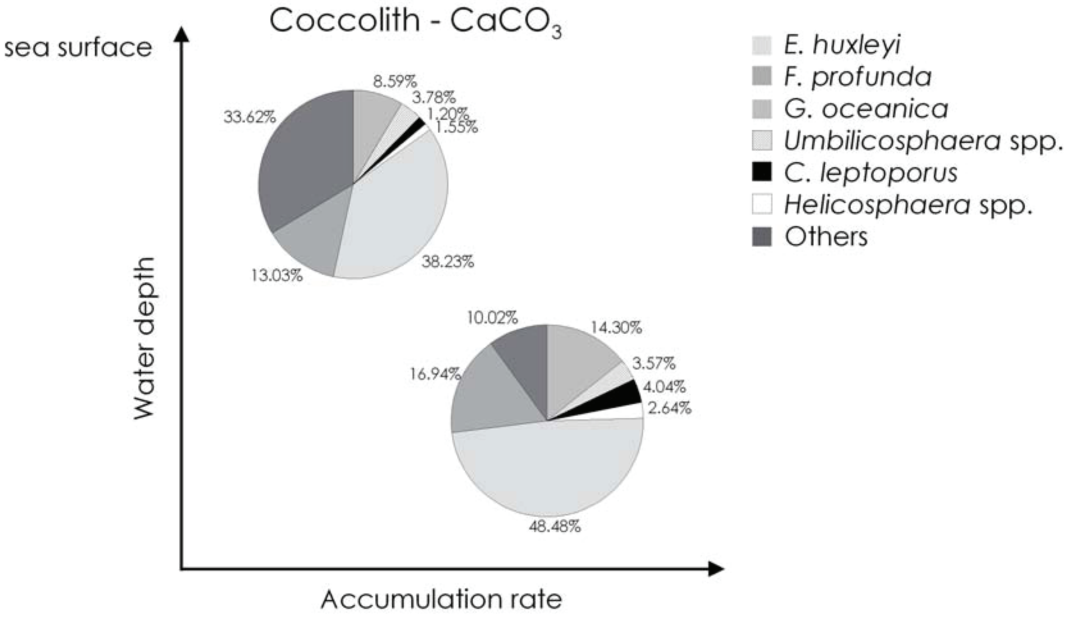


Fig. 2.15 Species contributing to the coccolith derived carbonate flux, presented in their relative abundance. The mean coccolith derived carbonate flux is slightly smaller in the trap.

2.5.3 Coccolith fluxes versus surface sediment accumulation

A good correlation between the flux of coccoliths and the accumulation in the sediment can be seen, despite a slight discrepancy in numbers and species composition. In general, coccolith fluxes recorded in the trap are slightly higher than the coccolith accumulation in the underlying sediment. The annual coccolith flux at 2200 m water depth was about a three-fold of the coccolith accumulation rate in the sediment (Fig. 2.14). The higher flux of coccoliths within the sediment trap samples is based on the higher abundance of more fragile and small-sized coccolithophores species, as species of the genus *Syracosphaera* (Fig. 2.16). The absence of these more delicate-structured coccoliths in the sediment might be caused by the enhanced dissolution especially at the sediment-water interface and by the destruction due to mechanical impact on the fragile structures. Nevertheless, coccolith and coccolith-$CaCO_3$ flux and accumulation rate (Fig. 2.14) as well as the relative contributions of single species (Fig. 2.15) are in 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 hundreds years, thus seasonal characteristics maybe overprinted by the 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, as *Helicosphaera spp.* and *C. leptoporus*.

Compared to other upwelling regions, the contribution of coccoliths to the total carbonate content of the sediment (15%) is relatively low off Cape Blanc. Off SW-Africa the contribution of coccoliths adds up to 23% (Boeckel, 2003) and in the Canary Island region to 26% (Sprengel *et al.*, 2000).

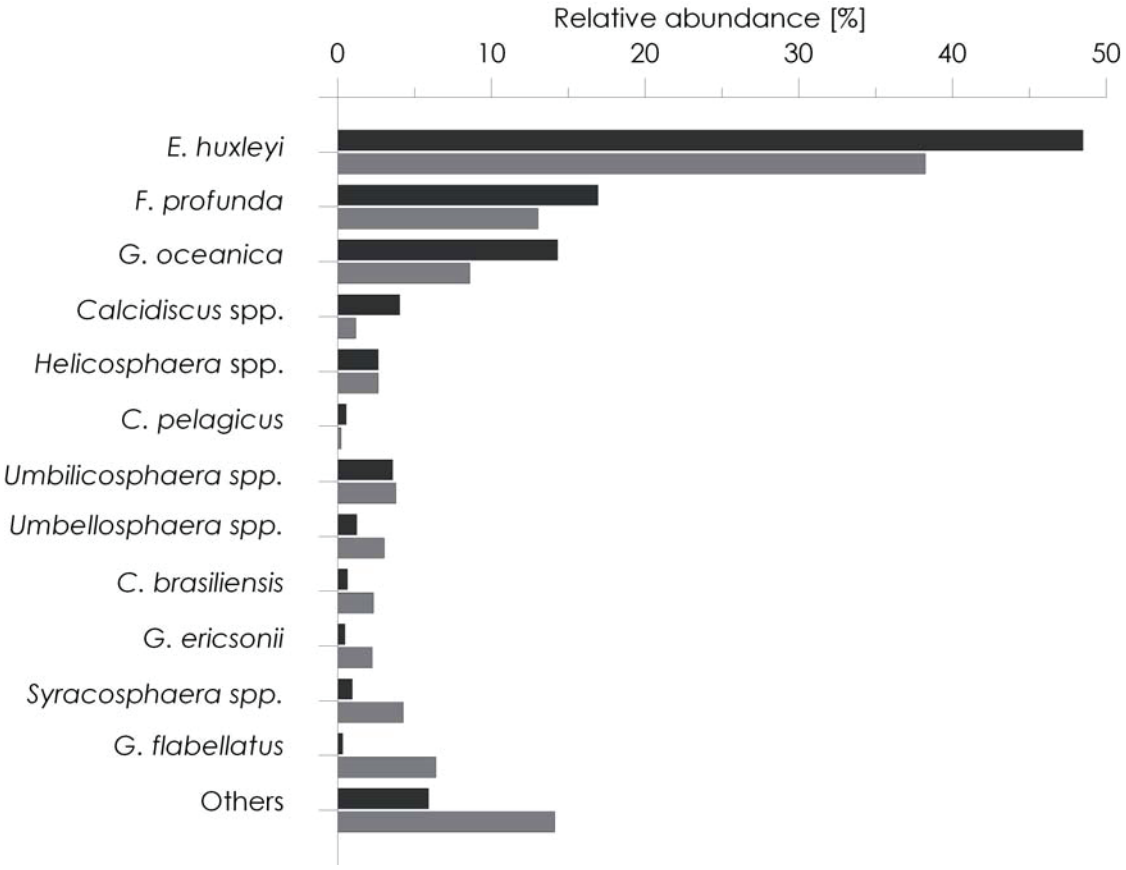


Fig. 2.16: Comparison of relative abundance between sediment trap samples (light grey) and underlaying holocene surface sediment samples (dark grey)

Conclusions

The study of settling coccolithophore assemblages from a year-round (1988 – 1989) moored sediment trap off NW-Africa revealed the following main outcomes:

- The coccolith flux shows seasonal changes with maxima in summer and winter and minima in fall and spring. The relatively diverse assemblage consisted of 63 identified heterococcolith-bearing species, one species in its hetero- and holococcolith bearing state, and one species bearing holococcoliths.
- Minimum coccolith flux corresponds to maximum sea surface temperature (SST) and high flux of coccoliths occurs during low SST. Maximum coccolith fluxes reflects an oceanic setting in which influencing factors, such as wind strength, upwelling intensity, nutrient content, and light availability of the surface waters were of medium value.
- The maximum fluxes of diatoms, coccoliths and silicoflagellates occurred during different seasons, starting with diatoms in fall followed by coccoliths in winter and finally silicoflagellates in winter. It is concluded that diatoms reacted first to additional nutrients; whereas coccolithophores dominated afterwards when average hydrographical and climatic conditions prevailed. The complex setting of the NW-African upwelling, nevertheless, represents an example of Margalef's Mandala and its extension by Balch (2004).
- *Emiliania huxleyi* was the dominant species. Morphometric measurements revealed a unimodal distribution of *E. huxleyi* coccoliths. The majority of the specimens belong to the variety *E. huxleyi* type A and only few specimens belonging to type C.
- Species of the lower photic zone, *Florisphaera profunda* and *Gladiolithus flabellatus* increased in winter and were most abundant during minimum insolation and minimum water turbulence. The sizes of the nannoliths 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 patterns with *C. leptoporus* dominating and strongly fluctuating during the year indicating a broader tolerance to the changing environmental conditions. *C. quadriperforatus* and *C. leptoporus* small show similar seasonal pattern, high flux in summer and low in fall/winter. However, *C. quadriperforatus* reaches its maximum earlier in summer. The assumed additional input of nutrients seems to favour their occurrence.
- Decreased relative abundance of *G. oceanica* and of *G. muellerae* indicate the reduced influence of cold, nutrient enriched and turbulent waters. The documented decrease in wind strength supports the assumption.

- The flux of holococcoliths parallels the measured lithogenic flux. Off Cape Blanc the lithogenic material appear to be coupled to the organic carbon fluxes. The high sinking speeds as a consequence of the high organic matrix loading may oppose the degradation and disintegration of holococcospheres and finally holococcoliths.
- The mean coccolith derived carbonate based on broad morphometric measurements adds up to 4.9 g $m^{-2}y^{-1}$. Compared to other oceanic regions, the mooring location represents a meso-eutrophic environment. The proportion of coccolithophores to the total carbonate flux accounts for 18% in the upwelling region of NW-Africa. It is in range with the upwelling region of SW-Africa, however less compared to the Canary Island region (41%).
- A good correlation between the coccolith flux and the accumulation in the underlying surface sediment can be seen. Nevertheless, in respect of species composition, relative and absolute abundances small discrepancies 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 carbonate that is less compared to upwelling region off SW-Africa (23%) and the Canary Island region (26%).

Acknowledgement

We are grateful to Dr. B. Boeckel the intensive discussions and valuable suggestions on the manuscript. M. Krysta is thanked for the technical support for the preparation of the samples. This research was funded by the Deutsche Forschungsgesellschaft as part of European Graduate College “Proxies in Earth History” EUROPROX, Bremen Universität.

III. Seasonal dynamics of coccolith fluxes and species assemblage off Cape Blanc (NW-Africa)

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(to be submitted to Deep Sea Research I)

Abstract

The coccolithophore assemblage of sediment traps moored off Cape Blanc (21°08.7'N 20°41.2'W) covering three years (March 1989 to November 1991) are studied to reveal the species composition, inter- and intraseasonal changes and influencing factors. A diverse assemblage of at least 74 species was identified with *Emiliania huxleyi, Florisphaera profunda,* and *Gephyrocapsa* spp. dominating the assemblage. In addition a significant change in assemblage took place with an increased flux of *Ophiaster* spp. and *Acanthoica* spp. (winter 1990/1991).

In general, during winter season most of the yearly exported coccolith flux settles. By contrast during summer and fall the proportion of the yearly coccolith flux was reduced. The settling of the coccoliths is associated with the enhanced lithogenic fluxes during winter and spring at this region. Different coccolithophore assemblages could be distinguished within the study period revealing distinct species composition in association with changing environmental parameters. A rather constant assemblage revealed only small changes in species composition reflecting the variable hydrographic condition. The significant change in winter 1990/1991 is assumed to be the result of a significant high occurrence of *Ophiaster* spp., *Acanthoica* spp., and *Syracosphaera* spp. in the surface waters accompanied with an enhanced transport into the deep. The coccolithophore fluxes display the highly dynamic region off Cape Blanc by the change in range as well as in species composition.

Keywords: coccolithophores, plankton fluxes, seasonality, sediment trap, ecological preferences

3.1 Introduction

The upwelling region off NW-Africa is one of the prominent eastern boundary current systems located at the eastern edge of the North Atlantic Subtropical Gyre. Upwelling is mostly persistent throughout the year off Cape Blanc (20°N) (Gabric *et al.*, 1993; Mittelstaedt, 1991; Schemainda *et al.*, 1975; van Camp *et al.*, 1991). In this area surface water masses of elevated pigment concentration extend far offshore as a result of primary production deflected offshore in filaments, upwelled nutrients, and in situ growth of phytoplankton (Gabric *et al.*, 1993; Lange *et al.*, 1998). These "*giant filaments*" persist year round but vary in intensity (van Camp *et al.*, 1991).

One major group within the modern phytoplankton are coccolithophores that not only succeed in oligotrophic regions of the oceans but also flourish in high productive regions (Broerse *et al.*, 2000b; Brown and Yoder, 1994; Giraudeau and Bailey, 1995; Kleijne, 1993; Mitchell-Innes and Winter, 1987; Siegel *et al.*, 2007; Stoll *et al.*, 2007). Due to their exo-skeleton consisting of minute calcite scales, the coccoliths, they play an important role within the global carbonate cycle. The export of the coccoliths to the deep floor occurs via fecal pellet or marine snow massively contributing to the fine-grained carbonate of deep sea sediments.

Table 3.1: Cape Blanc sediment traps: location, deployment and water depths, sampling durations and intervals

Mooring	Trap type Opening	Position	Water depth	Trap depth	Sampling duration	Samples x days
CB 2	Mark VI (1.17 m²)	21°08.7'N 20°41.2'W	4092 m	3502 m	Mar 15 89 – Mar 24 90	22 x 17
CB 3	Kiel SMT 230 (0.5 m²)	21°08.3'N 20°40.3'W	4094 m	3557 m	Apr 29 90 – Apr 08 91	16 x 21.5
CB 4	Kiel SMT 230 (0.5 m²)	21°08.7'N 20°41.2'W	4108 m	3562 m	May 03 91– Nov 19 91	20 x 10

Within the fossil record the varying occurrence of coccolithophores provides a basis for climatic and paleoceanographic studies.

The prerequisites for their use as paleooceanographic tool are their sensitivity to ecological parameters and the knowledge about ecological affinities of the different species. It has been shown that settling biogenic material rapidly transfers the production signal to depth, yielding coupling between surface and deep oceans (Bory *et al.*, 2001). A successful method to measure the downward fluxes is sediment trapping which allows to reveal seasonal and interannual differences in the coccolith fluxes (Dutkiewicz *et al.*, 2001; Haidar *et al.*, 2000; Sprengel *et al.*, 2002; Ziveri *et al.*, 2000a,b).

In this study we aim to characterize the coccolithophore assemblage of one major upwelling region in the Atlantic with respect to assemblage composition and inter- and intraseasonal changes in fluxes.

3.2 Study area

The mooring station (Table 3.1) was deployed in the marginal sector of the Canary Current (CC) as a branch of the subtropical gyre that detaches from the continental slope between 25° and 21°N and flows south westerly, supplying the North Equatorial Current (NEC) at the latitude of Cap Verde (Barton, 1998). However, south of the area, where the CC detaches, a cyclonic gyre of surface water exists persisting throughout the year (between 15° and 22°N). This mesoscale cyclonic gyre changes its position and extension within the seasons, being furthest north in autumn to winter and south in summer (Barton, 1998).

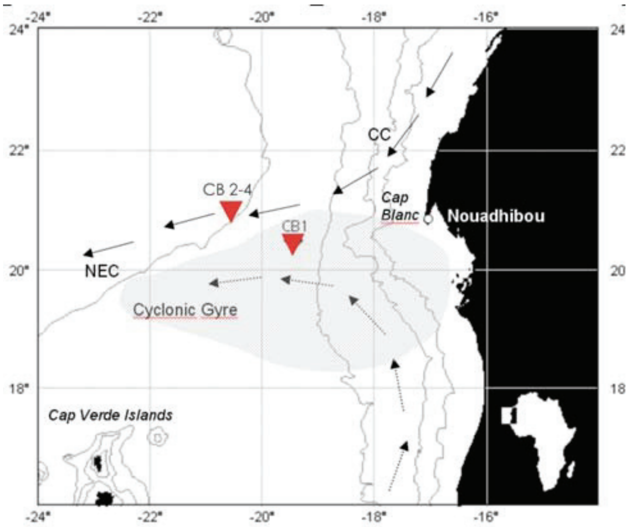


Fig. 3.1: Mooring location, bathymetry, schematic near-surface circulation at Cape Blance off NW-Africa (CC=Canary Current, NEC=North Equator Current); shaded area indicates the area of a gyre that changes its postion and circulation pattern throughout the year (Gabric *et al.*, 1993)

The source of the upwelled water alters between the salty and nutrient-poor North Atlantic Central Water (NACW) and the less saline, warmer, and nutrient rich South Atlantic Central Water (SACW) off Cape Blanc. The frontal zone between NACW and SACW fluctuates within 21°-23°N (Barton and Hughes, 1982; Lange *et al.*, 1998) under-

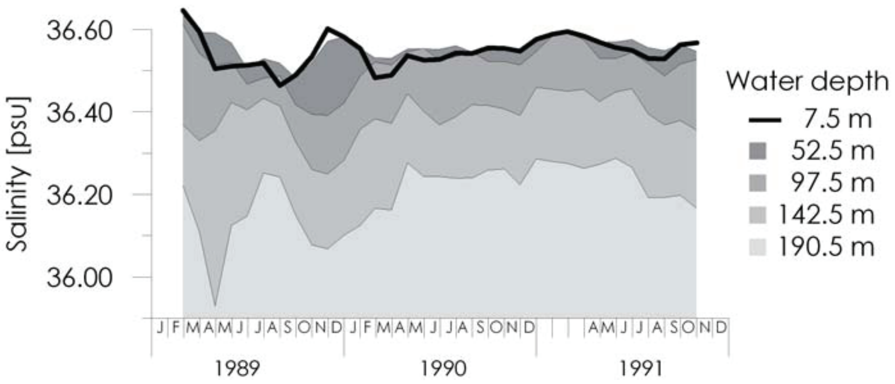


Fig. 3.2: Salinity profile at the mooring station from January 1989 to January 1992 data from http://ingrid.ldeo.columbia.edu/SOURCES/.UMD/.Carton/.goa/.beta7

going spatial and temporal changes. Accordingly, the nutrient content of the upwelled surface water near Cape Blanc fluctuates depending on the origin of the water. In 1989 to spring 1990, the surface waters (water depth 7.5m and 52.5m) differ in its characteristics compared to the deeper waters (Fig. 3.2). The salinity in the surface waters increased whereas in the deep the salinity decreased. From spring 1990 to winter 1991 salinity changes at different water depths were less pronounced with a parallel pattern at different depth.

The upwelling process off NW-Africa is induced by the trade winds which vary in strength and occurrence throughout the year. During the sampling period the pattern of the wind speed measured at Nouadhibou airport, (Mauritania) can be divided into distinct intervals (Fig. 3.3a). From March 1989 until March 1990 a pronounced pattern existed with maxima in summer (June 1989) and minima in autumn (November 1989). Subsequently, wind speed increased and fluctuated only moderately without well-defined minima or maxima. In general, the prevailing wind direction was from northeast to northwest with the northeast direction persisting in (autumn) winter.

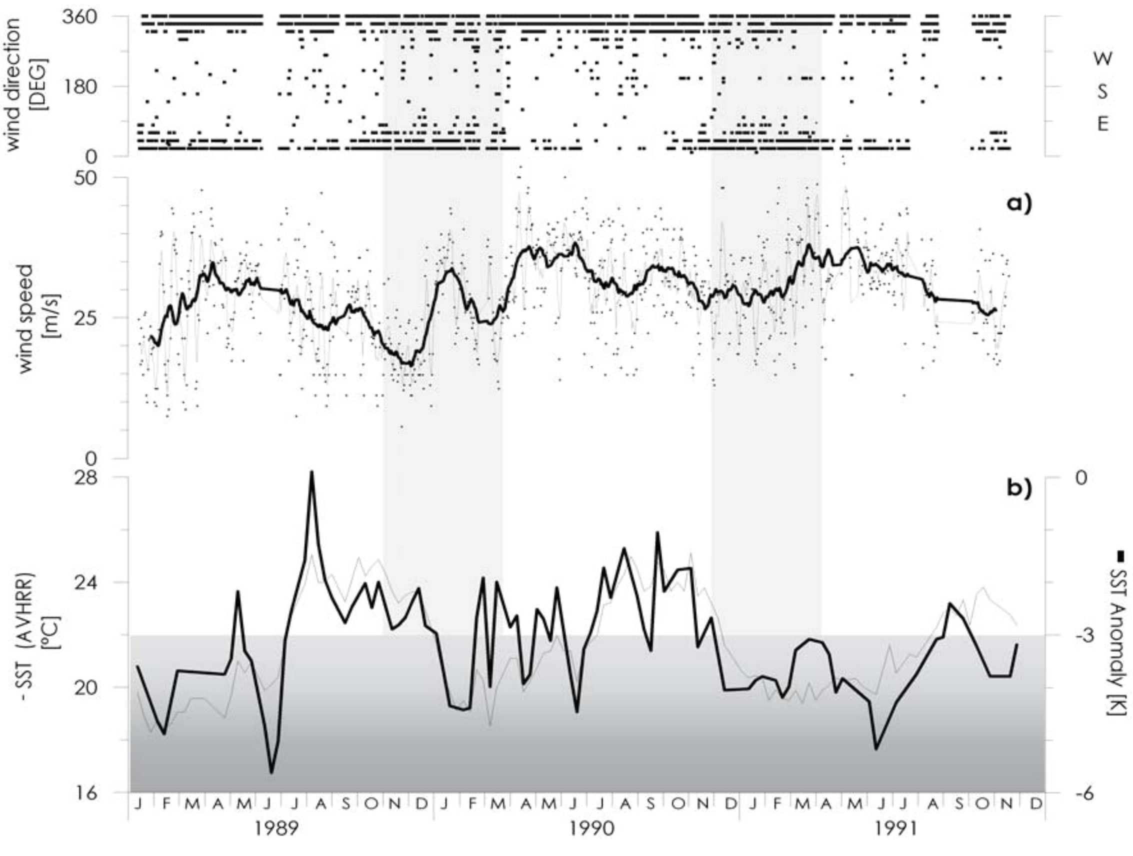


Fig. 3.3: **a)** Wind direction and wind speed measured at Nouadhibou ariport, Maritania (data from Ratmeyer pers. comm.); fine line 3 point moving average; thick line is function of polynomial)
b) Sea sSurface temperature (SST) (AVHRR data from http://ceanwatch.pfeg.noaa.gov/) and SST Anomaly (= SST difference derived from SST at the mooring location and open ocean station (40°W) according to Speth *et al.* (1978)
Shaded areas indicate time periods of upwelling favourable winds.

In general, the sea surface temperature difference (SST anomaly) between the mooring location and an open ocean station (40°W) can be used to define time periods of upwelling (Nykjær and van Camp, 1994). Speth *et al.* (1978) classifies a difference of -3K (and lower) as upwelling. Thus, strong upwelling occurs in summer 1989 and 1991 whereas in summer 1990 it was reduced. However, fluctuating weak upwelling lasted from winter to summer 1990, whereas during 1991 upwelling continued from winter to fall (Fig. 3.3b).

3.3 Material and Methods

3.3.1 Quantification of coccolith flux

The deployment of the sediment trap, as well as the initial treatment of the collected samples is described in detail by Fischer *et al.* (1996). The processing of the samples for coccolith study using scanning electron microscopy followed the method of Andruleit (1996). Depending on the particle content of the samples 1/640 to 1/6400 split of the original were filtered. In an arbitrarily chosen transection each coccolith and coccosphere were counted until a total number of at least 500 coccoliths was reached. Qualitative and quantitative analyses of the coccolithophores were performed at x3000 magnification using a Zeiss DSM 940A at 10kV accelerating voltage. Each individual was identified to the lowest taxonomic level as possible. The coccoliths were taxonomically classified based on Cros (2001) and Young *et al.* (2003).

The coccosphere fluxes were further converted into coccolith fluxes to consider the small fluxes of coccospheres as well. Therefore, species-specific values of mean coccolith numbers per coccosphere were used as in Boeckel and Baumann (2008).

3.3.2 Statistical methods

To evaluate the species abundances and community structure statistical analyses were carried out that are included in the multivariate statistical package CANOCO 4.54 for windows. Detrended correspondence analysis (DCA) was initially applied, which is based on the assumption that the most important environment gradient is responsible for the largest variation in species composition. In case of a unimodal response the abundance of species either increases or decreases within the limited range of values of an environmental variable (van Wijngaarden *et al.*, 1995).

To characterize the associations between different species within the assemblage Correspondence Analysis (CA) was made. Furthermore, to determine the effect of particular (measured) environmental variables on the species composition, a constrained unimodal ordination method (Canonical Correspondence Analysis, CCA) was carried out using the entire data set of absolute abundances, after defining the linear or unimodal distribution by detrended canonical correspondence analysis (DCCA).

The final axes of ordination diagrams represent linear combinations of the environmental and species data. In general, species lines pointing in the same direction indicate positive correlation with each other, i.e. species occur in similar samples and hence in similar seasonal patterns. In case of opposing directions a negative correlation exists, and perpendicular lines indicate lack of correlation. Species plotted close to the centre of the diagram are most likely not affected by the environmental gradients (van Wijngaarden *et al.*, 1995). To avoid covariance of the analysed environmental parameters Monte Carlo permutation test with 199 permutations were included in the analysis.

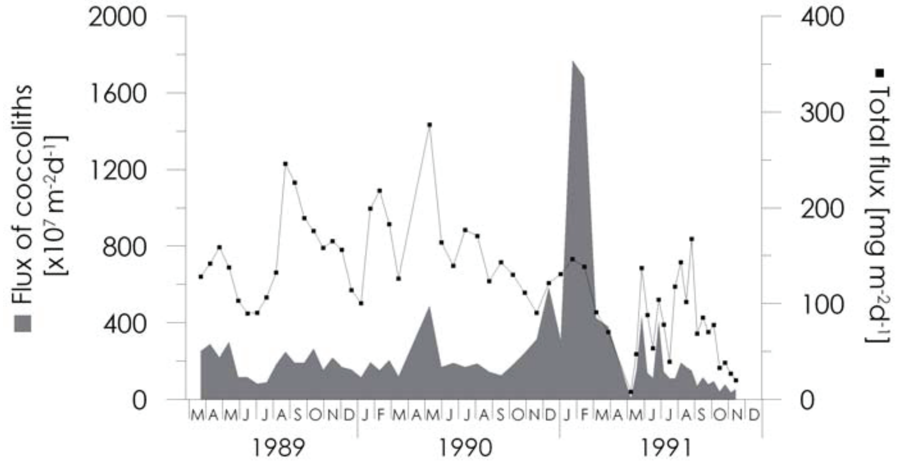


Fig. 3.4: Coccolith flux and total flux of CB2-4 (data of total flux from Fischer *et al.*, 1996)

3.4 Results

The flux of coccoliths varied seasonally and interannually (Fig. 3.4). In general, low numbers of coccoliths were present in (late) summer or autumn. The flux of coccoliths varied significantly with the highest flux of 1.77 $x10^{10}$ liths $m^{-2}d^{-1}$ occurring in January/February 1991 and lowest flux of 9.5 $x10^{7}$ liths $m^{-2}d^{-1}$ in May 1991. Between March 1989 and November 1991 a mean flux of 2.3 $x10^{9}$ $m^{-2}d^{-1}$ was recorded.

3.4.1 Seasonal and interannual variability in coccolithophore fluxes

A diverse coccolithophore assemblage was present. In total 74 heterococcolith-bearing species and seven holococcolith-bearing species were identified. Six species were found in their holo- and heterococcolith bearing stage. All counted specimens were excellently preserved with no signs of dissolution. The identified species that were dominant (or most abundant) and frequently found are listed in Table 3.2. All identified species are listed in Appendix A. For the results and interpretation those species were considered that show a minimum relative abundance of 5%. The exception is the genus *Calcidiscus*. The single species were not as abundant but were considered due to their significance for their contribution to the calcium carbonate flux derived by coccolithophores.

The dominant species were *Emiliania huxleyi, Florisphaera profunda,* and *Gephyrocapsa* spp. (Fig. 3.5). However, temporary further genera were important with respect to high fluxes, *Ophiaster* spp. and *Acanthoica* spp. (January/February 1991).

The overall pattern of the fluxes is divided into three intervals. The first one, from March 1989 until winter 1990/91, is characterized by fluctuating fluxes in which average values for the different species are evident. The second interval covers the winter months of 1990/91 and shows maximum coccolith fluxes. Subsequently the third interval is characterized by significantly decreased fluxes (Fig. 3.5).

The second interval exhibits differences in fluxes of certain species. In December 1990 the flux of *Umbellosphaera tenuis* increased followed by a rapid decrease and subsequently average values in January/February 1991. *Florisphaera profunda* also increased in December and slightly decreased in January/February 1991, however, the fluxes persisted in high numbers. In January to February *E. huxleyi*, *Ophiaster* spp., *Acanthoica* spp., and *Algirosphaera* spp. increased significantly as well as the fluxes of *Calciosolenia* spp, *Umbilicosphaera hulburtiana*, and *Calcidiscus leptoporus*. A considerable increase in fluxes of *Gephyrocapsa ericsonii* and holococcolithophores occurred in February 1991 (Fig. 3.5).

Table 3.2: Identified taxa of coccolithophores frequently found (*in >90% of the samples)and holococcolithophores

Taxa

Acanthoica spp.*
*Algirosphaera** sp.
Alisphaera sp.
Calciosolenia spp.*
*Calcidiscus leptoporus**
Calcidiscus leptoporus (small)
C. quadriperforatus
Calciopappus spp.
C. pelagicus
Discosphaera tubifera *
*Emiliania huxleyi**
*Florisphaera profunda**
*Gephyrocapsa ericsonii**
G. muellerae
*G. oceanica**
*Gladiolithus flabellatus**
Helicosphaera spp.*
*H. carteri**
H. hyalina
Michaelsarsia elegans
Ophiaster spp.*
Palusphaera spp.
Papposphaera spp.
Rhabdosphaera spp.
Syracosphaera spp.*
*S. anthos**
S. corolla
S. delicate
S. nana
S. nodosa
S. prolongata
*S. pulchra**
*S. tumularis**
U. annulus
*U. hulburtiana**
U. foliosa
*U. sibogae**
*U. irregularis**
*U. tenuis**

74 heterococcolith-bearing species

6 species in its hetero- and holococcolith stage

C. quadriperforatus – *Syracolithus quadriperforatus*
H. carterii – *S. catilliferus*
H. walichii – *S. dalmaticus*
*S. anthos** – *Periphyllophora mirabilis*
S. bannockii – *Zygosphaera bannockii*
*S. pulchra** – *Daktylethra pirus*
– *Calyptrosphaera oblonga*

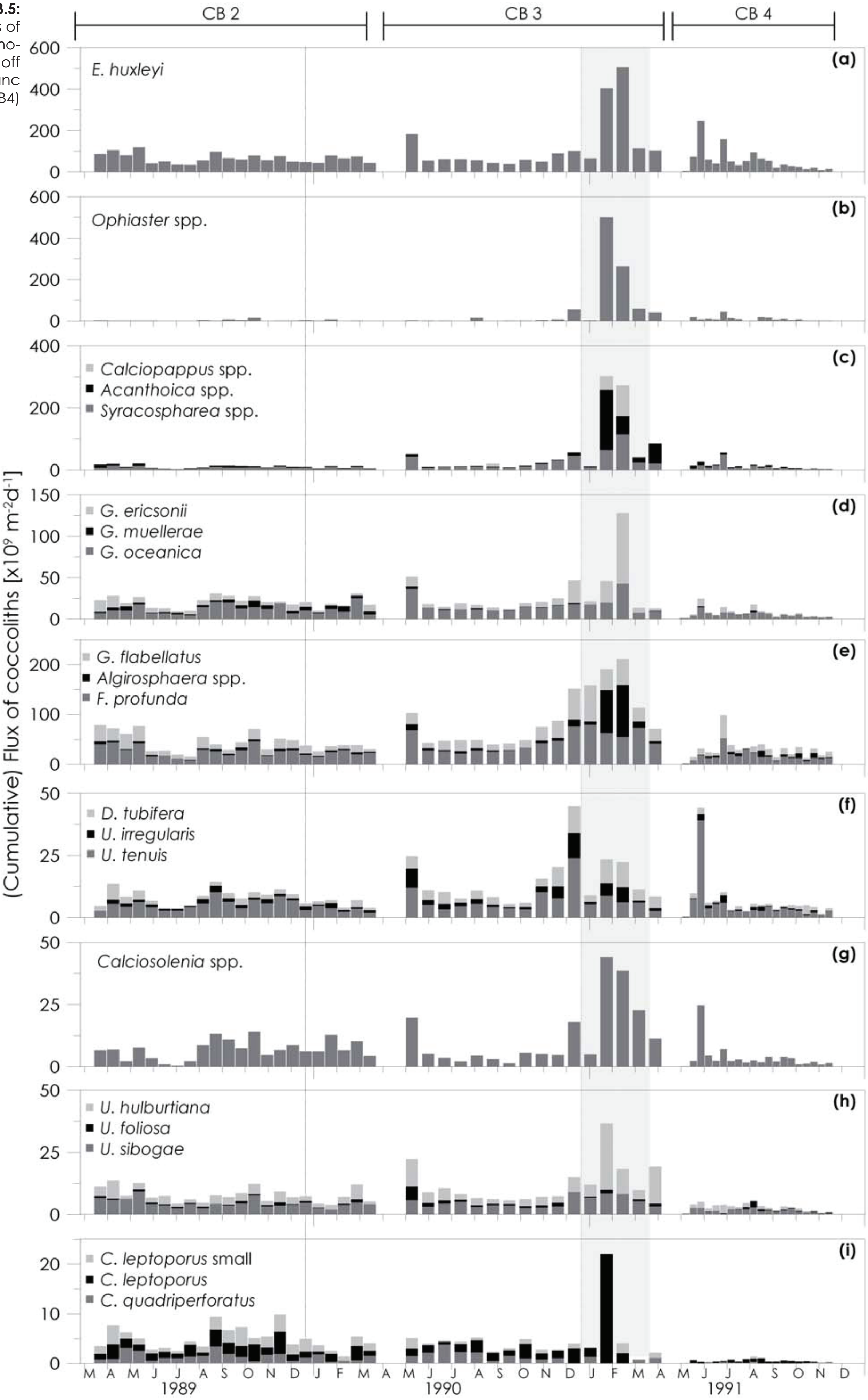
7 holococcolith-bearing species

Calyptroplithophora papillifera
Calyptrosphaera cialdi
Homozygosphaera triarcha
Sphaerocalyptra sp.
Syracolithus sp.
Syracolithus schilleri
Poritectolithus

In general, the assemblage was dominated by *E. huxleyi* with an average contribution of 34% (17-56%). A distinct minimum was observed in December 1990. At the same time *F. profunda* and *Gladiolithus flabellatus* had their maximum. In winter 1990/91 (January to March) *Gephyrocapsa* spp., *G. flabellatus*, *F. profunda, Umbellosphaera* spp., *Umbilicosphaera* spp., *Calcidiscus quadriperforatus*, and *C. leptoporus* displayed a minimum in relative abundances. During winter 1990/1991, the increase of specific species, that were usually present only in small numbers, results in a change in relative abundances (compare Fig. 3.5 and Fig. 3.8).

In general, *Ophiaster* spp. and the closely related genus *Calciopappus* spp. contributed only little to the assemblage (~4%, <1% respectively). However, in winter 1991 the relative abundance increased significantly adding up to a maximum of 28% for *Ophiaster* spp. and 7% for *Calciopappus* spp..

Fig. 3.5: Fluxes of cccolithophores off Cape Blanc (CB2-CB4)



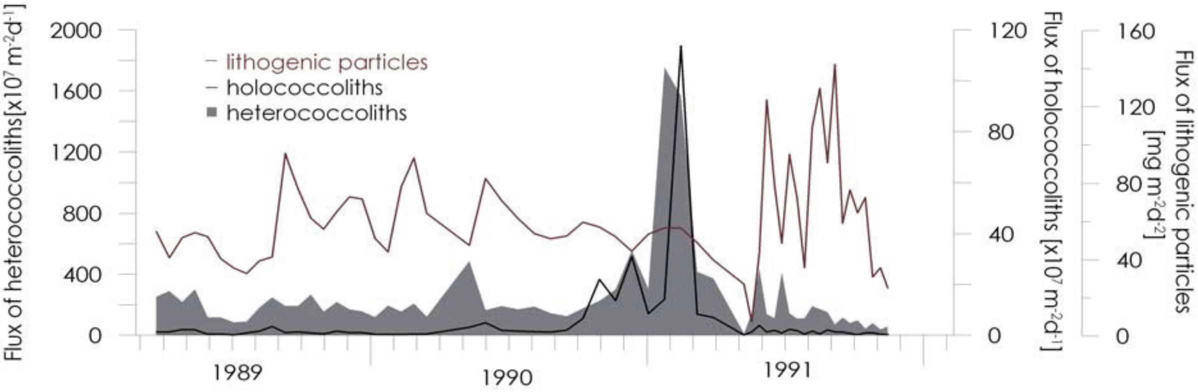


Fig. 3.6: Fluxes of holococcoliths and heterococcoliths and flux of lithogenic particles

3.4.2 Statistical Results

Based on the detrended correspondence analysis (DCA), some species showed a unimodal distribution (*G. muellerae*, *Acanthoica* spp., *C. quadriperforatus*, *Calciopappus*, *Ophiaster*, *S. pulchra*, and *Holococcolithophores*), whereas for the rest a linear distribution could be assumed. However, the assemblage as a whole revealed a linear distribution.

The initial analysis (DCCA) of the influence of environmental variables – nitrate at 50m water depth (N50 data by world ocean atlas – WOA), SST by AVHHR, and organic carbon (C_{org}) (Fischer *et al.*, 1996) – resulted in a unimodal distribution. The abundance and species composition of the coccolithophore community rather increased/decreases only within a limited range of the influencing parameters than in a linear response. The variability within the assemblage structure was accordingly analysed by canonical correspondence analysis (CCA). The ordination diagram in form of a biplot displays species and environmental variables (Fig. 3.7).

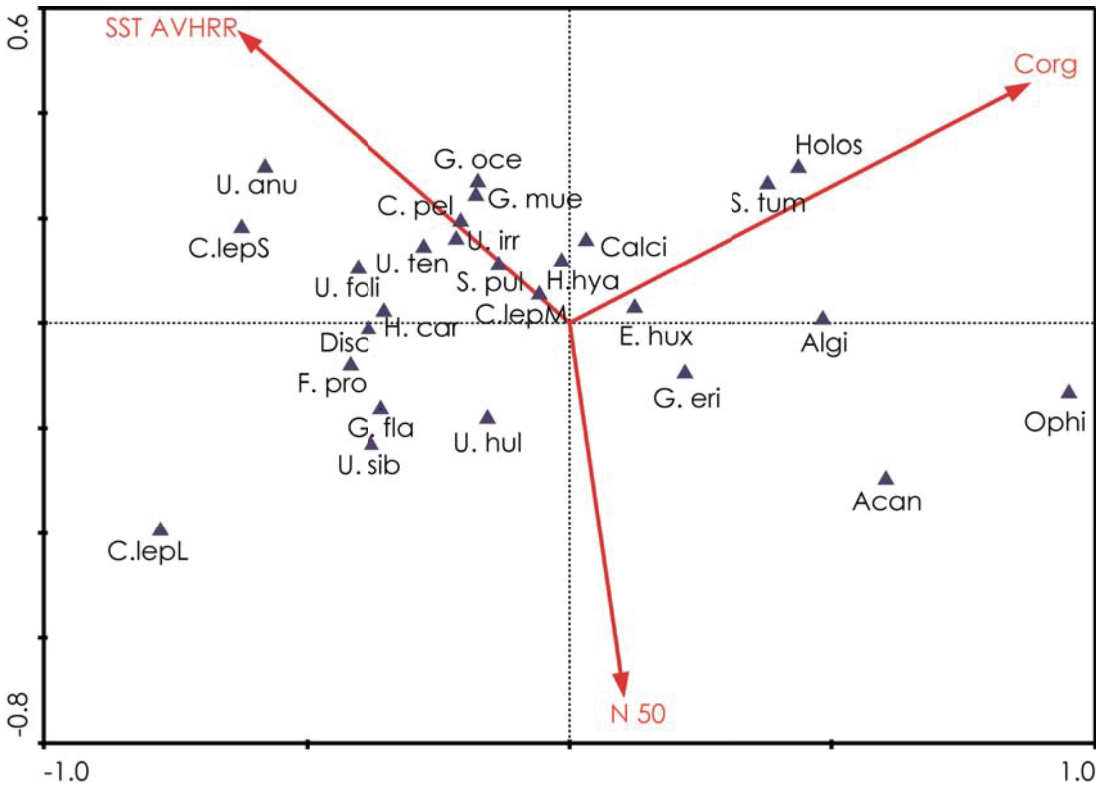
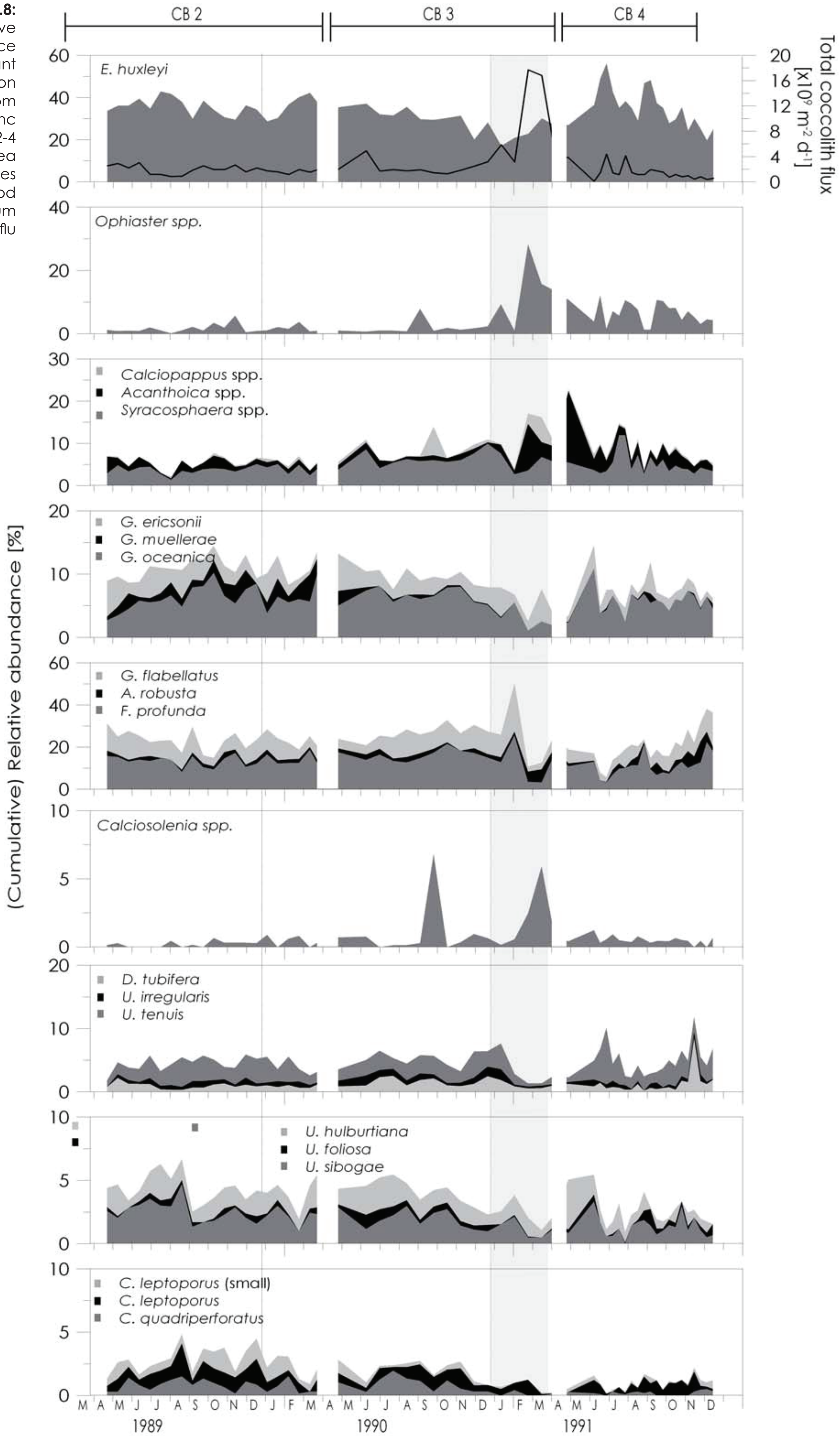


Fig. 3.7: Ordination diagramm derived by CCA based on the fluxes of the the dominant and frequently present species of CB1-4 Sea surface temperature by AVHRR, organic carbon (Corg) of the samples, nitrate in 50m water depth

Fig. 3.8: Relative abundance of dominant and common species from Cape Blanc (CB 2-4 Shaded area indicates time period of maximum coccolith flu



3.5 Discussion

3.5.1 Coccolith fluxes and seasonal patterns

The annual fluxes of coccoliths off Cape Blanc were extremely variable and lacked a simple and evidently seasonal cycle. This is basically due to the variable hydrographic condition in this area: the frontal system of the two deep water masses (NADW and SADW), changing coastal upwelling conditions during the year, and the occurrence, development and movement of filaments ("*giant filaments*") (Barton *et al.*, 1998; Kostianoy and Zatsepin, 1996; Mittelstaedt, 1991). Within the frontal zone small scale eddies of surface water exist consisting of mixed water characteristics according to their origin, either the nutrient enriched, less saline and warmer SACW or the salty and nutrient-poor NACW. The coastal upwelling persists year-round off Mauritania, however, varying in strengths and in direction of the trade winds. The upwelled coastal water forms filaments meandering far offshore. These *giant filaments* (Gabric *et al.*, 1993) vary in composition and movement direction. Thus, the flux of coccoliths reflects this highly variable system without (yet) disclosing a 'simple' and delimited pattern but revealing some tendencies.

One of these is the trend of increasing coccolith flux during time of significant SST change (Fig. 3.9), presumably at times when the water column stratifies or stratification breaks down. A change in SST could also indicate changing influence of the coastal upwelling, that is a relaxation or increase of the upwelling (Giraudeau *et al.*, 1993). Stratification of the water column or its breakdown during strong temperature changes is accompanied with changes in nutrient availability in the surface waters, or turbulences (mixing) of the water column. Satellite images of SST reveal intense and highly variable jets, filaments, and eddies in the studied area, which affect the regional nutrient load of the surface water (Kostianoy and Zatsepin, 1996; van Camp *et al.*, 1991). As a consequence a turbulent mixing process between nutrient rich coastal and poor offshore waters occurrs (Marchesiello *et al.*, 2004). The coccolith fluxes reflect this changing environment.

A second trend is the main season in which most of the coccoliths settle. The comparison of each sample with respect to their proportional contribution to the annual coccolith flux displays winter and spring to be the important seasons for the downward fluxes, whereas in summer and fall the proportions are smaller. Ratmeyer *et al.* (1999b) observed highest lithogenic fluxes during winter and spring. This could explain the main settling period of the coccoliths associated with the processes involved in scavenging small particles within the water column (Nowald *et al.*, 2006).

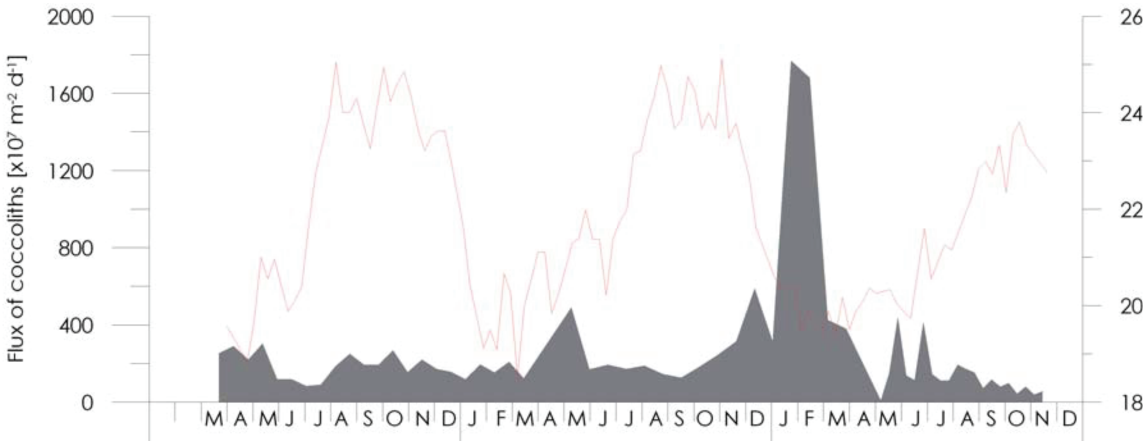
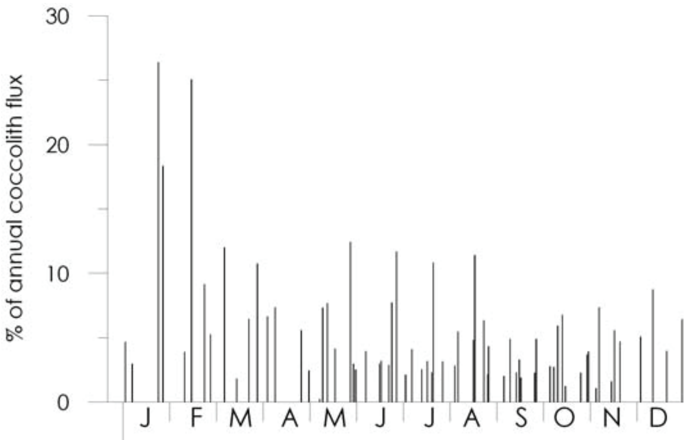


Fig. 3.9: Flux of coccoliths of CB1–4 and SST at the mooring location based on AVHRR data

Fig. 3.10: To obtain the season in which the largest part of the yearly downward flux takes place the proportion of the fluxes of each sample (CB1-4)to the specific annual coccolith flux is calculated and graphed parallel in one annual cycle

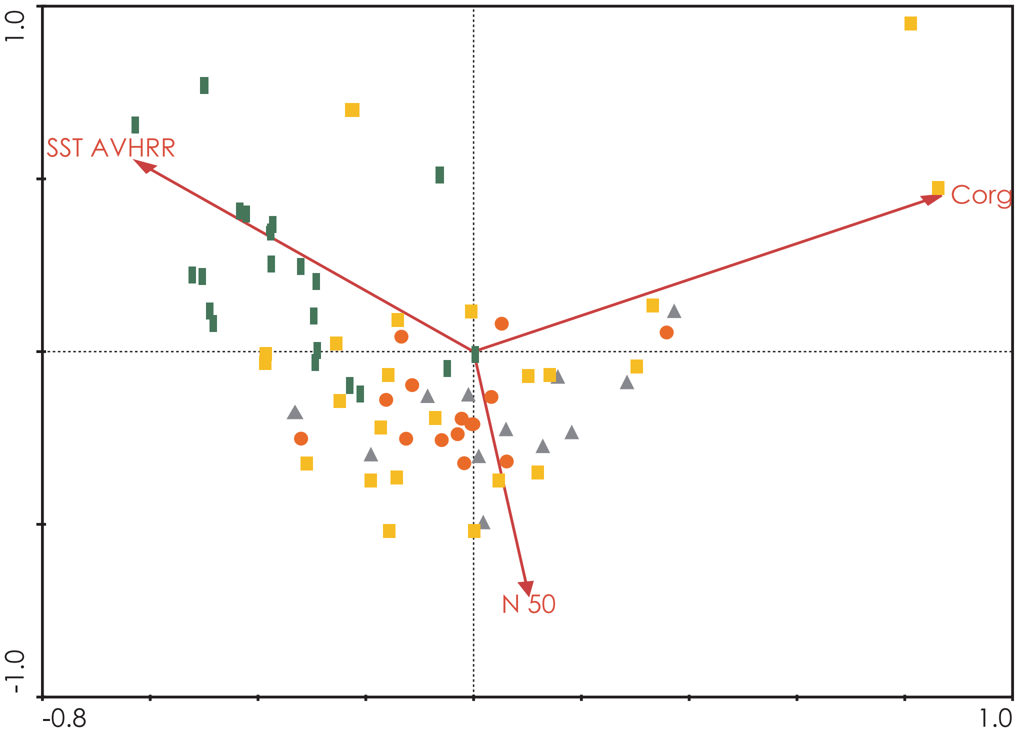


However, the strong intraseasonal differences of the fluxes in respect to their annual proportion further indicate the high variability of the region during the year (Fig. 3.10). In contrast, the absolute coccolith fluxes of the Canary Island region showed a distinct seasonality with high fluxes during late winter to early spring, whereas further south of Cape Blanc seasonal maximum fluxes were observed in spring (Bory *et al.*, 2001; Sprengel *et al.*, 2000). Offshore the Cape Blanc upwelling all the coccolithophore flux is more variable with a less pronounced seasonal pattern than in other sediment trap studies (Andruleit, 2007; Broerse *et al.*, 2000a; Haidar and Thierstein, 2001; Triantaphyllou *et al.*, 2005).

Predominant environmental parameters were studied with respect to their influence on the variability of the coccolithophore fluxes. The results showed that the combination of various factors rather than single specific parameters determine the coccolithophore assemblage. One exception seems to exist in fall. These samples cluster closely together with certain affinity to the SST. Thus, the variability of the coccolithophore fluxes is quite well explained by the fluctuations in SST. Spring samples seem to be related to the nutrient availability. In the remaining seasons the nutrient content of the surface waters also seems to influence the assemblage strongly, however, exceptions are also evident (Fig. 3.11).

Fig. 3.11: Ordination biplot with the coccolith flux and environmental variables based on CCA N50 (nitrate at 50m depth, WOA), SST of the AVHRR sataset and C_{org} of the trap samples

Green bars are samples of fall seasons, grey triangle of winter season, organe circles of spring, and yellow squares of summer seasons



3.5.2 Change of the annual coccolith fluxes and its species composition

Even though the coccolith fluxes fluctuated strongly the assemblage revealed rather constant species composition for the time period from spring 1989 to fall 1990 during the first interval. Subsequently a distinct change in species composition is recorded (winter 1990/1991), followed by an interval with similar assemblage as before. As a result we distinguish three time periods.

Besides the dominant species *E. huxleyi*, the common species *F. profunda, G. flabellatus, G. oceanica,* and *G. ericsonii* determined the assemblage. *C. quadriperforatus*, *C. leptoporus*, *Umbilicosphaera* spp., *Umbellosphaera* spp., *D. tubifera* contributed likewise constantly to the assemblage but in a smaller proportion (Fig. 3.8). Besides these species *G. muellerae*, *C. leptoporus* (small), and *U. foliosa* are of interest due to their changing abundances. *G. muellerae* and the small morphotype of *C. leptoporus* which are associated with nutrient enriched waters are present in larger proportions. Their presence points toward periods of nutrient enrichment, most probably upwelled waters due to the preference of *G. muellerae* to cold water conditions as well (Boeckel and Baumann, 2008). The salinity profile supports the occurrence of water masses in the beginning (until 1990) different to the subsequent months (Fig. 3.2). The increased abundance of these species reflects the strong upwelling impulse characterizing the first part of the interval (Fig. 3.3). In the following months *U. foliosa* which prefers oligotrophic conditions (Boeckel and Baumann, 2008) is slightly increased in proportion, whereas *G. muellerae* disappears, and *C. leptoporus* (small) is significantly reduced. This changes documents the reduced upwelling intensity concluded for that time. Thus the coccolith fluxes of this first interval seem to precisely indicate the differences in environmental condition by the changes in species composition.

The second interval is predominantly characterized by a remarkable increase of small sized taxa, *Ophiaster* spp. and *Acanthoica* spp. that *s*were well preserved as in all samples. However, there was an increase by the factor four compared to the beginning in settling velocity starting in fall 1990 (Müller and Fischer, 2001), thus reducing the time period of possible dissolution. Also the additional increased flux of holococcoliths and abundances of further small size species such as *Syracosphaera* spp. and *Calciosolenia* spp. supports the conclusion of less dissolution as usual.

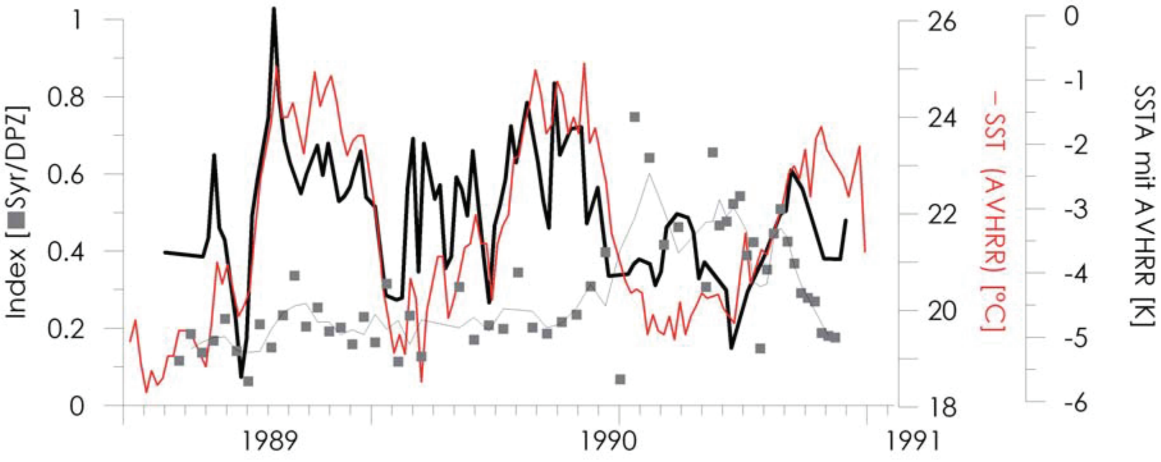


Fig. 3.12: Ratio of *Syracosphaera* spp. to species of the lower photic zone (*F. profunda, G. flabellatus,* and *Algirosphaera* spp.) in correspondence to SST anomaly and SST

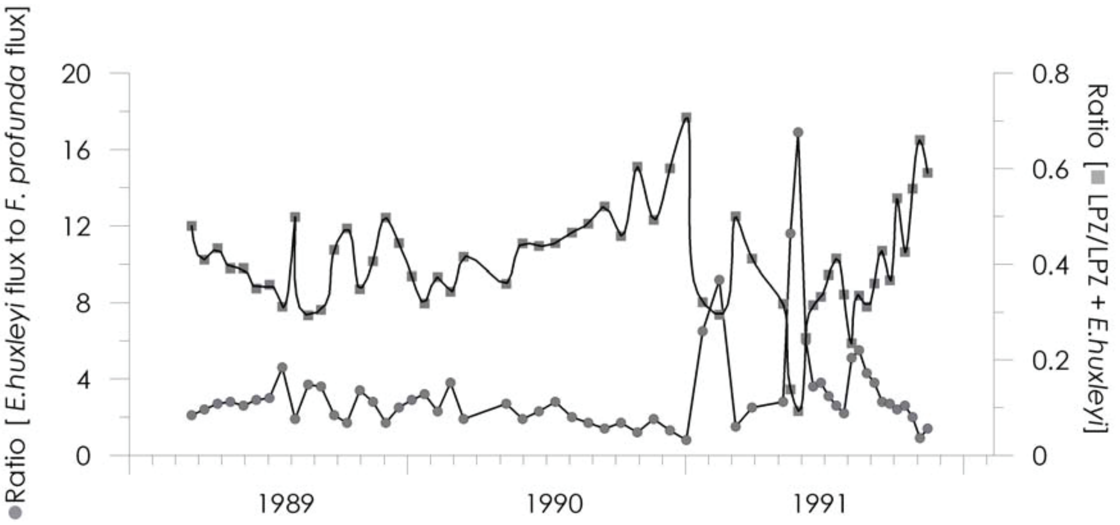


Fig. 3.13: Ratio of lower photic zone species vs sum of lower photic zone species (*F. profunda, G. flabellatus*, and *Algirosphaera* spp.)and *E. huxleyi* in correspondence to the ratio between *E. huxelyi* and *F. profunda*

Furthermore, the increased abundance of species with similar ecological preferences is remarkable. *Syracosphaera* spp. and holococcoliths seem to flourish in shallow surface waters (Cros, 2001), as *Ophiaster hydroideus* (Haidar and Thierstein, 2001). *Ophiaster* spp. and *Acanthoica* spp. are influenced strongly by same parameters as revealed by the CCA (Fig. 3.7). The ratio between *Syracosphaera* spp. versus species of the lower photic zone indicates a shift during winter 1990/1991. During the remaining seasons a relatively constant ratio prevailed even though the surrounding environment was characterized by strong changes (Fig. 3.12). This shift may indicate an increase occurrence of surface living species opposing a reduced lower photic zone assemblage.

A concurrent change in abundance of *E. huxleyi* and *F. profunda* and other lower photic zone species (*F. profunda, G. flabellatus,* and *Algirosphaera* spp.) ratio is noticed (Fig. 3.13). These species differ in their environmental preferences. *E. huxleyi* is a cosmopolitan species, that tends to favour rather mature waters (Townsend *et al.*, 1994) than freshly upwelled waters, but flourishes in a wide range of environmental conditions. *F. profunda* is found in correspondence to stratified waters close to the nutricline (Molfino and McIntyre, 1990). Besides the winter season of 1990/1991 the ratio was rather constant.

The stated shift indicates a change in environmental condition influencing species differently. However, to transfer changes in the plankton assemblage to the deep fast settling is a prerequisite. Due to their size coccoliths have to settle in aggregates to be found in the deep, either via of fecal pellets or of marine snow. A quantitative analysis of fecal pellets was not carried out in this study. The scavenge processes resulting in marine snow are described by Nowald *et al.* (2006). Due to their large abundance small particles are preferable scavenged during sinking. A trigger mechanism in that region is the input of wind transported dust which is coupled with the input of high-density lithogenic material. The terrigenous grains collide with the phytodetritus in the water column that lead to higher sinking rates. The comparison of coccolith fluxes and the lithogenic material during the study period however, reveals a decreasing input in winter 1990/1991. Consequently an increased scavenging due to the dust load is unlikely (Fig. 3.6).

Coccolith concentration, the ratio of total coccolith flux to total flux, results from production of coccolithophores in the surface waters, dilution of the collected material and of dissolution process of the coccoliths. The studied samples revealed a constant coccolith concentration except during winter 1990/1991 (Fig. 3.14). Here, a significant increase in coccolith concentration occurred.

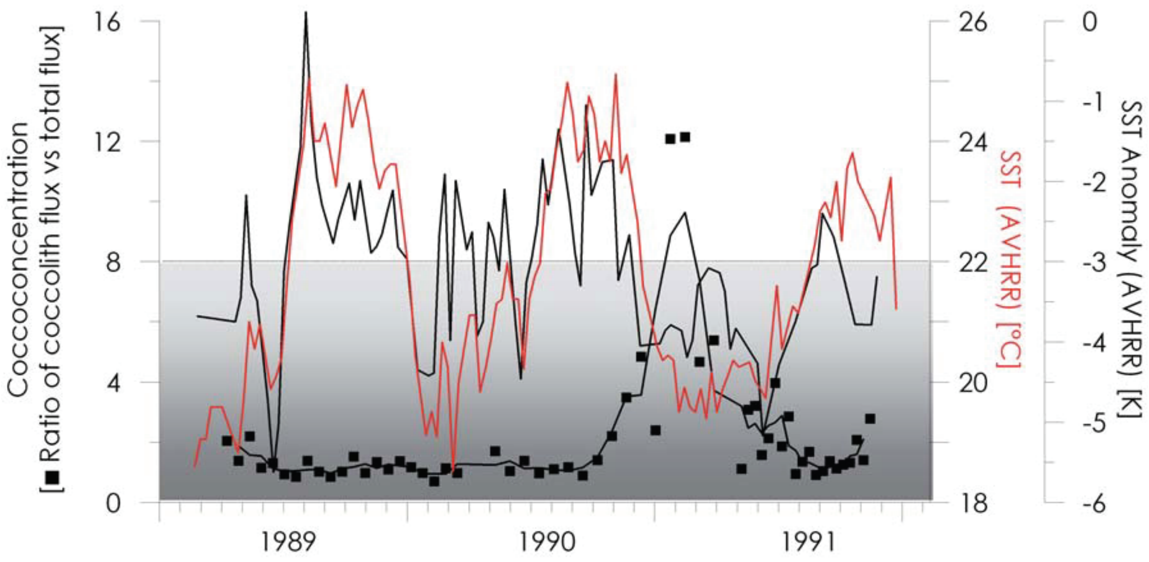


Fig. 3.14: Coccolithconcentration calculated for CB 1 to CB 4 in comparison to SST anomaly and SST. Grey bar indicates increasing upwelling Solid black line is the running average(width 3).

Due to the shift in species composition and the elevated concentration of well preserved coccoliths which stayed constant throughout the remaining study period, we assume that an increase in occurrence of small sized and upper photic zone taxa took place accompanied with a fast settling process. Nowald *et al.* (2006) describes such events as *pulse-like sedimentation events* which may be triggered by phytoplankton blooms.

The last interval (from spring 1991 to fall 1991) seems to be a *recovering* phase with slightly elevated proportion of *E. huxleyi* which is known to prosper faster than the other species in a positively changing environment (Westbroek *et al.*, 1993). However, extreme condition still prevailed as seen in the significantly decreased total fluxes, increased lithogenic fluxes and very low coccolith fluxes. However, the coccolithophore assemblage converges to the former (1989 to 1990) composition.

Conclusion

The study of a three year deployed sediment trap off Cape Blanc revealed a diverse and variable coccolithophore flux that reflects the prevailing hydrographic conditions of this dynamic offshore upwelling region. The following conclusion can be drawn:

- The coccolith fluxes vary in occurrence and amount revealing significantly increased fluxes in winter 1990/1991. The season in which most of the annual coccolith flux settles is winter and to a lesser content spring, however, the variability within the winter samples are large. In summer and fall the proportion on the yearly coccolith flux is small. A relation between coccolith fluxes and the scavenge process of lithogenic material which are increased in winter and spring is assumed.
- High coccolith fluxes occurred during changing sea surface temperature. The level of stratification and consequently the availability of nutrients seems an important relation to the observed coccolith fluxes. In general, environmental parameters in combination rather than distinct single parameters seem to explain the changes in coccolith fluxes. The combination of nutrient availability, stratification and SST changes explain the variability of the assemblage. Yet, the relevance of the single factors may change during the season. Outstanding is the good correspondence of SST variability and the variability of fall samples.
- During the study interval different intervals were distinguished characterized by specific assemblage that point at the variable and changed hydrography of the region. At the beginning, rather constant species composition of the coccolith fluxes prevailed displaying only (small) changes. The seasonality in upwelling, as well as in water characteristics which were recognized can explain these changes respectively the coccolithophore assemblage.
- In winter 1990/1991 a shift towards smaller sized coccoliths took place within the species composition of the fluxes. A significantly high flux of *Ophiaster* spp. and *Acanthoica* spp. was present. A fast settling process is assumed due to the good preservation of the small and delicate coccoliths accompanied with an increase occurrence of the species in the water column.
- The last interval is characterized by significantly reduced coccolith fluxes. However, the assemblage converges towards the species composition of the former composition.

Appendix A

The taxonomic list comprises all taxa encountered in the samples and are listed in alphabetical order. Full bibliographic references can be found in Young *et al.*, 2003.

Acanthoica Lohmann 1903
Acanthoica acanthifera Lohmann 1902
Acanthoica quattrospina Lohmann 1903
Algirosphaera robusta (Lohmann 1902) Norris 1984
Alisphaera Heimdal 1973
Alisphaera unicornis Okada & McIntyre 1977
Calcidiscus leptoporus (Murray & Blackmann 1898) Loeblich & Tappan 1978
Calcidiscus leptoporus (small type)
Calcidiscus leptoporus ssp. *quadriperforatus* (Kamptner 1937) Geisen *et al.* 2002
Calciopappus rigidus Heimdal in Heimdal & Gaarder 1981
Calcioppappus caudatus Gaarder & Ramsfjell 1954
Calciosolenia brasiliensis Lohmann 1919
Calciosolenia murrayi Gran 1912
Ceratus cristatus Kamptner 1950
Coccolithus pelagicus (Wallich 1877) Schiller 1930
Coronosphaera Gaarder in Gaarder & Heimdal 1977
Coronosphaera binodata (Kamptner 1927) Gaarder in Gaarder & Heimdal 1977
C. mediterranea (Lohmann 1902) Gaarder in Gaarder & Heimdal 1977
Discosphaera tubifera (Murray & Blackman, 1898) Ostenfeld 1900
Emiliania huxleyi (Lohmann 1902) Hay & Mohler 1967
Florisphaera profunda Okada & McIntyre 1980
Gephyrocapsa ericsonii McIntyre & Bé 1967
Gephyrocapsa muellerae Bréhéret 1978
Gephyrocapsa oceanica Kamptner 1943
Gladiolithus flabellatus (Halldall & Markali, 1955) Jordan & Chamberlain 1993
Helicosphaera carteri (Wallich 1877) Kamptner 1954
Helicosphaera hyalina Gaarder 1970
Helicosphaera walechii (Lohmann 1902) Okada & McIntyre 1977
Hyaster perplexus (Bramlette & Riedel 1954) Bukry 1973
Michaelsarsia elegans Gran 1912
Oolithotus antillarum (Cohen 1964) Reinhardt in Cohen & Reinhardt 1968
Oolithotus fragilis (Lohmann 1912) Marini & Müller 1972
Ophiaster (Gran 1912) Manton & Oates 1983
Palussphaera Lecal 1965
Pappomonas Manton & Oates 1975
Papposphaera lepida Tangen 1972
Papposphaera Tangen 1972
Pontosphaera Lohmann 1902
Pontosphaera multipora (Kamptner 1948) Roth 1970
Reticulofenestra sessilis (Lohmann 1912) Jordan & Young 1990
Rhabdosphaera Haeckel 1894
Rhabdosphaera clavigera Murray & Blackman 1898

Rhabdosphaera stylifer Lohmann 1902
Rhabdosphaera xiphos (Deflandre & Fert 1954) Norris 1984
Syracosphaera (Lohmann 1902) Lemmerman 1903
Syracosphaera ampliora Okada & McIntyre 1977
Syracosphaera anthos (Lohmann 1912) Janin 1987
Syracosphaera bannockii (Borsetti & Cati 1976) Cors *et al.* 2000
Syracosphaera borealis Okada & McIntyre 1977
Syracosphaera corolla Lecal 1966
Syracosphaera delicata Cros *et al.* 2000
Syracosphaera dilatata Jordan *et al.* 1993
Syracosphaera halldalii Gaardner in Gaarder & Hasle 1971
Syracosphaera histrica Kamptner 1941
Syracosphaera lamina Lecal-Schlauder 1951
Syracosphaera marginaporata Knappertsbusch 1993
Syracosphaera molischii Schiller 1925
Syracosphaera nana (Kamptner 1941) Okada & McIntyre 1977
Syracosphaera nodosa Kamptner 1941
Syracosphaera noroitica Knappertsbusch 1993
Syracosphaera ossa (Lecal 1966) Loeblich & Tappan 1968
Syracosphaera pirus Halldal & Markali 1955
Syracosphaera prolongata Gran 1912
Syracosphaera pulchra Lohmann 1902
Syracosphaera rotula Okada & McIntyre 1977
Syracosphaera tumularis Sánchez-Suárez 1990
Turrilithus Jordan *et al.* 1991
Umbellosphaera irregularis Paasche in Markali & Paasche,1955
Umbellosphaera tenuis (Kamptner 1937) Paasche in Markali & Paasche 1955
Umbilicosphaera annulus (Lecal 1967) Young & Geisen n. comb.
Umbilicosphaera foliosa (Kamptner 1963) Geisen in Sáez *et al.* 2003
Umbilicosphaera hulburtiana Gaarder 1970
Umbilicosphaera sibogae (Weber-Van Bosse 1901) Gaarder 1970

HOLOCOCCOLITHS
Calyptrolithophora papillifera (Halldal 1952) Heimdal in Heimdal & Gaarder 1980
Calyptrosphaera cialdii Borsetti & Cati 1976
Calyptrosphaera oblonga Lohmann 1902
Daktylethra pirus (Kamptner 1937) Norris 1984
Homozygosphaera triarcha Halldal & Markali 1955
Poritectolithus Kleijne 1991
Sphaerocalyptra Deflandre 1952
Syracolithus Deflandre 1952
Syracolithus catiliferus (Kamptner 1937) Deflandre 1952
Syracolithus dalmaticus (Kamptner 1927) Loeblich & Tappan 1966
Syracolithus quadriperforatus (Kamptner 1937) Gaarder 1962
Syracolithus schilleri (Kamptner 1927) Loeblich & Tappan 1963
Teralithoides quadrilaminata (Okada & McIntyre 1977) Jordan, Kleijne & Heimdal 1993
Zygosphaera bannockii (Borsetti & Cati 1976) Heimdal 1982

IV. Seasonal variations of the coccolith fluxes off Chile (30°S) under 'normal' and El Niño conditions

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(to be submitted to Deep Sea Research I)

Abstract

The coccolithophores flux collected by a sediment trap moored off Chile (30°S 73°W) under the influence of El Niño (1997/98) and under 'normal' hydrographic conditions (July 1993 to July 94) was studied. During 'normal' conditions the coccolith export revealed a high flux period from spring to summer and a low flux period in fall to winter. A diverse coccolithophorid assemblage of 68 species dominated by *Emiliania huxleyi* existed. In addition, *Florisphaera profunda, Calcidiscus spp.*, and *Gephyrocapsa oceanica*, and *G. muellerae* were common.

During the season a significant change in coccolithophore assemblage was observed. The absolute flux of *Umbilicosphaera sibogae*, *Gephyrocapsa oceanica*, *F. profunda*, *G. muellerae*, *Helicosphaera spp.*, and *Calcidiscus leptoporus* (small morphotype) changed indicating a warm, less nutrient enriched, and turbulent water intrusion.

During the 1997/98 El Niño event, the pronounced alteration between high and low flux period of coccoliths was missing revealing a strong fluctuating seasonal flux pattern of (most) species. A significant shift in species composition with respect to relative and absolute abundances took place. *E. huxleyi* decreased in relative abundance, whereas *F. profunda* increased. The absolute flux of *C. leptoporus* small, *U. sibogae* increased in contrast to the decrease in *G. oceanica* and *Syracosphaera spp.* flux. Off Chile, the change of the coccolithophorid assemblage reflects in detail the transformed environment by the El Niño event.

Even though, the general structure of the coccolithophorid community such as observed species, number of identified species, and the mean flux did not differ significantly to 1993/94.

The coccolith-derived carbonate added up to 9.4 g $m^{-2}y^{-1}$ and 5.9 g $m^{-2}y^{-1}$ for the 'normal' and the El Niño years respectively, accounting for 27% and 34% of the total carbonate flux.

Keywords: El Niño; sediment trap; coccolithophorid assemblage; carbonate flux; Chile

4.1 Introduction

High productivity regions cover only 15% of the world oceans, however, they produce roughly half of the global export production (Peinert *et al.*, 1989). In respect to the global carbon cycle coccolithophores should be considered due to their direct influence via photosynthetic activity and carbonate production (Westbroek *et a.l.*, 1993; Thierstein and Young, 2004).

Within the East Boundary Current systems, the Peru-Chile Current has a pronounced productivity (Escribano *et al.*, 2004; Hebbeln *et al.*, 2000) which in turn results in a substantial flux of biogenic matter to the sea floor (Hebbeln *et al.*, 2000). The settling of biogenic material is directly related to surface production and reflects the seasonality of that production (Deuser *et al.*, 1990). Consequently, the quantity and composition of the sinking matter, as measured with sediment traps, are functions of variable components within the overlying pelagic system (Delesalle *et al.*, 2001; Legendre and Rassoulzadegan, 1996; Peinert *et al.*, 1989). The sediment trap material provide invaluable information of the seasonal variations in abundance and species composition of the plankton, as described for coccolithophores (Broerse *et al.*, 2000c; Samtleben and Bickert, 1990; Sprengel *et al.*, 2002; Ziveri *et al.*, 1995).

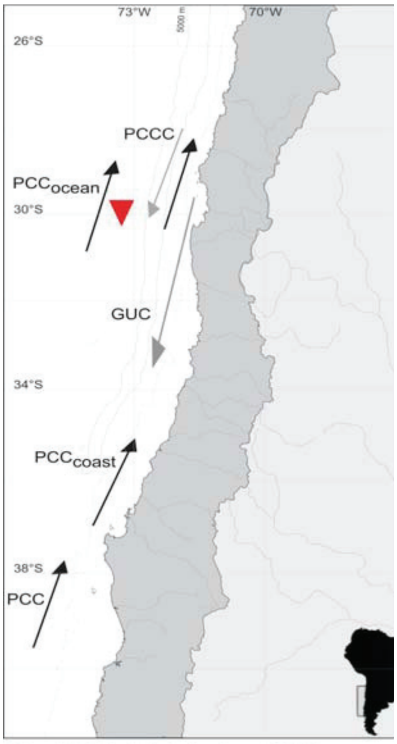
The Humboldt Current System experiences strong temporal changes including quasi-weekly upwelling favourable wind events, intraseasonal changes effecting the depth of the nutricline and interannual changes associated to El Niño (Montecino *et al.*, 2002).

This study deals with the export of coccolithophores off Chile. Two investigated periods differing significantly in the prevailing hydrographic condition are discussed: a time-series in 1993/94 as an example for 'normal' hydrographic condition and a time-series in 1997/98 as an example for a strong El Niño event. The study focuses on (1) (possible) change in coccolithophore assemblage which could be reflecting El Niño, (2) ecological affinities of coccolithophores being visible due to the change in hydrographic condition and (3) the estimation of carbonate export production derived by coccoliths.

4.2 Regional Setting

4.2.1 General Hydrography

The regional oceanography of the southeast Pacific has been described by Shaffer *et al.* (1995) and by Strub *et al.* (1998), whereas the seasonal climatology of the oceanographic conditions has been reported by Blanco *et al.* (2001). In general, the area is dominated by the northward flowing Peru-Chile Current (PCC, Subantarctic Surface Water) (Fig. 4.1). Off the Chilean coast the PCC is divided into an oceanic and a coastal branch, separated by the poleward flowing Peru-Chile Counter Current (Subtropical Surface Water) that flows 100-300 km offshore. Close to the coast, the poleward flowing Gunther Undercurrent (Equatorial Subsurface Water) underlay these surface water masses. It is the source of the upwelled water with its nutrient-rich Equatorial Subsurface Water (Morales *et al.*, 1996).



Scale: 1:8017511 at Latitude 0° Source: GEBCO.

Fig. 4.1: Mooring location (▼) off Chile and current system

(PCC = Peru-Chile Current, PCCcoast = coastal branch of PCC, PCCocean = oceanic branch of PCC, GUC = Gunther Undercurrent, PCCC = Peru-Chile Counter-Current)

Even though, the mooring site is not placed within the coastal upwelling cell, high pigment concentrations have been found (Fig. 4.2) due to filaments that extend hundreds of kilometres offshore (Montecino *et al.*, 2002). During a 'normal' condition coastal fronts are well developed (Escribano *et al.*, 2004). In general, highest mean chlorophyll concentration in September parallels strong westerly winds and lowest sea surface temperatures (Fig. 4.2).

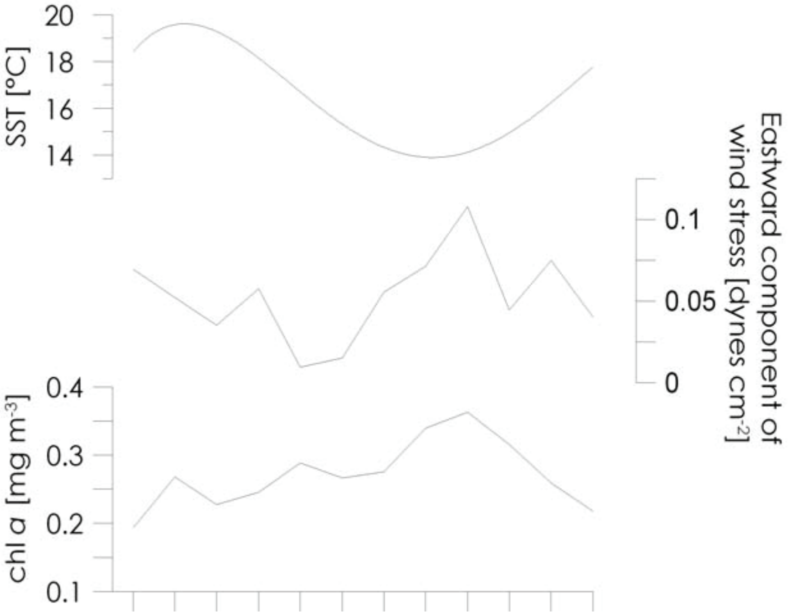


Fig. 4.2:
Mean seasonal cycles of sea surface temperatures (SST, Levitus Ocean Atlas data), eastward component of wind stress (Hellerman data data from Hallermann Taux http://iridl.ldeo.columbia.edu/SOURCES/.RC/) and chl *a* pigment concentration of surface water (MoDis data) at the mooring station in the Peru-Chile Current

4.2.2 The El Niño event 1997/98

At intervals of 2-7 years the whole system in the Pacific is disturbed by El Niño events, resulting in a considerable warming of the water masses (Escribano *et al.*, 2004; Ramage, 1986) and in modified circulation patterns and water properties (Strub *et al.*, 1998). In general, coastal fronts weaken or disappear, and the photic layer deepens. Based on the changes in the coastal water properties the thermocline, oxycline and oxygen minimum zone deepen. Upwelling may continue, but the nutrient supply to the surface waters is reduces as the upwelled water origins above the deepened nutricline (Blanco *et al.*, 2002).

In 1997/98 the Peru-Chile Current was subject to one of the most intense El Niño recorded and with major climatic impact felt around the world (McPhaden, 1999). Strong chl-*a* anomalies were associated with sea surface temperature (SST) anomalies (Carr *et al.*, 2002b). The dramatic changes started in April 1997 and culminated in a first peak of SST anomalies exceeding 2°C in July to August 1997. Upwelling favourable winds persisted but Δ SST was 1-2°C weaker than in 1996 (Carr *et al.*, 2002b). Between September and October 1997 a phase of relaxation occurred, with wind forcing still persisting but slightly decreasing (Escribano *et al.*, 2004; Rutllant *et al.*, 2004b). A second and more pronounced peak of anomalous SST persisted, the coastal fronts were weaker or disappeared, and the photic layer deepened. Satellite derived studies revealed a decrease in chl. *a* concentration. Between February and May 1998 a transitional phase occurred with upwelling favourable winds weakening slightly and Δ SST starting to change sign that in turn indicated upwelling of colder water (Carr *et al.*, 2002b; Escribano *et al.*, 2004). It was not until the trade winds in the eastern Pacific abruptly returned to near normal strength in May 1998 that the cold subsurface waters could be efficiently upwelled and El Niño demised (McPhaden, 1999). Con-

Fig. 4.3:
Sea Surface Temperature (Reynold & Smith) of 1993/94 (solid line) and 1997/98 (fine line)

sequently in May 1998 SST anomaly rapidly decreased and turned over in the development of a La Niña (negative SST anomalies) starting in September 1998. In general, upwelling continued, but the deepened nutricline dropped under the depth of the origin of the upwelled water. Consequently, the input of new nutrients into the photic zone was limited since the upwelled water was less enriched in nutrients (Carr, 2003; Escribano *et al.*, 2004).

The previous description of the El Niño development in 1997/98 focused on the phenomenon and situation off central Chile, the mooring location. As stated before, the mooring location is close to the upwelling cell, however, not located within the coastal band. Fig. 4.3, documents the increased SST at the mooring station during the sampling period (data from IGOSS nmc Reyn_SmithOIv2 weekly Sea Surface Temperature).

4.3 Material and Methods

The investigated sediment traps were moored off Chile (30°S 73°W) in a water depth of 2300m and 2600m, respectively (Table 4.1). Traps CH 3-1 and CH 4-1 (in the following referred to as CH3/4) provided a continuous 12 months' record of particle flux under 'normal', i.e. cold conditions with a sample duration of 8 respectively 9 days. The combined record of trap CH 10-2 and CH 11-1 (in the following named as CH 10/11) covered 18 months including the time period of the 1997-98 El Niño event. The sample duration was longer (12 and 13 days). The deployment of the sediment trap, as well as the treatment of the collected samples is described in detail by Hebbeln *et al.* (2000).

The measurements of the current speed 20 m underneath the sediment trap revealed a current velocity of <10 cm s^{-1} over the entire interval investigated, indicating no or only little effect on the trapping efficiency (Baker *et al.*, 1988; Hebbeln *et al.*, 2000).

For the processing of the samples for scanning electron microscopy the method of Andruleit (1996) was followed. Depending on the particle content of the samples between 3/12500 and 1/250 of the original material were used. Qualitative and quantitative analyses of the coccolithophores were performed at x3000 magnification using a Zeiss DSM 940A at 10kV accelerating voltage. Along an arbitrarily chosen traverse transect each coccolith and coccosphere were counted until a total number of at least 500 coccoliths were reached. Each individual was identified down to the lowest taxonomic level as possible. The coccolithophores were taxonomically classified based on Cros (2001) and Young *et al.* (2003). The coccolith and coccospheres were converted into coccolith-carbonate contents on the basis of

Table 4.1: Mooring location, duration and water depth of the studies sediment traps

Mooring	Position	Trap depth	Water depth	Sampling duration
CH 3-1	30°01.5'S 73°11.0'W	2333m	4360m	22.07.1993 – 18.01.1994
CH 4-1	30°00.3'S 73°10.3'W	2303m	4330m	25.01.1994 – 04.07.1994
CH 10-2	29°59.9'S 73°16.8'W	2578m	4500m	14.02.1997 – 01.11.1997
CH 11-1	29°58.8'S 73°18.1'W	2526m	4442m	15.11.1997 – 01.07.1998

mean estimates of species specific coccolith masses. To gain the estimates each coccosphere was converted into coccoliths based on species specific values (Boeckel and Baumann, 2008). To compare coccolithophores with fluxes of further plankton groups the coccolith counts were converted into sphere, thus representing whole organisms.

Size measurements for morphometric analysis were made directly on the TV-screen at a magnification of x5,000 or x10,000 by using an internal Zeiss measuring system, leading to a resolution of about 0.1-0.2 µm. For all species distal shield size of at least 20 selected specimens were measured on six of the 40 samples from sediment traps CH3/4, so that in total more than 150 coccoliths were measured for *Umbilicosphaera sibogae*, *U. foliosa* and *Calcidiscus leptoporus*. Calcium carbonate masses of further species to estimate the coccolithophorid derived carbonate flux were taken from Young and Ziveri (2000).

4.4 Results

4.4.1 Coccolithophores flux during 'normal' condition (1993/94)

The flux of coccospheres varied significantly during a high flux period (from June to December 1993) and was generally low from January to June 1994. The flux reached a maximum of 37x10^{6}coccospheres m^{-2}d^{-1} in November (Fig. 4.4). In total, coccospheres of 14 species were found (Table 4.2). The most abundant and frequent species was *Emiliania huxleyi*. Spheres of *Calcidiscus leptoporus* (small morphotype) were present only during the high flux period whereas spheres of *Syracosphaera spp.* and *S. molischii* were only present during the low flux period.

Due to the small amount of coccospheres found, coccospheres were converted into coccoliths based on species specific values. This coccolithophorid flux was in general characterized by seasonal pattern of distinct high and low flux intervals that corresponded to the total flux.

The high flux period started in August 1993 and lasted until December. The average coccolith flux was 436x10^7 m^{-2}d^{-1}. A low flux period with an average flux of 76x10^7 liths m^{-2}d^{-1} lasted from January 1994 until (at least) the end of the deployment time in June. The maximum flux of 799x10^7 liths m^{-2}d^{-1} was in November 1993, whereas the minimum flux of 23x10^7 liths m^{-2}d^{-1} occurred in May 1994 (Fig. 4.5).

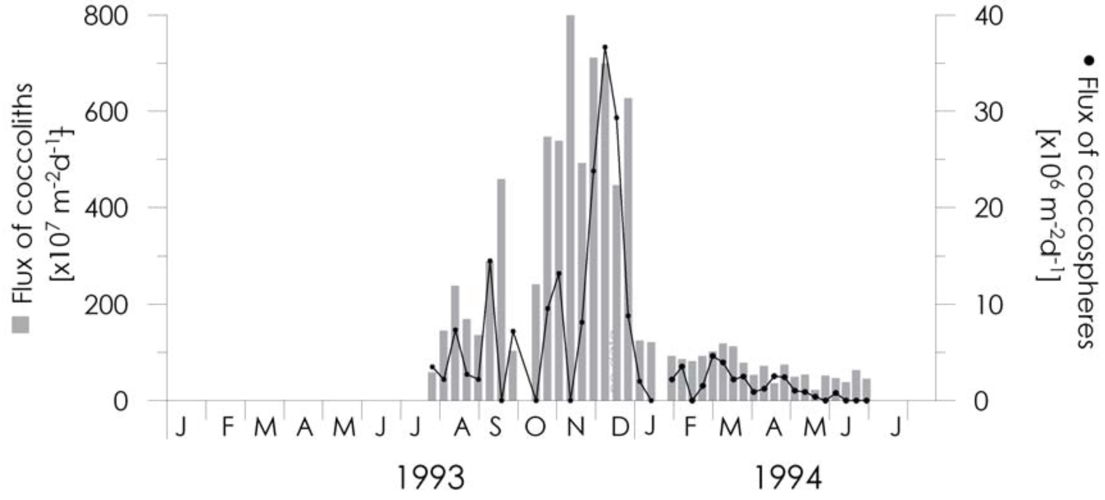
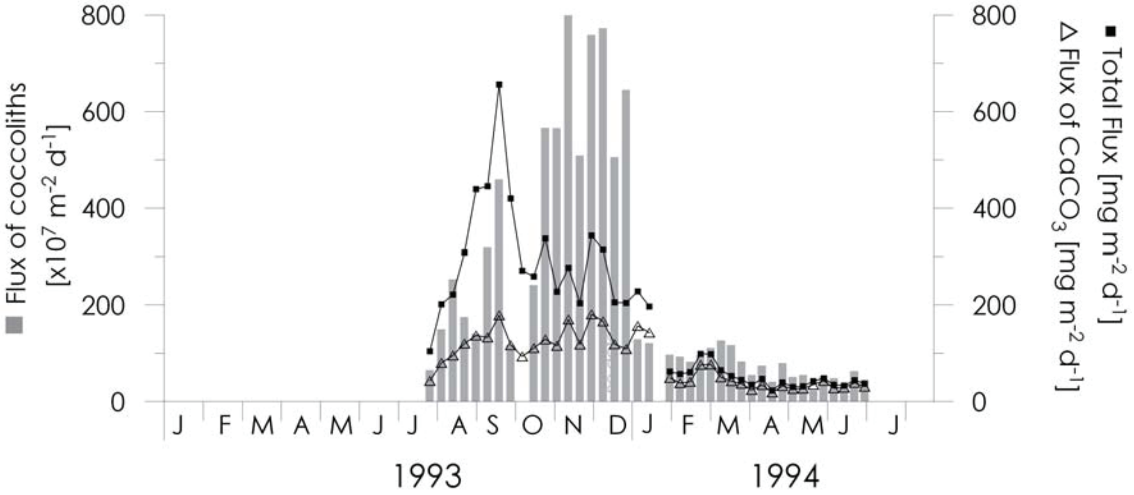


Fig. 4.4:
Flux of counted coccoliths and coccospheres of CH3/4 ('normal' condition)
(The mid-dates of the sampling periods have been used for the graphical presentation)

Fig. 4.5: Total flux of coccoliths, total flux and total carbonate flux of CH3/4 ('normal' condition)



The coccolithophorid assemblage revealed a diverse species composition. In total, 65 heterococcolith-bearing species, one species in its hetero- and holococcolith stage (*Syracosphaera pulchra –Calyptrosphaera oblonga*), and one holococcolithophore (*Teralithoides quadrilaminata*) were identified. A maximum of 42 heterococcoliths were observed in one sample. Species found in each samples are listed in Table 4.2.

Table 4.2: Identified taxa of coccolithophores found frequently (* found in each sample; + complete spheres found)

1993/1994 Non El Niño condition	1997/1998 El Niño
*Calciosolenia brasiliensis**	*C. brasiliensis*
*Calcidiscus leptoporus**	*C. leptoporus**
C. leptoporus (small morphotype) +*	*C. leptoporus* (small morphotype)*
C. quadriperforatus	*C. quadriperforatus*
Coronosphaera spp.+	
*Emiliania huxleyi** +	*E. huxleyi** +
*Florisphaera profunda** +	*F. profunda**
*Gephyrocapsa ericsonii** +	*G. ericsonii** +
*G. muellerae** +	*G. muellerae** +
*G. oceanica** +	*G. oceanica**
*Helicosphaera carteri**	*H. carteri** +
H. hyalina +	
H. pavimentum +	
Oolithotus antillarum	*O. antillarum*
Ophiaster spp.+	*Ophiaster spp.*
Rhabdosphaera spp.	*Rhabdosphaera spp.*
Rhabdosphaera clavigera	*R. clavigera*
*Syracosphaera spp.** +	*Syracosphaera spp.** +
S. anthos +	
S. molischii +	*S. ossa*
S. pulchra	*S. pulchra*
	Umbilicosphaera hulburtiana
*Umbilicosphaera sibogae**	*U. sibogae*
Umbellosphaera tenuis	*U. tenuis*
65 heterococcolith-bearing species	65 heterococcolith-bearing species
1 species in its hetero- and holococcolith stage	1 species in its hetero- and holococcolith stage
S. pulchra – Calyptrosphaera oblonga	*H. carteri – Syracolithus catilliferus*
1 holococcolith-bearing species	1 holococcolith-bearing species
Teralithoides	*S. schilleri*

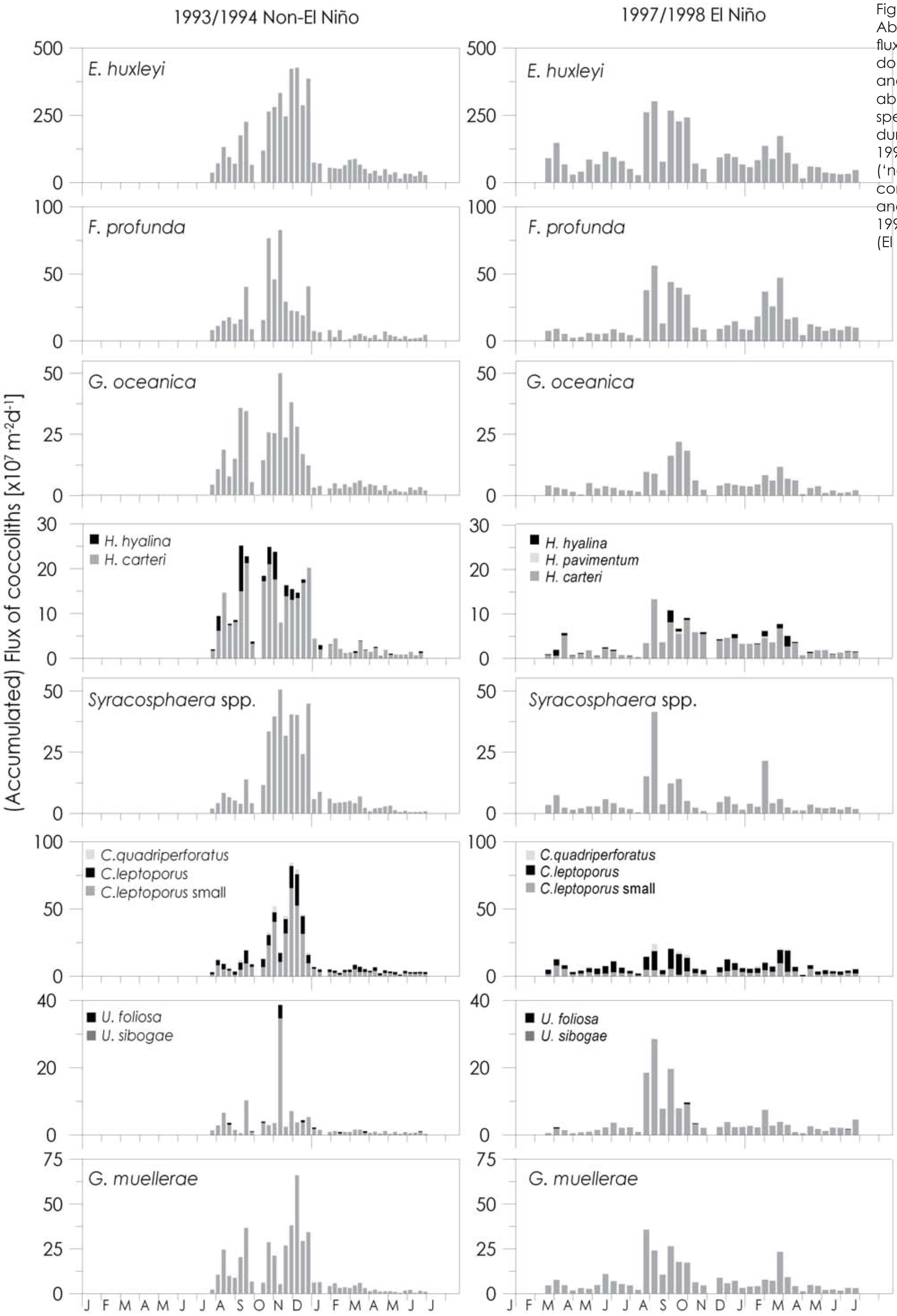
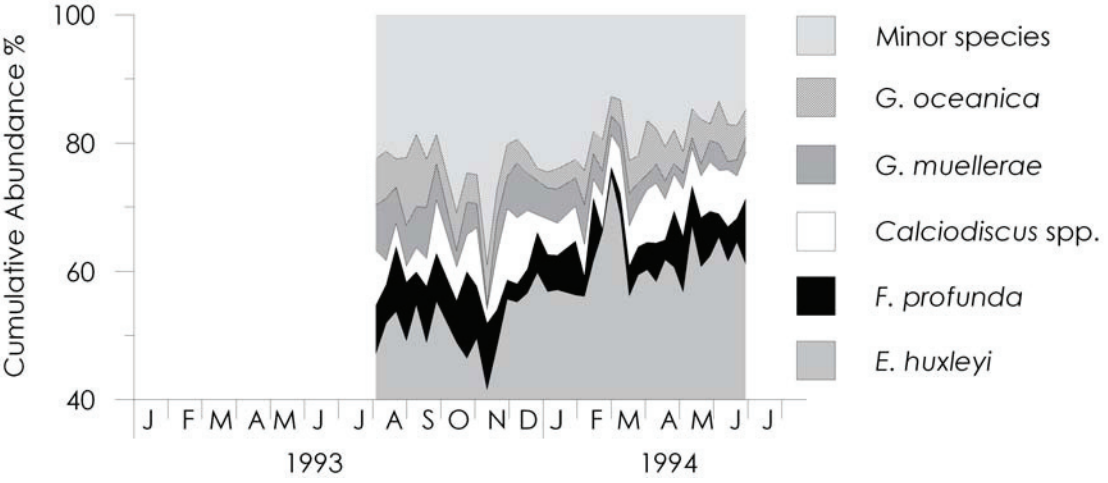


Fig. 4.6: Absolute flux of dominant and abundant species during 1993/94 ('normal' condition and 1997/98 (El Niño)

Fig. 4.7: Relative abaundance of dominant species of coccolithophores during CH3/4 ('normal' condition)



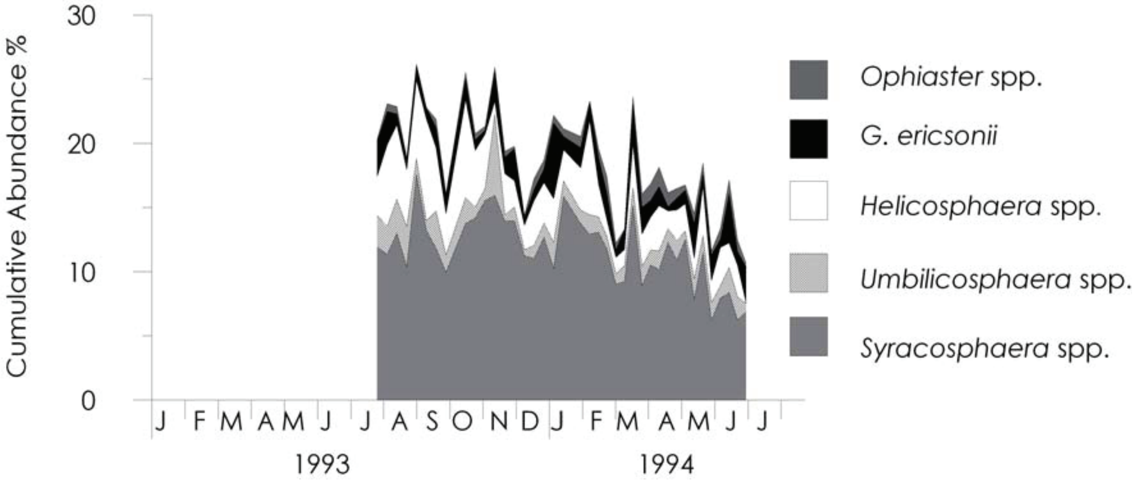
The dominant and common species, *Emiliania huxleyi*, *Florisphaera profunda*, *Calcidiscus leptoporus*, *Gephyrocapsa oceanica*, and *G. muellerae* revealed the alternation of high and low flux period with differences in duration and fluctuation during the high flux interval.

During the high flux period a mean of 34 heterococcolith-bearing species were observed, compared to 29 heterococcolithophores (mean) during the low flux period (Fig. 4.6).

The coccolithophorid assemblage was dominated by *E. huxleyi* with a mean of 57% (42-74%), *F. profunda* 6% (14-0.5%), *Calcidiscus spp.* 6% (11-2%), *G. oceanica* 5% (11-2%), and *G. muellerae* 4% (10-1%). Within the year an increase in relative abundance of *E. huxleyi* was observed associated with a decrease of the relative abundance of the 'minor' species.

Within the group of 'minor' species (Fig. 4.7) *Syracosphaera spp.* with a mean of 6% (12-1%), *Umbilicosphaera spp.* 2% (6-0.5%), *Helicosphaera spp.* 3% (8-0%), *Gephyrocapsa ericsonii* 2% (6-0%), and *Ophiaster spp.* 1% (6-0%) were more abundant (Fig. 4.8). The genus *Syracosphaera* showed a decreasing trend during 1994 (low flux period).

Fig. 4.8: Relative abundance of abundant species during CH3/4 ('normal' condition)



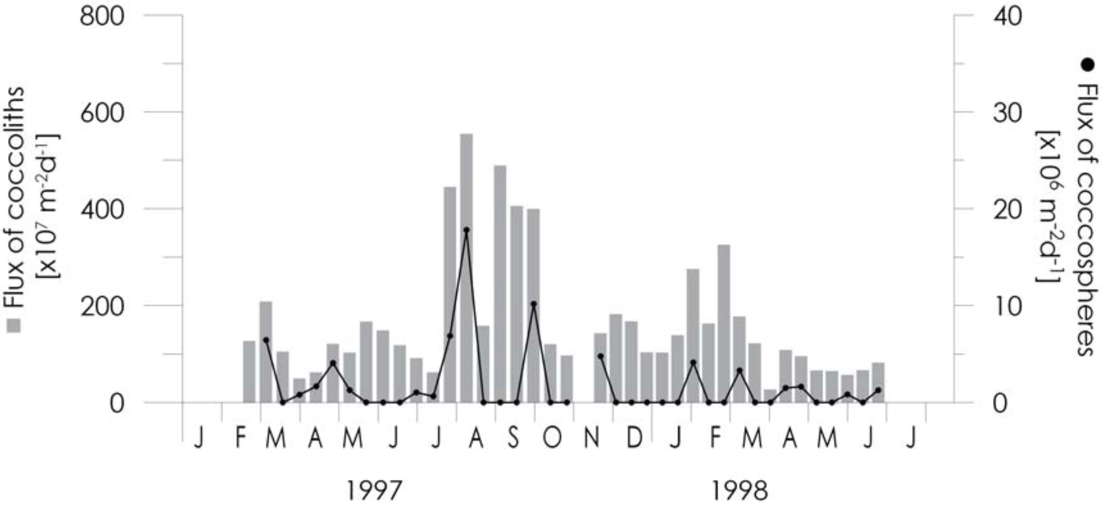


Fig. 4.9: Flux of counted coccoliths and coccospheres of CH10/11, El Niño condition

4.4.2 Coccolithophores flux during the El Niño event (1997/98)

The flux of coccospheres varied significantly during 1997/98 with a maximum in August ($18\text{x}10^6$spheres $m^{-2}d^{-1}$) (Fig. 4.9). In total, coccospheres of seven species were found (see Table 4.2) with those of *E. huxleyi* being the most abundant and frequent.

From January 1997 to June 1998 the coccolithophorid flux and the total flux varied strongly revealing times of elevated fluxes (July/August 1997, September/October 1997, January/February 1998). Maximum flux of up to $555\text{x}10^7$ liths $m^{-2}d^{-1}$ occurred in August 1997 whereas minimum flux was $27\text{x}10^7$ coccoliths $m^{-2}d^{-1}$ during March/April 1998 (Fig. 4.10).

The assemblage was again diverse with 65 heterococcolith-bearing species, one species in its holo- and heterococcolith stage (*Helicosphaera carteri – Syracolithus catilliferus*) and one holococcolith-bearing species (*Syracolithus schilleri*). The most abundant sample persisted out of 36 heterococcoliths and one species in its' holo- and heterococcolith stage (*Helicosphaera carteri – Syracolithus catilliferus*). In average, a sample contained 30 heterococcolith-bearing species (Table 4.2).

In austral spring the absolute fluxes of (most) dominant species were reduced, thus the high flux period (compared to 1993) was missing. As an exception, the absolute flux of *U. sibogae* increased and of *G. muellerae* stayed almost the same. Nevertheless, the mean coccolithophorid flux was only slightly reduced. However, the flux pattern fluctuated more during the season.

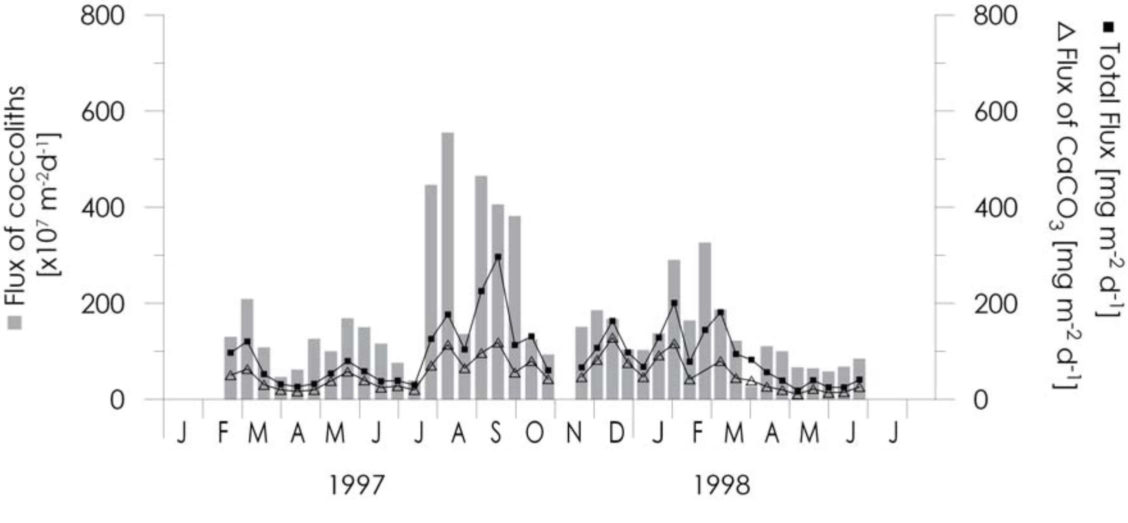


Fig. 4.10: Total flux of coccoliths, total flux and carbonate flux of CH10/11, El Niño condition

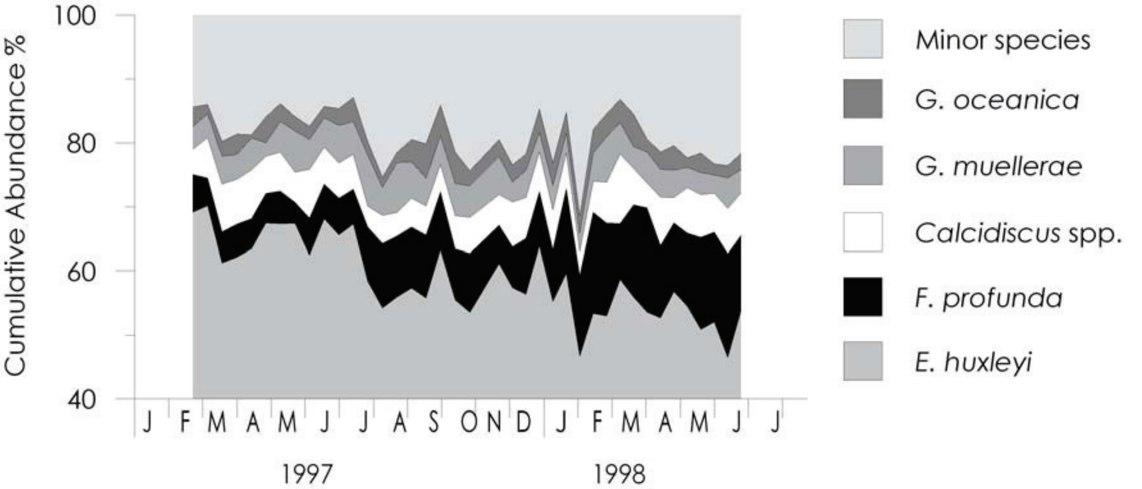


Fig. 4.11: Relative abundance of the dominant species during CH10/11; El Niño condition

The assemblage was again dominated by *E. huxleyi* (mean of 59%; 70-46%). Other commonly found taxa were *F. profunda* (mean of 9%; 16-3%), *Calcidiscus spp.* (mean of 6%; 11-3%), and *G. muellerae* (mean of 5%; 8-2%). This time, *E. huxleyi* showed a decreasing trend in austral summer, whereas *F. profunda* an increasing.

The relative abundance of *G. oceanica* (3;5-0.5%), *Syracosphaera spp.* (3; 7-1%), *Umbilicosphaera spp.* (3; 6-1%), *Helicosphaera spp.* (2; 6-1%), *G. ericsonii* (1; 4-0%), and *Ophiaster spp.* (1; 3-0%) was a reduced in 1997/98 compared to 1993/94 and fluctuated more during the season.

4.5 Discussion

4.5.1 Variation in coccolithophores assemblage during El Niño

The study period of 1993/94 was within the 1990 to 1995 ENSO phenomenon (Trenberth and Hoar, 1996). However, SST values as well as the Southern Oscillation Index (SOI) and Multivariate ENSO Index (MEI) reveal that normal conditions, i.e. non El Niño or La Niña condition (Blanco *et al.*, 2002) prevailed off Chile.

In general, the coccolithophorid assemblage was diverse but dominated by the cosmopolitan *Emiliania huxleyi* over the entire period. In 1993/94 the maximum flux of *E. huxleyi* occurred in November/December (Fig. 4.6). Before, in September 1993, diatoms had their

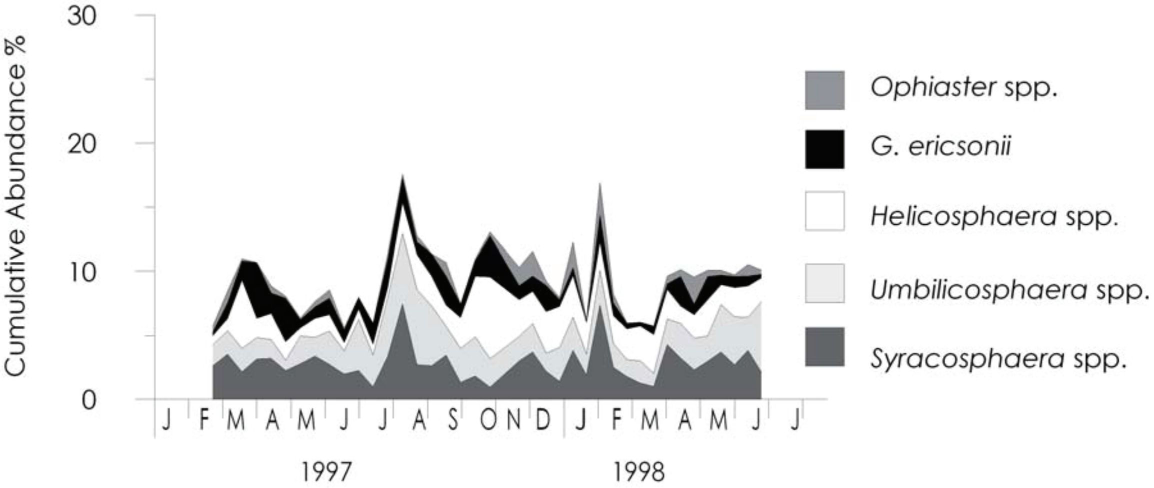


Fig. 4.12: Relative abundance of more abundant species of CH10/11; El Niño condition

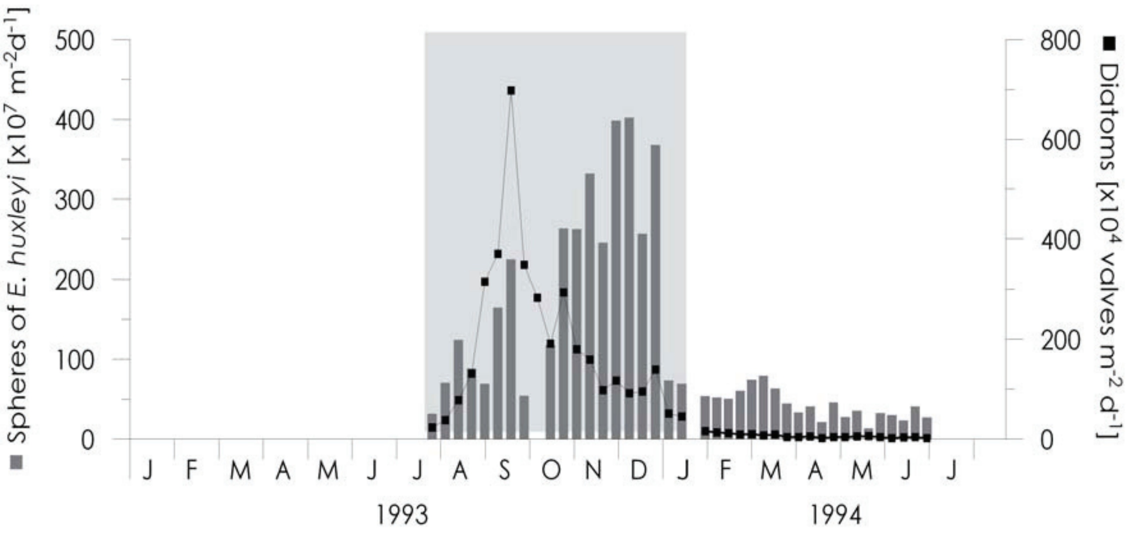


Fig. 4.13: Comparison of *E. huxleyi* flux and diatom fluxes of CH3/4 ('normal' conditions)

Data of diatoms from Romero *et al.* (2001)

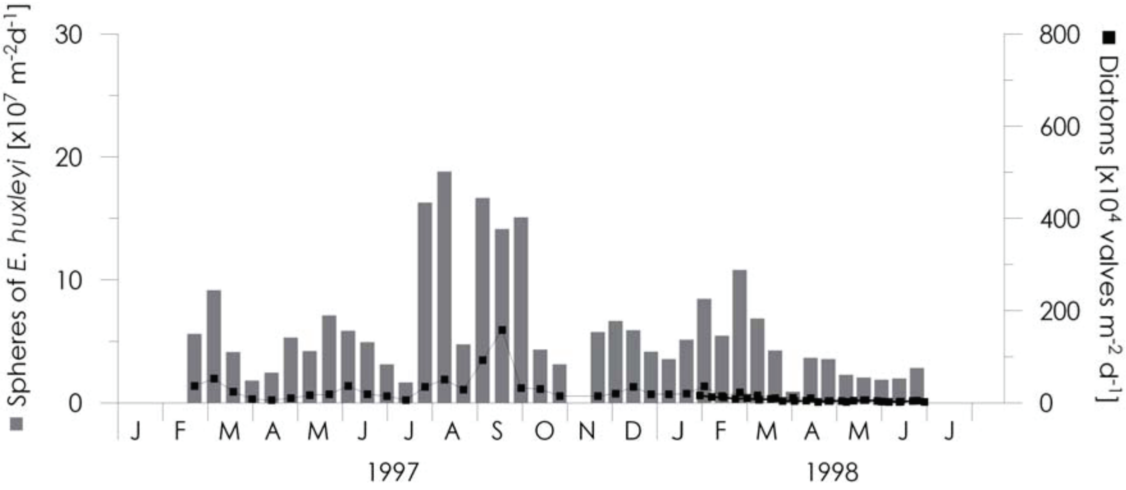


Fig. 4.14: Comparison of *E. huxleyi* flux and diatom fluxes during El Niño (data from Romero *et al.* (2001)

maximum flux (Romero *et al.*, 2001). To compare these different phytoplankton groups one has to convert them in individual units, diatoms in valves that consist of several single coccoliths differing in numbers (Winter and Siesser, 1994).

Figure 4.13 illustrates the succession of *E. huxleyi* and diatoms flux during 'normal' condition off Chile with diatoms being first in the year and *E. huxleyi* following after a significant decrease in diatom flux. This study deals with settling material, however, it displays observations made in surface waters of other oceanic regions. There *E. huxleyi* increased rapidly and enormously after blooms of diatoms (Thierstein and Young, 2004).

During El Niño, the fluxes of *E. huxleyi* and of diatoms lack this succession (Fig. 4.14). The maximum of *E. huxleyi* occurred earlier in the year, in July/August and again in September/ October. During El Niño 1997/98 upwelling still occurred, however, the upwelled water was less nutrient-rich due to the deepening of the nutricline (Carr *et al.*, 2002b; McPhaden, 1999).

The relaxation of the anomalous hydrographic condition in September/October 1997 may be reflected by the increase in diatom and *E. huxleyi*. In association with the still on-going upwelling favourable winds but the less nutrient enriched upwelled waters the intensity was reduced. In general, the (mean) flux of *E. huxleyi* as well as the overall coccolithophorid flux was only slightly reduced during El Niño but fluctuated strongly. The El Niño event caused variability in upwelling intensity and frequency, in both time and space (Escribano *et al.*, 2004) that cause the fluctuations. Further upwelling favourable winds still occurred during the mature El Niño (McPhaden, 1999; Rutllant *et al.*, 2004a; Ulloa *et al.*, 2001).

In 1993/94 the flux of *F. profunda* varied within the season (Fig. 4.6). Its mean relative abundance was similar during the high and low flux period (7.4% and 5.5% respectively) (Fig 4.15). In both time periods the different environmental conditions seem to have small influence on the low photic zone species. During winter/spring of the El Niño event in 1997/98, absolute flux of *F. profunda* was higher than in 1993/94 ('normal' condition). The first peak of the El Niño event (September/October) (Carr *et al.*, 2002b) took place. The accompanied deepening of the nutricline and increase in SST seems to favour this species with its habitat in deeper water layers and in association of the nutricline (Okada and Honjo, 1973).

From January to July 1998 an increase in relative abundance of *F. profunda* was observed (Fig. 4.15). The ongoing low nutrient content of the surface waters, as well as the deepening of the nutricline during the mature El Niño event (Carr *et al.*, 2002b) and the adaptation of *F. profunda* to the deep seems favourable to its occurrence and abundance within the coccolithophorid assemblage during the El Niño event.

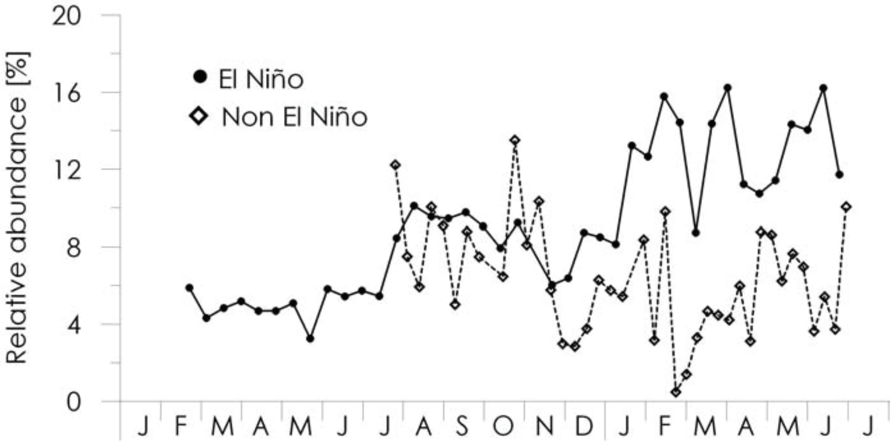
In accordance with the additional nutrient input in September 1993 the total flux of *G. oceanica* increased significantly. During the 'low flux' period of 1994, with reduced nutrient content due to stratified surface water, the flux of *G. oceanica* was also minimum. *G. oceanica* which is found in regions of elevated nutrients (Andruleit *et al.*, 2003; Broerse *et al.*, 2000c) is associated to eutrophic conditions. Further *G. oceanica* seems to be able to coup with strong mixing and turbulences of surface water (Boeckel *et al.*, 2006; Jordan and Winter, 2000).

During El Niño *G. oceanica* was found in lower quantities reflecting the changed environmental conditions of significantly reduced nutrient input and temperature increase compared to non El Niño condition. During the season, elevated numbers are associated with time periods of slightly enhanced nutrient input either based on relaxation of the El Niño event or/and on the influence of upwelling. The periods of elevated fluxes correspond to time intervals of elevated fluxes of *G. muellerae* which in turn indicates cold water properties (Findlay and Flores, 2000; Flores *et al.*, 1997; Lototskaya *et al.*, 1998).

In the present study *G. muellerae* were found in high numbers during the upwelling season in 1993, when cold surface temperature was predominant. In contrast, the low flux period in 1994 reveal low numbers of *G. muellerae* corresponding to higher SST (Fig. 4.3, Fig. 4.6).

During the El Niño the flux of *G. muellerae* was significantly reduced. Concurrently the intrusion of warm waters to the coast and the deepening of the nutricline beneath the origin of the upwelled water reduced the input of cold and nutrient-rich waters reaching offshore (Halpern, 2002; McPhaden, 1999). In summary, *G. muellerae* indicates the upwelling intensity in 1993/94 with cold and nutrient rich water as well as the occurrence of warm and nutrient-

Fig. 4.15: Relative abundance of *F. profunda*



poorer water of 1997/1998.

The flux of the genus *Helicosphaera* was documented distinguishing three discrete species: *H. carteri*, *H. hyalina* and *H. pavimentum* (Fig. 4.6). During the upwelling period of 1993/94 the flux of *H. carteri* was high, whereas strongly reduced during the El Niño event. The association of *H. carteri* to mesotrophic conditions would explain these changes.

However, the indication of *H. hyalina* being more frequent in an upwelling environment cannot be supported by our data. In both study intervals absolute numbers were very low. Nevertheless, during the initiation of the upwelling period in September 1993 low quantities were exhibit and higher ones afterwards.

The group of *Syracosphaera* is diverse and in their ecological preferences basically unknown taxonomic grouping. Within this study 15 species of the genus *Syracosphaera* were identified (Table 4.3). In total, a higher abundance was encountered during 'normal' oceanic condition than during the El Niño event. Studies of plankton size distribution during the El Niño of 1997/98 revealed a species composition consistent with species of preceding or succeeding years, however, a shift in abundances towards small sized species occurred (Montecino and Quiroz, 2000). Within the (already small) nanoplankton this trend cannot be noticed. The abundance of the small sized *Syracosphaera* is decreased during El Niño.

Table 4.3: Identified taxa of the genus *Syracosphaera* regardless their absolute and relative fluxes (+ found only 1997/98)

Syracosphaera
S. anthos
S. ampliora $^+$
S. borealis
S. corolla
S. dilatata group
S. delicata
S. halldali
S. histrica
S. lamina
S. marginaporata
S. molischii
S. nana
S. nodosa
S. ossa
S. prolongata
S. pulchra
S. rotula
S. tumularis

Calcidiscus leptoporus in its heterococcolith-bearing stage can be grouped into three – *C. lep-*

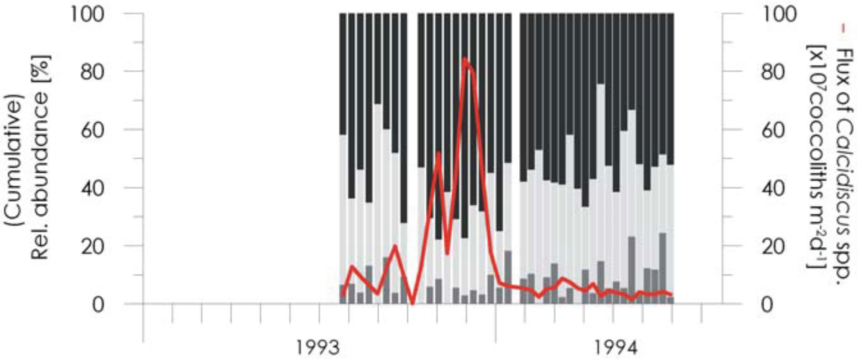


Fig. 4.16: Relative abundance of ■ *C. leptoporus* small, □ *C. leptoporus*, and ▨ *C. quadriperforatus* during 'normal' condition (CH3/4) (100% corresponds to total flux of *Calcidiscus spp.*)

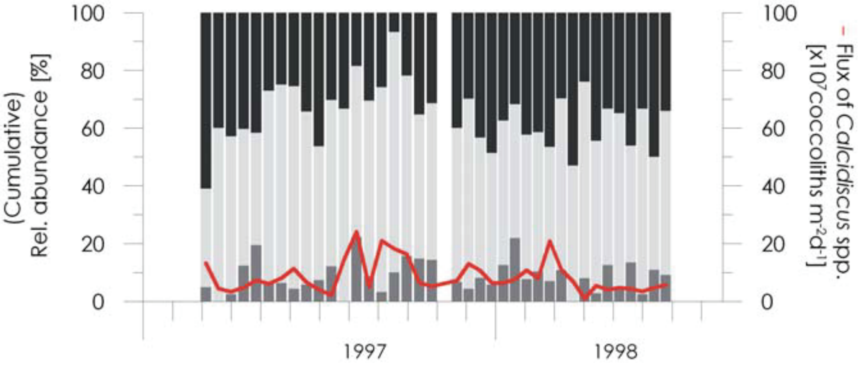


Fig. 4.17: Relative abundance of ■ *C. leptoporus* small, □ *C. leptoporus*, and ▨ *C. quadriperforatus* during El Niño (CH10/11) (100% corresponds to total flux of *Calcidiscus spp.*)

toporus small morphotype, the intermediate *C. leptoporus* and the large *C. quadriperforatus* as introduced by Geisen *et al.* (2002a). Coccoliths of all three types were found in the present study, as well as spheres of *C. leptoporus* and *C. leptoporus* small morphotype. During 'normal' hydrographic conditions the small morphotype dominated regardless of absolute fluxes and the prevailing different environmental conditions.

During the El Niño event the flux of *C. leptoporus* small decreased significantly resulting in the dominance of the intermediate *C. leptoporus*. A broad study of surface sediment and correlating environmental gradients revealed a strong association of the small morphotype to upwelling and dynamic conditions, whereas *C. leptoporus* (intermediate) exhibited a broad tolerance to its surrounding conditions (Boeckel *et al.*, 2006). The dominance and slight increase of the small morphotype during high flux period during 1993/94 and the shift towards *C. leptoporus* during the El Niño support these findings. In return, the reduced fertilization of the surface water due to the deepening of the nutricline is reflected in this change (Fig. 4.16, Fig. 4.17).

Within our study *U. sibogae* has a twofold higher mean flux during El Niño than during non-El Niño conditions (4.24 x10^7 respectively 2.1 x10^7 liths $m^{-2}d^{-1}$[1]). *U. sibogae* is observed in subtropical and tropical regions associated with warm, saline, slightly mixed upper waters of an oligotrophic environment (Okada and McIntyre, 1979; Ziveri *et al.*, 2004; Ziveri *et al.*, 1995). Consequently, the increase in absolute flux reflects the occurred shift in hydrographic condition that is in accordance with the warmer and more oligotrophic condition of the surface water during 1997/98 (Escribano *et al.*, 2004).

In summary, the coccolithophore assemblage mirrors remarkably the different hydrographic conditions caused by the strong El Niño of 1997/98 that contrasts studies of phyto- and zooplankton revealing unclear or minor changes in species composition (Hidalgo and Escribano, 2001; Ulloa *et al.*, 2001).

4.5.2 Short time variability in coccolithophores assemblage

Within the study period 1993/94 a short but distinct *event* took place when the assemblage changed significantly (Fig. 4.6). In November 1993 a sharp increase in flux of *U. sibogae*, *G. oceanica* and *F. profunda* was observed whereas *G. muellerae*, *Helicosphaera spp.* and *C. leptoporus* (small morphotype) decreased significantly. *U. sibogae* and *G. muellerae* both reflect sea surface temperature conditions. *U. sibogae* favours warm waters whereas *G. muellerae* is often found in cold surface waters. Consequently, the drastic increase of *U. sibogae* corresponds to the strong decrease of *G. muellerae* pointing towards a strong influence of warm surface water. Furthermore, the abundance of *Helicosphaera spp.* and *C. leptoporus* (small morphotype) was reduced. In general, these species reflect (meso-)eutrophic nutrient conditions of the surface waters indicating in this case a reduction of the nutrient content. The increased flux of *U. sibogae*, a species associated to more oligotrophic conditions, supports this.

Additionally, a significant increase in flux of *G. oceanica*, also an indicator for nutrient enriched environments in many regions increased. However, its correlation to turbulent mixing seems slightly more important than the correlation of nutrient content (Boeckel *et al.*, 2006). Thus, the increase is interpreted as an impulse of turbulent water mixing.

As a result one can hypothesize a strong influence of warm, nutrient-depleted and turbulent

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[1] The maximum in 1993 was not considered for this calculated mean (with consideration the mean amounts to 2.9 x10^7 liths $m^{-2}d^{-1}$) since it is interpreted as an exceptional event which is described in Chapter 4.5.2.

surface water. Halpern (2002) showed that intrusion of near-surface warm layer is possible in times of a weakening of prevailing westward wind stress, and a lowering of the thermocline which in turn would explain the increase of *F. profunda* during the event. Even a short time change in the coccolithophores assemblage points to distinct and well defined water properties off Chile.

4.5.3 Estimation of coccolith derived carbonate

The mean calculated coccolith-$CacO_3$ fluxes amount to 25.96 mg $m^{-2}d^{-1}$ during 'normal' hydrographic condition and to 16.43 mg $m^{-2}d^{-1}$ during the El Niño event of 1997/98 (Fig. 4.18). The contribution of coccolithophorid flux to the total carbonate flux differ little between 1993/94 'normal' condition with 28% (8-60%) and El Niño event with 33% (8-72%). The present estimates are higher than recent approximations of González and co-authors (2004) who estimated coccoliths to add up to 11% (mean) of the total carbonate for the same sediment trap. The estimation is based on calculations regarding the fluxes of *E. huxleyi* and *C. pelagicus*. *E. huxleyi* represents a species occurring in high numbers and *C. pelagicus* for a species with a high specific carbonate weight. However, our findings as well as previous detailed studies show that the coccolith derived carbonate flux differs significantly based on the used values for the species specific carbonate content (Baumann, 2004). Thus, a detailed species composition of the coccolithophores assemblage, as well as morphometric measurements were used for the present estimates.

The annual coccoliths derived carbonate fluxes in the upwelling region off Chile amounts to 9.5 g m^{-2} during 'normal' conditions and to 5.9 g m^{-2} during the El Niño of 1997/98. In contrast, the yearly mean carbonate flux derived by coccoliths in other upwelling regions account for 4.9 g $m^{-2}y^{-1}$ off NW-Africa (Köbrich and Baumann, subm.), 3 g $m^{-2}y^{-1}$ off Somalia (Broerse *et al.*, 2000b) and 2.7 g $m^{-2}y^{-1}$ for an oligotrophic site in North Atlantic (Broerse *et al.*, 2000a). Furthermore, the proportion of coccolithophores to the total carbonate export differs significantly. In the upwelling area off NW-Africa and off Somalia the contribution of coccoliths to the total carbonate flux accounts for 18% and 13% respectively, compared to 24% in the North Atlantic. In the upwelling region off Chile it amounts to 27% respectively 34% during El Niño. Thus off Chile, coccolithophores reach higher annual mean fluxes, as well as a higher contribution to the overall carbonate export.

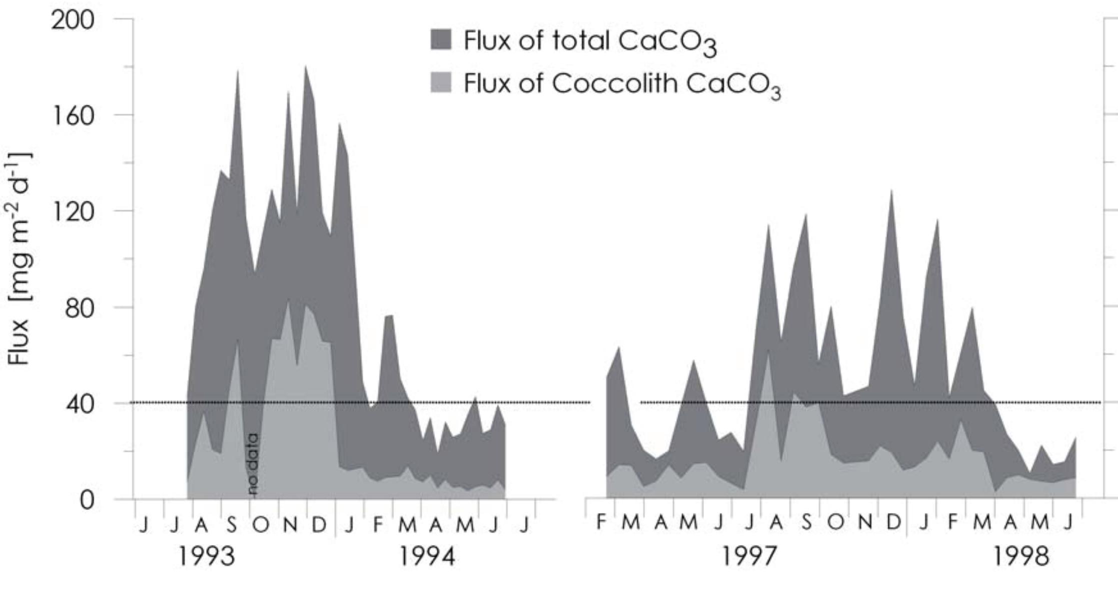

Fig. 4.18: Total carbonate flux and calculated coccolith derived carbonate flux

Conclusions

- During the study period of ‘normal’ hydrographic condition (1993/94) the coccolithophorid flux pattern can be divided into a high flux period in austral spring and summer and a low flux period in fall and winter revealing same species composition. In contrast, the flux during the El Niño event of 1997/98 lacked this alteration. The mean flux of (most) dominant species was only slightly reduced and continuously fluctuating regardless of the season.
- Coccolithophorid assemblage showed short time variation during the 'normal' year. There was a significant increase in abundance of *U. sibogae*, *G. oceanica*, and *F. profunda*. At the same time *G. muellerae*, *Helicosphaera spp.*, and *C. leptoporus* (small morphotype) decreased. Presumably the change reflects an intraseasonal variation in sea-surface water condition. It is hypothesized that the intrusion of warm water led to this alteration in species composition.
- The relative abundance of *G. oceanica*, *G. muellerae*, *Helicosphaera spp.* and *Syracosphaera spp.* decreased significantly during El Niño whereas *U. sibogae* and *F. profunda* increased. Based on the ecological preferences of the species, these changes correspond to the warmer sea-surface temperatures and the deepening of the nutricline during this time.
- A diverse coccolithophorid assemblage was present under El Niño as well as under 'normal' hydrographic conditions. However, a shift in relative and absolute abundances took place during the El Niño event mirroring the changes in sea-surface water condition.
- The annual mean coccolith-derived carbonate flux amounts to 9.5 g m^{-2} and 5.9 g m^{-2} during ‘normal’ and El Niño respectively. In turn it contributes to 27% and 34% to the total carbonate flux. Thus off Chile, coccolithophores reach higher annual mean carbonate fluxes, as well as a higher contribution to the overall carbonate export compared to upwelling regions off NW-Africa or Somalia.

V. Synthesis

In order to determine the position of coccolithophores within the plankton community (structure) a conversion of coccoliths to coccospheres as cell equivalent is necessary. Although coccoliths were well persevered in the studied sediment trap samples, complete coccospheres were rare. Especially off NW-Africa the correlation of coccoliths to the sum of converted and counted coccospheres was in cases small (CB2). Compared to the upwelling off Chile (r^2=0.99) the correlation is weaker off NW-Africa (r^2=0.72) (Fig. 5.1). The highly variable system of the NW-African upwelling region and the accompanied fluctuating coccolith fluxes seem reasons for this strong variability (see chapter 2.1). However, the summarized treatment of the numerous counts (71 samples for Cape Blanc) reveal a good correlation (r^2=0.72). It is the basis for the following consideration of the plankton community's structure respectively changes in the upwelling regions of Cape Blanc and Chile. The conclusions are drawn based on the general aspects of the environmental parameters such as SST, SST anomaly, upwelling, wind conditions, and nutrient availability (as depicted in Chapter 2.1) and by comparing the fluxes of different plankton groups (in specific foraminifera, pteropods, diatoms, and silicoflagellates).

5.1 Coccolithophores and plankton community off Cape Blanc

During sediment trapping the survey of the plankton communities in the surface water is possible over a longer period of time. The settling of the biogenic material is directly related to surface production and reflects the seasonality of that production (Deuser *et al.*, 1990). The knowledge of the ecological affinities or seasonal patterns of extant species is essential for paleo – ecological studies using fossil assemblages in marine sediments.

The long term deployments of the CB sediment traps and their intensive studies offers the unique possibility to compare (the fluxes of) different plankton groups, such as diatoms, silicoflagellates, coccolithophores, and planktonic foraminifera (Fischer *et al.*, 1996; Müller and Fischer, 2001; Romero *et al.*, 2002b; Žaric *et al.*, 2005). Further processes may be re-

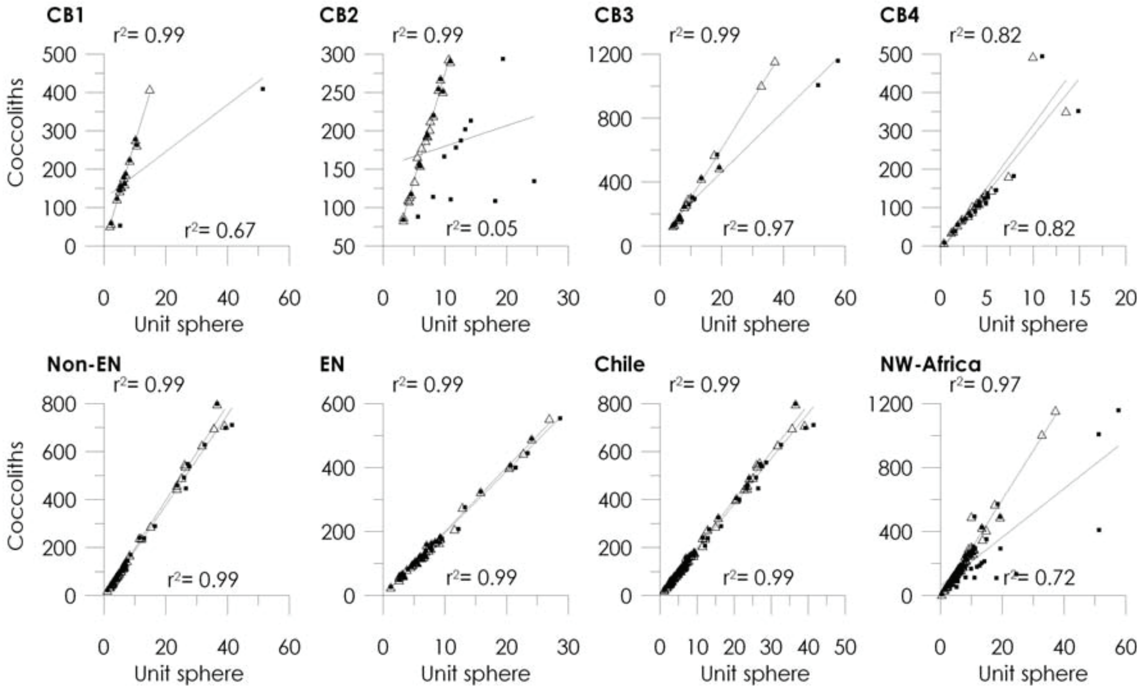

Fig. 5.1: Relationship between coccoliths and coccospheres (■ counted liths vs counted and converted spheres ▼ counted liths vs converted spheres) Data of coccolith numbers per sphere from Boeckel and Baumann (2008)

Non-EN are the samples of trap CH4/4, EN (El Niño) the samples of CH 10/11

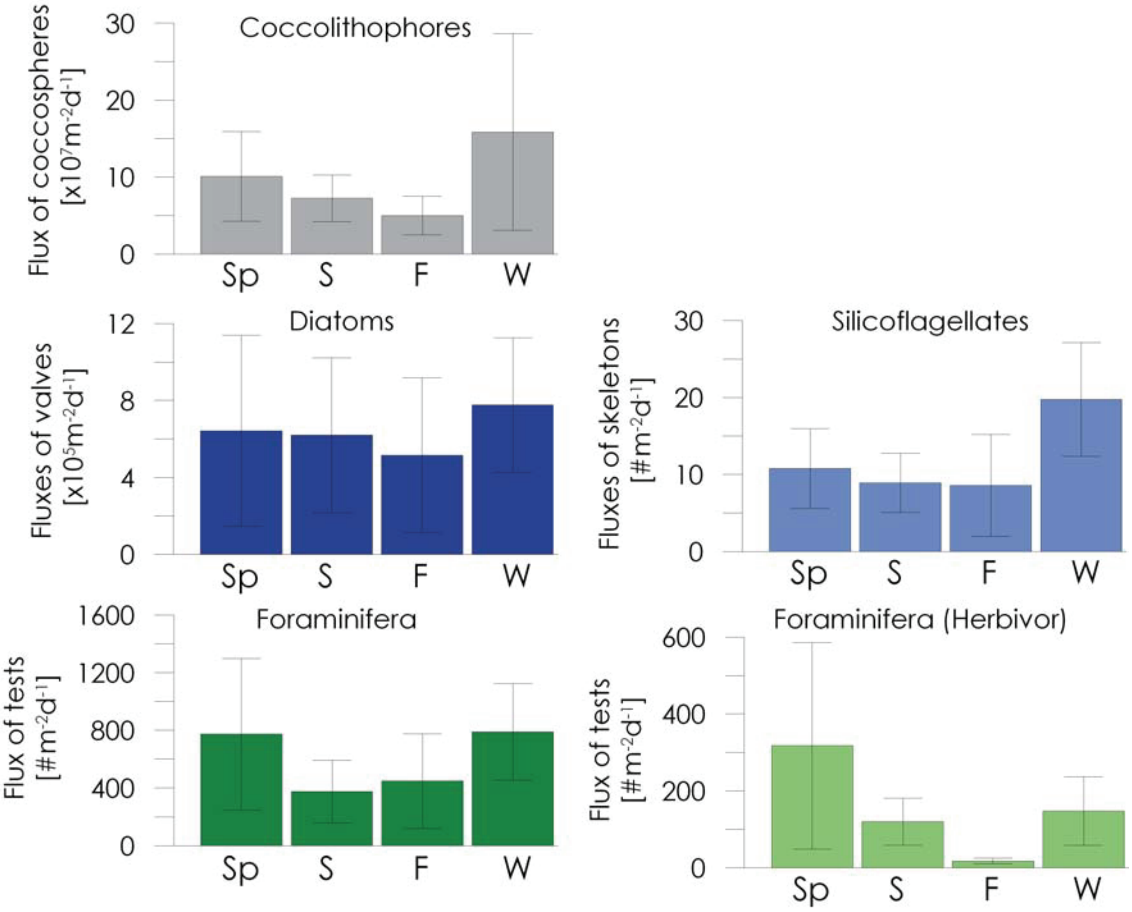

Fig. 5.2: Fluxes of different plankton groups displayed in their seasonal occurrences off Cape Blanc (CB1-4) (bars indicate standard deviation). Data of coccospheres this study; data of diatom and silicoflagellate fluxes by Romero *et al.* (2002b); fluxes of planktonic foraminifera were kindly provided by B. Donner (Marum), Herbivor Foraminifera summarize the fluxes of *Globigerina bulloides* and Neogloboquadrina pachyderma

vealed which influence the occurrence and/or the fluxes of the different organism groups despite their intrinsic species specific ecological preferences. Figure 6 displays the fluxes of carbonate producers such as coccolithophores and foraminifers and silica producers such as diatoms and silicoflagellates distinguished by their seasonal rates. Even though a high variability is present which is most probably due to the variable oceanographic setting of the area (Chapter 2.1) and due to the complex downward processes (Nowald *et al.*, 2006) seasonal patterns are evident.

As described in detail (chapter III.) highest coccosphere fluxes are documented in winter, followed by spring. In summer and fall low numbers of coccospheres are present. For silicoflagellates and diatoms the same pattern is valid even though for diatoms it is not as concise developed. The fluxes of foraminifera are different. Their maximum flux is in spring. Focusing on herbivore foraminifera taxa the seasonality is even more pronounced (Fig. 5.2). Even though the fluxes off Cape Blanc experience diverse processes during the long way to the

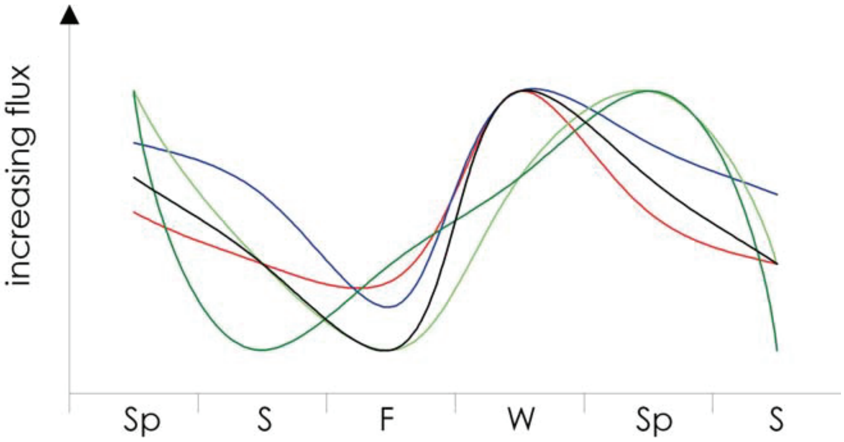

Fig. 5.3: Schematic pattern of a seasonal cycle of the fluxes of coccolithophres (black line), diatoms, silicoflagellates, planktonic foraminifera, and herbivore foraminifera

sediment traps (for example dilution, dissolution, grazing, drifting) the following pattern for a seasonal cycle can be identified: The phytoplankton fluxes reach their maximum in winter and their minimum in fall, with a peculiarity for diatoms exist. After the maximum in winter there exists another high flux period in spring/summer. Planktonic (herbivore) foraminifera nourish on the phytoplankton and reveal consequently their maximum flux after the phytoplankton in spring (Fig. 5.3).

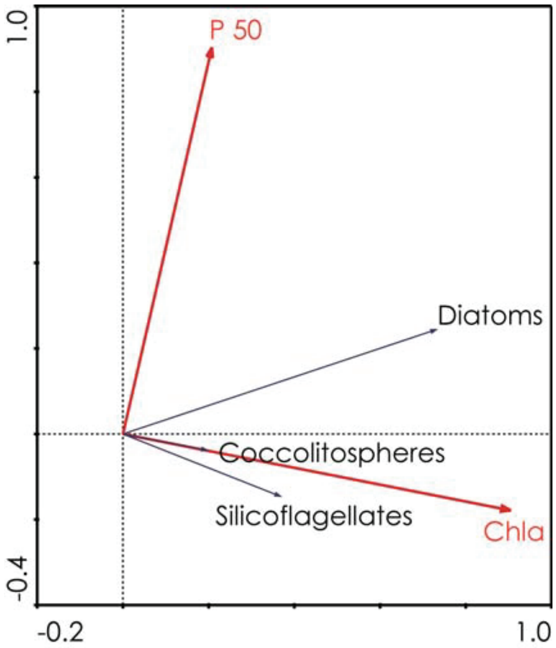

Fig. 5.4: Ordination diagram based on RDA and the fluxes of coccospheres, diatoms and silicoflagellates of the CB 1-4 sediment traps (Köbrich unpublished data)

P50 is phosphate in 50m water depth) and chl a of surface water; both data from world ocean atlas

For this reason the prevailing abiotic factors such as irradiance, wind (velocity and direction), sea surface temperature and nutrients were compared in order to reveal the influencing factors (see Appendix for detailed illustration). A summary is given in Table 5.1. The upwelling intensity was determined by using SST anomaly (Speth *et al.*, 1978), as well as the wind conditions (see Appendix). The additional nutrient input is coupled to the intensity of the coastal upwelling events and the occurrence and development of filaments (Gabric *et al.*, 1993; Lange *et al.*, 1998). Besides insolation, the mean irradiance experienced by phytoplankton is influenced by the intensity of upwelling and wind speed, thus by the strength of turbulences and mixing of the water column (Dugdale and Wilkerson, 1985; Nelson and Conway, 1979). In general the light regime seems important in controlling the use of inorganic nutrients in the northwest African upwelling system (Nelson and Conway, 1979).

These findings are supported by redundancy analysis (RDA) deciphering the variability within the specific phytoplankton fluxes (Fig. 5.4). The influence of nutrients is stronger for diatoms than coccolithophores and silicoflagellates. The good correspondence of the variability of the chl-*a* concentration of the surface waters and the variability within the coccolithophore assemblage is may be interpreted as a signal for the productivity. In addition it could be an indication for the meandering (and still being productive) *giant filaments* which in turn is an indirect signal for the coastal upwelling situation (Gabric *et al.*, 1993; Gabric *et al.*, 1996).

	Spring	Summer	Fall	Winter
Flux of coccoliths	average	high	minimum	maximum
Upwelling	strong	weakening	no	average
(additional) Nutrients	high	low	low	average
Irridiance (in water column)	low	high	low	average

Table 5.1: Summary of the interaction of light, nutrient and wind determining the flux of coccoliths at the mooring station during the seasons. Wind data and insolation data see Appendix

Off Cape Blanc the occurrence of the phytoplankton revealed by their fluxes seem therefore strongly influenced by irridiance, wind effecting upwelling and additional nutrient supply. Due to the seasonal cycles of diatoms, silicoflagellates and coccolithophores a relationship to these factors is revealed, with coccolithophores flourishing in a surrounding characterized by mesoscale light condition (irradiance) and wind induced influences (turbulences, upwelling, additional nutrients). Silicoflagellates showed a quite similar response, however, changes in fluxes were (often) earlier within the year. This was interpreted as a slightly lower optimum for the parameters. But it could also be explained by different settling processes. Fluxes of diatoms were high throughout most of the seasons indicating a good and fast response to their surrounding. In detail their first peak during the year often coincided with the first additional input of nutrients, respectively (assumed) break down of the water column. Even though the study was carried out by investigating dead and decayed material it is in good correspondence to Margalef's Mandala and description by models (Balch, 2004; Gregg and Casey, 2007; Margalef, 1978; Thierstein and Young, 2004).

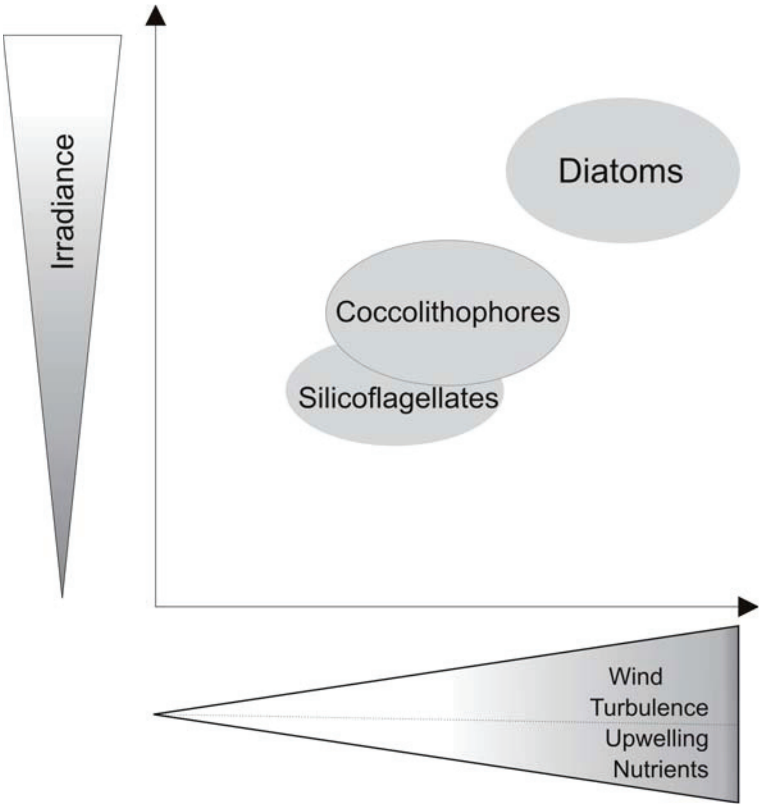

Fig. 5.5: Summary of the preferences of diatoms, coccolithophores and silicoflagellates revealed by the results of the sediment traps (CB1-4). The interaction of light (irradiance) and wind which determine the fluxes is in correspondence to Margalef's Mandala (Balch, 2004; Margalef, 1978; Thierstein and Young, 2004).

5.2 Phytoplankton community flux and El Niño

The complex microplankton succession must be understood in detail before each of its components, diatoms, coccolithophores and planktic foraminifera (and others), can be used as a paleoceanographic proxy (Schiebel *et al.*, 2004). The interpretation of fluxes or seasonal occurrences of coccolithophores and planktic foraminifera will add information on oceanographic as well as environmental characteristics due to the individual ecological preferences of these plankton groups. The combination of different trophic levels extends the outcome of an ecological study. Seasonality is of particular importance to understand teleconnections of a climatic dipole like ENSO.

The study of the sediment trap samples collected off Chile (30°S) with respect to fluxes during El Niño and 'normal' conditions creates the possibility to combine the results of foraminifera, diatom and coccolithophore fluxes. All three plankton groups of the same sediment trap has been studied (Marchant *et al.*, 2004; Romero *et al.*, 2001). In the following, a comprehensive view to the possible development respectively succession based on the prevailing hydrographic conditions will be given.

During the 'normal' condition in 1993/94 study period an increase in upwelling favourable winds induced a first input of nutrients resulting in a bloom of diatoms (Romero *et al.*, 2000) (*Fig.* 5.6). Diatoms have a fast response to changing environmental (favourable) conditions resulting in rapid new production (rates). In the beginning of the winter 1993 enhanced upwelling lead to the flourishing of diatoms which reached their maximum within September, as the silicoflagellates flux (Romero *et al.*, 2000). Thus, the maximum pigment chl-*a* concentration being present in September/October observed with MODIS can be explained by the maximum flux of the diatoms.

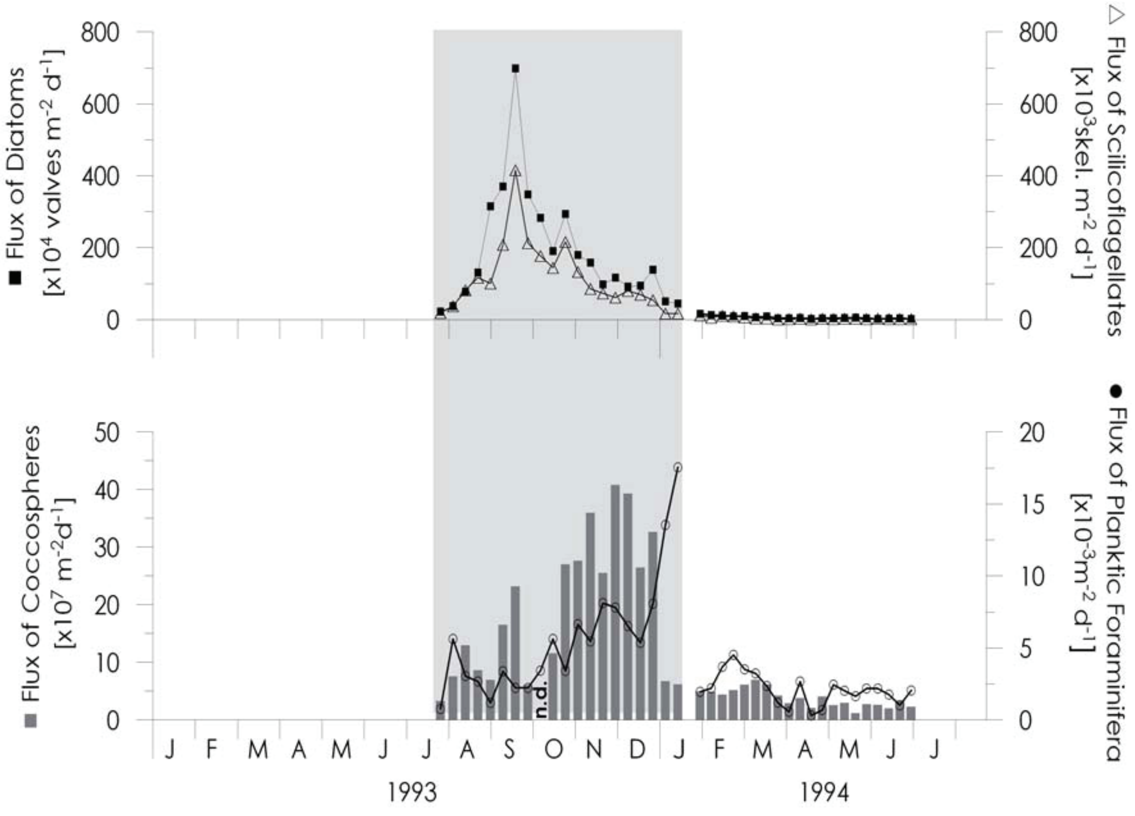

Fig. 5.6:
Flux of coccolithophore (sphere units), foramnifera, diatom and silicoflagelate flux during 1993/94 ('normal' condition) shaded area indicates upwelling conditions (Hebbeln *et al.*, 2000);
n.d.: no data

Table 5.2: Correlation to the calculated axes based on the statistical analysis (PCA) of total fluxes of diatoms, scilicoflagellates, coccolithophores, and planktonic foraminifera (CH3/4 'normal' condition)

Plankton group	AX1	AX2	AX3
Diatoms	0.9728	0.0016	-0.0222
Silicoflagellates	1	-0.0001	0
Planktonic Foraminifera	0.0314	0.9995	-0.0014
Coccolithophores	0.4355	0.3817	0.8153
Interpretation	nutrients	(variability of) SST	(turbulence light availability)

By the end of September a first temporarily depletion of nutrients (or components of essential nutrients) may have occurred resulting in a sharp decrease in the flux of the siliceous phytoplankton.

Given that continuous upwelling impulses followed, as reported by Rutllant *et al.* (2004), and was indicated by the isotopic signal of foraminifera of the sediment traps, the high flux period continued due to the additional nutrient input until the end of January (Marchant *et al.*, 2004). Coccolithophores which are known to inhabit more successfully mesotrophic environments and medium turbulent waters (Balch, 2004; Margalef, 1978), had their maximum flux in November/December.

The dramatic decrease in January coincides with the maximum flux of foraminifera. Foraminifera as secondary producers feed inter alia on phytoplankton. In general, the control of meso-zooplankton occurs typically later in the seasonal cycle due to the comparatively slow development of copepods (Rost and Riebesell, 2004). The seasonal flux pattern of the samples is in agreement with the interrelation of foraminifera and diatom flux. High foraminifera flux is known to negatively correlate with diatoms, as well as to record mesotrophic conditions (Schiebel *et al.*, 2004).

Fig. 5.7: Flux of diatoms, scilicoflagellates and coccolithophorids, planktic foraminifera of sediment traps off Chile during El Niño of 1997/98

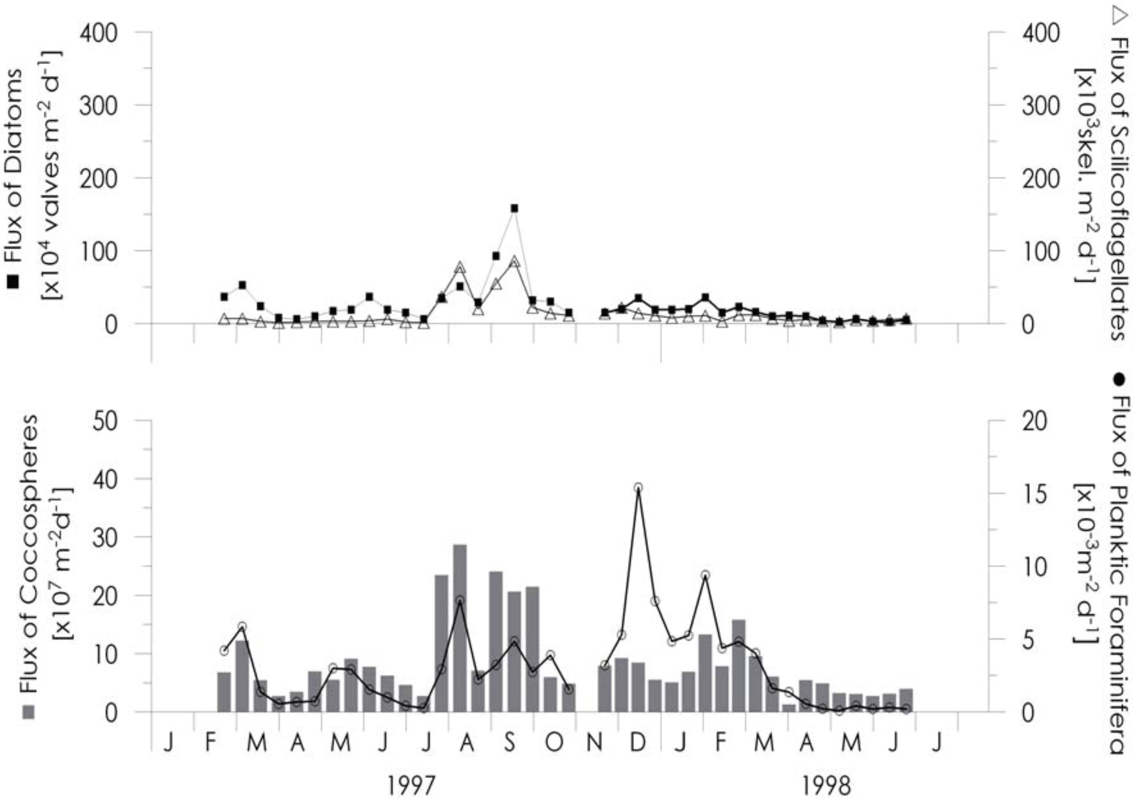

Table 5.3: Correlation to the calculated axes based on the statistical analysis (PCA) of total fluxes of diatoms, scilicoflagellates, coccolithophores, and planktonic foraminifera

Plankton group	AX1	AX2	AX3
Diatoms	0.156	0.9656	1
Silicoflagellates	0.1269	0.8453	0.9969
Planctonic Foraminifera	1	1	1
Coccolithophores	0.1951	0.6252	0.7602

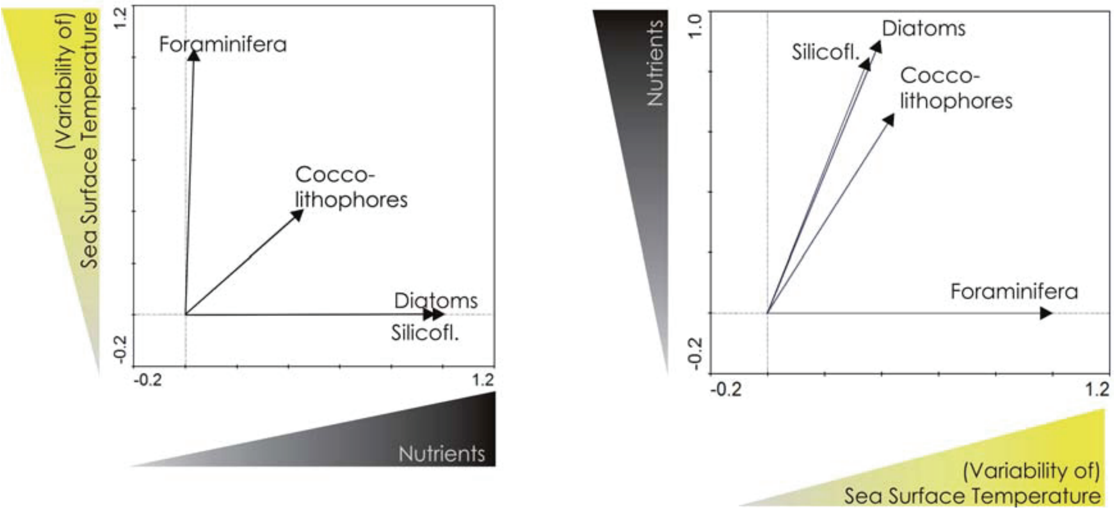

Fig. 5.8: Statistical analysis (PCA) for the data of CH3/4 ('normal' condition) (left diagramm), for data El Niño right diagramm

As a result we found the distinct plankton succession in the fluxes that was hypothesized by Marchant *et al.* (2004). It is characterized by diatoms flourishing during intense upwelling utilizing the additional nutrient input first. Thereafter, coccolithophores dominate; during the time of medium upwelling or within (slightly) nutrient depleted surface water. Predators (i.e. foraminifera) follow the phytoplankton bloom of diatoms and coccolithophores (Fig. 5.9).

The analysis of the variability of the samples in respect of their absolute abundance can characterize the general ecological preferences of the different plankton groups. The statistical analysis due to Principal component analysis (PCA[1]) (Canoco 4.5) reveals the interdependence (results Table 5.2, Table 5.3). Due to the virtually accordance of axe 1 to diatoms/silicoflagellates this axe is interpreted as nutrient availability (Fig. 5.8). Axe 2 that is in (almost) congruent with foraminifera is interpreted as temperature. The interesting outcome is the 'in between' position of the coccolithophores as a group. Even though this analysis is based on data of 'dead' material the 'average' position of coccolithophores within a habitat characterized by different abiotic factors is evident and confirmed (Balch, 2004; Margalef, 1978).

A 'succession' of the different plankton groups is not observed during 1997/98. The year is characterized by the strong and fast developing El Niño event (Carr *et al.*, 2002b; McPhaden, 1999). The total flux was significantly decreased by 60% as was the flux of diatoms (by 75%) (Romero *et al.*, 2001). All the studied organism groups, i.e. coccolithophores (this study), sili-

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[1] Principal component analysis (PCA) was performed, which determines gradients (axes) of variability that explains the variance of the analysed data. This analyse is based on the assumption that the most important gradient (i.e. environmental gradient) is responsible for the largest variation within the analysed data (in this case species composition). Further the environmental gradient causes a linear variance of the species composition (or analysed data) or the variance of the species assemblage represents a linear course at the moment of detection (if a data assemblage lies within the linear trend was detected by detrended correspondence analysis (DCA)). The first two axes represent the most prominent underlying gradients and are determined by a two way weighted averaging algorithm. All statistical analyses applied are included in the multivariate statistical package CANOCO 4.5.

ceous phytoplankton (Romero *et al.*, 2001) and foraminifera (Marchant *et al.*, 2004) revealed the similar fluctuating seasonal flux pattern (Fig. 5.7). A first maximum occurred earlier in the year compared to 1993. Maximum fluxes in the winter season and wind measurements indicate upwelling events even within the mature El Niño phase (McPhaden, 1999). Further during winter, a short relaxation of the El Niño event took place (Carr *et al.*, 2002a). However, due to the deepening of the thermocline and nutricline the upwelled water was less nutrient rich. As a result seems the reduced the maximum flux of diatoms that was not as striking as in 1993/94. In contrast, the coccolithophorid flux revealed same annual mean fluxes for the El Niño event and during ‘normal’ condition (3.6 and 3.7 x10^{11} coccoliths m^{-2} respectively). Thus, coccolithophores, known to inhabit mesotrophic waters, were not as much affected with respect to their fluxes. Since a more oligotrophic regime seems to have prevailed, a higher dominance of pico- and nanoplankton in the inshore areas during summer/winter 1997 and summer 1998 was suggested (Iriarte and González, 2004). The present findings with constant flux of coccolithophores but significantly reduction of diatoms support the hypothesis for a shift towards smaller phytoplankton also for this more oceanic position.

The sharp decrease in August 1997 may be a result of a temporary nutrient depletion of the surface waters resulting after the first bloom of phytoplankton consisting of diatoms and coccolithophores. Furthermore, it coincides with a first seasonal peak of foraminifera (Marchant *et al.*, 2004). The following elevated fluxes seem to reflect the upwelling event of the normal winter period. However, the winter upwelling seems to be less pronounced due to the lower nutrient content of the upwelled water. During the subsequent months, the El Niño event took place fluctuating in intensity for the mooring location (Carr *et al.*, 2002a). As a result, the influence of the warm water and the deepening of the nutricline varied. Still upwelling events took place differing in the additional nutrient input as well as in the propagation of filaments meandering offshore (Carr *et al.*, 2002a). Furthermore in 1997/98 a pronounced high flux of foraminifera was observed that exceeded the flux of the study period of 1993/94. The predator forcing is enhanced and can explain decreases of the phytoplankton fluxes during January and February (Marchant *et al.*, 2004).

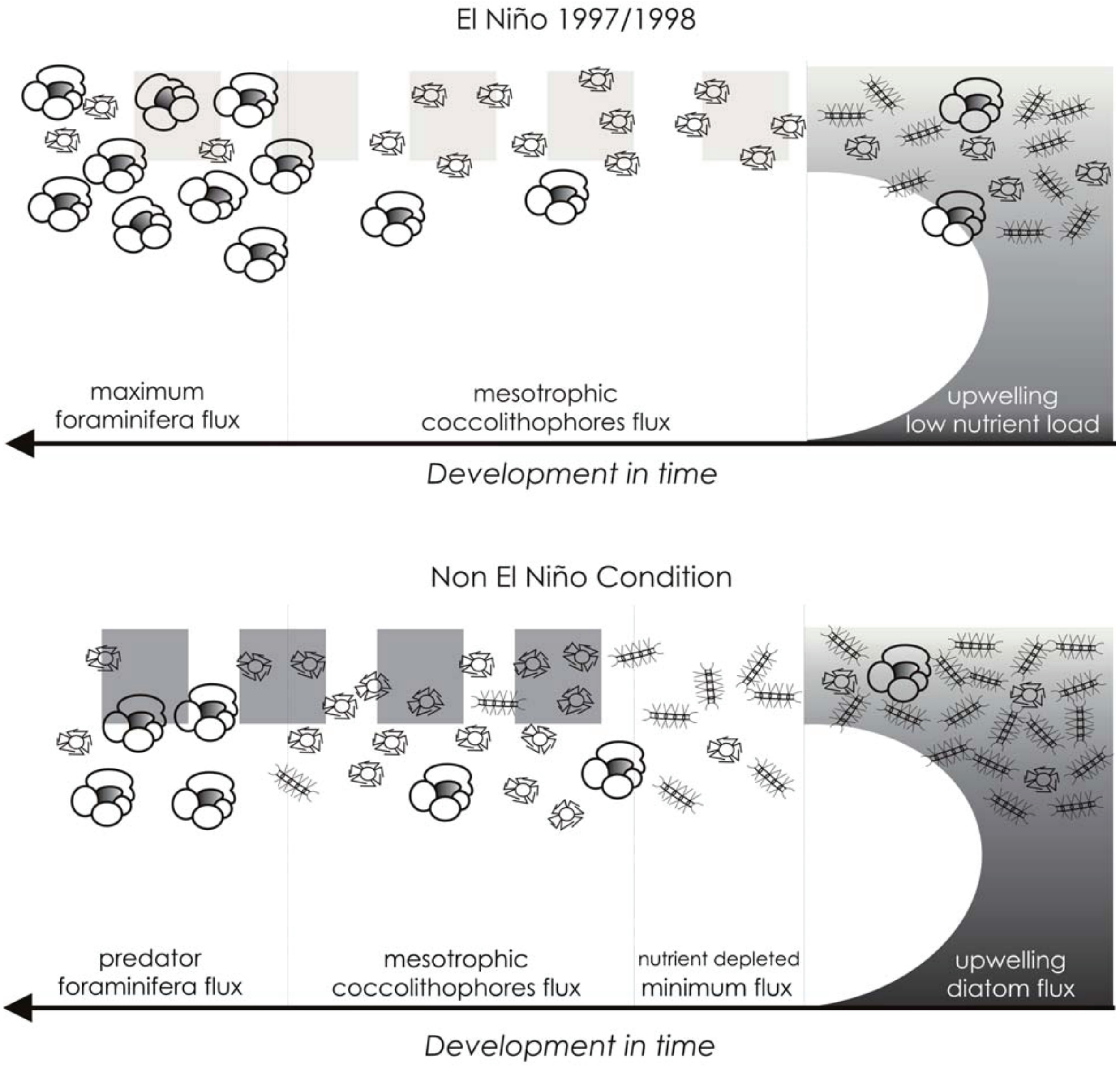


Fig. 5.9:
Schematic overview of the dynamics of differen plankton groups during the El Niño event of 1997/98 and during 1993/94 ('normal' condition shading indicates upwelled water, darkness corresponds with nutrient content)

coccolithophore
foraminifera
diatom

5.3 Carbonate Fluxes

Milliman (1993) estimated the carbonate export production to range between 2-5 g $m^{-2}y^{-1}$ in the central ocean gyres and 30-40 g $m^{-2}y^{-1}$ in the eastern upwelling zones. The carbonate fluxes measured off Chile reached 30 g $m^{-2}y^{-1}$ (Marchant *et al.*, 2004). In contrast the yearly carbonate flux at the Cape Blanc mooring location was lower with 22 g $m^{-2}y^{-1}$ (Fischer *et al.*, 1996). The deployment station of the Chile sediment traps was closer at the coastal upwelling region than the CB traps to the Mauritania upwelling zone. The sediment traps off Cape Blanc were influenced only occasionally by the meandering filaments. Further north of Cape Blanc, in the Canary Island region (ESTOC traps) the carbonate flux was significant lower with a yearly flux of 8.7 g m^{-2}, which is regarded as a more oligotrophic site (Sprengel *et al.*, 2000). Stations comparable in carbonate fluxes and their position close to upwelling zones are located off Somalia (MST-9) (Broerse *et al.*, 2000b) and Namibia (NU) (Romero *et al.*, 2002b) with a yearly carbonate flux of 22 and 21 respectively. In contrast, the mooring station in the North Atlantic (NABE-48) (Broerse *et al.*, 2000) has a yearly carbonate flux of 11 g m^{-2}.

Foraminifera, coccolithophores and to a lesser extend pteropods and calcareous dinoflagellate cysts contribute to the stated carbonate fluxes. To identify the proportion of the coccolithophores their coccolith mass fluxes have to be determined. Due to the small size of coccolithophores weighing of single spheres is impossible. Due to the availability of the coccolith fluxes, the shape-factor method (Young and Ziveri, 2000) is more applicative. Here, the specific shapes of the coccoliths, as well as the length of the coccolith and the density of calcite are incorporated in the calculation of the coccolith carbonate masses. Based on own biometric measurements of specific species the two upwelling regions can be compared with respect to their coccolith carbonate fluxes.

Off Cape Blanc the annual coccolith–carbonate flux of the slightly more coastal trap site CB1 amounts to 4.9 g $m^{-2}y^{-1}$ and further offshore to 5.7 g $m^{-2}y^{-1}$ (based on CB 2-4) respectively 3.1 g $m^{-2}y^{-1}$ (based on CB9, respectively CB3 and 4 upper trap, unpublished data by Köbrich). Higher fluxes are present off Chile where the annual coccolith–carbonate fluxes add up to 9.5 g m^{-2}, only to 5.9 g m^{-2} during the El Niño year (Fig. 5.10) The more coastal position of CH3/4 and CH10/11 seems an explanation for the higher annual fluxes compared to the NW-African study region. The differences of the coccolith–carbonate fluxes between the El Niño year and during a ‘normal’ year are based on the extreme decrease in fluxes during El Niño (see chapter IV).

The fluxes of Cape Blanc (CB1) closer to the coast are higher than the fluxes further offshore moored. The annual flux of 5.9 g m^{-2} based on CB 2-4 may be slightly overestimated as an annual average due to the extraordinarily high fluxes during the winter season 1990/1991. This maximum coccolith flux was not observed with the same range in the upper trap, consequently the coccolith flux resulted in lower coccolith–carbonate mass. In general, sediment traps in deeper waters are considered to be more reliable in collecting vertical particle fluxes (Feely *et al.*, 2004). The estimates show the range the carbonate fluxes of coccolithophores can obtain in this region. Thus, annual mean estimates may be problematic if taken as basis for global carbonate budgets or model inputs (Gregg and Casey, 2007). In comparison to the upwelling influenced regions off Namibia

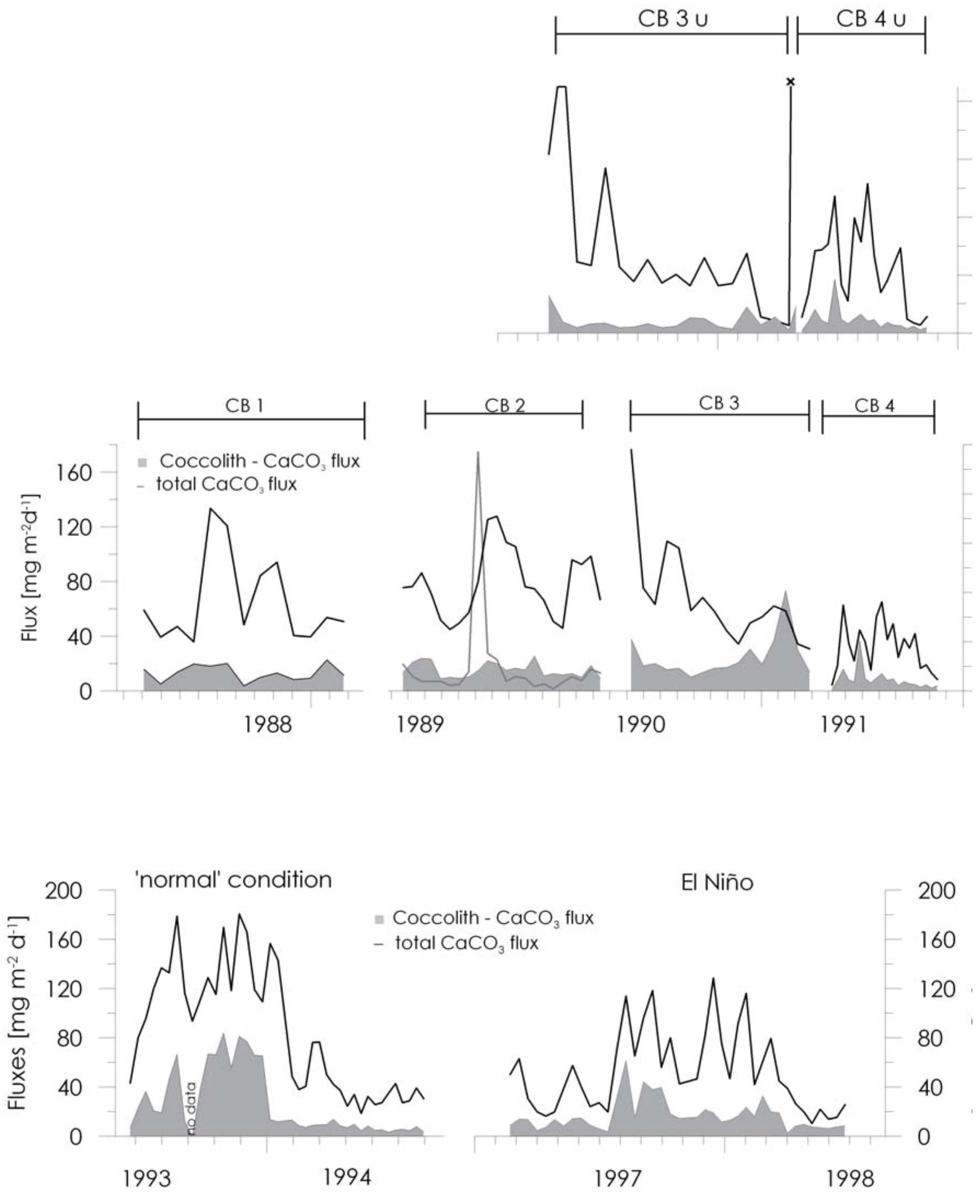


Fig. 5.10 Estimated coccolith carbonate fluxes, total carbonate, and flux of aragonit fluxes (pteropods, data only for CB2 shown) off Cape Blanc and off Chile (CB3 u and CB 4 u, deployment det´pth 730m, 733m) unpublished data by Köbrich)

(3.8 m^{-2}y^{-1}) and Somalia (3 g m^{-2}y^{-1}), the Cape Blanc study area displays same fluxes, whereas the coccolith–carbonate fluxes of the Chile upwelling are almost twice as high during El Niño and three times during 'normal' conditions. At the equatorial Pacific yearly fluxes of 6.4 g m^{-2} are reported (Tanaka and Kawahata, 2001), whereas at the Arabian sea higher annual fluxes of 10.4 up to 24.0 g m^{-2} (Ramaswamy and Gaye, 2006).

The seasonal pattern of the coccolith – carbonate fluxes of Cape Blanc is rather constant throughout the years (Fig. 5.10). However, remarkable exceptions also exist as seen in the maximum coccolith-carbonate flux in winter 1990/1991 and the pteropod aragonite maximum in summer 1989 (Fig. 5.10) (Kalberer *et al.*, 1993). In general, fluxes arise from either increased production in the surface layers or increased downward transport of the produced (Waniek *et al.*, 2005). The existing specific hydrography in the Cape Blanc upwelling region with the formation giant filaments and the resulting patchy occurrence of blooms

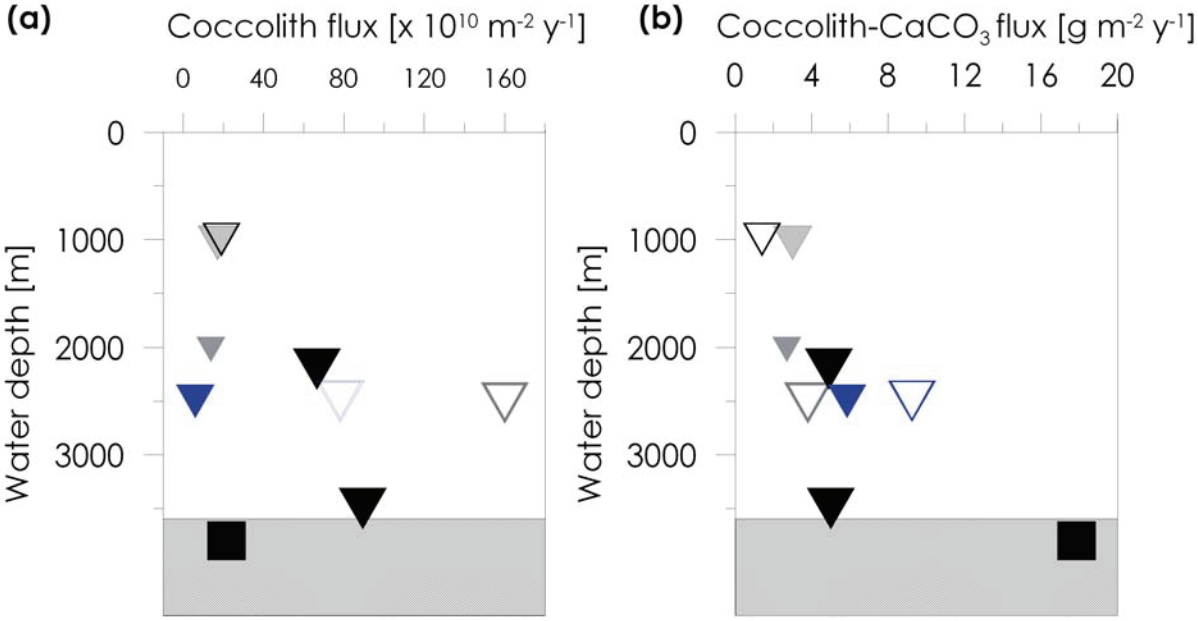


Fig. 5.11: **(a)** Comparison of average coccolith flux/ accumulation **(b)** average coccolith-carbonate flux /accumulation recorded in sediment traps off Cape Blanc (▼CB1, ▼CB2-4 -3500m), in N. Atlantik (▼NABE), off ▽Namibia (NU, at the ▽Canary Island region (ESCTOC), off ▼Somalia (MST), and off ▽Chile (▼Chile El Niño) and surface sediment at the mooring station CB1(■GeoB 1121)

may explain the exceptional high fluxes at certain times. In addition, a phenomenon regularly observed off Cape Blanc is the pulse like sedimentation of particles that increase the mean settling velocity tremendously (Nowald *et al.*, 2006). In turn a fast settling reduces the time of possible dissolution processes (Berelson, 2001). The pulse like sedimentation events are often associated with the presence of blooms (Nowald *et al.*, 2006). As discussed in chapter III, the significant increase in fluxes of well preserved fragile coccoliths suggest a higher production in the surface water and a fast(er) settling of this material into the deep.

Similarly, the coccolith–carbonate fluxes off Chile during 'normal' hydrographic conditions seem to result from fast settling coupled with increased surface water production. The pattern of coccoliths-carbonate flux as well as of the total flux is revealed a high and low phase during the season except during the El Niño event. The El Niño event is characterized by the vast changes in climatic and oceanic environment.

Even though the two studied upwelling region display at times comparable conditions, differences also exist, especially the comparison of the coccolith fluxes with the resulting coccolith–carbonate fluxes (Fig. 5.11). The flux of coccoliths during El Niño off Chile is significantly lower than off Cape Blanc, however, the estimated coccolith–carbonate is almost the same. The coccolithophore species composition explains the apparent discrepancy (Fig. 5.12). Especially the massive species of the genus *Helicosphaera* and of *Calcidiscus* contribute to the coccolith–carbonate off Chile, whereas off Cape Blanc other small sized species add significantly to the coccolith fluxes, but only little to the coccolith mass (referred as others in Fig. 5.12). Even though the fluxes of coccoliths differed in the single time-series of Cape Blanc, the important species in respect to carbonate content and their contribution to the coccolith-carbonate are within the same range (Fig. 5.12).

The measured carbonate fluxes and the estimated coccolith – carbonate fluxes allow to determining the contribution of coccolithophores to the overall carbonate flux of the upwelling region. The proportion of coccolithophores to the total carbonate varies with time and region. The mean contribution of the coccolith–carbonate fluxes of Cape Blanc ranges from 18% for CB1 to 34% for CB9 (Fig. 5.13a). The overall contribution of coccoliths to the carbonate fluxes varies even stronger with 7% to 125% (Fig. 5.13a). The contribution of coccolithophores to the carbonate flux off Chile adds up to 27% ('normal' condition) and

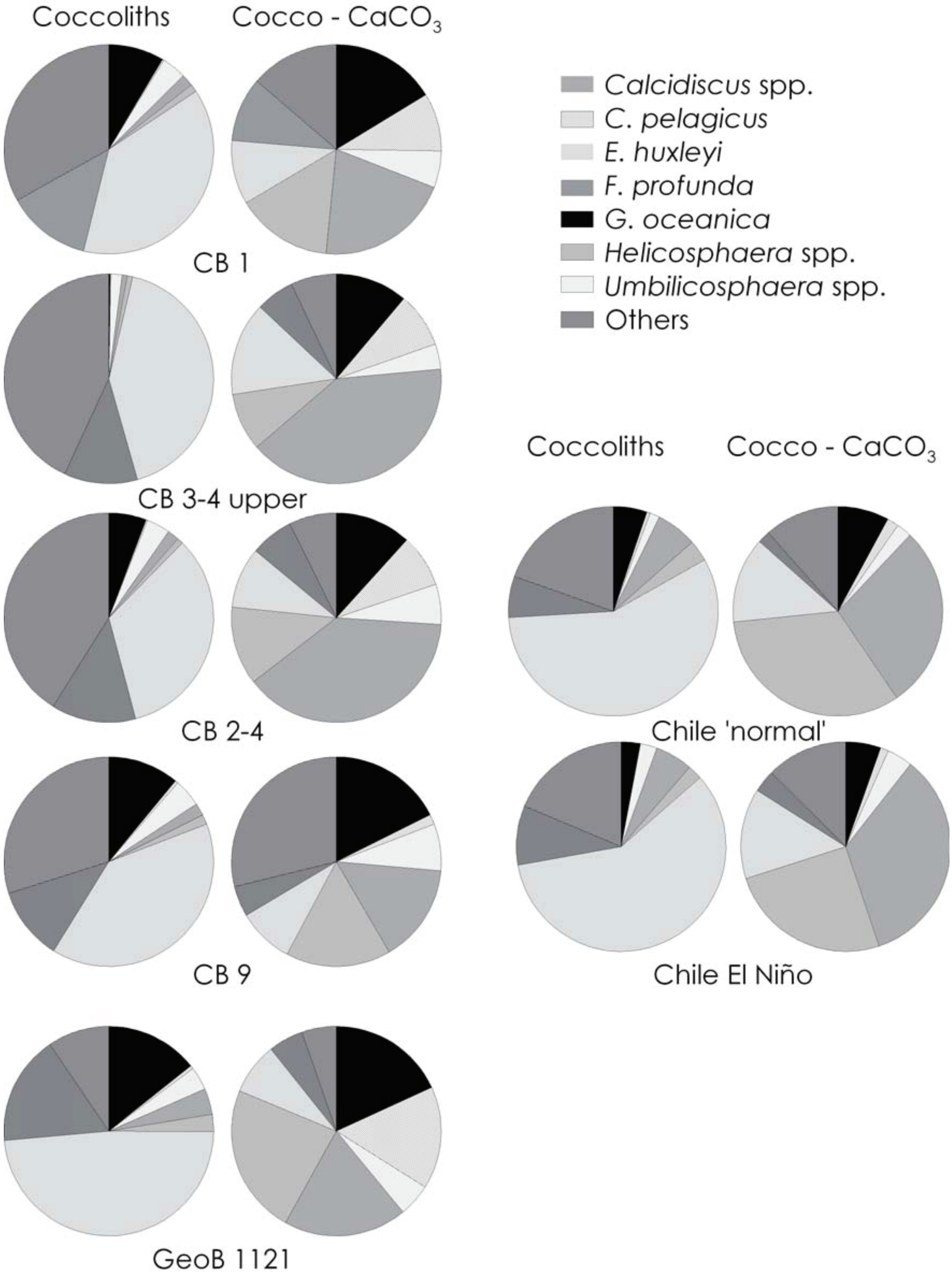


Fig. 5.12: Relative contribution of Species to the coccolith fluxes (annual mean) and to the coccolith-carbonate

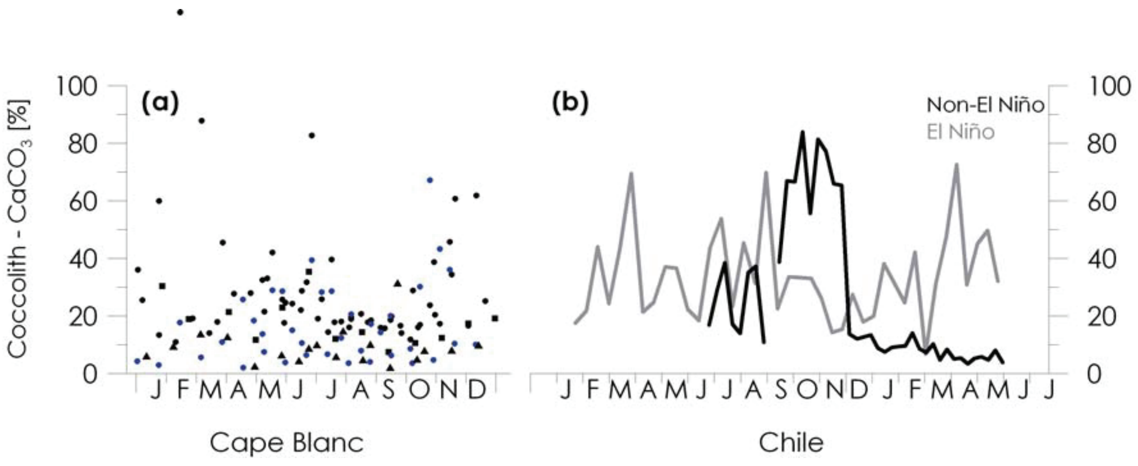


Fig. 5.13: Coccolit-carbonate contribution to total carbonate flux for the studied sediment traps Cape Blanc and Chile

(■ CB1,●CB 2-4 ▼ CB9 and ● CB 3-4 upper trap unpublished data by Köbrich

34% during El Niño with (Fig. 13b). Coccolith–carbonate flux calculations can only provide estimates because of substantial errors in coccolith volume calculations of around 40-50% (Young and Ziveri, 2000). In addition, the incorporation of coccoliths in aggregates such as fecal pellets or marine snow leads to an underestimation of the coccolith–carbonate in the samples (Beaufort and Heussner, 1999; Knappertsbusch and Brummer, 1995). Additionally, fragmentation of coccoliths and the exclusion of coccolith fragments from the counts lead also to an underestimation of the coccolith carbonate (Broerse *et al.*, 2000a). The resulted overestimation in winter 1990/1991 may be due to the inaccuracy of the shape factor. This factor is an important magnitude in determining the species specific carbonate and is best determined for only certain species (Young and Ziveri, 2000).

The estimated coccolith-carbonate fluxes of these two major upwelling regions add up to a larger contribution to the total carbonate flux as Schiebel (2002) presents for the global budget. Here only 12% of the annual carbonate flux of the open-marine carbonate inventory is related to coccolithophores. Broerse (2000) describes this proportion as a first estimation which excludes several regions, for examples such as those with major *E. huxleyi* blooms. Further recent studies of upwelling region report higher contribution of coccolithophores to the overall carbonate fluxes ranging from 23% (South Atlantik), 26% (Mediterranean Sea) to 51.2% (Arabian Sea) (Boeckel and Baumann, 2008, Ramaswamy and Gaye, 2006; Triantaphyllou *et al.*, 2005). In each study the variability of the fluxes is evident revealing in times by far larger contribution of coccolithophores to the carbonate fluxes.

VII. Future Perspectives

To study and evaluate the changes between the standing stocks of the surface water production by collecting plankton samples, the settling particles by sediment trapping, and the settled assemblage by examine the underlying surface sediments is one prerequisite for the interpretation of the paleo-signature found in sediment cores (Andruleit *et al.*, 2004). During the cruise M58/2b samples taken from varies stations and water depth off Mauritania expand the existing plankton samples archived at the geological department of Universität Bremen. First unpublished samples yield besides a species composition similar to the traps, so far undescribed species (see Plate 18). The deployment of sediment traps in two different water depths as present off Cape Blanc records the fluxes of the settling particles simultaneously. Differences in settling processes which might influence the species composition and coccolith-carbonate fluxes can be observed (Berelson, 2001). Furthermore, samples of underlying surface sediments have been studied in respect to the occurrence of calcareous dinoflagellates cysts (Richter *et al.*, 2007). To use the same locations and study the coccolithophore content would allow comparison of two carbonate producers. Altogether, a large sample pool is available to compare three water compartments (surface-water column-sediment). To characterize this highly productive upwelling region is an important step towards the calculation of the export production of coccolithophores, respectively biogenic carbonate. The verification of this export (and its formation) is critical to the success of hydrodynamic models which predict these (or future) exports (Jackson *et al.*, 2005).

CBi a sediment trap moored at the upwelling region of Mauritania and deployed at the same time as CB offers the opportunity to directly compare the coccolithophore fluxes of the coastal upwelling and further offshore (Meinecke *et al.*, 2004). The study would increase our knowledge of the ecological affinities of the single species and of the coccolithophore community. It would also raise the possibility of determination of the influences of transport processes into the deep as well as offshore due to filaments (Alvarez-Salgado *et al.*, 2007). These aspects build an important base for future modelling studies in which marginal regions as well as the variability of regions stand to the fore (Boyd and Trull, 2007).

The Cape Blanc deployment offers a unique possibility to obtain a more or less continuous data set of fluxes for the past ten years. In this study the first four years were intensively studied showing strong interannual variability of the general flux patterns including coccolithophores and further organism fluxes. An interesting subsequent issue is if there is a changing trend within the amount and composition of the coccolithophores fluxes due to climatic anomalies or climate change. First hint gave the reduced diatom flux within the first years (1988-1991) (Fischer *et al.*, 1996). Furthermore, the response of marine calcification to changes in water CO_2 and acidification of the world oceans is of special interest (Barker *et al.*, 2003) and recent studies indicate the responds of coccolithophores to it (Iglesias-Rodriguez *et al.*, 2008). Since coccolithophore species react differently to an increase in pCO_2 (Langer *et al.*, 2006; Riebesell, 2000), the observation of whole coccolithophore assemblages (and their fluxes) of an important upwelling region could give information on shifts within the species composition or within the plankton community structure.

The use of satellite derived data such as chlorophyll-a, biomass, and primary production in addition to coccolithophore occurrence respectively fluxes serves as further basis for the estimation of the proportion of coccolithophores on primary production (Behrenfeld and

Falkowski, 1997). During the last years the satellite imagery (CSCZ, SeaWiFS, and MoDIS) increased the knowledge about the primary production rates in the world oceans (Carr, 2002a; Hoepffner *et al.*, 1999). With the aid of satellite imagery climatic anomalies as for example El Niño can be monitored in detail (McPhaden, 1999). These strong climatic events with its world wide impact may also influence primary production outside the direct affected area (Enfield and Mayer, 1997; Gerten and Adrian, 2002). To amend the interpolation of satellite signals the coccolith occurrence of this major upwelling region could be used (Balch *et al.*, 2005).

Thus the detailed study of the offshore coccolithophore community structure over a decade in comparison to the living community with its observation via satellite imagery and in comparison to the coastal upwelling would describe an important oceanic region in respect to export production of an important phytoplankton group.

VII. Plates

It has been shown that many apparently globally distributed coccolithophores are composed of genotypically discrete species (or sub-species) often with similar morphologies but with rather strong ecological differences (Geisen et al., 2004). This applies to some of the species studied here. Knowledge of the morphological size variation in living oceanic coccolithophore species as well as of their ecological affinities is a prerequisite for paleontological and paleoceanographical studies. Further these data, that is size measurements, are needed for a more exact determination of spe-cies-specific carbonate fluxes.

Where available, diagrams display the variability of length, width or numbers of elements of the coccoliths. These characteristics document for the first time the coccolithophore assemblage off Cape Blanc and off Chile (30°S) in detail.

One aim of the present study was to characterize the coccolithophore flora off major upwelling re-gions represented by the east current systems off NW-Africa and off Chile. In the following plates the variety of the assemblage, variability of single species, and undocumented species are dis-played. Together with SEM images, information on several species is given. In some cases the in-formation is an extract of the before shown, in others new data on morphological measurements are shown. As a result a direct comparison between the two upwelling sites or/and between the different time intervals is possible. The focus is to characterize the species and to gain an overview as well as to raise the information and the specific ecological descriptions available to date.

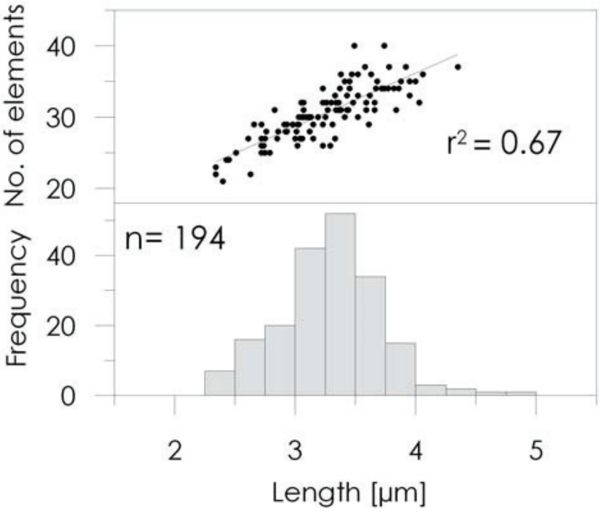
ISOCHRYSIDALES: *NOELAERHABDACEAE*: EMILIANIA

Emiliania huxleyi

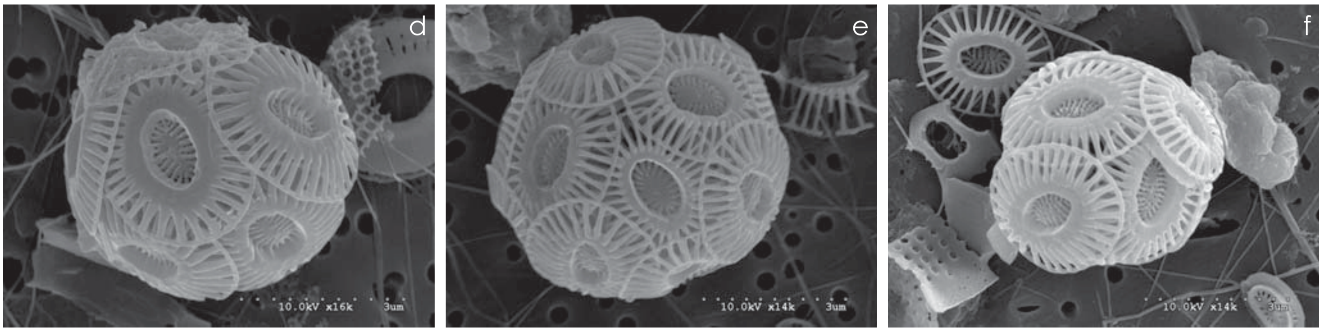
In general *E. huxleyi* dominates the coccolith assemblage in the studied sediment traps off Cape Blanc as well as off Chile.

Out of the CB1 trap samples, the morphology of 194 coccoliths was measured. The result shows a unimodal distribution (Fig. 7.1). The coccolith sizes range from 2.5–4.9 µm with a mean of 3.3 µm (Fig. 7.1). Varieties as given by Young and Westbroek (1991) have not been distinguished in the studies during counting. However, the majority of the measured specimens are (probably) *E. huxleyi* type A (Plate I Fig. 7.a–f; in part overcalcified). Specimens with more delicate rays indicate that *E. huxleyi* type C (Plate I Fig. 7.l) and type B (Plate I Fig. 7.j–k) also occur. One criterion to distinguish type B and type C is size with type C being smaller than type B. The dividing line is fluently, so in some cases the classification is hard to implement. Therefore, morphotypes with a similar appearance as type B and C but intermediate in size are named *E. huxleyi* B/C type (Plate I Fig. 7.i). In Plate I Figure 7.g) *E. huxleyi* type B (left) and type A (right, overcalcified) can be compared

Fig. 7.1: Size variation and frequency distribution (at 0.25 µm intervals) of *E. huxleyi* (194 coccoliths of CB1 trap samples)



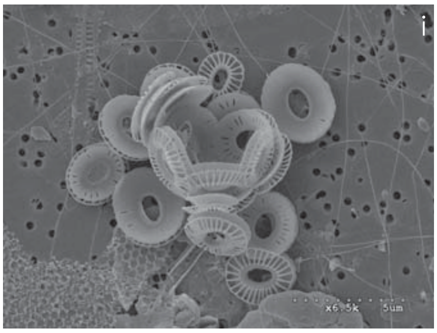
E. huxleyi



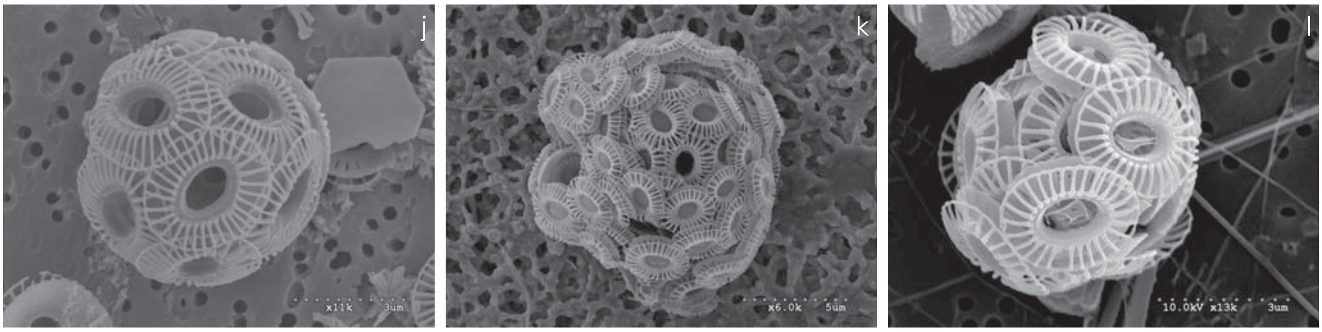
E. huxleyi

E. huxleyi

E. huxleyi



E. huxleyi



E. huxleyi

PLATE I - NOELAERHABDACEAE: *EMILIANIA*

ISOCHRYSIDALES: *NOELAERHABDACEAE*: GEPHYROCAPSA

Gephyrocapsa spp.

In the present studies the three species *Gephyrocapsa ericsonii, G. muellerae,* and *G. oceanica* were distinguished. *G. oceanica* was dominant either off Cape Blanc or off Chile. Surprisingly off Cape Blanc only seldom coccoliths of *G. muellerae* – characterizing cold water properties – were found. Off Chile the three species were present in all samples.

148 specimens of *Gephyrocapsa* from the Cape Blanc samples were measured morphologically. In addition, *G. oceanica* was separated into smaller and larger types following the description of Bollmann (1997) who morphologically analysed *Gephyrocapsa* of Holocene assemblages and revealed six dominant associations. Small *G. oceanica* coccoliths are medium-sized, 3.1–4.4 µm long and have a large bridge angle of 49–74°, whereas lengths of large-sized *G. oceanica* generally range from 4.2–5.9 µm. These specimens also have a large bridge angle of 49–83° (Fig. 7.2a). (*G. oceanica* occurred primarily in the phenotype represented in image a–d) Plate 2, but phenotype shown in image e–f) also frequently occurred). *G. ericsonii* coccoliths are 1.6–2.7 µm long and have a medium-large bridge angle of about 18–47°. These measurements exactly fit into the ”traditional” scatterplot-scheme of bridge angle vs. length presented by Samtleben (1980) (Fig. 7.2a).Overall, lengths and widths of the placoliths are extremely well correlated (r^2=0.99). A bivariate scatterplot of length versus bridge angle clearly separate the three modes into discrete clusters and correspond to the above-mentioned species (Fig. 7.2).

The described morphotype by Bollmann (1997) appear to have distinct environmental preferences with respect to temperature and productivity. Out of the proportion of the phenotypes we calculated the sea surface temperature (SST) (Bollmann, 1997). Figure 7.2b illustrates the SST from the world ocean atlas (WOA), SST based on alkenon concentrations (Müller and Fischer, 2001), and SST based on Gephyrocapsa morphotypes. The SST estimations by alkenones show a shift of 25 days to the SST of the WOA (Müller and Fischer, 2001). The SST based on the morphotypes misses the increase and maximum temperature in summer.

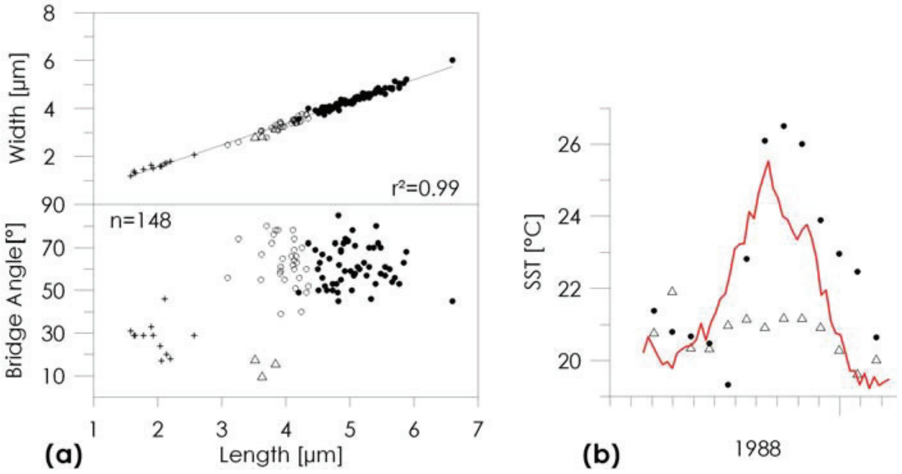
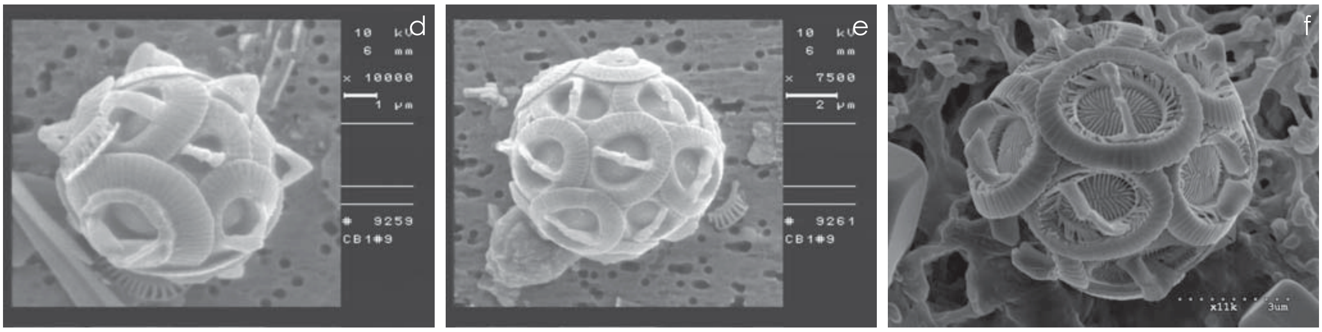


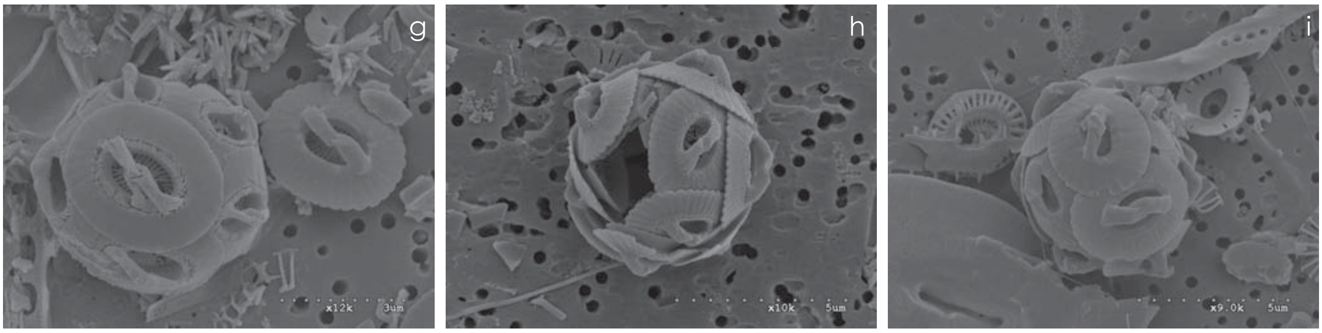
Fig. 7.2: **(a)** Coccolith size variation data of length versus bridge angle and width versus length measured in *Gephyrocapsa spp.* (+ *G. ericsonii*, ▲*G. muellarae*, ○ *G. oceanica* small, ● *G. oceanica* large).

(b) Sea surface temperature (—) from WOA, △ calculated after Bollmann (1997), and ● derived by alkenon concentrations (Müller and Fischer, 2001)

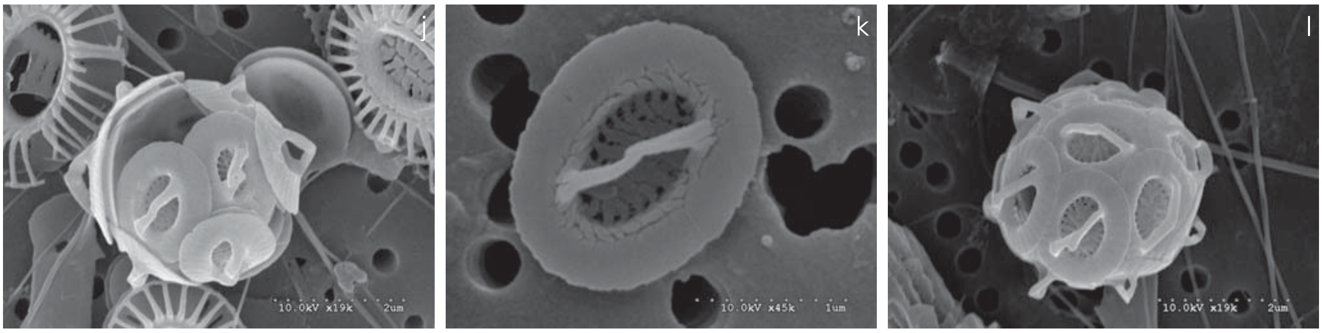
G. oceanica



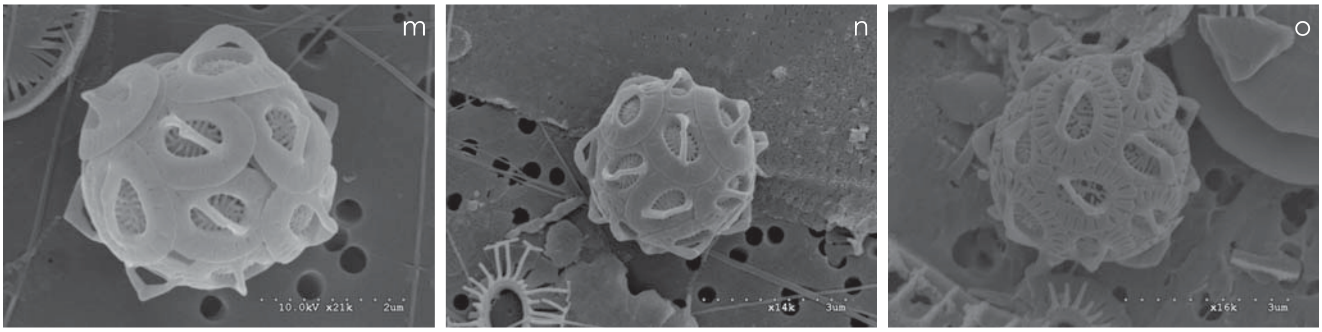
G. oceanica



G. ericsonii



G. ericsonii



G. ericsonii

Plate 2 - Noelaerhabdaceae: *Gephyrocapsa*

COCCOSPHAERALES: *COCCOLITHACEAE*: COCCOLITHUS

Coccolithus pelagicus

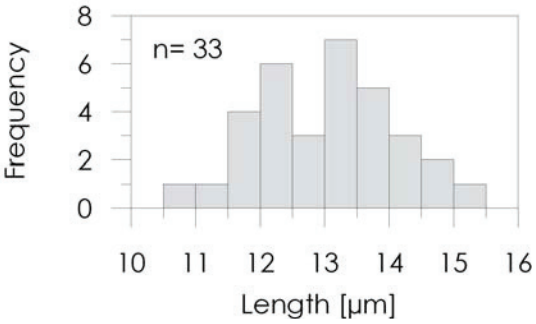


Fig. 7.3: Size variation and frequency distribution (at 0.25 µm intervals) of *C. pelagicus*

Even though *Coccolithus pelagicus* was found only in 52 out of 72 samples off Cape Blanc in very low numbers, the species has its importance as carbonate producer due to its massive placoliths. Also off Chile, *C. pelagicus* was scarce during 'normal' oceanic condition, as well as during El Niño (9 out of 40 samples, respectively 7 out of 40). The measurement of few specimens revealed a size variation between 10.82 µm and 14.77 µm in length and central area of 8.23–12.49 µm (Fig. 7.3).

The subdivision into *C. pelagics* ssp. *braarudii* and ssp. *pelagicus* is supported by morphological, biogeographical and cultural data (Geisen *et al.*, 2004). Following this description the encountered species were *C. pelagicus* ssp. *braarudii.*

COCCOSPHAERALES: *CALCIDISCACEAE*: CALCIDISCUS

Calcidiscus spp.

The coccoliths of *Calcidiscus* have been routinely distinguished (*C. quadriperforatus*, *C. leptoporus*, and *C. leptoporus* small) and were present in most samples off Cape Blanc, whereby their relative proportions fluctuated (Fig. 7.4). In addition, off Chile during 'normal' condition *C. leptoporus* and *C. leptoporus* small were found in all samples and *C. quadriperforatus* was missed only three times. During El Niño *C. quadriperforatus* was missed five times and the others were again present the whole sampling period (Fig. 7.5).

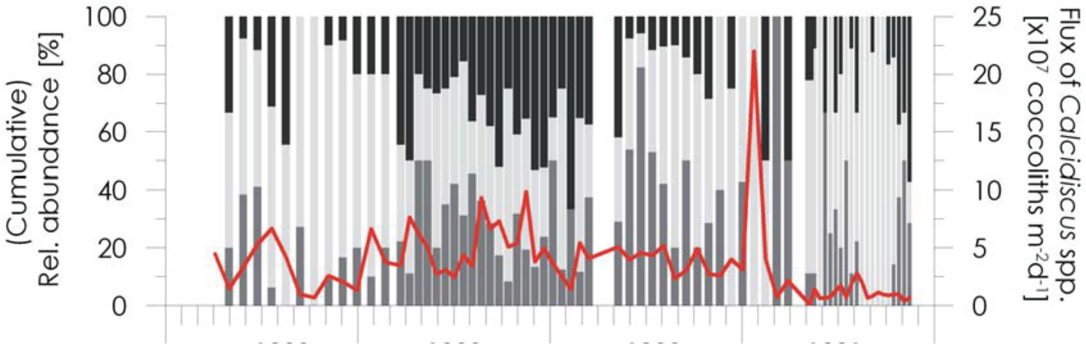


Fig. 7.4: Relative abundance of █ *C. leptoporus* small type, ░ *C. leptoporus*, and ▓ *C. quadriperforatus*, and flux of the *Calcidiscus* spp. (—)

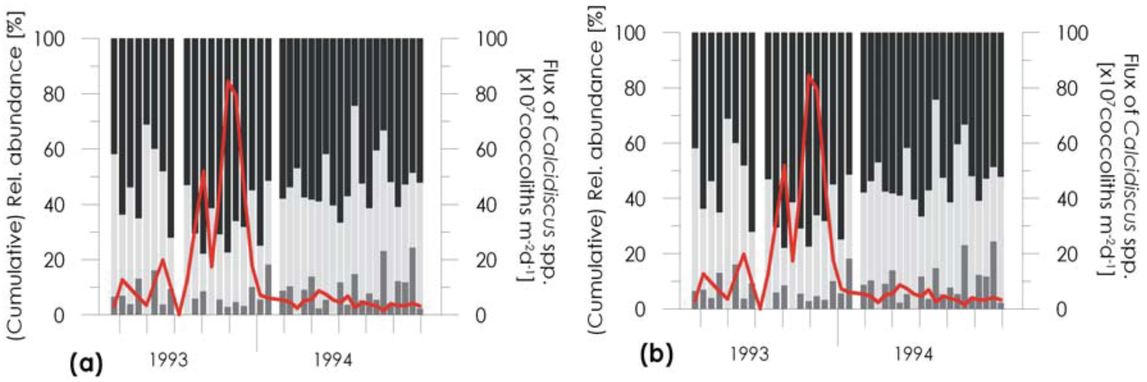
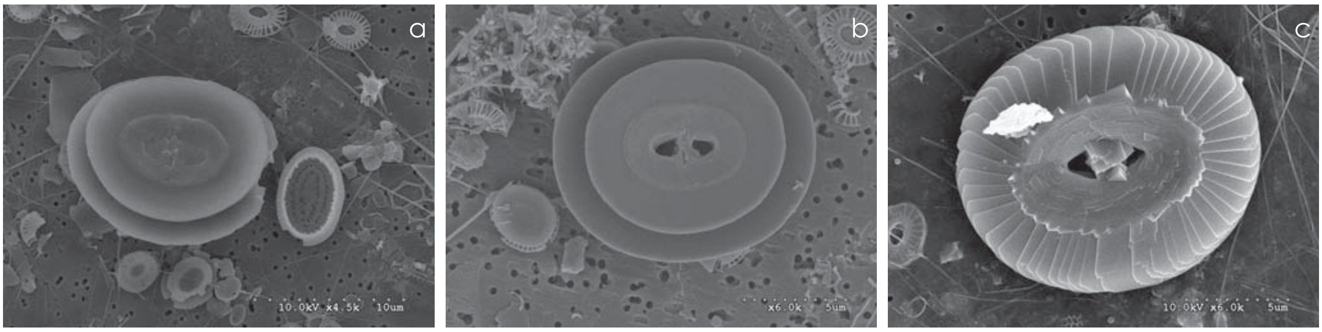
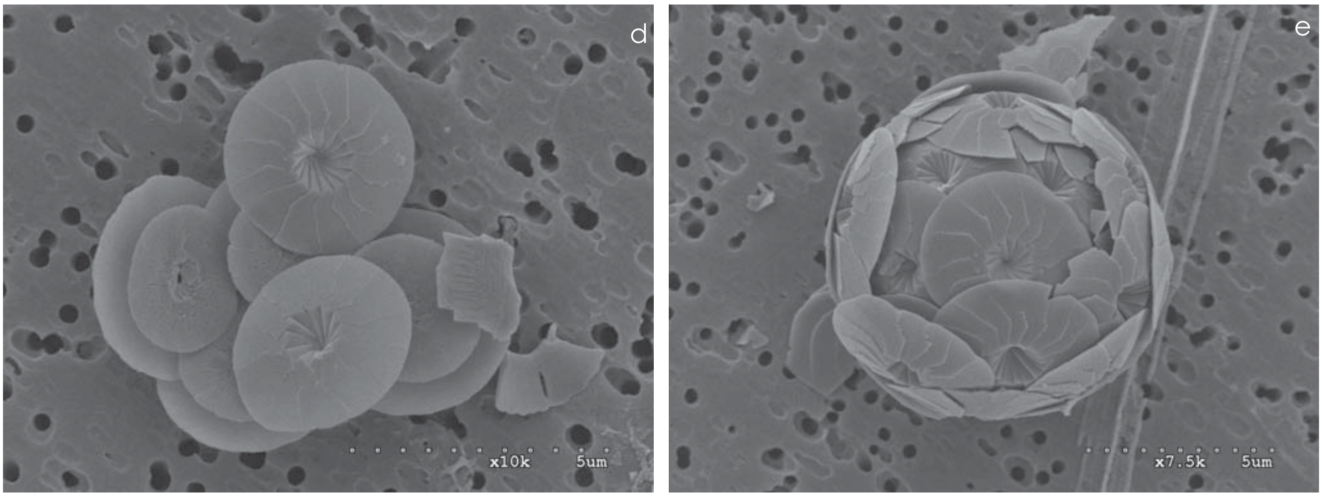


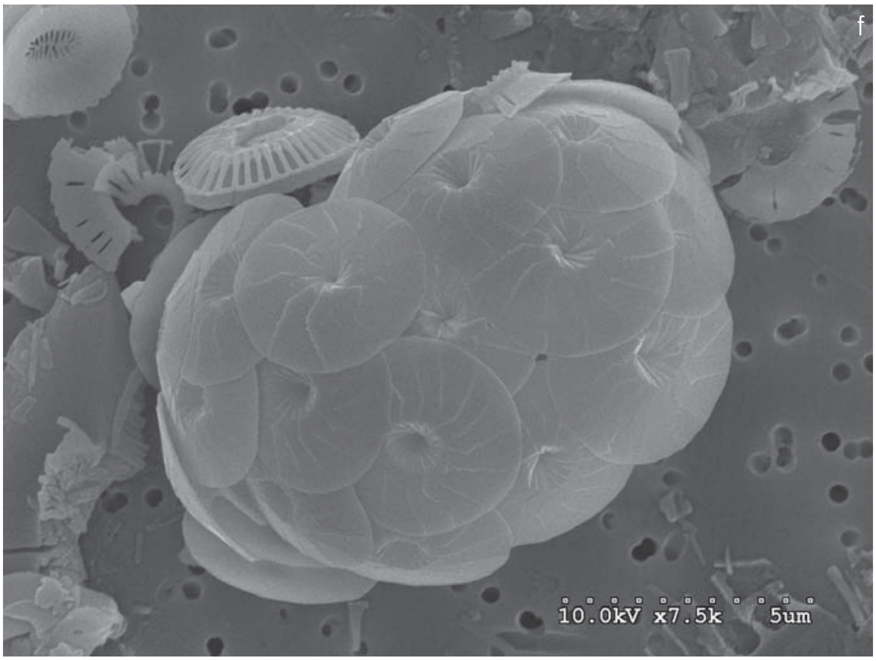
Fig. 7.5: Rel. abundance of █ *C. leptoporus* small type, ░ *C. leptoporus*, and ▓ *C. quadriperforatus*, and the flux of *Calcidiscus spp.* (—) **(a)** 'normal' condition, **(b)** El Niño



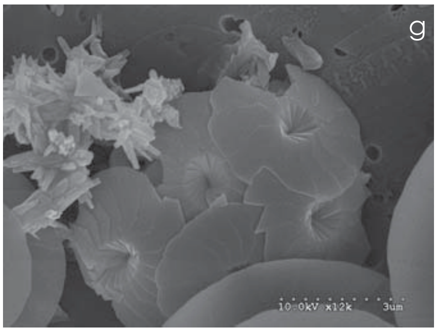
C. pelagicus



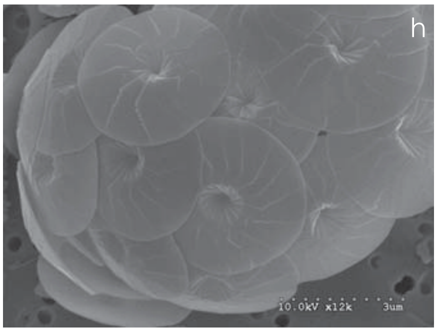
C. leptoporus



C. leptoporus



C. leptoprus



C. leptoprus

Plate 3 - Coccolithaceae: *Coccolithus* & *Calciduscus*

Calcidiscus spp.

The morphology of 130 placoliths of heterococcolith-bearing stage of *C. leptoporus* (CB samples) groups into three indistinct clusters with minimum overlap at 5 µm and 8 µm (Fig. 7.6). But even when considering and counting these morphotypes as distinct species – with *C. leptoporus* small type, the intermediate *C. leptoporus* and the large *C. quadriperforatus* as introduced by Geisens *et al.* (2002) – their sizes still vary significantly, with overall sizes 3.4–5.5 µm, 5.1–8.4 µm, and 6.9–11.4 µm, respectively (Fig. 7.6).

Off Chile the morphotypes or species clearly separate into *C. quadriperforatus* (7.29–10.10 µm), *C. leptoporus* (3.96–5.81 µm), and *C. leptoporus* small type (1.07–3.7 µm). The small morphotype attracts further attention. Its flux is higher off Cape Blanc (mean flux 1.1x10^{7} m^{-2}d^{-1}) than off Chile. Furthermore, the fluxes differ between the El Niño year (1997/98) (mean of 9.5 x10^{7} m^{-2}d^{-1}) and during the year of 'normal' oceanic condition (1993/94) (mean 3 x10^{7} m^{-2}d^{-1}) (Fig. 7.5).

The different morphotypes or species have not been counted separately so far in most coccolith counts. As a consequence, the comparison of different data sets is difficult. The dominance of the large, intermediate or small forms reveal different ecological preferences: *C. leptoporus* seems to be related to low temperature and nitrate content, *C. quadriperforatus* seems to be opportunistic (increase with increasing temperature and nutrient availability) (Boeckel and Baumann, 2008). The small morphotype seems to increase in relative abundance with increase in nutrient content of the surface water, temperature and stratification of the water column (Renaud *et al.*, 2002). In the present studies the three morphotypes were routinely counted. The holococcolith form *Syracolithus quadriperforatus* was found only once in the CB trap samples (in CB2#10).

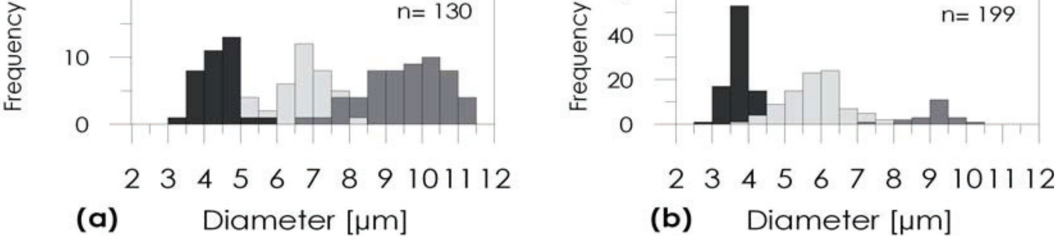
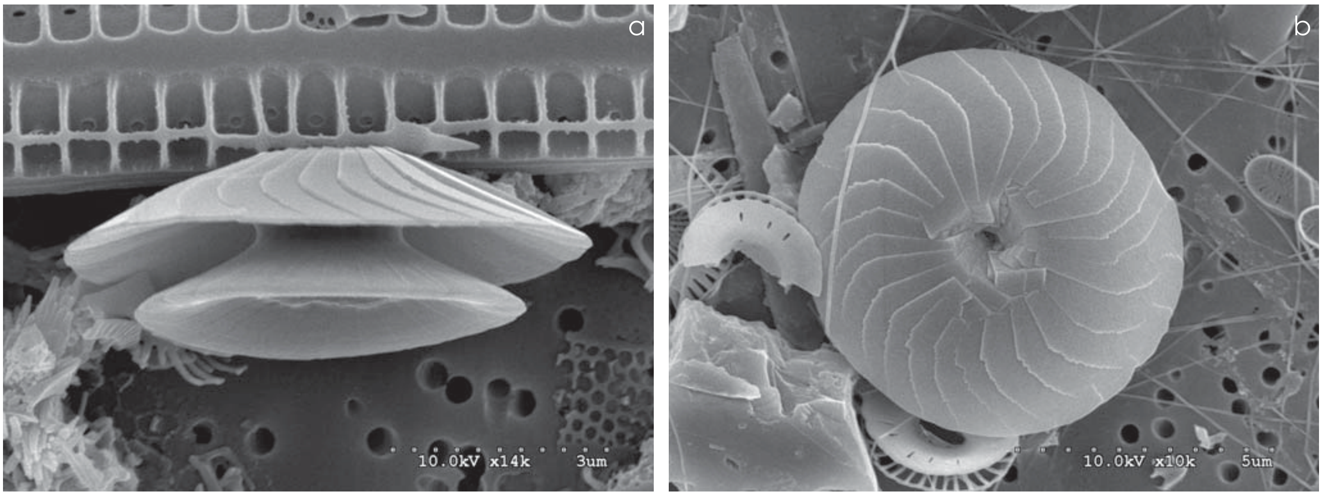
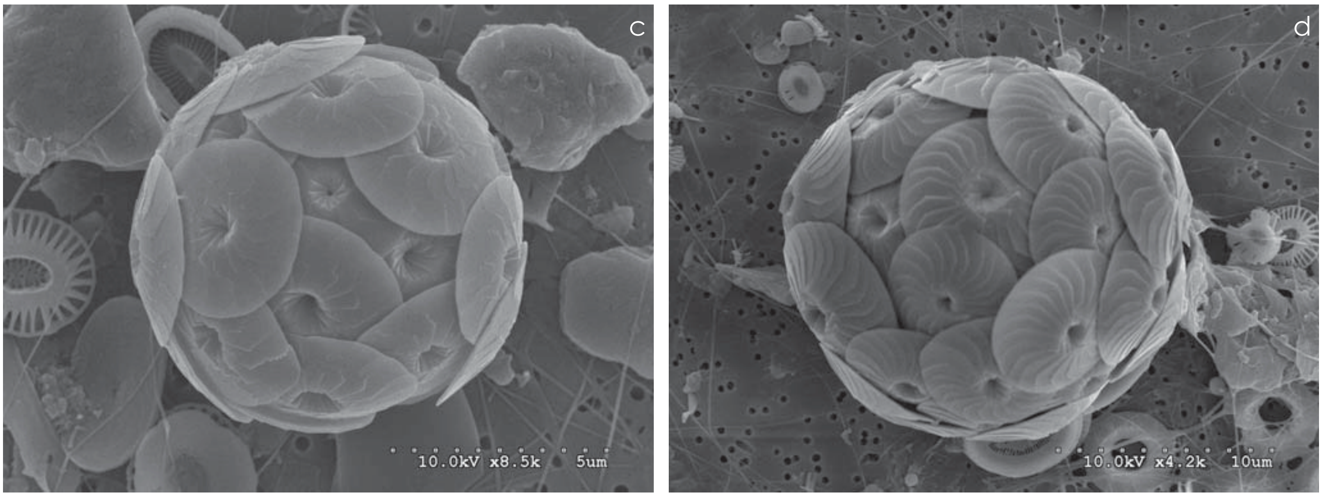


Fig. 7.6: Scatter plot of diameter versus pore size, diameter versus number of elements in the distal shield of the genus *Calcidiscus*, and frequency size distribution (at 0.5 µm intervals) of **(a)** Cape Blanc, and **(b)** Chile trap samples (+ *C. leptoporus* small, ○ *C. leptoporus*, ▲ *C. quadriperforatus*)

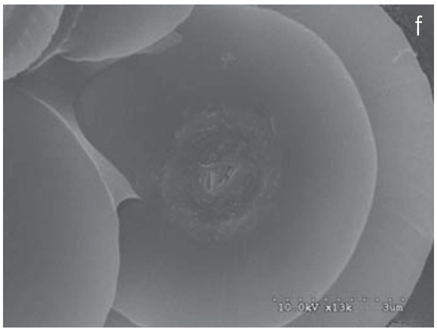


C. leptoporus

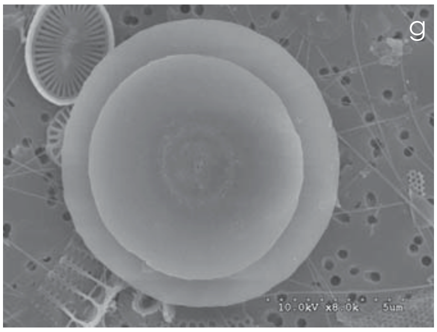


C. leptoporus

C. quadriperofratus



C. quadriperforatus



C. quadriperforatus

Plate 4 - Coccolithaceae: *Calciduscus*

COCCOSPHAERALES: *CALCIDISCACEAE*: OOLITHOTUS

Oolithotus antillarum

O. antillarum was rare and found only in one third of the Cape Blanc samples, whereas off Chile during the species was found frequently both study intervals (36 times during 'normal' condition respectively 34 times out of 40 during El Niño).

COCCOSPHAERALES: *CALCIDISCACEAE*: HYASTER

Hyaster perplexa

H. perplexa was seldom found in both upwelling regions (nine times off Cape Blanc and eight times off Chile).

COCCOSPHAERALES: *CALCIDISCACEAE*: UMBILICOSPHAERA

Umbilicosphaera sibogae, U. foliosa & U. hulburtiana

U. sibogae is the dominating species of the genus *Umbilicosphaera* in both upwelling regions. *U. sibogae* was present in all samples off Cape Blanc except once and *U. foliosa* was frequent, altogether missed in ten samples (out of 71) and especially during spring 1990. Off Chile, there was a significant difference between the two species: *U. sibogae* was present in all samples, whereas *U. foliosa* was rare. *U. foliosa* was found more often during 'normal' condition (12 out of 40) and only five times in 40 samples during El Niño. Only in 1993 austral spring ('normal' condition) a (max) flux of *U. foliosa* was recorded (8x107 $m^{-2}d^{-1}$).

In the morphometric study of 124 coccoliths the two species show distinct variation in diameter, element numbers, and size of the central area (Fig. 7.7). The distal shield of *U. sibogae* is 3.1–5.1 µm wide and consists of 20–32 elements. Proximal shields are larger than the distal shields having a mean of 4.9 µm. The distal shield of *U. foliosa* is 5.0–6.8 µm in diameter with a mean of 5.8 µm, and consists of 28–37 elements. The distribution of each of the varieties is unimodal with a mean of 4.4 µm (*U. sibogae*) and 5.8 µm (*U. foliosa*), respectively. In general the findings of the morphometric measurements fit to previously published morphological data on this species (Baumann and Sprengel, 2000; Kleijne, 1993).

U. hulburtiana is present during the whole sampling period off Cape Blanc with maximum fluxes during winter 1990/1991. Off Chile, *U. hulburtiana* occurs only in half of the samples during 'normal' oceanic condition (1993/94). The frequency increases during El Niño (3/4th of the samples).

The sizes of 69 basin-shaped endothecal heterococcoliths show a clear unimodal distribution pattern (Fig. 7.7 c). In general, mean coccolith length in the samples varies from 4.3–7.5 µm with mean of 6.0 µm. Mean coccolith width in the samples varies from 3.1–5.3 µm with an overall mean of 4.2 µm. The sizes are in the same range as previously observed (Baumann and Sprengel, 2000).

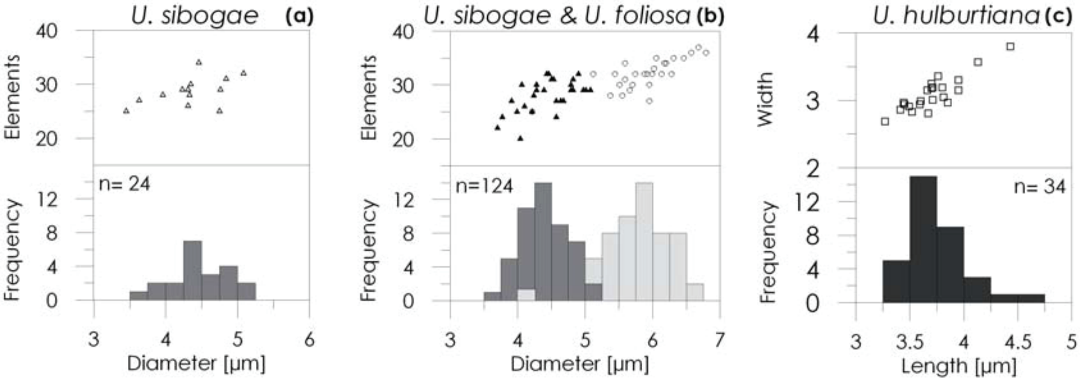
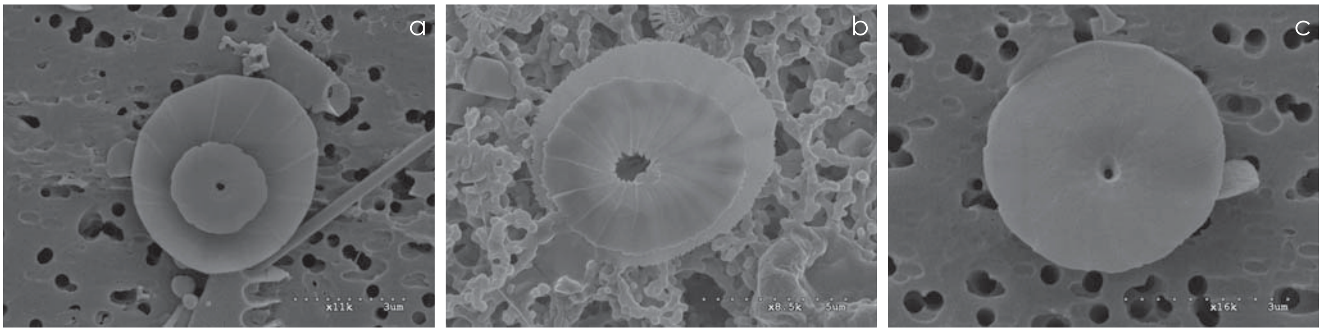
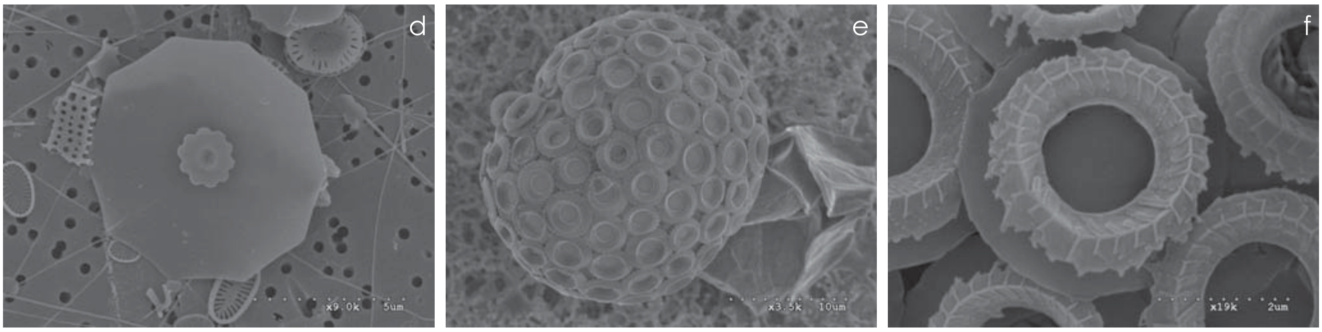


Fig. 7.7:
(a) Scatter plot of diameter versus number of elements in the distal shield of *U. sibogae* and frequency size distribution (Chile 'normal' condition)
aasa(b) Scatter plot of ▮ *U. sibogae* (▲) and of ▯ *U. foliosa* (○), and frequency size distribution **(c)** Scatter plot of length versus width of *U. hulburtiana* and frequency size distribution of Cape Blanc samples (at 0.25 µm intervals)



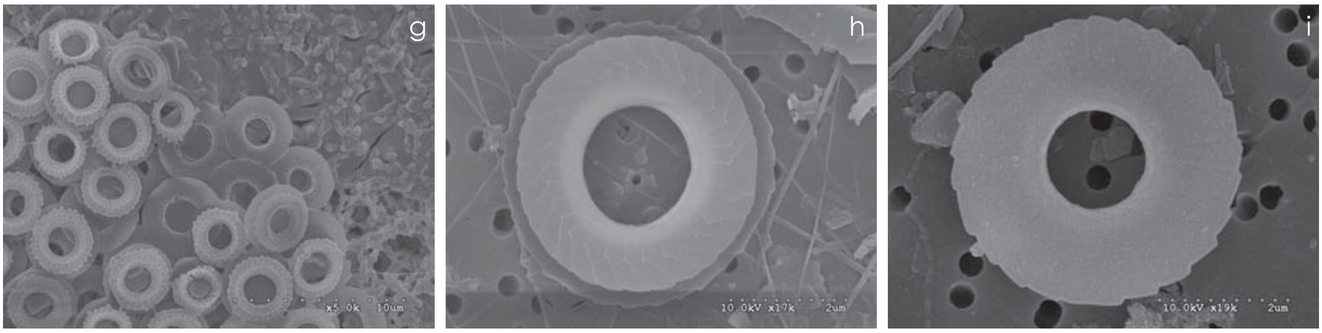
O. antillarum



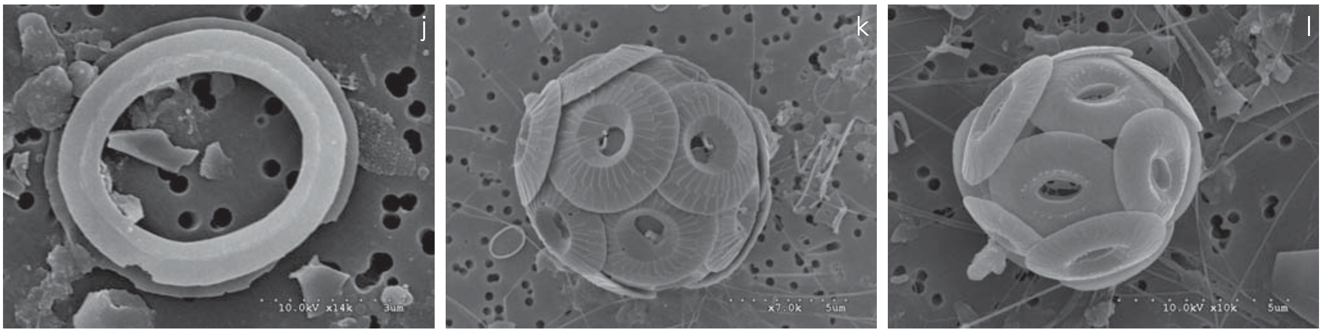
H. perlexa

U. sibogae

U. sibogae



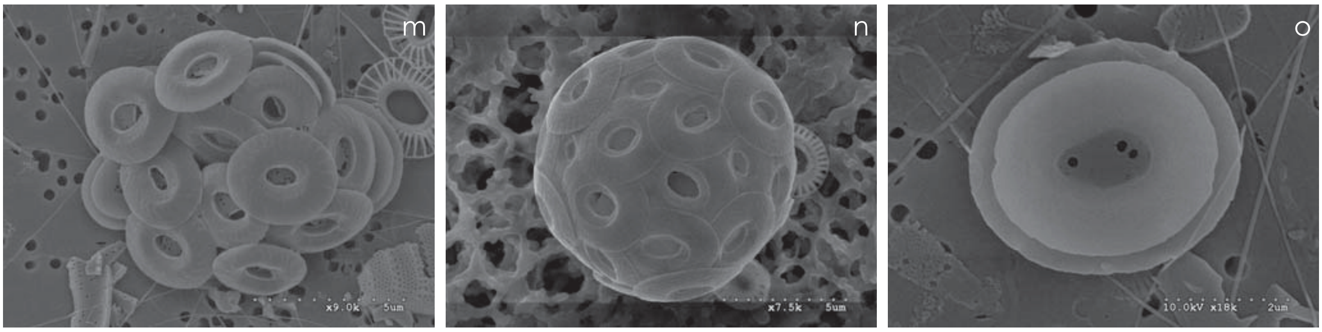
U. sibogae



U. anulus

U.foliosa

U. hulburtiana



U. hulburtiana

Plate 5 - Calcidiscaceae: *Oolithotus & Hyaster & Umbilicosphaera*

ZYGODISCALES: *HELICOSPHAERACEAE*: HELICOSPHAERA

Helicosphaera carteri

H. carteri is the dominant species within the genera in both upwelling regions being present in all seasons and displaying the same seasonal pattern as the overall coccolith fluxes (Fig. 7.9). However, the absolute as well as the relative abundances of *H. carteri* was different in the studied upwelling regions. It ranged from 0.2–2.8% in the samples off Cape Blanc, and off Chile from 1–7.9%.

Due to the massive construction the contribution of *Helicosphaera spp.* to the coccolith derived carbonate is of importance in both upwelling regions. Off Cape Blanc; 2.2–28.2% of the coccolith carbonate was due to the flux of Helicosphaera species and off Chile 9–52% during El Niño (1997/98) and 12.9– 61% during 'normal' condition (1993/94).

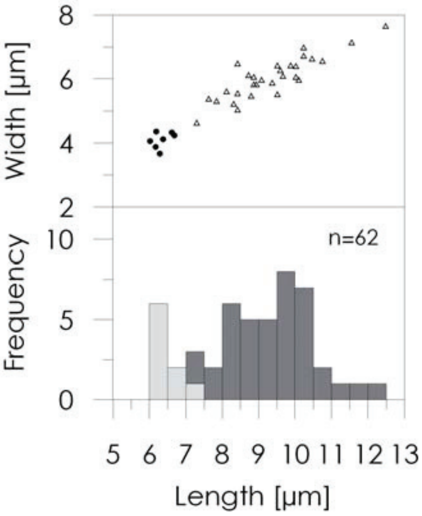


Fig. 7.8: Scatter plot of width versus length of ■ *H. carteri* (●) and □ *H. hyalina* (Δ) and frequency size distribution (at 0.5 µm intervals); Cape Blanc sediment trap samples

H. hyalina

H. hyalina was found in almost half of the samples (45%) off Cape Blanc with no obvious seasonal preference. The occurrence off Chile was slightly higher (65%) and displayed no difference between El Niño and non-El Niño conditions (Fig. 7.9).

The few specimen morphologically measured revealed a large size range of *H. carteri*. *H. hyalina* was smaller in length and width but the correlation of width versus length fit well in each species (Fig. 7.8).

H. pavimentum

H. pavimentum was only found within the Chile samples and encountered only seldom.

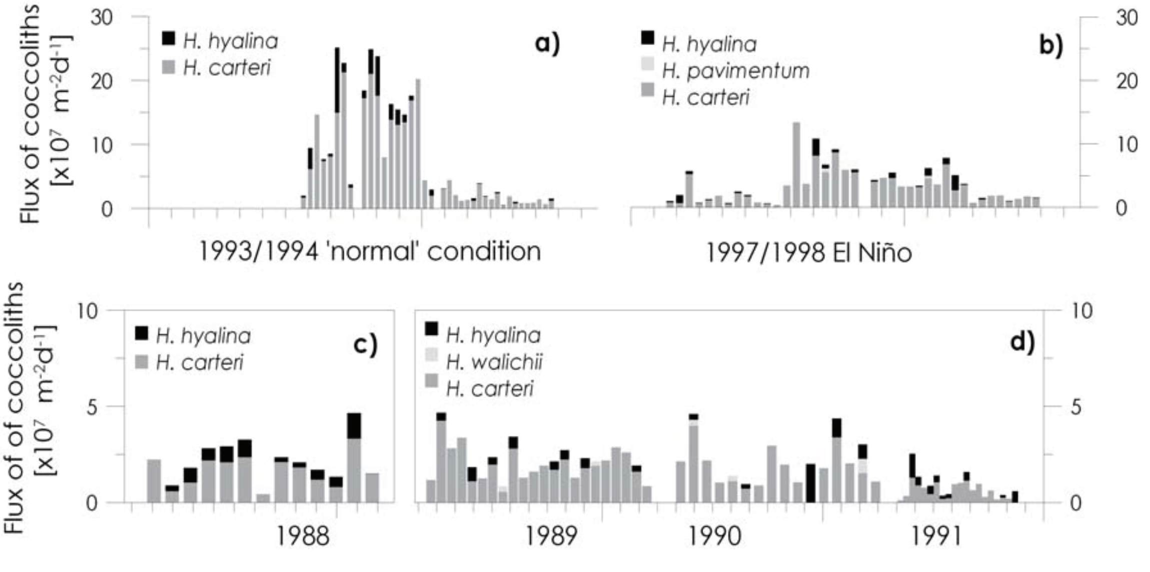
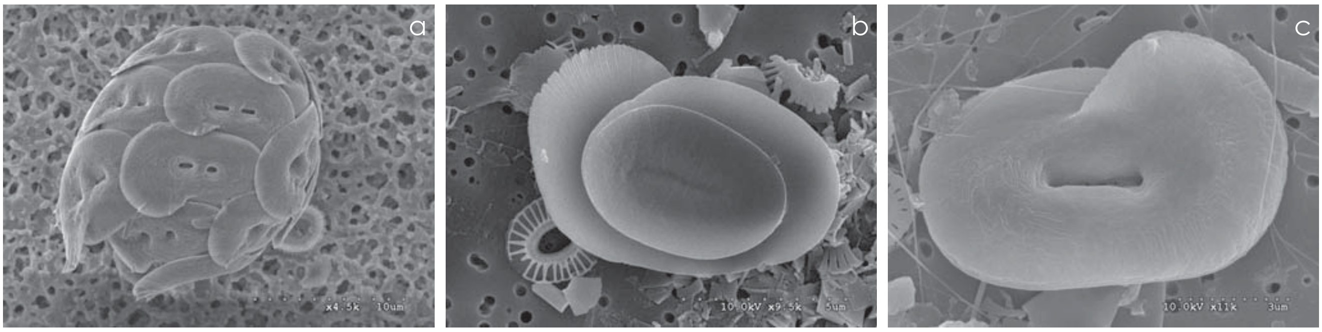


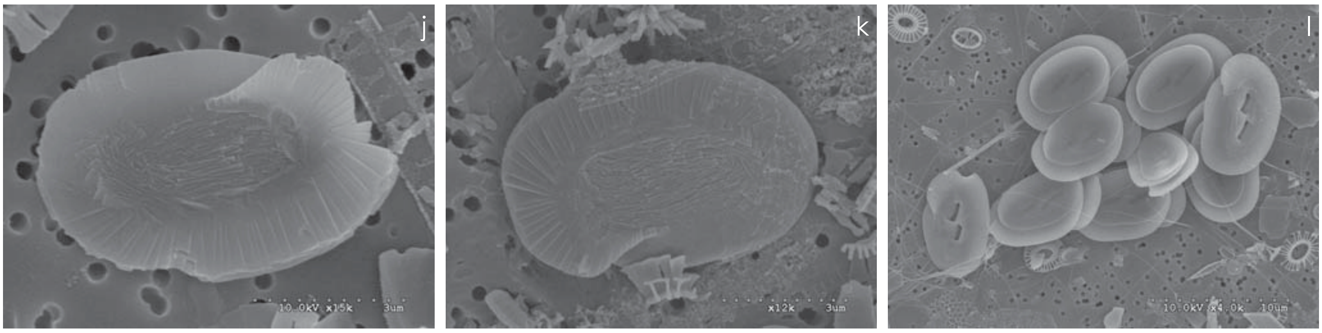
Fig. 7.9: **(a)** Flux of *H. hyalina, H. carteri,* and *H. pavimentum* during 'normal' oceanic condition and **(b)** during El Niño off Chile. The flux of *H. hyalina, H. carteri*, and *H. walichii* off Cape Blanc is shown in **(c)** and **(d)**



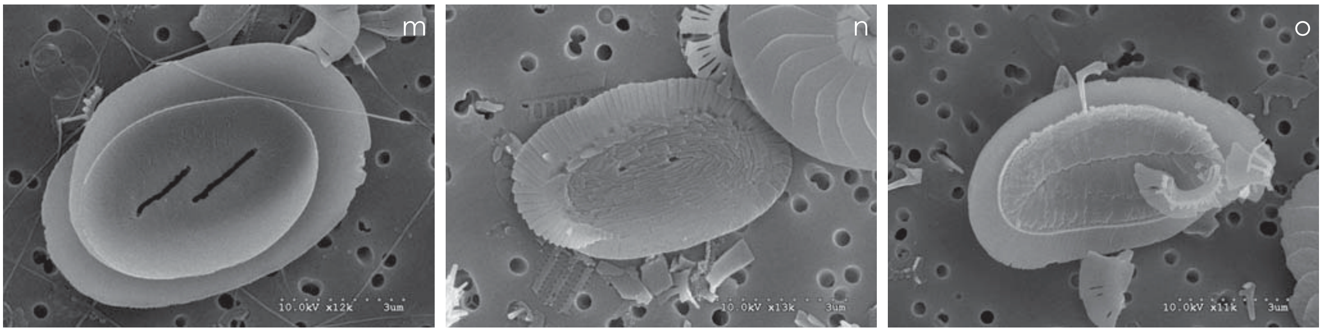
H. carteri

H. carteri

H. carteri *H. hyalina*



H. hyalina *H. hyalina* *H. wallechii*



H. wallechii *H. pavimentum* *H. pavimentum*

Plate 6: Helicosphaeraceae: *Helicosphaera*

ZYGODISCALES: *PONTOSPHAERACEAE*: PONTOSPHAERA

Pontosphaera spp.

In general, species of the genus *Pontosphaera* were present only in few samples and low numbers. However, its presence must be noticed due to the high specific carbonate mass and therefore its contribution to the coccolith derived carbonate flux. *Pontosphaera spp.* occurred in one third of the samples off Cape Blanc throughout the whole sampling period with no evidence for a preferable season. Off Chile, *Pontosphaera spp.* was just as rare during El Niño, but during 'normal' oceanic condition more than half of the samples (26 out of 40) contained *Pontosphaera spp.*

P.japonica

P. japonica was only found due to the extensive taxonomic study of the Cape Blanc samples and was not contained in the counts.

P. multipora

P. multipora was found in three samples off Cape Blanc and only once (CH11/1) off Chile.

P. syracosana

Off Cape Blanc *P. syracosana* was seldom, found only three times. In contrast the species was present in one fourth of the samples off Chile, however, no specific seasonal preferences was determined.

ZYGODISCALES: *PONTOSPHAERACEAE*: SCYPHOSPHAERA

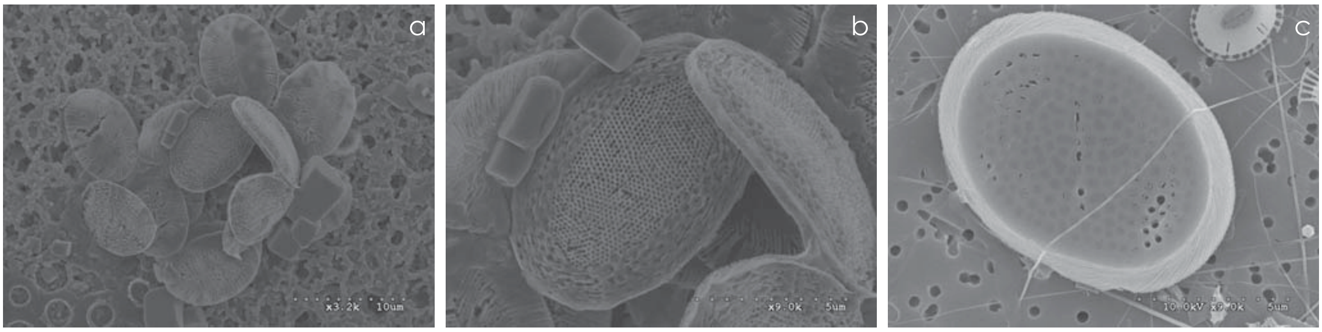
Scyphosphaera apsteinii

Only within the CB2 (twice) and CB3 (four times) samples *S. apsteinii* was found.

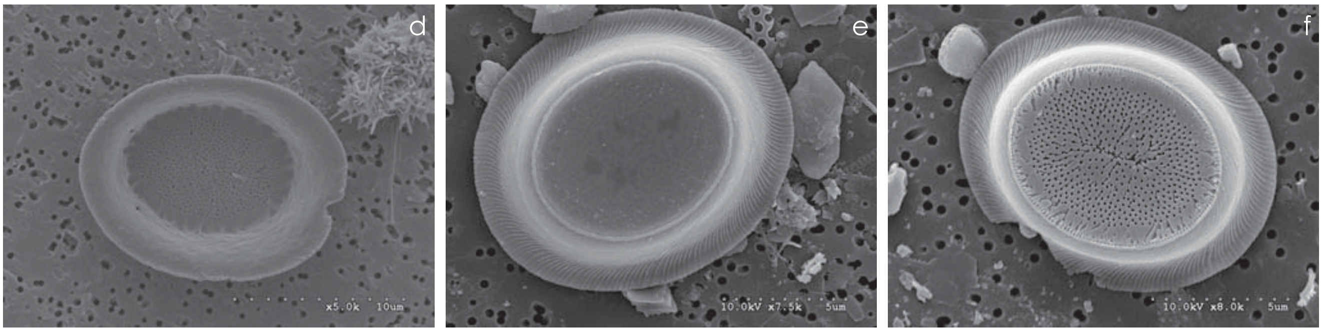
SYRACOSPHAERALES : SYRACOSPHAERACEAE: CALCIOPAPPUS

Calciopappus spp.

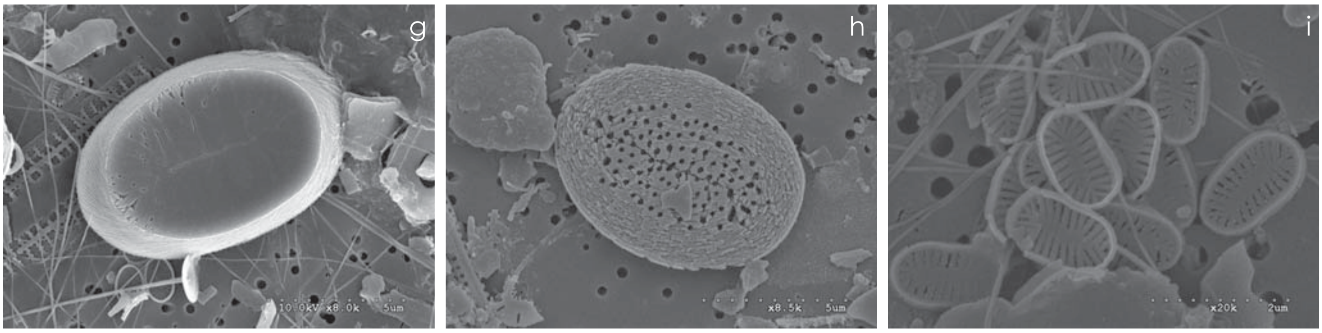
During the study the species *C. caudatus* and *C. rigidus* were found. Together, they were found commonly off Cape Blanc, whereas off Chile rather seldom (one fourth of the samples).



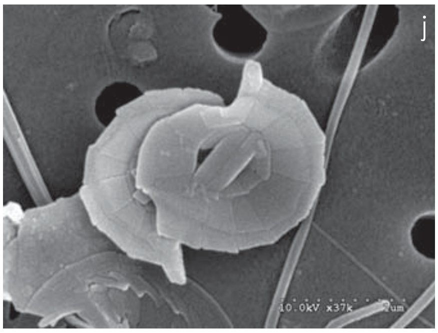
Pontosphaera japonica — Pontosphaera japonica — P. multipora



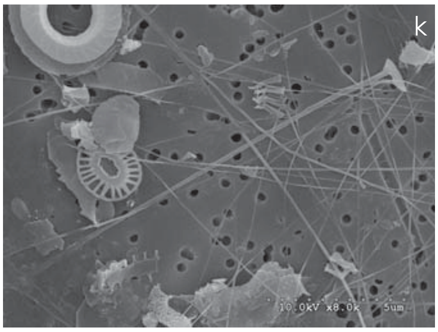
P. syracusana



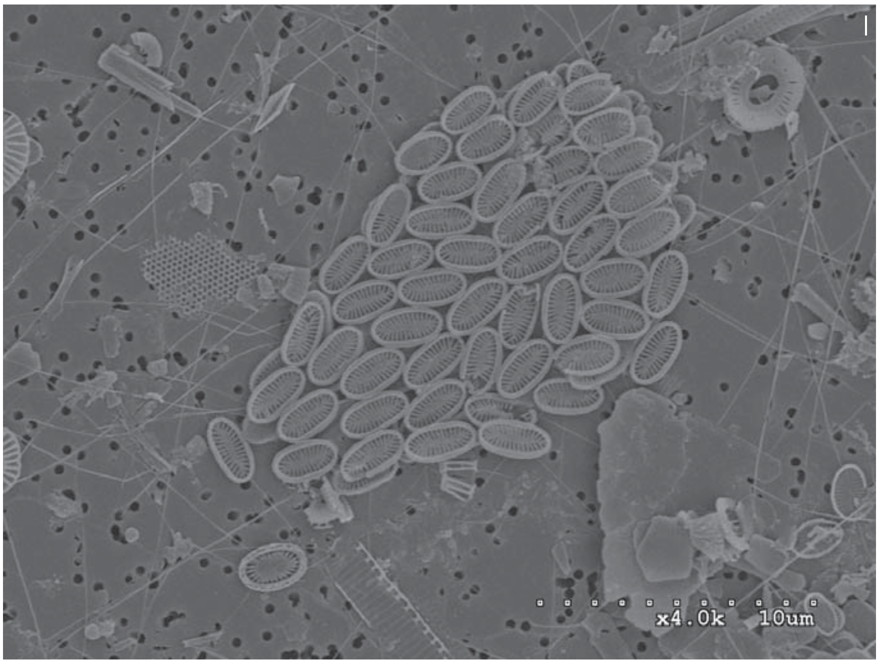
P. discopora — Scyphosphaera apsteinii — Calciopappus caudatus



C. caudatus



C. caudatus



Michaelsarsia elegans

PLATE 7 - PONTOSPHAERACEAE: *PONTOSPHAERA & SCYPHOSPHAERA*
SYRACOSPHAERALES - SYRACOSPHAERCEAE: *CALCIOPAPPUS & MICHELSARSIA*

SYRACOSPHAERALES: *SYRACOSPHAERACEAE*: MICHAELSARSIA

Michaelsarsia elegans

Michelsarsia elegans were present frequently in the samples. *M. elegans* and *M. adriaticus* were counted as *Michaelsarsia spp.* In general, coccoliths of *Michelsarsia spp.* were encountered more often in samples from NW-Africa (46 out of 71) than from Chile (only four respectively eight out of 40 samples of each study interval).

M. adriaticus

M. adriaticus was unambiguously identified in few samples from Chile during El Niño condition. The species is identified without difficulty only if whole coccospheres are preserved. Therefore both species were listed as *Michaelsarsia spp.*.

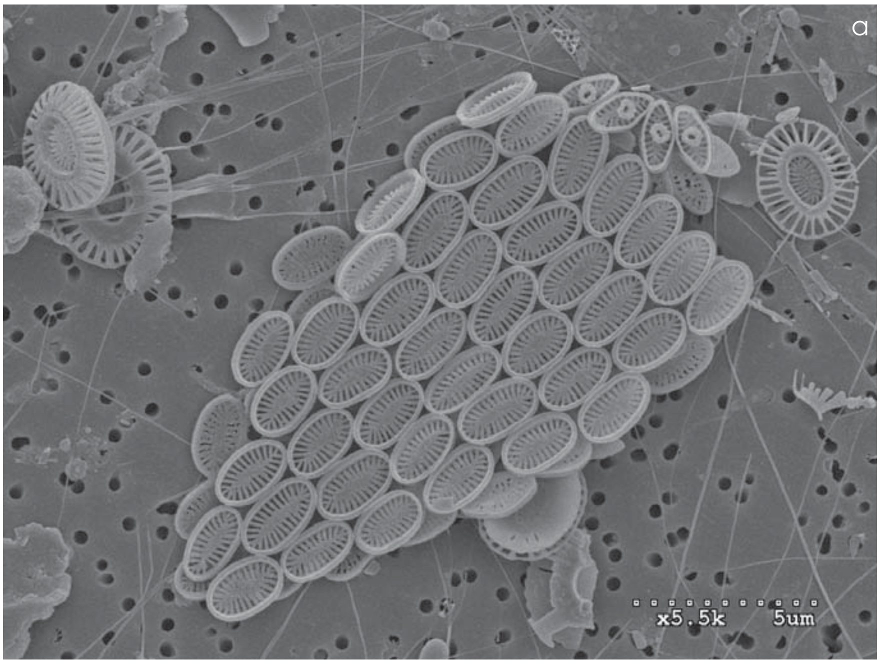
SYRACOSPHAERALES: *SYRACOSPHAERACEAE*: OPHIASTER

Ophiaster spp.

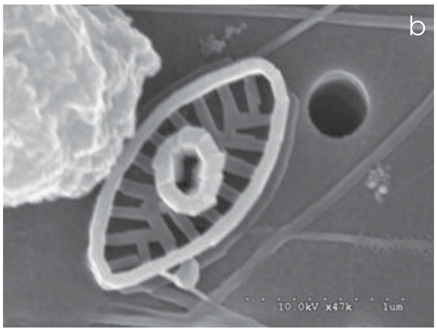
The genera *Ophiaster* was present in all samples obtained off Cape Blanc, whereas off Chile *Ophiaster* was present in three quarters of the samples regardless of El Niño condition prevailing or not.

The coccosphere of *Ophiaster* specimen is composed of numerous (50–80) rather small (1.1–1.3 µm) body caneoliths (Cros, 2002). Within the study of the Cape Blanc assemblage an extraordinary flux of *Ophiaster* was observed with an max of $5x10^9$ coccoliths $m^{-2}d^{-1}$). This maximum flux revealed several different species (unfortunately we were not able to define them to a lower taxonomic level). In Fig d) Plate 7 two spheres of different species are depicted with three different coccoliths, the body coccoliths, the circumpolar coccoliths (white arrows), and antiapical coccoliths (red arrows). The right coccosphere also possesses an antiapical coccolith.

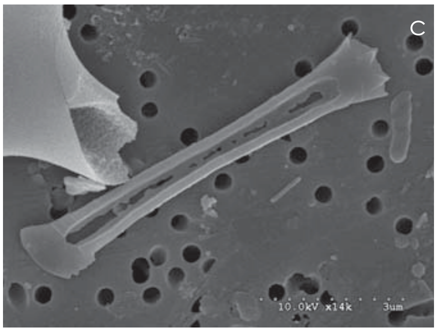
The Image e) and f) in Plate 9) represent elongated coccolith (osteolith) with coccolith and the coccolith in image f) forming the osteolith.



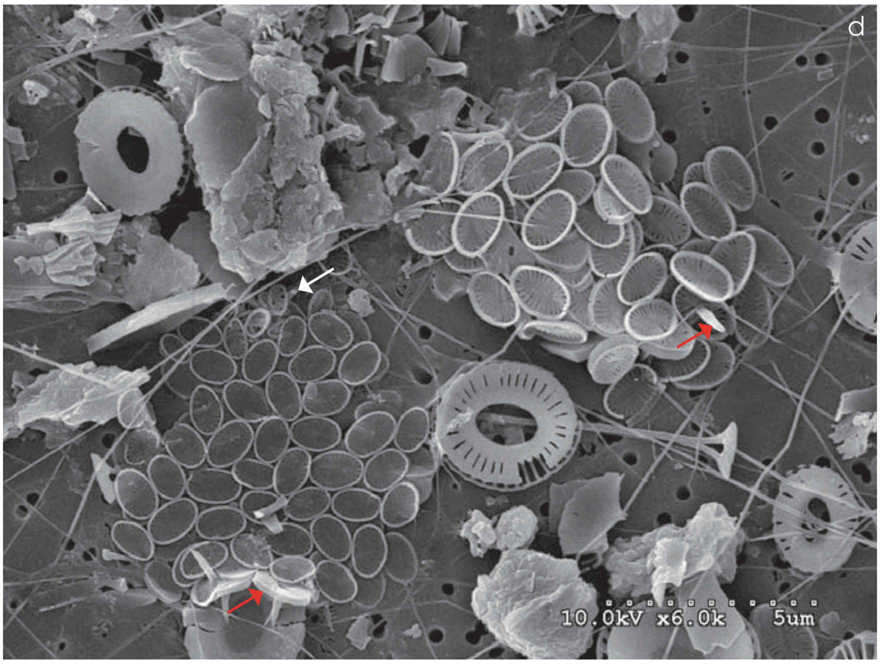
M. adriaticus



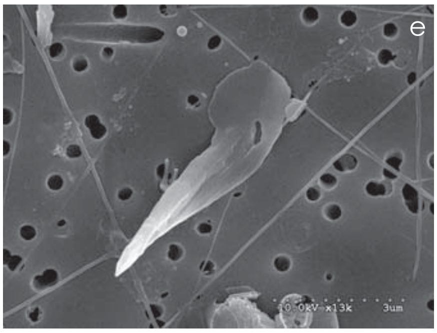
M. adriaticus



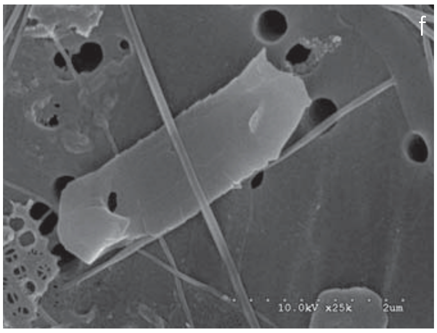
M. adriaticus



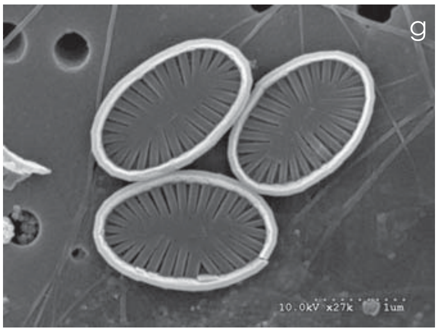
Ophiaster spp.

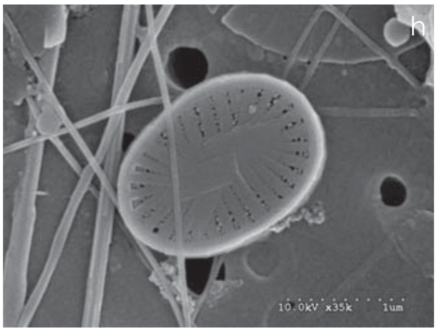


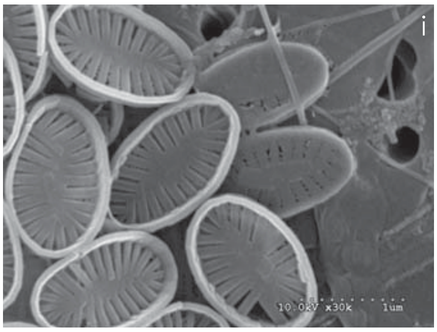
Ophiaster spp.



Ophiaster spp.







Ophiaster spp.

PLATE 8 - Syracosphaeraceae: *Michelsarsia & Ophiaster*

O. hydroideus

To classify the genus *Ophiaster* up to species rank requires whole coccospheres. Within the maximum flux of *Ophiaster* different species were revealed. The sample of *O. hydroideus* was found in CB 3(#15).

O. cf formosa

Most probably the image on the right represents a sphere of *O. formosa*. It was found in CB 3 (#15).

Image f) Plate 9 shows exothecal (white arrow).

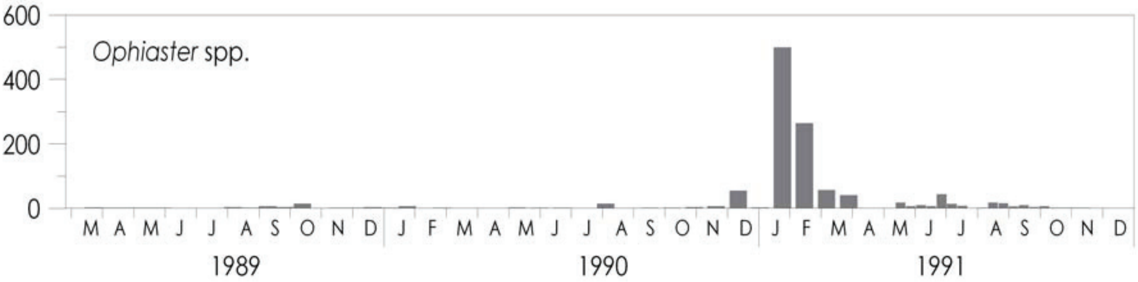
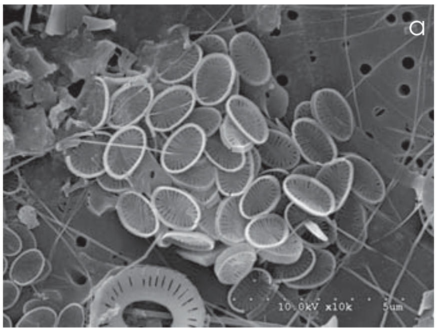
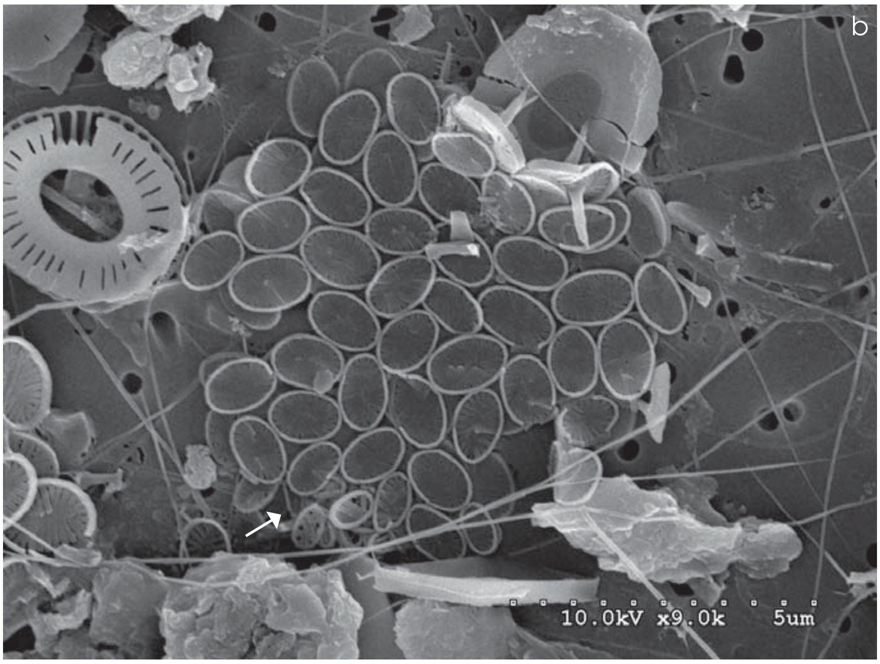


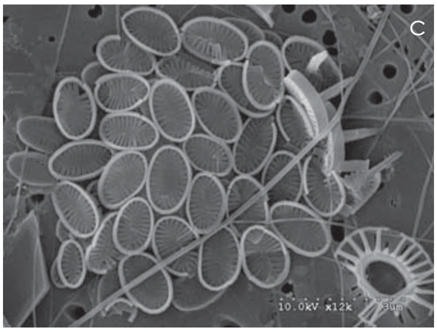
Fig. 7.10: Flux of *Ophiaster spp.* off Cape Blanc during the sampling period 1989 to 1991 (CB 2 to CB 4). The maximum in 1991 occurred during maximum of the total coccolith flux



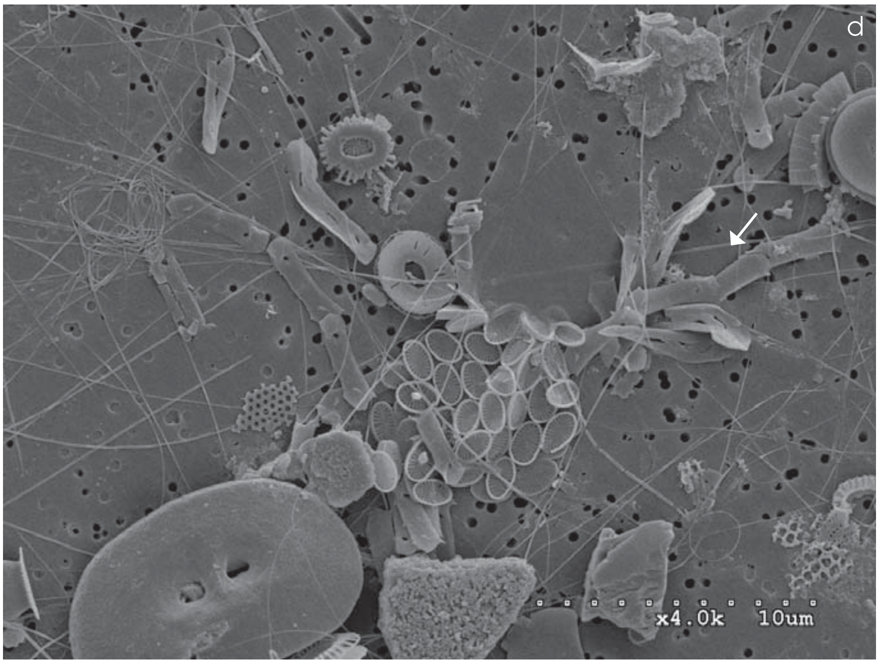
Ophiaster spp.



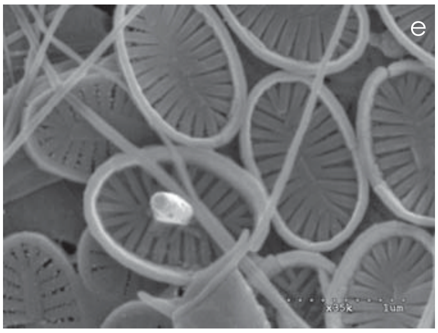
Ophiaster spp.



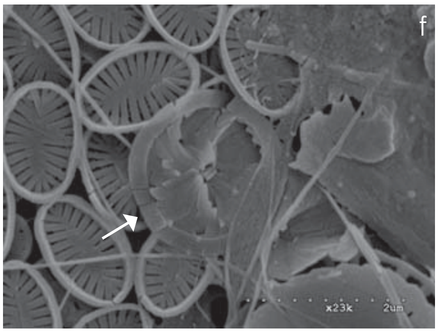
Ophiaster spp.



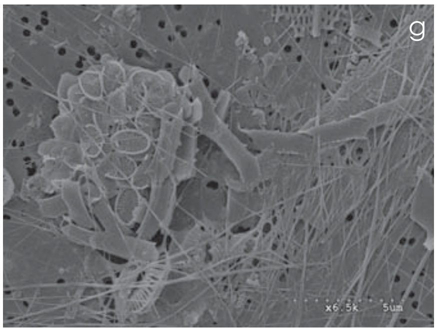
Ophiaster hydroideus



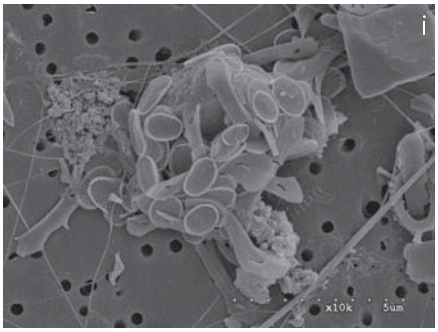
Ophiaster spp.



Ophiaster spp.



Ophiaster



O. cf formosus

PLATE 9 - SYRACOSPHAERA: *OPHIASTER*

Syracosphaera

Small *Syracosphaera* species that were not further classified were found in all samples of both upwelling regions. In all samples species of *Syracosphaera* were found. Even the speciefic species changed from sample to sample, in general same number of *Syracosphaera* species were present at both upwelling regions revealing a divers composition (Fig. 7.11).

The genus *Syracosphaera* is diverse with forms small as *S. nana* (1.4–1.6 µm) and *S. anthos* (2.2–2.8 µm) and large forms like *S. pulchra* (5.2– 5.6 µm), *S. lamina* (3.4–3.8 µm), and *S. tumularis* (3.5–3.8 µm) (Cros, 2001). To identify the small coccoliths up to species level is hard, especially if only single coccoliths are present and/or working without a SEM.

S. nodosa

S. nodosa was found in almost each sample of Cape Blanc, from spring 1990 until fall 1991 (CB3 and CB4), but was seldom in 1988 to 1989. *S. nodosa* was found by far less frequent off Chile (only one fourth of the samples) regardless of the prevailing oceanic condition.

The image d, f) in Plate 10 shows the exothecal coccoliths of *S. nodosa* being well preserved.

S. nana

S. nana was frequently present in the samples from Cape Blanc; however, a noticeable decrease in occurrence during the CB 2 deployment (1989) exists. Off Chile, the species was found consistently throughout the deployment regardless the oceanic prevailing condition, but all in all only in one third respectively one fourth of the samples.

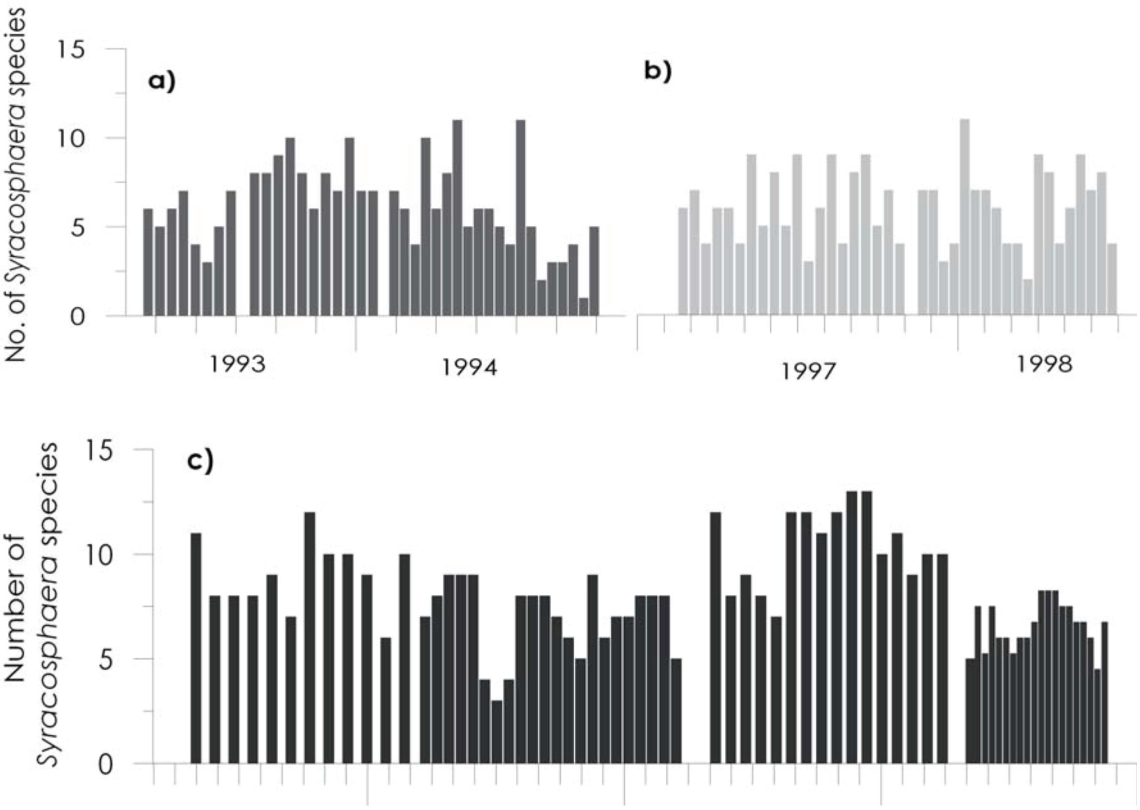
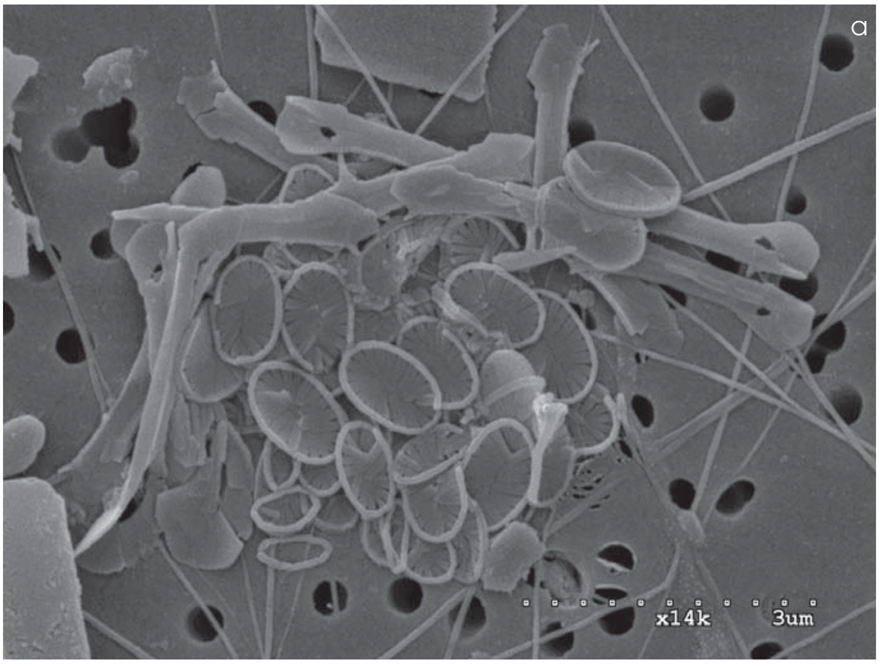
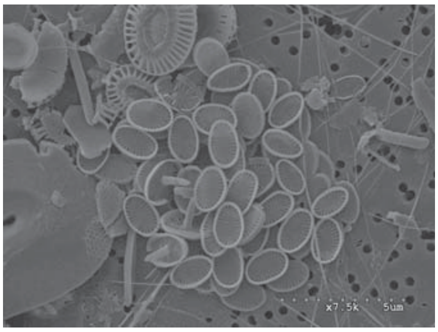


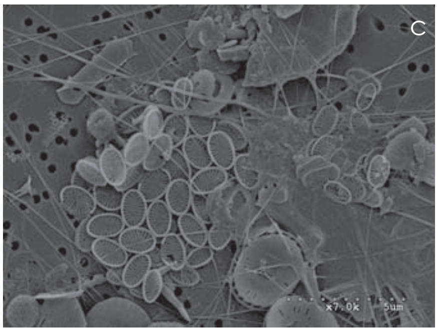
Fig. 7.11: The amount of identified species of the genus *Syracosphaera* within the samples of the sediment traps **(a)** off Cape Blanc (CB 1 to CB 4 **(b)** off Chile ('normal' condition) and **(c)** off Chile during El Niño



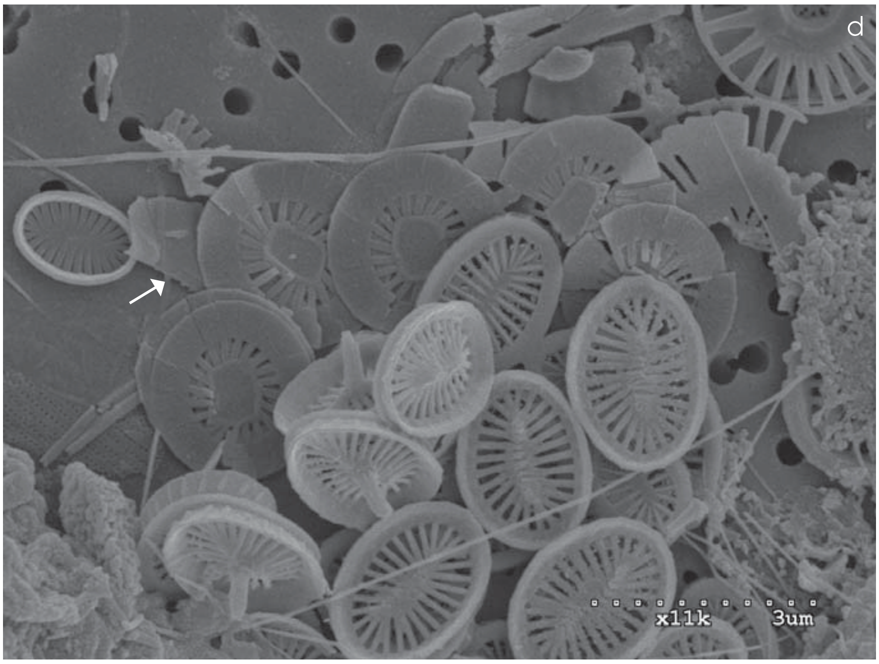
Ophiaster spp.



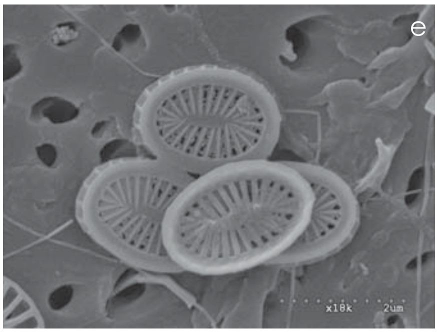
Ophiaster spp.



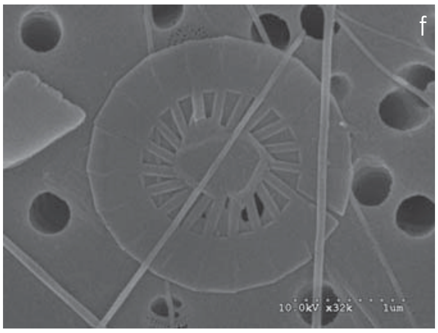
Ophiaster spp.



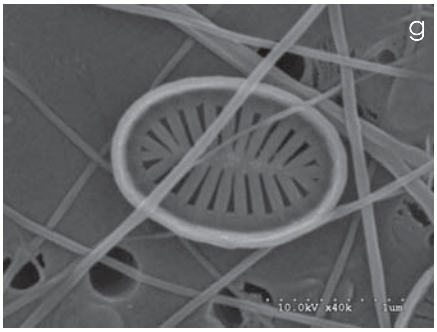
S. nodosa



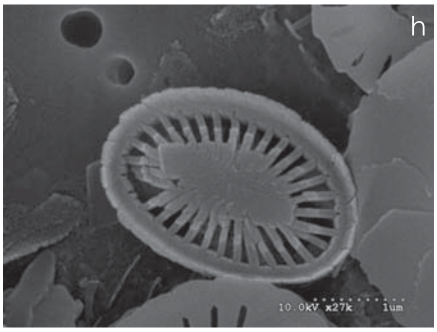
S. nodosa



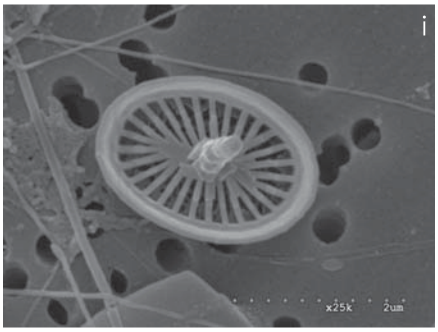
S. nodosa



S. nana



S. anthos



S. anthos

PLATE 10 - SYRACOSPHAERACEAE: *OPHIASTER & SYRACOSPHAERA*

S. anthos

S. anthos was found in almost every sample off Cape Blanc (68 out of 71). Noteworthy, is the maximum flux of *S. nana* coinciding with maximum (total) coccolith flux off Cape Blanc in winter 1990/1991 (Fig. 7.12). Off Chile, *S. anthos* was also a common species.

S. tumularis

S. tumularis was frequently found off Cape Blanc with a distinct maximum flux in 1991 (22.4x10^7 coccoliths $m^{-2}d^{-1}$). In contrast off Chile *S. tumularis* was rare during 'normal' oceanic condition. In samples of the El Niño interval the frequency of *S. tumularis* occurrence increased slightly but not the absolute fluxes (Fig. 7.13).

In plate 10 further fragile exothecal coccoliths of *S. anthos* (c), *S. lamina* (e), and *S. tumularis* (f) are presented.

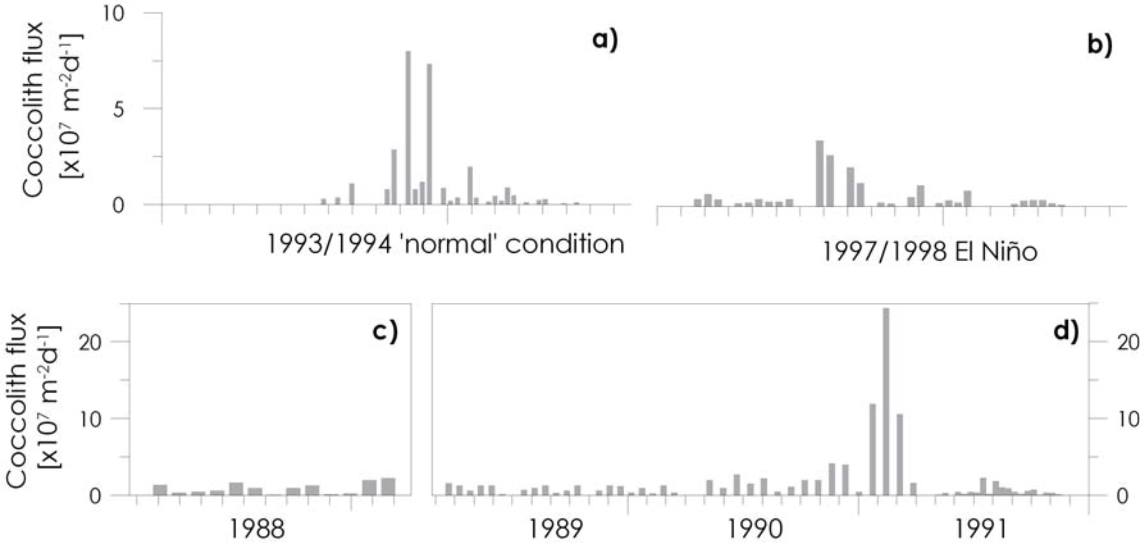


Fig. 7.12: **(a)** Flux of *S. anthos* off Chile during 'normal' oceanic condition, **(b)** during El Niño, **(c)** off Cape Blanc in 1989 (CB1), and **(d)** during the sampling period 1989 to 1991 (CB 2 to CB 4)

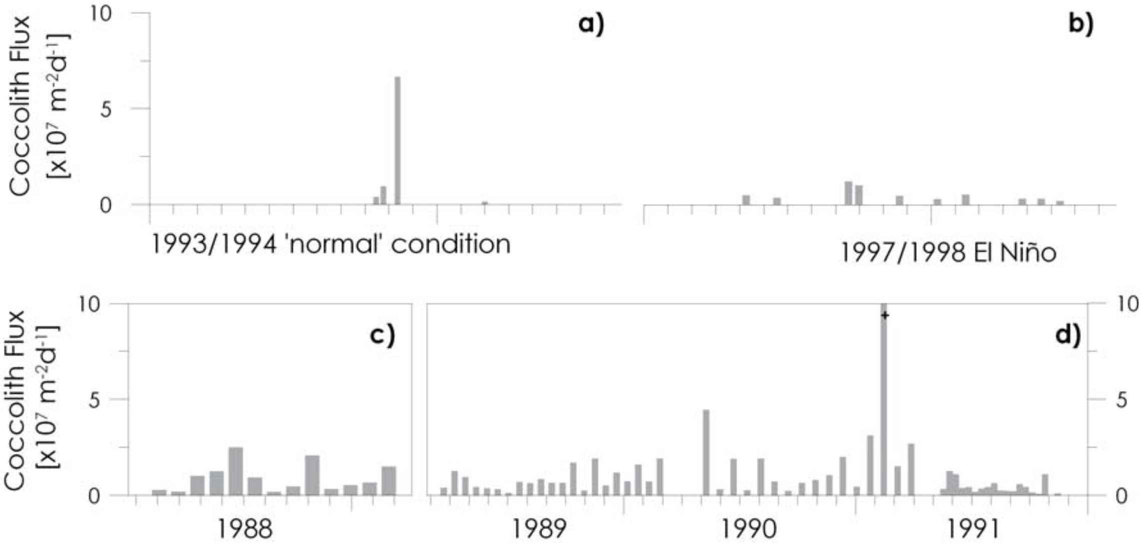
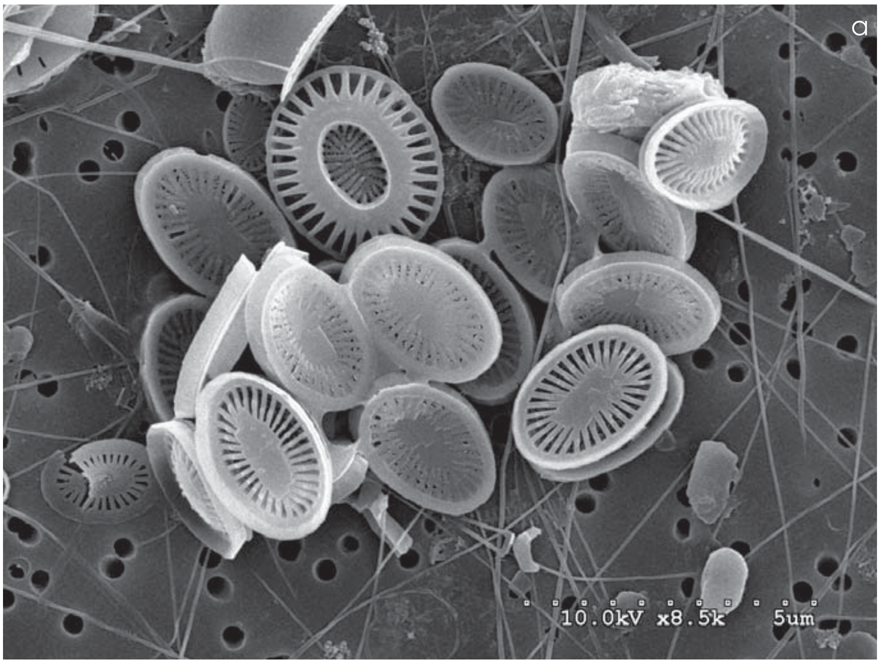
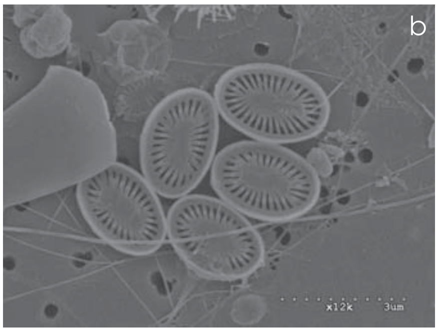


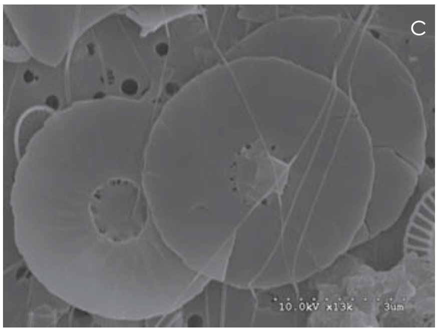
Fig. 7.13: **(a)** Flux of *S. tumularis* off Chile during 'normal' oceanic condition, **(b)** during El Niño, **(c)** off Cape Blanc in 1989 (CB1), and **(d)** during the sampling period 1989 to 1991 (CB 2 to CB 4) (+ maximum flux 22.35x10^7 $m^{-2}d^{-1}$



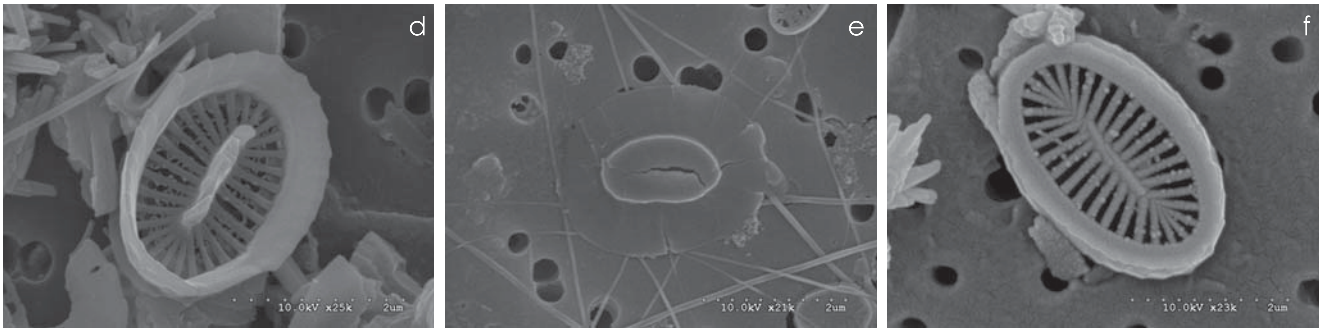
S. anthos



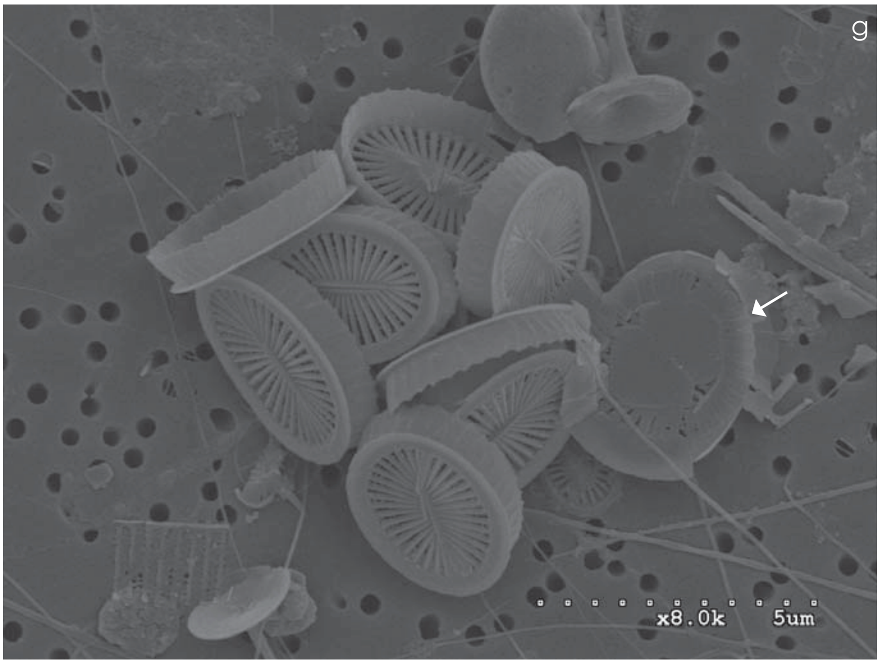
S. anthos



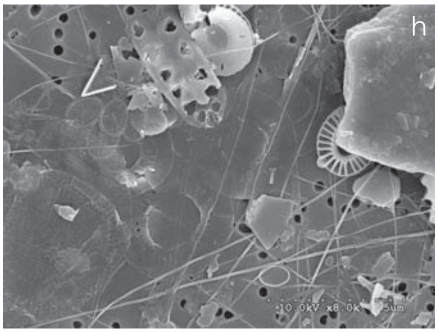
S. anthos



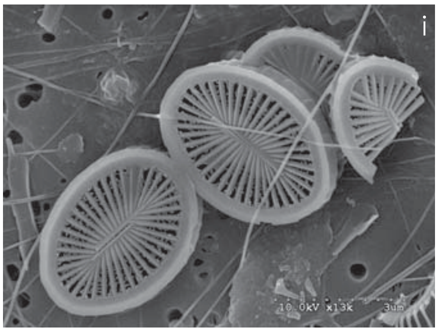
S. lamina



S. tumularis



S. tumularis



S. tumularis

PLATE 11 - SYRACOSPHAERACEAE: *SYRACOSPHAERA NODOSA GROUP*

S. banockii

S. banockii was found only off Cape Blanc in eight samples with four times in the CB1, thus the more coastal located sediment trap deployment.

S. orbiculus

The displayed species was only found in CB3 and only due to the intense taxonomic study of these samples.

S. delicata

S. delicate was identified in half of the Cape Blanc samples with a higher frequency during the CB3 and CB4 deployment. Off Chile, *S. delicate* was found only in samples represent 'normal' oceanic condition.

S. pulchra

S. pulchra is the dominant species of the genus *Syracosphaera* in respect of frequency, flux and importance for the coccolith derived carbonate in both upwelling regions studied. *S. pulchra* was nearly present in each sample (only missed twice in the different sampling periods) (Fig. 7.14).

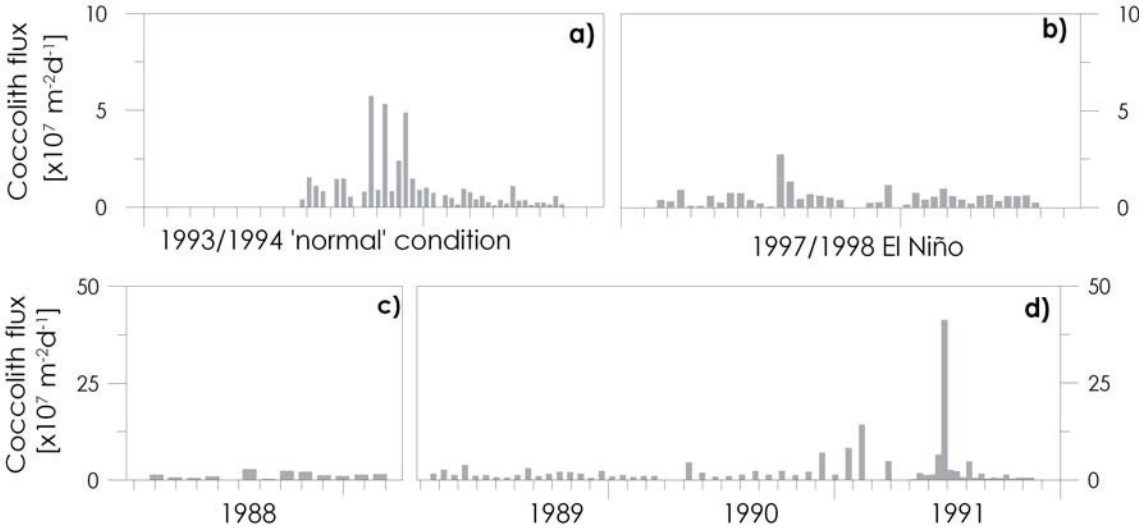
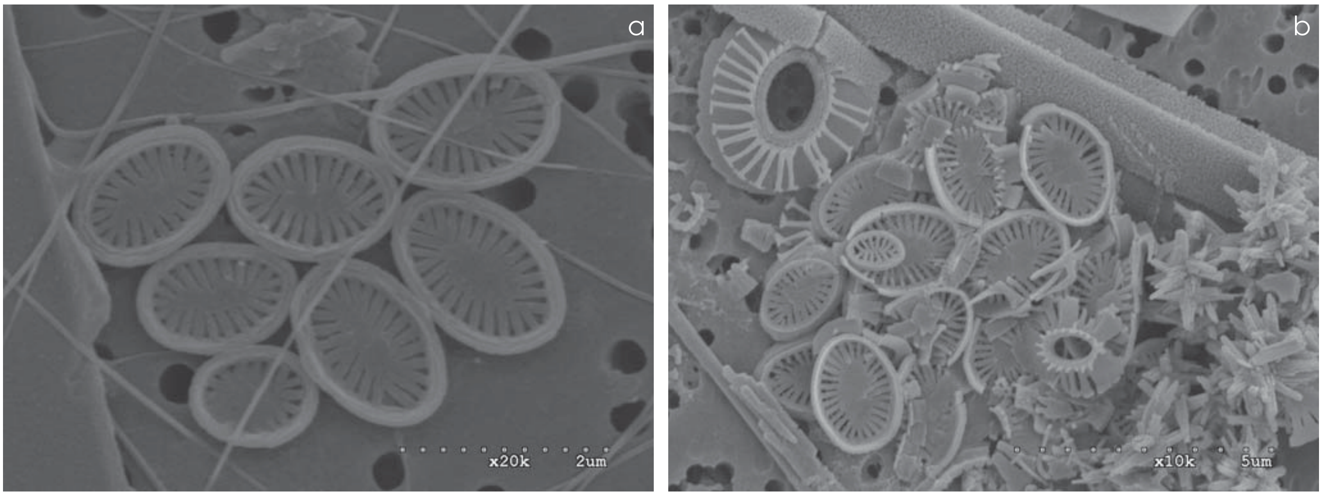
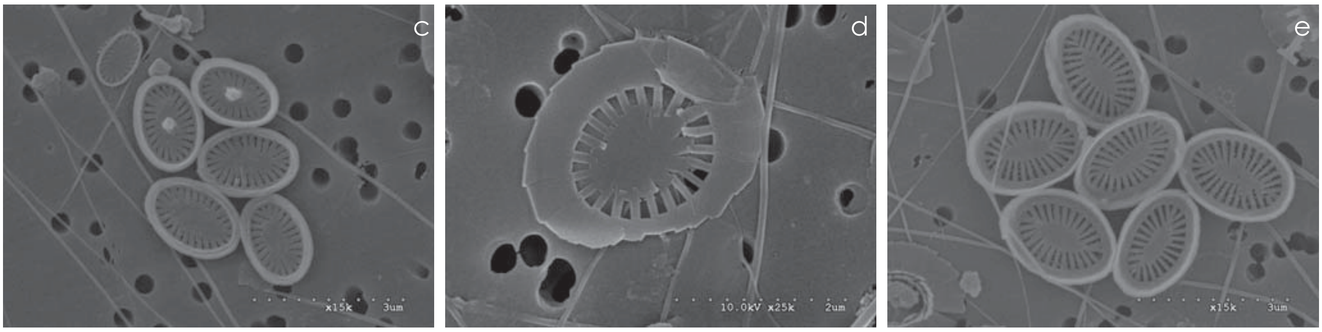


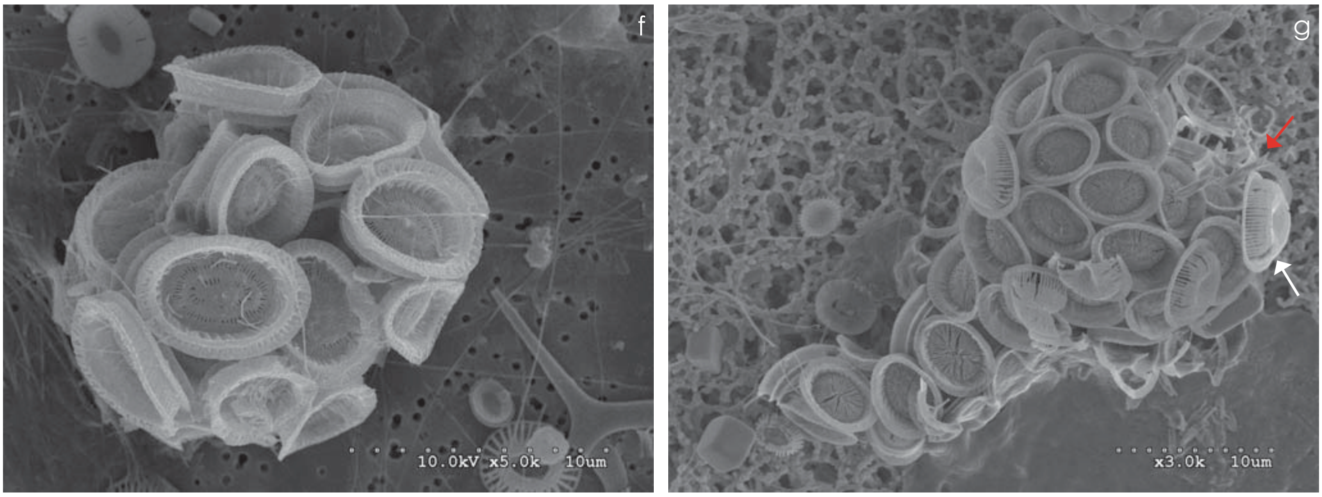
Fig. 7.14: **(a)** Flux of *S. pulchra* off Chile during 'normal' oceanic condition, **(b)** during El Niño, **(c)** off Cape Blanc in 1989 (CB1), and **(d)** during 1989–1991 (CB2–CB4)



S. banockii *S. cf orbiculus*



S. banockii *S.delicata* *S. orbiculus*



S. pulchra

S. pulchra

PLATE 12 - SYRACOSPHAERACEAE: *SYRACOSPHAERA* NODOSA & PULCHRA GROUP

S. pulchra

The sizes of 55 basin-shaped endothecal heterococcoliths (from Cape Blanc samples) show a clear unimodal distribution pattern (Fig. 7.15). In general, coccolith length in the samples varies from 4.3–7.5 µm with mean of 6.0 µm. Coccolith width in the samples varies from 3.1–5.3 µm with an overall mean of 4.2 µm. The lengths and widths are strongly correlated to each other, with a correlation coefficient of r^2=0.91. The sizes are in the same range as previously observed in the Canary Islands region (Baumann and Sprengel, 2000) and in other oceanic areas (Geisen *et al.*, 2002).

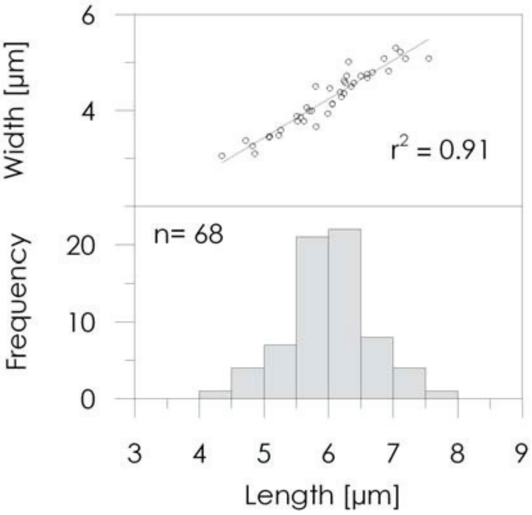
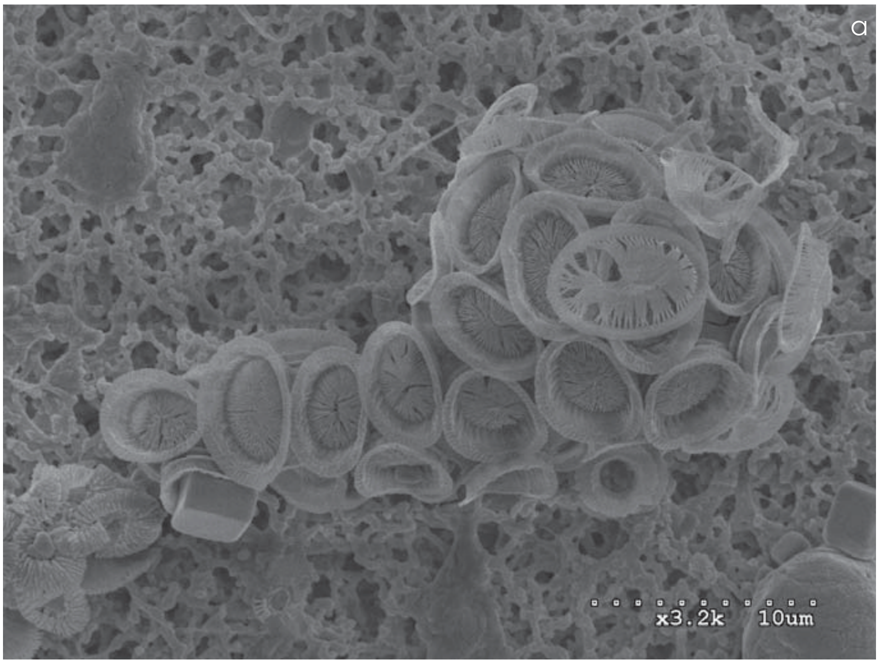
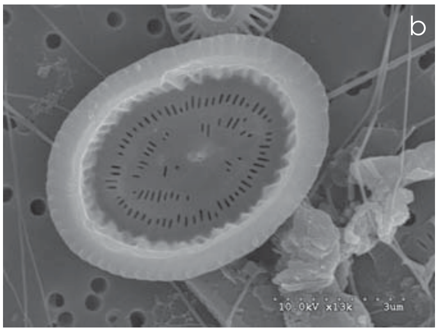


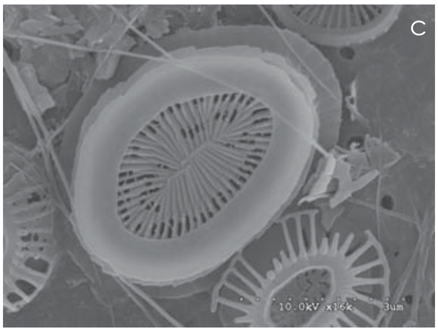
Fig. 7.15 : Scatter plot and frequency distribution (at 0.5 µm intervals) of the endothecal heterococcoliths of *S. pulchra* of Cape Blanc samples



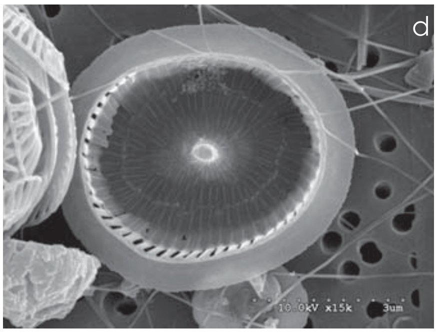
S. pulchra



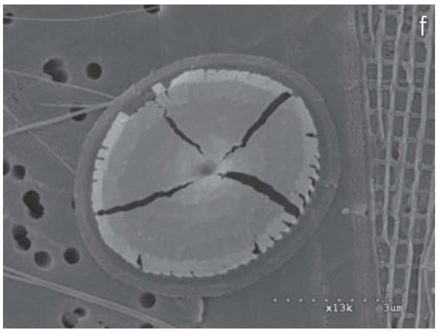
S. pulchra

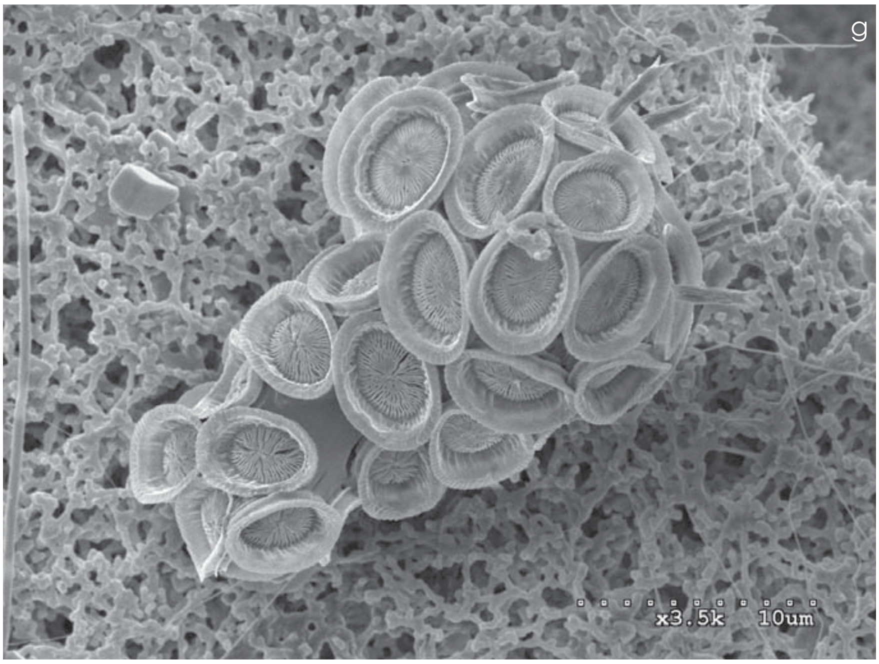


S. pulchra

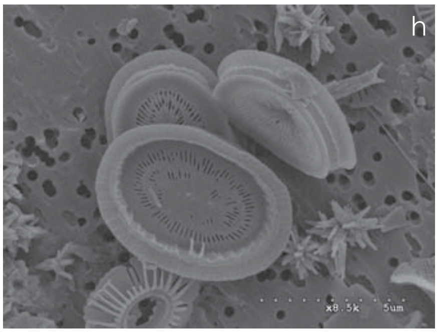


S. pulchra

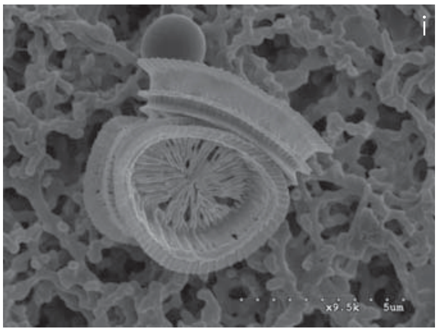




S. pulchra



S. pulchra



S. pulchra

Plate 13 - Syracosphaeraceae: *Syracosphaera* pulchra group

S. histrica

S. histrica is a rare *Syracosphaerales* but was more often found off Cape Blanc than off Chile.

S. pirus

During the counts, the species was found only in one sample derived from NW–Africa.

S. prolongata

S. prolongara was found more frequently in Cape Blanc samples than in Chile samples. Noticeable is the complete lack of *S. prolongata* off Chile during time of low overall coccolith flux regardless of the presence of El Niño (Fig. 7.16).

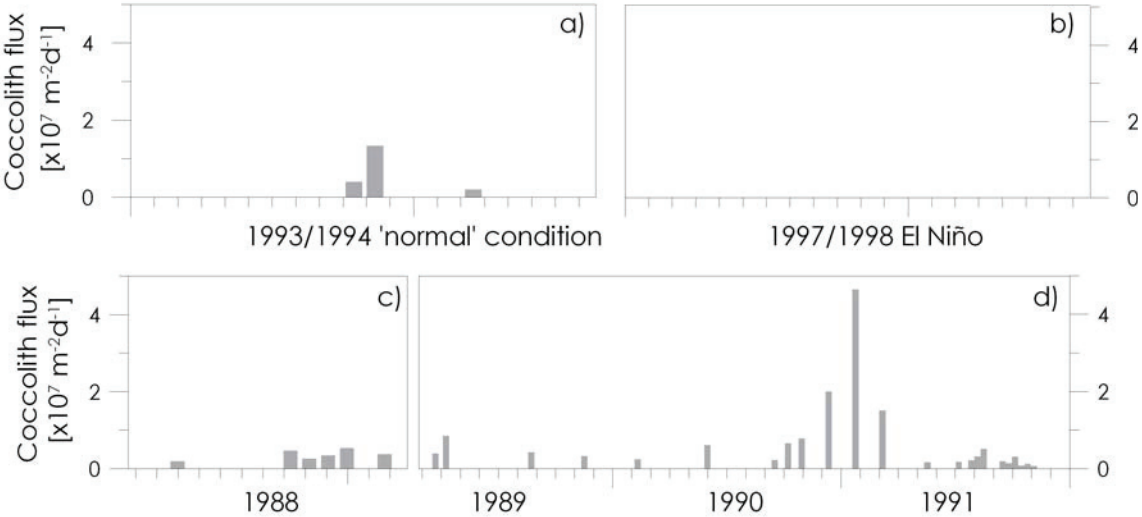
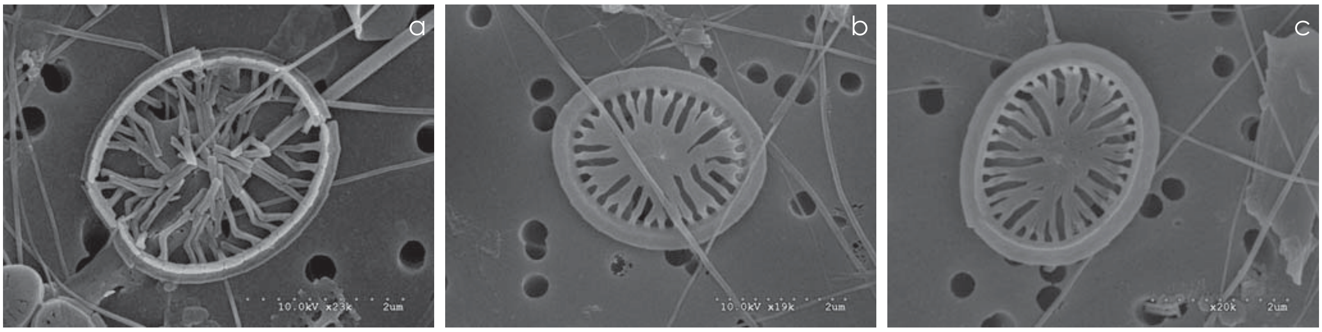
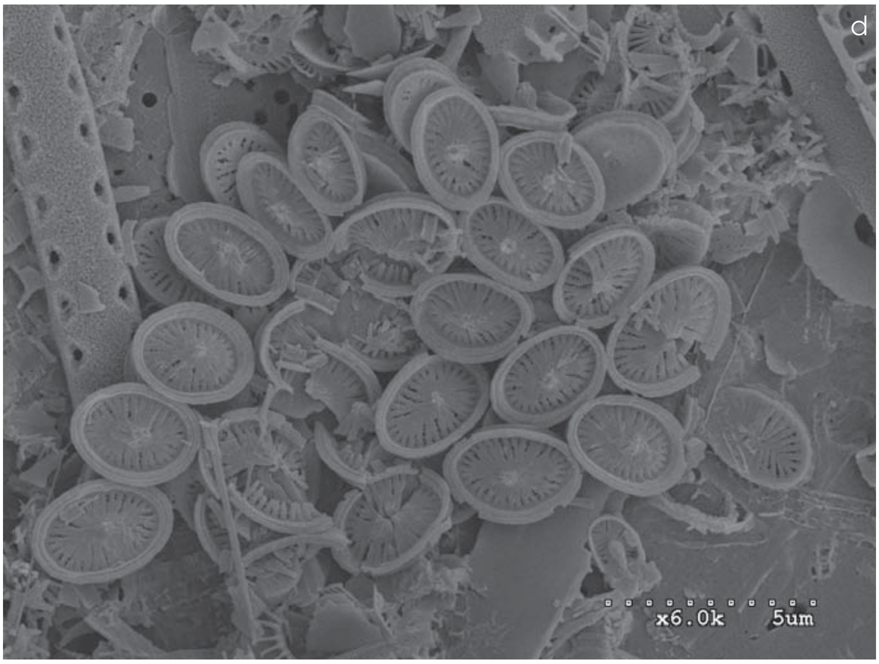


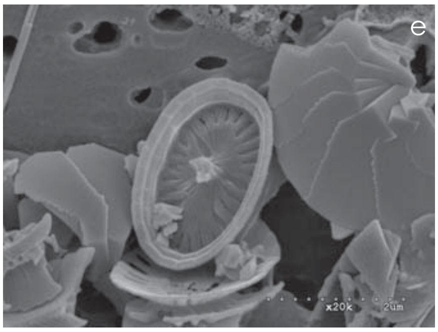
Fig. 7.16: **(a)** Flux of *S. prolongata* off Chile during 'normal' oceanic condition, **(b)** during El Niño, **(c)** off Cape Blanc in 1989 (CB1), and **(d)** during the sampling period 1989–1991



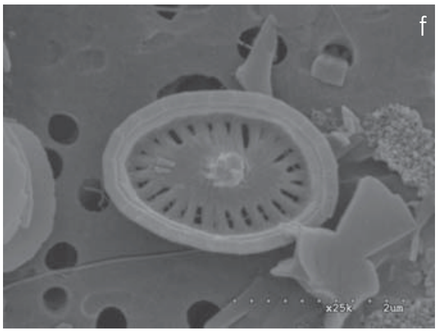
S. histrica



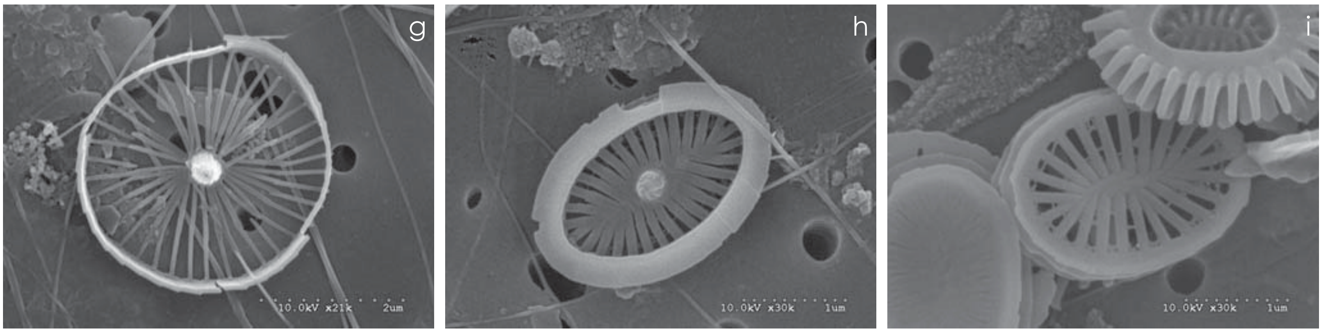
S. histrica



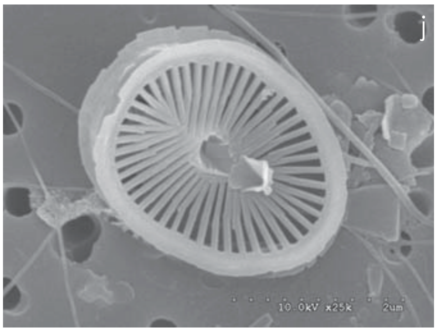
S. histrica



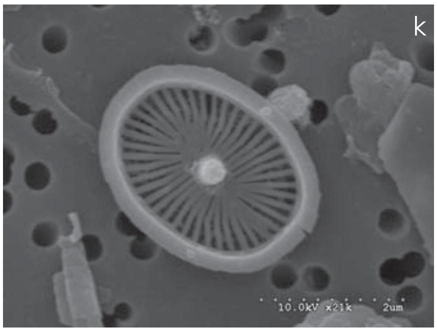
S. histrica



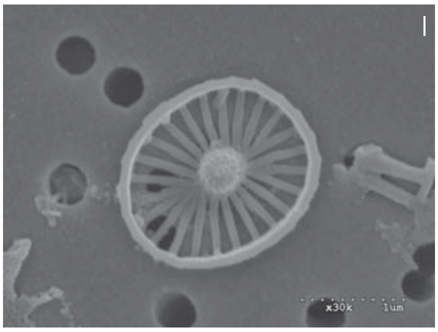
S. prolongata



S. prolongata



S. prolongata



S. pirus

Plate 14 - Syracosphaeraceae: *Syracosphaera* pulchra group

S. noroitica

The continuous presence of *S. noroitica* during fall and winter 1990/91 is outstanding. Ten out of sixteen samples arise from that time.

S. cf type G

The documented species were found in samples of NW-Africa. In Plate 15 Fig g) an exothecal (left) and a body coccolith (right) of *Syracosphaera* cf *type D* of Kleijne (1993) is shown. During the counts the species were not distinguished and merged to *Syracosphaera spp.*.

S. cf type D

As *S.* cf *type G*, *S.* cf *type D* was identified in samples of Cape Blanc for photo documentation. In Plate 15 Figure g) a exothecal besides a body coccolith is shown.

S. corolla

S. corolla, a rather large *Syracosphaera* species was commonly present in the Cape Blanc samples. During summer 1990 no specimen was found off Cape Blanc (Fig. 7.17). The highest flux was recorded off Chile during 'normal' oceanic condition and maximum total coccolith flux.

In Plate 15 Fig h) j) exothecal of *S. corolla* and body coccoliths are shown in Fig i).

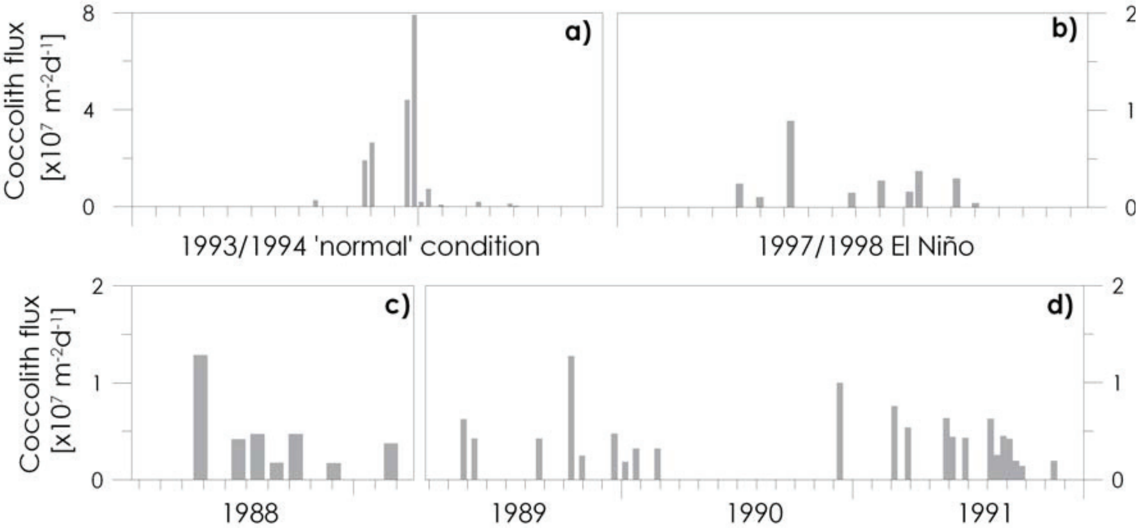
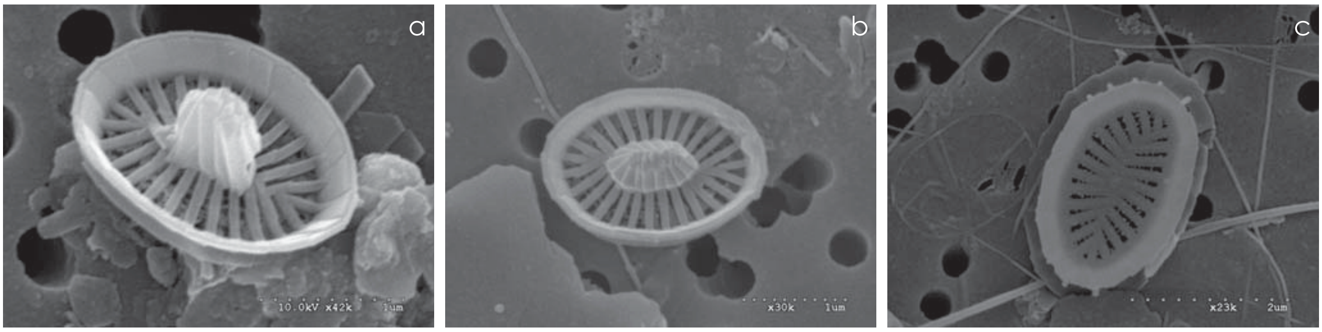
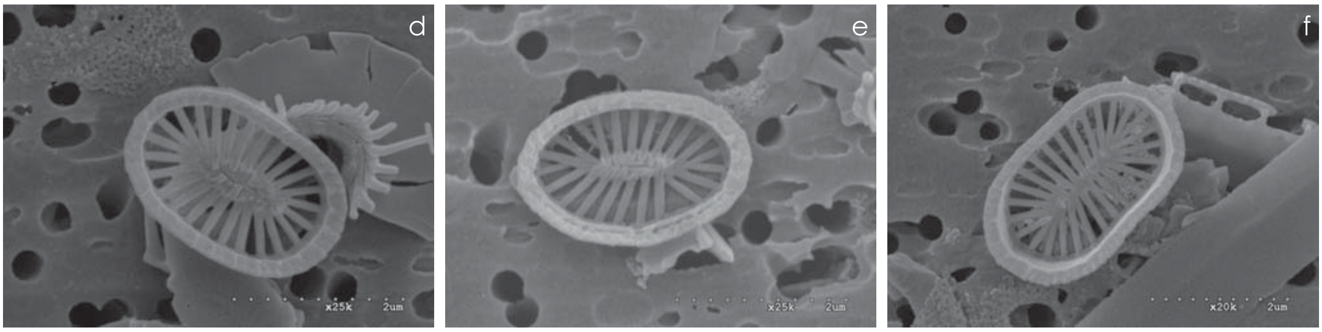


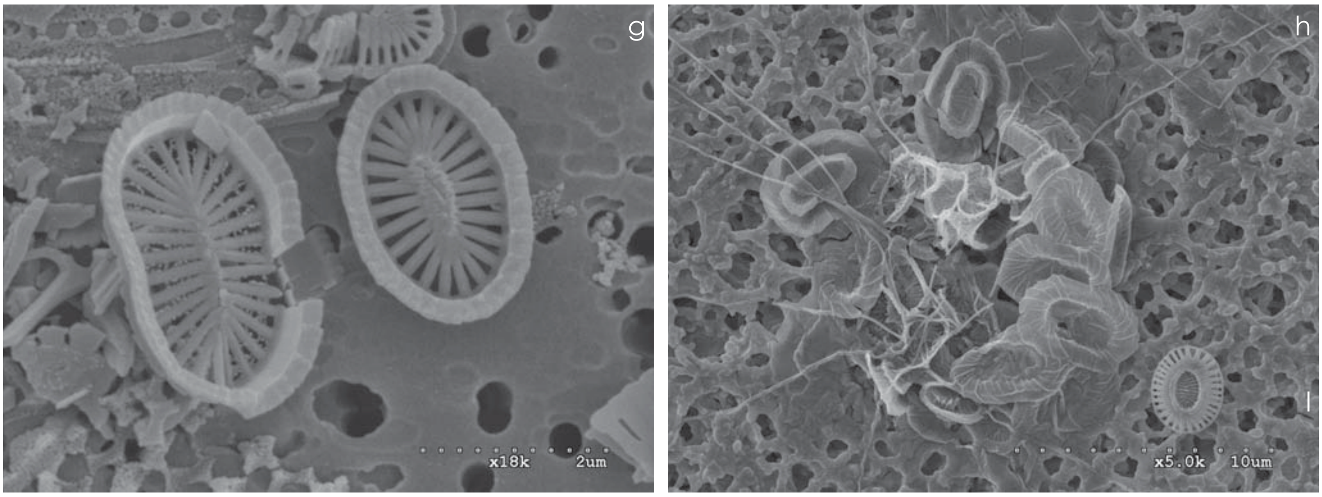
Fig. 7.17: **(a)** Flux of *S. corolla* off Chile during 'normal' oceanic condition, **(b)** during El Niño, **(c)** off Cape Blanc in 1989 (CB1), and **(d)** during the sampling period 1989 –1991



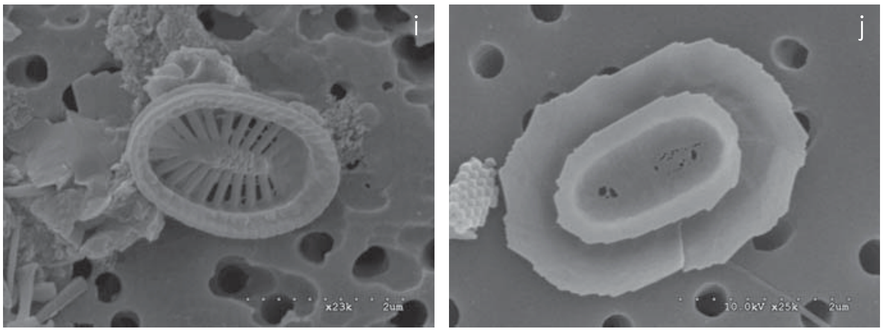
S. noroitica *S. cf type G* *S. dilata group*



S. cf type D



S. cf type D *S. corolla*



S. corolla *S. corolla*

PLATE 15 - SYRACOSPHAERACEAE: *SYRACOSPHAERA* PULCHRA GROUP

S. molischii

Off Chile, *S. molischii* is found frequently, whereas the species was (rarely) found off Cape Blanc (Fig. 7.18). *S. molischii* was encountered regularly in different morphotypes (type I-III).

S. ossa

S. ossa was found in both upwelling regions but more frequent off Chile. More samples (half of the samples) of the El Niño study period exhibit the species whereas only in one fourth of the samples of the 'normal' time period the species was present. Off Cape Blanc, the frequent presence of *S. ossa* from fall 1990 until the end of the study is striking.

S. cf epigrosa

This species was found in a sample derived from Cape Blanc offshore, but was not present in the counting.

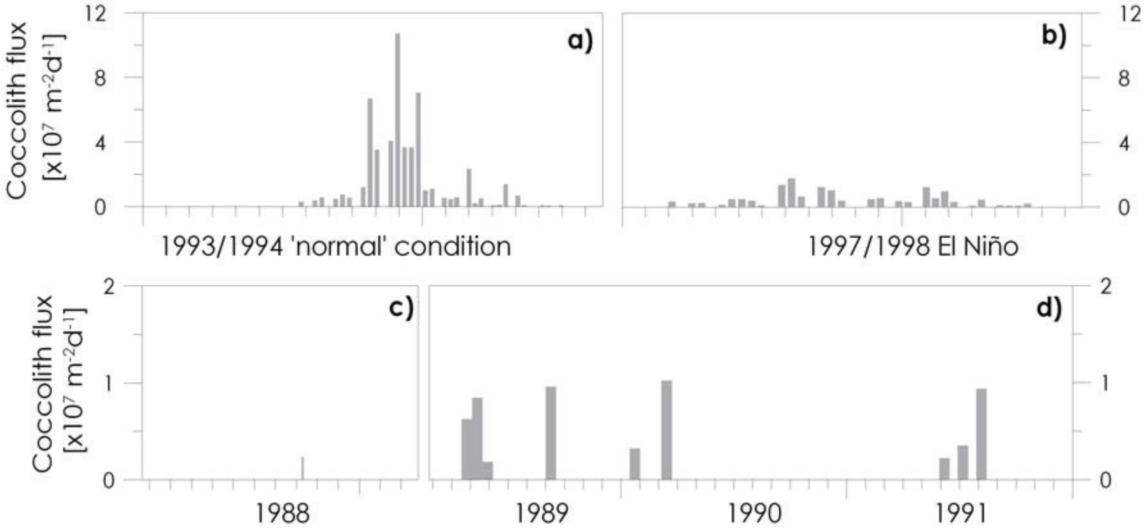


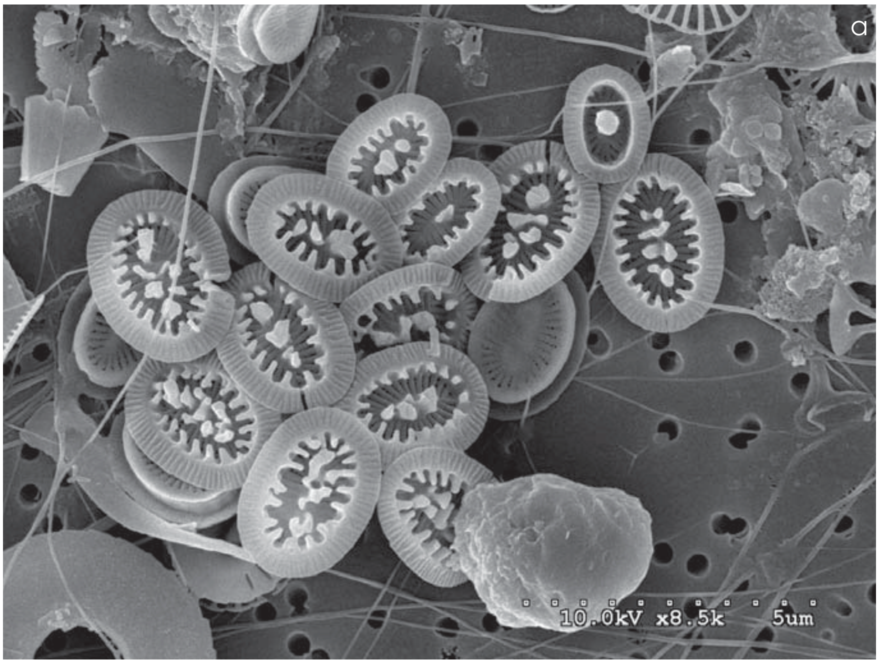
Fig. 7.18: **(a)** Flux of *S. molischii* off Chile during 'normal' oceanic condition, **(b)** during El Niño, **(c)** off Cape Blanc in 1989 (CB1), and **(d)** during the sampling period 1989–1991

S. corrugis

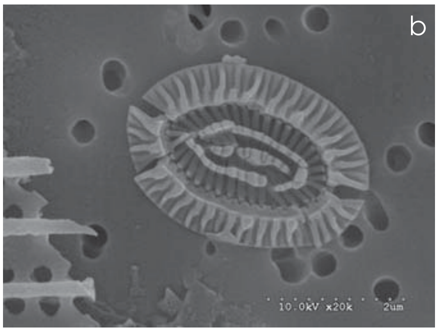
This species was found in a sample derived from Cape Blanc offshore, but was not found during the counting.

S. halldalli

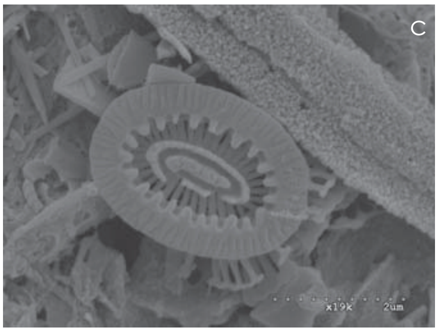
S. halldalli was found more often in samples derived from the Cape Blanc region than from Chile. Especially during spring and summer 1990 the species occurred frequently.



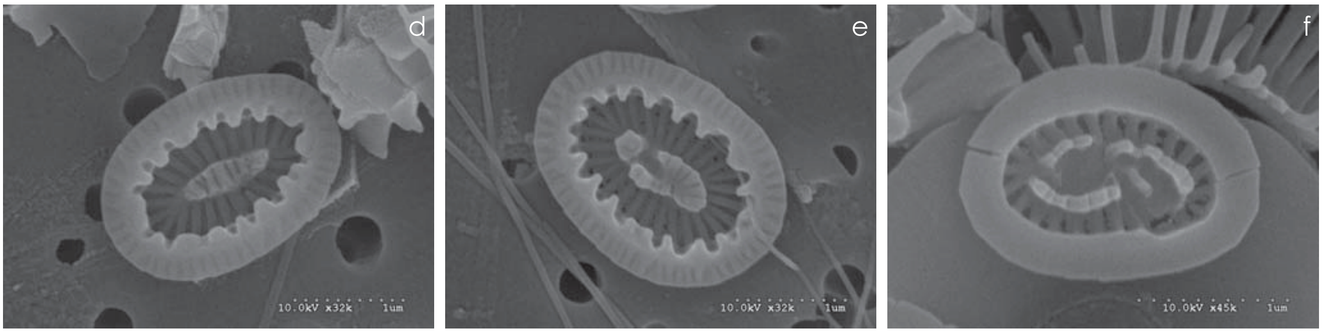
S. molischii type II



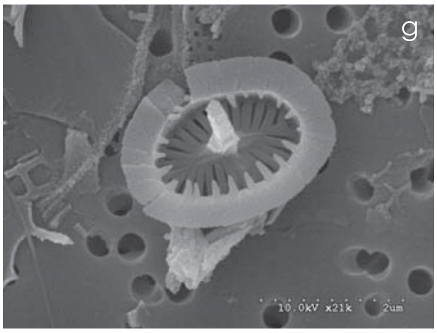
S. molischii type I



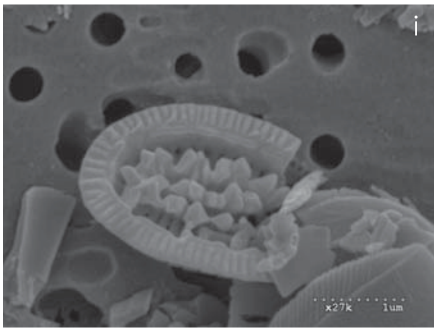
S. molischii type II



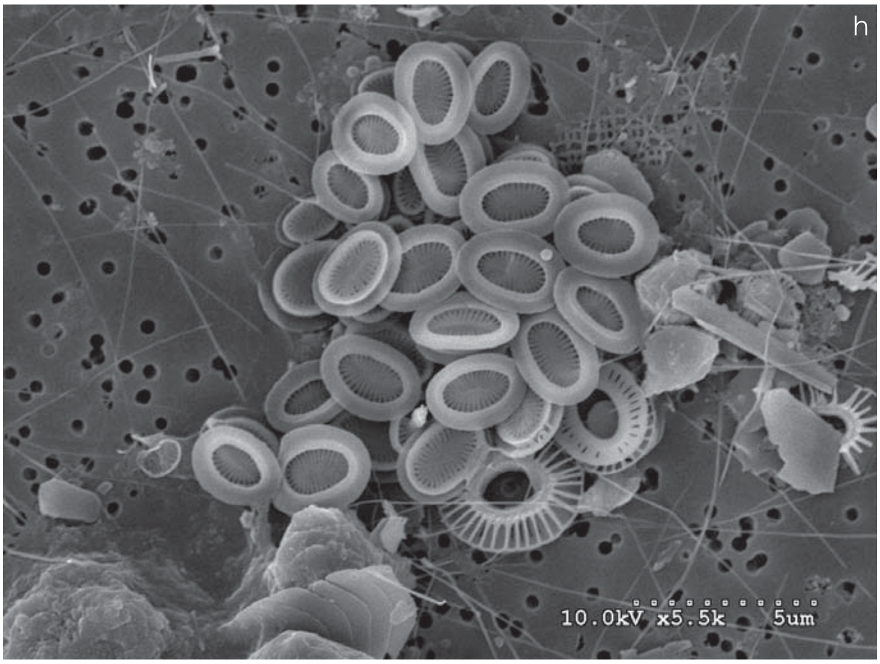
S. molischii type III



S. molischii



S. cf epigrosa



S. ossa

PLATE 16 - SYRACOSPHAERACEAE: *SYRACOSPHAERA* MOLISCHII GROUP

Slightly more species of the genus *Syracosphaera* were encountered in the Cape Blanc samples (Fig. 7.19). In addition, the frequency of the particular species within the two upwelling regions is different. Especially the more massive species such as *S. pulchra*, *S. tumularis*, and *S. prolongata* were found more often in samples of Cape Blanc than of Chile. *S. tumularis* revealed further a higher frequency in the Chile samples of the El Niño time period than of the 'normal' period. *S. ossa*, *S. borealis*, and *S. rotula* showed also different frequency during the two study periods of Chile (Fig. 7.19).

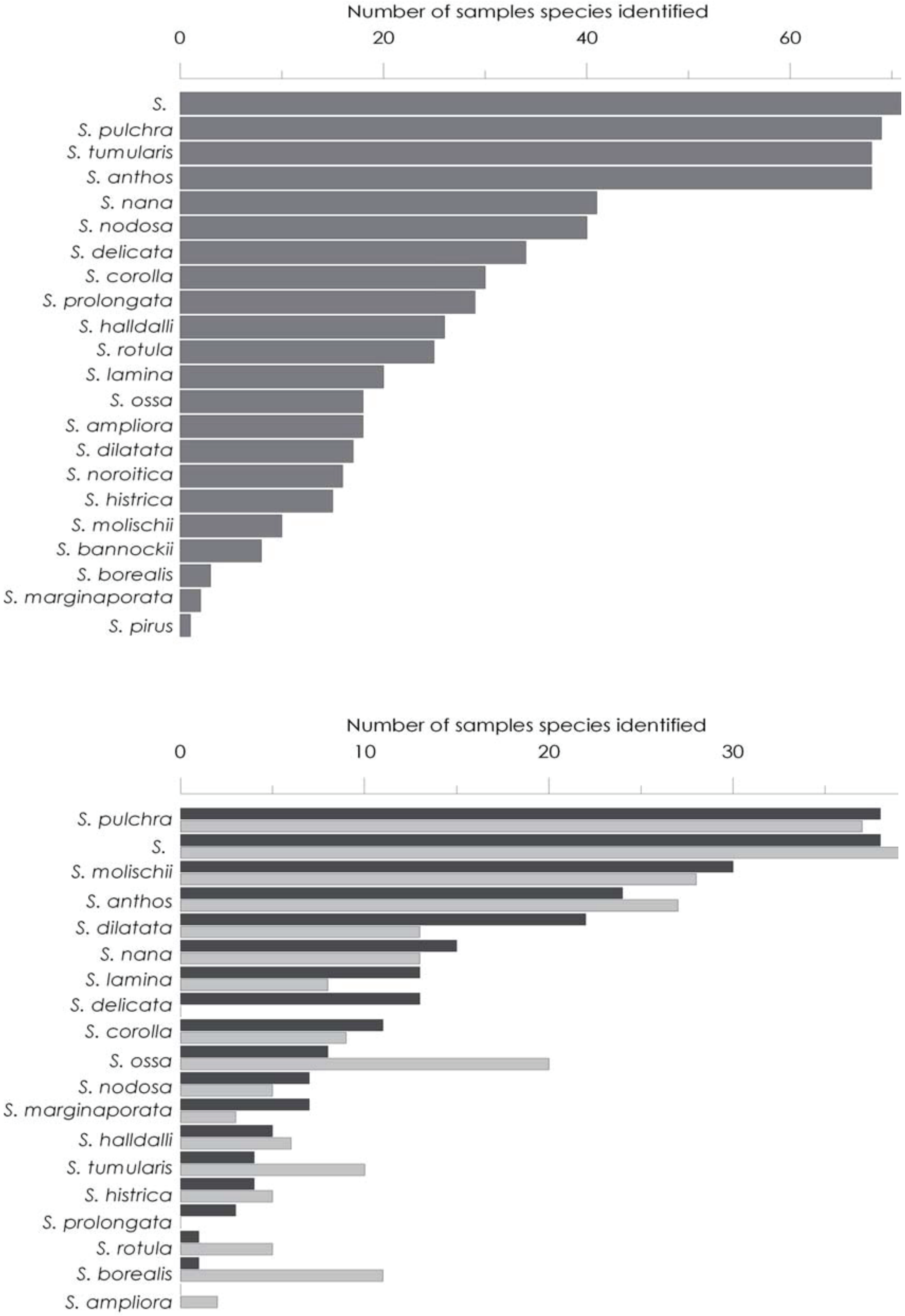
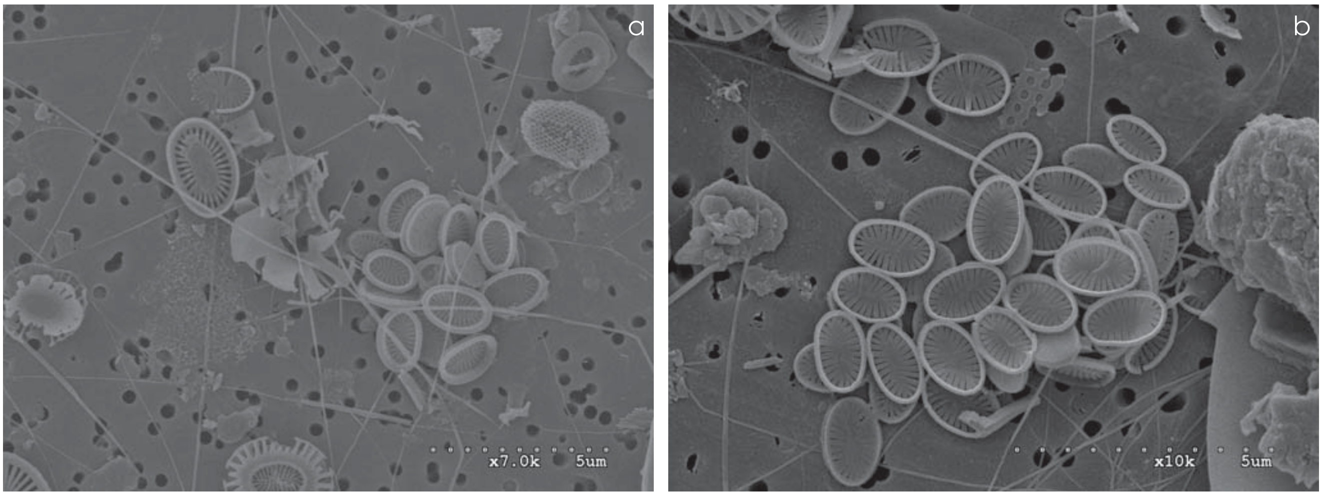
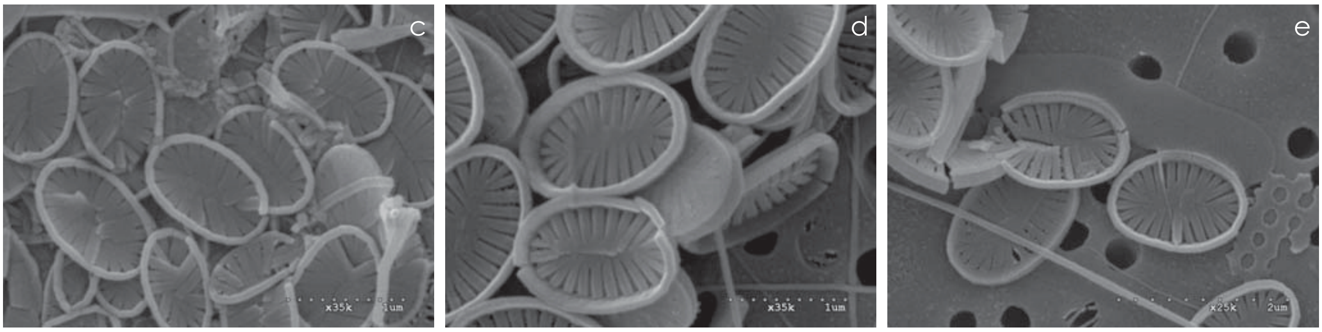


Fig. 7.19: **(a)**The frequencies of identified *Syracosphaera* species were found in the Cape Blanc samples. The samples off Cape Blanc (CB 1 to CB 4) amount to 71. **(b)** The frequencies of identified *Syracosphaera* species were found in samples of Chile. The samples during 'normal' oceanic condition (dark grey bars) amount to 38, the samples of the El Niño study period to 39 (light grey bars). In case of uncertainty or inability to identify a *Syracosphaera* to species level it was determined as *S.*



Syracosphaera Spp.

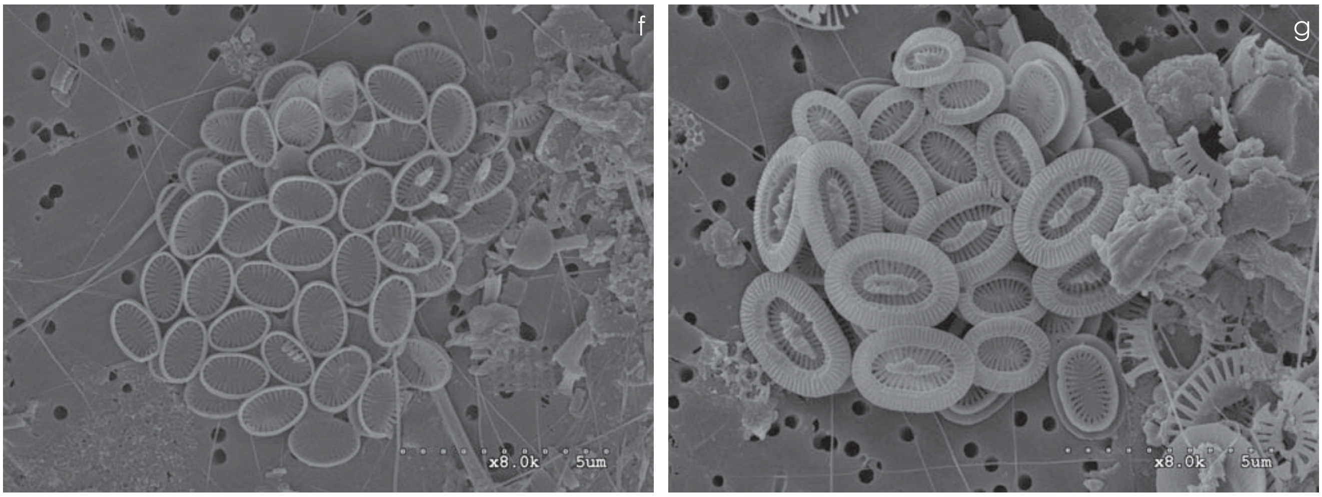
Syracosphaera Spp.



Syracosphaera Spp.

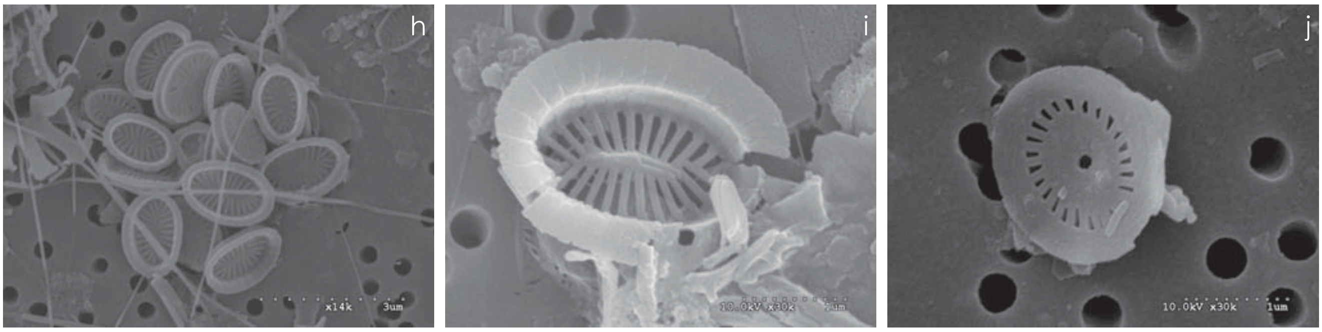
Syracosphaera Spp.

Syracosphaera Spp.



Syracosphaera Spp.

S. corrugis



Syracosphaera Spp.

S. halldalli

Syracosphaera Spp.

Plate 17 - Syracosphaeraceae: *Syracosphaera*

Syracosphaera nov. spec.

The species displayed in Plate 18 Fig. 7.a)–e) was found only in samples from Chile (CH3#14,#15,#17,#18). It maybe related to *S. borealis* because of the wide flange. Due to its form it may also be grouped to *S. marginaporata* and/or *S. rotula*.

Syracosphaera nov. spec.

In Plate 18 Fig f)–k) an undescribed coccosphere which was found repeatedly in the plankton samples off Cape Blanc is pictured. The coccoliths' width varied between 1.58 µm, 1.59 µm, and 1.89 µm, 1.94 µm and the length between 2.46 µm, 2.70 µm, and 2.92 µm.

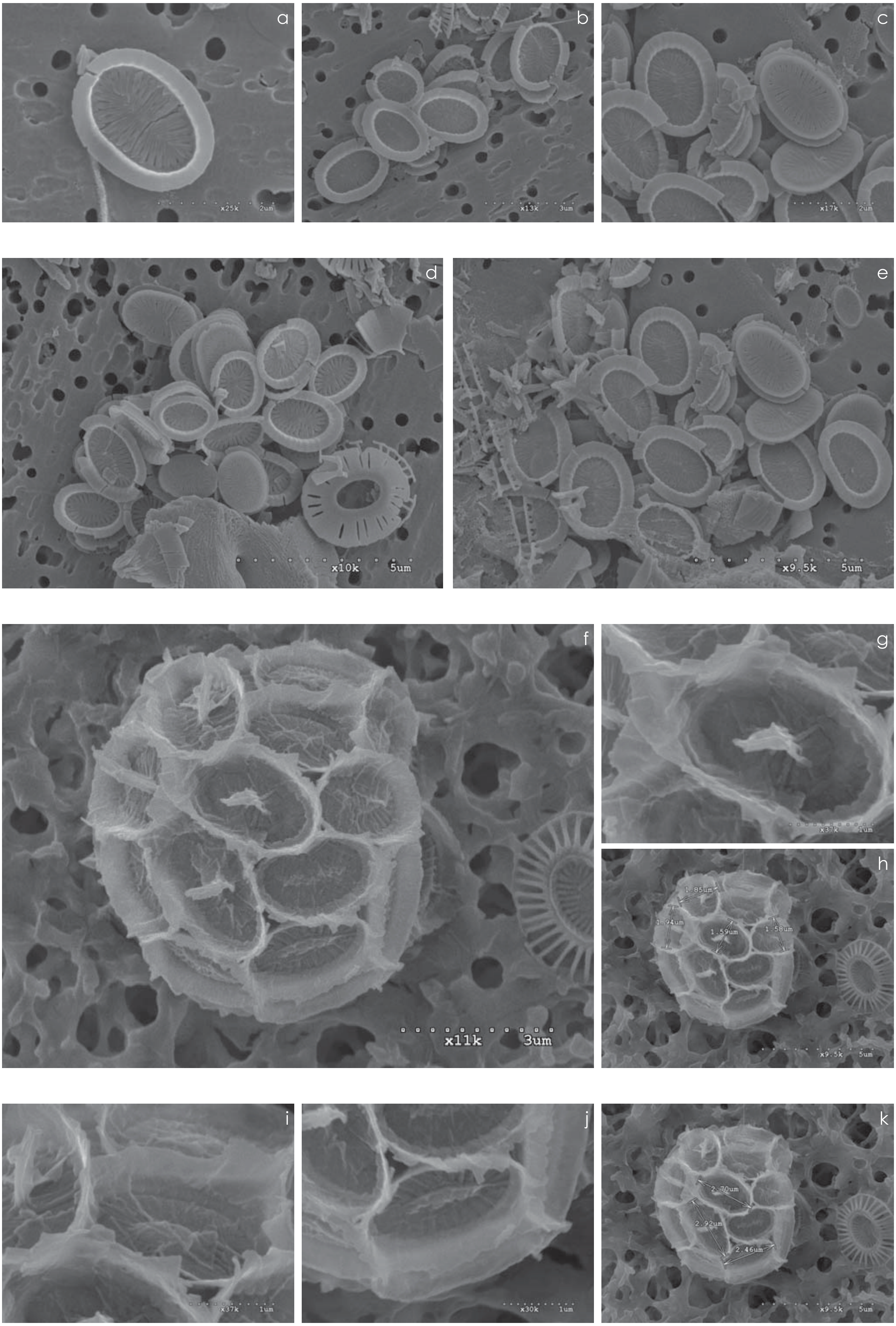


Plate 18 - Syracosphaeraceae: *Syracosphaera nov spec*

SYRACOSPHAERALES: *SYRACOSPHAERACEAE*: CORONOSPHAERA

Coronosphaera mediterranea

In both upwelling regions *C. mediterranea* were regularly found (off Cape Blanc in one third of the samples and off Chile in almost half of the samples). Besides the species *C. mediterranea*, *C. binodata* was (seldom) found.

SYRACOSPHAERALES: *CALCIOSOLENIACEAE*: CALCIOSOLENIA

Calciosolenia brasiliensis

C. brasiliensis was found in nearly all samples of both upwelling regions (except of three samples off Chile). In both region the fluxes of *C. brasiliensis* revealed similar pattern to the overal coccolith fluxes (Fig. 20).

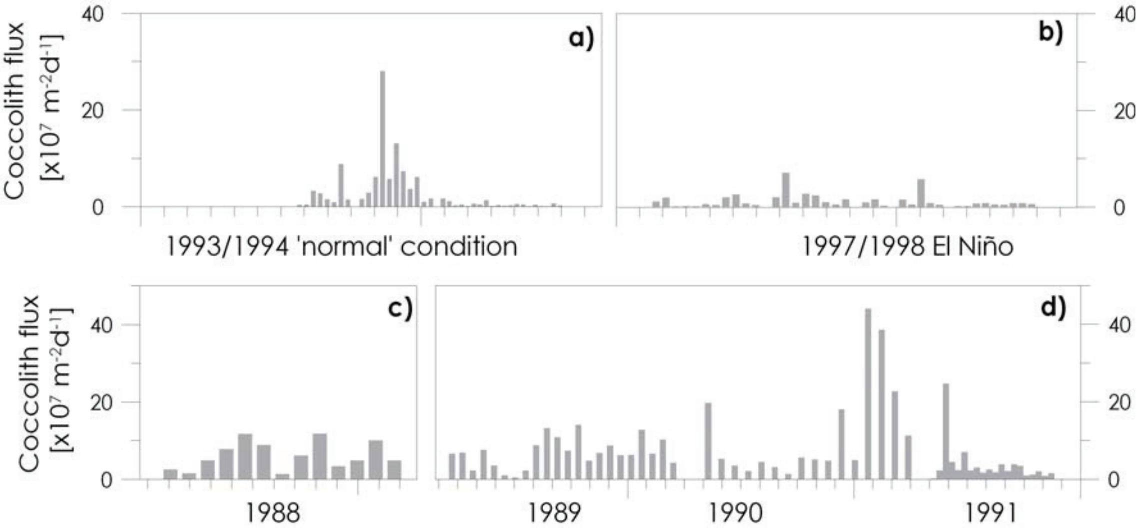
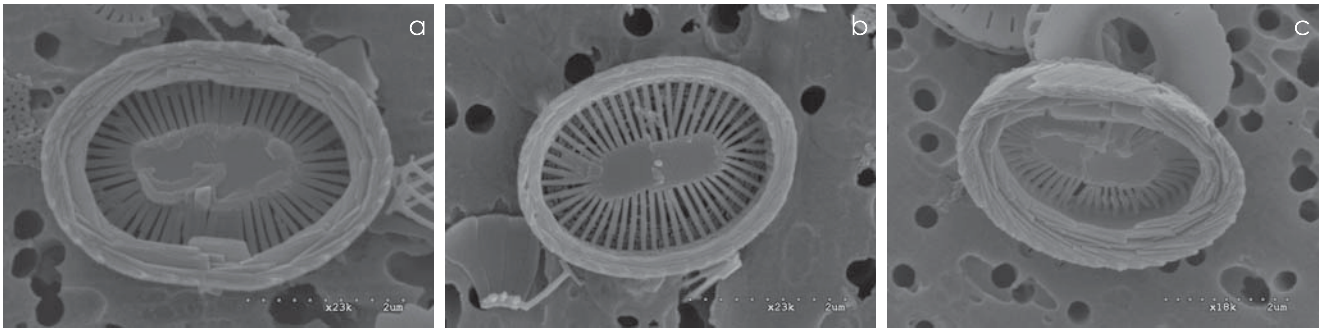
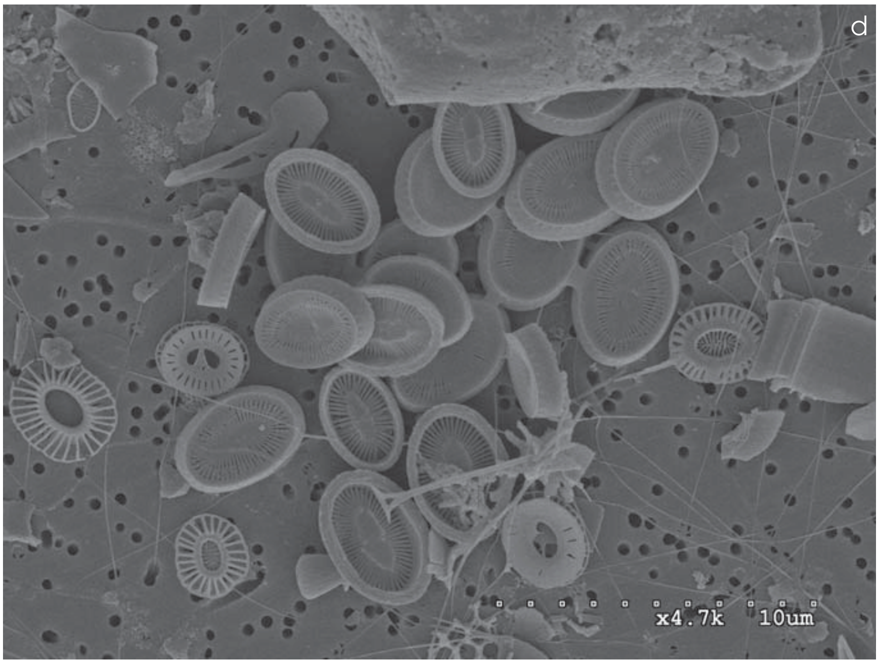


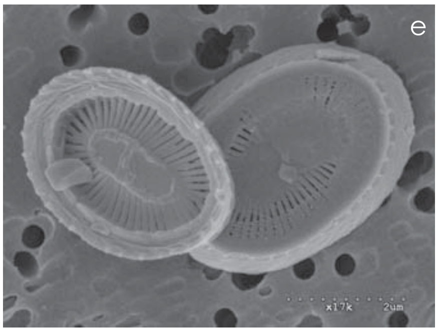
Fig. 7.20: **(a)** Flux of *Calciosolenia* off Chile during 'normal' oceanic condition, **(b)** during El Niño, **(c)** off Cape Blanc in 1989 (CB1), and **(d)** during the sampling period 1989–1991



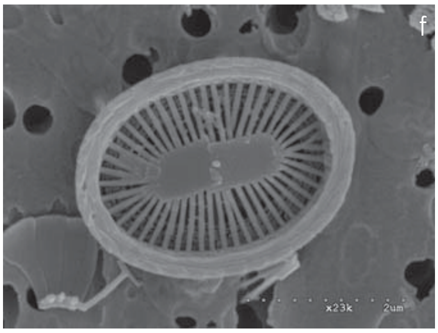
Coronosphaera mediterranea



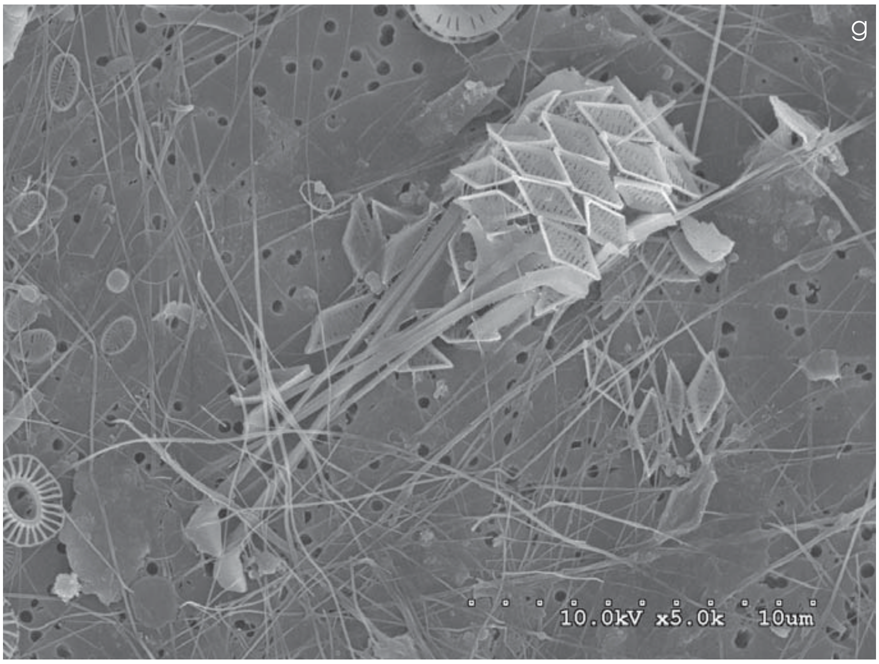
C. mediterranea



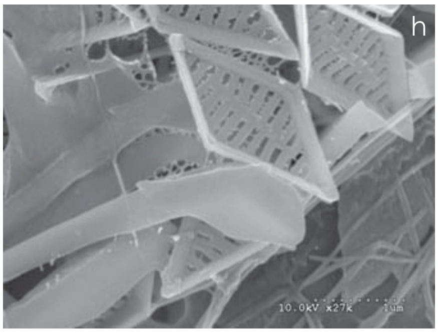
C. mediterranea



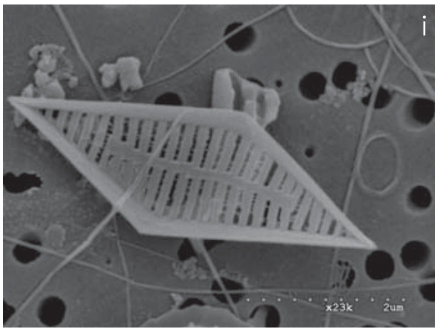
C. mediterranea



Calciosolenia brasiliensis



C. brasiliensis



C. brasiliensis

PLATE 19 - SYRACOSPHAERALES, GENUS INCERTAE SEDIS: *CORONOSPHAERA*
CALCIOSLENIACEAE: *CALCIOSOLENIA*

C. murrayi

C. murrayi was more often identified in samples off Chile than off Cape Blanc but all in all rather seldom. Off Chile the species occurred more often during times of ‘normal’ condition.

SYRACOSPHAERALES: *RHABDOSPHAERACEAE:* RHABDOSPHAERA

Rhabdosphaera spp.

The genus *Rhabdosphaera* is present throughout the whole study period in both upwelling regions even though in varying numbers and frequency. Focusing on the single species draws a different picture: *R. xiphos* is found off Chile during ‘normal’ oceanic condition whereas it is absent during El Niño. Off Cape Blanc, a significant increase of *R. xiphos* is observed during maximum total coccolith flux (winter 1990/1991) (Fig 7.21).

R. clavigera & R. sytlifera

R. clavigera was rarely absent in the samples. Only in CB1 and CB4 it was missed once in a while, whereas from 1989 to 1990 it was continuously present. Off Chile (almost) each sample contained the species. *R. stylifera* was less frequent present in both study areas (roughly half of the Chile samples and two third of the Cape Blanc samples).

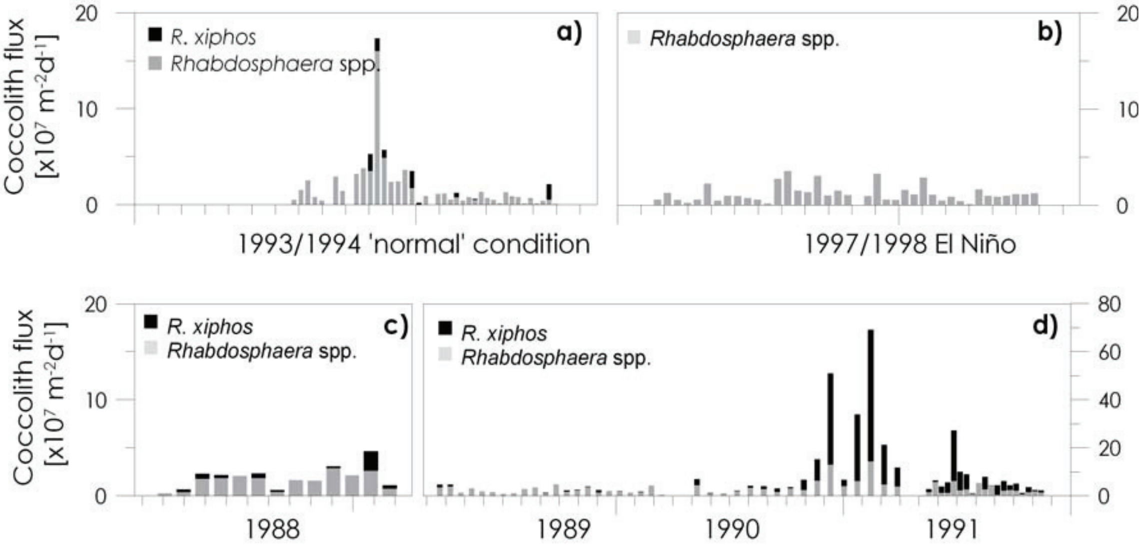
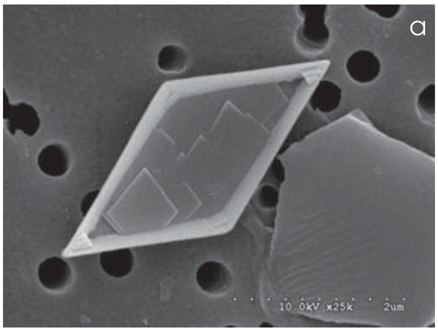
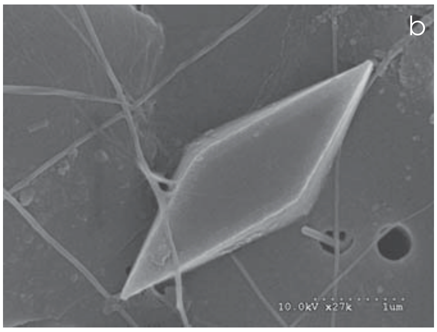


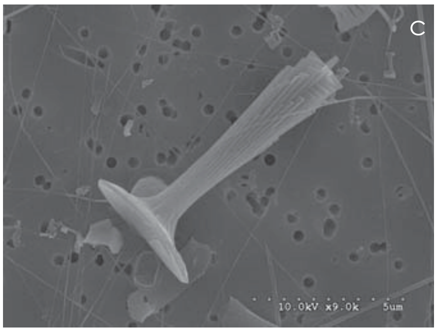
Fig. 7.21: **(a)** Flux of *Rhabdosphaera spp.* (consisting of *R. clavigera* and *R. stylifera*) and *R. xiphos* off Chile during ‘normal’ oceanic condition, **(b)** during El Niño, **(c)** off Cape Blanc in 1989 (CB1), and **(d)** during the sampling period 1989–1991



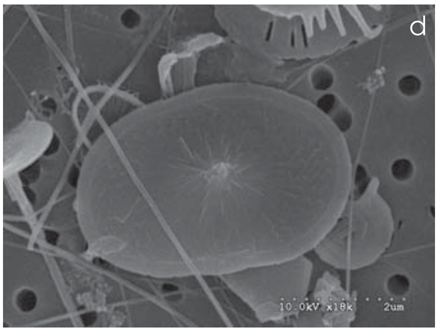
C. murrayi



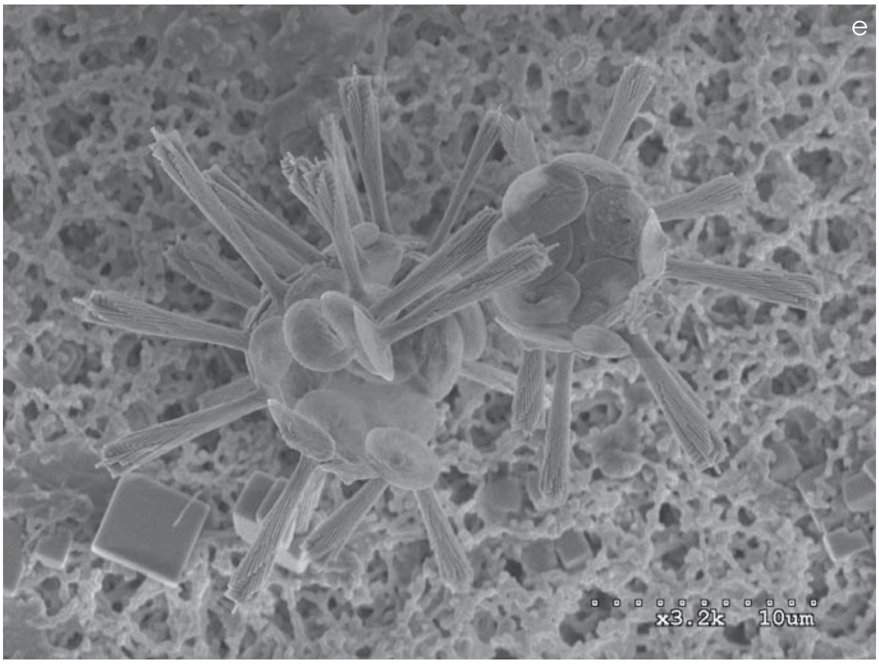
C. murrayi



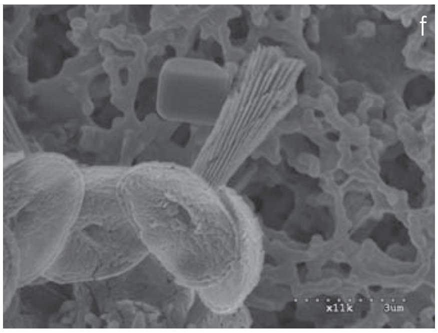
Rhabdosphaera clavigera



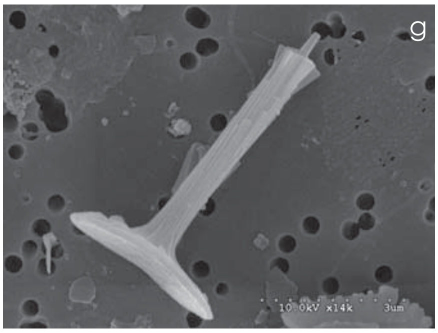
Rhabdosphaera



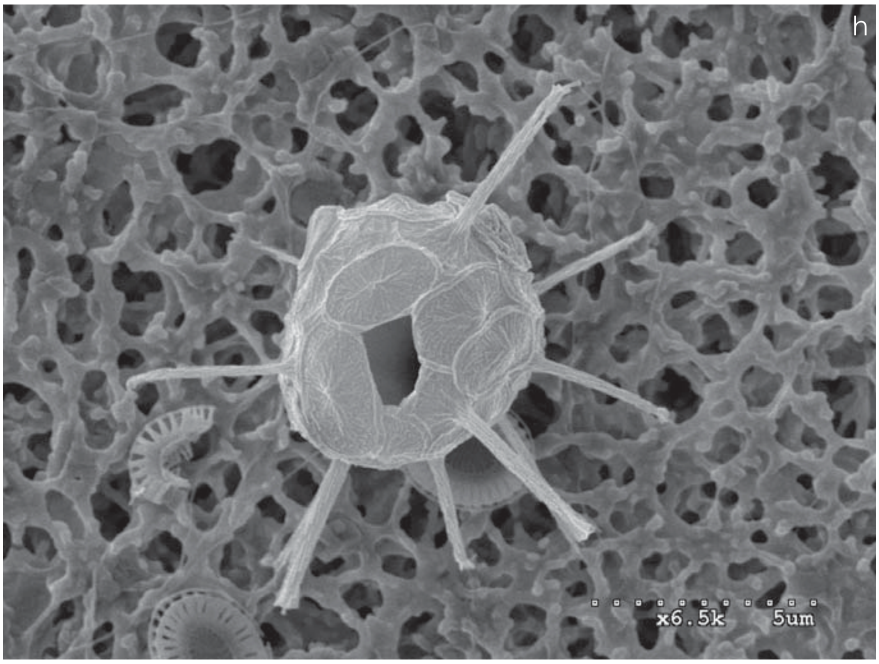
R. clavigera



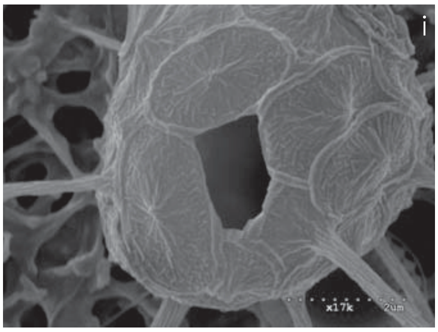
R. clavigera



R. stylifera



R. sytlifera



R. stylifera

PLATE 20 - CALCIOSOLENIACEAE:*CALCIOSOLENIA*
RHABDOSPHAERACEAE: *RHABDOSPHAERA*

SYRACOSPHAERALES: *RHABDOSPHAERACEAE:* PALUSPHAERA

Palusphaera

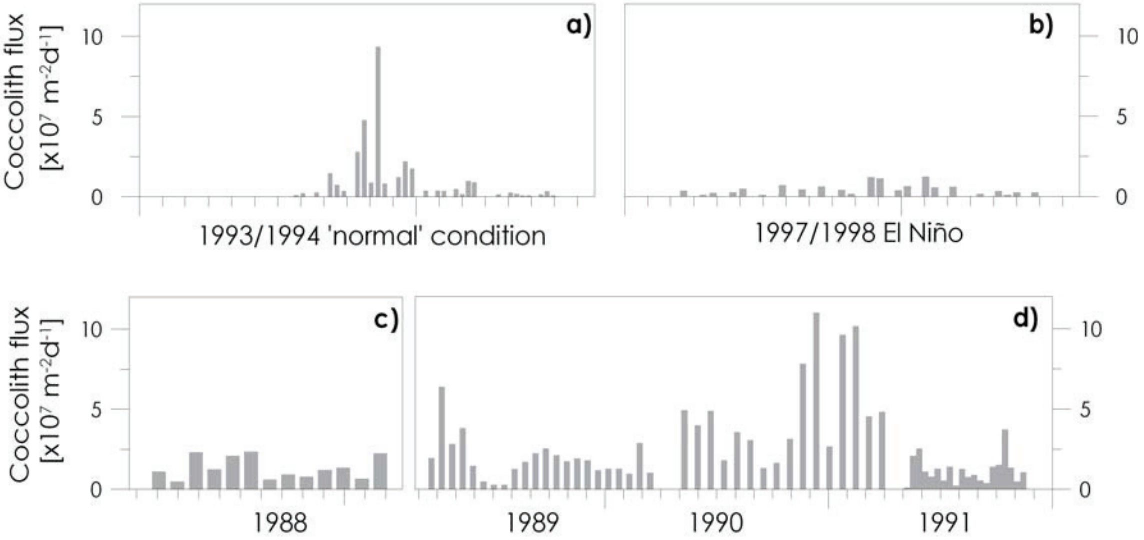
Palusphaera spp. was found off Cape Blanc especially during the first two deployments (1988-1989) and afterwards rather seldom. Off Chile, the species was seldom found during 'normal' condition (half of the samples) and even less frequent during El Niño (11 out of 40 samples)

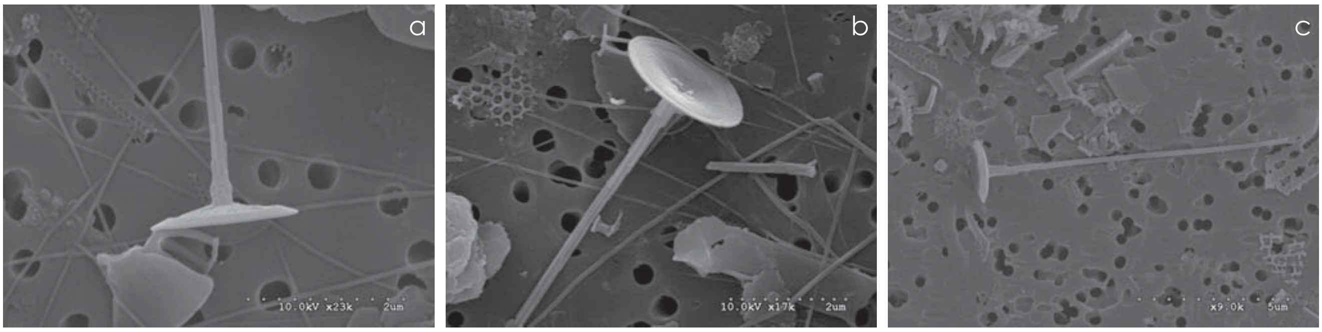
SYRACOSPHAERALES: *RHABDOSPHAERACEAE:* DISCOSPHAERA

Discosphaera tubifera

D. tubifera was found in all samples comprised of the Cape Blanc sediment trap and frequently found off Chile. In comparison, off Cape Blanc the flux was higher than off Chile (Fig. 7.22).

Fig. 7.22: **(a)** Flux of *D. tubifera* off Chile during 'normal' oceanic condition, **(b)** during El Niño, **(c)** off Cape Blanc in 1989 (CB1), and **(d)** during the sampling period 1989–1991





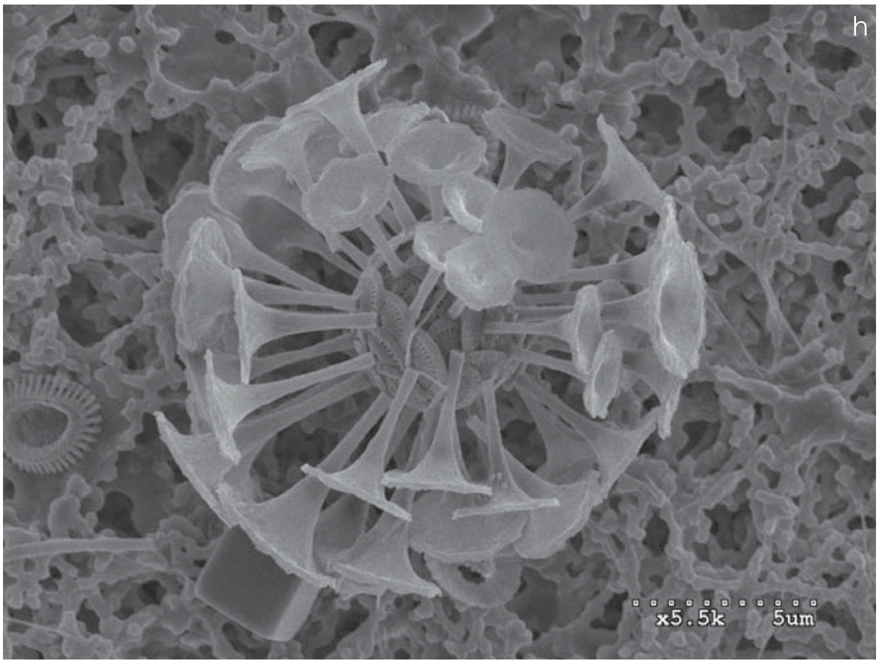
Palusphaera

Palusphaera

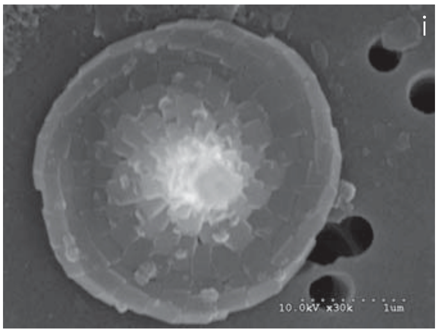
D. tubifera

D. tubifera

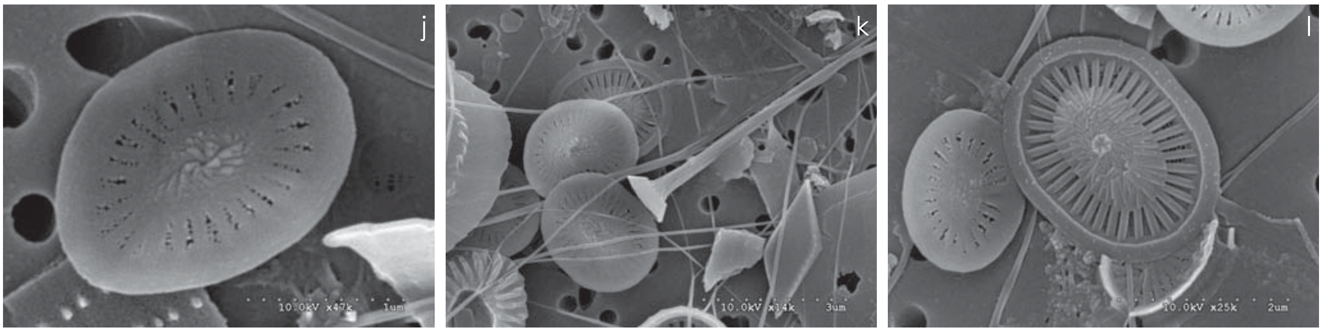
D. tubifera



D. tubifera



D. tubifera



Acanthoica quattrospina

PLATE 21 - RHABDOSPHAERACEAE: *PALUSPHAERA, DISCOS PHAERA & ACANTHOICA*

SYRACOSPHAERALES: *RHABDOSPHAERACEAE:* ACANTHOICA

Acanthoica spp.

Species of the genus *Acanthoica* were found in each sample derived from Cape Blanc study area with a significant maximum during winter 1990/1991 (Fig. 7.23). Off Chile *Acanthoica* was a frequently found genus, and was absent only in one third of the samples regardless of the prevailing oceanic condition.

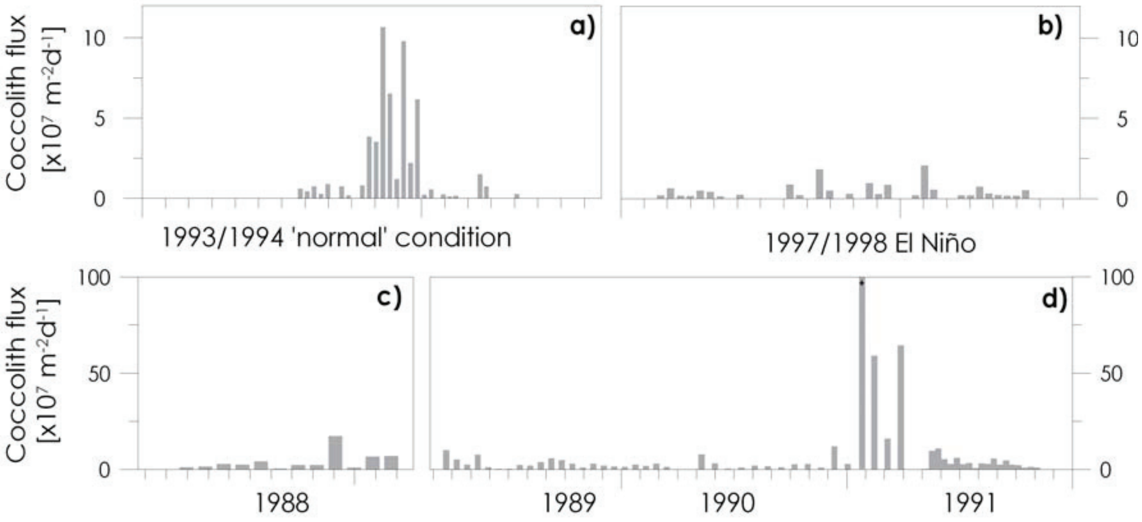
Species of the genera found were *A. quattrospina, A. acanthifera*, and *A. maxima*.

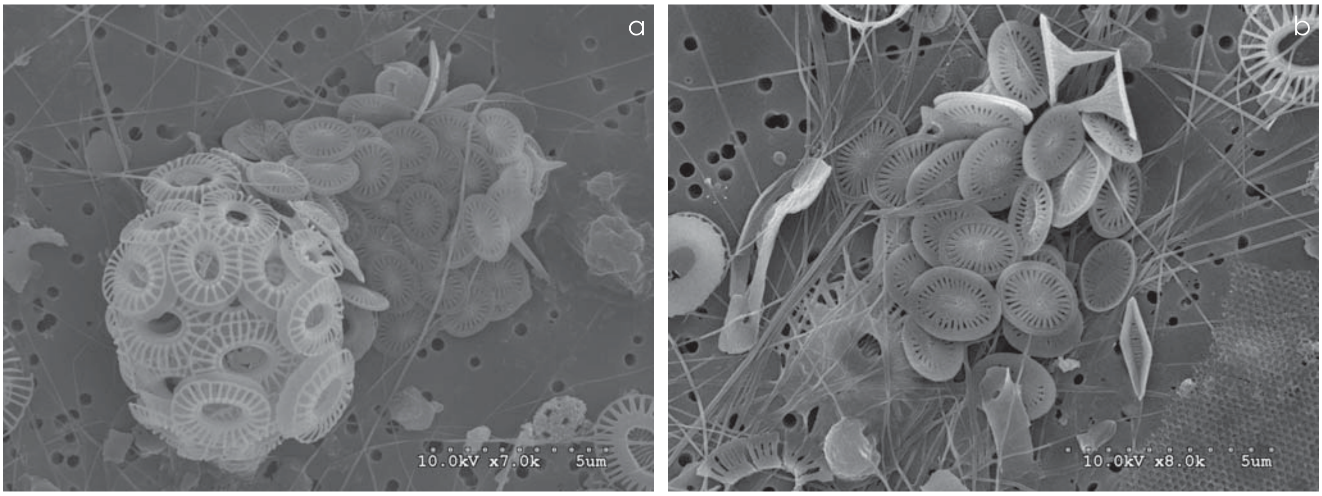
SYRACOSPHAERALES: *RHABDOSPHAERACEAE:* ALGIROSPHAERA

Algirosphaera robusta

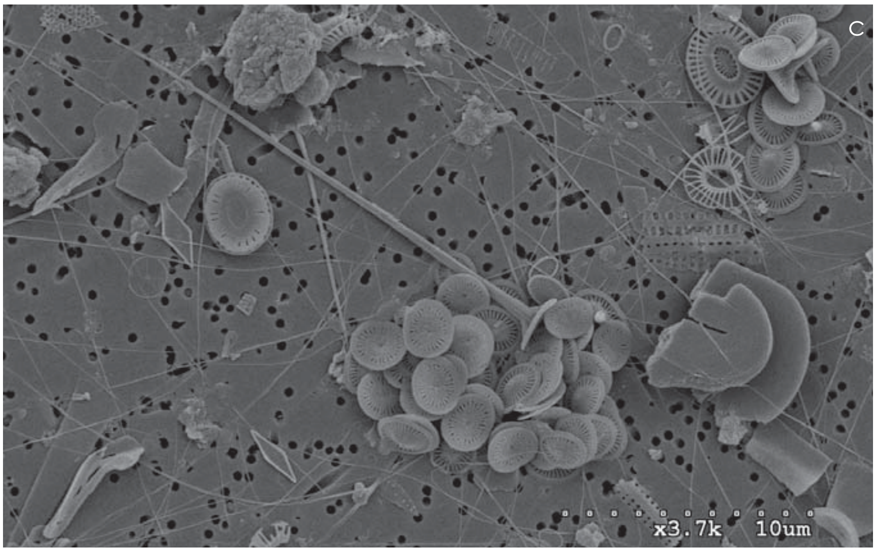
A. robusta was found in (nearly) all samples (except three) of the Cape Blanc sediment trap. Off Chile, there is a difference between samples of the 'normal' oceanic condition study period and samples of the El Niño event. During El Niño it was less frequent and found only in half of the samples, whereas during 'normal' condition *A. robusta* was quite frequent (in 29 samples out of 40).

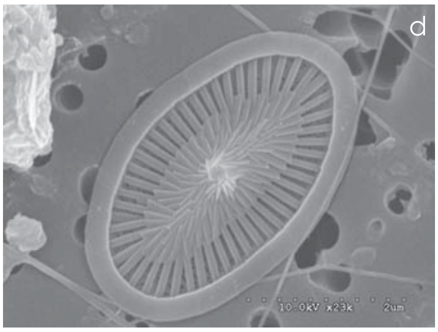
Fig. 7.23: **(a)** Flux of *Acanthoica spp.* off Chile during 'normal' oceanic condition, **(b)** during El Niño, **(c)** off Cape Blanc in 1989 (CB1), and **(d)** during the sampling period 1989 –1991





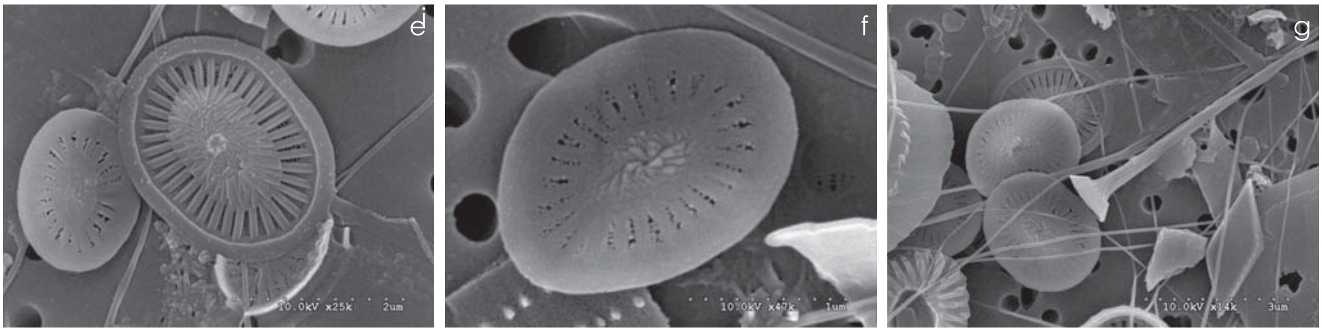
Acanthoica *Acanthoica*



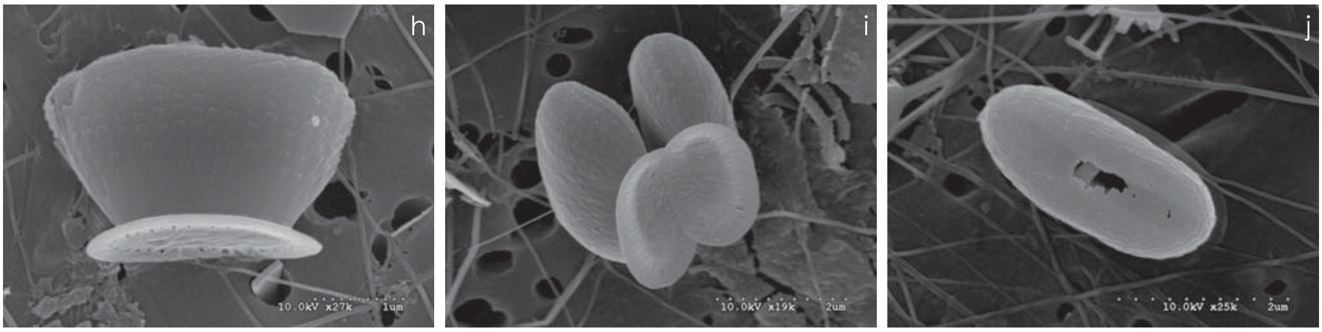


A. maxima

Acanthoica



A. quattrospina



Algirsophaera robusta

PLATE 22 - Rhabdosphaeraceae: *Acanthoica, Algirosphaera*

HETEROCCOLITHS INCERTAE SEDIS: *UMBELLOSPHAERACEAE:* UMBELLOSPHAERA

Umbellosphaera irregularis & U. tenuis

U. tenuis was present in all samples derived from the Cape Blanc area. *U. irregularis* was missed only in two samples. Off Chile, U. tenuis was more common than *U. irregularis* but both species were less frequently found compared to NW-Africa. There is also a difference between El Niño samples and non-El Niño samples in respect to the occurrence of *U. irregularis*. Less samples of the El Niño study period contained coccoliths of *U. irregularis* (5 vs. 16 samples) (Fig 7.24).

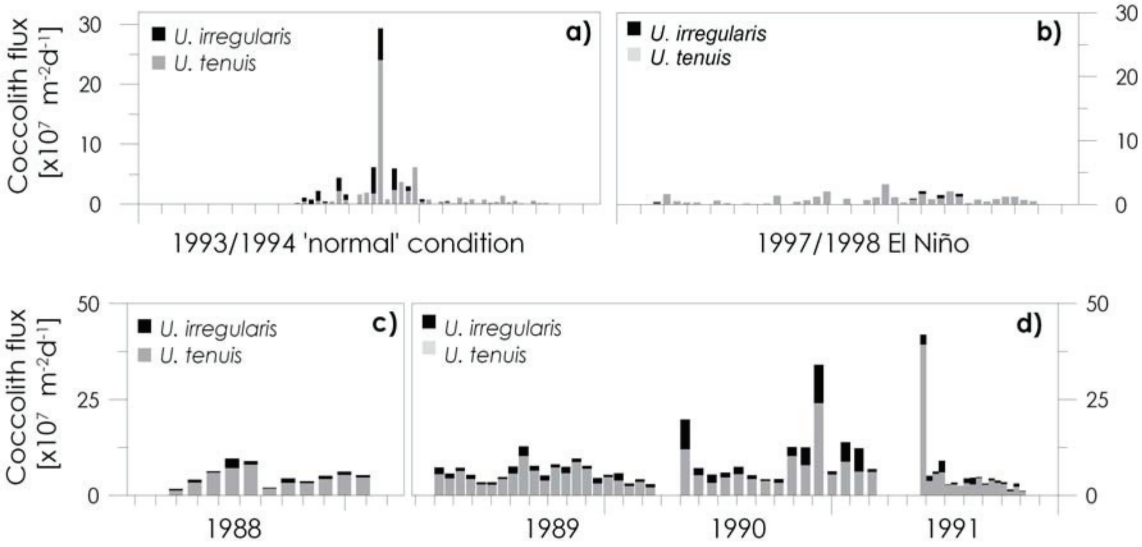
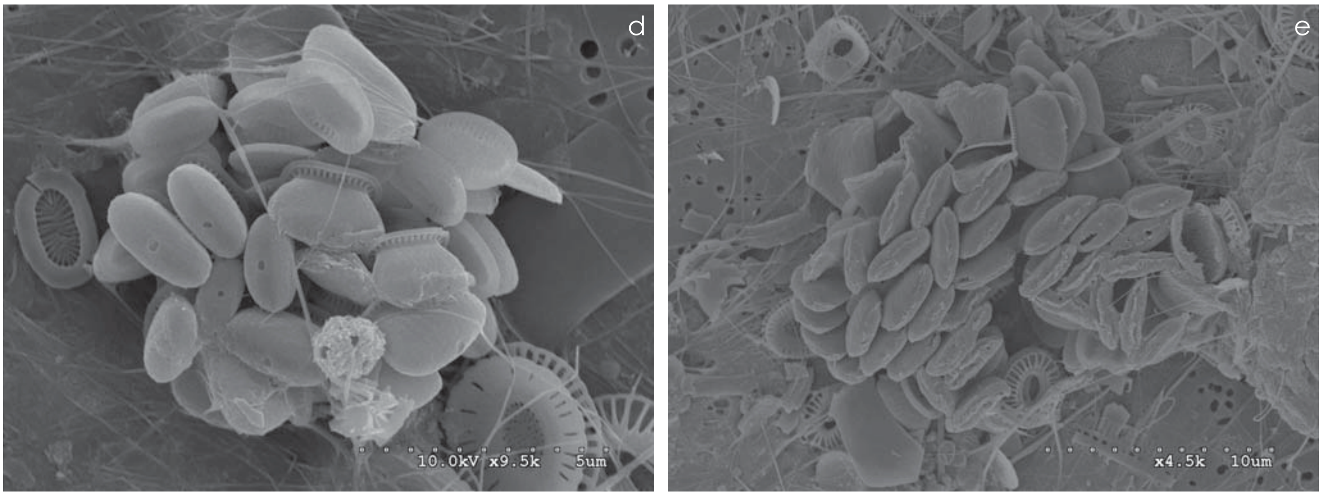
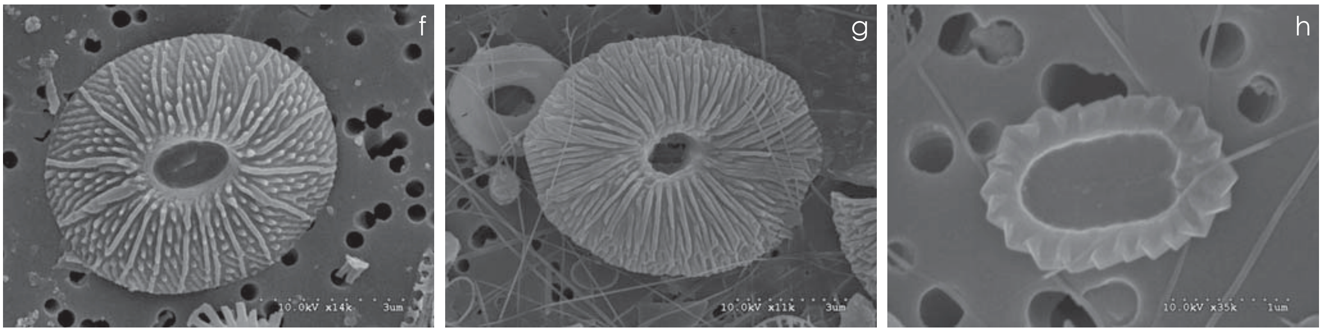


Fig. 7.24: **(a)** Flux of *U. irregularis* and *U. tenuis* off Chile during 'normal' oceanic condition, **(b)** during El Niño, **(c)** off Cape Blanc in 1989 (CB1), and **(d)** during the sampling period 1989–1991

A. robusta



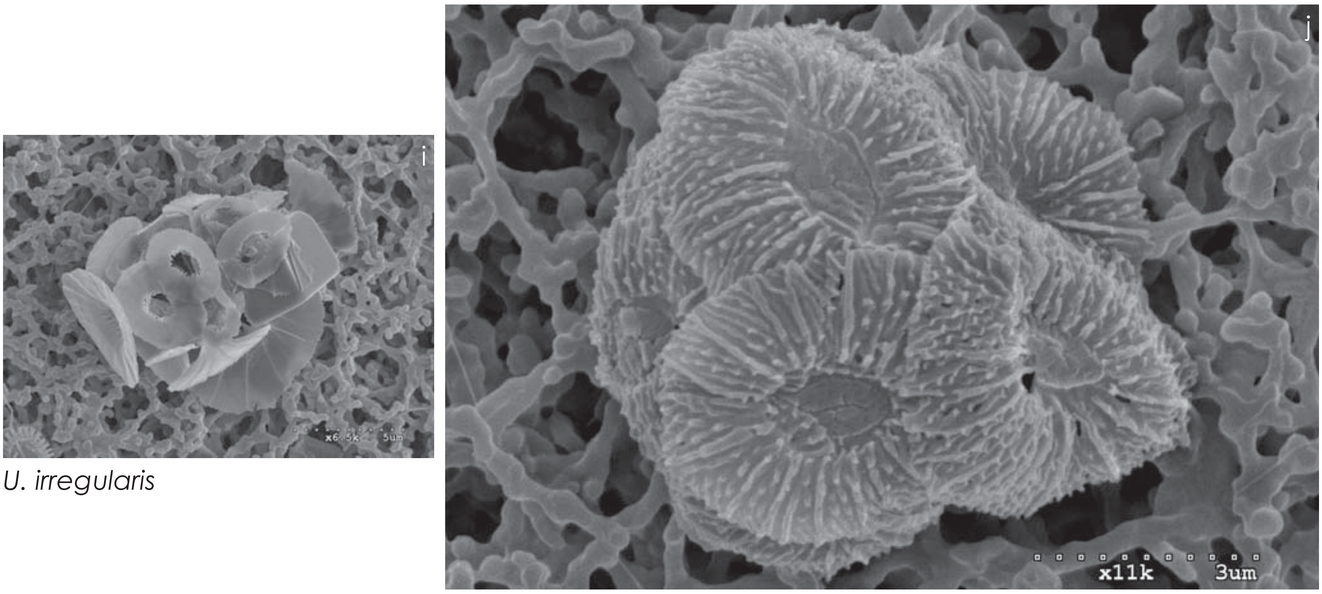
A. robusta



Umbellosphaera tenuis type I

U. tenuis

U. tenuis



U. irregularis

U. tenuis

PLATE 23 - Rhabdosphaeraceae: *Algirosphaera*
Umbellosphaeracaea: *Umbellosphaera*

HETEROCCOLITHS INCERTAE SEDIS: *NARROW RIMMED PLACOLITHS*: TURRILITHUS

Turrilithus

The pictured species was found (once) in a sample derived from CB 3 (#16).

NANNOLITHS: *NANNOLITHS INCERTAE SEDIS*: FLORISPHAERA

Florisphaera profunda

F. profunda was found in all samples regardless of the upwelling region or the prevailing oceanic condition.

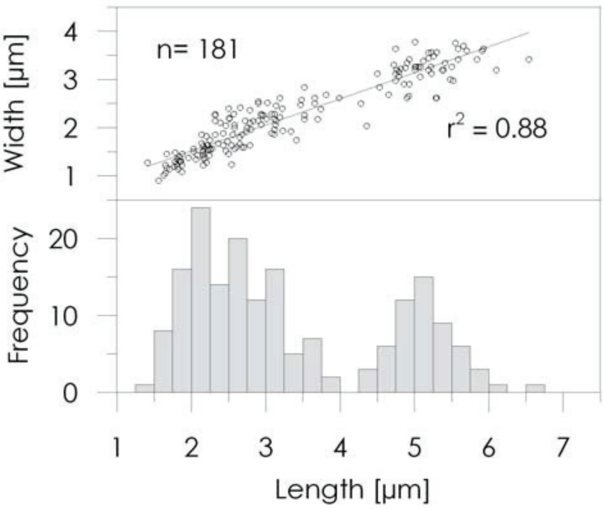


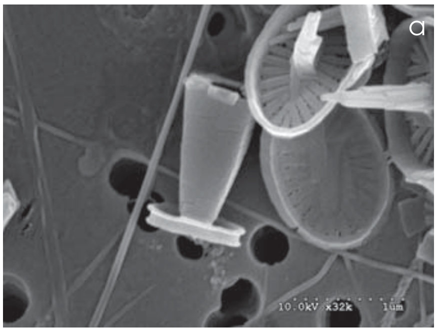
Fig. 7.25: Coccolith size variation data and frequency distributions (at 0.25 µm intervals) of all measured *F. profunda* (CB1)

Overall, nannolith lengths in the studied sediment trap samples are 1.4–6.4 µm with a mean size of 3.4 µm (Fig. 7.25). The width varies from 0.9–3.8 µm with an overall mean of 2.2 µm. In contrast to previous findings of Baumann and Sprengel (2000), length and width of the nannoliths are very well correlated (r^2=0.88) although the sizes are exactly in the same range as observed in the Canary Islands region. In addition, the scatterplot and the frequency distribution clearly document a bimodal distribution pattern indicating that two varieties of *F. profunda* are present in the investigated samples, with var. *elongata* forming larger coccoliths (e.g. Reid, 1980). The latter is between 4.3–6.5 µm in size, whereas nannoliths of 1.4–3.9 µm may correspond to *F. profunda* var. *profunda.* A wide range in size of this species has already been described and has lead to its subdivision (Okada and Honjo, 1973). However, it is not yet exclusively proven whether the distinct size morphotypes correspond to typological varieties and what biological significance they have.

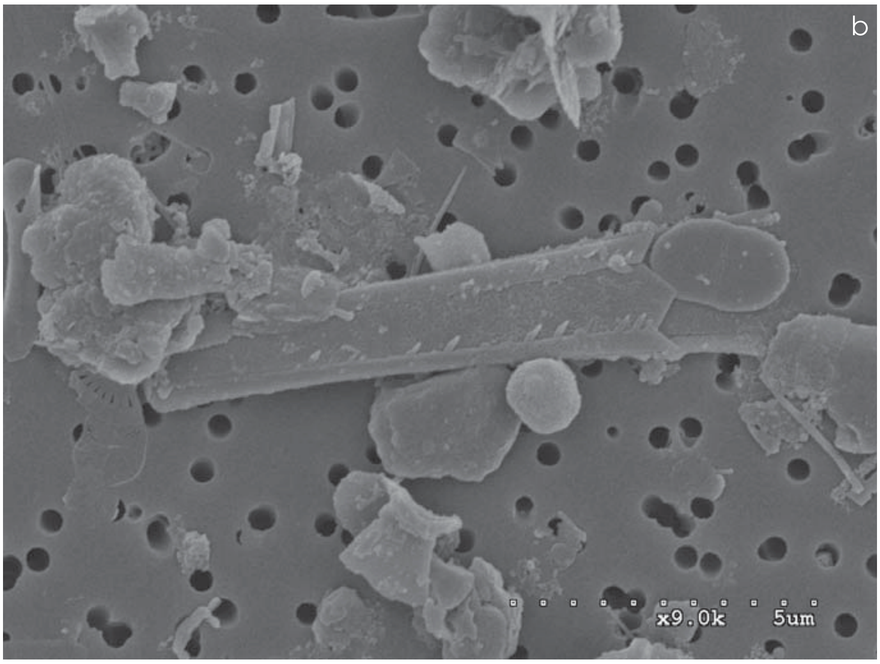
NANNOLITHS: *NANNOLITHS INCERTAE SEDIS*: GLADIOLITHUS

Gladiolithus flabellatus

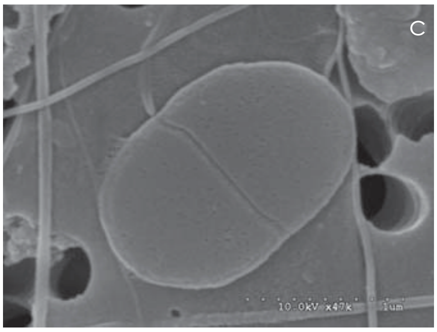
G. flabellatus was found in all samples of the Cape Blanc deployment, whereas only in two thirds of the Chile samples CH3/4 and even less of the El Niño samples (only in 22 samples).



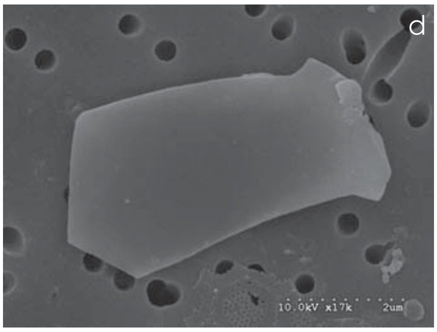
Turrilithus



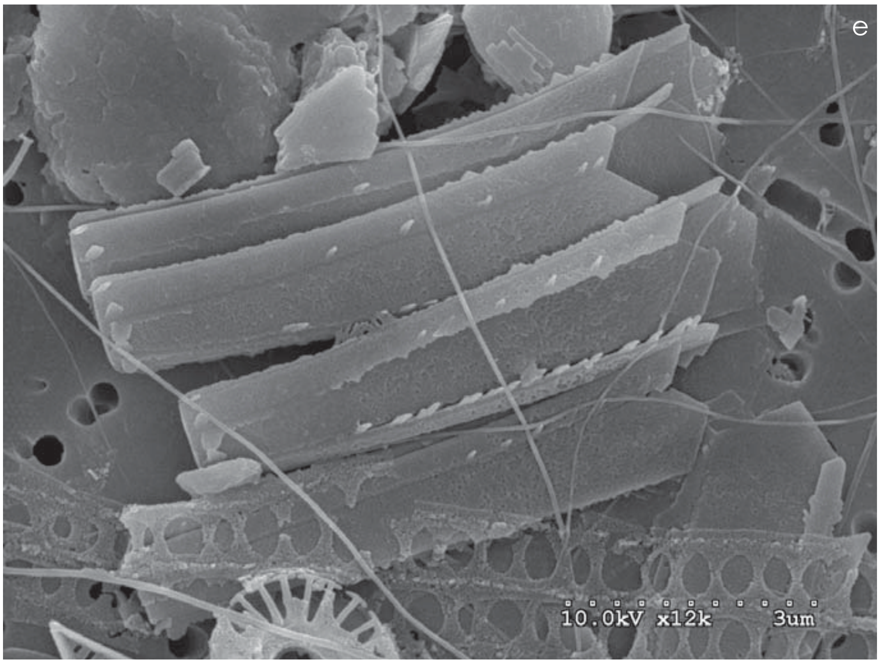
G. flabellatus



Gladiolithus flabellatus



Florisphaera profunda



G. flabellatus

PLATE 24 - Placoliths: *Turrilithus*
Nannoliths: *Florisphaera & Gladiolithus*

HOLOCOCCOLITHS: *CALYPTROSPHAERACEAE*: SYRACOLITHUS

Syracolithus catilliferus

In general the occurrence of holococcoliths was always quite seldom and varied in flux. *S. catilliferus* were found in eight samples (out of 71) derived from Cape Blanc area. Off Chile, the species was found only in 'El Niño' samples. There, in total three samples contained *S. catilliferus*.

S. dalmaticus

S. dalmaticus was found only in 1988 and 1991 in samples of the Cape Blanc sediment trap whereas off Chile *S. dalmaticus* was not found in any sample.

HOLOCOCCOLITHS: *CALYPTROSPHAERACEAE*: CALYPTROLITHINA

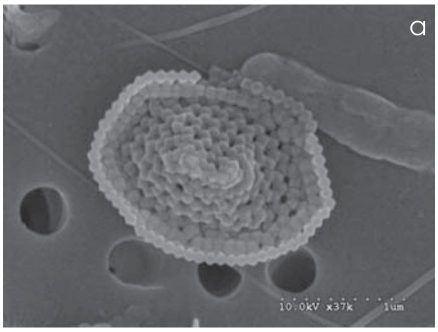
C. multipora

The pictured species was found in a sample of the CB3 deployment (#16).

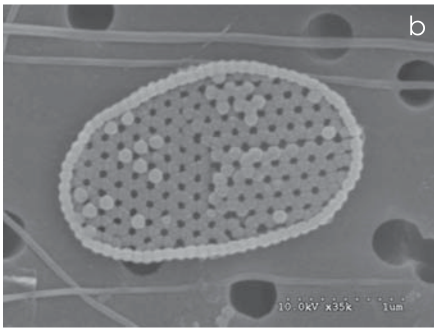
HOLOCOCCOLITHS: *CALYPTROSPHAERACEAE:* DAKTYLETHRA

Daktylethra pirus

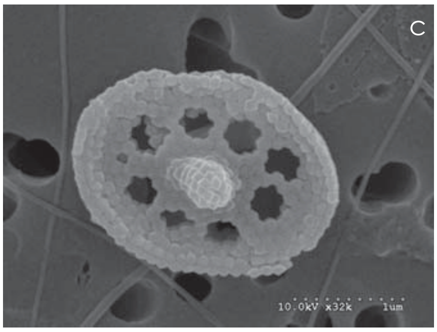
D. pirus was found (quite) regularly but only off Cape Blanc at the more oceanic site (CB2–CB4).



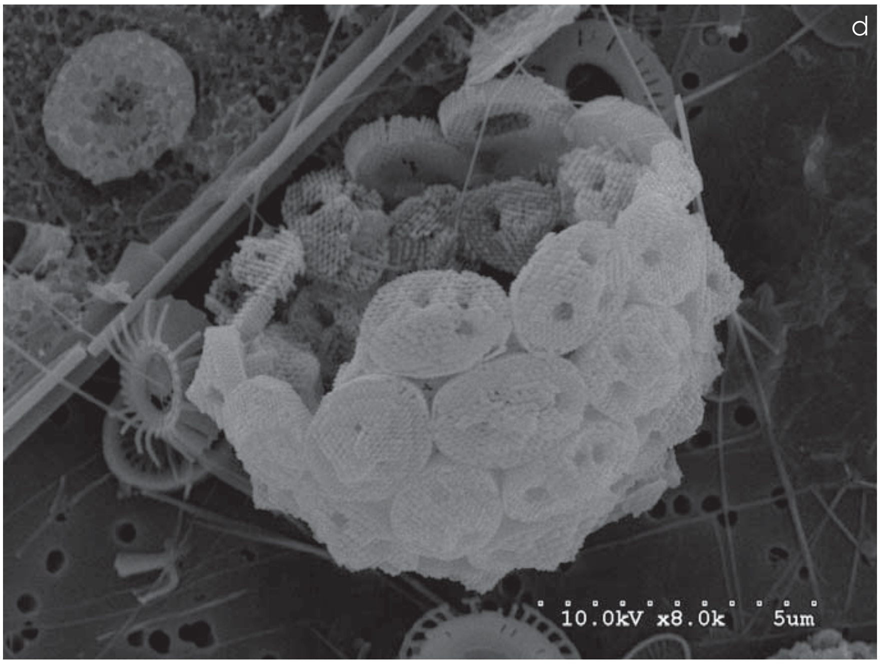
Calyptrolithina divergens



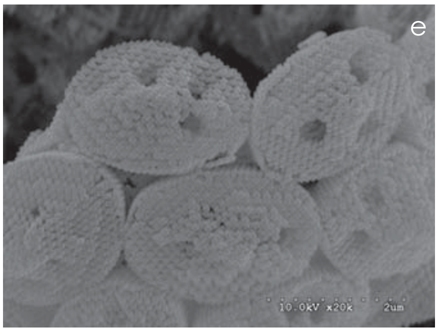
Syracolithus catilliferus



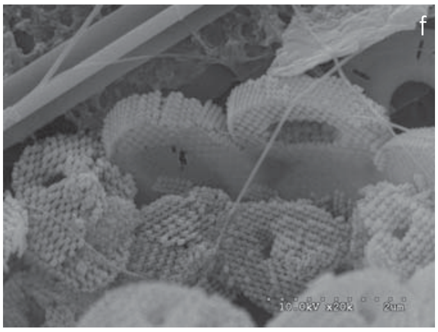
Calyptrolithina cf multipora



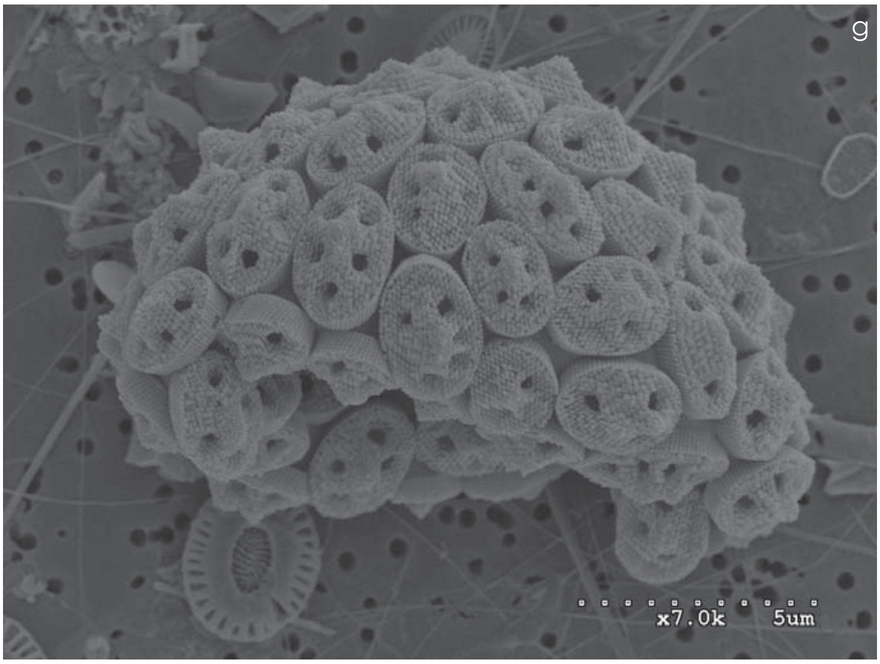
Syracolithus



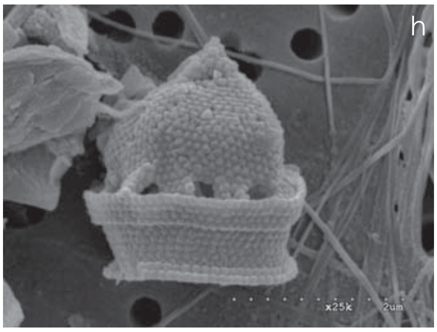
Syracolithus



Syracolithus



Syracolithus dalmaticus



Daktylethra pirus

PLATE 25 - HOLOCOCCOLITHS

Appendix

Fig. I: Wind velocity and direction at Nouhadibou airport (Mauritania) data Rathmeyer pers. comm.

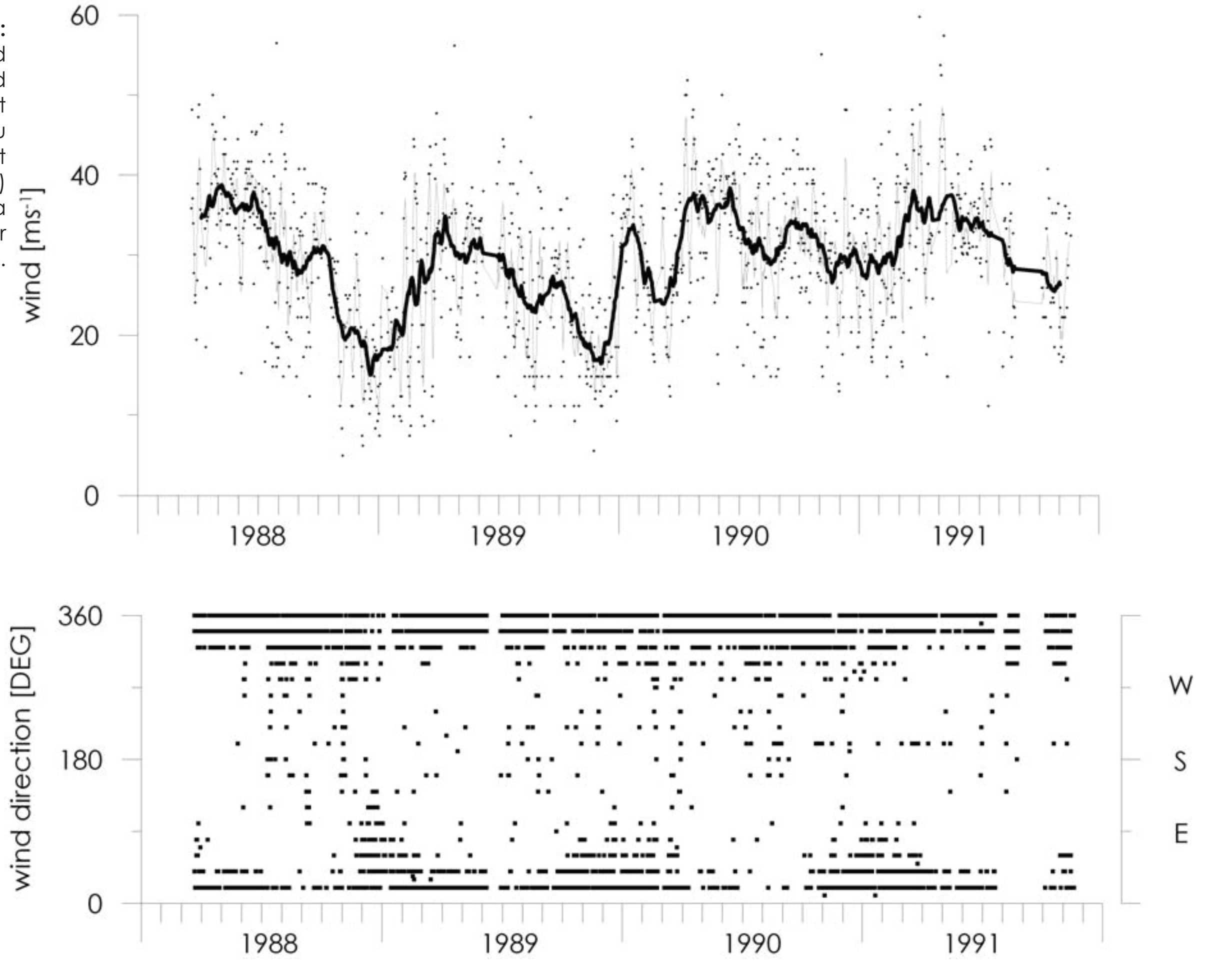


Fig. II: SST and SST anomaly for the sediment trap location off Cape Blanc (data set: AVHRR)

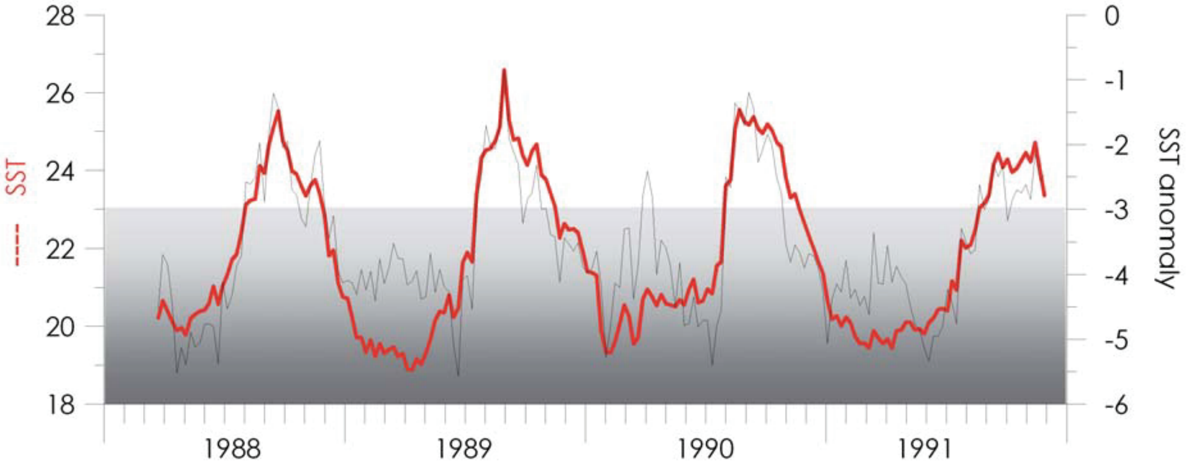


Fig. III: Insolation for the sediment trap location off Cape Blanc data: *NASA Surface meteorology and Solar Energy: Daily Data*

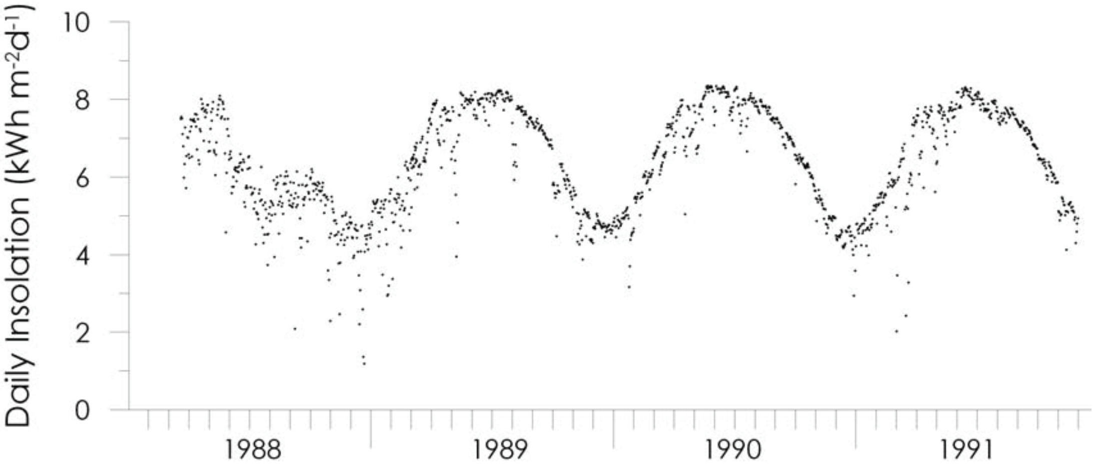
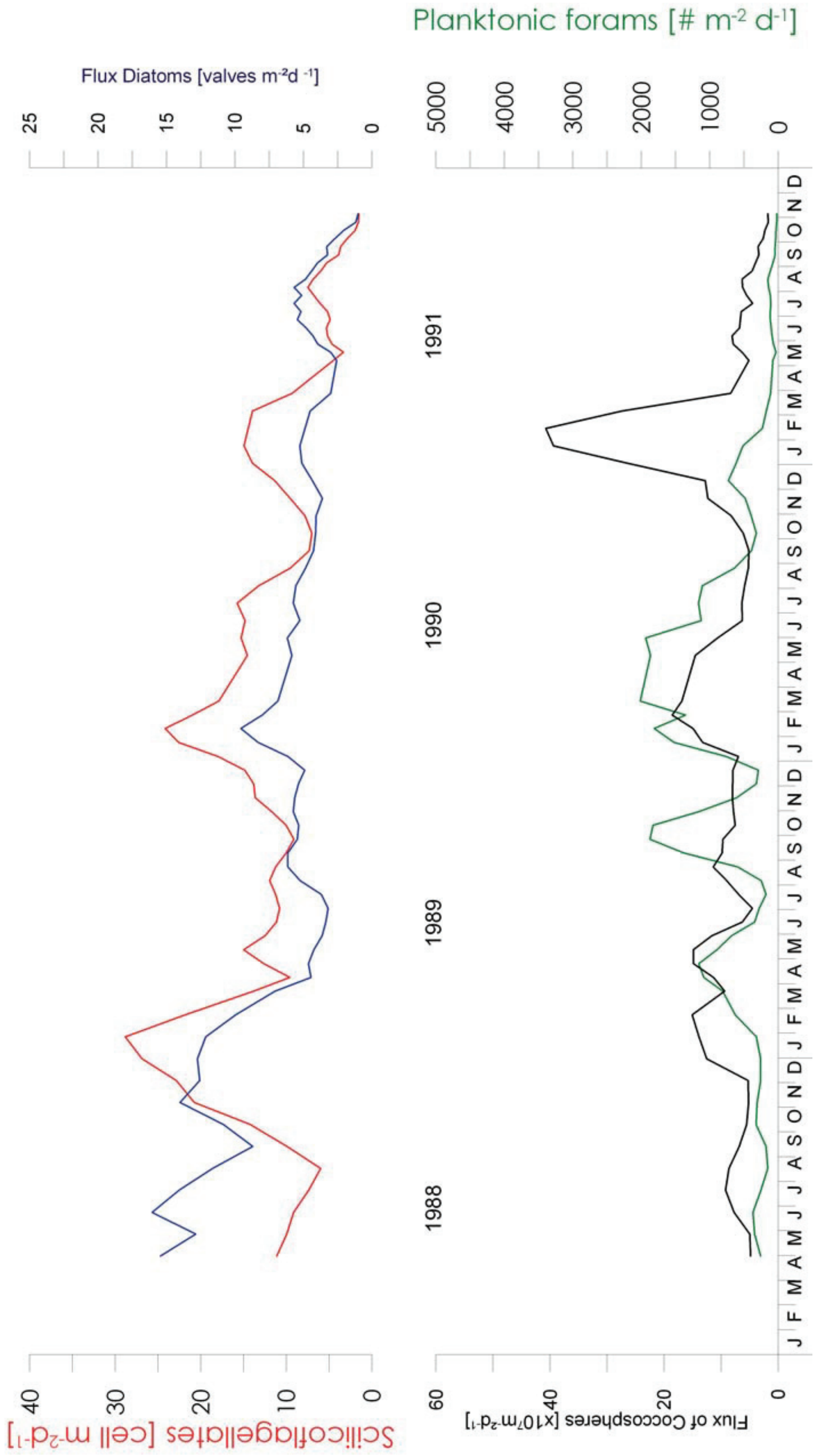


Fig. IV: Plankton fluxes of sediment trap CB1-4

data by Romero et al. 2002b, Donner (pers. comm.), and this study



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