Characteristics of calcareous dinoflagellate cyst assemblages in a major upwelling region (NW Africa)

Spatial distribution, fluxes and ecology

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Summary

This study of calcareous dinoflagellate cysts from the upwelling area off the NW African margin aimed to gain detailed information about environmental preferences of the single species, which will be important and useful for future palaeoenvironmental and palaeoceanographic reconstructions within upwelling areas, and to refine our knowledge of calcareous dinoflagellates cysts production and ecology, especially interannual variations and seasonality of cyst assemblages and abundances in a high production area. Therefore, dinoflagellate cyst fluxes, their spatial distribution in surface sediments, and ecological preferences of calcareous dinoflagellates in one of the most productive Eastern Boundary Current systems, the upwelling region off NW Africa, were studied and compared.

The well defined investigation region contains a productivity gradient from the eutrophic NW African upwelling zones to the oligotrophic offshore regions. The area is characterized by high biological productivity and low sea surface temperatures, both varying seasonally and interannually. Especially off the capes (Cape Ghir, Cape Yubi and Cape Blanc) upwelling filaments develop, contributing to the mixing of coastal with offshore oceanic water. The nutrient-rich upwelled waters as well as the contribution of terrigeneous material (mostly Saharan dust) determine the nutrient supply into the euphotic zone and thus strongly influence phytoplankton production. These environmental properties create a unique setting for phytoplankton growth.

The distribution patterns of calcareous dinoflagellate cyst species in Holocene surface sediment samples from the upwelling region off the Moroccan coast between Cape Ghir and Cape Yubi, encompassing the Canary Islands were investigated. In order to determine the ecological significance and the palaeoenvironmental reconstruction potential of each cyst species, their relationships with known environmental (physical and trophic) parameters of the overlying (sub-)surface waters have been analysed. Relative abundances and accumulation rates have been determined and verified by statistical methods. The comparison between the statistical analyses of both the relative and the accumulative approach shows that cyst accumulation rates present a much more causal relationship between calcareous dinoflagellate cyst production and the environmental parameters of the upper water column than relative or absolute abundances, as commonly used in previous analyses. The species-specific geographic distribution patterns of nine observed species, *Thoracosphaera heimii*, *Leonella granifera*, *Calciodinellum levantinum* and *Calciodinellum albatrosianum*, paratabulated *Calciodinellum albatrosianum, Calciodinellum elongatum, Pernambugia tuberosa, Scrippsiella regalis* and *Scrippsiella* spp., reflect the highly variable onshore-offshore gradients of the environmental

parameters. In general, high accumulation rates of calcareous dinoflagellate cysts were found around and south of 29°N and offshore the westernmost Canary Island La Palma, with slightly lower accumulation rates in the upwelling filaments off Cape Yubi and Cape Ghir, indicating species' preference for regions beyond the active upwelling zones.

To enhance the still limited ecological knowledge of modern calcareous cysts producing dinoflagellates, time-series, based on sediment traps moored off Cape Blanc (Mauritania), were studied. In total cyst fluxes of three annual cycles (1990-1991, 1998-1999) were determined, in order to reveal production and transport mechanisms on calcareous dinoflagellate cysts and relationships between cyst fluxes and (sub)surface environmental properties. Cyst production shows seasonal and interannual variation corresponding to upper water column conditions. In general, high fluxes were observed during times of waning upwelling filaments and higher sea surface temperatures, whereas cyst fluxes decreased when water column mixing increased due to the strengthen influence of upwelling filaments. Moderate turbulence is, however, tolerated by most of the dinoflagellates. Additionally, good correlations between cyst fluxes and nutrient supply are apparent. Especially *Leonella granifera* reacts to the higher input of important land-derived elements or nutrients by remarkable enhanced cyst production.

The sediment trap moorings gave the unique opportunity to investigate the changes of the cyst fluxes through the water column due to trap deployments in two different water depths. Relatively high sinking velocities of the cysts were estimated, indicating a fast transport in aggregates as the main export mechanism to the deep ocean. To expose possibly alterations of the finally deposited cyst assemblage, a comparison of cyst fluxes with abundances of the surface sediment directly below the trap position was carried out. Cyst accumulation rates in the surface sediment were considerably lower than in the deeper sediment trap. Differences in relative abundances between sediment trap and surface sediment assemblages, particularly the large loss of *L. granifera* reaching only up to 3 % in surface sediment samples compared to about 30% at deeper trap level, are probably caused by transport, preferential dissolution and variability in cyst production.

This thesis increase the basic knowledge of calcareous cysts producing dinoflagellates, especially based on the comparative approach of this study: cyst fluxes and underlying surface sediments, well-defined surface sediments samples, modern vs. Holocene assemblages. The results of this research permit more dependable reconstructions within upwelling areas, and confirm the application of calcareous dinoflagellates as very useful proxies for detailed palaeoenvironmental and –oceanographic reconstructions.

Zusammenfassung

Ziel der vorliegenden Arbeit über kalkige Dinoflagellatenzysten aus dem Auftriebsgebiet vor der Küste NW Afrikas war es, weitreichende Informationen über die ökologischen Präferenzen einzelner Arten zu erhalten. Dieses Wissen bildet die Basis für zukünftige Rekonstruktionen der Paläoumwelt und Paläoozeanographie, besonders in Auftriebsgebieten. Der Fokus lag auf der Zystenproduktion und der Ökologie kalkiger Dinoflagellaten mit Schwerpunkt auf die saisonalen und jährlichen Schwankungen der Zystenvergesellschaftungen und -häufigkeiten in einem Hochproduktionsgebiet. Zu diesem Zweck wurden die Flussraten der Dinoflagellatenzysten, ihre räumliche Verteilung in holozänen Oberflächensedimenten und die ökologischen Vorlieben kalkiger Dinoflagellaten in einem der produktivsten Oberflächenströmungssysteme der östlichen Ozeanränder, dem Auftriebsgebiet vor der Nordwest-Afrikanischen Küste, untersucht und verglichen.

Das Untersuchungsgebiet weist einen deutlichen Produktivitätsgradienten von der eutrophen afrikanischen Küste zu oligotrophen ozeanischen Bereichen auf. Die Region ist durch eine hohe Bioproduktivität und niedrige Wasseroberflächentemperaturen charakterisiert, die saisonalen und jährlichen Schwankungen unterliegen. Besonders vor den Kaps (Kap Ghir, Kap Yubi und Kap Blanc) entstehen Auftriebsfilamente, die zum Transport des küstennahen Wassers in den offenen Ozean beitragen. Das nährstoffreiche Auftriebswasser sowie der Eintrag von terrigenem Material (hauptsächlich Staub aus der Sahara) bestimmen das Nährstoffangebot in der euphotischen Zone und beeinflussen damit sehr stark die Phytoplanktonproduktion. Diese Einflüsse machen das Gebiet einzigartig im Hinblick auf Wachstum und Ausbreitung des Phytoplanktons.

Die Verteilungsmuster einzelner Arten kalkiger Dinoflagellatenzysten in holozänen Oberflächensedimenten aus dem Auftriebsgebiet vor der Küste Marokkos, zwischen Kap Ghir und Kap Yubi, einschließlich der Kanarischen Inseln, wurden untersucht. Um die ökologische Bedeutsamkeit der einzelnen Zystenarten und ihr Potential für die Rekonstruktion der Paläoumwelt innerhalb des hier untersuchten ausgeprägten Hochproduktionsgebietes zu ermitteln, wurden ihre Korrelationen zu bekannten Umweltparametern des Oberflächenwassers bestimmt. Relative Häufigkeiten und Akkumulationsraten wurden berechnet und durch statistische Methoden untermauert. Der Vergleich der beiden Ansätze zeigt, dass kausale Zusammenhänge zwischen Zystenbildung und Umweltparametern der oberen Wassersäule durch Zystenakkumulationsraten besser erklärt werden als durch relative und absolute Häufigkeiten, die in vorherigen Studien Verwendung fanden. Die artspezifischen geographischen Verteilungsmuster der neun identifizierten Arten, nämlich *Thoracosphaera heimii*, *Leonella granifera*, *Calciodinellum levantinum* and *Calciodinellum albatrosianum*,

Calciodinellum albatrosianum (paratabuliert), *Calciodinellum elongatum, Pernambugia tuberosa, Scrippsiella regalis* and *Scrippsiella* spp. spiegeln die Umweltparameter-Gradienten zischen Küste und offenem Ozean wider. Im Allgemeinen wurden hohe Zystenakkumulationsraten um und südlich von 29°N und vor der Küste der westlichsten Kanareninsel La Palma gefunden. Etwas niedrigere Akkumulationsraten wiesen die Auftriebsfilamente vor Kap Yubi und Kap Ghir auf. Dies bedeutet einen Vorzug der Arten auf Gebiete außerhalb der aktiven Auftriebszonen.

Um das noch unvollständige Wissen über die Ökologie rezenter Kalkzysten produzierender Dinoflagellaten zu erweitern, wurden Zeitserienuntersuchungen aus einer Sedimentfalle vor Kap Blanc (Mauretanien) durchgeführt. Hierbei wurden Zystenflussraten aus insgesamt drei Jahreszyklen (1990-1991, 1998-1999) untersucht, um Auswirkungen von Produktions- und Transportmechanismen auf die kalkigen Dinoflagellatenzysten sowie Wechselwirkungen zwischen dem Zystenexport und den Verhältnissen in der oberen Wassersäule zu ermitteln. Generell wurden hohe Flussraten während geringerer Einflüsse der Auftriebsfilamente sowie höherer Oberflächenwassertemperaturen beobachtet. Mit zunehmendem Einfluss der Auftriebsfilamente und dem damit verbundenem stärkeren Durchmischen der oberen Wasserschichten nahm der Zystenexport ab. Allerdings wurden mittlere Turbulenzen des Oberflächenwassers von fast allen Arten toleriert. Ferner scheinen die Zystenflussraten durch das Nährstoffangebot beeinflusst zu werden. Besonders deutlich zeigt dies *Leonella granifera*, die auf eine zunehmende Zufuhr von terrigenen Spurenelementen oder Nährstoffen mit deutlich erhöhten Zystenflussraten reagiert.

Die Untersuchung von Sedimentfallenproben aus zwei unterschiedlichen Wassertiefen eröffnet die außerordentliche Möglichkeit, Veränderungen in der Vergesellschaftung der Zysten während des Transports durch die Wassersäule zu ermitteln. Die Berechnung von relativ hohen Sinkgeschwindigkeiten deutet auf einen schnellen Transport in Aggregaten als hauptsächlichen Exportmechanismus in die Tiefsee hin. Um mögliche Veränderungen in der Artenvergesellschaftung der endgültig abgelagerten Zysten aufzuzeigen, wurden die Zystenflussraten mit dem Zystenvorkommen in dem, unter der Falle liegenden, Oberflächensediment verglichen. Die Akkumulationsraten der Zysten im Oberflächensediment waren deutlich geringer als in der unteren Sedimentfalle. Unterschiede zwischen den relativen Häufigkeiten der Artenvergesellschaftungen in der Sedimentfalle und im Oberflächensediment, besonders der starke Verlust bei der Art *L. granifera*, die im Sediment nur ca. 3% der Artenzusammensetzung erreicht, im Vergleich zu ungefähr 30% in der tieferen Sedimentfalle, wurden wahrscheinlich durch Transport, spezifische Lösungsprozesse und die Variabilität in der Zystenbildung verursacht.

Die vorliegende Arbeit erweitert das ökologische Wissen über Kalkzysten produzierender Dinoflagellaten, besonders durch den vergleichenden Charakter der Untersuchungen, in dem Zystenexport dem Oberflächensediment gegenübergestellt wird bzw. räumlich abgegrenzte Oberflächensedimentproben oder aber rezente und holozäne Vergesellschaftungen miteinander verglichen werden. Die Ergebnisse dieser Arbeit lassen detaillierte Rekonstruktionen von Paläoumweltbedingungen, insbesondere in Auftriebsgebieten, zu und bekräftigen die Verwendung kalkiger Dinoflagellatenzysten als Proxies in der Paläozeanographie.

Contents

Chapter 1: Introduction 1

Calcareous cyst-producing dinoflagellates 2

Study Area 5

Structure of this thesis 8

Chapter 2: Calcareous dinoflagellate cyst distribution in surface sediments from upwelling areas off NW Africa, and their relationships with environmental parameters of the upper water column. 11

Richter, D., Vink, A., Zonneveld, K.A.F., Kuhlmann, H. and Willems, H., 2007

Marine Micropaleontology 63, 201-228

Chapter 3: Calcareous dinoflagellate cysts production in response to variations in upwelling intensity and lithogenic input from sediment trap material off Cape Blanc (NW Africa). 53

Richter, D. and Zonneveld, K.A.F.

To be submitted to Journal of Nannoplankton Research

Chapter 4: Seasonal variations in the calcareous dinoflagellate cyst production: A sediment trap study from the upwelling-influenced area off Cape Blanc 71

Richter, D., Vink, A., Meier, K.J.S. and Zonneveld, K.A.F.

To be submitted to Journal of Plankton Research

Chapter 5: Conclusions and future perspectives 93

Methodical approach 93

Ecological Information 94

Prospects of future research 95

References 97

Appendix: The (palaeo-) environmental significance of modern calcareous dinoflagellate cysts: a review 109

Zonneveld, K.A.F., Meier, K.J.S., Esper, O., Siggelkow, D., Wendler, I. and Willems, H., 2005.

Paläontologische Zeitschrift 79(1), 61-77

Danksagung 139

Introduction

The anthropogenic impact on the global climatic system has become one of the main fields of interest in recent times. To understand and predict future changes on Earth's climate, it is essential to research present as well as past processes causing climatic alterations (Florides and Christodoulides, 2009) .

A fundamental part of the climate system are the world oceans, promoting the heat transfer on the planet by ocean currents, and playing a central role for primary productivity, which affects the exchange of the greenhouse gas CO_2 between the atmosphere and the ocean (Hays et al., 2005). Reconstructions of past oceanographic and climatic variations are often based on the actualistic principle, making the basic assumption that past processes can be inferred from present-day observations, which means that ecological preferences of individual marine micro-organisms did not change over well-defined time scales and microfossil assemblages from the sedimentary record (i.e. coccoliths, diatoms, foraminifers) can reflect the environmental and hydrographic circumstances in which these organisms were produced (Fischer and Wefer, 1999 and references therein).

One of these environmentally sensitive organism groups which are suited for palaeoceanographic reconstructions are dinoflagellates, which form part of the phytoplankton community. They live in the upper water column of lakes and oceans where enough light for photosynthesis and nutrients are available. Several dinoflagellates produce geologically preservable cysts, which are either organic-walled, calcareous or rarely siliceous, as part of their life cycle (Taylor, 1987; Fensome et al., 1993, 1996)

Research on calcareous dinoflagellate cysts (dinocysts), their distribution and ecology is making a lot of progress in recent years. Studies of sediment-surface and sediment-trap samples as well as sediment cores have improved the general applicability and significance of calcareous dinocysts as proxies for palaeoenvironmental, palaeoclimatic, palaeoecological and palaeo–oceanographic reconstructions, at least during the Quarternary. It has been shown that dinoflagellates that produce well-preserving calcareous cysts react very sensitively to variations of environmental parameters, such as temperature, salinity, stratification in surface waters and nutrient supply (Zonneveld et al., 1999, 2000, 2005; Esper et al., 2000; Vink et al., 2000, 2001, 2002; Wendler et al., 2002a; Hildebrandt-Habel and Streng, 2003; Meier and Willems, 2003; Meier et al., 2004a; Vink, 2004). Therefore alterations in the dinoflagellate cyst assemblage can reflect environmental and hydrographic changes in the upper water column. Together with diatoms and coccolithophorids, dinoflagellates are major contributors to the marine eukaryotic phytoplankton and therefore play an important role as primary producers. Besides planktonic

foraminiferas and coccolithophores, calcareous dinoflagellates are important contributors to carbonate primary productivity in the equatorial Atlantic and offshore NW Africa (Kerntopf, 1997; Schiebel, 2001).

Most studies on calcareous dinocysts have been focussed on oligotrophic and mesotrophic regions (e.g. Vink, 2004 and references therein). Studies from upwelling areas were, so far, conducted only in the Arabian Sea (Wendler et al., 2002a,b,c) and the Benguela upwelling region (Zonneveld et al., 2000). Moreover, calcareous dinocyst studies on sediment trap material, providing information on relationship between cyst production and their individual environmental preferences, exist from the Mediterranean Sea (Montresor et al., 1998), from the western Atlantic Ocean and the Sargasso Sea (Dale, 1992), from the Northern Atlantic Ocean (Ziveri et al., 2000), the North-Western Pacific (Tanimura and Shimada, 2004), and the Arabian Sea (Wendler et al., 2002a), with the last one being the only study from a upwelling influenced area, so far. To establish dinoflagellate as a proxy for detailed palaeoceanographic reconstructions, it is essential to investigate as many different oceanic areas as possible. Especially from the highly productive areas of the Eastern Boundary Current (EBC) systems little is known about the calcareous dinoflagellate ecology, cyst production, and aspects of transport and dissolution.

Calcareous cyst-producing dinoflagellates

Dinoflagellates are a diverse group of eukaryotic, generally unicellular protists that typically occur as motile cells with two dissimilar flagella (one transverse and one longitudinal) and a characteristic nucleus, the so called dinocaryon (Fensome et al., 1993; 1996). They are widely abundant in almost all aquatic, but mainly in marine environments ranging from the tropics to the subarctic and from inner neritic to deep oceanic environments, reaching highest diversity in the tropics and neritic temperate waters (Dale, 1992; Stover et al., 1996).

The complex cell wall contains either cellulosic, non-fossilisable thecal plates within amphiesmal vesicles (termed thecate or armored dinoflagellates) or lacks thecal plates (termed unarmored or naked dinoflagellates). The arrangement of thecal plates is used to refer to tabulation, which is species-specific and forms a major taxonomic criterion. The cyst wall can entirely or partly reflect the tabulation pattern of the motile cell that formed the cyst (Fensome et al. 1993, 1996).

Reproduction of most motile dinoflagellates species, which are normally haploid cells, involves relatively simple mitotic, asexual cell division (Fensome et al., 1996). As part of their life cycle, many dinoflagellate species produce non-motile, geologically preservable cysts

(dinocysts), whose walls are built of organic material, silica or calcite (the latter are further referred to as the 'calcareous dinocysts'). So far, about 30 modern species of calcareous dinocysts are known (Vink, 2004). Calcareous dinocysts can be subdivided into two groups based on their life-cycle (Fensome et al., 1993, 1996): sexual resting cysts and vegetative coccoid cysts (Meier et al. 2007). The first group is characterised by alternating generations of thecate swimming stages and non-motile calcareous cysts that are produced after sexual fusion of two haploid thecae and forming a diploid planozygote (Fig.1). Continuous cyst production with short resting periods is observed in many oceanic species and has been proposed to be an adaptation to prevent sinking into unfavourable water depths in the open ocean (Meier et al. 2007). In the second group, i.e. *Thoracosphaera heimii* and *Leonella granifera,* calcareous vegetative coccoid cells are the dominant life-cycle stages (Fig. 2; Tangen et al. 1982, Inouye and Pienaar 1983, Meier et al. 2007). These presumably haploid vegetative cysts are metabolically and/or reproductively active in contrast to resting cysts (Fensome et al., 1996). Due to their asexual reproduction they show higher production rates, and usually *T. heimii* dominates the assemblages by an order of magnitude, with the exception of the Arabian Sea, where *L. granifera* can dominate fluxes (Wendler et al. 2002).

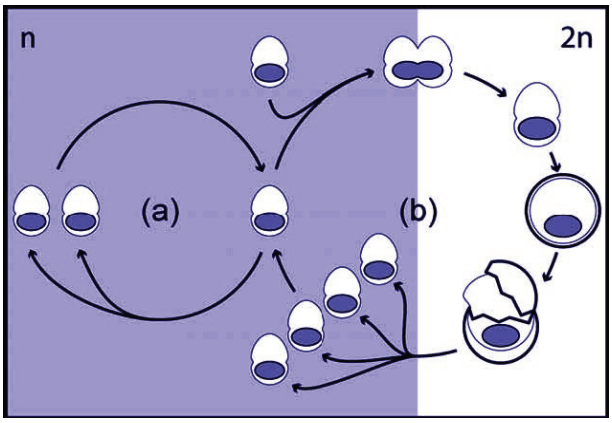

Fig. 1: Simplified life-cycle of calcareous dinoflagellates. Within the vegetative life-cycle phase (a) the motile stages are haploid (n) and reproduce by mitotic division. The fusion of two haploid motile cells results in the formation of a diploid (2n) planozygote that subsequently undergoes encystment (b). After excystment, four haploid daughter cells are formed by meiotic division (after Meier et al., 2007).

Processes regulating encystment of dinoflagellates as part of their sexual life cycle are barely understood and apparently vary from species to species. For species studied in culture, factors triggering cyst formation have been recently discussed (Godhe et al., 2001; Olli and Anderson, 2002, Meier et al., 2004). Changing environmental parameters such as day length, light intensity and/or temperature as well as endogenous rhythms might influence the sexual cycle and cyst formation (Godhe et al., 2001; Sgrosso, 2001), but especially nutrient depletion (nitrate and/or phosphate) is one of the main parameters inducing encystment (Anderson and Lindquist, 1985; Pfiester and Anderson, 1987; Olli and Anderson, 2002). Nevertheless, formation of cysts has often been observed following exponential population growth and commonly occurs after blooms, when nutrients in the water column are not depleted (Ishikawa

and Taniguchi, 1996; Montresor et al., 1998; Kremp and Heiskanen, 1999; Godhe et al., 2001). However, encystment is not only associated with sexual reproduction, but also with surviving unfavourable conditions such as an anoxic environment, low temperatures or darkness (Anderson et al., 1987; Sarjeant, 1987; Bravo and Anderson, 1994).

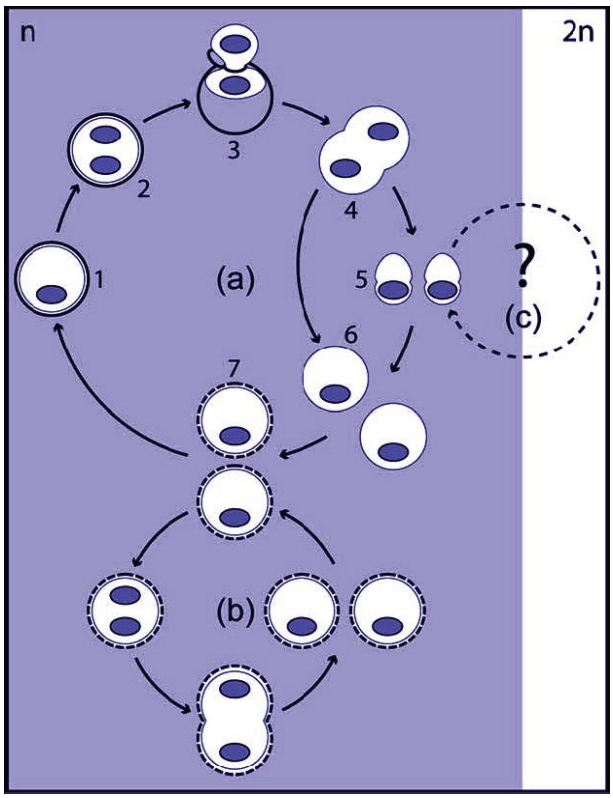

Fig. 2: Simplified life-cycle of *Leonella granifera* and *Thoracosphaera heimii*. Presumably haploid (n) calcareous vegetative cells (a, 1–2) are the dominant life-cycle stages. After a cell emerges from the calcareous shell (a, 3), it divides (a, 4) and forms directly aplanospores (a, 6) or through the production of planospores (a, 5). The aplanospores start calcification (a, 7), weakly calcified cells are capable of mitotic division (b). Sexuality might occur in a separate sexual cycle (2n) starting from the planospore stage (c) (after Meier et al., 2007).

After completing a dormancy period, in which the cyst is not able to hatch and metabolic processes are reduced, the protoplast leaves through an excystment aperture known as archeopyle and a new phase of vegetative reproduction starts. The dormancy period is species-specific and can range from about 12 hours to 12 months (Pfiester and Anderson, 1987), but there are also cysts remaining vital for almost a decade (Lewis et al., 1999). For excystment several factors such as light availability, temperature, oxygen concentration or endogenous rhythms are responsible (Binder and Anderson, 1986; Kremp and Anderson, 2000).

As most calcareous dinoflagellates have so far been found to be photoautotrophic organisms (Tangen et al., 1982; Binder and Anderson, 1987; Montresor et al., 1994), i.e. they are dependent on light for their metabolism and thus, they generally thrive in the upper water column where sufficient light is available for photosynthesis. Therefore, it may be assumed that the calcareous dinoflagellate abundance and production will be mainly determined by the ecological properties of the near-surface waters.

Study Area

The studied area is situated in the eastern North Atlantic Ocean within the Eastern Boundary Current (EBC) system off the NW African continental margin, which belongs to the four most important EBC systems. These ecosystems are characterized by their high primary production, reaching about 2% of the global marine production, although their areas constitute only 0.3 % of the global ocean, and thus are very important for fisheries. After the Benguela Current the CC is the second most productive EBC, with a total annual primary production of 0.33 Gt of carbon per year (Carr, 2002).

The surface sediment samples were obtained the Moroccan coast comprising the region from 27° to 32°N and 9° to 18°W, encompassing the Canary Islands. The coastline of this area is characterized by two cape locations: Cape Ghir and Cape Yubi. The sediment traps are deployed off Cape Blanc, Mauritania (Fig. 3), in water depths of approximately 730m and 3560m.

The major surface current along the Northwest African continental margin is the southward flowing Canary Current (CC), which is fed by the Azores Current, and forms the easternmost branch of the North Atlantic subtropical gyre. The Canary Islands represent a barrier to the equatorward flowing CC, resulting in a variety of mesoscale phenomena (Barton et al., 1998). At Cape Blanc the CC detaches from the African coast and turns westward under the influence of the northward flowing Equatorial Countercurrent to contribute to the North Equatorial Current (Mittelstaedt, 1991; Barton, 1998). South of Cape Blanc a mesoscale permanent cyclonic gyre persists, whose position and extension vary with the seasons (determined by the seasonally varying strength of the CC and Equatorial Countercurrent), extending the furthest north in autumn and winter but becoming the largest in summer (Fig. 3; Mittelstaedt, 1991; Gabric, 1993; Barton, 1998).

The high productivity of the region is fuelled by trade-wind driven coastal upwelling of cool and nutrient-enriched waters (Mittelstaedt, 1991). The coastal upwelling undergoes seasonal variability due to seasonal variations in the intensity of the NE trade winds, which are related to the position of the Intertropical Convergence Zone (ITCZ) and the associated Azores High, reaching their northernmost position in summer and their southernmost position in winter (Hernández-Guerra and Nykjær, 1997). Thus, north of 25°N upwelling generally happens in summer and fall, whereas fairly steady and strong winds lead to year-round upwelling with maxima in spring and summer between 20°N and 25°N (Mittelstaedt, 1991; Van Camp et al., 1991; Nykjær and Van Camp, 1994, Barton et al., 1998). Actual upwelling is usually restricted to waters over the shelf and the upper slope within a narrow band of 20 to 30 km (Mittelstaedt, 1991; Barton et al., 1998). Controlled by wind stress, surface currents, and coastal morphology,

upwelling filaments develop transporting cool, upwelled water up to several hundred kilometres offshore (Van Camp et al., 1991; Johnson and Stevens, 2000). Particularly at the cape locations these filaments are strongly pronounced and spread towards the open ocean, e.g. the quasi-permanent strong upwelling filament off Cape Ghir (Hagen et al., 1996). Off Cape Blanc "giant filaments" with very high chlorophyll-*a* concentrations extend about 450 km offshore, which are present throughout the year but vary seasonally and interannually (Van Camp et al. 1991, Barton, 1998).

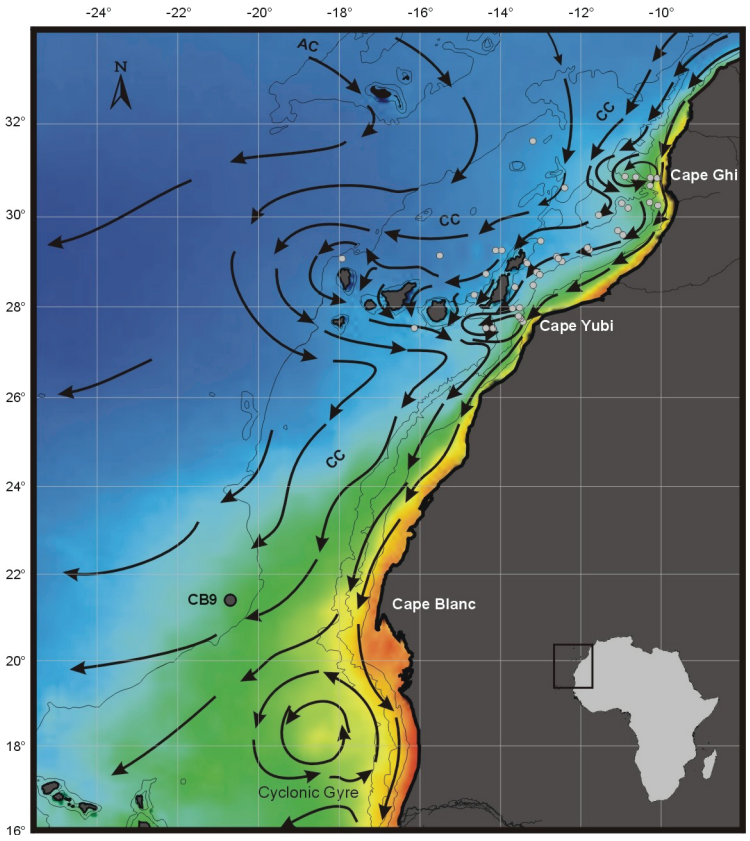

Fig. 3: Location of investigation area and study site CB; with depth contour lines (100, 1000, 2000 and 4000 m). Arrows indicate schematic surface water circulation (after Mittelstaedt, 1991). The average chlorophyll-a concentration between 1997 and 2004 is shown (obtained from the SeaWiFS Project / NASA Goddard Space Flight Center). Yellow to red = > 2 mg m^{-3}; green to blue = 0.5–2 mg m^{-3}.

In the northern region the main source of upwelled waters is the North Atlantic Central Water (NACW; Mittelstaedt 1991; Barton, 1998). Around Cape Blanc the confluence of the CC and the poleward flowing countercurrent cause a transition between the NACW and the South Atlantic Central Water (SACW; Mittelstaedt, 1991; Klein and Tomczak, 1994). The SACW has a higher nutrient content, is less saline and slightly cooler than the NACW (Barton, 1998). Consequently, the source of upwelled waters determines the nutrient input into the surface

waters by upwelling, and therefore influences productivity of the euphotic zone.

Additionally, a high input of aeolian dust from the central Sahara supplies nutrients and trace elements to the investigation area. Saharan dust is regularly transported under the influence of the westward Harmattan or Saharan Air Layer and the trade winds from the African continent over the North Atlantic Ocean (Fig. 4; Swap et al., 1996; Moulin et al., 1997; Ratmeyer et al., 1999; Middleton & Goudie, 2001). Biogeochemical processes, nutrient dynamics and oceanic productivity may be strongly affected by dust (Middleton and Goudie, 2001), as it is a source of trace nutrients such as iron (Pittman, 2002; Sarthou et al., 2003), which is essential for phytoplankton growth and enhanced primary productivity (e.g. Boyd et al., 2000).

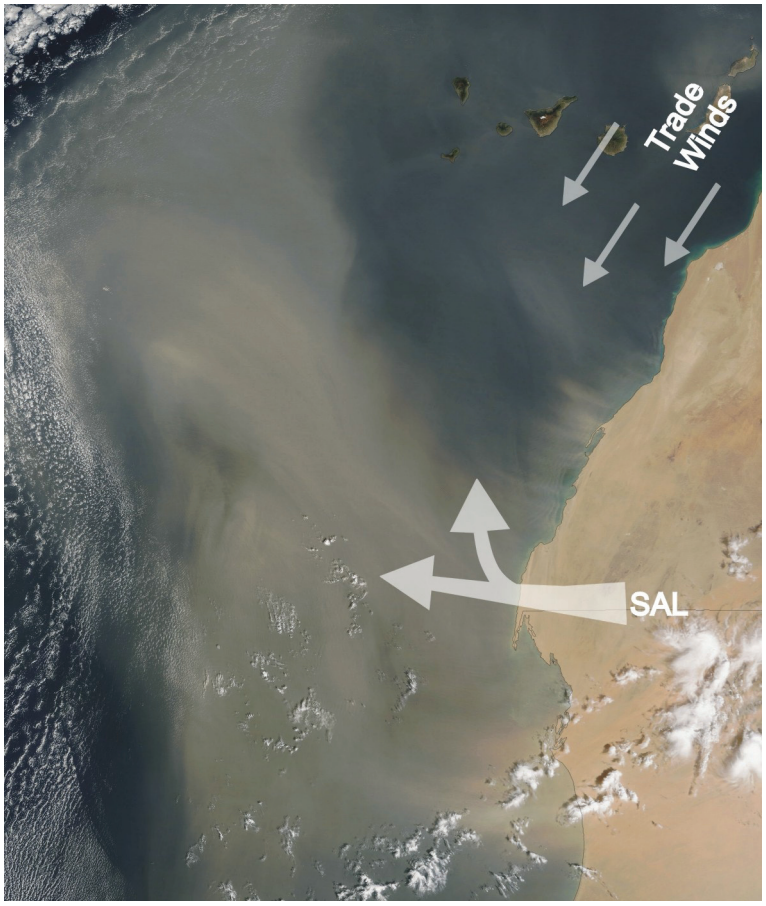

Fig. 4: True-colour image of a sand storm swept off the NW African continental margin captured by MODIS flying aboard NASA's Terra satellite. Arrows mark the present-day relevant wind systems: the Saharan Air Layer (SAL), carrying Saharan sand towards the west and north, and the NE trade winds.

In summary, the upwelling processes off NW Africa, associated with the variability of the trade winds, changes significantly seasonally and interannually. Upwelling filaments off the capes develop correspondely (Kostianoy and Zatsepin, 1996). Additionally, the source of upwelled waters (either NACW or SACW) as well as Saharan dust input determine the nutrient supply into the euphotic zone and thus strongly influence phytoplankton production.

Structure of this thesis

In this study, for the first time, surface sediment samples from the upwelling area off the Moroccan coast as well as sediment trap samples from the upwelling influenced area off Cape Blanc, Mauritania, were quantitatively analysed for their calcareous dinocyst content in relation to environmental properties of corresponding surface waters in order to enhance our existing knowledge on cyst species diversity, their geographic distribution and ecology.
In detail, the main objectives of the present study were:

- Acquisition of information on recent calcareous dinocyst associations in surface sediments from the upwelling influenced area of NW Africa.
- Mapping of present day spatial distribution patterns of single species and determining their relationships with environmental parameters of the (sub)surface waters in order to improve the still incomplete knowledge on modern dinocyst distribution and to establish the ecological significance and palaeoenvironmental reconstruction potential.
- Evaluation of sediment trap material and estimation of dinoflagellate cyst fluxes.
- Identification of seasonal patterns of calcareous dinoflagellate cyst fluxes
- Verification of ecological preferences and relationships between cyst fluxes and hydrographical conditions.
- Assessment of effects of different production, transport and dissolution mechanisms on cyst fluxes.

The results are described and discussed in chapters 2 to 4, represented by three manuscripts. Additionally, the appendix of this thesis includes a further publication, which is closely related to the main research topic, This review paper was a joint effort of the working group of Historical Geology and Palaeontology, in which I made a significant contribution about the ecology of calcareous dinoflagellates (under my maiden name D. Siggelkow).

Manuscript 1: ***Calcareous dinoflagellate cyst distribution in surface sediments from upwelling areas off NW Africa, and their relationships with environmental parameters of the upper water column***

This chapter focuses on recent calcareous dinocyst associations in surface sediments from the upwelling zone off Morocco. With the help of well-constrained sedimentation rates cyst accumulation rates were calculated, thus providing a precise estimation of actual calcareous dinoflagellate cyst production in the upper water column. Based on relative abundances and accumulation rates, geographic distribution patterns of the dinocyst assemblages are presented, and possible ecological preferences of the different species are determined using statistical multivariate ordination techniques. Substantial differences in cyst distribution patterns are observed, partly confirming previous results on cyst ecology but also providing new information which will be helpful for future palaeoenvironmental reconstructions within upwelling areas.

Manuscript 2: ***Calcareous dinoflagellate cysts production in response to variations in upwelling intensity and lithogenic input from sediment trap material off Cape Blanc (NW Africa)***

The determination of calcareous dinocyst fluxes was the main aim of the study of a sediment trap located close to the coastal upwelling area off Cape Blanc. The cyst fluxes of individual species have been compared with physical and trophic parameters from *in situ* measurements as well as with sea surface temperature data and chlorophyll-*a* concentrations obtained from online databases. The cyst fluxes relate to seasonal variations in intensity and duration of upwelling filaments and associated seasonal changes of environmental properties of the surface waters. Furthermore, a good correlation between nutrient supply through high Saharan dust input and dinocyst fluxes is revealed. This study shows that calcareous dinocysts respond very sensitively to rapid environmental changes.

Manuscript 3: ***Seasonal variations in the calcareous dinoflagellate cyst production: A sediment trap study from the upwelling-influenced area off Cape Blanc***

The objective of this chapter is to investigate production, transport and dissolution mechanisms of calcareous dinoflagellate cysts and the factors which influence their abundance between production in the upper water column and final deposition in the bottom sediment. Observations on sediment trap moorings deployed in two different water depths adjacent to the coastal upwelling region off Cape Blanc are presented By comparing the time shift of major flux peaks, sinking velocities of dinocysts were estimated. Finally, a comparison with the cyst assemblages in the surface sediment directly below the trap position reveals differences in

absolute and relative abundance Processes altering the identified cyst assemblage were determined and characterized.

Appendix: ***The (palaeo-) environmental significance of modern calcareous dinoflagellate cysts: a review***

This paper represents the state of the art of calcareous dinoflagellates cysts, and gives an overview of known data on calcareous dinoflagellate ecology, morphology, and taxonomy, demonstrating their applicability as proxies for palaeoenvironmental reconstruction.

Calcareous dinoflagellate cyst distributions in surface sediments from upwelling areas off NW Africa, and their relationships with environmental parameters of the upper water column

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Abstract

Only very few studies have focussed on the spatial distribution and ecology of calcareous dinoflagellate cysts (dinocysts) in upwelling areas. Here, distributions of individual calcareous dinocyst species in surface sediment samples from the coastal upwelling zone off NW Africa and their relationships with known environmental parameters of the (sub-)surface waters have been analysed in order to enhance our knowledge on their modern distribution patterns and to determine the ecological significance and palaeoenvironmental reconstruction potential of each calcareous dinocyst species within this exemplary high-productivity region. In addition to calculating relative cyst abundances, well-constrained sedimentation rates have allowed the calculation of dinocyst accumulation rates (cysts cm^{-2} ka^{-1}) for most of the surface sample positions, thus providing a much more accurate estimation of actual calcareous dinocyst production in the upper water column than could be warranted in similar studies so far. Distinct differences in the geographic distribution patterns of nine species were observed. In general, high accumulation rates of calcareous dinocysts were found around and south of 29°N and offshore the westernmost Canary Island La Palma, with slightly lower accumulation rates in the upwelling-influenced areas off Cape Yubi and in the upwelling filament area off Cape Ghir. Multivariate ordination techniques were applied in order to compare the cyst accumulation rates of individual species with physical parameters (temperature, salinity, density, mixed layer depth) and the trophic state (nitrate, phosphate and chlorophyll concentrations) of the overlying (sub-)surface waters. All species were found to relate significantly to one or more of the environmental parameters, partly confirming previous results on cyst ecology but also providing new information which will be useful for future palaeoenvironmental reconstructions within upwelling areas.

Keywords: calcareous dinoflagellate cysts; surface sediments; NW Africa; accumulation rates; statistical analyses; ecology

1. Introduction

Many dinoflagellate species produce geologically preservable calcareous or organic-walled cysts as part of their life cycle. Recent studies have shown that modern calcareous cyst-producing dinoflagellates react sensitively to environmental change, and that their cysts (dinocysts) can be very useful for the establishment of detailed palaeoceanographic reconstructions, at least during the Quaternary (Zonneveld et al., 1999, 2000, 2005; Esper et al., 2000; Vink et al., 2000, 2001, 2002; Wendler et al., 2002a; Meier and Willems, 2003; Vink, 2004; Meier et al., 2004a). However, most of these studies have focused on dinocyst distribution patterns and their relationships with environmental parameters in oligotrophic and mesotrophic regions (e.g. Vink, 2004 and references therein). So far, studies from upwelling areas were conducted only in the Arabian Sea (Wendler et al., 2002a,b,c) and the Benguela upwelling region (Zonneveld et al., 2000). In order to extend the existing knowledge on calcareous dinocyst ecology and palaeoenvironmental significance into new, previously unanalysed upwelling areas, we have thus focussed on the lateral distribution of calcareous dinocysts in surface sediments from the upwelling region off NW Africa (Morocco), and compared these distributions with environmental (physical and trophic) characteristics of the upper water column using statistical multivariate ordination techniques.

Previous ecological studies focussing on recent dinocyst distributions in surface sediments and their relationships with subsurface water parameters have always been based on relative (%) or absolute (cysts g^{-1}) abundances (e.g. Vink et al., 2000; Zonneveld et al., 2000; Wendler et al., 2002c; Vink, 2004). Both methods do not adequately reflect actual cyst production in the upper water column, as relative abundances are very sensitive to the so-called "closed-sum effect" (i.e. that an absolute increase in one species automatically leads to a relative decrease of all other species), and absolute abundances are susceptible to differences in sedimentation rate, which are bound to be large especially when coastal to offshore transects are taken into account. More direct relationships between cyst production and individual environmental preferences can be determined through culturing experiments (e.g. Karwath et al., 2000a; Meier et al., 2004b), sediment trap studies (e.g. Dale, 1992a,b; Dale and Dale, 1992; Montresor et al., 1998; Wendler et al., 2002a; Tanimura and Shimada, 2004) and isotope analyses (Friedrich and Meier, 2003; Zonneveld, 2004). Here we follow another approach. With the help of exact dating of subsurface sediments and the determination of well-constrained

sedimentation rates, we were able to calculate accumulation rates of calcareous dinocysts (cysts cm^{-2} ka^{-1}) for most of the analysed sample positions. Based on the assumption that secondary processes such as cyst transportation and selective preservation have not greatly altered the cyst assemblages qualitatively or quantitatively (see Discussion section), we can thus use surface sediment cyst accumulation rates to establish a more causal relationship between cyst production and the environmental parameters of the upper water column than could be warranted in previous analyses.

1.1. Oceanographic settings of the studied area

The investigation area encompassing the Canary Islands off NW Africa comprises the region from the Moroccan shelf between Cape Yubi and Cape Ghir to the westernmost Canary Islands Hierro and La Palma, as shown in Figure 1. The most important oceanographic surface water current is the Canary Current, which forms the easternmost branch of the North Atlantic subtropical gyre and flows southward over the continental shelf along the coast of NW Africa (e.g. Stramma, 1984; Stramma and Siedler, 1988; Barton, 1998; Johnson and Stevens, 2000).

The area is characterised by the presence of year-round coastal upwelling of cool and nutrient-enriched waters (Mittelstaedt, 1991). Actual upwelling is usually restricted to waters over the shelf and the upper slope within a narrow band of 20 to 30 km (Mittelstaedt, 1991). Thus, primary production is high on the shelf and decreases towards the oligotrophic oceanic waters of the subtropical gyre. The intensity of the Canary Current, as well as the strength and duration of coastal upwelling, depends on seasonal variations in the intensity and position of the NE trade winds, which are coupled with the meridional shift of the Azores High. The areas off Cape Ghir (~31°N) and Cape Yubi (~27°N) experience strong upwelling in summer and autumn and less intense upwelling in winter and spring (Mittelstaedt, 1991; Nykjær and Van Camp, 1994; Hernández-Guerra and Nykjær, 1997). Between the capes upwelling is less pronounced, as winds are directed primarily onshore (Hernández-Guerra and Nykjær, 1997).

Based on data from the World Ocean Atlas 1994 Data Set (National Oceanographic Data Centre, Washington D.C.), sea surface temperatures (SST) in the investigated area range from 17°C to 19°C in winter and from 20°C to 23°C in summer (Appendix A), with lowest temperatures around Cape Ghir and highest temperatures in the south-western oceanic part of the investigated area. Sea surface salinity (SSS) fluctuates between 36.25 and 36.78 p.s.u. only (Appendix A). Despite these minor variations, an E-W gradient is clearly recognisable, i.e. near the coast between the capes salinity is lowest and near the westernmost Canary Islands salinity is highest. The gradient develops due to upwelling of relatively fresh Central Water near the

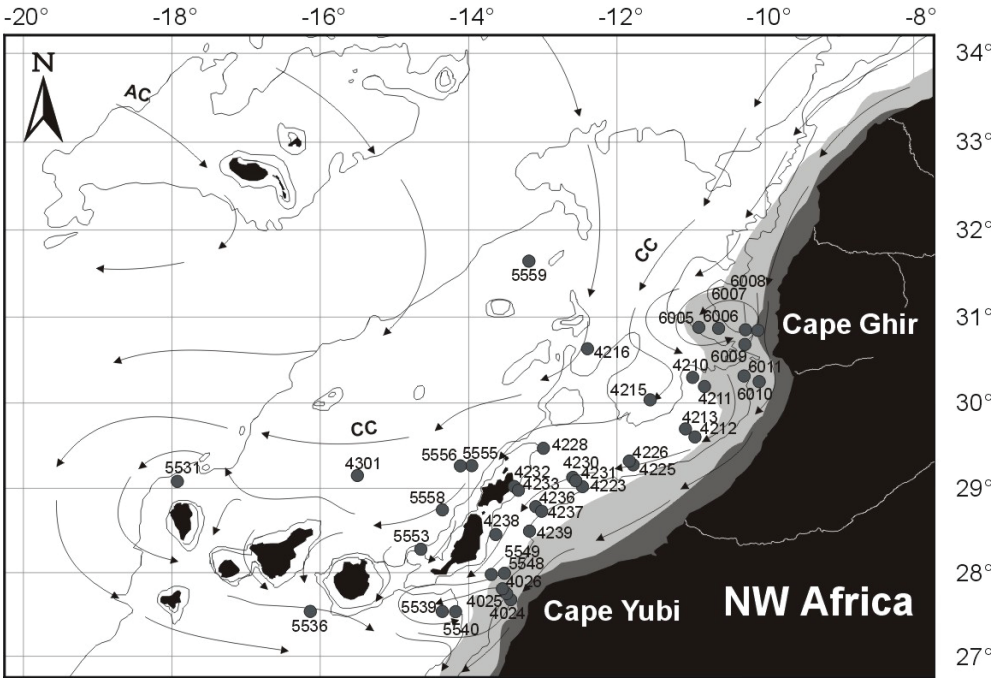

Fig. 1: Map of the investigation area with depth contour lines (100, 1000, 2000 and 4000 m). Circles show surface sediment sample locations and numbers (the prefix 'GeoB' has been omitted for clarity). Arrows indicate surface water currents after Mittelstaedt (1991): AC = Azores Current; CC = Canary Current. The coastal upwelling area and upwelling filaments are shown based on average chlorophyll-a concentration between 1997 and 2004 (obtained from the SeaWiFS Project / NASA Goddard Space Flight Center). Dark grey shading = > 2 mg m^{-3}; light grey shading = 0.5–2 mg m^{-3}.

coast, followed by evaporation and consequently a salinity increase as the waters are transported offshore (Hagen et al., 1996). It is more conspicuous in the summer season and in surface waters than in the winter season and at 75 m water depth. The mixed layer depth and its associated thermocline are relatively deep in spring (down to 180 m) but shallow in summer and winter (5 to 90 m). The mixed layer is generally shallower near the coast than in offshore areas, indicating that (sub-)surface waters are more stratified near the coast and less stratified in the upwelling filaments and the offshore regions. The distribution of nutrients, explained by concentrations of phosphate and nitrate, changes with increasing water depth. At sea surface, nitrate concentration is relatively high around Cape Ghir, decreases toward southern direction and has lowest values at Cape Yubi. At 75 m water depth nitrate distribution shows an opposite gradient, with lowest concentrations at Cape Ghir and increasing values towards south-western direction and at Cape Yubi. Nitrate concentrations at 100 m water depth are still high at Cape Yubi but are also enhanced between the Capes. In contrast, phosphate concentration at sea surface is low off the capes and increases between them and in offshore direction. Phosphate concentration at 75 m water depth is very similar, but with slightly enhanced values at Cape

Ghir. At 100 m water depth, the values increase at Cape Ghir and west of Tenerife and decrease between the capes. Terrigenous sediments are transported into the investigated oceanic areas either through aeolian dust input or through fluvial supply. Presently, fluvial supply to the Atlantic Ocean occurs mainly in the northern area off Cape Ghir, e.g. by the Souss River. South of 29°N, arid conditions prevail on the continent and aeolian dust deriving from the Saharan region dominates the terrigenous input (Schütz et al., 1981; Sarnthein et al., 1982; Swap et al., 1996; Holz et al., 2004; Kuhlmann et al., 2004).

The Canary Current system contains filaments and eddies which are formed due to the meandering nature of the Canary Current. They transport cool, upwelled water up to several hundred kilometres offshore (van Camp et al., 1991; Johnson and Stevens, 2000). Most of the filaments develop near the capes of the African coast, e.g. the quasi-permanent strong upwelling filament off Cape Ghir (Hagen et al., 1996). High chlorophyll-a pigment concentrations indicating high primary productivity are observed in filaments as well as in the zone of coastal upwelling (van Camp et al., 1991; Davenport et al., 1999). The main source of the upwelled water (coming from depths between 100 and 300 m) is North Atlantic Central Water (NACW) (Mittelstaedt, 1983), which is relatively cool (ca. 7°C to 14°C) and salinities range between 34.9 and 35.9 p.s.u. (Poole and Tomczak, 1999). Water masses below this layer (e.g. Antarctic Intermediate Water (AIW) and below that, very salty Mediterranean Outflow Water) have no significant influence on (sub-)surface water conditions.

A northward-flowing undercurrent has been reported along the African slope between 20°N and 34°N (e.g. Mittelstaedt, 1991; Barton, 1998; Johnson and Stevens, 2000), which is less than 100 km wide and has a vertical extension of several hundred meters (Barton, 1998). Off the Moroccan coast, it flows at depths of around 1000 m and transports substantial admixtures of South Atlantic Central Water (SACW) in its upper part and AIW in its deeper part (Mittelstaedt, 1989). Bottom water masses are comprised either of North Atlantic Deep Water (NADW) flowing in a southerly direction between 2000 m and 3800 m, or Antarctic Bottom Water (AABW) which flows in a north-easterly direction below 3800 m water depth.

2. Material and methods

2.1. Material and laboratory preparation

Surface sediment samples were collected from the upper centimetre of forty multicores which were obtained during METEOR cruises M37/1, M38/1, M42/4 and M45/5, and VICTOR HENSEN cruise VH96/1 (Fig. 1, Table 1). For thirty of the forty sites, surface sedimentation

rates could be calculated based on the stratigraphy of gravity cores that were retrieved from the same sites. The sedimentation rates vary between 1.92 cm ka^{-1} far offshore, 3–6 cm ka^{-1} in the area between the capes, and about 10 cm ka^{-1} in the upwelling filament off Cape Yubi (Table 1). At site GeoB 6007 near Cape Ghir, a very high sedimentation rate of ~85 cm ka^{-1} was documented, as this site is located in a small sedimentation trough (Kuhlmann et al., 2004). All the tops of the gravity cores were found to contain sediments of Holocene age (Kuhlmann et al., 2004). We therefore assume that our studied material was deposited during recent to sub-recent times, varying in age from about 100 or less years in the upwelling-influenced region to approximately 500 years in the open ocean.

Table 1
Core and cruise number, geographical position, water depth and sedimentation rates of the investigated surface sediment samples

Core GeoB	Cruise	Latitude (°N)	Longitude (°W)	Water depth (m)	Sed. rate (cm ka^{-1}) (Kuhlmann et al., 2004; this study)
4024-3	VH 96/1	27.68	13.43	98	
4025-1	VH 96/1	27.75	13.49	504	
4026-1	VH 96/1	27.81	13.54	990	
4210-2	M 37/1	30.30	10.98	1959	3.67
4211-1	M 37/1	30.19	10.82	1773	3.83
4212-3	M 37/1	29.60	10.95	1256	4.42
4213-1	M 37/1	29.70	11.08	1547	2.92
4215-1	M 37/1	30.04	11.55	2106	3.00
4216-2	M 37/1	30.63	12.40	2325	3.83
4223-1	M 37/1	29.02	12.47	777	11.17
4225-3	M 37/1	29.28	11.78	1281	4.25
4226-1	M 37/1	29.32	11.83	1400	4.17
4228-1	M 37/1	29.47	12.99	1633	6.67
4230-1	M 37/1	29.13	12.60	1316	5.50
4231-2	M 37/1	29.09	12.56	1207	7.75
4232-1	M 37/1	29.02	13.39	1161	6.42
4233-2	M 37/1	28.98	13.33	1303	6.00
4236-2	M 37/1	28.78	13.10	1030	6.83
4237-1	M 37/1	28.73	13.02	800	6.50
4238-2	M 37/1	28.45	13.64	1185	4.25
4239-1	M 37/1	28.49	13.18	881	10.75
4301-1	M 38/1	29.15	15.50	3614	5.06
5531-1	M 42/4	29.08	17.93	3301	4.67
5536-3	M 42/4	27.54	16.14	3456	6.50
5539-2	M 42/4	27.54	14.36	2202	
5540-3	M 42/4	27.54	14.18	2035	9.92
5548-3	M 42/4	27.99	13.52	1162	8.83
5549-2	M 42/4	27.98	13.70	1454	11.25
5553-2	M 42/4	28.28	14.65	3397	
5555-2	M 42/4	29.27	13.96	2837	6.00
5556-3	M 42/4	29.27	14.11	3170	4.33
5558-2	M 42/4	28.75	14.35	2471	
5559-1	M 42/4	31.65	13.19	3178	1.92
6005-1	M 45/5	30.88	10.90	1781	
6006-2	M 45/5	30.87	10.63	1282	5.92
6007-1	M 45/5	30.85	10.27	899	86.75
6008-2	M 45/5	30.85	10.10	355	
6009-1	M 45/5	30.68	10.28	579	
6010-1	M 45/5	30.25	10.08	406	
6011-2	M 45/5	30.32	10.29	993	6.83

The laboratory preparation of the calcareous dinocysts follows the method described by Vink et al. (2000). 1 cm^3 of the sediment was oven-dried and approximately 400 mg of the dried sediment was wet-sieved and split into two fractions (5–20 µm and 20–75 µm) to concentrate relatively large but rare species in one fraction and the small but abundant specimens of *Thoracosphaera heimii* in the other fraction. 50 µl from 15 ml of the larger fraction and 100 µl from exactly 100 ml of the smaller fraction were placed upon slides and embedded in SPURR's resin. The cysts were counted using a light microscope with polarised light and a gypsum plate (Janofske, 1996). One whole slide per fraction and sample was counted. If a slide contained less than 200 specimens,

additional slides were analysed. Raw count data are provided in Appendix B. We calculated relative cyst abundances for all of the samples, as well as cyst accumulation rates (cysts cm^{-2} ka^{-1}) for the thirty samples with known sedimentation rates.

2.2. Statistical methods

Geographic distribution maps based on (i) the relative abundances of calcareous dinocyst species (excluding *T. heimii* from the total cyst sum due to its overwhelming dominance in the assemblage); and (ii) accumulation rates of all species and *T. heimii*, were produced (Figs. 2–10). To determine potential relationships between dinocyst distribution patterns and environmental parameters, redundancy analyses (RDA) were carried out on the entire datasets as well as on accumulation rates of single species using the statistical package CANOCO for Windows (CANOnical Community Ordination: version 4.02, author C.J.F. Ter Braak 1992, Wageningen, The Netherlands). We carried out the RDA on relative abundance data (RDA rel) for a direct external comparison with available distribution data from other regions (e.g. from the entire South Atlantic; Vink, 2004), as well as for a methodological internal comparison with the results from accumulation rate data. However, we assume that the RDA on accumulation rate data (RDA acc) provides a better estimation of the factors influencing actual cyst production in the upper water column. The choice for using redundancy analyses for the current datasets was based on the outcome of initial detrended correspondence analyses (DCA), which calculated a linear type of ecological response for the calcareous dinocysts in both datasets; i.e. the species appear to react linearly to changing environmental gradients in both datasets (see Hill and Gauch, 1980; Jongman et al., 1987). This outcome is not surprising as the environmental gradients are relatively short in the restricted area off NW Africa.

The principle aim of a RDA is to directly relate the species' distributions to known environmental parameters of the overlying (sub-)surface waters (e.g. Figs. 11 and 12). The correlation coefficient between a species and the environmental gradient corresponds to the cosine of the angle between the cyst response line and the gradient line: a positive score of a species represents an increasing abundance of the species along the gradient, and a negative score the opposite. Species lines pointing in the same direction indicate that the species are positively correlated with each other, i.e. that they occur in similar samples and hence have similar distribution patterns. Lines pointing in opposite directions indicate a negative correlation, and perpendicular lines indicate lack of correlation. Species that plot close to the centre of the diagram are most likely not affected by the environmental gradients.

The environmental parameters used in the RDA are summarised in Table 2 and are: (a)

water depth at the sample location; (b) mean temperatures, salinities, densities, phosphate and nitrate concentrations at three different water depths (0 and 75 m as standard, and an additional depth of 100 m for phosphate and nitrate concentrations because of frequent thermocline-related increased concentrations at this depth); (c) mixed layer depth (as a measure of stratification, i.e. a shallow mixed layer indicates stronger subsurface stratification); and (d) sea surface chlorophyll-a concentration. Mean temperatures, salinities, mixed layer depths and chlorophyll-a concentrations were obtained for two periods of the year (i.e. hypothetical seasons): summer (= July to September) and winter (= January to March). These time periods were chosen to chart the seasonality of the area (with strong upwelling occurring during summer and spring and less intense upwelling during the winter months), rather than taking a yearly average in which seasonal variations in environment are lost (see Appendix A). All environmental data were obtained from the World Ocean Atlas 1994 Data Set, National Oceanographic Data Centre, Washington D.C. (http://ingrid.ldgo.columbia.edu/SOURCES/.LEVITUS94/) and the SeaWiFS Project from the NASA Goddard Space Flight Center (http://seawifs.gsfc.nasa.gov/SEAWIFS.html).

The ranking of environmental variables according to their importance in significantly influencing the species' distributions (Table 3), and the detection of covariance between the parameters involved, is based on the principle of forward selection. Both the marginal effects (representing the amount of variance explained by that variable, uncorrected for possible covariance) and the conditional effects (representing the amount of variance explained by that particular variable only, after the elimination of covariance) were calculated for each variable. Furthermore, the significance of each environmental variable was judged from a Monte Carlo permutation test with 199 permutations. These tests serve to minimise problems associated with covariation due to the small spatial and seasonal contrasts between environmental parameters in the investigated area, and thus lower the risk of potential overrepresentation of insignificant variables in the dataset. Because of the small size of the investigated area and hence the close proximity of all sites, an additional problem which may lead to overrepresentation of environmental variables in the analysis is the occurrence of spatial autocorrelation – the tendency of sites close to each other to resemble one another more than randomly selected sites (Fortin and Jacquez, 2000; Legendre, 1993; Telford and Birks, 2005). However, we assume that even in the presence of autocorrelation, the analysed environmental dataset will provide helpful information; the potential effects of overrepresentation of variables being reduced by only taking those environmental variables whose eigenvalues are $\geq 15\%$ into consideration.

3. Results

3.1. Geographic distributions of calcareous dinocyst species

Eight species/taxa of calcareous dinocysts, in addition to the vegetative coccoid species *Thoracosphaera heimii*, were observed regularly in the samples, but in different abundances. These are *Leonella granifera*, *Calciodinellum levantinum*, *Calciodinellum albatrosianum*, paratabulated *Calciodinellum albatrosianum*, *Calciodinellum elongatum*, *Pernambugia tuberosa*, *Scrippsiella regalis* and a group of spiny cysts (*Scrippsiella* spp.) containing several different species or morphotypes which cannot be attributed to *S. regalis* (mainly *Scrippsiella trochoidea*). Calcareous dinocysts were present in almost every sample. Only one sample (GeoB 4024-3) was barren. This sample originates from the coastal area off Cape Yubi which is characterised by river influence that brings nutrients, sand and fresh water into the coastal system.

Generally high accumulation rates of calcareous dinocysts and *T. heimii*, in total reaching up to 19.000.000 specimens cm^{-2} ka^{-1}, were observed around and south of 29°N and offshore the westernmost Canary Island La Palma, whereas slightly lower rates occur in the upwelling-influenced areas off Cape Yubi and in the upwelling filament area off Cape Ghir (Figs. 2–10). *T. heimii* strongly dominates the total association due to its high reproduction rates and may form 88–98% of the assemblage. Off NW Africa, it has a widespread distribution without a clear distribution pattern, although slightly higher accumulation rates are observed south of 29°N and beyond the upwelling filaments (Fig. 2).

L.granifera, *C. levantinum* and *C. albatrosianum* are the most common dinocyst species in the assemblages (Fig. 3, 4 and 5, respectively). *L. granifera* may form up to 66% of the cyst association (i.e. excluding *T. heimii*), especially in the shelfward areas. Highest accumulation rates are found on the broad shallow shelf north of Cape Yubi (Fig. 3). Cysts of *C. levantinum* constitute 25–60% of the total cyst association, but may form up to 70% off Cape Ghir (Fig. 4) and in the southern, more offshore areas. However, the highest accumulation rates are found in the southern region (below 29°N) off Cape Yubi and not off Cape Ghir. The distribution pattern of *C. albatrosianum* based on both relative abundances and accumulation rates is very similar to that of *C. levantinum*. Accumulation rates are also highest in the southern region, but a more prominent transition from higher to lower accumulation rates at ca. 29°N is present (Fig. 5).
C. albatrosianum paratabulated has a comparable geographic distribution to that of *C. albatrosianum* (Fig. 6), with highest values in the southern area. However, accumulation rates drop much more sharply in an offshore direction than those of either *C. albatrosianum* or *C. levantinum*, showing a generally more shelfward distribution. *P.*

tuberosa is a relatively rare species off NW Africa. Only few specimens were found in the coastal areas, with higher relative abundances and accumulation rates occurring in regions further offshore (Fig. 7). Another uncommon species is *C. elongatum* (Fig. 8). Relative abundances and accumulation rates increase slightly in the area between the upwelling filaments and further offshore. Cysts of *S. regalis* are also rare in the dataset and show a rather patchy relative distribution, with highest values in the northern part of the studied region (Fig. 9). In contrast, accumulation rates are the highest in the shelfward areas and on the broad shelf off Cape Yubi, i.e. in the southern part of the area. The uncommon group of spiny cysts (*Scrippsiella* spp.) has a very clear distribution pattern and occurs in highest relative abundances and accumulation rates in the upwelling filaments off both capes (Fig. 10).

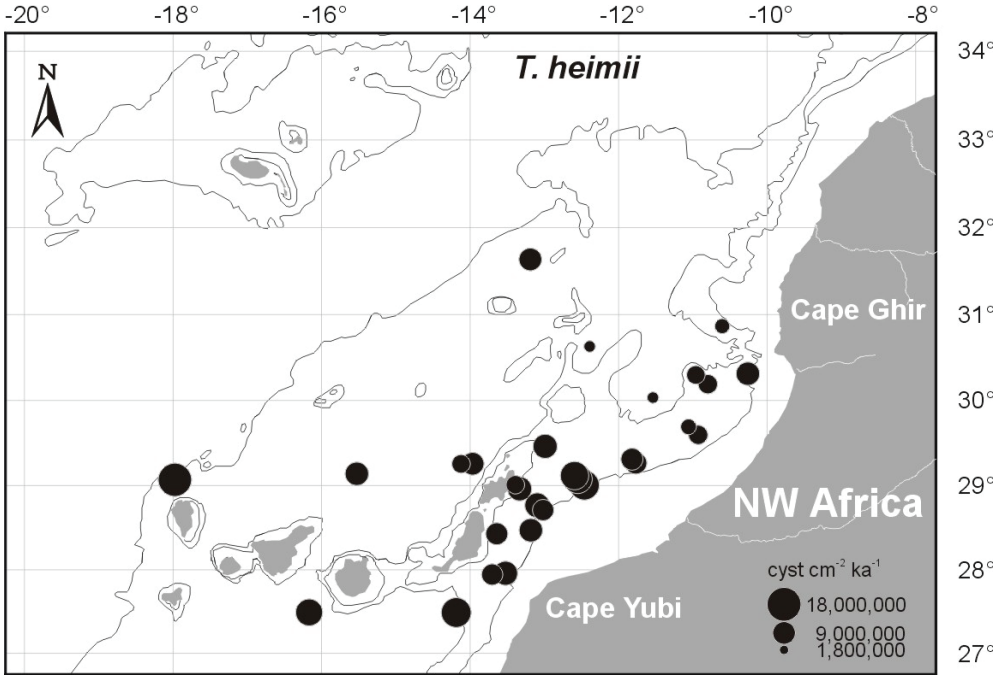

Fig. 2: Surface sediment distribution map of *Thoracosphaera heimii* based on accumulation rates.

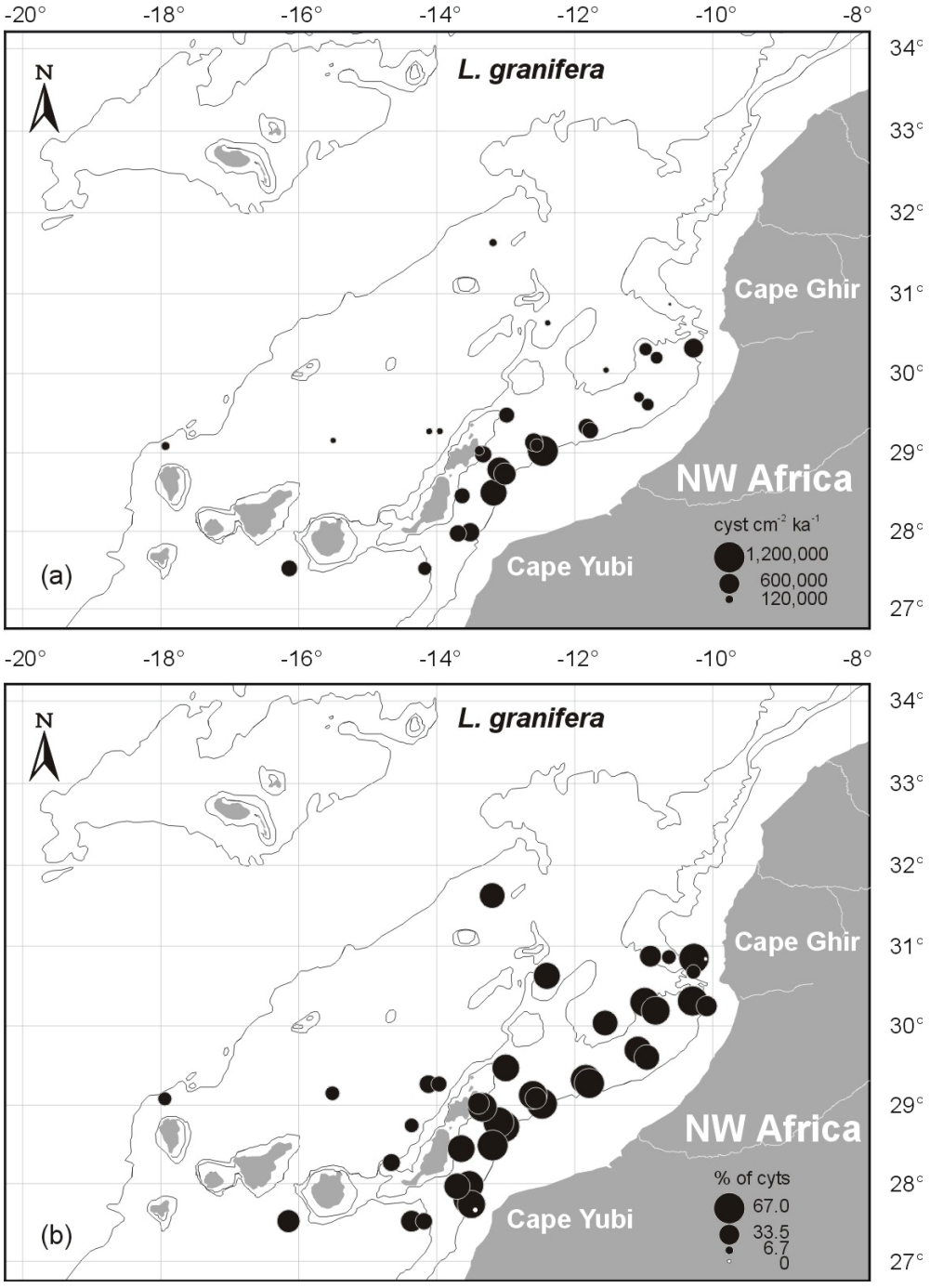

Fig. 3: Surface sediment distribution maps of *Leonella granifera* based on (a) accumulation rates, and (b) relative abundances as % of total dinocysts (excluding *Thoracosphaera heimii*).

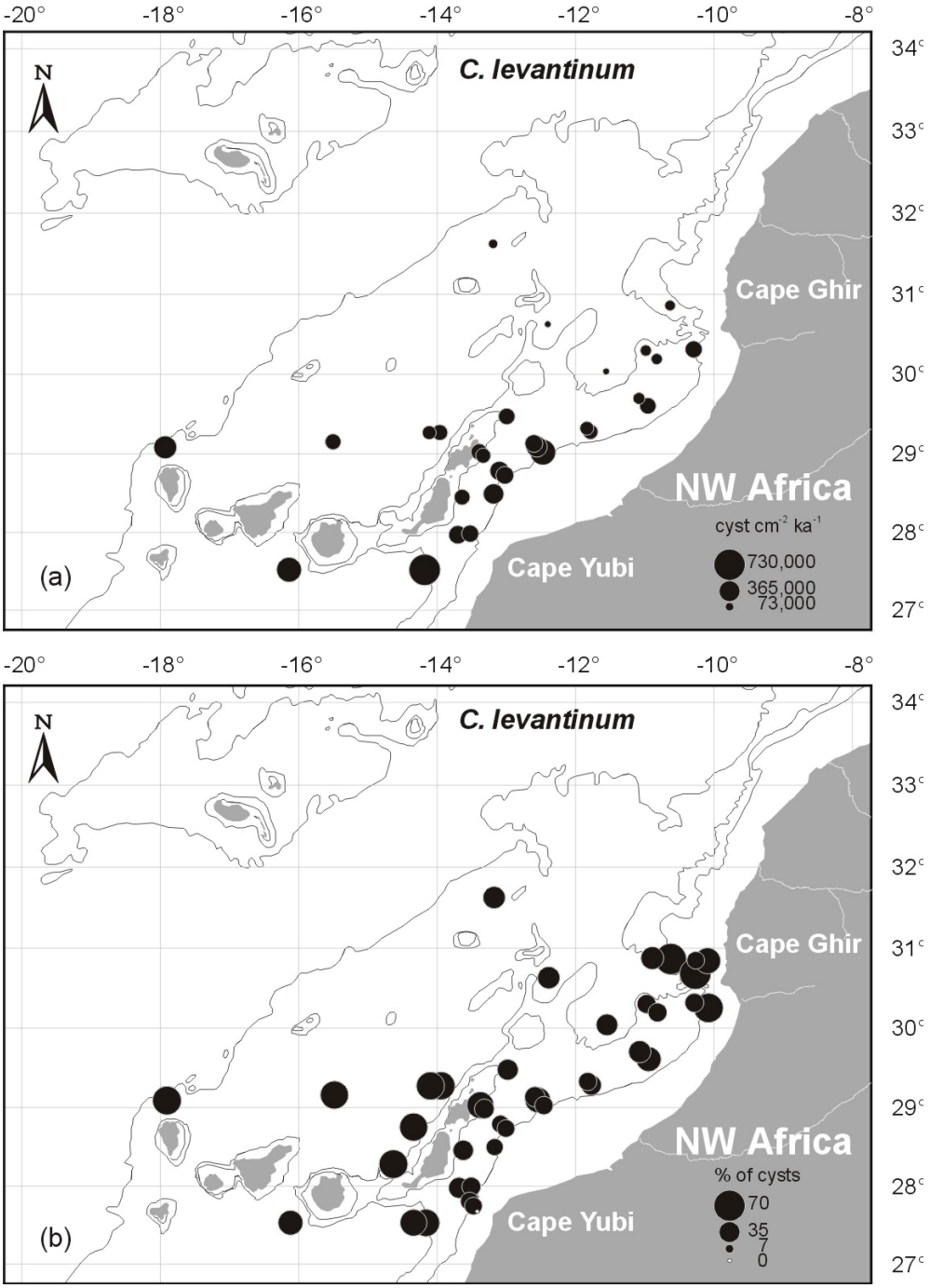

Fig. 4: Surface sediment distribution maps of *Calciodinellum levantinum* based on (a) accumulation rates, and (b) relative abundances as % of total dinocysts (excluding *Thoracosphaera heimii*).

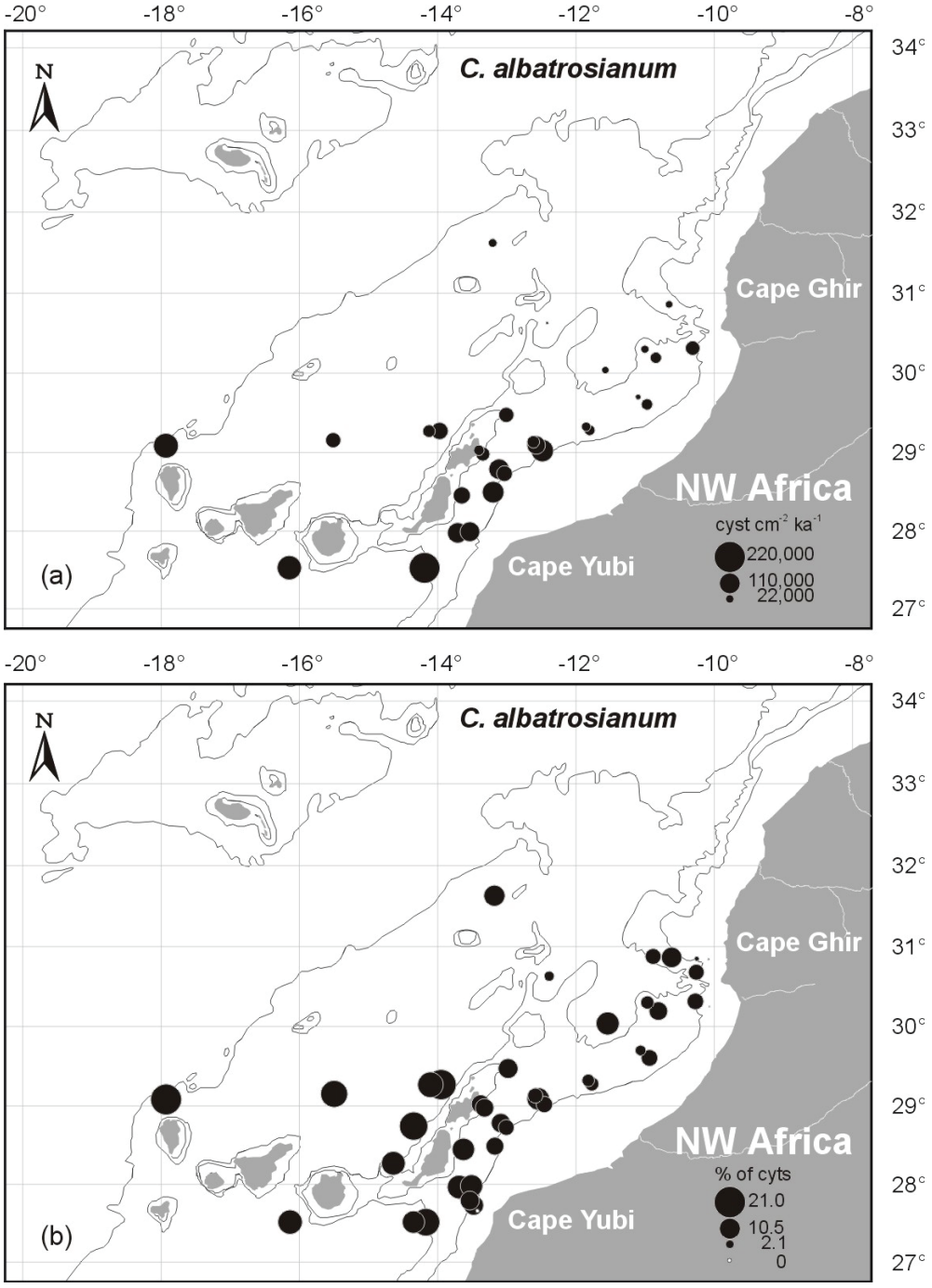

Fig. 5: Surface sediment distribution maps of *Calciodinellum albatrosianum* based on (a) accumulation rates, and (b) relative abundances as % of total dinocysts (excluding *Thoracosphaera heimii*).

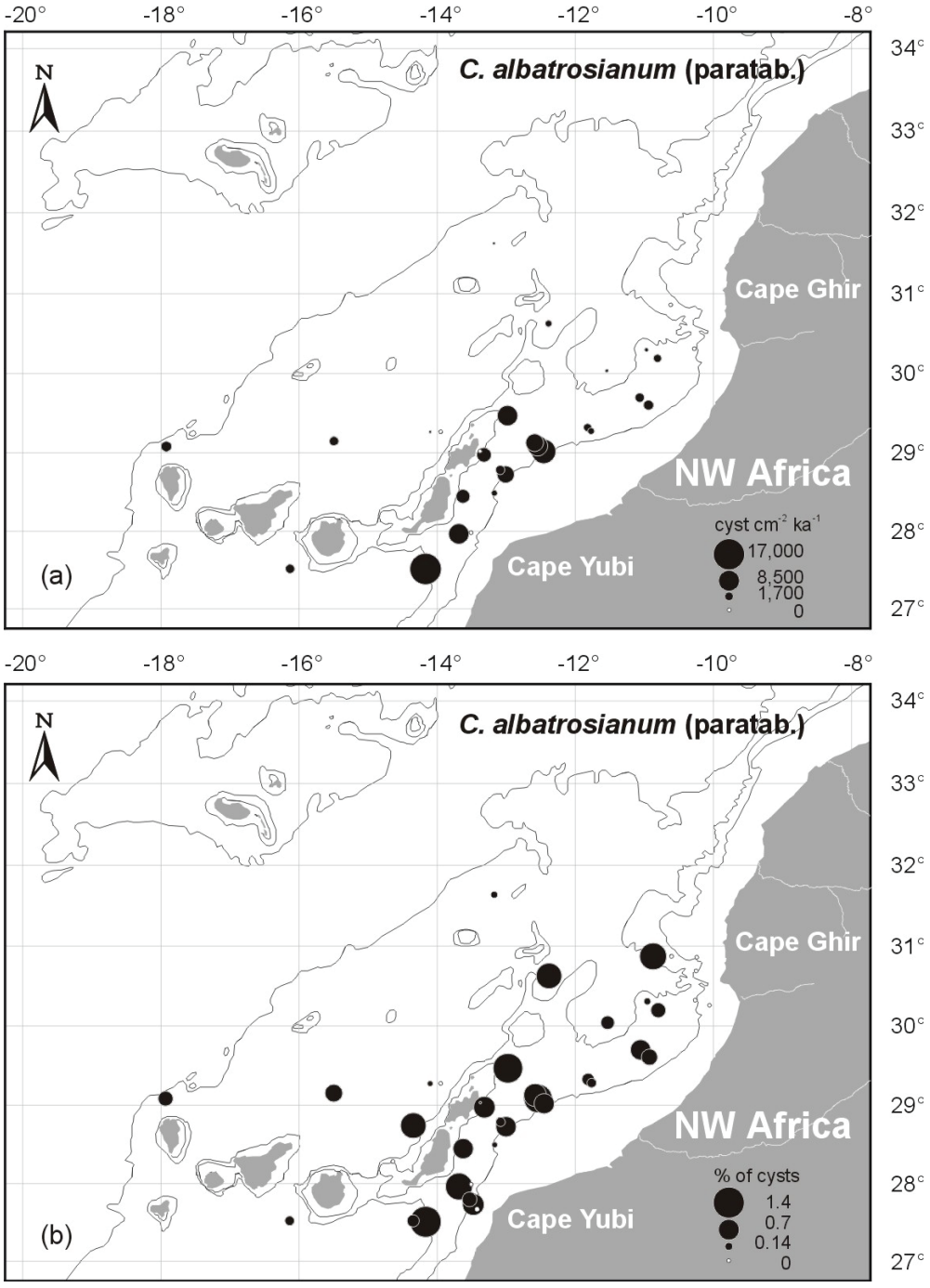

Fig. 6: Surface sediment distribution maps of paratabulated *Calciodinellum albatrosianum* based on (a) accumulation rates, and (b) relative abundances as % of total dinocysts (excluding *Thoracosphaera heimii*).

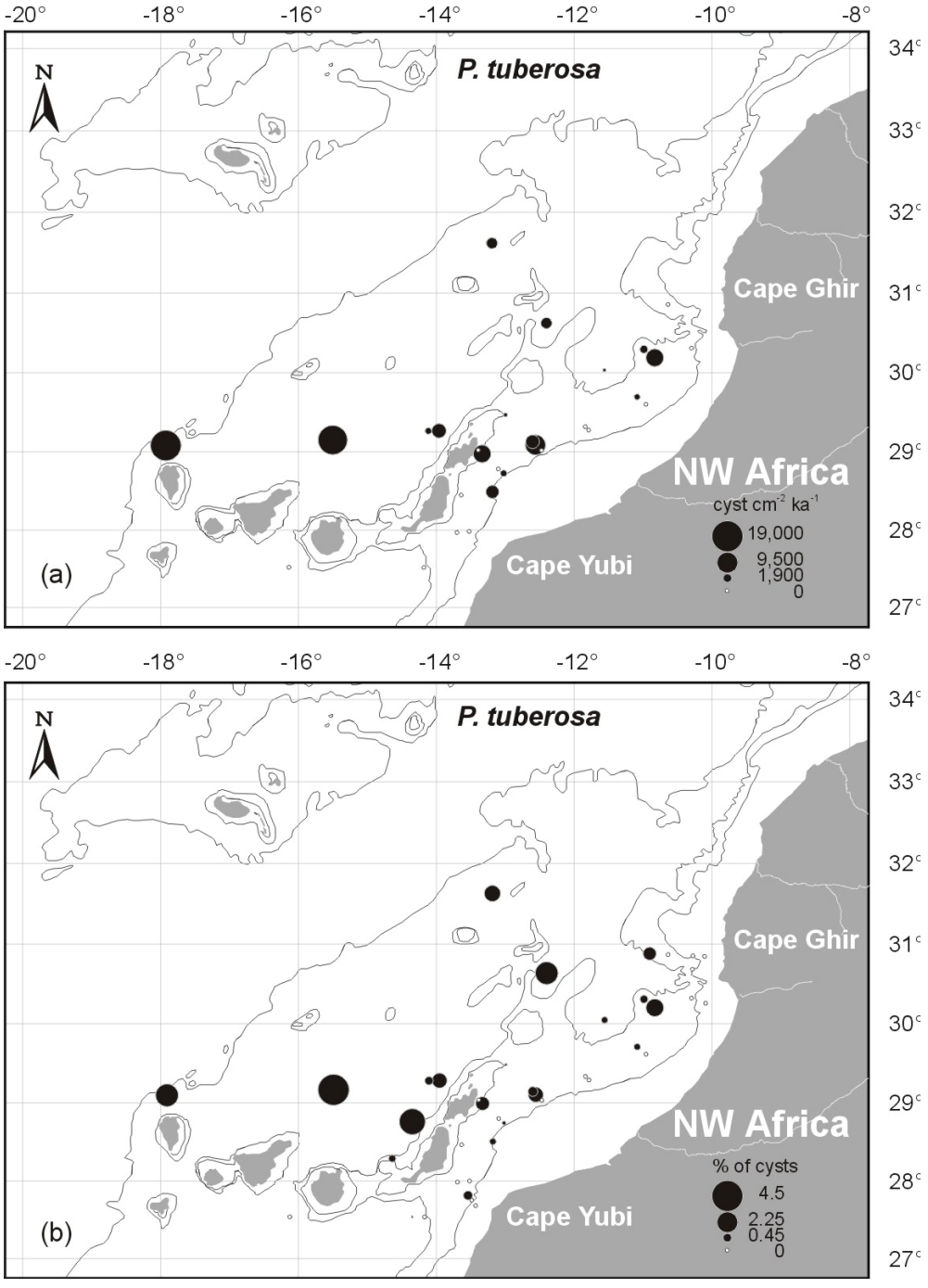

Fig. 7: Surface sediment distribution maps of *Pernambugia tuberosa* based on (a) accumulation rates, and (b) relative abundances as % of total dinocysts (excluding *Thoracosphaera heimii*).

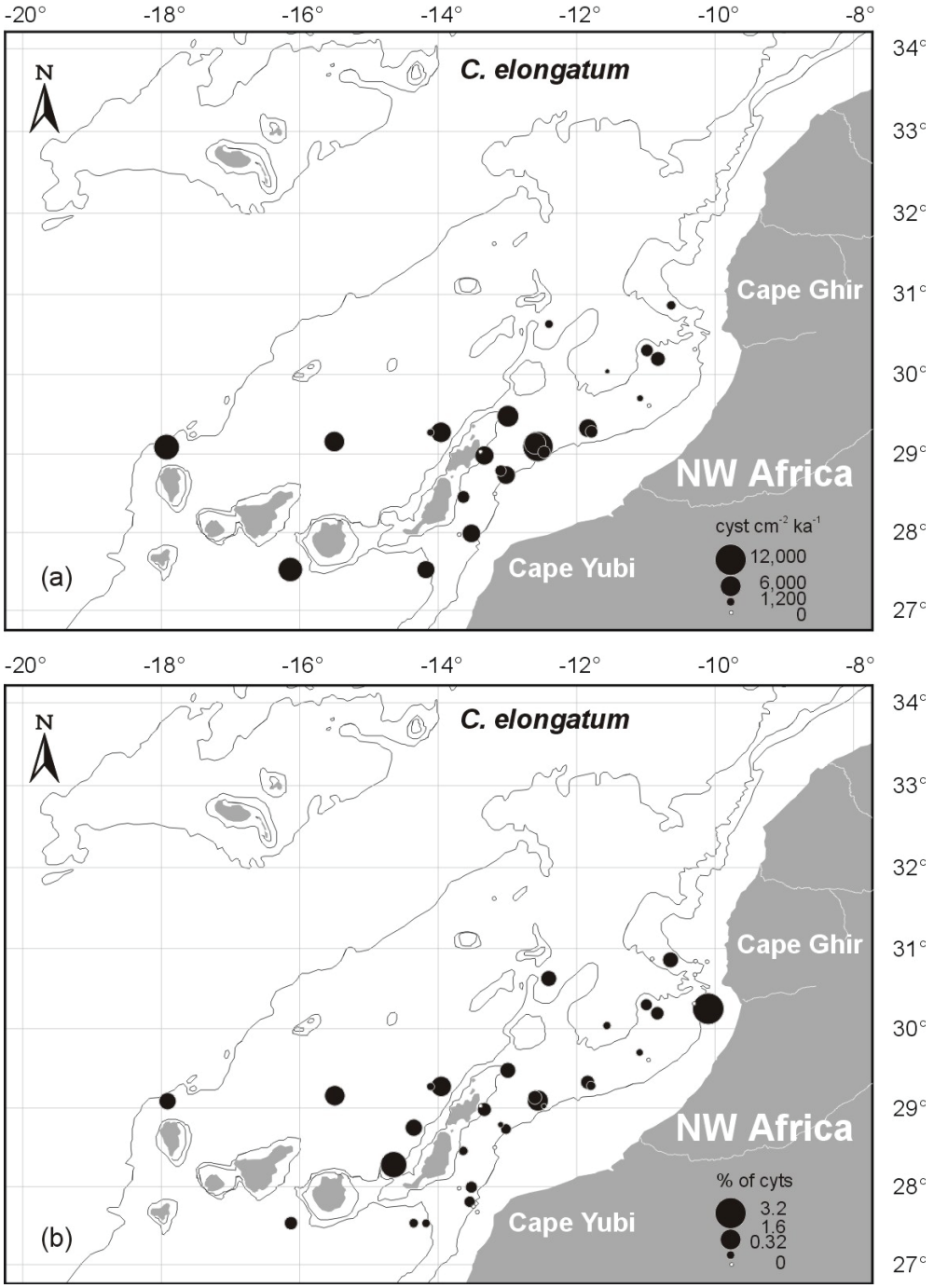

Fig. 8: Surface sediment distribution maps of *Calciodinellum elongatum* based on (a) accumulation rates, and (b) relative abundances as % of total dinocysts (excluding *Thoracosphaera heimii*).

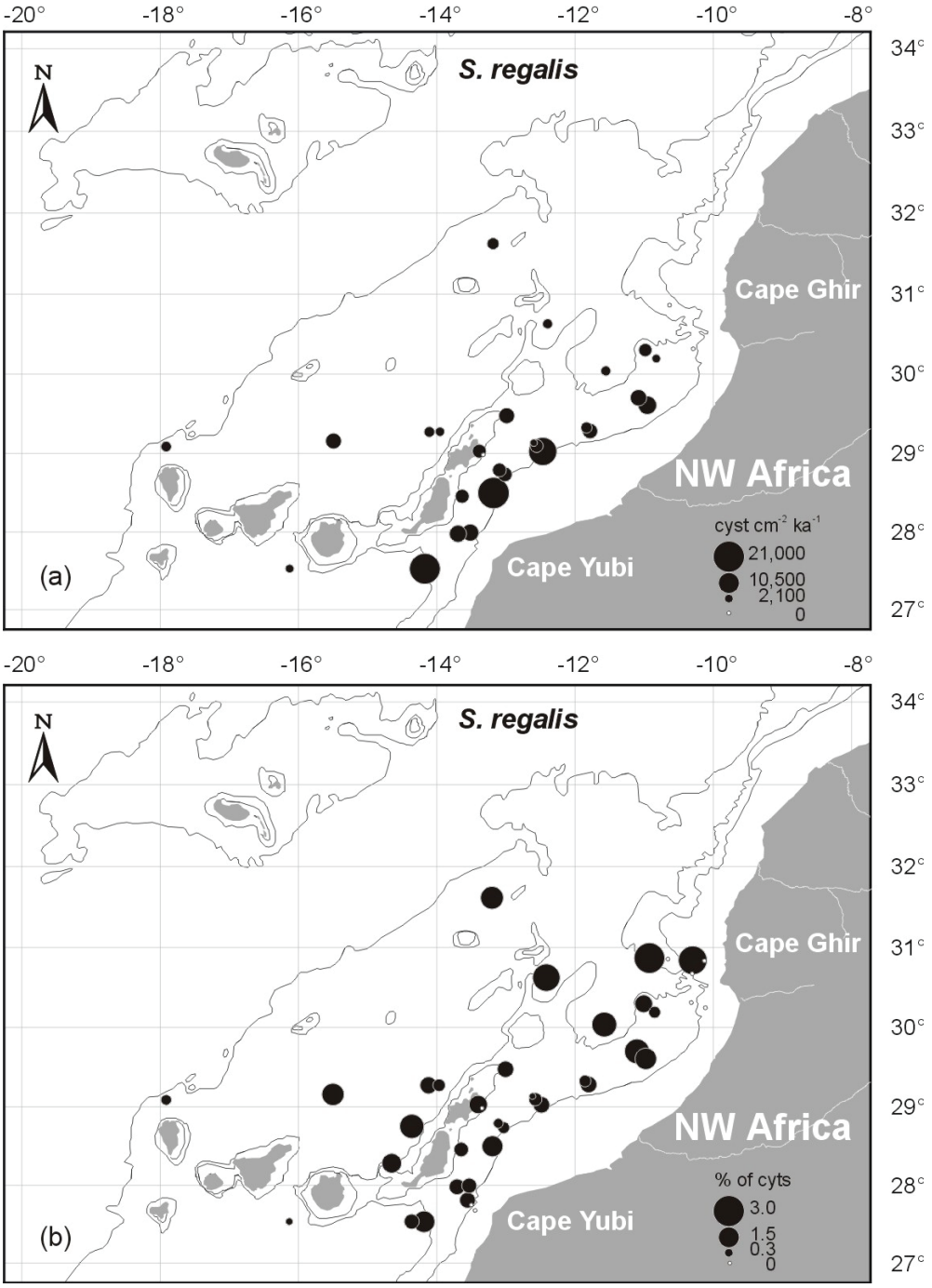

Fig. 9: Surface sediment distribution maps of *Scrippsiella regalis* based on (a) accumulation rates, and (b) relative abundances as % of total dinocysts (excluding *Thoracosphaera heimii*).

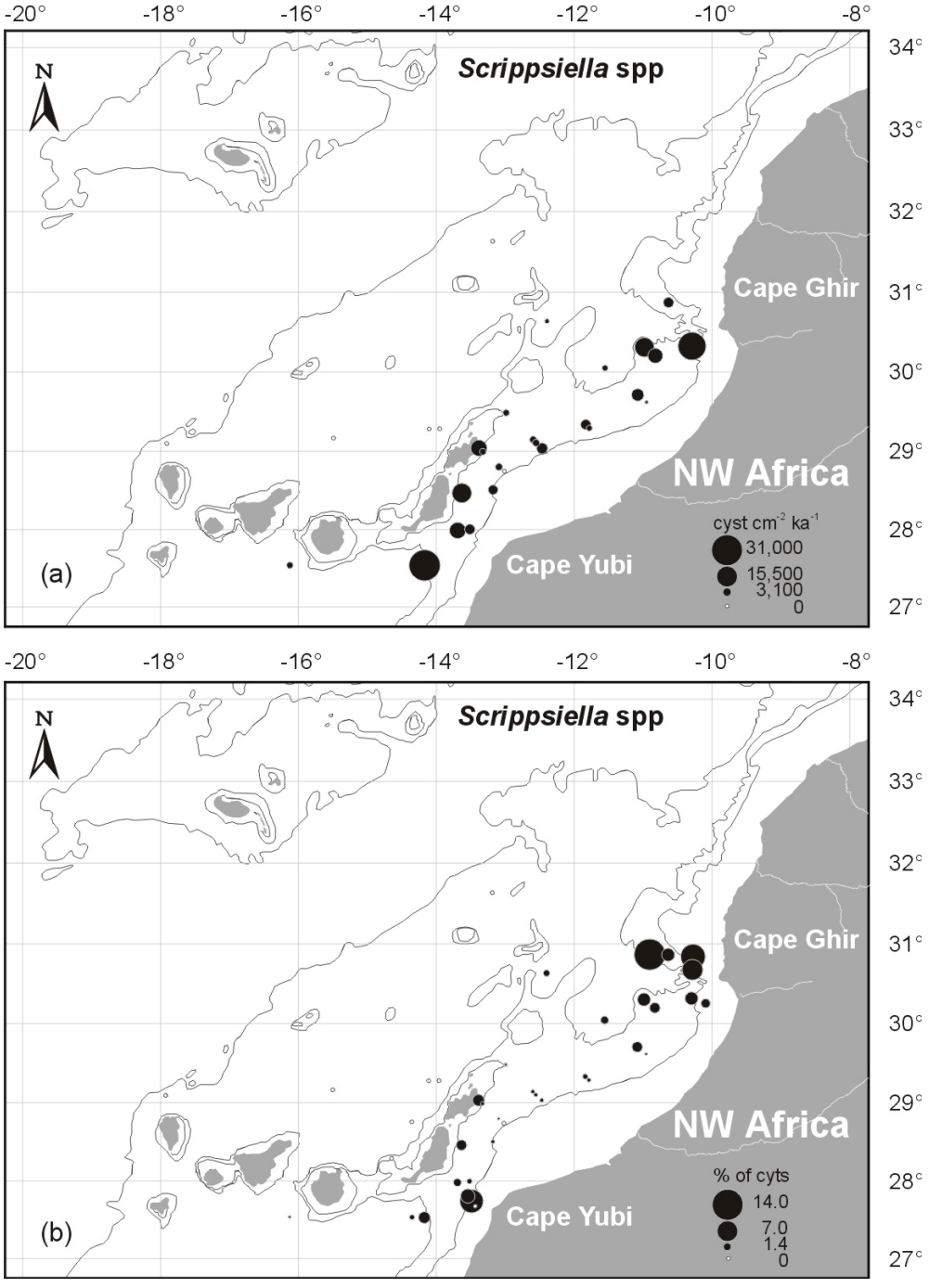

Fig. 10: Surface sediment distribution maps of *Scrippsiella* spp. based on (a) accumulation rates, and (b) relative abundances as % of total dinocysts (excluding *Thoracosphaera heimii*).

3.2. Statistical analyses

In the RDA rel and RDA acc analyses, *Thoracosphaera heimii* counts have been excluded from the calculations as their exceedingly high abundances overshadow the whole assemblage and cause a single most significant direction of variation. Furthermore, due to the exceptional position of sample GeoB 6007 in a high-sedimentation trough, this sample has been excluded from the statistical analyses. GeoB 4024, 4025, 6008, 6009 and 6010 were also omitted due to their statistically insufficient dinocyst concentrations, most likely caused by dilution at these sites.

The results of the statistical analyses are shown in figures 11 (RDA rel) and 12 (RDA acc). In RDA rel, the first axis explains 79.9% of the total variance in species composition, whereas the second axis explains only 2.1% and is thus insignificant. The distributions of the significant environmental variables and the dominant species *Leonella granifera* and *Calciodinellum levantinum* around the first axis (Fig. 11), in addition to the insignificance of the second axis, effectively show that this analysis summarises the antagonistic relationship between these two species only, thus obscuring relationships with all other species which generally form less than 30% of the cyst assemblage. This is a typical problem associated with the "closed-sum effect" of relative abundances where only few species, of which two are much more dominant than the rest, are involved. Therefore, the results of the analysis can only be used to explain the distributions of *L. granifera* and *C. levantinum*.

The variables best explaining the opposing distributions of *L. granifera* and *C. levantinum* are summarised in Table 3. The seasonal temperature and salinity variables at 0 and 75 m water depth covary very strongly. Thus, the temperature variables T75 win and T75 sum, as well as the salinity variables at 0 and 75 m water depth (S0 win and S0 sum; S75 win and S75 sum) have been taken as single parameters. In the resulting analysis, WD, PO_4^{3-}-100, S0 win/sum, T0 sum, Z mix sum, S75 win/sum, T0 win, Chl win and T75 win/sum appear to be the most significant marginal parameters determining the variation in the species composition (in decreasing order of importance), each explaining ≥ 15% of the variation (Table 3). However, when the amount of variability explained by only one particular variable is calculated through forward selection (thus eliminating covariance effects), only two variables show a significance ≥ 10%: WD and Zmix sum (Table 3). Moreover, PO_4^{3-}-0 turns out to be a significant parameter when considered alone in the absence of covariance, with a significance of 7%. The relative abundances of *L. granifera* correlate negatively with WD and Zmix sum, but positively with PO_4^{3-}-0 (Fig. 11; Table 4), thus indicating that highest abundances are found primarily in the more shelfward areas where a shallow mixed layer depth (indicating stratified subsurface water conditions) and relatively high surface phosphate concentrations predominate. Furthermore,

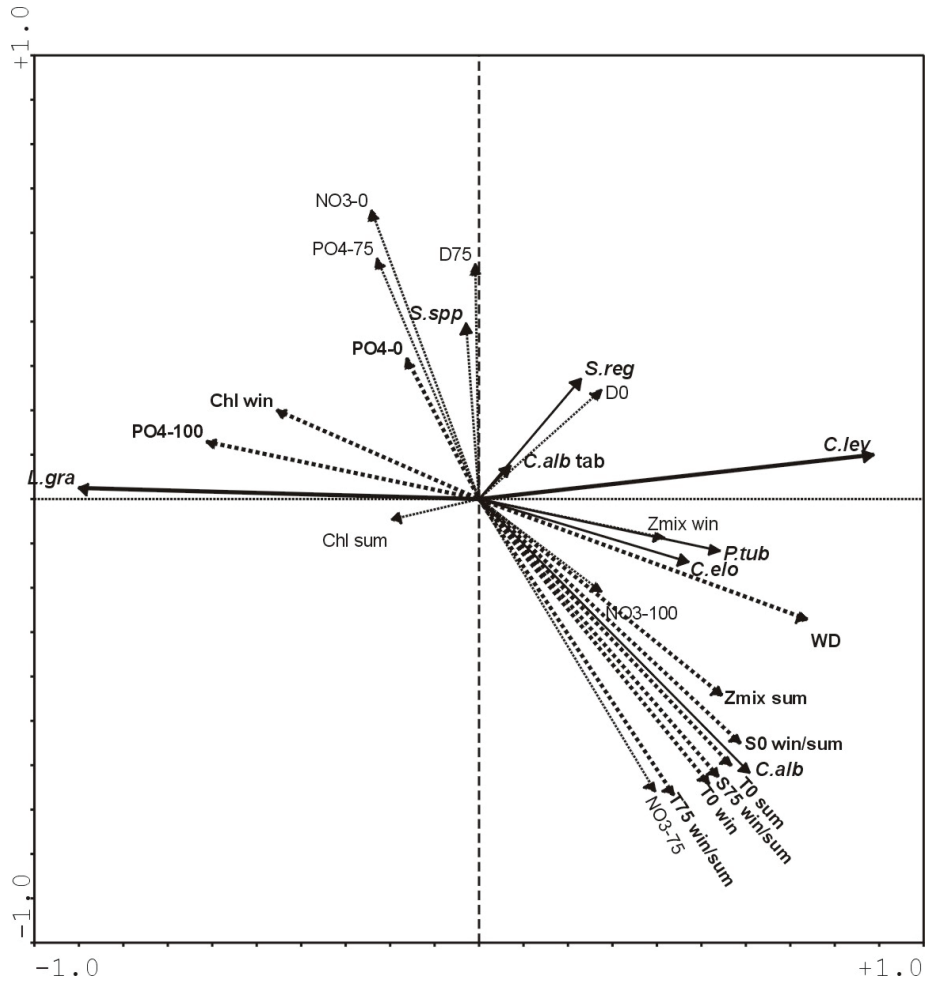

Fig. 11: Redundancy analysis diagram showing the relative abundances of calcareous dinocyst species in relation to known environmental parameters of the upper water column (RDA rel). Values along the first and second axes correspond to standard deviations. See Table 2 for an explanation of variable abbreviations. The arrows of parameters significantly influencing species' distributions (marginally and conditionally) are indicated in bold.

when considering the marginal effects, *L. granifera* abundance correlates positively with PO_4^{3-}-100, and Chl win, and negatively with the salinity variables S0 win/sum and S75 win/sum, and the temperature parameters T0 win, T0 sum and T75 win/sum (Table 4). This indicates high abundances in regions with relatively high nutrient concentrations at 100 m water depth as well as at the sea surface and where subsurface temperatures and salinities are relatively low. *C. levantinum*, on the other hand, shows a completely opposite trend, indicating a relationship with greater water depths, relatively high temperature and salinity, and a relatively deep mixed layer, but low nutrient and winter chlorophyll-a concentrations in subsurface waters.

In RDA acc, 82.2% of the total variance in species' distributions can be explained by the first two axes, with 65.6% explained by the first and 16.6% by the second axis. *L. granifera* and

C. levantinum now plot perpendicular to one another rather than as opposites, showing that the results of this analysis are generally less dominated by these two species. In addition to the redundancy analysis carried out on the whole dataset, RDAs were carried out on single species to determine their specific individual relationships with environmental parameters (i.e. the marginal and conditional effects) which are potentially blurred when dominating species are included in the dataset. The most important relationships between species and environmental parameters based on the entire dataset (Fig. 12; Table 3) as well as individual analyses of single species are summarised in Table 4. As the analyses were carried out on a slightly reduced number of sample sites in comparison with RDA rel, covariation characteristics between parameters are slightly different, and an additional covariance is observed between the salinity values S75 win/sum and T0 win (most likely related to the upwelling process, as the upwelling of relatively fresh Central Water lowers surface water temperature). In the resulting analysis for

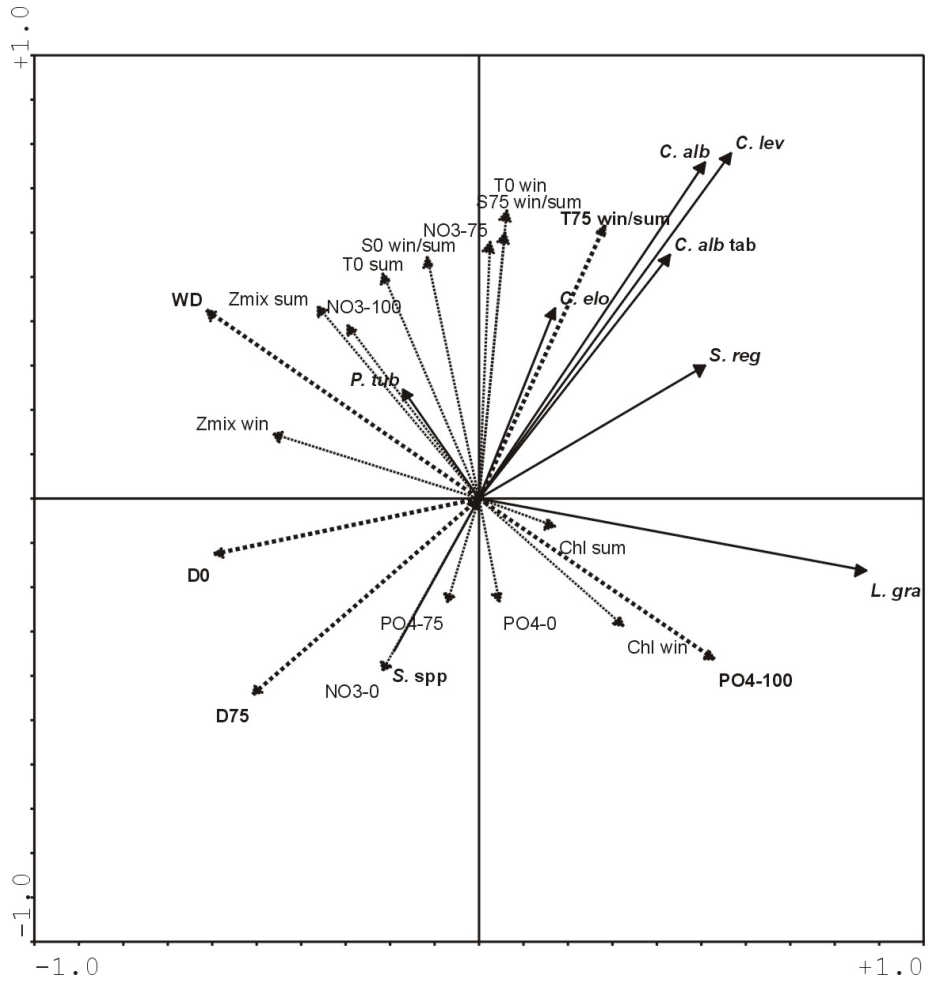

Fig. 12: Redundancy analysis diagram showing the accumulation rates of calcareous dinocyst species in relation to known environmental parameters of the upper water column (RDA acc). Values along the first and second axes correspond to standard deviations. See Table 2 for an explanation of variable abbreviations. The arrows of parameters significantly influencing species' distributions (marginally and conditionally) are indicated in bold.

Table 2
Description of the environmental parameters used in the statistical analyses (values listed in AppendixA)

Parameter	Description	Unit
WD	water depth at sampling site	m
T0 win	sea surface temperature in winter	°C
T0 sum	sea surface temperature in summer	°C
T75 win	sea temperature at 75 m water depth in winter	°C
T75 sum	sea temperature at 75 m water depth in summer	°C
S0 win	sea surface salinity in winter	p.s.u.
S0 sum	sea surface salinity in summer	p.s.u.
S75 win	salinity at 75 m water depth in winter	p.s.u.
S75 sum	salinity at 75 m water depth in summer	p.s.u.
D0	sea surface density	g cm-3
D75	density at 75 m water depth	g cm-3
Zmix win	mixed layer depth in winter	m
Zmix sum	mixed layer depth in summer	m
NO3--0	nitrate concentration at sea surface	micromolar
NO3--75	nitrate concentration at 75 m water depth	micromolar
NO3--100	nitrate concentration at 100 m water depth	micromolar
PO43--0	phosphate concentration at sea surface	micromolar
PO43--75	phosphate concentration at 75 m water depth	micromolar
PO43--100	phosphate concentration at 100 m water depth	micromolar
Chl win	chlorophyll-a concentration in winter	mg m-3
Chl sum	chlorophyll-a concentration in summer	mg m-3

the entire dataset, WD, D0, PO_4^{3-}-100 and D75 appear to be the most significant marginal parameters determining the variation in the species composition, each explaining ≥ 15% of the variation (Table 3). However, only WD and T75 win/sum are significant when conditional effects are taken into account. Mixed layer depth (Z mix) is an insignificant parameter for cyst accumulation in this case. Nevertheless, additional analyses carried out on single species' accumulation rates do show that each species has its own significant relationships with environmental parameters (Table 4).

Only two parameters appear to influence *L. granifera* accumulation conditionally: low WD and low S75 win/sum (and thus low T0 win). In fact, the conditional effect of WD on all species' distributions when considering the whole dataset (Fig, 12; Table 3) is due to the strong weighting of this species' preference for shallow waters in comparison to all other species which are either not influenced by water depth or rather prefer greater water depths (e.g. *Pernambugia tuberosa*: Table 4). Focussing on the marginal parameters, accumulation rates of *L. granifera* also correlate positively with PO_4^{3-}-100 and negatively with D0, Zmix win and Zmix sum. All other parameters do not appear to significantly influence the distribution. This indicates that highest accumulation occurs in the more shelfward areas, where surface winter temperature and density is relatively low, phosphate concentration in 100 m water depth is relatively high and where a shallow mixed layer depth predominates in the upper water column, indicating stratified subsurface water conditions. These results fit well with those derived from RDA rel, although RDA acc has allowed a more stringent selection of important controlling parameters.

Accumulation rates of *C. levantinum* are positively related to T75 win/sum, T0 sum, Zmix sum and PO_4^{3-}-100 (Table 4). When marginal effects are taken into account, positive relationships also exist with S75 win/sum, T0 win and NO_3^--75, and a negative relationship with

Table 3
Significance of environmental parameters in determining species' distribution based on relative abundances (RDA rel: left-hand column) and accumulation rates (RDA acc: right-hand column

RDA rel			**RDA acc**		
Marginal Effects [a]			*Marginal Effects* [a]		
Variable	Lambda 1		Variable	Lambda 1	
WD	0.42		WD	0.27	
PO_4^{3-}-100	0.29		D0	0.23	
S0 win/sum	0.28		PO_4^{3-}-100	0.21	
T0 sum	0.26		D75	0.2	
Zmix sum	0.24		Zmix win	0.14	
S75 win/sum	0.23		T75 win/sum	0.12	
T0 win	0.22		Zmix sum	0.12	
Chl win	0.16		Chl win	0.08	
T75 win/sum	0.16		NO_3^--100	0.08	
Zmix win	0.14		T0 win	0.07	
NO_3^--75	0.13		T0 sum	0.06	
D0	0.06		S75 win/sum	0.06	
NO_3^--100	0.06		S0 win/sum	0.06	
NO_3^--0	0.05		NO_3^--75	0.06	
PO_4^{3-}-75	0.05		NO_3^--0	0.06	
Chl sum	0.03		Chl sum	0.02	
PO_4^{3-}-0	0.02		PO_4^{3-}-75	0.01	
D75	0.01		PO_4^{3-}-0	0.01	

Conditional Effects [b]			*Conditional Effects* [b]		
Variable	Lambda A	*P* value	Variable	Lambda A	*P* value
WD	0.42	0.01	WD	0.27	0.02
Zmix sum	0.11	0.02	T75 win/sum	0.24	0.01
PO_4^{3-}-0	0.07	0.03	T0 sum	0.02	0.4
T0 win	0.02	0.31	D75	0.02	0.28
D0	0.02	0.23	PO_4^{3-}-100	0.02	0.39
T0 sum	0.01	0.56	Chl sum	0.02	0.35
PO_4^{3-}-100	0.02	0.35	Chl win	0.04	0.15
NO_3^--100	0.01	0.5	NO_3^--100	0.04	0.14
Zmix win	0.01	0.4	PO_4^{3-}-0	0.03	0.11
Chl win	0	0.5	NO_3^--75	0.03	0.12
Chl sum	0.04	0.17	S75 win/sum	0.03	0.15
NO_3^--0	0.01	0.39	Zmix win	0.01	0.46
T75 win/sum	0.01	0.31	S0 win/sum	0.03	0.13
S75 win/sum	0.01	0.23	Zmix sum	0.01	0.49
NO_3^--75	0.03	0.2	T0 win	0	0.67
D75	0.01	0.42	D0	0.01	0.84
PO_4^{3-}-75	0	0.73	PO_4^{3-}-75	0	0.76
S0 win/sum	0	0.78	NO_3^--0	0	0.76

See Table 2 for an explanation of variable abbreviations. Significant marginal and conditional environmental parameters have been highlighted.

[a] Marginal effects represent the amount of variance explained by the variable, uncorrected for covariance.

[b] Conditional effects represent the amount of variance explained by that particular variable only. The P value indicates the significance of the variable (at and above the 5% significance level, $P \leq 0.05$).

D0, D75 and NO_3^--0. Thus, highest accumulation rates are found in areas where (sub-)surface temperatures are relatively high, but densities are low; the mixed layer is relatively deep (i.e. unstratified) and nutrients are available at depth. These data fit only partly with those obtained from RDA rel for *C. levantinum*, where a negative relationship with nutrients at depth and a positive relationship with water depth are postulated. This discrepancy is probably due to the fact that RDA rel has been mostly influenced by the abundance distribution of *L. granifera*.

Calciodinellum albatrosianum plots very close to *C. levantinum* in the RDA (Fig. 12), thus showing similar environmental preferences, although the distribution of this species is conditionally affected by high T75 win/sum and low Chl win only. Taking marginal effects into account, positive relationships are also found with T0 win, T0 sum, S0 win/sum, S75 win/sum and NO_3^--75, and negative relationships with D0, D75, NO_3^--0 and PO_4^{3-}-75. Thus, highest accumulation rates of

Table 4
Significant correlations between dinocyst abundances (relative and accumulative) and known environmental parameters of the upper water column, as determined from RDA rel (Fig. 11) and RDA acc (Fig. 12) as well as additional RDAs of single species' accumulation rates

RDA rel	*L.gra*	*C.lev*	RDA acc	*L.gra*	*C.lev*	*C.alb*	*C.alb tab*	*P.tub*	*C.elo*	*S.reg*	*S.*spp
WD	--	++	WD	--				++			
T0 win	--	+	T0 win		++	++		++	++		
T0 sum	--	++	T0 sum		+	+		++	++		
T75 win/sum	-	+	T75 win/sum		++	++		+	++		
S0 win/sum	--	+	S0 win/sum			++		++			
S75 win/sum	--	+	S75 win/sum	-	++	++		++	++		
D0			D0	--	-	-	-			-	
D75			D75		--	--	-			-	
Zmix win			Zmix win	-			-				
Zmix sum	--	+	Zmix sum	-	+			+			
NO_3^--0			NO_3^--0		-	--	-				
NO_3^--75			NO_3^--75		+	++		+			
NO_3^--100			NO_3^--100								
PO_4^{3-}-0	+	-	PO_4^{3-}-0								--
PO_4^{3-}-75			PO_4^{3-}-75			-					
PO_4^{3-}-100	++	--	PO_4^{3-}-100	++	+		-	--			
Chl win	+	-	Chl win			-		--			++
Chl sum			Chl sum								+

See Table 2 for an explanation of variable abbreviations. Variables which have a conditional effect on cyst distributions (i.e. after the elimination of covariance) have been highlighted (significance ≥ 7%; P value ≤ 0.05); other relationships reflect marginal effects of parameters on each species' distribution (significance ≥ 15%).
+ = positive correlation (significance ≥ 15%) ; ++ = very positive correlation (significance ≥ 20%);
− = negative correlation (significance ≥ 15%) ; −− = very negative correlation (significance ≥ 20%)

C. albatrosianum are found in areas with relatively high (sub-)surface water temperatures and low surface water nutrient/chlorophyll-a concentrations; in combination with relatively high salinity and relatively low density. Mixed layer depth appears to have no direct influence on the accumulation of this species.

Although the distribution of the paratabulated form of *C. albatrosianum* shows similarities to those of the above two species, relationships with environmental parameters are less pronounced, perhaps due to the rareness of this morphotype. Moreover, parameters relating conditionally to the accumulation rates of *C. albatrosianum* paratabulated turn out to be quite different: these being low D0, Zmix win, NO_3^--0 and low PO_4^{3-}-100. Taking marginal effects into consideration, a negative relationship with D75 also becomes apparent. Thus, highest accumulation rates occur in areas with a shallow mixed layer depth, low subsurface water densities, relative low surface nitrate concentrations and low phosphate concentrations at 100 m water depth.

Accumulation rates of *P. tuberosa* relate to PO_4^{3-}-100 only when conditional effects are considered, showing that low phosphate concentration in 100 m water depth is an important factor controlling the distribution of this species. However, a whole string of marginal positive relationships occur with water depth, T0 sum, T0 win, T75 win/sum, S0 win/sum, S75 win/sum, Zmix sum and NO_3^--75, whereas a negative relationship occurs with Chl win. Thus, provided

that water temperatures are relatively high, highest accumulation rates of this species are found in offshore, oligotrophic areas with high subsurface water salinities, a deep mixed layer depth in summer, and high nitrate concentrations but low phosphate concentrations at depth.

Accumulation rates of *Calciodinellum elongatum* show a positive conditional correlation with T0 win. Marginal positive correlations also exist with the other temperature parameters T0 sum, T75 win/sum and S75 win/sum (and thus T0 win). However, none of the other parameters seem to significantly influence its distribution, effectively showing that relatively high subsurface water temperature is the main factor controlling its distribution.

Accumulation rates of *Scrippsiella regalis* are negatively correlated with D0 and D75 only, thus indicating clear environmental preferences for less dense subsurface waters. None of the other parameters seem to have a great influence on its distribution. In contrast, accumulation rates of *Scrippsiella* spp. are only positively related to Chl win when conditional effects are taken into account. Additional marginal relationships exist with relatively high Chl sum and low PO_4^{3-}-0. Thus, highest accumulation rates of this species occur in areas with relatively high chlorophyll-a concentrations, but with relatively low surface phosphate concentrations.

An additional RDA has been carried out on the accumulation rates of *Thoracosphaera heimii* only. The accumulation rates of this species correlate positively with T75 win/sum, S75 win/sum (and thus T0 win), T0 sum, NO_3^--75 and Zmix win, but negatively with D75. This indicates highest accumulation rates in areas where temperatures, salinities and nitrate values in 75 m water depth are relatively high but where densities are low, and where the winter mixed layer depth is relatively deep (i.e. unstratified).

5. Discussion

5.1. Transport and dissolution

Aspects of cyst transport and the possibility of (selective) dissolution of calcareous dinocysts in the South Atlantic Ocean and the Arabian Sea have been discussed in detail in several studies (Vink et al., 2000; Zonneveld et al., 2000; Wendler et al., 2002b,c; Vink, 2004) and will not be handled in great detail here. Principally, little is currently known on the mechanisms of lateral and vertical transport of calcareous dinocysts through the water column. The investigation of seasonal fluctuation patterns in cyst accumulation in a sediment trap off Cape Blanc revealed an average sinking velocity of ~1.62 cm s^{-1} = 140 m d^{-1} between the upper (730 m) and the lower (3557 m) trap (Siggelkow et al., 2002). These sinking rates are much higher than those previously determined through sinking experiments for *Scrippsiella*

trochoidea, where rates of 0.013 and 0.008 cm s^{-1} were determined for individual cysts with and without spines, respectively (Anderson et al., 1985), implying that these cysts would take almost a year to settle down to the bottom of a 4000-m-deep ocean. We assume that in natural environments, transport in faecal pellet form or through agglomeration in organic matter or 'marine snow' (Honjo, 1976; Honjo et al., 1982; Lampitt et al., 1993) accelerates the sinking velocity. Another form of cyst transport is through dispersion by surface and deep water currents. In the sediment trap off Cape Blanc (Siggelkow et al., 2002), fluctuations in cyst accumulation rates of the most common species are very similar in the upper and lower trap, although a lag of about 21 days between the traps was observed. However, the accumulation rates in the lower trap were found to be two to four times as high as those in the upper trap, depending on the species. This discrepancy may result from lateral transport, although it could also simply reflect the larger catchment area of the lower trap in comparison to the upper trap, which lies close to the sea surface. The latter explanation is strengthened by the fact that species composition and relative abundances hardly change from the upper to the lower trap, which would be unlikely in the case of lateral transport from other regions. Nevertheless, these results do suggest that a bias for higher accumulation rates in deeper samples could very well have occurred in our study region, implying that the use of relative abundances may be more robust when comparing surface sediment cyst data from regions with greatly varying sample depths. Moreover, lateral transport of calcareous dinocysts cannot be ruled out in regions affected by eddies and filaments, influencing both the relative and absolute cyst records in those cases. Indeed, offshore transport of fish larvae into oceanic waters within an upwelling filament near the Canary Islands has been observed to occur (Rodríguez et al., 1999), although intact parts of the offshore flow may also return back to the coastal region by recirculation around the eddy (Barton et al., 1998). Conversely, calcareous cyst distribution may be influenced by processes that occur after deposition on the sea floor (e.g. slumping, bioturbation, winnowing), depending on several factors such as bottom current velocity, sedimentation rate and the topography of the sea floor. Clearly, transport effects cannot be adequately assessed until more concerted process-oriented studies are carried out. In the mean time, the only valid argument against large-scale lateral transport is the fact that most species distributions in surface sediments clearly reflect the overlying surface water hydrography without a significant offset between the two (e.g. Vink, 2004).

Dinocyst assemblages can be influenced by (selective) dissolution within the water column or at the sediment/water interface (e.g. Wendler et al., 2002b). Milliman et al. (1999) suggest that a considerable dissolution of about 60% of the calcium carbonate already occurs in the upper water column as a result of either biological processes within guts and faeces of grazers, or increased degradation of organic matter within marine snow or aggregates, which

would cause local formation of carbonate-dissolving waters. However, models simulating coccolith dissolution in copepod guts suggest insignificant dissolution as long as grazing is continuous (Jansen and Wolf-Gladrow, 2001). In a scenario involving alternating grazing and non-grazing, the model delivers dissolution values of up to ~25%. In pre- or post-bloom situations, when grazing pressure is assumed to be higher, up to ~14% of standing stock calcite can be dissolved in copepod guts. From this, Jansen and Wolf-Gladrow (2001) conclude that calcite dissolution in copepod guts does not constitute the majority of carbonate dissolution in the water column, but may form a significant portion nonetheless. Furthermore, Jansen et al. (2002) found dissolution within marine snow or aggregates to be insignificant as the size, settling velocity and porosity of the aggregates were unfavourable for the production of a carbonate-dissolving microenvironment around the particles. Thus, we assume that dissolution of calcareous dinocysts in the water column has been of minor importance only.

It is more likely that the calcareous dinocyst assemblage has been influenced by dissolution processes at the sediment/water interface below and around the calcite lysocline, due to deep water undersaturation with respect to CO_3^{2-}. Using aragonitic pteropods and the fragmentation state of planktic foraminifera, Meggers et al. (2002) reconstructed a rise of the aragonite compensation depth (ACD) in the upwelling region off Morocco to a water depth of 355 m off Cape Ghir and 1300 m off Cape Yubi. Offshore, the ACD is located at a depth of 3200 m. However, aragonite is much more susceptible to dissolution than calcite, so that aragonitic pteropods would be expected to dissolve at a shallower depth than calcareous dinocysts. Furthermore, Vink et al. (2000) have shown that most cyst species are actually quite resistant against dissolution, with many specimens still occurring intact around and below the calcite lysocline. Off NW Africa, the calcite lysocline is located at greater depths, approximating the transition from NADW to AABW at ~3800 m. As the deepest samples of our investigation area are influenced by NADW only, which is saturated with respect to calcium carbonate (Broecker and Peng, 1989), we assume that deep water undersaturation has not significantly corroded the cysts. As most of our samples derive from high-productivity areas, dissolution through the bacterial degradation of organic matter is more likely to have occurred. Wendler et al. (2002b) showed that *Thoracosphaera heimii* and *Calciodinellum levantinum* were the most sensitive to degradation-related dissolution in the highly productive NE Arabian Sea. However, in our samples deriving directly from the upwelling cells/filaments off NW Africa, *T. heimii* and *C. levantinum* are the most abundant species, together with *L. granifera*. Accumulation rates are generally low, but this could just as well be the result of the greater (sub-)surface water turbulence, which can seriously hamper cyst production (Wendler et al., 2002a). As our study region is (i) less productive than the NE Arabian Sea (determined from satellite data and nutrient data from the Levitus atlas), and (ii) influenced by seasonally

fluctuating upwelling intensity rather than year-round deep water mixing, as indeed is the case in the SW Arabian Sea where dissolution was found to be much less of a problem (Wendler et al., 2002a), we assume that (selective) cyst dissolution has not been as prominent as in the NE Arabian Sea. In fact, values for the accumulation rates of the dissolution-sensitive species *T. heimii* off NW Africa are quite comparable to those found in a Late Quaternary core from the oligotrophic western Tropical Atlantic (Vink et al., 2001), or indeed to those found in the carbonate-preserving oxygen minimum zones of the highly productive NE and SW Arabian Sea upwelling regions (Wendler et al., 2002b), which are all assumed to have undergone negligible dissolution. Thus, although cyst dissolution cannot be cancelled out, it is improbable that dissolution has affected the recent cyst distribution patterns to a large extent.

5.2. Dinocyst distribution in relation to environmental factors

Recent studies on the ecology of calcareous cyst-producing dinoflagellates, based mainly on relative and/or cyst g^{-1} absolute abundances, have shown that individual species react in their own specific way to combinations of environmental parameters (e.g. Wendler et al., 2002c; Meier and Willems, 2003; Vink, 2004), and should therefore always be considered separately in ecological and palaeoenvironmental analyses. Our data strongly support these interpretations; the following environmental affinities of species becoming apparent from the highly productive NW African margin:

Thoracosphaera heimii. This species dominates the calcareous dinocyst assemblage in the entire area, presumably due to its ability to produce large numbers of shells within short time periods (Tangen et al., 1982). It shows a widespread distribution in the region off Morocco (Fig. 2), although accumulation rates are somewhat higher beyond the upwelling cells and in the southern region of the investigated area, where water temperatures are slightly higher (18°C to 23°C). In these areas, nutrients are still available due to offshore transport within upwelling filaments and eddies, but surface water masses are more stratified than within the upwelling cells themselves. The RDA analysis on acculumation rates of *T. heimii* does indeed show that the distribution of this species off NW Africa relates strongly to relatively high temperature throughout the water column, a relatively deep mixed layer and high NO_3^- concentration at 75 m water depth.

Growth experiments carried out on *T. heimii* have revealed a temperature preference between 14°C and 27°C (Karwath et al., 2000a). Maximal growth rates were reached at temperatures around 27°C, but over a longer period of time (80 days) the greatest numbers of cysts were produced at relatively low temperatures around 16°C. In investigations of surface

sediment samples from the South and equatorial Atlantic Ocean, Vink (2004) described *T. heimii* as a species that prefers water temperatures ranging from 14°C to 26°C, and a high nutrient availability. Our "relatively high temperatures" off NW Africa range from 18°C to 23°C and are thus completely in line with previous observations. Nevertheless, we observe that accumulation rates of *T. heimii* are lower in the northern part of the analysed area despite its lower temperatures which approach optimum laboratory growth temperatures, showing that temperature alone does not determine its distribution. Wendler et al. (2002a,c) inferred from surface sediment and sediment trap studies from the SW Arabian Sea coastal upwelling area that highest abundances of *T. heimii* occurred within mature upwelled waters beyond the region/time of active upwelling. Such a region is characterised by relatively high nutrient concentrations but also by reduced water turbulence and agitation, which appears to be more favourable for shell production. Off NW Africa, the generally low accumulation rates of *T. heimii* within and around the upwelling cells at Cape Ghir and Cape Yubi, and the relationship of this species with a relatively deep mixed layer and subsurface nutrients in regions beyond the upwelling cells, correspond very well with the results from the SW Arabian Sea. Our results thus strengthen the original hypothesis of Wendler et al. (2002a) that the production of *T. heimii* is controlled by water column stability and nutrient supply rather than by temperature, at least within coastal upwelling regimes. Furthermore, the strong relationship with a deep mixed layer and NO_3 concentrations at 75 m water depth supports previous observations that *T. heimii* preferentially lives in the deeper parts of the photic zone, where nutrients are available and competition with other phytoplankton is less. In the South and equatorial Atlantic, for example, highest amounts of *T. heimii* shells with cell content were found at depths between 50 and 100 m (Karwath et al., 2000b).

Leonella granifera. This species also occurs in high relative abundances throughout the studied area, but highest accumulation rates are reached in the more shelfward areas, especially on the broad shelf north of Cape Yubi between the two main upwelling cells, where water masses are generally more stratified (Fig. 3). Accumulation rates are relatively low in the upwelling cells themselves, and offshore this species is also less abundant. Nevertheless, its widespread distribution and high relative abundance which exceeds 50% of the cyst assemblage in most areas cause a total dominance of this species in the RDA rel analysis. Results of the RDA rel and RDA acc analyses are comparable and imply that this species prefers relatively shallow, nutrient-rich areas, with a shallow mixed layer depth, low salinity at 75 m water depth, low SST, and low surface water density (Table 4). The conditional relationship with water depth is very strong (significance of 36%).

L. granifera has previously been found to occur in high abundances in the upwelling zones of the NE and SW Arabian Sea (Wendler et al., 2002c), the Benguela upwelling system

(Zonneveld et al., 2000), the Amazon outflow area (Vink et al., 2000) and in the Gulf of Guinea (Vink, 2004). In all cases, absolute abundances were observed to be higher in the most shelfward regions, gradually decreasing towards deeper, offshore areas. Our data support these previous observations. As water depth itself is unlikely to have a great effect on *L. granifera* physiology and ecology, we assume that other biotic or abiotic factors related to water depth must be involved. It is not the upwelling process itself which controls its distribution, as both the Amazon outflow area and the Gulf of Guinea are not influenced by upwelling at all, and abundances of *L. granifera* in active upwelling areas such as the SW Arabian Sea and our study area are generally lower within the upwelling cells than in the less turbulent, albeit nutrient-rich filaments and surrounding areas. A relationship with temperature has often been described for this species, but appears to be non-causal as more and more information on distributions of this species in different regions becomes available (e.g. Vink, 2004). For example, high abundances of *L. granifera* are found in regions with annual SST's between 22°C and 28°C (NE Arabian Sea; Amazon outflow area; Gulf of Guinea), but may also be found in regions where temperatures are significantly lower (15°C to 20°C), e.g. in the upwelling areas of the SW Arabian Sea, Benguela and off NW Africa. In laboratory culturing experiments, however, fossilisable cysts of *L. granifera* were produced within a smaller temperature range of between 18°C and 24°C, which, in comparison to the field data, suggests either a distinct seasonality in cyst production or cyst production at deeper, cooler water depths within the photic zone (Meier et al., 2004b). Unfortunately, it is still not clear at which water depths *L. granifera* lives, and thus whether it reacts to surface water conditions or those of deeper water layers. Whatever the case, the (sub-)surface water temperatures in our study area fall exactly within the range determined by culture experiments and may thus have stimulated high cyst production, even though temperature itself has probably not been a major controlling factor for its distribution. Salinities are generally relatively low in regions of maximal *L. granifera* abundance, but again studies have shown that these conditions are not necessarily essential for its distribution (e.g. Vink, 2004).

Based on its distribution in the South and equatorial Atlantic Ocean and comparisons with distributions in other regions, Vink (2004) states that exceptionally high abundances of *L. granifera* ultimately occur in regions characterised by nutrient enrichment and/or the input of land-derived nutrients and minerals to the ocean (i.e. through river and/or aeolian dust input), perhaps in combination with density stratification which inherently occurs in all regions with high *L. granifera* abundance. Off NW Africa, lithogenic material may have been transported into the ocean via several of the river and wadi systems that occur along the Moroccan coast, e.g. the Souss River flowing into the Ocean at Cape Ghir and draining the Atlas Mountains. However, material transport from most of these systems is insignificant under the present arid

climate (Kuhlmann et al., 2003), so that river input has probably had a negligible influence on the distribution of *L. granifera*. Another source of terrestrial nutrients and minerals is the relatively constant aeolian dust input from the Saharan Region (Schütz et al., 1981; Swap et al., 1996; Moulin et al., 1997), which is not restricted to a special part of the investigated area but rather seems to settle over all shelf and offshore regions equally (Holz et al., 2004). Thus, if dust input would have had a controlling influence on the distribution of *L. granifera* in the investigated area, similar abundances would be expected in the shelfward and offshore regions, which is not the case. Nevertheless, analyses of sediment trap material off Cape Blanc show clear positive relationships between *L. granifera* abundance and lithogenic influx (chapter 4), and so we assume that lithogenic components do play an important role in the physiology of this species – even though its exact role cannot be verified or tested in combination with the other water depth-related factors which appear to have a stronger influence on its final distribution off NW Africa. Based on the results of the statistical analyses and the observations discussed above, we suggest that shelfwardly-enhanced nutrient concentrations (high PO_4^{3-}-0; PO_4^{3-}-100; Chl win) due to weak coastal upwelling of relatively fresh and cool Central Water (low S75 win/sum, low T0/75) between the strong upwelling cells at Cape Yubi and Cape Ghir, in combination with a shallow mixed layer, relatively stratified conditions in the upper water column and perhaps dust input from the mainland, have determined the distribution of *L. granifera* off NW Africa.

Calciodinellum levantinum. This species is abundant in all analysed samples (25–60% of the total cyst association), but highest accumulation rates occur in the southern part of the investigated area (Fig. 4), where (sub-)surface water temperatures are somewhat higher than in the northern areas (temperature range 18°C to 23°C). The accumulation of *C. levantinum* is conditionally related to high water temperature (T75 win/sum; T0 sum), a deep summer mixed layer and high PO_4^{3-} concentration at 100 m water depth (Table 4). Its conditional relationship with high T75 win/sum is very strong (significance of 41%); showing that especially temperatures appear to be very important for the distribution of this species off NW Africa. Parameters marginally influencing *C. levantinum* distribution are high salinity at 75 m water depth (and/or high T0 win), high NO_3^- concentration at 75 m water depth but low NO_3^- concentration at the surface, and low density at sea surface and at 75 m water depth.

In contrast to our findings, previous studies have related the distribution of *C. levantinum* to relatively cool (sub-)surface water annual temperatures between 13°C and 20°C. Furthermore, its distribution ranges from nutrient-enriched environments (e.g. Benguela; Arabian Sea) to oligotropic environments (e.g. mid-Atlantic gyres; Mediterranean Sea), indicating that it is one of the most opportunistic and widespread of all calcareous cyst species (Zonneveld et al., 2000; Wendler et al., 2002c; Meier and Willems, 2003; Vink, 2004). Nevertheless, absolute abundances of *C. levantinum* have so far been found to be low in areas of

active coastal upwelling (e.g. Wendler et al., 2002a,c). Off NW Africa, high accumulation rates were also not reached in the upwelling cells themselves, even though the species does appear to marginally tolerate the high nutrient concentrations and/or turbulence associated with upwelling and thus forms up to 70% of the dwindling cyst association in the upwelling cell off Cape Ghir. In general, the distribution of *C. levantinum* in our study area is more comparable to that in a nutrient-poor environment; relating to offshore areas beyond the influence of upwelling, i.e. where temperatures are higher, the mixed layer is deep and well-mixed and where nutrients are available at depth but are relatively depleted at the sea surface – thus supporting the notion of *C. levantinum* as a thermocline-dwelling species. However, the strong conditional relationship of this species with the highest temperatures of the region, i.e. in the range of 18°C to 23°C, is somewhat surprising in the light of most current evidence which would predict exactly the opposite. The relationship may not be causal but might simply be indicative of a strong preference of this species for the regions beyond the influence of active upwelling, which is better reflected in subsurface water temperature and Zmix than in nutrient concentrations which can derive from various sources (e.g. deep chlorophyll maximum; dust input) and are thus not necessarily related to upwelling processes alone.

Calciodinellum albatrosianum. The distribution of *C. albatrosianum* is very similar to that of *C. levantinum* (Fig. 5), although highest accumulation rates are much more restricted to the southern part of the analysed area (i.e. south of 29°N). Despite their similar distributions, accumulation rates of *C. albatrosianum* are two to three times lower and statistically relate to different parameters than those of *C. levantinum*; showing a very strong positive conditional relationship with temperature at 75 m water depth (significance of 56%) and low winter chlorophyll-a concentration (Table 4). Marginal relationships have furthermore been found with high SST, low subsurface water salinities and densities, and generally low nutrient concentrations.

This species is considered to be a typical warm water species, occurring in highest abundances in the South and equatorial Atlantic where annual SSTs are high (25°C to 28°C) and subsurface water temperatures (i.e. at 75 m water depth) range from 17°C to 26°C (Vink, 2004). However, culturing experiments reveal a much lower temperature range for optimal cyst production and fossilisation, ranging from 16.1°C to 21.7°C (Meier et al., 2004b). Off NW Africa, accumulation rates of *C. albatrosianum* relate very strongly to high T75 (~19°C) and high T0 (~23°C); thus relating to higher temperatures than predicted by the culturing experiments, but slightly lower temperatures than predicted by the comprehensive South Atlantic surface sediment analysis of Vink (2004). Moreover, *C. albatrosianum* can adapt to a wide range of nutrient levels within its generally warm (sub-)surface water environment (e.g. high nutrient levels in the NE Arabian Sea; low nutrient levels in the mid-Atlantic gyres).

Conversely, within eutrophic environments, accumulation rates in the warm NE Arabian Sea area of deep water mixing were found to be twice as high as those in the cool SW Arabian coastal upwelling area, which was assumed to be mainly temperature-related (Wendler et al., 2002c). Despite the results of the culturing experiments, we thus assume that the temperature range off NW Africa is still within the lower range of preference of *C. albatrosianum*, explaining (i) why accumulation rates are 2–3 times lower than those of *C. levantinum*, even in the slightly warmer offshore areas, and (ii) why *C. albatrosianum* distribution is much more restricted to the southern part of the studied area than that of *C. levantinum*. Our results thus continue to support previous findings that temperature is the most important factor influencing *C. albatrosianum* production and distribution. Apart from temperature, a clear relationship with the nutrient-poor offshore areas beyond the areas of active upwelling is also evident off NW Africa.

Paratabulated ***Calciodinellum albatrosianum***. This rather uncommon morphotype was originally created in order to accommodate all paratabulated forms of the oceanic cyst species *C. albatrosianum* which could not be allocated to the neritic species *Calciodinellum operosum*, based on their differences in surface crystal structure and geographic distribution. Indeed, paratabulated *C. albatrosianum* was found to exhibit a very similar distribution pattern to *C. albatrosianum* in the South and equatorial Atlantic, thus strengthening the hypothesis that the two could be genetically linked (Vink, 2004). At a first glance, *C. albatrosianum* paratabulated also has a comparable geographic distribution to that of *C. albatrosianum* off NW Africa (Fig. 6), although accumulation rates drop much more sharply in an offshore direction. However, parameters relating significantly to the accumulation of this morphotype are quite different. Paratabulated *C. albatrosianum* is found in greater abundances where the mixed layer depth is shallow and (sub-)surface water densities, surface nitrate concentrations and phosphate concentrations at 100 m are low (Table 4). It is striking that no correlation with subsurface water temperature is found. The differences between distributions and environmental preferences of *C. albatrosianum* and the paratabulated form hint at the possibility that several of the specimens counted as this morphotype may have been confused with the neritic species *C. operosum*. As such, the shelfward distribution off NW Africa (Fig. 6) may have been "created" due to the admixture of *C. operosum* in samples closer to the neritic areas rather than reflecting the distribution of the paratabulated morphotype only, which has so far been observed in warm, oligotrophic environments rather than in cool, nutrient-rich upwelling systems (Vink, 2004). These results emphasise the potential problems which arise when two morphologically very similar but environmentally totally different species/morphotypes occur in one area and are not distinguishable from one another; and highlight the necessity to be cautious with both the determination and the interpretation of such specimens. More detailed morphological and

genetic analyses are required to improve and secure their future correct identification.

Pernambugia tuberosa. This species occurs in low relative and absolute abundances in the region off NW Africa and has a chiefly offshore distribution (Fig. 7), with many of the shelfward samples being completely barren of this species. In the RDA acc analysis, *P. tuberosa* relates conditionally to PO_4^{3-}-100 only (significance of 34%), showing that low phosphate concentration at 100 m water depth may be the most important controlling factor for its distribution (Table 4). However, when marginal effects are also taken into account, this species' accumulation relates to high water depth, high (sub-)surface temperatures and salinities, a deep mixed layer, high nitrate concentrations at 75 m but low phosphate concentrations at 100 m water depth, and low chlorophyll-a concentrations in winter.

In studies from the South and equatorial Atlantic, the most important factor influencing the distribution of *P. tuberosa* was found to be oligotrophy throughout the entire water column, as this species occurred in high abundances only in nutrient-poor regions along the eastern Brazilian coast and in the mid-Atlantic Gyres (Vink, 2004). *P. tuberosa* was found in highest abundances within a relatively restricted annual temperature range of 21°C to 28°C, although temperature was not considered to be a significant parameter influencing its distribution based on statistical analyses with subsurface water parameters. Nevertheless, culture experiments show that fossilisable cysts of *P. tuberosa* are produced within a similarly high temperature range of 22.3°C to 27.6°C in the laboratory (Meier et al., 2004b). Furthermore, relatively high salinities in the range of 36–37 p.s.u. were assumed to significantly influence its distribution. Off NW Africa, *P. tuberosa* does not relate as strongly to nutrient-depleted conditions despite its completely oceanic distribution; showing a negative correlation with subsurface water phosphate but a somewhat surprising positive correlation with nitrate. However, chlorophyll-a concentrations are the lowest of the entire area in the regions where *P. tuberosa* accumulation rates are the highest (Appendix A), showing that phytoplankton production is low there despite relatively high nitrate concentrations. Perhaps the low phosphate concentrations had a limiting effect on phytoplankton production in general but did not hamper *P. tuberosa* production. If this is the case, its relationship with oligotrophy is still warranted. Moreover, this species shows strong relationships to high temperature in our analysis. Annual SST ranges from 18°C to 23°C in its area of maximum abundance, and is thus at the lower end of the temperature range considered to be more favourable for *P. tuberosa* production in the South and equatorial Atlantic as well as in the laboratory. This could well be the reason for its low relative abundance in our study area, in addition to the relatively high nutrient concentrations and/or resulting greater competition which may be on the limiting edge of their tolerance range. (Sub-)surface salinities have values around 36.5 p.s.u. and are thus within the range considered as optimal for *P. tuberosa* production.

Calciodinellum elongatum. Low abundances of this species are found in the southern offshore areas and in the somewhat shallower area between the two upwelling filaments off NW Africa (Fig. 8), showing a distribution quite similar to that of *C. albatrosianum*. In the statistical analyses, strong relationships with relatively high (sub-)surface water temperatures become apparent, in addition to relatively high salinity and nitrate concentration at 75 m water depth (Table 4).

In previous studies, *C. elongatum* has been described in high relative abundances (5-15%, but reaching up to 20% of the total cyst association in one sample) from the relatively warm (20°C to 22°C), extremely saline (~39 p.s.u.) and oligotrophic eastern Mediterranean Sea (Meier and Willems, 2003). In the South and equatorial Atlantic Ocean, lower abundances (up to 5% of the association) were found in purely oligotrophic areas where relatively high annual (sub-)surface temperatures (22°C to 27°C) and salinities (36 to 37.5 p.s.u.) predominate (Vink, 2004). Our relationship with relatively high temperatures and salinities fit these observations quite well, but its occurrence in the shelfward areas where nutrients are available show that the species is more adaptable and less restricted to purely oligotrophic areas than was supposed previously. Slightly higher temperatures in the southern part of the analysed area could explain why *C. elongatum* is mainly distributed there, as these temperatures are at the lower end of what has been determined for this species so far.

Scrippsiella regalis. Cysts of *S. regalis* are rare in the dataset and show a rather confusing distribution pattern as relative abundances are highest in the northern part of the studied region around Cape Ghir, whereas accumulation rates are the highest in the shelfward areas and on the broad shelf to the north of Cape Yubi, i.e. in the southern part of the area (Fig. 9). As if this is not confusing enough, accumulation of *S. regalis* only shows a significant negative correlation with (sub-)surface water density, all other parameters apparently having an insignificant effect on its distribution (Table 4).

In the Mediterranean Sea, high abundances of *S. regalis* (up to 40% of the total cyst association) are related to relatively high nitrate concentration and reduced salinity at 75 m water depth, which in the case of the Mediterranean is still 37 to 38 p.s.u. (Meier and Willems, 2003). SSTs vary from ca. 18°C to 22°C. This distribution contrasts that of the South and equatorial Atlantic, where Vink (2004) found this species to relate to cool (14°C to 21°C), well-mixed, relatively fresh (34.5 to 36 p.s.u.) and oligotrophic (sub-)surface waters. The species thus apparently tolerates large variations in salinity and nutrient content, which is also shown by our distribution. For example, the high relative abundances of *S. regalis* off Cape Ghir attest to its ongoing competitiveness at the mercy of other cyst species in this relatively cool and productive area, as shown by its highest chlorophyll-a concentrations, especially in summer (Appendix A). However, accumulation rates are highest in the southern, more shelfward regions

where temperatures are somewhat higher and densities lower. Nevertheless, nutrient concentrations are still elevated here and the distribution thus shows that *S. regalis* is much less restricted to oceanic and oligotrophic regions than was suggested by Vink (2004). In a broad perspective, and judging from its common distribution in the southern South Atlantic, its very low concentrations in the equatorial Atlantic and its return to common values in the North Atlantic off NW Africa and in the Mediterranean Sea, temperature seems to be the most restrictive factor controlling its distribution. However, our temperature range is simply too small to detect such a relationship offshore Morocco.

***Scrippsiella* spp**. This rare group contains all spiny calcareous cysts which are not attributable to *S. regalis*, for a large part containing specimens of the neritic species *Scrippsiella trochoidea*. Although it is unsure whether and/or how many different species/morphotypes may have been bundled into this single group, a very clear restricted distribution pattern exists with highest relative abundances and accumulation rates in the upwelling filaments off both capes (Fig. 10). Accumulation rates are also elevated in the shelfward regions compared to the offshore areas where this group is absent. Nevertheless, a clear relationship with water depth does not emerge from the statistical analyses. Instead, accumulation rates are conditionally related to relatively high winter chlorophyll-a concentrations only. Marginally, this group furthermore relates to low surface water phosphate and high summer chlorophyll-a concentrations.

In the Arabian Sea, Wendler et al. (2002c) defined a group of spiny cysts including mainly *S. trochoidea* but also containing specimens of *S. regalis*, so that the resulting distribution pattern could have merged both an oceanic and a coastal signal. However, they found the group of spiny cysts to be abundant in zones of active upwelling and allocated it to eutrophic environments in which a high seasonality and low temperatures persist. Similar results were found in the Benguela upwelling region, where relatively high abundances of *Rhabdothorax* spp., including all spiny species, were related to high nutrient concentration and strong seasonality (Zonneveld et al., 2000). Even in the whole South and equatorial Atlantic dataset, spiny cysts were related to relatively low annual SST's (12°C to 19°C), high nutrient concentrations throughout the entire water column and high density at 75 m water depth (Vink, 2004). Although our statistical results do not support these studies very well, the relationship to elevated chlorophyll-a concentrations, which are typical for the upwelling influenced areas off the capes, confirm observations of high abundances in upwelling regions. However, further studies are required to differentiate between the spiny cysts observed off NW Africa, which appear to represent morphological variations mainly of *S. trochoidea* based on the results of this and previous studies.

6. Conclusions

In this study, relative abundances and accumulation rates of calcareous dinocyst species in surface sediment samples from the coastal upwelling zone off NW Africa have been determined and multivariate ordination techniques were applied on both datasets. The comparison between both approaches shows that dinocyst accumulation rates provide more trustworthy ecological information than relative abundances in the area off NW Africa, due to the overwhelming dominance of the two species *Leonella granifera* and *Calciodinellum levantinum* and their negative influence on the percentage abundances of all other species through the "closed-sum effect". Thus, information and trends shown by the less abundant species cannot be revealed or are not unambiguous. Furthermore, relative abundances in samples from regions with high sedimentation rates, where only a few cysts are found due to dilution (e.g. off Cape Ghir), tend to overestimate and/or provide a distorted image of actual cyst abundance. More intricate differences and trends in cyst distribution are revealed through the analysis of accumulation rates, suggesting that they provide a more accurate estimation of actual calcareous dinocyst production in the upper water column than can be warranted by the relative approach. However, the risk of cyst enrichment in bottom sediments due to lateral transport and/or resuspension processes can still by no means be excluded. Nevertheless, our data show that the ecological information obtained from accumulation rate analysis approaches a more realistic scenario of cyst production within the limits of the uncertainties involved and thus allows us to emend and/or refine known ecologies for each species, which in turn is essential for their future application in palaeoecologic and palaeoceanograpic reconstructions.

Our results partly support and refine previous studies on calcareous dinocyst ecology, but also highlight new aspects of calcareous dinocysts in upwelling regimes. The distribution of *Thoracosphaera heimii* appears to be more closely related to water column stability and nutrient availability beyond the regions of active upwelling than to (sub-)surface water temperature. The distribution of *Leonella granifera* also appears to be controlled by nutrient availability, but is restricted to the more shelfward areas where salinities are relatively low and the mixed layer depth is shallow. In contrast to the results of previous studies, temperature is considered not to be of major importance for its distribution. The potentially important role of lithogenic influx on the ecology and distribution of this species could not be discarded or verified with the present study. Further studies on this subject are necessary as this species could be an important indicator of land-derived mineral and nutrient input into the ocean. Our results for *Calciodinellum levantinum* show a somewhat surprising relationship with relatively high water temperatures, which is different to former studies in which this species was rather related to the cooler regions (e.g. Vink, 2004). This could be due to the species' preference for regions beyond

the influence of upwelling. Relationships with a deep mixed layer and higher nutrient concentrations at depth fit with those of previous studies and continue to support the notion of *C. levantinum* as a thermocline-dwelling species. The definition of *Calciodinellum albatriosianum* as a typical warm-water species (Wendler et al., 2002c; Vink, 2004) is validated by its distribution off NW Africa. Distributions of *Pernambugia tuberosa* and *Calciodinellum elongatum* also fit previous observations from the South and equatorial Atlantic Ocean (Vink, 2004), where a preference for regions with relatively high water temperatures is similar to that in our study area. However, both species are less restricted to oligotrophic areas than was assumed previously. This is especially true for *C. elongatum*, which occurs mainly in the relatively shallow, nutrient-enriched area between the two upwelling filaments off NW Africa. *P. tuberosa*, on the other hand, occurs in the offshore areas where nitrate concentrations are not comparatively low but where phosphate is potentially limiting. The distribution of *Scrippsiella regalis* off NW Africa is not unambiguous but clearly shows that this species is less restricted to oceanic and oligotrophic areas than has been documented so far. We suggest that relatively low temperature may be the main factor controlling its distribution on a regional scale. *Scrippsiella* spp. shows a clear distribution within the shelfward and upwelling influenced areas and is clearly the most competitive of all analysed species. Most of the specimens counted in this group are probably attributable to the neritic species *Scrippsiella trochoidea*.

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Appendix A

Raw data; environmental parameters. See Table 2 for an explanation of variable abbreviations.

sample	WD	T0 win	T0 sum	T75 win	T75 sum	S0 win	S0 sum	S75 win	S75 sum	D0	D75	Zmix win	Zmix sum	NO_3^--0	NO_3^--75	NO_3^--100	PO_4^{3-}-0	PO_4^{3-}-75	PO_4^{3-}-100	Chl win	Chl sum
4024-3	98	17.8278	20.9278	17.9680	18.0076	36.6197	36.4828	36.4866	36.3672	0.0259183	0.0266086	107.8378	21.5510	0.5703	2.2335	2.5410	0.0612	0.1159	0.1774	1.6098	6.5273
4025-1	504	17.8667	21.0111	17.9680	18.0076	36.6197	36.4828	36.4866	36.3672	0.0259183	0.0266086	107.8378	21.5510	0.5703	2.2335	2.5410	0.0612	0.1159	0.1774	1.2550	5.3245
4026-1	990	17.9333	21.0444	17.9680	18.0076	36.6197	36.4828	36.4866	36.3672	0.0259183	0.0266086	107.8378	21.5510	0.5703	2.2335	2.5410	0.0612	0.1159	0.1774	0.8144	3.0279
4210-2	1959	17.5111	20.7667	17.0832	16.7278	36.4959	36.4018	36.3855	36.2295	0.0261638	0.0268166	145.6061	18.7959	1.2027	1.6114	2.0628	0.0828	0.1327	0.1741	0.3931	0.2489
4211-1	1773	17.5500	20.6167	17.0832	16.7278	36.4959	36.4018	36.3855	36.2295	0.0261638	0.0268166	145.6061	18.7959	1.2027	1.6114	2.0628	0.0828	0.1327	0.1741	0.4142	0.2715
4212-3	1256	17.6833	20.5611	17.2613	16.7175	36.3041	36.1570	36.3328	36.1509	0.0258906	0.0267318	49.6921	12.2611	1.5224	1.7830	2.8480	0.1110	0.1681	0.1819	0.3932	0.2336
4213-1	1547	17.7000	20.7222	17.3782	17.0315	36.3723	36.2407	36.4032	36.2388	0.0259288	0.0267559	53.6550	12.9376	1.3294	1.7123	2.4598	0.1032	0.1654	0.1767	0.3783	0.2045
4215-1	2106	17.7111	21.0889	17.2677	17.0957	36.4650	36.3846	36.4293	36.2892	0.0260715	0.0268017	107.7545	17.6783	1.1642	1.6698	2.2113	0.0950	0.1474	0.1720	0.3453	0.1705
4216-2	2325	17.7389	21.4722	17.4228	17.4345	36.4952	36.4284	36.4761	36.3530	0.0260676	0.0267977	105.6766	18.8385	1.0792	1.8417	2.2360	0.0991	0.1427	0.1659	0.2945	0.1684
4223-1	777	17.8611	21.0611	17.5742	17.4598	36.4137	36.3055	36.4661	36.3262	0.0259353	0.0267476	51.3151	13.5464	1.1399	1.7803	1.9879	0.1091	0.1480	0.1724	0.3505	0.2322
4225-3	1281	17.7889	20.9056	17.3782	17.0315	36.3723	36.2407	36.4032	36.2388	0.0259288	0.0267559	53.6550	12.9376	1.3294	1.7123	2.4598	0.1032	0.1654	0.1767	0.3829	0.2056
4226-1	1400	17.8000	21.1056	17.3782	17.0315	36.3723	36.2407	36.4032	36.2388	0.0259288	0.0267559	53.6550	12.9376	1.3294	1.7123	2.4598	0.1032	0.1654	0.1767	0.3373	0.1823
4228-1	1633	18.0167	21.5833	17.5742	17.4598	36.4137	36.3055	36.4661	36.3262	0.0259353	0.0267476	51.3151	13.5464	1.1399	1.7803	1.9879	0.1091	0.1480	0.1724	0.2584	0.1411
4230-1	1316	17.9056	21.2222	17.5742	17.4598	36.4137	36.3055	36.4661	36.3262	0.0259353	0.0267476	51.3151	13.5464	1.1399	1.7803	1.9879	0.1091	0.1480	0.1724	0.3148	0.1845
4231-2	1207	17.9056	21.2222	17.5742	17.4598	36.4137	36.3055	36.4661	36.3262	0.0259353	0.0267476	51.3151	13.5464	1.1399	1.7803	1.9879	0.1091	0.1480	0.1724	0.3148	0.1845
4232-1	1161	18.0714	21.4571	17.7135	17.8084	36.5219	36.4325	36.5160	36.3992	0.0260051	0.0267512	97.4713	17.5307	0.9411	1.9196	2.1923	0.0982	0.1382	0.1713	0.2945	0.1664
4233-2	1303	18.0714	21.4571	17.8669	17.9078	36.5025	36.3854	36.5080	36.3859	0.0259039	0.0266846	74.9747	15.4727	0.8648	1.9434	2.0772	0.0940	0.1327	0.1857	0.2945	0.1664
4236-2	1030	18.0167	21.2333	17.8669	17.9078	36.5025	36.3854	36.5080	36.3859	0.0259039	0.0266846	74.9747	15.4727	0.8648	1.9434	2.0772	0.0940	0.1327	0.1857	0.3538	0.2366
4237-1	800	17.9667	21.1667	17.8669	17.9078	36.5025	36.3854	36.5080	36.3859	0.0259039	0.0266846	74.9747	15.4727	0.8648	1.9434	2.0772	0.0940	0.1327	0.1857	0.3668	0.2578
4238-2	1185	18.1056	21.4778	17.8669	17.9078	36.5025	36.3854	36.5080	36.3859	0.0259039	0.0266846	74.9747	15.4727	0.8648	1.9434	2.0772	0.0940	0.1327	0.1857	0.3002	0.1915
4239-1	881	17.9889	21.1667	17.8669	17.9078	36.5025	36.3854	36.5080	36.3859	0.0259039	0.0266846	74.9747	15.4727	0.8648	1.9434	2.0772	0.0940	0.1327	0.1857	0.4088	0.2995
4301-1	3614	18.6333	22.3333	18.0328	18.4550	36.6623	36.6096	36.6067	36.5288	0.0260649	0.0267422	124.7612	24.7664	0.8420	2.2516	2.4917	0.0898	0.1312	0.1586	0.1818	0.1018
5531-1	3301	19.0056	22.8333	18.4017	18.9614	36.7522	36.7400	36.6931	36.6260	0.0260682	0.0267163	132.8859	29.4464	0.9167	2.5658	3.0234	0.0906	0.1233	0.1469	0.1820	0.1052
5536-3	3456	18.9889	22.1722	18.5441	19.0400	36.7200	36.6459	36.6686	36.6141	0.0259466	0.0266359	113.5065	24.4150	0.8309	2.3583	2.6371	0.0926	0.1416	0.1750	0.2744	0.1568
5539-2	2202	18.3778	21.4889	18.1453	18.3930	36.6251	36.5119	36.5583	36.4705	0.0259265	0.0266275	107.5683	21.3361	0.6528	2.1613	2.3187	0.0688	0.1270	0.1726	0.3425	0.3626
5540-3	2035	18.3056	21.4056	18.1453	18.3930	36.6251	36.5119	36.5583	36.4705	0.0259265	0.0266275	107.5683	21.3361	0.6528	2.1613	2.3187	0.0688	0.1270	0.1726	0.3872	0.4179
5548-3	1162	18.0167	21.2000	17.9680	18.0076	36.6197	36.4828	36.4866	36.3672	0.0259183	0.0266086	107.8378	21.5510	0.5703	2.2335	2.5410	0.0612	0.1159	0.1774	0.5400	1.0442
5549-2	1454	18.1333	21.3000	17.9680	18.0076	36.6197	36.4828	36.4866	36.3672	0.0259183	0.0266086	107.8378	21.5510	0.5703	2.2335	2.5410	0.0612	0.1159	0.1774	0.3827	0.4780
5553-2	3397	18.4778	21.9000	18.0154	18.2574	36.5996	36.5028	36.5627	36.4663	0.0259674	0.0266934	104.8141	20.1285	0.7686	2.0371	2.2068	0.0836	0.1314	0.1724	0.2873	0.1462
5555-2	2837	18.3222	21.8722	17.7135	17.8084	36.5219	36.4325	36.5160	36.3992	0.0260051	0.0267512	97.4713	17.5307	0.9411	1.9196	2.1923	0.0982	0.1382	0.1713	0.2293	0.1304
5556-3	3170	18.3722	21.9167	17.8646	18.1414	36.6015	36.5301	36.5630	36.4673	0.0260455	0.0267498	114.3409	21.4722	0.8476	2.0736	2.3259	0.0913	0.1336	0.1651	0.2222	0.1239
5558-2	2471	18.4500	21.9000	18.0154	18.2574	36.5996	36.5028	36.5627	36.4663	0.0259674	0.0266934	104.8141	20.1285	0.7686	2.0371	2.2068	0.0836	0.1314	0.1724	0.2447	0.1359
5559-1	3178	17.6389	21.8500	17.4002	17.7018	36.5648	36.5521	36.5118	36.4203	0.0261468	0.0268213	133.0168	28.0624	0.9869	2.2021	2.4298	0.0917	0.1333	0.1544	0.2412	0.1090
6005-1	1781	17.3167	20.6222	17.0832	16.7278	36.4959	36.4018	36.3855	36.2295	0.0261638	0.0268166	145.6061	18.7959	1.2027	1.6114	2.0628	0.0828	0.1327	0.1741	0.4623	0.4541
6006-2	1282	17.2167	20.4222	17.0832	16.7278	36.4959	36.4018	36.3855	36.2295	0.0261638	0.0268166	145.6061	18.7959	1.2027	1.6114	2.0628	0.0828	0.1327	0.1741	0.4954	0.8056
6007-1	899	17.0611	20.2167	17.0832	16.7278	36.4959	36.4018	36.3855	36.2295	0.0261638	0.0268166	145.6061	18.7959	1.2027	1.6114	2.0628	0.0828	0.1327	0.1741	0.9119	2.2031
6008-2	355	16.9611	20.1944	17.0832	16.7278	36.4959	36.4018	36.3855	36.2295	0.0261638	0.0268166	145.6061	18.7959	1.2027	1.6114	2.0628	0.0828	0.1327	0.1741	1.9935	4.6444
6009-1	579	17.1389	20.2000	17.0832	16.7278	36.4959	36.4018	36.3855	36.2295	0.0261638	0.0268166	145.6061	18.7959	1.2027	1.6114	2.0628	0.0828	0.1327	0.1741	0.8802	2.2502
6010-1	406	17.2778	19.9667	17.0832	16.7278	36.4959	36.4018	36.3855	36.2295	0.0261638	0.0268166	145.6061	18.7959	1.2027	1.6114	2.0628	0.0828	0.1327	0.1741	0.8071	1.9296
6011-2	993	17.3333	20.0889	17.0832	16.7278	36.4959	36.4018	36.3855	36.2295	0.0261638	0.0268166	145.6061	18.7959	1.2027	1.6114	2.0628	0.0828	0.1327	0.1741	0.5650	0.7906

Appendix B

Raw data; cyst counts

sample	fraction	weight (g)	*T. heim*	*L. gra*	*C. lev*	*C. alb*	*C.alb* par	*P. tub*	*C.elo*	*S. reg*	*S.* spp	counted cysts	multipl. factor	total cysts	total cysts/g
4024-3	>20 µm	0.3026	0	0	0	0	0	0	0	0	0	0	300	0	3305
	<20 µm		0	0	0	0	0	0	0	0	0.5	0.5	2000	1000	
4025-1	>20 µm	0.3009	28	7	7.75	3.25	0.25	0	0	0	3	49.25	150	7387.5	196535
	<20 µm		49.5	2	0.25	0	0	0	0	0	0	51.75	1000	51750	
4026-1	>20 µm	0.3021	88	13	30	10.5	0.75	1	1	1.75	7	153	150	22950	1061569
	<20 µm		278	15	3.75	1	0	0	0	0	0	297.75	1000	297750	
4210-2	>20 µm	0.3090	244	28	46.25	5.75	0.25	1	1.5	3	8.5	338.25	150	50738	1999150
	<20 µm		270.5	10	2.5	0.5	0	0	0	0	0	283.5	2000	567000	
4211-1	>20 µm	0.3320	172.5	26	45.75	9.75	1	4.5	2	1.5	5.75	268.75	150	40312.5	2038592
	<20 µm		304.5	10	2.75	1	0	0	0	0	0	318.25	2000	636500	
4212-3	>20 µm	0.3028	20	15	70.25	6	1.75	0	0	6.25	0.5	119.75	100	11975	1809142
	<20 µm		759	25	16.75	3	0	0	0	0	0	803.75	667	535833	
4213-1	>20 µm	0.3076	150	17	67.25	7	2.5	1.25	1	8.25	7.75	262	100	26200	2047139
	<20 µm		287	10	4.5	0.25	0	0	0	0	0	301.75	2000	603500	
4215-1	>20 µm	0.6574	58	3	59.75	17	1	1	1	7	4.25	152	100	15200	1090204
	<20 µm		338.25	8	3.25	1.25	0	0	0	0	0	350.75	2000	701500	
4216-2	>20 µm	0.3939	68.5	7	35.5	2.75	1	1	1	2.5	1	120.25	150	18037.5	935612
	<20 µm		342.75	7	0.5	0	0	0.25	0	0	0	350.5	1000	350500	
4223-1	>20 µm	0.3260	41	27	44.75	15	2.25	0	0.5	3.5	1	135	150	20250	1500767
	<20 µm		213.25	16	4.5	0.75	0	0	0	0	0	234.5	2000	469000	
4225-3	>20 µm	0.3311	513	34	91.75	16.75	1	0	2	5.25	1.5	665.25	100	66525	2428345
	<20 µm		349	15	4.25	0.5	0	0	0	0	0	368.75	2000	737500	
4226-1	>20 µm	0.3084	423.5	32	84.75	13	1.25	0	4	3	3.75	565.25	100	56525	2493596
	<20 µm		336.5	16	3.25	0.5	0	0	0	0	0	356.25	2000	712500	
4228-1	>20 µm	0.3007	49	12	66.25	14.25	4.25	0.25	3.5	3.5	1	154	100	15400	1929332
	<20 µm		538.5	18	6.25	2	0	0	0	0	0	564.75	1000	564750	
4230-1	>20 µm	0.3053	997	82	125.25	14.5	4	3	4	1	1.5	1232.25	100	123225	2974861
	<20 µm		378.5	11	2.25	0.75	0	0	0	0	0	392.5	2000	785000	
4231-2	>20 µm	0.3025	424	51	117.5	17	3.5	4	5	2	1	625	100	62500	2107438
	<20 µm		281.5	3	2	1	0	0	0	0	0	287.5	2000	575000	
4232-1	>20 µm	0.4213	123.5	24	93	13.5	0	0	0	3.5	7	264.5	100	26450	1060883
	<20 µm		202.5	4	3.25	0.5	0	0	0	0	0	210.25	2000	420500	
4233-2	>20 µm	0.3233	528	44	94.75	23	2.75	4.25	3	0	1.25	701	100	70100	2017012
	<20 µm		279	10	1.5	0.5	0	0	0	0	0	291	2000	582000	
4236-2	>20 µm	0.3254	443	62	105	22	1	0	1	2.5	1.25	637.75	100	63775	1857022
	<20 µm		249.25	17	2.5	1.5	0	0	0	0	0	270.25	2000	540500	
4237-1	>20 µm	0.3970	60.5	18	58.75	17	2.5	0.5	2	2.25	0	161.5	150	24225	1413665
	<20 µm		243.75	20	4	0.75	0	0	0	0	0	268.5	2000	537000	
4238-2	>20 µm	0.3168	71	26	73.25	16	3.25	0	2	4	11	206.5	100	20650	2377367
	<20 µm		346	13	5	2.25	0	0	0	0	0	366.25	2000	732500	
4239-1	>20 µm	0.4005	52	21	60	13.25	0.25	1	0	5.25	1	153.75	150	23063	1041355
	<20 µm		355.5	32	4.25	2.25	0	0	0	0	0	394	1000	394000	

Appendix B (Continued)

sample	fraction	weight (g)	*T. heim*	*L. gra*	*C. lev*	*C. alb*	*C.alb par*	*P. tub*	*C.elo*	*S. reg*	*S.* spp	counted cysts	multipl. factor	total cysts	total cysts/g
4301-1	>20 µm	0.3002	155	7	120.75	30.25	1.75	12	5	5.75	0	337.5	150	50625	4262575
	<20 µm		602.5	4	6	1.75	0	0.25	0	0	0	614.5	2000	1229000	
5531-1	>20 µm	0.3189	647.5	11	145	46	1.25	9	4	1.5	0	865.25	150	129787.5	4112692
	<20 µm		1161	7	9.75	4	0	0	0	0	0	1181.75	1000	1181750	
5536-3	>20 µm	0.2598	65.5	10	108.5	36.5	1.25	0	5	1.5	1.25	229.5	75	17212.5	2483497
	<20 µm		588.5	19	16.25	4.25	0	0	0	0	0	628	1000	628000	
5539-2	>20 µm	0.2590	61	5	120.75	24.25	1.5	0.25	2	4.5	3.5	222.75	75	16706.25	2134001
	<20 µm		253	7	6.5	1.5	0	0	0	0	0	268	2000	536000	
5540-3	>20 µm	0.2957	455	19	94.5	30.25	0.5	0	1	4.5	7	611.75	150	91762.5	1779718
	<20 µm		414	7	10.25	2.75	0.5	0	0	0	0	434.5	1000	434500	
5548-3	>20 µm	0.2585	18	3	19.5	7.5	0	0	1	1.5	1	51.5	150	7725	1307447
	<20 µm		308.5	15	4.75	2	0	0	0	0	0	330.25	1000	330250	
5549-2	>20 µm	0.3022	66	17	42	11.25	0	0	0	1.5	2	139.75	150	20962.5	909042
	<20 µm		239.5	10	2.5	1.5	0.25	0	0	0	0	253.75	1000	253750	
5553-2	>20 µm	0.3068	69	6	120.75	18.5	0	1	7	4	0	226.25	150	33937.5	2887671
	<20 µm		830	10	9	3	0	0	0	0	0	852	1000	852000	
5555-2	>20 µm	0.4157	495	13	94.5	21.75	0	2.5	3	1.25	0	631	150	94650	1795526
	<20 µm		641.25	4	3.75	2.75	0	0	0	0	0	651.75	1000	651750	
5556-3	>20 µm	0.3078	286	24	87.5	20	0.25	1.5	1	3.5	0	423.75	75	31781.25	1818653
	<20 µm		512.5	5	8.25	2.25	0	0	0	0	0	528	1000	528000	
5558-2	>20 µm	0.3144	302	17	58.75	20.5	1.75	2.75	2	3.5	0	408.25	150	61237.5	2373529
	<20 µm		673.5	2	7.25	1.75	0	0.5	0	0	0	685	1000	685000	
5559-1	>20 µm	0.3020	185	24	44.75	8.5	0.25	2	0	4.5	0	269	150	40350	5578974
	<20 µm		1618	15	8.5	2.75	0	0.25	0	0	0	1644.5	1000	1644500	
6005-1	>20 µm	0.3000	178.5	8	32	3.25	1	1	0	3	7.5	234.25	150	35137.5	1313792
	<20 µm		176	2	0.75	0.25	0	0	0	0	0.5	179.5	2000	359000	
6006-2	>20 µm	0.2998	174	9	21.25	5.25	0	0	0.5	0	1.5	211.5	150	31725	747915
	<20 µm		95	0	1.25	0	0	0	0	0	0	96.25	2000	192500	
6007-1	>20 µm	0.3015	14	4	5.25	0.25	0	0	0	1	3.5	28	150	4200	233665
	<20 µm		62.5	3	0.75	0	0	0	0	0	0	66.25	1000	66250	
6008-2	>20 µm	0.3000	8	0	2	0	1	0	0	0	1	12	150	1800	49333
	<20 µm		6.5	0	0	0	0	0	0	0	0	6.5	2000	13000	
6009-1	>20 µm	0.3006	20.5	1	16.75	2.75	0	0	0	0	3	44	150	6600	189953
	<20 µm		47.5	1	2	0	0	0	0	0	0	50.5	1000	50500	
6010-1	>20 µm	0.3000	25	5	7.25	0	0	0	0.5	0	0.25	38	100	3800	105167
	<20 µm		27.5	0	0.25	0	0	0	0	0	0	27.75	1000	27750	
6011-2	>20 µm	0.3002	312	50	66	7	0	0	0	0	7.5	442.5	150	66375	1490256
	<20 µm		181.25	8	0.5	0.75	0	0	0	0	0	190.5	2000	381000	

Calcareous dinoflagellate cysts production in response to variations in upwelling intensity and lithogenic input from sediment trap material off Cape Blanc (NW Africa)

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Abstract

So far, only a few studies have focussed on seasonal production of calcareous dinoflagellate cyst in relationship to environmental conditions of the upper water column and the final deposition in the bottom sediment. In this study cyst fluxes were calculated from sediment trap material collected from June 1998 to November 1999 at a site off Cape Blanc located close to the coastal upwelling area. The cyst fluxes of individual species have been compared with physical and trophic parameters from in situ measurements and with sea surface temperature data and chlorophyll a-concentrations obtained from online databases.

The assemblage consist of nine calcareous dinoflagellate cysts species. Four main species (*Thoracosphaera heimii*, *Leonella granifera*, *Calciodinellum levantinum* and *Calciodinellum albatrosianum*) occurred in all samples. The fluxes of the most abundant species could be differentiated to be distinctive for time intervals characterized by either a low or a high total biological production. High total cyst fluxes were observed during times of less intense upwelling and higher surface water temperatures, whereas cyst fluxes decrease when water column mixing increases due to the influence of intensified coastal upwelling. However, up to certain point enhanced turbulence is tolerated by the dinoflagellates. Nutrient supply appears to stimulate growth of all calcareous dinoflagellate species and subsequent cyst formation. This is most pronounced for *L. granifera*, which reacts to the higher input of important land-derived elements or nutrients by remarkable enhanced cyst production.

Keywords: calcareous dinoflagellate cysts, sediment trap, seasonal patterns, Cape Blanc, ecology

1. Introduction

The development of calcareous dinoflagellate cysts (dinocysts) for late Quaternary palaeoenvironmental and palaeoclimatic reconstructions over the last decades is based on studies that compare modern calcareous cyst distribution patterns in surface sediments with environmental parameters of the overlying water masses. These studies have shown that cyst production reacts sensitively to changing environmental parameters (Höll et al., 1999; Vink, 2004; Zonneveld et al., 2005; Richter et al., 2007). Calcareous cysts have been found frequently in the upper water column of the open ocean, and culturing experiments have shown that all of the modern species are photoautotrophic and continuously form cysts under normal growth conditions (e.g. Janofske and Karwath, 2000; Karwath et al., 2000 a,b; Meier et al., 2004b). However, only little information is presently available on seasonal production of calcareous dinocysts as well as on the influence of the environment on the initial production in the upper water column and the final deposition in the bottom sediment. These factors are, however, extremely important for the (palaeo)environmental interpretation of sedimentary cyst records. A way to obtain this information is to study the seasonal calcareous dinocyst flux collected by sediment traps and compare this signal with changes in physical parameters of the overlying water column.

So far, relationships between cyst production and environmental factors has been determined in sediment trap studies in the Mediterranean Sea (Montresor et al., 1998); the northwestern Pacific (Tanimura and Shimada, 2004) and the Arabian Sea (Wendler et al., 2002a) with the latter one being the only upwelling influenced region so far. In the Atlantic Ocean, calcareous dinocysts from sediment trap material have been studied for sites in the western Atlantic Ocean and the Sargasso Sea (Dale, 1992) and off Cape Blanc (chapter 4). Apart from this, the total calcareous dinocyst flux (mistakenly documented as "*Thoracosphaera heimii*" (Ziveri, pers. comm., 2008) has been investigated in traps in the Northern Atlantic Ocean (Ziveri et al., 2000). In order to extend the knowledge of calcareous dinocyst production in relation to variations in physical parameters in the upper water column, cyst fluxes were calculated from sediment trap material collected from a site in the upwelling influenced high production area off Cape Blanc from June 1998 to November 1999 (trap CB 9; see Fig. 1).

Based on their life-cycle the presently known calcareous dinocysts can be subdivided into two types (Fensome et al. 1996). The first group of sexual resting cysts is characterised by alternating generations of thecate swimming stages and non-motile calcareous cysts that are produced after sexual fusion of two thecae and in which metabolic processes are greatly reduced. In many oceanic species permanent cyst production with relatively short resting times is observed and has been suggested as an adaptation to prevent sinking into adverse water

depths in the open ocean (Meier et al. 2007). In the second group, calcareous vegetative coccoid cysts are the dominant life-cycle stages, i.e. *Thoracosphaera heimii* and *Leonella granifera* (Tangen et al. 1982, Inouye and Pienaar 1983, Meier et al. 2007). These species show higher production rates due to their asexual reproduction, and usually *T. heimii* overshadows the assemblages by an order of magnitude, with the exception of the Arabian Sea, where *L. granifera* can dominate fluxes (Wendler et al. 2002c). For easier reading, we refer to calcareous dinocysts for both sexual resting and vegetative coccoid cysts.

1.1. Oceanographic settings

Off the NW African margin coastal upwelling of cool, nutrient-rich waters occurs due to the interaction of the NE trade winds and the southward flowing Canary Current (CC; Fig.1). Between 20°N and 25°N upwelling persists throughout the year with maximum intensities during spring and autumn attributed to the strong north eastern trade winds, (Speth et al., 1978; Mittelstaedt, 1991; Nykjær and Van Camp, 1994). Within a 20-30 km broad coastal band "primary upwelling", the actual upwelling into the surface water layers, takes place, which is separated by a front from the Canary Current (Hagen, 1981) where "secondary upwelling" may occur (Mittelstaedt, 1991). At Cape Blanc (21°N) the CC separates from the coast and moves south-westwards to the open ocean (Barton, 1998). South of Cape Blanc a large cyclonic gyre occurs throughout the year, whose position varies seasonally (Gabric et al., 1993; Barton, 1998) and which is associated

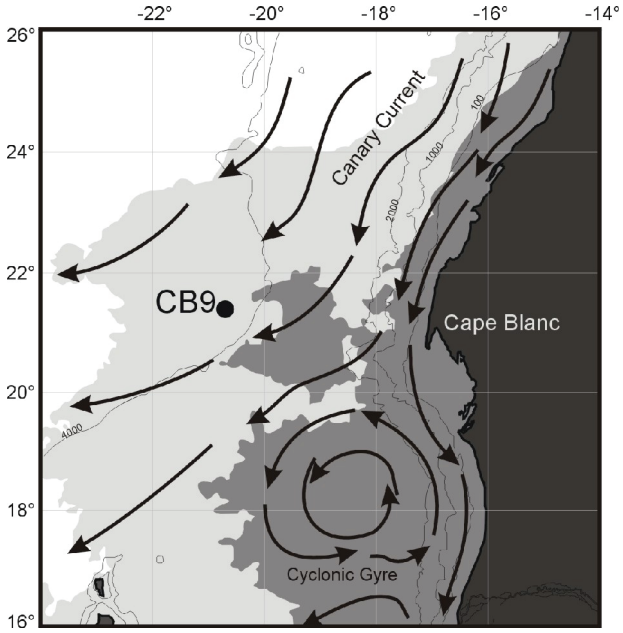

Fig. 1: Position of the sediment trap CB9 with depth contour lines (100, 1000, 2000 and 4000 m) and idealized surface circulation in spring (modified after Mittelstaedt, 1991). The Coastal upwelling area and upwelling filaments, as indicated by SeaWiFS-derived chlorophyll-a concentrations averaged from spring 1999, are outlined (dark grey shading > 2.0 mg m^{-3}, light grey shading 2.0 – 0.5 mg m^{-3}).

with a poleward flowing counter current (Mittelstaedt, 1991; Van Camp et al., 1991). The confluence of the CC and the counter current causes filaments (Mittelstaedt, 1991), which are characteristic for surface waters at the studied trap site off Cape Blanc. These "giant filaments" transport cool nutrient-rich subsurface waters from the coastal upwelling zone into oligotrophic offshore regions and extend at least 450 km offshore (Van Camp et al., 1991). An average velocity of 0.07 m s-1 was determined for a filament migrating from the coast to the trap position (Helmke et al., 2005), but small scale internal velocities may reach values between 0.35 and 2.18 m s-1 (Kostianoy and Zatsepin, 1996).

Off Cape Blanc the upwelled waters come from depths between 100 and 300 m (Mittelstaedt, 1983). Subsurface waters consists of North Atlantic Central Water (NACW) with a southward transition to South Atlantic Central Water (SACW) at around 20°N (Klein and Tomczak, 1994; Mittelstaedt, 1983; Mittelstaedt, 1991). The SACW has a higher nutrient content, is less saline and slightly cooler than the NACW (Barton, 1998).

Apart from nutrient supply to the upper water layers through upwelling, nutrient and trace elements are transported into the area in the form of aeolian dust. Saharan dust is regularly transported under the influence of the trade winds from the central Sahara over the North Atlantic Ocean (Swap et al., 1996; Moulin et al., 1997; Ratmeyer et al., 1999; Middleton & Goudie, 2001). This dust has a major influence on the nutrient dynamics and oceanic productivity in the investigation area (Middleton and Goudie, 2001) as it is a source of trace nutrients such as iron (Pittman, 2002; Sarthou et al., 2003), which is essential for phytoplankton growth and enhanced primary productivity (e.g. Boyd et al., 2000). From August to September 1998 and from February to April 1999 high supply of lithogenic material has been detected (Fig. 2).

2. Material and methods

2.1. Sediment trap material and data

Calcareous dinocyst associations and fluxes have been determined from sediment trap material collected from a site adjacent to the region of coastal upwelling off Cape Blanc (CB9, 21°15.2'N 20°42.2'W, Fig.1, Appendix 1). The trap was deployed 541 m above the seafloor (at a water depth of 3580 m) to prevent input from particle resuspension.

Sediment trap sampling occurred from June 1998 to November 1999 in time intervals of 1x7.5, 18x27.5 and 1x11.5 days. The sampling cups were poisoned with HgCl2 to stop biological

activity and stored in darkness at 4°C until further investigations (for sample treatment see Fischer et al., 1996a and Helmke et al., 2005). One sub-sample of each of the twenty original trap samples (1/125 split of samples 1-19, 1/25 split of sample 20) was investigated for calcareous dinocysts within this study.

Calcareous dinocyst fluxes have been compared with following environmental parameters: (a) total particle flux to the sediment trap (including fluxes of opal concentration, organic carbon, nitrate and organic material), (b) biogenic opal and (c) lithogenic material (all in situ measurements, Appendix 2) as well as (d) sea surface temperature (SST), (e) sea surface temperature anomaly (SSTA, see below) and (f) chlorophyll-a concentration as a measure of productivity. Recent evaluation on the particle fluxes in CB9 have shown that both fluxes of organic carbon and carbonate reflect the total particle flux. Furthermore, all peaks of organic carbon were associated with elevated lithogenic material flux. Detailed information on particle fluxes and chlorophyll-a data is given in Helmke et al. (2005).

Based on the sea surface temperature (SST), a simple estimate of times of intensified upwelling or rather the extent of upwelling influence can be performed by calculating the mean temperature difference between coastal and mid-ocean areas, known as Sea Surface Temperature Anomaly (SSTA; Speth et al., 1978). These anomalies give an indication of the duration of the upwelling events and the amount of upwelled waters carried into offshore regions. For the sampling period, SSTA was estimated by calculating the SST difference between the trap position (21°30'N 20°30'W) and the open ocean (21°30'N 40°30'W). Time intervals during which SSTA is equal to or less than -3.5 K are defined as intervals of intense upwelling (Speth et al., 1978). During the study intervals of relatively weak influence of upwelling occurred from the middle of July to the end of November 1998 and from August to October 1999. Between the middle of January to the beginning of August 1999 intensified upwelling influence was observed. The latter period is also characterised by enhanced chlorophyll-a concentrations (Fig. 3). SST data was obtained from http://iridl.ldeo.columbia.edu/SOURCES/.IGOSS/.nmc/.Reyn_SmithOIv2/.weekly/.

Variations in the intensity of the upwelling filaments are not only reflected by the SSTA changes (as described above) but also by surface phytoplankton biomass production (expressed by chlorophyll-a data) and export of organic carbon to the deep sea (Helmke et al., 2005). Based on the comparison of chlorophyll-a peaks at the sea surface and particle sedimentation peaks in trap CB9, Helmke et al. (2005) calculated an average time lag of 47.6 days (ranging between 21 and 61 days) between production and deposition. In this study, the data of sea surface temperature (SST), sea surface temperature anomaly (SSTA) and chlorophyll-a has been shifted for the estimated time lag of about 47 days in order to make it comparable to the dinocyst fluxes into the trap.

2.2. Laboratory preparation

The solution containing the trap material was briefly homogenised ultrasonically (maximally 60 seconds to avoid damage to the cysts), and filtered through a 5 µm polycarbonate filter using a vacuum pump system. The residue was transferred into a test tube with some drops of NaOH to keep the mixture alkaline and some drops of ethanol to avoid contamination by fungi during storage. The sediment was left to settle for about 24 hours. After settling, the material was concentrated to 5-6 ml. The solution was then transferred into a centrifuge glass and centrifuged at 2500 rpm, for 8 minutes. After decanting the water from the centrifuge glasses, the suspension was transferred into an Eppendorf-cup which was again centrifuged for 8 minutes at 2500 rpm. After centrifuging, the water in the Eppendorf-cups was reduced to 1,0 ml. 50 or 100 µl of the material were brought onto slides. After drying the material, it was embedded in SPURR's resin and placed in an oven at 75°C to polymerise the resin. The cysts were counted using a light microscope with polarised light. One whole slide per sample was counted. If a slide contained less than 200 specimens, additional slides were analysed. We followed the taxonomy given in Vink (2004). The morphological group of *Scrippsiella* spp. used in this study corresponds to Rhabdothorax sp. used in Vink (2004). Cyst fluxes (in cysts/ m^2/day) of each split were calculated.

3. Results

Nine calcareous dinocysts species were identified from sediment trap material. The most abundant species are *Thoracosphaera heimii* and *Leonella granifera*, followed by *Calciodinellum levantinum* and *Calciodinellum albatrosianum* (App.1). Cyst fluxes in comparison with particle fluxes and SST/A values are depicted in Figs. 2 and 3. Particle fluxes measured off Cape Blanc were published by Helmke et al. (2005). Cyst fluxes per trap sample and particle fluxes are also indicated in App. 1.

In general, two periods with different calcareous dinocyst fluxes were distinguished. From June 1998 to March 1999 (sample no. 1-11), calcareous dinocysts were more abundant (high flux period). During the high flux period SST and SSTA are generally enhanced (Fig. 3). From April 1999 to November 1999 (sample no. 12-20) cyst fluxes decreased (low flux period, Fig. 2). The low flux period is characterised by generally lower SST/A values. However, with increasing SST/A values in September 1999 cyst fluxes do not increase again. Although the rare species are only found in a few samples, similar trends were visible. Especially paratabulated

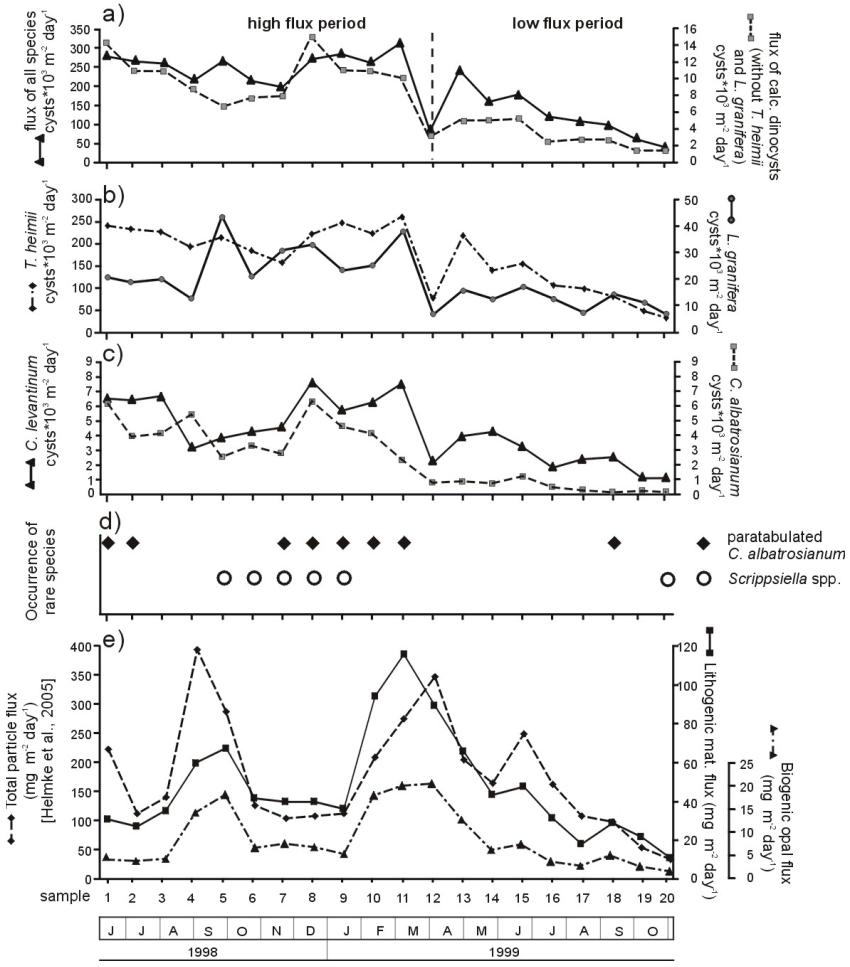

Fig. 2: Cyst fluxes of a) all calcareous dinoflagellate species (both including and excluding *T. heimii* and *L. granifera*), b) *T. heimii* and *L. granifera*, c) *C. levantinum* and *C. albatrosianum* and occurrence of d) paratabulated *C. albatrosianum* and Scrippsiella spp. in relation to e) particle input (total particle flux, lithogenic material and biogenic opal flux).

Calciodinellum albatrosianum and the group of *Scrippsiella* spp. reveal higher abundances from June 1998 to March 1999, but lower abundances or totally absence in samples from April 1999 to November 1999 (App. 1, Fig. 2). *Pernambugia tuberosa*, *Calciodinellum elongatum* and *Scrippsiella regalis* occur in only three to four samples, thus, results for these species are not very reliable and have been excluded from the following considerations.

Thoracosphaera heimii strongly dominates the calcareous dinoflagellate assemblage throughout the whole sampling period (>80%). From June 1998 to March 1999 (samples 1 to 11) cyst fluxes are generally high. Fluxes are slightly enhanced in June/July 1998 and January/February 1999, at times of descending SSTA. From May 1999 cyst fluxes decrease and stay at a lower level till October 1999 (samples 14 to 20; Tab. 1, Fig. 2). Relationships with particle fluxes were not observed

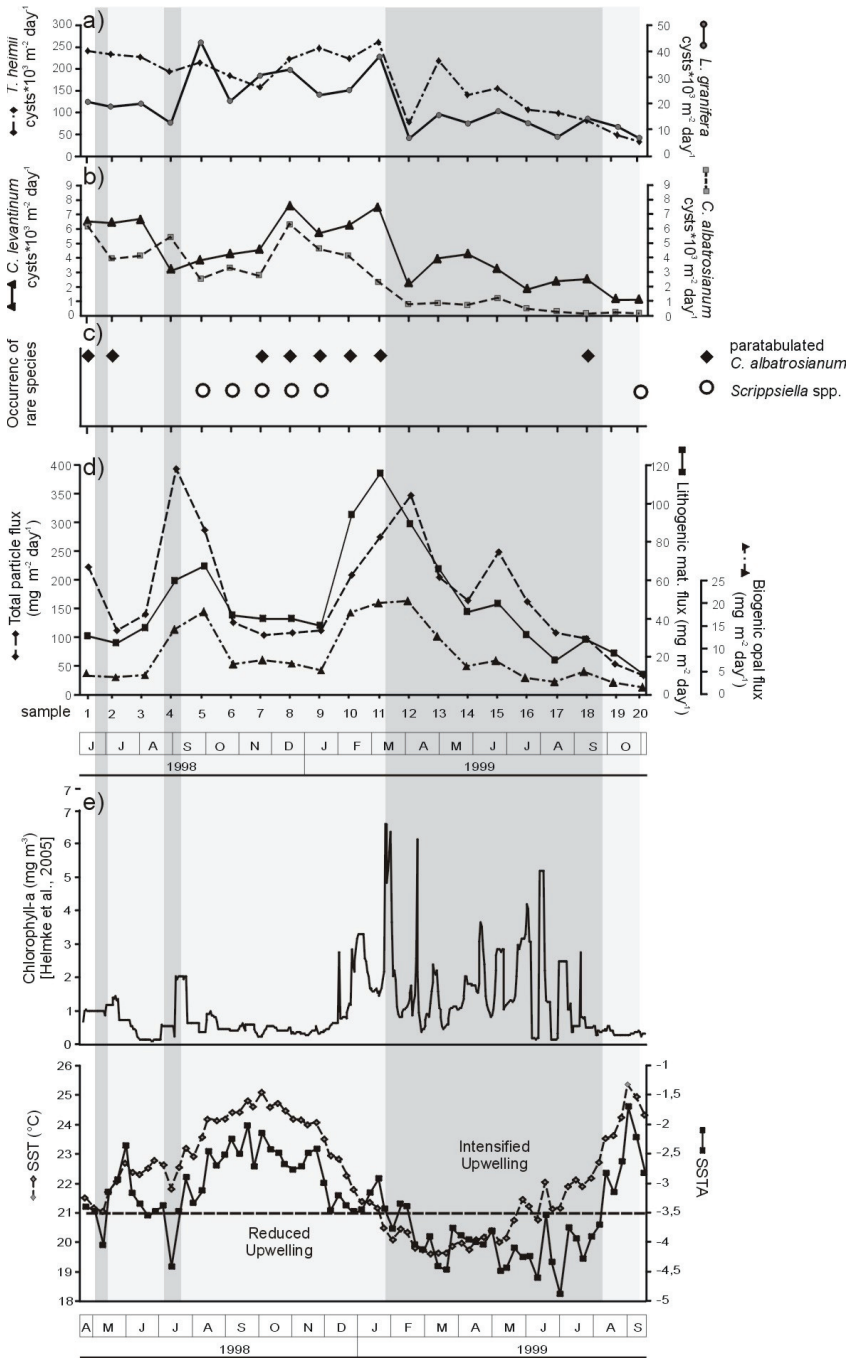

Fig. 3: Cyst fluxes of a) *T. heimii* and *L. granifera*, b) *C. levantinum* and *C. albatrosianum* and occurrence of c) paratabulated *C. albatrosianum* and Scrippsiella spp. in relation to d) particle input (total particle flux, lithogenic material and biogenic opal flux) and e) Sea Surface Temperature, Sea Surface Temperature Anomaly and chlorophyll-*a* concentration (corrected for 47 days time lag between SST, SSTA and chlorophyll-*a* and deep sediment trap fluxes).

Leonella granifera is the second most abundant species (6-19 % of the total association, but >60% of the association without *T. heimii*, Tab.1). In the high flux period two distinct peaks in September 1998 (sample 5) and March 1999 (sample 11) are evident, corresponding to intervals with high input of lithogenic material and biogenic opal. Also in the low flux period,

cysts of *L. granifera* are more abundant when lithogenic fluxes are higher. Furthermore, this species reveals higher cyst fluxes in samples deposited at higher SST and SSTA, and low cyst fluxes when SST/A is reduced.

Cyst fluxes of *Calciodinellum levantinum* do not show a distinct correlation to the studied parameters. In general, higher cyst fluxes of *C. levantinum* are observed from June 1998 to March 1999 (samples 1 to 11) and lower fluxes from April to November 1999 (samples 12 to 20 ; Fig. 2). In comparison to SST and SSTA (corrected for ca. 47 days), cyst fluxes are higher in the first period of high SST/A values (June 1998 to February 1999) and decrease with declining SST/A. Also *Calciodinellum albatrosianum* shows highest cyst fluxes from June 1998 to March 1999 (samples 1 to 11). From April to November 1999 cyst fluxes are significantly lower (samples 12 to 20). The cyst fluxes of *C. albatrosianum* can also be related to elevated SST and SSTA values (Tab. 1, Fig. 2). Even though cysts of *Scrippsiella* spp. and paratabulated *Calciodinellum albatrosianum* were found in only in six to eight samples, respectively, these species reveal higher occurrence during times of increased SST and SSTA values, but low particle fluxes.

4. Discussion

4.1. Aspects of transport and dissolution

Off Cape Blanc two major vertical particle transport mechanisms were described (Nowald et al., 2006): (1) A constant flux of particulate matter mainly in form of large, coagulated particles aggregates, which were observed within the entire water column. This continuous and almost vertical flux from the sea surface to the sea floor pass through relatively fast, and a lateral advection is supposed to be small. (2) Transfer through “sinking events”, which are characterised by fast mass transport of large amounts of particulate matter within a short period of time, and in which material from surface waters sinks at higher rates and more abundant small particles were scavenged more efficiently. This form of transport promotes an elevated concentration of large particles aggregation with sinking velocities higher than 35 m d^{-1}. The particle sinking rate is very much dependent on the nature of the particles (Siegel et al., 1990). It can be assumed that in natural environments also dinocysts are transported in large particle aggregates in form of faecal pellets or through flocculation and agglomeration in structureless organic matter (Honjo, 1976; Honjo et al., 1982; Lampitt et al., 1993; Mudie, 1996), which may accelerate the sinking velocity. Furthermore, carbonate producers may react

as an effective ballast mineral for organic carbon (Ziveri et al., 2007, Fischer et al., 2009 a; Fischer and Karakas, 2009), which may also contribute to high particle sinking rates. Off NW Africa particle sinking rates are generally very high and show high interannual variability (Ratmeyer et al., 1999; Müller and Fischer 2001; Helmke et al., 2005; Fischer and Karakas, 2009). Recent studies on calcareous dinocyst fluxes between an upper (730m) and a lower trap (3560m) at the CB position (from April 1990 to November 1991) also revealed relatively high sinking velocities of 130-280 m d^{-1} (chapter 4). Highest particle sinking rates of 280 m d^{-1} reached in 1991 probably result from high lithogenic material input (Fischer et al., 1996a). Based on the correlation of sea surface chlorophyll-a peaks and particle sedimentation peaks in trap CB9, Helmke et al. (2005) estimated an mean time lag of 47.6 days ranging between 21 and 61 days. This corresponds to an average particle sinking velocity of 75 m d^{-1} (with values between 59 and 170 m d^{-1}) to the trap deployment depth of 3580 m (Helmke et al., 2005; Fischer and Karakas, 2009), revealing that sinking velocities in 1998/1999 were reduced compared to 1990/1991. We assume that dinocysts investigated within this study were transported within the same velocity range as described by Helmke et al (2005).

In March 1999 high chlorophyll-a fluxes, combined with high lithogenic and carbonate input could have caused a fast sedimentation event. During this period (sample 11) cyst production is enhanced and decrease abruptly afterwards (sample 12). Fast sedimentation processes or transport events as described by Nowald et al. (2006) are connected with high biomass production and thus carbonate building primary producers, reacting as ballast for organic carbon (Fischer et al., 2009a). Additionally the strengthening of upwelling and high lithogenic particle fluxes, which in turn are influenced by scavenging processes (Stolzenbach, 1993; Ratmeyer et al., 1999) may accelerate the downward transport, i.e. a fast settling sedimentation event or a sinking cloud can be caused (Nowald, 2006, Fischer et al., 1996b, 2009a,b; Fischer and Karakas, 2009). These transport events last only a few hours to a few days (Fischer et al., 1996 b), however time resolution of sediment trap data (with sampling intervals of 27 days) is not high enough to detect such en event. Therefore, further studies on this subject would be necessary to investigate this relationship.

Moreover, sediment trap results may be impaired by lateral particle advection (Fischer and Wefer, 1991). Horizontal diffusion and particle sinking rates influence the particle fluxes into the trap (Siegel et al., 1990). Although analyses of grain size distributions in upper and lower sediment traps at CB position lead to the conclusion that vertical particle transport through the water column occurred fast and undisturbed by lateral input (Ratmeyer et al., 1999), Fischer et al. (2009 a) stated that significant lateral advection of particles from near-shore environments within the surface waters is evident. This is revealed by an advective transport of

chlorophyll within the Cape Blanc filament obtained by SeaWifs satellite data (Helmke et al., 2005). Thus, sediment trap data does not exactly reflect the downward particle flux of a certain limited area, but rather from various distances around the sediment trap position (Siegel et al., 1990; Fischer et al., 2009 a). However, deeper traps at CB position were influenced by almost constant currents with low velocities, and thus flux data from these depths can be analysed with respect to seasonality and interannual variability (Fischer et al., 1996a).

Within the water column calcareous dinocyst assemblages can be altered by (species-selective) dissolution (e.g. Wendler et al., 2002b and references therein). However, we suggest that off NW Africa dissolution of dinocysts in the water column above 3580 m was kept to a minimum, as the trap was located above the calcite lysocline (Key et al., 2004). Furthermore, calcareous dinocysts were well preserved, and also studies on calcareous dinocysts fluxes in CB3 and CB4 did not reveal any indication for dissolution (chapter 4).

4.2. Calcareous dinocyst production vs. particle fluxes and upwelling parameters

The surface waters at the trap site off Cape Blanc are influenced by seasonal varying oceanic circulation (Mittelstaedt, 1991; Van Camp et al., 1991), changing upwelling intensity and accordingly primary productivity due to variations in the strength of the NE trade winds (Ratmeyer et al., 1999), and variable dust input from the Sahara through the NE trades (Fischer et al., 1996a; Ratmeyer et al., 1999). Even though the sediment trap was not moored within the actual coastal upwelling band itself, it was influenced by coastal upwelling events due to the passage of giant filaments that contain packages of upwelled waters (Gabric et al., 1993, Van Camp et al., 1991). The offshore waters in the investigated area are characterised by mesoscale turbulent water motions (unstable jets, filaments and eddy formation) as revealed by satellite images of SST (Van Camp et al., 1991; Kostianoy and Zatsepin, 1996), and even within the filaments active upwelling processes may occur (Hagen et al., 1996). However, Marchesiello and Estrade (2009) suggested reduced eddy activity in the Canary Current system, but efficient dispersion a few hundreds of kilometres away from the coast. Such turbulent processes affect the dinoflagellate assemblage due to moving entire populations and modifying environmental factors such as light, temperature or nutrients conditions (Sullivan & Swift, 2003). Since nutrients are not being depleted on the shelf, nutrient supply is still high within the filaments in comparison to surrounding areas, and in situ growth of phytoplankton takes place (Gabric et al., 1993).

In CB9 the same dominant species of calcareous dinoflagellate cysts are observed as reported in trap studies from the Arabian Sea (Wendler et al., 2002a) and the Pacific Ocean

(Tanimura and Shimada, 2004), and therefore seem to be characteristic for temperate to subtropical oceans. In general, high cyst fluxes of calcareous dinocysts are observed during times of upwelling relaxation, which are characterised by relatively high SST and SSTA values, and low overall productivity (chlorophyll-a concentration) (Fig 3). Cyst fluxes are still enhanced during times of significant SST and SSTA decrease (in March 1999), probably at times at the transition between reduced upwelling and the passing of upwelling filaments (Fig. 3), additionally transporting nutrients into the surface waters. This indicates that calcareous dinoflagellates are able to produce high numbers of cysts up to certain point of upwelling intensity. During times of passing filaments (March to September 1999), resulting in more turbulent conditions in the upper water column, the cyst fluxes decrease. This decrease is probably caused by a combination of different factors: (1) Turbulence is known to be an important factor influencing dinoflagellate growth and cyst production (Gibson and Thomas, 1995; Gibson, 2000; Meier et al., 2004; Ross and Sharples, 2007). Strong turbulences hamper the build-up of a standing stock of phototrophic dinoflagellates in the Arabian Sea (Wendler et al., 2002a,c). The low cyst fluxes at times of intensified upwelling activity might therefore be the result of intense turbulence of the upper water column preventing cyst production. Also in sediment trap and surface sediment samples analyses off Somalia highest cyst production rates were found at times of upwelling relaxation or in regions offshore the major upwelling cells, when nutrient supply is relatively high and stratification of the upper water column is strong (Wendler et al., 2002a,b). Nevertheless, if strong turbulence would have been the only steering factor, enhanced cyst production could be expected to occur at the end of our study period (September-October 1999) when upwelling decreased in the upper water column. This is however not the case. A possible explanation could be that during this interval the lithogenic input and associated trace elements and nutrients were relatively low, indicating that increased cyst fluxes only occur when high nutrient (trace element) concentrations are available but less intense turbulences in the upper water column exist. This would be in agreement with sediment trap analysis from the Arabian Sea, where calcareous dinocyst fluxes were minimal in second half of the autumn monsoon, indicated by strong stratification but nutrient depletion (Wendler et al., 2002c). (2) Thecate dinoflagellates in the motile stage reach swimming speeds of up to 1.2 m h^{-1} (Kamykowski et al., 1992). In comparison the filaments migrate seaward with an average velocity of 250 m h^{-1} (Helmke et al., 2005), and small scale internal velocities may reach even higher values up to several km h-1 (Kostianoy and Zatsepin, 1996). These high flow velocities (in relation to dinoflagellate swimming speeds) are possibly unfavourable for dinoflagellates. Since dinoflagellates have a Reynolds number smaller than 1, and are therefore bound to their surrounding water masses (Zonneveld et al., 2005), it is further likely, that water masses, which are preferred by dinoflagellates, are displaced by waters arriving with the filament and

accordingly the dinoflagellates. Thus, less dinoflagellates occur in the trap catchment area. (3) Light limitation due to turbulent vertical mixing, high primary production (Dugdale and Wilkerson, 1985, Gabric et al., 1993), and lithogenic material (dust) input (February/March 1999) may be responsible for the decreasing cyst fluxes in March/April 1999. As dinoflagellates are part of the phytoplankton and thus light-driven primary producers, light limitation may hamper their optimum growth. However, time resolution in the sediment trap is not adequate to reveal an exact correlation. (4) A pulsed sedimentation event (as discussed above) is likely to cause a downward transport of high amounts of dinoflagellates from where a recovery of the dinoflagellate population is unlikely within a short period of time.

In contrast to other calcareous dinoflagellate species *Thoracosphaera heimii* is able to produce large numbers of shells in a relatively short period of time (Tangen et al., 1982) and therefore dominates the calcareous dinocyst assemblage during the entire sampling period. Relatively constant cyst fluxes from June 1998 to April 1999 through times of different particle and nutrient input as well as changing SST and upwelling conditions verify the very broad range of ecological tolerance of *T. heimii*. It is adapted to a wide range of temperatures (between 14 and 27°C) and nutrient supply (Karwath et al., 2000b; Vink, 2004). Nevertheless, we observed slightly enhanced cyst fluxes during times of decreasing SSTA values in the beginning of March 1999 indicating the strengthening of upwelling filaments (accompanied with changes in nutrient availability and vertical mixing of the upper water column). Since calcareous non-motile cells are the dominant life-cycle stage of *T. heimii* (Meier et al., 2007), it might be possible that this species is more successful under rather turbulent conditions, which can cause enhanced nutrient intake through overcoming diffuse transport restrictions (Thomas and Gibson, 1990). However, strong turbulences and nutrient depletion (May to October 1999) seem to hamper cyst production.

Life-cycle and reproduction pattern of the second most abundant species *Leonella granifera* are comparable to those of *T. heimii* (Meier et al, 2007). The positive correlation between cyst fluxes of this species and lithogenic material input that may originate from Saharan dust indicate that this species reacts positively to an increased supply of land-derived minerals or nutrients to the photic zone, e.g. the trace element iron, which may stimulate phytoplankton production (Boyd et al., 2000). But also higher SST and less intense influence of upwelling filaments and thus reduced vertical mixing appear to have a positive effect on this species. During times of decreased SST and strengthened upwelling, when general nutrient concentration is high, cyst production is reduced. As cyst fluxes of *L. granifera* do not increase with increasing SST, less intensified upwelling, but low lithogenic input in September/October 1999, the effect of temperature alone seems not to increase production of *L. granifera* but an elevated concentration of nutrients appears to be essential to maintain cyst production. Also in

previous studies it has been assumed that *L. granifera* is influenced by terrestrial nutrient (trace elements) input into the Atlantic Ocean and the Arabian Sea, but also by relatively high temperature and strong stratification (Vink, 2004; Wendler et al., 2002c). Furthermore, correlations with biogenic opal, comprising mostly marine diatoms (Romero et al., 2000) suggest that factors controlling production of both *L. granifera* and diatoms may be quite similar but further investigations are needed to verify the assumption.

Cyst fluxes of both *Calciodinellum levantinum* and *Calciodinellum albatrosianum* reveal no distinct correlations with particle fluxes (Fig.2). Cyst production rates of *C. levantinum* attain highest values form fall 1998 to spring 1999 during times of both elevated and decreasing SST and SSTA (Fig. 3), implying that this species is adapted to a broad range of water temperatures and appears to tolerate turbulent conditions to some extent. From April to November 1999, when water temperatures are lowest and thus vertical mixing is intensified due to the stronger influence of upwelling filaments, cyst fluxes decline, showing that *C. levantinum* is negatively affected by turbulent water conditions. Our results support previous observations, where absolute abundances of *C. levantinum* have been found to be low under the turbulent conditions of coastal upwelling areas (Wendler et al., 2002c; Richter et al., 2007). Furthermore, earlier studies have shown that the distribution of *C. levantinum* ranges from nutrient-enriched environments (e.g. Benguela; Arabian Sea) to oligotropic environments (e.g. mid-Atlantic gyres; Mediterranean Sea), indicating that it is one of the most opportunistic and common of all calcareous cyst species (Zonneveld et al., 2000; Wendler et al., 2002c; Meier and Willems, 2003; Vink, 2004).

In our study temperature and upwelling intensity (i.e. filament activity) as indicated by SSTA seem to be the most obvious factor influencing *Calciodinellum albatrosianum*, as fluxes of this species are relatively high in times with high SST/A and strongly drop off with declining SST/A values. From this we assume high water temperature combined with diminished turbulence positively affect *C. albatrosianum*. Results from the Atlantic Ocean and the Arabian Sea show that above all warm water temperatures have a significant effect on the distribution of *C. albatrosianum* (Wendler et al., 2002a; Vink, 2004; Richter et al., 2007). However, cyst production of this species does not increase with upwelling relaxation and increasing temperature in September/October1999. This can result from the loss of 80 to 95% of cysts in samples 12 to 20 in relation to the average amount in samples 1 to 11 (maybe triggered by a fast settling transport event). It is possible, that this species can not build up a standing stock of cysts again in a short period of time and that reaction to changed environmental condition do not occur immediately.

Although paratabulated *C. albatrosianum* occurs in only eight samples, this species can similar to *C. albatrosianum* be related to warm surface waters and moderate turbulence.

Furthermore, cysts of this species are found almost only in samples in which total particle and lithogenic fluxes were decreased, suggesting that also nutrient-poor surface water conditions have a positive influence on cyst production, which is in accordance with results from surface sediment samples from the South and equatorial Atlantic Ocean, where this species has been observed in warm and oligotrophic environments rather than in cool, nutrient-rich upwelling systems (Vink, 2004).

The group of *Scrippsiella* spp., containing mainly spiny cysts of the neritic species *S. trochoidea*, can be related to warm (sub)surface water temperatures and water column stability. This contrasts with results from the Arabian Sea and the Atlantic Ocean, where similar groups of spiny cysts were abundant in zones of active upwelling (Wendler et al., 2002c; Richter et al., 2007). Since cysts of this group are rare in our dataset, direct comparisons to existing studies may be imprecise.

5. Conclusions

This study of calcareous dinoflagellate cyst fluxes in a sediment trap off Cape Blanc represents relationships between cyst production and variations in influence of upwelling events due to the offshore meandering giant filaments (Gabric et al., 1993, Van Camp et al., 1991) as well as nutrient supply by Saharan dust input. A high flux period of cysts is observed in the first time interval of relatively high SST and SSTA values, indicating diminished upwelling filament accompanied with reduced turbulent and rather stratified water conditions. Subsequent a low flux period can be reported, during a period of stronger influence of coastal upwelling and decreased SST. Although cyst production rates generally decrease when rather turbulent water condition prevail, times of significantly SST/A change, probably at the transition of a passing upwelling filament, when turbulence is not too strong and nutrient supply is enhanced, appear to be favourable for cyst production. This indicates that moderate turbulence is tolerated by most of the species. *Calciodinellum albatrosianum* is the only species, which can generally be related to high sea surface temperatures. Furthermore, nutrient supply seems to stimulate growth and subsequent cyst formation of almost all calcareous dinoflagellate species. As cyst fluxes of *Leonella granifera* as well as *Calciodinellum levantinum* and *Thoracosphaera heimii* do not increase in times of re-stratification and rising SST, but low lithogenic influx, enhanced nutrient concentration appears to be essential to sustain cyst production. Our results indicate that both higher nutrient supply and rather stable water condition due to a diminished influence of upwelling filaments are favourable for cyst production. Only cyst fluxes of *L. granifera* exhibit clear advantages to lithogenic input, as it shows maximal cyst production during months with

enhanced contribution of lithogenic material (mainly Saharan dust). This species probably requires important land-derived minerals or micro-nutrients such as the trace element iron for optimum growth..

Interannual variations and seasonality of dinoflagellate cyst production in upwelling areas should be studied more intensively to refine our understanding of dinoflagellates. Especially the Cape Blanc deployment offers a unique possibility to attain a more or less continuous data set of fluxes for the last two decades.

Acknowledgments

We thank everyone in the working group of Historical Geology and Palaeontology of the University of Bremen for their general support and openness to discussion. Special thanks are due to Sebastian Meier for a critical review and helpful suggestions. This research was funded by the German Research Foundation (DFG) within the framework of the DFG Research Center 'Ocean Margins'. All data presented in this study will be online available from the public database Pangaea (http://www.pangaea.de).

Appendix 1

Cyst fluxes (cysts m^{-2} day^{-1}) and particle fluxes (mg m^{-2} day^{-1}; Helmke et al., 2005)

sample	*T. heimii*	*L. granifera*	*C. levantinum*	*C. albatrosianum*	paratabulated *C. albatrosianum*	*S.* spp	*P. tuberosa*	*C. elongatum*	*S. regalis*
CB 9 #1	242750	21000	6500	6250	500	0	0	1000	0
CB 9 #2	234886	19091	6409	3955	239	0	0	273	0
CB 9 #3	228545	20182	6682	4159	0	0	68	0	0
CB 9 #4	193636	12727	3182	5455	0	0	0	0	0
CB 9 #5	216273	43909	3818	2591	0	273	0	0	0
CB 9 #6	185182	21273	4227	3341	0	136	0	0	0
CB 9 #7	158318	31091	4636	2795	409	68	0	0	0
CB 9 #8	223091	33273	7705	6341	614	273	0	0	136
CB 9 #9	250091	23455	5727	4636	68	273	273	0	0
CB 9 #10	224864	25364	6273	4159	205	0	273	0	0
CB 9 #11	264273	38455	7568	2386	136	0	0	0	0
CB 9 #12	73023	7091	2114	852	0	0	0	0	0
CB 9 #13	220773	16364	4023	955	0	0	0	0	0
CB 9 #14	141273	12818	4227	818	0	0	0	0	0
CB 9 #15	157091	17455	3341	1295	0	0	0	273	273
CB 9 #16	106773	12818	1909	545	0	0	0	0	0
CB 9 #17	99682	7636	2386	341	0	0	0	0	0
CB 9 #18	81750	14727	2523	205	34	0	0	0	0
CB 9 #19	47795	11455	1125	307	0	0	0	0	0
CB 9 #20	32870	6978	1076	212	0	33	0	33	33

Total particle flux	Opal	C_{org}	N_{total}	Organic material	$CaCO_3$	Lithogenic material
221.47	4.03	3.52	0.40	7.04	180.11	30.28
112.44	3.81	3.04	0.39	6.09	75.81	26.73
139.29	4.21	5.82	0.71	11.63	88.50	34.96
390.98	14.19	12.28	1.60	24.57	292.63	59.59
284.87	18.06	11.42	1.33	22.84	177.12	66.85
125.05	6.52	6.01	0.64	12.02	65.11	41.42
103.62	7.47	5.22	0.56	10.45	46.33	39.37
106.80	6.73	5.17	0.58	10.35	50.09	39.64
112.25	5.24	3.83	0.45	7.67	63.33	36.01
207.93	17.90	9.07	1.04	18.15	78.48	93.40
273.58	20.03	9.71	1.17	19.43	119.42	114.71
344.56	20.57	10.49	1.36	20.98	214.72	88.30
203.33	12.69	7.99	0.98	15.99	109.85	64.80
163.16	6.12	5.26	0.66	10.52	103.30	43.23
247.13	7.31	7.28	0.98	14.57	177.80	47.45
161.76	3.59	5.24	0.66	10.48	116.87	30.83
108.18	2.74	3.91	0.37	7.81	79.68	17.95
96.64	4.90	4.13	0.46	8.27	54.80	28.67
52.85	2.49	2.39	0.28	4.78	24.14	21.44
33.57	1.46	1.29	0.15	2.59	18.50	11.02

Seasonal variations in calcareous dinoflagellate cyst production: A sediment trap study from the upwelling area off Cape Blanc

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Abstract

Production, transport and dissolution mechanisms of calcareous dinoflagellate cysts determine the nature of fossil assemblages used in palaeoenvironmental reconstructions, but only limited direct observations from sediment traps are so far available. First observations on sediment trap moorings deployed in two different water depths adjacent to the coastal upwelling region off Cape Blanc are presented, showing seasonal and interannual variations of calcareous dinoflagellate cyst production in relation to upper water column conditions. Relatively high sinking velocities of 150-280 m d^{-1} indicate fast transport in aggregates as a main export mechanism to the deep ocean. In the investigated period from April 1990 through November 1991, high fluxes occur during times of less intense upwelling but still enhanced nutrient supply (August to November 1990). Moderate turbulence during these times is apparently tolerated by most of the dinoflagellates. High nutrient supply results in notably enhanced cyst fluxes especially of *Leonella granifera*. Cyst fluxes of *Scrippsiella* spp, *Calciodinellum levantinum*, and *P. tuberosa* revealed indications for transport within the filaments from more coastal areas. Comparison with abundances in the surface sediment directly below the trap position show that the average assemblage recovered during the investigated 19 month period is not entirely representative of the at most 300 year accumulation of cysts on the sea floor. Differences in relative abundance between sediment trap and surface sediment assemblages are due to transport, selective dissolution and variability in interannual cyst production.

Keywords**:** calcareous dinoflagellate cysts, sediment trap, seasonal patterns, ecology

1. Introduction

Dinoflagellates belong to one of the three main eukaryotic phytoplankton groups together with diatoms and coccolithophores (Falkowski et al. 2004). They can be found in almost all aquatic milieus from fresh water to marine environments, even in sea ice or wet sand. About half of the modern genera are found to be photoautotrophic and are, therefore, important as primary producers (e.g. Taylor 1987). Several dinoflagellate species produce geologically preservable cysts made of organic or calcareous material as part of their life cycle (Fensome et al., 1993). The usability of calcareous dinoflagellate cysts (dinocysts) as tools for paleoceanographic and -environmental reconstructions has been improved in many recent studies (Zonneveld et al., 1999, 2000, 2005; Esper et al., 2000; Vink et al., 2000, 2001, 2002; Wendler et al., 2002a; Meier and Willems, 2003; Vink, 2004; Meier et al., 2004a, Richter et al., 2007). Despite these advances, information about seasonal fluctuations of calcareous dinocyst production, the environmental factors influencing them and aspects of transport and dissolution through the water column is still sparse. This information is, however, essential to complete our knowledge of the ecology of dinoflagellates. Analyses of sediment trap material can reveal direct relationships between dinocyst production and the environmental conditions of surrounding water masses. Until now, sediment trap studies involving calcareous dinoflagellate cyst analyses have only been carried out in the Mediterranean Sea (Montresor et al., 1998), the northwestern Pacific Ocean (Tanimura and Shimada, 2004), the Western Atlantic Ocean and the Sargasso Sea (Dale, 1992), and the Arabian Sea (Wendler et al., 2002a), with the last one being the only study from upwelling regions so far.

Calcareous dinoflagellate cysts can be subdivided into two groups based on their life-cycle (Fensome et al. 1996): sexual resting cysts and vegetative coccoid cysts (Meier et al. 2007). The first group is characterised by alternating generations of thecate swimming stages and non-motile calcareous cysts that are produced after sexual fusion of two thecae. Continuous cyst production with short resting periods is observed in many oceanic species and has been proposed as an adaptation to prevent sinking into unfavourable water depths in the open ocean (Meier et al. 2007). In the second group, i.e. *Thoracosphaera heimii* and *Leonella granifera,* calcareous vegetative coccoid cells are the dominant life-cycle stages (Tangen et al. 1982, Inouye and Pienaar 1983, Meier et al. 2007). Due to their asexual reproduction they show higher production rates, and usually *T. heimii* dominates the assemblages by an order of magnitude, with the exception of the Arabian Sea, where *L. granifera* can dominate fluxes (Wendler et al. 2002). For easier understanding, we refer to calcareous dinocysts for both sexual resting and vegetative coccoid cysts.

The main aim of this study is to evaluate the environmental factors influencing

calcareous dinocyst abundance from their production in the upper water column to their final deposition in the bottom sediment. For these purposes we have investigated upper and lower sediment trap material from the upwelling-induced high production area off Cape Blanc (collected in 1990/1991) as well as from the surface sediment below the trap position. Relationships between dinocyst fluxes and environmental conditions of the surface waters (e.g. SST), as well as potential effects of (lateral) transport and (species-specific) dissolution through the water column, can be deduced in this way. Cyst fluxes observed in sediment trap studies are rarely reflecting only the original production signal, but also the influence of dissolution and transport.

1.1. Oceanographic setting

The sediment trap moorings were located within the outer filamentous mixing area of the coastal upwelling system off Cape Blanc, NW Africa (21°N). This region is strongly influenced by the southward flowing Canary Current (CC), which is the eastern limb of the subtropical gyre (Fig. 1). Between 25°N and 21°N the CC departs from the continental margin and at a latitude of around 15°N the current turns westward to contribute the North Equatorial Current (Barton, 1998). South of Cape Blanc a mesoscale permanent cyclonic gyre persists, whose position and extension vary seasonally, being furthest north in autumn and winter and largest in summer (Mittelstaedt, 1991; Gabric, 1993; Barton, 1998).

The CC transports North Atlantic Central Water (NACW) from the north into the investigated area. The confluence of the CC and a poleward flowing countercurrent, carrying less saline, slightly cooler and nutrient-rich South Atlantic Central Water (SACW), cause a transition between NACW and SACW at latitudes around Cape Blanc (Mittelstaedt, 1991; Barton, 1998). Furthermore, off Cape Blanc “giant filaments”, extending up to 450 km offshore and transporting cool and nutrient-rich water from the coastal upwelling zone, are favoured by this convergence and regional recirculations (Van Camp et al., 1991; Gabric et al., 1993).

Due to the fairly steady and strong trade winds off northwest Africa upwelling occurs throughout the whole year with upwelling maxima in spring and summer (Speth et al., 1978; Mittelstaedt, 1991; Van Camp et al., 1991; Nykjær and Van Camp, 1994). Within a narrow 20 to 30 km band along the coast “primary upwelling”, the actual upwelling into the surface water layer, takes place. “Secondary upwelling” may occur further offshore along the shelf break (Mittelstaedt, 1991). In the region off Cape Blanc upwelled waters come from depths around 200 m and consist of NACW and SACW (Mittelstaedt, 1983; 1991).

Apart from nutrient supply to the upper water layers through upwelling, a further likely

source of nutrients is the trade wind-induced input of aeolian dust, originating from the central Sahara, into the Atlantic Ocean (Swap et al., 1996; Ratmeyer et al., 1999; Middleton & Goudie, 2001).

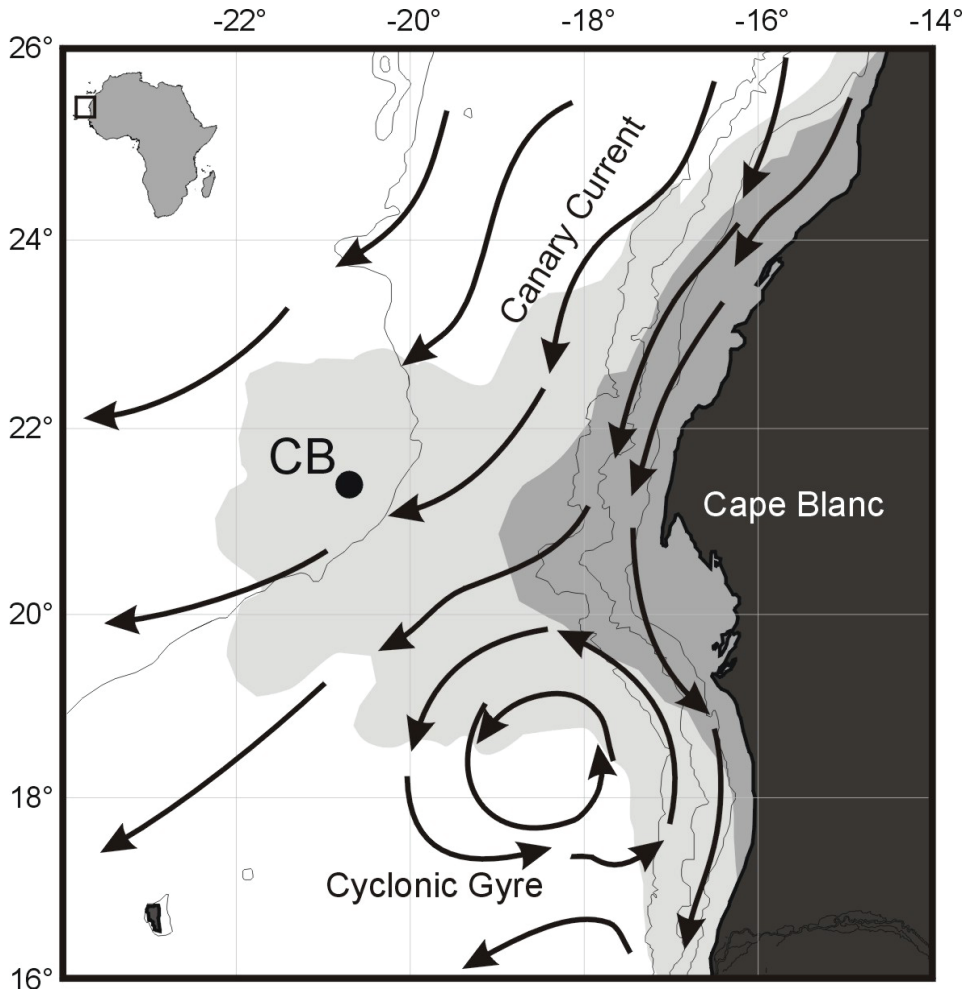

Fig. 1: Location of study site CB; with depth contour lines (100, 1000, 2000 and 4000 m). Arrows indicate schematic surface water circulation (after Mittelstaedt, 1991). The coastal upwelling area and upwelling filament are shown based on average chlorophyll-a concentration between 1997 and 2004 (obtained from the SeaWiFS Project / NASA Goddard Space Flight Center). Dark grey shading = > 2 mg m^{-3}; light grey shading = 0.5–2 mg m^{-3}.

2. Material and methods

2.1. Material

Calcareous dinocyst associations and fluxes have been determined using sediment trap material from a site adjacent to the coastal upwelling region off Cape Blanc (21°09'N, 20°41'W). The investigated samples were collected from two consecutive moorings (CB3,

CB4) deployed from April 1990 to November 1991 in two different water depths (upper traps: CB3/4u at 730m; lower traps: CB3/4l at 3560m). The exact deployment data for the traps are given in Tab.1. Determination of particle flux rates are presented in detail in Wefer and Fischer (1993) and Fischer et al. (1996a). Additionally, two surface sediment samples from the sediment below the trap position has been analysed for their calcareous dinocyst content (GeoB 4302-9, GeoB 6103-2, water depth 4120m).

Table 1
Deployment and surface sediment data.

Mooring	Trap type Opening	Position	Water depth	Trap depth	Sampling duration	Samples x days
CB 3	Kiel SMT 230 0.5m²	21°08.3'N 20°40.3'W	4094 m	730 m 3557 m	08.04.90-30.04.91 29.04.90-08.04.91	18x21.5 16x21.5
CB 4	Kiel SMT 230 0.5m²	21°09.0'N 20°41.0'W	4108 m	733 m 3562 m	03.05.91-19.11.91 03.05.91-19.11.91	20x10 20x10

Surface sediment sample	Cruise	Position	Water depth
GeoB 4302-9	M38/1	21°13.4'N 20°42.0'W	4112 m
GeoB 6103-2	M46/1	21°17.0'N 20°43.0'W	4120 m

2.2. Laboratory preparation

The sediment trap material was briefly homogenised ultrasonically and filtered through a 5 µm polycarbonate filter using a vacuum pump system. Thereafter the material on the filter was transferred into a 20 ml test tube with some drops of NaOH to keep the mixture alkaline and some drops of ethanol to avoid contamination by fungi. The sediment was left to settle for about 24 hours. After settling, the water from the test tube was decanted to 5-6 ml. The solution was then transferred into a centrifuge glass and centrifuged at 2500 revolutions per minute, for 8 minutes. After decanting the water from the centrifuge glasses, the suspension was transferred into an Eppendorf-cup which was again centrifuged for 8 minutes at 2500 revolutions per minute. After centrifuging, the water in the Eppendorf-cups was reduced to exactly 1 ml.

The preparation of the calcareous dinocysts from the surface sediment followed the method described by Vink et al. (2000). In this method, 1 cm^3 of oven-dried sediment was weighed, wet-sieved and split into two fractions (5 to 20 µm and 20 to 75 µm) to concentrate the relatively small but abundant cysts of the species *Thoracosphaera heimii* in one fraction and

all larger cysts in another fraction.

In both methods, 50 or 100 µl of the material were brought onto slides. After drying the material, it was embedded in SPURR's resin and placed in an oven at 75°C to polymerise the resin. The cysts were counted using a light microscope with polarised light (Janofske, 1996). One whole slide per sample and fraction was counted. If a slide contained less than 200 specimens, additional slides were analysed.

2.3. Methods of analyses

Holocene sedimentation rates off Cape Blanc vary between 3 cm ka^{-1} and 22 cm ka^{-1} (Krastel et al., 2006; Winn et al., 1991), we therefore assume the studied sample was deposited during recent to sub-recent times, comprising a time interval of at most 300 years. Because of the highly varying sedimentation rates an averaged sedimentation rate of 0.08 g m^{-2} day^{-1} (based on Winn et al., 1991) has been used to convert absolute cyst abundance into cyst fluxes (cysts m^{-2} day^{-1}).

Calcareous dinocyst fluxes have been compared with the following environmental parameters: (a) total particle flux to the sediment trap (including fluxes of opal concentration, organic carbon, nitrate and organic material), (b) calcium carbonate ($CaCO_3$), (c) lithogenic material, and (d) opal flux (all in situ measurements; Fischer et al., 1996). Additionally, for comparison with dinocyst fluxes of the upper traps the following factors have been used: (e) sea surface temperature (SST) and (f) sea surface temperature anomaly (SSTA). Weekly Sea Surface Temperature data were obtained from http://iridl.ldeo.columbia.edu/SOURCES/.IGOSS/.nmc/.Reyn_SmithOIv2/.

Upwelling areas are characterised by lower SST than those in surrounding regions. Variations in upwelling intensity can therefore easily be shown by the sea surface temperature anomaly (SSTA), the mean SST difference between coastal water and water further offshore at the corresponding latitude (Speth et al., 1978; Speth and Detlefsen, 1982; Nykjær and Van Camp, 1994). In our study we calculated SSTA by subtracting mid-ocean SST from SST at trap site to obtain an upwelling index for this position. Differences in SST equal to or less than -3 K are indicative of upwelling periods (Speth et al., 1978; Helmke & Davenport, 2003). Thus, periods of strong influence of upwelling filaments indicated by cold water intrusions occur in spring/summer (March to July 1990 and April/March to July 1991), whereas upwelling filament intensity was reduced from August to December 1990 and from August to November 1991. Fluctuating less intense upwelling filaments were identified from April to May 1990 and from

December 1990/January 1991 to March 1991 (Fig. 2).

3. Results

Nine calcareous dinoflagellate cyst species were recognized in the sediment trap material. In all samples calcareous dinocysts were well preserved. The most abundant species were, in order of appearance, *Thoracosphaera heimii*, *Leonella granifera*, *Calciodinellum levantinum* and *Calciodinellum albatrosianum*. Less abundant and rare species were paratabulated *Calciodinellum albatrosianum, Calciodinellum elongatum, Pernambugia tuberosa, Scrippsiella regalis* and a group of spiny cysts (*Scrippsiella* spp.), containing several different morphotypes of the *Scrippsiella trochoidea* species complex (Montresor et al. 2003, Gottschling et al. 2005). Cyst fluxes in comparison with SST/A and particle fluxes are shown for the upper and lower traps in Figs. 2 and 3, respectively. Particle fluxes measured off Cape Blanc were published by Wefer and Fischer (1993) and Fischer et al. (1996a). Cyst fluxes per trap sample are also indicated in App. 1.

The fluxes of calcareous dinocysts vary significantly throughout the sampling period. In general, highest fluxes were observed from April 1990 to February/March 1991 at both trap levels. After March 1991 cyst fluxes decreased considerably. Species-specific differences in seasonal and interannual cysts production can be observed. Individual dinocyst fluxes in CB3 were approximately 2 to 15 times higher than in CB4 at comparable times of the year. Furthermore, cyst accumulation rates recorded in the bottom traps were 2 – 12 times as high as those in the upper traps, depending on the species (Figs. 2, 3). Between the upper and lower trap cyst fluxes an one cup time lag of 21 days for CB3 and 10 days for CB4 is evident (Fig. 4).

Thoracosphaera heimii strongly dominates the total association throughout nearly the entire sampling period, accounting for 66 % to 94 % of the total assemblage. The *T. heimii* fluxes generally follow the total mass flux and correlate well with the input of $CaCO_3$, lithogenic material, and biogenic opal in CB4. However, poorer correlations are apparent in CB3. Cyst fluxes in upper trap decrease in winter/spring 1991 with decreasing SST/A values. In CB4 (spring to autumn 1991) cyst fluxes diminish. lowest fluxes were recorded in March/April and from August to November 1991 (Fig. 2). In the deep traps *T. heimii* fluxes are relatively high in 1990, and increase in winter 1990/1991, reaching highest value in March 1991. In CB4l fluxes of this species were reduced by about a factor of three compared to CB3l (Fig. 3).

Leonella granifera is the second most abundant species, forming up to 43% of the entire association. Fluxes of this species correlate well with all particle fluxes (especially in the CB4 deployment). Upper trap fluxes are dominated by two distinctive peaks in April 1990 and

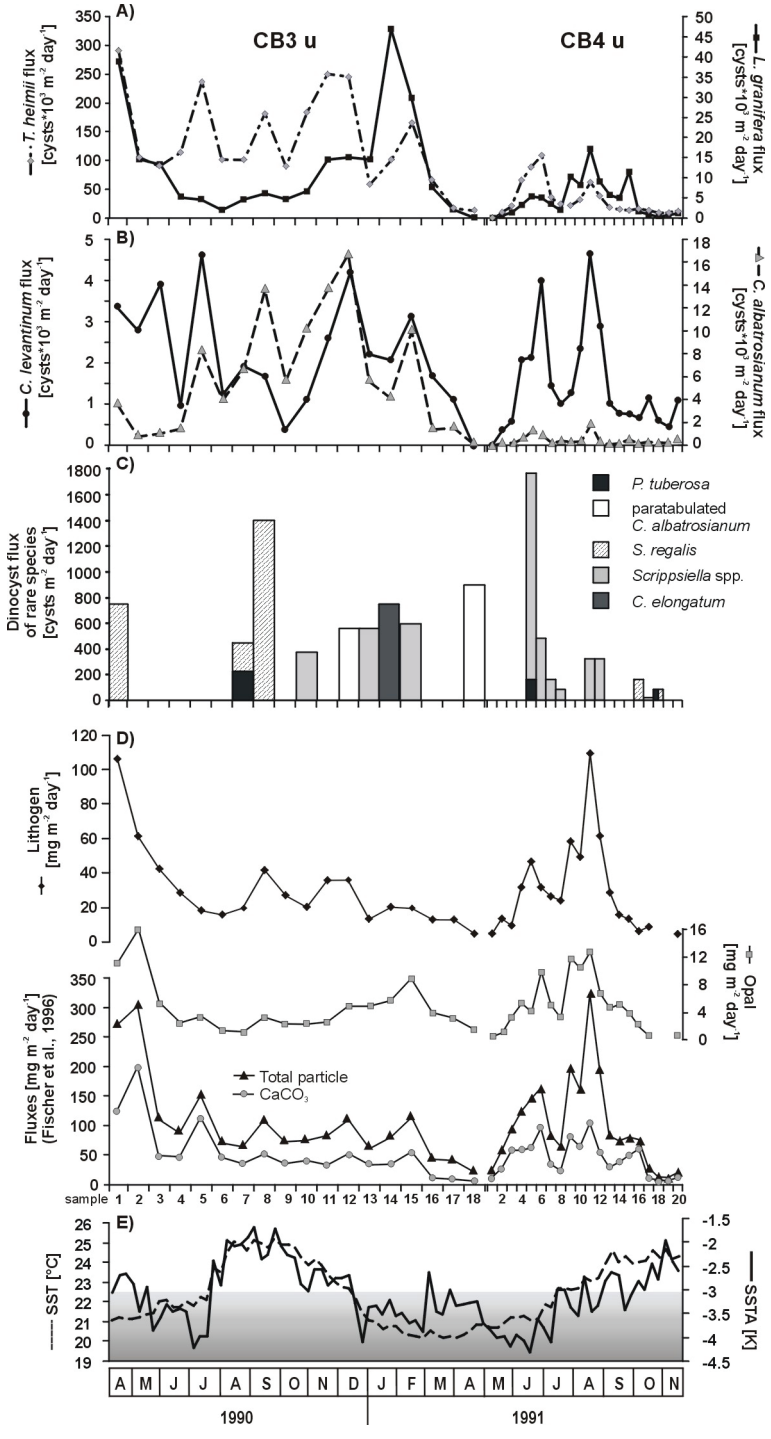

Fig. 2: Upper trap fluxes of calcareous dinoflagellate cysts: A) *T. heimii* and *L. granifera*; B) *C. levantinum* and *C. albatorsianum; C*) rare species in relation to D) lithogenic input, opal, carbonate and total particle flux, and E) Sea Surface Temperature Anomaly and Sea Surface Temperature.

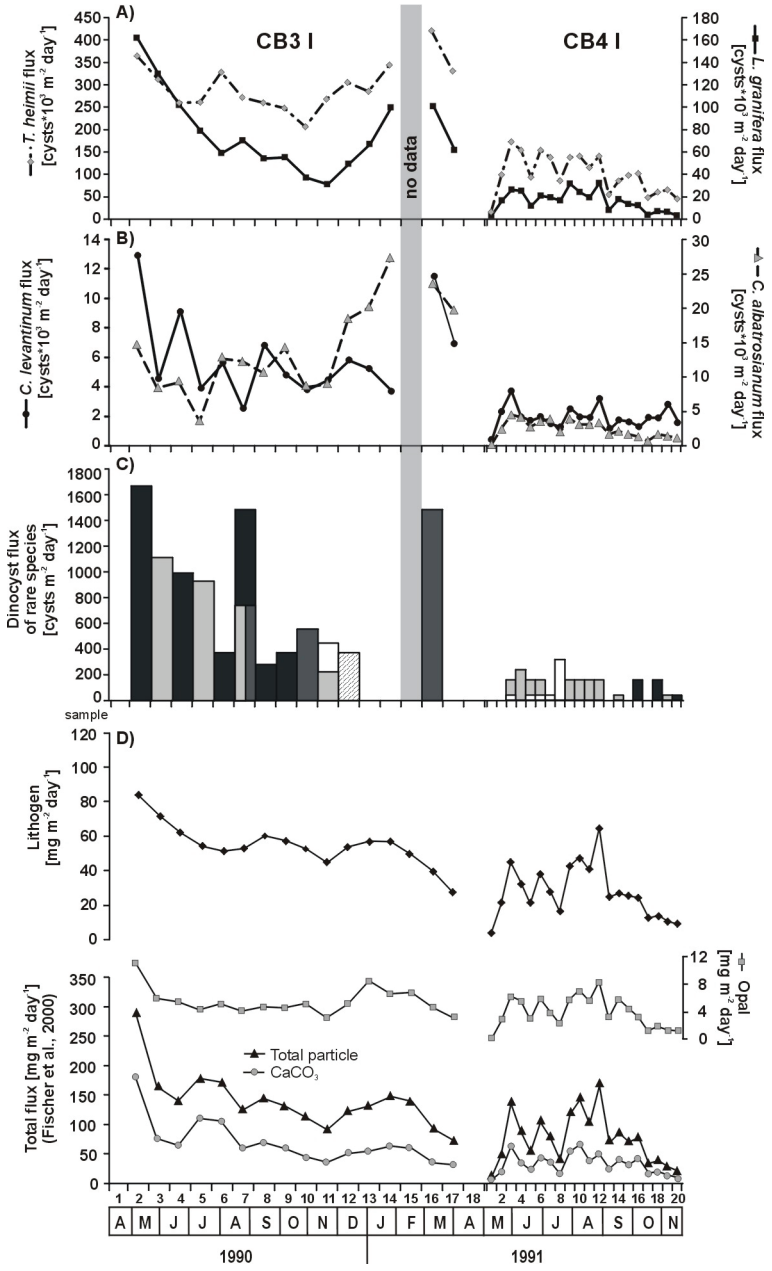

Fig. 3: Lower trap fluxes of calcareous dinoflagellate cysts: A) *T. heimii* and *L. granifera* ; B) *C. levantinum* and *C. albatrosianum*; C) rare species in relation to D) lithogenic input, opal, carbonate and total particle flux.

January/February 1991. In the period from May to December 1990, cyst fluxes are relatively low. After March 1991 cyst fluxes decrease. During periods of intermediate SST/A values (in April 1990, January 1991 and August 1991), fluxes of *L. granifera* are enhanced (Fig. 2). In the deeper trap, fluxes of *L. granifera* show a declining trend from April to November 1990, followed by an increase from November 1990 to January 1991. Fluxes in the CB4l fluctuate in

Table 2
Mean cyst fluxes in traps and surface sediments.

slide	4302-9	6103-2	CB3 upper	CB4 upper	CB3 lower	CB4 lower
T. heimii	54120	80013	134061	32786	297632	100436
L. granifera	880	2693	12775	4863	77075	15948
C. levantinum	2820	4620	2163	1534	6094	1925
C. albatrosianum	4320	5100	6117	479	14099	2438
rare species	47	200	363	191	787	114

sediment accumlation rate 0.08 g m-2 day-1

the entire sampling period (Fig. 3). In the lower traps, flux patterns of *L. granifera* and *T. heimii* are fairly similar.

Cysts of *Calciodinellum levantinum* are abundant in all samples. Cyst fluxes *C. levantinum* are in the same order of magnitude from 1990 to 1991, in contrast to all other species revealing notably decreased cyst fluxes in 1991. Highest cyst fluxes in upper traps were reached in July 1990, winter 1990/1991 and in summer 1991 (Fig. 2). In summer 1990, when SST/A values are highest, cyst fluxes decrease. Only in CB4u good correlations with particle fluxes are recognized. In deeper traps cyst fluxes reveal no distinct relationships with particle fluxes. However, in CB4l the observed peaks in spring, summer and autumn 1991 correspond to some extent to total particle and lithogenic fluxes at the same time (Fig. 3).

Cyst fluxes of *Calciodinellum albatrosianum* are substantially lower in CB4 compared to CB3, revealing the highest decrease of all species (Fig. 2). Maximum fluxes can be related to enhanced SST/A values. Cyst fluxes in CB4 deployment reflect to some degree all particle fluxes (total particles, $CaCO_3$, opal and lithogen). Cyst fluxes of *C. albatrosianum* and *T. heimii* show almost the same trends, especially in upper traps, correlating well with total particle flux.

Since rare species occurred only in a few samples in low amounts, their cyst fluxes do not reveal a clear response to environmental parameters or upwelling dynamics (Figs. 2, 3). Nevertheless, some relationships are visible. *Scrippsiella regalis* occur only during times of elevated SST and SSTA values (September 1990 and October/November 1991). On the contrary, the group of spiny cysts (*Scrippsiella* spp.) are found in higher abundance when SST/A is lower (January/February and June/July 1991). Cysts of *Pernambugia tuberosa* are obtained in higher numbers only in lower trap material. Highest abundances of this species are found in spring/summer 1990. Correlations to particle flux patterns could not be detected. Other calcareous dinocyst species are too seldom to reveal any seasonal production pattern.

The underlying surface sediments contain the same calcareous dinoflagellate cyst species as the sediment trap material. Relative abundances of both investigated samples (GeoB 4302-9, GeoB 6103-2) are quite similar. Compared to average cyst fluxes into the deeper sediment trap (especially compared to CB3l), cyst accumulation rates in surface sediments are

considerably lower (Tab. 2), differing by about 80% from the mean flux in CB3l. The largest loss is recorded for *L. granifera* (97-99%) followed by all rare species (75-94%) and *T. heimii* (73-82%; Tab. 3). In sediment samples relative abundances of *L. granifera* reach only 1.4 to 2.9 % (Fig. 5), whereas cysts of *L. granifera* account for up to 29% in the deeper trap. That means, that fluxes of *L. granifera* into the lower trap are on average a factor of 29 (GeoB 6103) to 88 (GeoB 4302) times higher than accumulation rates into the sediment (Tab. 3). Concentrations of *C. levantinum* and *C. albatrosianum* reveal the lowest loss, decreasing by about 2 and 3 times, respectively (Tab. 3).

Table 3
Ratios of mean cyst fluxes in traps and surface sediments.

slide	CB3u / 4302	CB4u / 4302	CB3u / 6103	CB4u / 6103	CB3lo / 4302	CB4lo / 4302	CB3lo / 6103	CB4lo / 6103
T. heimii	2.5	0.6	1.7	0.4	5.5	1.9	3.7	1.3
L. granifera	14.5	5.5	4.7	1.8	87.6	18.1	28.6	5.9
C. levantinum	0.8	0.5	0.5	0.3	2.2	0.7	1.3	0.4
C. albatrosianum	1.4	0.1	1.2	0.1	3.3	0.6	2.8	0.5
rare species	7.8	4.1	1.8	1.0	16.9	2.4	3.9	0.6

4. Discussion

4.1. Transport and dissolution

Off Cape Banc two transport mechanisms can be distinguished (Nowald et al., 2006): (i) A constant particulate matter flux mainly in the form of large, coagulated particle aggregates within the entire water column. This continuous and almost vertical flux from the sea surface to the sea floor occurs relatively fast, and a lateral advection is assumed to be small. (ii) Transport through “sinking events” that are characterised by a fast short-term mass transfer of large amounts of particulate matter within sinking clouds, in which material from surface waters sinks at higher rates and more abundant small particles are scavenged. This form of transport promotes an elevated concentration of large particles aggregation with sinking velocities higher than 35 m d^{-1}. Carbonate-secreting primary producers as well as dust input are considered to be important mineral ballast for organic carbon and thus influence particle sinking velocities and organic carbon transfer to depth (Fischer et al., 2009a).

Mean daily dinoflagellate cyst fluxes recorded in the deep sediment trap were up to 12 times as high as the fluxes observed in the upper one, depending on the species. This is particularly evident for *Leonella granifera*. Cyst fluxes and relative abundances of *L. granifera* increased in lower traps, especially in CB3l compared to CB3u. This discrepancy was probably caused by lateral transport of cysts from more shelf ward areas, along the shelf and continental slope, into the lower trap due to the higher catchment volume of the lower trap (Siegel et al.,

1990). In general, lateral particle advection may impair sediment trap results, especially upper trap fluxes may be affected by higher current velocities (Fischer et al., 1996a; 2009a). Earlier studies of grain size distribution between upper and lower traps at the same trap position showed that particle transport through the water column occurred rapidly and was undisturbed by lateral input, and that no alteration of particles during sinking took place in the investigated traps (Ratmeyer et al., 1999). However, Fischer et al. (2009a) stated that in CB3 deployment some lateral advection occurred, but in CB4 a mostly vertical sedimentation with a negligible lateral advection was recorded. However, indications for lateral particle transport are also given by the calcareous dinocyst fluxes. Off NW Africa intensified NE trades result in high lithogenic input of the surface waters (Ratmeyer et al., 1999), and increased nutrient supply is revealed by high biogenic opal and particle fluxes. The dinocyst association reflects the influence of

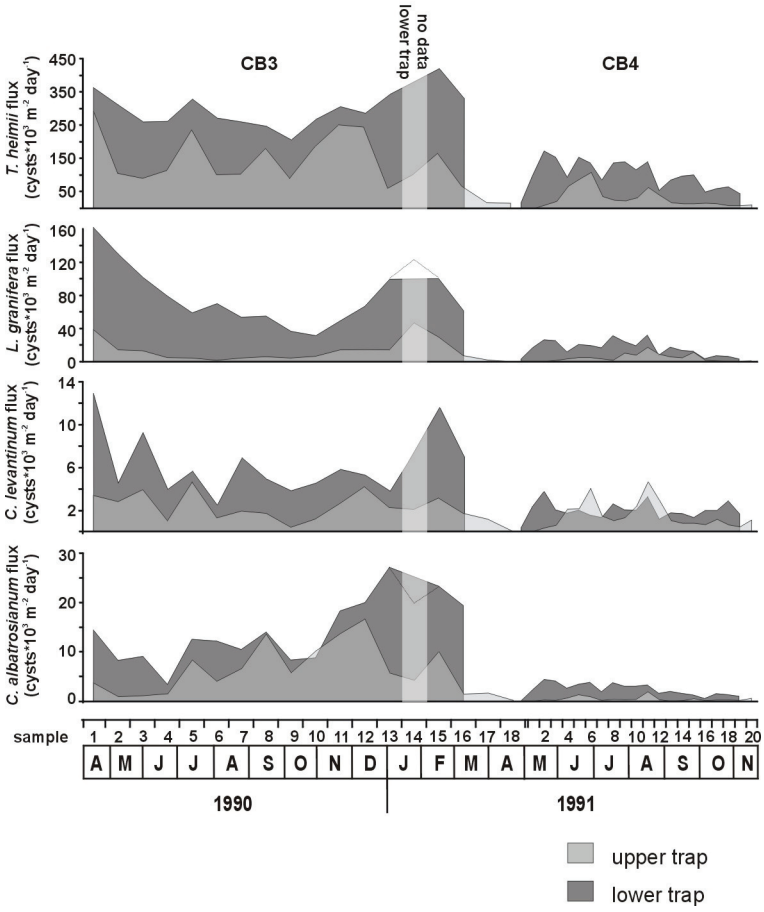

Fig. 4: Cyst fluxes of main species corrected for 21.5 days (CB3) and 10 days (CB4) between upper (light grey) and lower (dark grey) traps, respectively.

coastally derived nutrient-rich waters, which is apparent by the continuous flux of the group of spiny cysts, mostly consisting of the neritic species *S. trochoidea*.

There was an approximate one-cup time lag between the upper and lower trap (~10 days lag in CB4 and ~21.5 days lag in CB3) (Fig. 5), i.e. the cysts took about 10 days to 3 weeks, respectively, to settle through the water column from a depth of 730 m to 3557 m. These results are supported by previously determined estimations, where particle sinking rates of 150-280 m d^{-1} were calculated, corresponding to time lags of 10-20 days between upper and lower traps for CB4 and CB3 (Fischer et al., 1996a, 2009a; Ratmeyer et al, 1999; Müller and Fischer, 2001). By means of sinking experiments, Anderson et al. (1985) calculated sinking rates of 7 and 11 m day^{-1} for *Scrippsiella. trochoidea*, implying that these cysts would take at least eight months to settle down from 730 m to the deeper trap at 3557 m. We assume that in natural environments, transport in form of faecal pellets or through flocculation and agglomeration in structureless organic matter (Honjo, 1976; Honjo et al., 1982; Lampitt et al., 1993; Mudie, 1996) accelerates the sinking velocity. Moreover, recent analyses have shown that small scale carbonate producers may react as an effective mineral ballast for organic carbon, resulting in higher settling velocities (Ziveri et al., 2007; Fischer et al., 2009a).

Calcareous dinocyst assemblages can be altered by (species-selective) dissolution in sediments located below the calcite lysocline, due to deep water undersaturation with respect to calcite and/or within the water column, caused by biological processes within the guts and faeces of grazers, or by increased degradation of organic material within marine snow or aggregates resulting in a local formation of carbonate-dissolving waters (e.g. Wendler et al., 2002b and references therein). At both trap positions waters are still saturated with respect to calcite (Key et al., 2004). Although an obvious decrease of particle fluxes (Corg, biogenic opal, and carbonate) in CB4 deployment points towards some dissolution within the water column (Fischer et al., 2009a), cyst accumulation rates in the bottom trap increased. Furthermore, both calcareous dinocysts and coccoliths from the same lower sediment trap samples (Köbrich et al., 2008) were well preserved. Thus, we suggest that dissolution of cysts in the water column above 3560 m was kept to a minimum.

The concentration of cysts in the surface sediment directly below the trap position was lower than that in the lower trap (Tab. 2). In particular concentrations of *L. granifera*, *Thoracosphaera heimii* and the rare species diminish in surface sediments. At the depth of 4100m probably cyst dissolution set in around the calcite lysocline due to undersaturation with respect to carbonate ions in the deep water masses. Furthermore, especially in areas with high surface water productivity and export of organic carbon to the sea floor, carbonate dissolution due to organic matter degradation may also have a large effect on cyst preservation (Wendler et al., 2002b; Vink, 2004). Species-specific dissolution has been described for the high

productivity area of the NE Arabian Sea through the analysis of a sediment sample transect intersecting the intensive oxygen minimum zone, where *T. heimii* and *Calciodinellum levantinum* have been found to be the most sensitive species to degradation-related dissolution (Wendler et al., 2002b). In our study, cyst accumulation rates of *T. heimii* declined 4 to 5 times between CB3l and in the bottom sediment, whereas concentration of *C .levantinum* dropped 2 times, indicating that *T. heimii* is more susceptible for dissolution than the other species and that *C. levantinum* is more resistant. This is confirmed by surface sediment analyses from the Benguela upwelling system, revealing extremely high relative abundances of *C. levantinum*, and thus suggesting, that this species is more resistant to dissolution related to organic matter

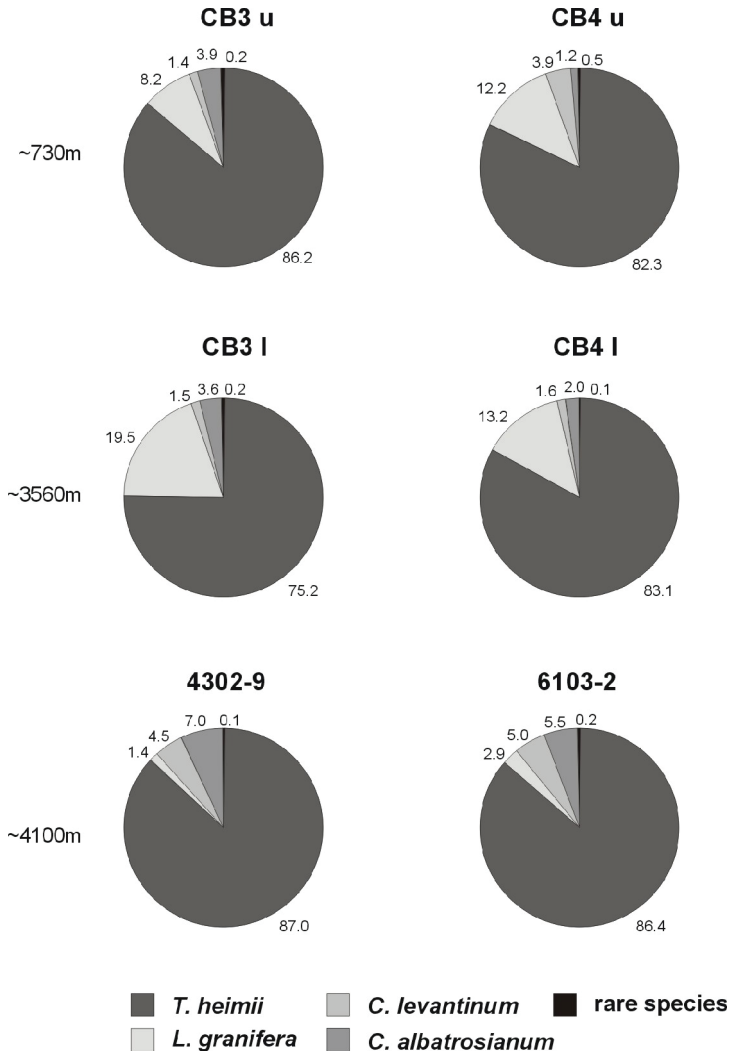

Fig. 5: Relative cyst abundances in sediment trap and surface sediment samples.

degradation than the other species (Vink, 2004).

The fact, that the largest loss in relative cyst abundances between the lower trap and the sediment sample has been documented for *L. granifera*, tentatively indicates a higher sensitivity of this species to dissolution. This suggestion is in contrast with earlier work on sediment trap material and surface sediment samples form the Arabian Sea (Wendler et al., 2002 a,b), where *L. granifera* was found to be the most resistant to dissolution compared to the other species. However, sedimentation rates off Cape Blanc differ strongly and comprise values between 3 cm ka^{-1} and 22 cm ka^{-1} (Krastel et al., 2006; Winn et al., 1991), and accordingly the time interval in which the upper centimetre of the investigated sediment was deposited vary between 45 and 300 years. Higher cyst production rates of *L. granifera* during the relatively short trap sampling period of approximately 19 months compared to the mean cyst accumulation rates in the last at most 300 years would lead to reduced relative abundances of this species in relation to the other species. Furthermore, if patches of *L. granifera* blooms are located away from the trap position, cyst fluxes would increase with depth in the sediment trap due to horizontal particle advection (Siegel et al., 1990), but would possibly not being reflected in the surface sediments.

4.2.Dinocyst production in relation to environmental parameters and particle fluxes

Off Cape Blanc surface waters are influenced by variations in upwelling intensity and thus primary productivity, associated with variations in the strength of the NE trade winds (Ratmeyer et al., 1999), seasonal variations in oceanic circulation (Mittelstaedt, 1991; Van Camp et al., 1991), and variable dust input from the Sahara through the NE trades (Fischer et al., 1996a; Ratmeyer et al., 1999). Even though the Cape Blanc sediment trap is not placed within the actual coastal upwelling system, the mooring is situated in a region that is affected by filaments that extend hundreds of kilometres offshore carrying coastally upwelled water with chlorophyll concentrations above 1 mg m^{-3} (Van Camp et al., 1991; Kostianoy and Zatsepin, 1996). The development of filaments and eddy formation result in mesoscale turbulent water motions in offshore waters off Cape Blanc (Van Camp et al., 1991; Mittelstadt, 1991; Kostianoy and Zatsepin, 1996), and even within the filaments active upwelling processes may occur (Hagen et al., 1996). However, Marchesiello and Estrade (2009) suggested reduced eddy activity in the Canary Current system, but efficient dispersion a few hundreds of kilometres away from the coast. Within the filaments nutrient supply is still enhanced and *in situ* growth of phytoplankton occurs, as nutrients are not exhausted on the shelf and transported offshore (Gabric et al., 1993).

In general, cyst fluxes in 1991 are reduced compared to 1990, possibly due to the

enhanced influence of upwelling filaments (Figs. 2 and 3). Upper water conditions during this period of time may have been unfavourable for calcareous dinoflagellates, as surface waters were rather turbulent. Compared to 1991 (CB4), 1990 (CB 3) was a relatively calm year, as not so many filaments were passing over the trap. Thus, dinocyst production is enhanced. During CB 4 (summer 1991), many more filaments were transported to the trap site, indicated by reduced SSTA values. These passing filaments either hampered cyst production or transported those further offshore. Studies on dinoflagellates have shown that they react sensitively to high turbulence (e.g. Thomas and Gibson, 1990, 1992; Sullivan and Swift, 2003). Cyst production rates in the Arabian Sea were positively related to reduced turbulence but still high nutrient concentrations in surface waters (Wendler et al., 2002a). However, cyst fluxes increased in January/February 1991 during a period of intensified but not strongest influence of upwelling filaments, signifying that up to a certain point of upwelling intensity calcareous dinoflagellates are able to produce high amount of cysts. Since the dominant life-cycle stages of *Thoracosphaera heimii* and *Leonella granifera* are calcareous vegetative coccoid cells (Tangen et al. 1982, Inouye and Pienaar 1983, Meier et al. 2007), and also *C. levantinum* and *C. albatrosianum* exposed continuous cyst production (Janofske and Karwath, 2000; Meier et al., 2007), these species may benefit from somewhat turbulent conditions, by moving the cells into favourable light and nutrient regimes. Moreover, correlation of cyst species with biogenic opal, comprising mostly marine diatoms (Romero et al., 2000), lead to the suggestion, that some factors controlling production of both phytoplankton groups may be quite similar, as also diatoms dominate in nutrient rich and turbulent environments (Margalef, 1978; Nave et al., 2001). However, this assumption has to be verified in further investigations.

However, cyst fluxes do not increase significantly in autumn 1991 when SST raise and upwelling is less intense. If strong turbulence would have been the only steering factor, increasing cyst fluxes could be expected to occur at the end of our study period (September-November 1991). The relatively low input of lithogenic matter and associated trace elements and nutrients in September 1991, may possibly lead to diminished cyst fluxes. This signifies that increased cyst fluxes only occur when high nutrient (trace element) concentrations are available but less intense turbulences in the upper water column exist. Our results confirm sediment trap analysis from the Arabian Sea, where calcareous dinocyst fluxes were minimal in the second half of the autumn monsoon, indicated by strong stratification but nutrient depletion (Wendler et al., 2002c).

Thoracosphaera heimii dominates the calcareous dinocyst assemblage in all samples, apparently due to its ability to produce a large number of shells in a short period of time (Tangen et al., 1982). Cyst fluxes of *T. heimii* vary throughout the entire sampling period, but were slightly enhanced during times of increased SST and less intense influence of upwelling

filaments, signifying the importance of less turbulent water conditions. Correlations with lithogenic and total particle fluxes indicate a certain significance of nutrient input for *T. heimii*. This species is assumed to have a broad range of ecological tolerance (Vink,2004). However, investigations of surface sediment samples off NW Africa (Richter et al., 2007) and sediment trap samples off Somalia (Wendler et al., 2002a) show that highest production rates of *T. heimii* is related to higher nutrient contribution and reduced water turbulence rather than to temperature changes. Although our result do not support this very well, the relationships with enhanced SST/ A values and total particle fluxes, indicate some preferences for higher nutrient supply and reduced turbulence.

Leonella granifera is highly abundant in almost all sediment trap samples. This species has a similar life cycle to *T. heimii*, thus having a high reproduction rate of cysts (Meier et al., 2007). Cysts fluxes of this species show a relationship with lithogenic material input, implying a preference of *L. granifera* for nutrient enrichment through (i) upwelling of nutrient-enriched waters and/or (ii) input of land-derived nutrients or minerals, i.e. aeolian dust input from the Saharan region (Swap et al., 1996; Moulin et al., 1997; Ratmeyer et al., 1999). Nutrients and minerals, above all iron, within the dust may lead to enhanced biomass production at sea surface (Boyd et al., 2000; Pittman, 2002; Sarthou et al., 2003). Relatively high abundances of *L. granifera* have been described in regions of substantial river input (Wendler et al., 2002c; Meier et al. 2004a; Vink, 2004). Also in the upwelling region off the Moroccan coast, a likely influence of land-derived nutrients and minerals through aeolian dust input from the Saharan region on cyst production has been described (Richter et al., 2007, chapter 2), supporting our observations.

At both trap depths cyst fluxes of *L. granifera* drop at times of raised SST and reduced upwelling intensity in summer 1990, but increase rapidly at the transition between reduced filament activity and the passing of filaments (Figs. 2, 3). When filament intensity become strongest, cyst fluxes decrease. These result suggest that up to a certain point turbulence is tolerated by *L. granifera*. However, too strong turbulences seem to hamper cyst production. In previous studies *L. granifera* has been described from the upwelling regions of the NE and SW Arabian Sea (Wendler et al., 2002c), the Benguela upwelling system (Zonneveld et al., 2000), the NW African upwelling area (Richter et al., 2007), the Amazon outflow area (Vink et al., 2000) and in the Gulf of Guinea (Vink, 2004). Results of all studies showed large quantities in the more shelfward zones and decreasing abundances towards offshore regions. However, surface sediment samples from the active upwelling zones in the SW Arabian Sea (Wendler et al., 2002c) and off NW Africa (Richter et al., 2007) revealed lower amounts of cysts than in the less turbulent, albeit nutrient-rich filaments and surrounding areas. As both the Amazon outflow region and the Gulf of Guinea are not influenced by upwelling at all, upwelling itself is not the

major factor controlling the distribution of *L. granifera*. Our data confirm these earlier findings. As cyst fluxes of *L. granifera* are reduced during the time period of highest SST and reduced filament activity (i.e. water column in summer/autumn 1990 is more stratified), a relationship of this species to relatively warm and stratified surface waters, as documented from the Arabian Sea (Wendler et al., 2002a) as well as from the South and equatorial Atlantic with SST between 25°C and 28°C (Vink, 2004), cannot be seen. However, field data from the NW African upwelling system revealed preferences of *L. granifera* to relatively low SST (Richter et al., 2007). In laboratory culturing experiments the majority of well-calcified cysts was produced within a temperature range of between 18°C and 24°C, leading to the suggestion, that this species is more related to a distinct seasonality in cyst production or cyst production is enhanced at deeper, cooler water depths within the photic zone. (Meier et al., 2004b). In this study cyst production is enhanced, when SST diminishes (between 20°C and 22°C), but upwelling intensity is not strongest, signifying . that enhanced nutrient concentrations due to dust input and moderate upwelling as well as rather cooler water temperatures have determined the cyst fluxes of *L. granifera*.

High flux rates of *C. levantinum* correspond to times of significant SST and SSTA change, apparently at times, when stratification builds up or breaks down, i.e. at the transition of rather calm conditions and the passing of filaments or the relaxation of filament activity. In addition, cyst fluxes correlate with total particle fluxes, which is dominated by carbonate and lithogenic components (Fischer et al., 1996). From our results we infer, that slightly enhanced upwelling intensity, lower surface water temperatures and nutrient-rich environments reflect the cyst production of *C. levantinum*. Our findings are in agreement with previous studies, where this species was related to relatively cool (13°C-20°C) and nutrient-rich environmental conditions (Vink, 2004). However, highest abundances of *C. levantinum* were not reached in zones of active coastal upwelling (Wendler et al., 2002a,c; Richter et al., 2007). Nevertheless, the higher abundances of *C. levantinum* in summer 1991, related to the enhanced input of lithogenic material may also be caused by higher production in more coastal areas and subsequent lateral transport within the filaments, as this species appears to be the most widespread and opportunistic of all calcareous dinocyst species with its distribution extended from oligotrophic (e.g. Mediterranean Sea, mid Atlantic gyres) to nutrient-enriched environments (e.g. Arabian Sea, Benguela and NW African upwelling systems; Zonneveld et al., 2000; Wendler et al., 2002c; Meier and Willems, 2003; Vink, 2004; Richter et al., 2007), and thus being the only of the oceanic species which can still compete in relatively shallow, nutrient-rich environments.

The cyst fluxes of *Calciodinellum albatrosianum* showed a clear relationship with warm (sub)-surface waters and reduced upwelling intensity, especially in upper trap samples (Fig. 2).

Correlations with particle fluxes are not distinctive. Striking relationship with relatively high SST was also shown by distribution pattern of *C. albatrosianum* from the Arabian Sea (Wendler et al., 2002c) as well as from South and equatorial Atlantic surface sediments (Janofske & Karwath, 2000; Zonneveld, 2000; Vink, 2004) and five late Quaternary cores from the same region (Esper et al., 2000). Furthermore, ccurrence of this species was positively related to higher temperatures in surface sediment samples from the upwelling region of NW Africa (Richter et al., 2007). Thus, previous considerations on *C. albatrosianum* as a typical warm water species can be confirmed within this study. Cyst fluxes of *C. albatrosianum* and *T. heimii* are quite similar, showing that these species have probably similar ecological preferences, although relationships of *T. heimii* with warm temperatures were not that obvious as for *C. albatrosianum.*

Cysts of *Scrippsiella regalis*, *Scrippsiella* spp. and *Pernambugia tuberosa* (as well as paratabulated *Calciodinellum albatrosianum* and *Calciodinellum elongatum*) occurred in minor abundances and in a few samples only, thus cyst fluxes are barely linked to particle fluxes (Figs. 2, 3). Cyst fluxes of *S. regalis* showed some tendencies to warmer temperatures and lowered upwelling intensity connected with reduced turbulences in upper water column. This pattern contrasts with distribution from the South and equatorial Atlantic, where relationship of this species with relatively cool (14°C to 21°C) and well mixed (sub-)surface waters became apparent (Vink, 2004). However, our results are uncertain due to the patchiness of occurrence of *S. regalis*.

All other spiny calcareous dinocysts (without *S. regalis*) were grouped together, but mainly consisting of the species *Scrippsiella trochoidea*, which is exclusively known from the neritic environment (Janofske, 2000). Compared to the other uncommon species, cysts of this group occurred quite often and revealed preferences for lower water temperatures. This species is probably transported within the filaments form more coastal areas. In the Arabian Sea (Wendler et al., 2002c) as well as in the Benguela upwelling region (Zonneveld et al., 2000), spiny cysts (containing all calcareous dinocysts with spines) were abundant in zones of active upwelling with relatively high nutrient concentrations, low temperatures and strong seasonality. Moreover, results from the upwelling area off Morocco exposed highest abundances of this group within the active upwelling filaments (Richter et al., 2007).

Cyst fluxes of *P. tuberosa* appeared in lower trap samples only in somewhat higher amount. If blooms of this species occurred is some distance from the trap position, sinking particles from this region will appear in the deeper trap due to lateral advection (especially obvious in CB3; Siegel et al., 1990; Fischer et al., 2009a). However, cyst abundances lacked a good correlation to particle fluxes, SST or SSTA, as cyst fluxes were higher in summer/autumn 1990 during times of low temperatures and enhanced upwelling intensity as well as higher

temperatures and upwelling relaxation. In earlier studies, *P. tuberosa* has been related to oligotrophic environments with relatively mixed (sub-)surface water conditions (Vink, 2004). Nonetheless, interpretation of relations to any factors is insufficient due to the scarcity of cyst of *P. tuberosa.*

5. Conclusion

In this study sediment trap samples from the upwelling influenced area off Cape Blanc have been investigated concerning their calcareous dinocyst content. For the first time we were able to examine samples from two different water depths during the same period of time, and thus to obtain insight into mechanisms that occur between cyst production in the upper water column and deposition on the sea floor. Cyst fluxes revealed fluctuating production pattern throughout the sampling time, reflecting the various hydrographic conditions, without disclosing the influence of single parameters. In general, fluxes decreased during times of passing filament, indicating preferences for less turbulent conditions. However, at the transition between low and high filament activity (i.e. moderate upwelling intensity) cysts fluxes were still enhanced. Thus, we suggest that up to a certain point turbulence may be favourable for cyst production, but too strong mixing of the water column hamper the development of a standing stock of calcareous dinoflagellates. Furthermore, cyst fluxes are correlated with total and lithogenic particle fluxes, implying significance of nutrients for calcareous dinoflagellates.

T. heimii cyst production was high throughout the whole sampling period. Although some preferences of this species to higher SST and to times during times the filament activity is diminished were revealed, not distinct correlations to upwelling dynamics and nutrient supply were observed. Production of *L. granifera* is clearly related to lithogenic matter, mainly consisting of Saharan dust. Higher cyst production is probably stimulated by the supply of the trace mineral iron within the dust. Furthermore, moderate turbulences through less intense upwelling also appears to be a controlling factor. Based on our results *L. granifera* can be used as an indicator for land-derived minerals and nutrients into the ocean in palaeoceanographic reconstructions. Cyst fluxes of *C. levantinum* are positively related to slightly enhanced upwelling intensity and lower surface water temperatures, supporting earlier studies on this species (e.g. Vink, 2004). Higher abundances during times of changing water column stratification, indicate that *C. levantinum* is more resistant to water column instability than the other investigated species. Since this species is adapted to different environmental regimes, it is likely that this species is transported within the filaments from more coastal areas, explaining the good relationships with the enhanced filament activity and the lithogenic material

contribution. The definition of *C. albatrosianum* as a typical warm water species is confirmed within this study. As similar trend for *T. heimii* and *C. albatrosianum* have been observed, these species may have comparable ecological preferences. Less abundant species reveal only weak relationship between cyst production and environmental parameters, thus interpretation of relations to any factors is inadequate. Nevertheless, some tendencies are visible. Cyst fluxes of *S. regalis* appears to be related to warmer SST's and lowered upwelling intensity, which is different from former studies in which this species was rather related to relatively cool (14°C to 21°C) and well mixed (sub-)surface waters (Vink, 2004). *Scrippsiella* spp. occurs mainly during times of relatively cool and turbulent water conditions, reflecting the higher cyst production of the neritic species *Scrippsiella trochoidea* in the active upwelling area and the transport within the upwelling filaments. Also the occurrence of *P. tuberosa* especially in deeper traps possibly results from lateral transport.

The comparison of the cyst flux patterns of the upper and the lower traps revealed average sinking velocities of 150-280 m d^{-1}. Thus, transport of cysts through the water column occurred rapidly, probably through agglomeration in organic matter or marine snow or in faecal pellet form (Honjo, 1976; Honjo et al., 1982; Nowald, 2006). Carbonate dissolution of dinocyst during transport through the water column has been of minor importance, but was probably evident in surface sediment samples around the calcite lysocline. Reduced relative abundances of *L. granifera* in the surface sediment directly below the trap position indicate, that not only species-selective dissolution changes dinocyst population, but that the average assemblage accumulated in the sediment trap is not entirely representative of the at most 300 year accumulation of cysts on the sea floor due to transport processes and variability in the interannual cyst production.

Our results sustain and improve earlier studies on calcareous dinoflagellate ecology. Within this study new aspects of calcareous dinocysts in upwelling areas and mechanisms of transport through the water column are exposed. However, the described dinocysts fluxes reflect the scope of the sampling period only and additional trap samples would undoubtedly modify the seasonal variations patterns to some extent.

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Appendix 1
Fluxes of calcareous dinoflagellate cysts in CB3 and CB4

	sample	*T.heimii*	*L.granifera*	*C.levantinum*	*C.albatrosianum*	P.tuberosa	paratabulated *C.albatrosianum*	*S.regalis*	*Scrippsiella* spp.	*C.elongatum*
upper trap	CB3u-1	290977	38698	3349	3721	0	0	744	0	0
	CB3u-2	104930	14512	2791	930	0	0	0	0	0
	CB3u-3	90419	13395	3907	1116	0	0	0	0	0
	CB3u-4	114140	5023	977	1535	0	0	0	0	0
	CB3u-5	236651	4465	4605	8372	0	0	0	0	0
	CB3u-6	101023	1953	1256	4047	0	0	0	0	0
	CB3u-7	102028	4465	1898	6698	223	0	447	0	0
	CB3u-8	180558	6140	1674	13674	0	0	1395	0	0
	CB3u-9	90419	4465	372	5767	0	0	0	0	0
	CB3u-10	183814	6698	1116	10233	0	0	0	372	0
	CB3u-11	249674	14512	2605	13767	0	0	0	0	0
	CB3u-12	243907	14791	4186	16744	0	558	0	0	0
	CB3u-13	59163	14512	2233	5721	0	0	0	558	0
	CB3u-14	101209	46884	2047	4279	0	0	0	0	744
	CB3u-15	165805	29767	3126	10121	0	0	0	595	0
	CB3u-16	66233	7442	1674	1488	0	0	0	0	0
	CB3u-17	17860	2233	1116	1674	0	0	0	0	0
	CB3u-18	14288	0	0	223	0	893	0	0	0
	CB4u-1	0	0	0	0	0	0	0	0	0
	CB4u-2	10320	320	340	240	0	0	0	0	0
	CB4u-3	21300	1520	580	220	0	0	0	0	0
	CB4u-4	66320	3360	2080	680	0	0	0	0	0
	CB4u-5	88720	5120	2120	1320	160	0	0	1760	0
	CB4u-6	108640	4960	4000	920	0	0	0	480	0
	CB4u-7	36480	3440	1440	200	0	0	0	160	0
	CB4u-8	24800	2000	1000	400	0	0	0	80	0
	CB4u-9	23040	10400	1280	360	0	0	0	0	0
	CB4u-10	32800	8000	2360	400	0	0	0	0	0
	CB4u-11	63200	17280	4640	1920	0	0	0	320	0
	CB4u-12	39040	8960	2880	320	0	0	0	320	0
	CB4u-13	18240	5760	1000	0	0	0	0	0	0
	CB4u-14	14880	4800	760	160	0	0	0	0	0
	CB4u-15	13840	11520	760	520	0	0	0	0	0
	CB4u-16	16560	1760	640	120	0	0	160	0	0
	CB4u-17	14320	1120	1140	280	0	20	0	0	0
	CB4u-18	9720	400	600	260	80	0	80	0	0
	CB4u-19	9200	640	440	180	0	0	0	0	0
	CB4u-20	11520	1040	1080	600	0	0	0	0	0
lower trap	CB3l-2	363907	161860	12837	14512	1674	0	0	0	0
	CB3l-3	311442	129488	4465	8372	0	0	0	1116	0
	CB3l-4	259473	101705	9178	9178	992	0	0	0	0
	CB3l-5	261209	78884	3907	3535	0	0	0	930	0
	CB3l-6	328186	58791	5581	12651	372	0	0	0	0
	CB3l-7	272372	70326	2419	12279	1488	0	0	744	744
	CB3l-8	259535	53860	6837	10605	279	0	0	0	0
	CB3l-9	247442	55070	4837	14140	372	0	0	0	0
	CB3l-10	206233	36837	3767	8512	0	0	0	0	558
	CB3l-11	268353	31256	4465	8930	0	447	0	223	0
	CB3l-12	305860	49116	5767	18419	0	0	372	0	0
	CB3l-13	285767	66977	5209	20093	0	0	0	0	0
	CB3l-14	343814	99721	3721	27287	0	0	0	0	0
	CB3l-15	n.d.	n.d.	n.d.	n.d.	n.d.	n.d.	n.d.	n.d.	n.d.
	CB3l-16	420465	100465	11535	23442	0	0	0	0	1488
	CB3l-17	330419	61767	6884	19535	0	0	0	0	0
	CB4l-1	16320	3040	320	200	0	0	0	0	0
	CB4l-2	99200	16560	2300	2440	0	0	0	0	0
	CB4l-3	173120	26400	3720	4520	0	40	0	160	0
	CB4l-4	154560	25120	2000	4160	0	0	0	240	0
	CB4l-5	93440	11840	1680	2720	0	40	0	160	0
	CB4l-6	154560	20640	1960	3560	0	40	0	160	0
	CB4l-7	137520	19520	1480	3920	0	40	0	0	0
	CB4l-8	86320	16640	1280	2040	0	320	0	0	0
	CB4l-9	137440	31360	2560	3880	0	0	0	160	0
	CB4l-10	141120	24320	2000	3120	0	0	0	160	0
	CB4l-11	115680	19360	1960	3120	0	0	0	160	0
	CB4l-12	140560	32160	3200	3400	0	0	0	160	0
	CB4l-13	54880	8000	1120	1680	0	0	0	0	0
	CB4l-14	86240	17600	1720	2080	0	0	0	40	0
	CB4l-15	97120	13440	1640	1680	0	0	0	0	0
	CB4l-16	101280	12320	1280	1360	160	0	0	0	0
	CB4l-17	48800	3680	1920	680	0	0	0	0	0
	CB4l-18	60160	7200	1920	1640	160	0	0	0	0
	CB4l-19	65520	6400	2820	1440	0	0	0	40	0
	CB4l-20	44880	3360	1620	1120	40	0	0	0	0

Conclusions and future perspectives

Numerous studies have proven the use of calcareous dinoflagellate cysts as proxies for p, palaeoclimatic, palaeoecological and palaeooceanographic reconstructions (Zonneveld et al., 1999, 2000, 2005; Esper et al., 2000; Vink et al., 2000, 2001, 2002; Wendler et al., 2002a; Hildebrandt-Habel and Streng, 2003; Meier and Willems, 2003; Meier et al., 2004a; Vink, 2004). However, the ecological knowledge of many species is still fragmentary. Thus, this comparative study has been carried out to understand the ecology, spatial distribution and fluxes of calcareous dinoflagellate cysts (dinocysts) in a major upwelling system (off NW Africa) better. From analyses of surface sediment samples (**chapter 2**), and from time-series sediment trap analyses (**chapter 3 and 4**) fundamental and new information have been obtained.

Methodical approach

The spatial distribution of calcareous dinoflagellate cysts from a well-defined area off the NW African coast has been investigated. Their relative and absolute abundances have been determined, and by means of well-constrained sedimentation rates dinocyst accumulation rates (cysts cm^{-2} ka^{-1}) were calculated (**chapter 2**). The comparison of both approaches (relative and accumulative) have shown, that the use of dinocyst accumulation rates provide much more trustworthy ecological information than only relative and absolute concentrations, as those may be negatively influenced by the so-called “closed-sum effect”, i.e. the absolute increase of one species leads to a relative decrease of all other species. Thus, information and trends shown by the less abundant species cannot be revealed or are uncertain. Furthermore, absolute abundances are susceptible to differences in sedimentation rates, which are exposed to be high in upwelling areas. This study of accumulation rates reflects a more realistic scenario of cyst production, although the possibility of cyst enrichment in surface sediments due to resuspension and/or lateral particle advection cannot be excluded.

Time-series sediment traps are a useful method to enhance and refine our knowledge of calcareous dinoflagellates cysts production and ecology, especially with respect to interannual variations and seasonality of cyst assemblages (**chapter 3 and 4**). By investigating sediment trap material from two different water depths (CB3-4; **chapter 4**), cyst fluxes as well as the sinking velocities of dinocysts through the water column were possible to calculate, and mechanisms of transport were elucidated. Relatively high sinking speeds of 150-280 m d^{-1} signify a fast transport in aggregates as a main export mechanism to the deep ocean.

Ecological information

From the analysis of species-specific cyst distribution patterns in surface sediment samples off the Moroccan coast (**chapter 2**), cyst relationships with environmental properties of the (sub)surface waters have been verified. The distribution of the dinocysts mirrors the onshore-offshore variance of the environmental parameters. The dinocyst fluxes in sediment traps revealed seasonal and interannual variations, implying relationships with passing and waning of upwelling filaments, i.e. variations in surface water turbulence and nutrient supply (**chapter 3 and 4**). Species-specific cyst fluxes revealed indications for lateral cyst transport from more coastal areas within the upwelling filaments. The comparison of cyst fluxes with cyst accumulation rates in the surface sediment exposed dissimilarity in absolute and relative abundances, which are due to transport, selective dissolution and variability in the interannual cyst production. Information on the ecology of dinoflagellates as important carbonate producers as well as of single species was gained.

Although cyst fluxes of *T. heimii* revealed only poor correlations with upwelling dynamic and environmental parameters, nutrient supply and diminishing filament activity are of certain importance. The investigation of surface sediment samples supports the close relationship of the distribution of *Thoracosphaera heimii* to water column stability and nutrient availability beyond the regions of active upwelling, resulting in highest accumulation rates (up to 18 x 10^6 cysts m^{-2} ka^{-1}) off the westernmost Canary Island La Palma and between the capes, where upwelling filaments are likely to develop.

Cyst fluxes of *Leonella granifera* derived from sediment trap samples (**chapter 3 and 4**) shows good relationships with enhanced lithogenic particle flux, leading to the assumption that terrigeneous components (micronutrients, such as iron) do play an essential role in this species' ecology and distribution. Moreover, the spatial distribution of this species revealed a lithogenic impact on species' accumulation with restriction to more shelfward areas. These results verify the ecology of *L. granifera* being an important indicator of land-derived mineral and nutrient contribution to the ocean (Wendler et al., 2002c; Vink, 2004).

Different ecological aspects of *Calciodinellum levantinum* could be gained by the study of cyst distribution in surface sediments and cyst fluxes in sediment traps. The spatial cyst distribution of *C. levantinum* reveals preferences for regions and times beyond the influence of upwelling, whereas sediment trap studies indicate that *C. levantinum* is more resistant to water column instability than the other investigated species. Since this species is known to be the most opportunistic and widespread species (Vink, 2004), these differences may simply reflect this species' adaptation to a broad range of environmental regimes. However, the good relationships with the enhanced filament activity and the lithogenic material contribution in the sediment

traps may possibly be the result of lateral transport within the upwelling filaments from more coastal areas. The definition of *Calciodinellum albatriosianum* as a typical warm-water species (Wendler et al., 2002c; Vink, 2004) is validated by both its distribution in surface sediments and cyst fluxes in sediment trap.

Less abundant species reveal weak relationship between cyst production and environmental parameters. However, tendencies are visible. Cyst fluxes of *S. regalis* appears to be related to warmer SST and decreased upwelling intensity, which differs from previous studies in which this species was related to relatively cool (14°C to 21°C) and well mixed (sub-)surface waters (Vink, 2004). The distribution of *S. regalis* off NW Africa is less restricted to oceanic and oligotrophic areas than has been documented so far (Vink, 2004). This study suggests that relatively low temperature may be ultimate factor controlling its distribution on a regional scale. *Scrippsiella* spp. occurs mainly during times of relatively cool and turbulent water conditions, reflecting the higher cyst production of the neritic species *Scrippsiella trochoidea* in zones of active upwelling and the transport within the upwelling filaments. Also the occurrence of *Pernambugia tuberosa* especially in deeper traps reflects probably lateral transport. The spatial distributions of *P. tuberosa* and *Calciodinellum elongatum* confirm previous observations from the South and equatorial Atlantic Ocean (Vink, 2004), where a preference for regions with relatively high water temperatures is similar to that in our study area. However, both species are less restricted to oligotrophic areas than was assumed previously (Vink 2004). Especially *C. elongatum* occurs mainly in the relatively shallow, nutrient-enriched area between the two upwelling filaments off NW Africa.

Prospects for future research

To study the distribution and ecology of calcareous dinocysts the considered oceanic compartments such as surface waters (plankton samples) in relation to the water column (sediment traps), cyst accumulation in subsurface sediments, and the burial in sediments resulting in archival storage, have to be taken into account.

Long-term field observations on plankton samples and sediment traps from different water depths could reveal different depth habitats of single species, and possible seasonally and interannually changes in cyst production, which in turn allows more accurate palaeoenvironmental reconstructions. The Cape Blanc deployment offers the unique possibility to obtain a more or less continuous data set of fluxes for the past two decades (Fischer et al., 2009a). 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 and transport processes which apparently influence the species composition can be observed. Additionally, time-series sediment traps deployed in more coastal areas could provide information about the species preferences within the active upwelling zones. In comparison with more oceanic sediment traps the amount of transport into the deep as well as offshore due to filaments (Alvarez-Salgado *et al.*, 2007) could be estimated. For example, CBi is a sediment trap deployed within the upwelling region off Mauritania at the same periods of time as the CB trap (Fischer et al., 2009c), offering the opportunity to directly compare coastal with offshore dinocyst fluxes. This approach would allow to verify different parameters such as upwelling intensity and turbulence, and would increase our knowledge of the ecological preferences of both single dinoflagellate species and the entire dinoflagellates assemblage. These aspects build an important base for future modelling studies concerning the variability of marginal regions (Boyd and Trull, 2007).

Since the last century, the anthropogenic impact on World's climate resulted in a rapid increase of atmospheric carbon dioxide (CO_2). The response of marine calcification to changes in water CO_2 and acidification of the world oceans is one major question to be solved (Guinotte and Fabry, 2008; Doney et al., 2009) First results of the response of planktonic foraminifera and coccolithophore are controversial (Iglesias-Rodriguez et al., 2008), whereas study of dinoflagellates cysts are missing to date.

The possible changes of small scale climatic variations within the amount and the composition of the calcareous dinoflagellate fluxes should be compared with down-core variations in calcareous dinoflagellate cyst accumulation and association, especially from upwelling regions, thus revealing potential long-term climatic and oceanographic changes.

As shown with this study, calcareous dinoflagellate cyst fluxes and distribution patterns mirror variations in upwelling intensity. However, in order to increase these ecological information, it is necessary to expand the surface sediment and sediment trap sampling to other high productive areas, continuing the detailed research on calcareous dinoflagellate ecology, which is of high benefit for more accurate palaeoenvironmental reconstructions.

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The (palaeo-) environmental significance of modern calcareous dinoflagellate cysts: a review

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Abstract

Increased interest in the environmental applicability of calcareous dinoflagellate cysts for palaeo-environmental studies arose in the last two decades, when it was discovered that they constitute a widespread and abundant group within the calcareous phytoplankton. As primary producers they are directly influenced by environmental parameters of the surrounding water masses, and therefore extremely suitable for detailed palaeo-environmental and -oceanographical reconstructions. During the last years, detailed investigations on their distribution in surface sediments of the South Atlantic Ocean, the Mediterranean Sea and the Arabian Sea were carried out, in order to reveal which environmental parameters influence their distribution. This, in turn, formed the base for palaeo-environmental and –oceanographical reconstructions. The compilation of the available data on calcareous dinoflagellate ecology, morphology, taxonomy and palaeo-environmental application presented here demonstrates their ample application potential as palaeo-environmental tools.

Keywords: calcareous dinoflagellate cysts, palaeo-environment,

Kurzfassung

Ein steigendes Interesse an der umweltrelevanten Einsetzbarkeit kalkiger Dinoflagellatenzysten für Paläoumweltstudien zeichnete sich in den letzten zwei Jahrzehnten ab, als man sie als weit verbreitete und häufige Gruppe innerhalb des kalkigen Phytoplanktons erkannte. Als Primärproduzenten werden sie direkt von den Umweltparametern der umgebenden Wassermassen beeinflusst und sind daher extrem nützlich für detaillierte Paläoumwelt- und

Paläozeanographie-Rekonstruktionen. Während der letzten Jahre wurden detaillierte Untersuchungen der Verbreitung kalkiger Dinoflagellatenzysten in Oberflächensedimenten des Südatlantiks, des Mittelmeeres und des Arabischen Meeres ausgeführt, um herauszufinden, welche Umweltparameter ihre Verbreitung beeinflussen. Dies wiederum bildete die Basis für Paläoumwelt- und Paläozeanographie-Rekonstruktionen. Die hier präsentierte Quintessenz der zur Verfügung stehenden Daten über Ökologie, Morphologie, Taxonomie und Paläoumwelt-Anwendung kalkige Dinoflagellaten zeigt ihr weitläufiges Anwendungspotential als Paläoumwelt-Werkzeug.

Schlüsselwörter: kalkige Dinoflagellatenzysten, Paläoumwelt

Introduction

Within the scope of the current concern about possible global change, the need of refining and applying proxy variables for establishing detailed palaeo-environmental and -climatic reconstructions is increasing. During the last decades, it has become evident that fossilisable remains of dinoflagellates (dinoflagellate cysts) form extremely suitable tools for approaching this (Versteegh 1994; Zonneveld et al. 1997; Grøsfjeld et al. 1999; Devillers & De Vernal 2000; Höll & Kemle-von Mücke 2000; Vink et al. 2001). Apart from being used in palaeoceanographic and -climatic studies, dinoflagellate cysts are applied and studied within a wide range of industrial environments such as, for instance, in the petroleum and gas exploration companies and the fishery industry. Recent developments in these fields increasingly demand detailed information about the life habit of dinoflagellates within the different stages of their life cycle. The industry therefore, often makes an appeal to the academic society at universities and research institutes to study dinoflagellate ecology and provide this information.

Until now the major interest was given to organic-walled cyst producing species and only since the last decade there is a growing interest for calcareous cysts. Ongoing research shows that calcareous cysts are, at times, tremendously abundant in tropical, subtropical and temperate oceanic environments where they can overwhelmingly dominate the total dinoflagellate cyst flux to the sea floor (e.g. Dale 1992; Dale & Dale 1992; Höll 1998) and neritic (Lewis 1991; Nehring 1994a, b; Montresor et al. 1998; Fig. 1). Quantitative analyses showed that they constitute not more than 4 wt-% of the total carbonate in sediments from the south Atlantic Ocean (Baumann et al. 2004). Nevertheless, they appear to be extremely suitable

for detailed reconstructions of palaeo-environmental and -oceanographic changes in oceanic environments, sometimes having an advantage over the traditionally used proxies (e.g. VINK et al. 2001).

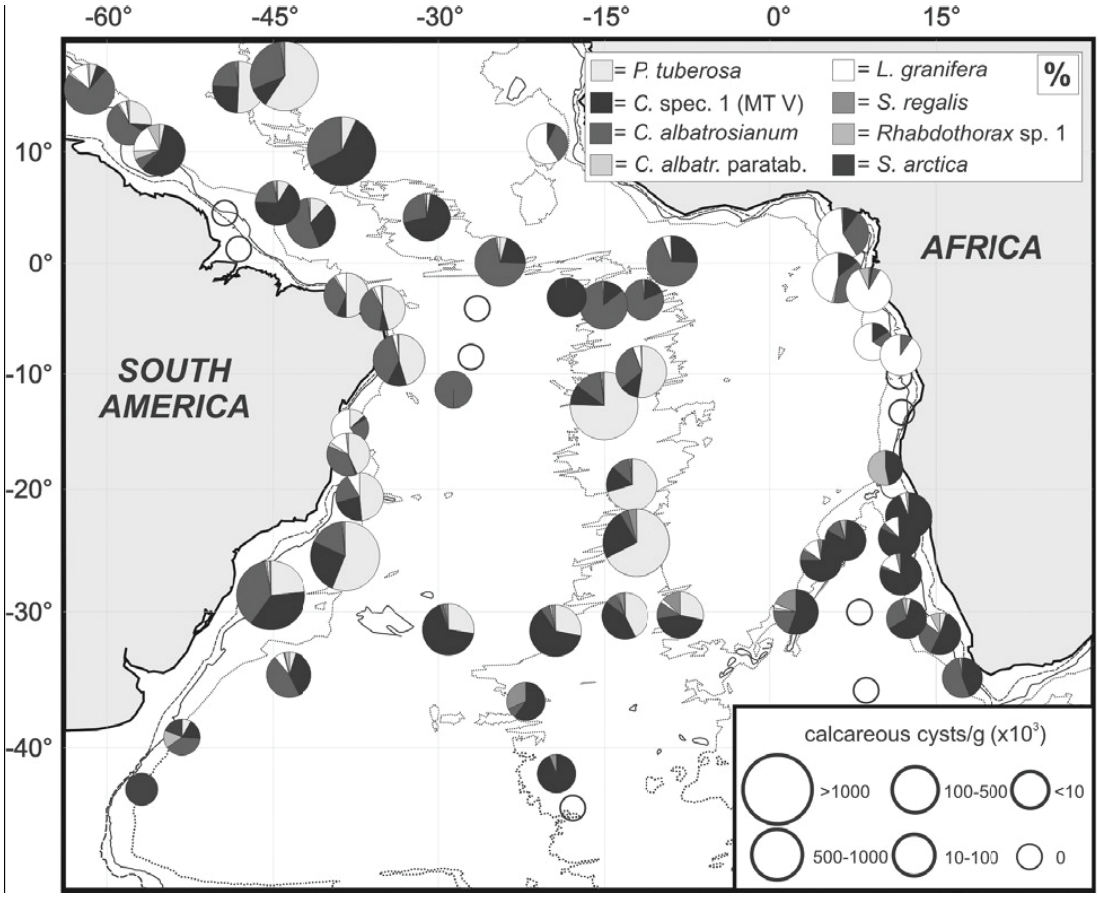

Fig. 1. Surface sediment distribution of calcareous dinoflagellate cyst species in the South Atlantic Ocean (Vink et al. 2004).

Within this paper we provide a state of the art of the presently known information on extant calcareous cyst producing dinoflagellates and their applicability for palaeo-environmental and palaeo-oceanographical reconstructions. An overview will be presented about information available on their (palaeo-)ecology, morphology and examples will be given about their applicability in palaeoceanographic research.

Life cycle

Dinoflagellates are a diverse group of eukaryotic, unicellular organisms (FENSOME et al. 1993). Together with diatoms and coccolithophores, they constitute the majority of the marine

phytoplankton and are important as primary producers. As part of their life cycle several dinoflagellate species are able to produce cysts made of organic or calcareous substances with a high fossilisation potential. Today there are about 30 modern species that are known to incorporate calcite into their cyst-wall (Tab. 1; Vink 2004). The presently known fossilisable calcareous cysts are of two functional types (Fig. 2). (1) Resting cysts representing a dormant stage in which normal metabolic processes are greatly reduced. They are generally very resistant to adverse conditions and can preserve well in sediments. In those cases which have been investigated, resting cysts result as part of the sexual reproduction cycle. (2) Vegetative cysts that are metabolically and/or reproductively active non-motile cells surrounded by a continuous wall (Fensome et al. 1993).

These cysts, especially resting cysts, may form a seed bank in aquatic sediments from which the motile stock can be renewed. Recent experiments have shown that cysts of some organic-walled producing dinoflagellate species can remain vital for almost a decade, which can be assumed for calcareous cysts as well (Lewis et al. 1999). To date all calcareous cyst producing dinoflagellates are thought to be photosynthetic (photoautotrophic or mixotrophic; Tangen et al. 1982; Binder & Anderson 1987; Montresor et al. 1994) indicating that they live in

Tab. 1 Extant calcareous cyst forming dinoflagellate species with characterisation of their archeopyle type and wall structure. O = oblique, T = tangential, R = radial, A = apical, M = mesoepicystal, E = epicystal.

Cyst name	Wall	Archaeopyle	Related theca	Cingulum
Bicarinellum tricarinelloides	?O	A		
Calcicarpinum bivalvum		A	*Pentapharsodinium tyrrhenicum*	P
Calcigonellum infula		E		S
Calciodinellum albatrosianum	T	M	*Calciodinellum albatrosianum*	S
Calciodinellum albatrosianum paratab.		M		
Calciodinellumelongatum	T	M	*Calciodinellum elongatum*	S
Calciodinellum levatinum	T	M	*Calciodinellum levantinum*	S
Calciodinellum operosum	T	M	*Calciodinellum operosum*	S
Calciperidinium asymmetricum		I		
Caracomia arctica	R	M		
Esiculifera carinata			*Ensiculifera carinata*	E
Follisdinellum splendidum				
Fuettererella cf. *tesserula*	T	A		
Lebessphaera urania	T	E		
Leonella granifera	R	A	*Leonella granifera*	S
Melodomuncula berlinensis	?O	A		
Pentadinellum oblatum		?A	*Ensiculifera mexicana*	E
Pernambugia tuberosa	O	E	*Pernambugia tuberosa*	P
Praecalcigonellum schizosaeptum		A		
Scrippsiella crystallina			*Scrippsiella crystallin*	S
Scrippsiella lachrymosa		M	*Scrippsiella lachrymosa*	S
Scrippsiella precaria			*Scrippsiella precaria*	S
Scrippsiella ramonii			*Scrippsiella ramonii*	S
Scrippsiella regalis	T	?E	*Scrippsiella regalis*	S
Scrippsiella rotunda		M	*Scrippsiella rotunda*	S
Scrippsiella tirfida		M	*Scrippsiella trifida*	S
Scrippsiella triquetracapitata	T	?M		
Scrippsiella trochoidea	T	M	*Scrippsiella trochoidea*	
Thoracosphaera heimii	T	A	*athecate*	athecate

the photic zone.

Dinoflagellates typically occur during a certain phase of their life cycle as motile biflagellate cells, possessing a transverse flagellum that encircles the body and a longitudinal flagellum that is orientated perpendicular to the transverse flagellum. This gives the organism a spiral motion. They can have dial vertical migration of several meters as results of endogenous rhythms and their geotactic and phototactic preferences (e.g. ANDERSON & STOLZENBACH 1985; LIEBERMAN et al. 1994; KAMYKOWSKI et al. 1998). Although this enables the algae to move through the water column, their size of about 7-50 µm results in a Reynolds number (Re) smaller than 1:

$$Re = (DxVx\rho)/\mu$$

where D is the length of the moving object, and V, ρ and µ are velocity, density and viscosity of the surrounding medium. In praxis this means that if a dinoflagellate stops moving its flagellae, it will immediately stop its movement. As such it is bound to its surrounding water mass. Another result is that they have problems crossing borders between media, for instance water masses with different densities. In consequence, their abundance and, in turn, the abundance of their cysts in sediments will be primarily be determined by the environmental properties of the (sub-) surface waters.

Encystment

Numerous issues concerning the encystment of dinoflagellates as part of the sexual life cycle remain to be solved. Especially the factors triggering sexuality and successive cyst formation are currently debated (e.g. GODHE et al. 2001; OLLI & ANDERSON 2002). In many culturing experiments it has been shown that sexuality and cyst formation can be induced by nutrient depletion of especially phosphate and nitrate (e.g. ANDERSON et al. 1984; OLLI & ANDERSON 2002). Nevertheless, in long-term field studies it has often been observed that maximum cyst formation occurs during, or just after periods of maximal

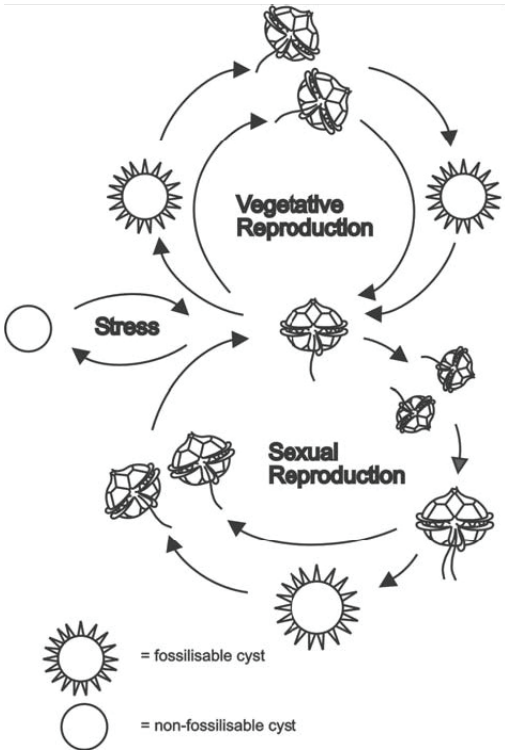

Fig. 2. Schematic illustration of cyst production in the life cycle of dinoflagellates.

vegetative cell division with nutrient concentrations not being depleted (e.g. Ishikawa & Taniguchi 1996; Montresor et al. 1998). Lower encystment success of *Scrippsiella* cf. *lachrymosa* has been reported to be related to low nutrient concentrations in culture media (Olli & Anderson 2002). It is suggested that a possible solution for this discrepancy could be that nutrient concentrations in the local water conditions surrounding the individual dinoflagellate specimens might be the crucial factor. Cells are thought to initiate sexuality as the intracellular pools of limiting nutrients reach critical levels due to a change in uptake at low ambient nutrient concentrations or due to some other environmental stress. However, in the field, the evidence on cyst formation in relation to nutrients is indirect and can often not be found (Kremp & Heiskanen 1999; Godhe et al. 2001). Furthermore, a recent study shows that nutrient limitation did not induce cyst formation for *Scrippsiella trochoidea* var. *aciculifera*, *Pentapharsodinium tyrrhenicum*, *Calciodinellum operosum* and S*crippsiella rotunda* under day length and temperature conditions unfavourable for encystment (Sgrosso et al. 2001). In this study nutrient concentration was not the primary factor influencing encystment but it steered the intensity of the responds. Other factors that might influence encystment of dinoflagellates are temperature, day length, irradiance and an endogenous encystment rhythm. It has been shown that several dinoflagellates are able to produce cysts in a narrow temperature window. Temperature itself however, is not a triggering factor. Recent studies on the encystment *Scrippsiella trochoidea* var. *aciculifera*, *Pentapharsodinium tyrrhenicum*, *Calciodinellum operosum* and *Scrippsiella rotunda* show an inverse relationship between day length at temperatures between 20°C and 25°C. This inverse relationship was not the result of a relationship with total daily irradiance and an increased cyst production was prevented by light breaks during the dark phase of the photocycle (Sgrosso et al. 2001). In general, encystment of dinoflagellates is not related to stress but is rather favoured by optimal conditions for vegetative growth.

After encystment, dinoflagellate resting cysts have a mandatory dormancy period through which newly formed cysts must proceed before they are physiologically capable of germination. The duration of this period is, species dependant, and can range from about 12h to 12 months (e.g. Pfiester & Anderson 1987). Within the cyst stage metabolic processes are greatly reduced. For the calcareous species *Scrippsiella trochoidea* it has been shown that metabolic activity reduced to 40% of the vegetative stage level in freshly formed cysts to about 1.5% in more maturated cysts (Binder & Anderson 1990).

The formation of vegetative cysts is dependent on an array of biotic and a-biotic factors. The relationship between the several a-biotic factors and the spatial and temporal distribution of calcareous resting cyst species in natural environments, as well as the effects of these factors on the formation of *Thoracosphaera heimii* will be discussed in chapter (palaeo-) ecological significance.

Excystment

Excystment can be triggered or inhibited by several factors such as temperature, light availability, oxygen concentration and endogenous rhythms. In culture conditions excystment can be often inhibited by cold storage whereas temperature increase might induce germination (e.g. Binder 1986; Pfiester & Anderson 1987; Kremp & Anderson, 2000). Each species has a specific temperature window in which germination can take place. Light availability is generally thought to be essential for germination and it has been shown that a pulse as short as one second might be sufficient (e.g. Binder & Anderson 1986; Nuzzo & Montresor 1999). Hatching of cysts is observed in culture experiments where the cysts were stored in the dark (e.g. Kremp & Anderson 2000). It is, however, hard to say if short light pulses of low radiance in these experiments were completely avoided. Anoxic conditions inhibit cyst germination in most, if not all, dinoflagellate species and germination is reduced under low oxygen conditions (Anderson et al. 1987; Kremp & Anderson 2000; Persson 2001).

One of the most intriguing questions within dinoflagellate research is how newly germinated dinoflagellates re-colonise the upper water masses. Following cyst formation the dinoflagellates become immobile and sink. The above described life cycle of producing a resting stage with a dormancy period seems an appropriate life strategy in neritic environments, especially in those areas where a period of unfavourable environmental conditions has to be bridged, e.g. in higher latitude regions. It seems however, to be a quite irrational strategy in open oceanic regions. With swimming speeds of around 0.03 to 2 m h^{-1} it would be impossible for a dinoflagellate to swim to the surface of the open ocean. Therefore oceanic dinoflagellates must have other mechanisms to reach the upper water masses, or cysts must have been hatched before a crucial depth is reached on which no return is possible.

Morphology and taxonomy of calcareous cyst forming dinoflagellates

The main morphological characters of the calcareous cyst stage are wall ultrastructure and type of the archaeopyle (e.g. Keupp 1981; Keupp & Versteegh 1989; Janofske & Karwath 2000; Meier et al. 2002; Streng et al. 2004.). The crystallographic orientation of the calcite crystals forming the cyst wall is considered to be genetically determined and therefore of high taxonomic value. Three types are recognised based on the orientation of the crystallographic c-axis of the crystals in the wall, which can be tangential, radial or oblique (Fig. 3A; Fig. 4; Tab. 1) (e.g. Kohring 1993; Janofske 1996). The archaeopyle is often the only morphological character of the cyst in which the theca tabulation is reflected. Based on which plate

homologues are reflected, different types of archaeopyles are defined: apical, intercalary, meso-epicystal and epitractal (Fig. 3B; STRENG ET AL. 2004).

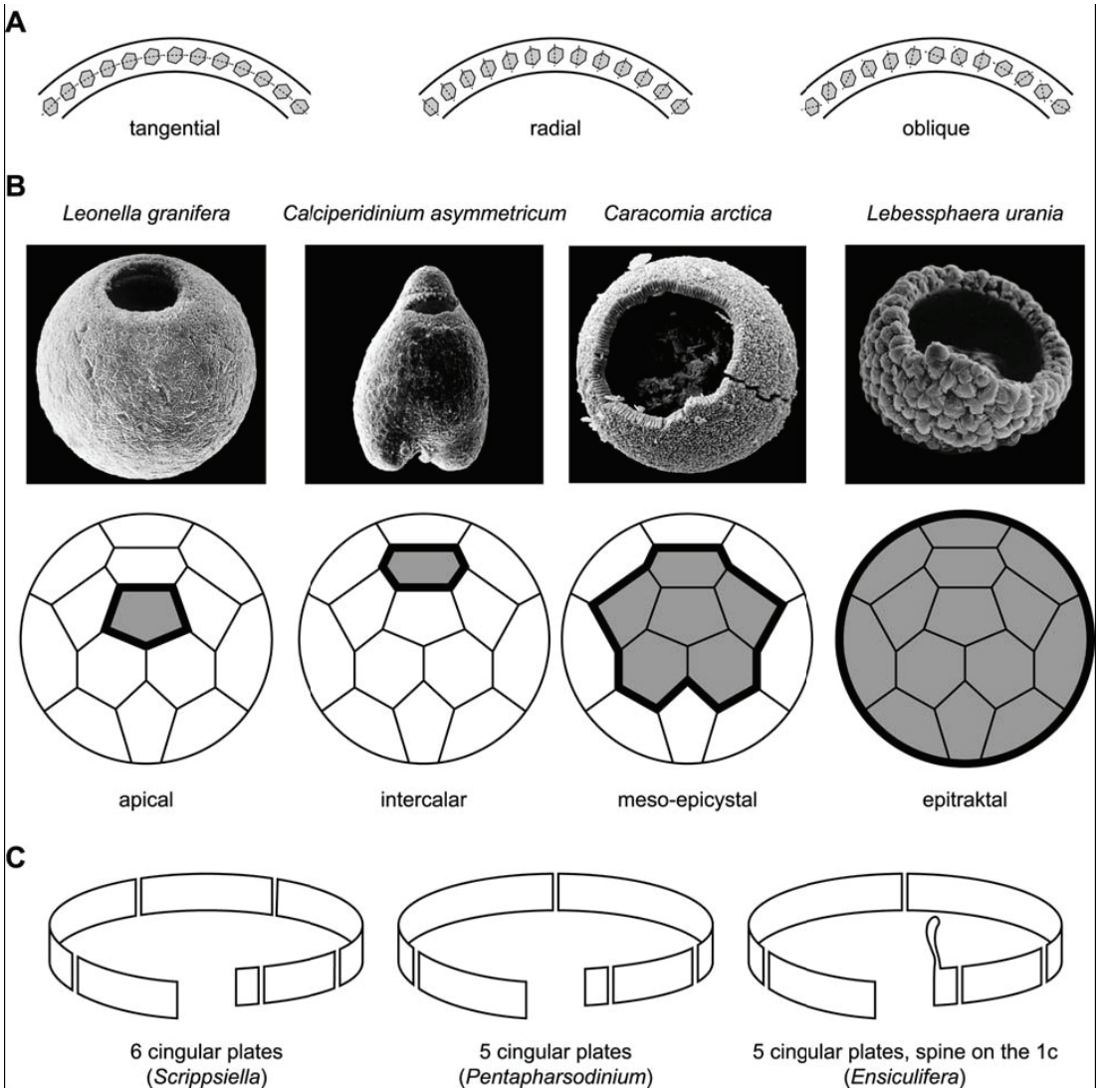

Fig. 3. Taxonomic important morphological characters in dinoflagellates producing calcareous cysts. – A: Crystallographic ultrastructure of the cyst wall (after Janofske 1996). – B: Archaeopyle types (after Streng et al. 2004.). C: Theca tabulation pattern in the cingulum (after Fensome et al. 1993).

For extant calcareous cyst producing dinoflagellates, also morphological characters of the theca are important in taxonomy. However, only little morphological variation occurs in the thecae, which are subdivided in the three genera *Scrippsiella*, *Pentapharsodinium* and *Ensiculifera*, based on the number and form of their cingular plates (Fig. 3C). However, these genera also include species that are not known to produce cysts or produce organic walled cysts (D'ONOFRIO et al. 1999), which questions, if the production of a calcareous cyst is a monophyletic character.

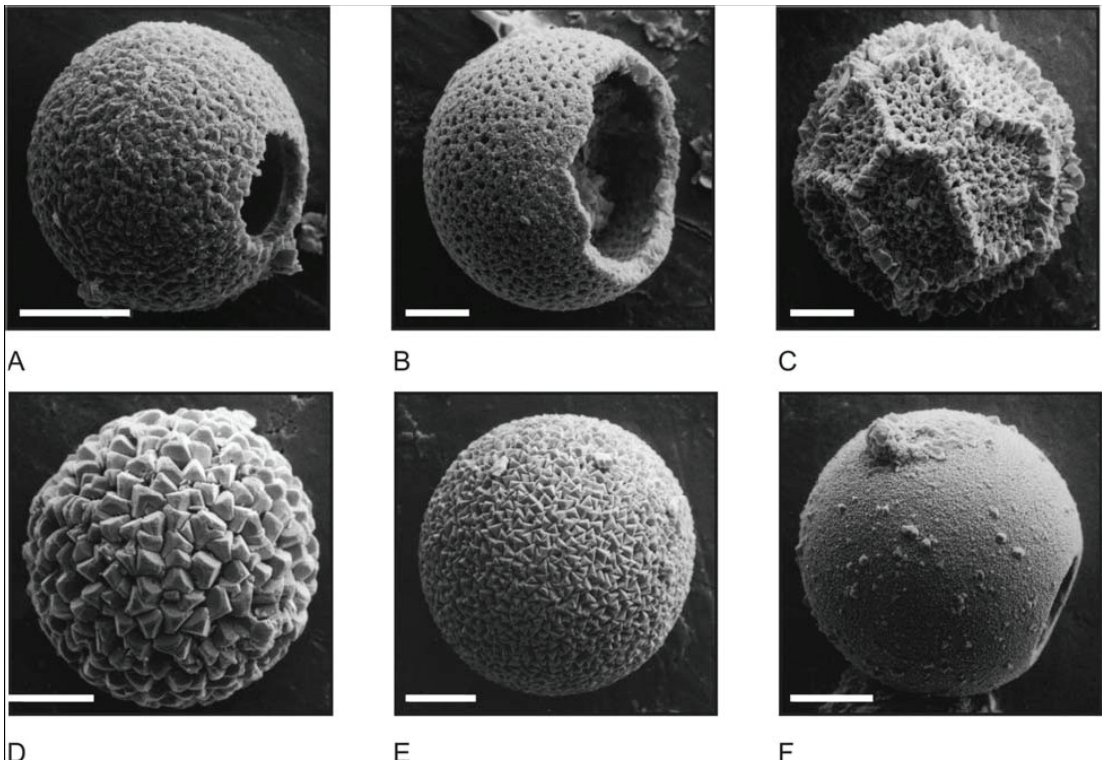

Fig. 4. Scanning electron microscope photographs of calcareous dinoflagellate cyst species/morphotypes (line bars represent 10µm).- **A**: *Thoracosphaera heimii.* - **B:** *Calciodinellum albatrosiana* - **C***: Calciodinellum operosum.* - **D**: *Pernambugia tuberosa.* - **E***: Calciodinellum* spec. 1. - **F**: *Leonella granifera.*

Due to the separate nomenclatures used for fossil cysts and extant vegetative cells, different stages in the life cycle of one organism have been described as separate species. In order to avoid double descriptions, the cyst-theca relationship was described for those species that are held in cultures (Lewis 1991; Montresor et al. 1997, d'Onofrio et al. 1999; Janofske & Karwath 2000; Meier et al. 2002). It was found, that most modern species of calcareous cyst producing dinoflagellates that were assigned to a wide variety of cyst species due to the morphological variability of their cysts, in fact have a *Scrippsiella*-type theca tabulation pattern (Tab. 1).A taxonomical species concept combining the characters of cysts and thecae is still under debate. Apart from the fact that the cyst-theca relationship is still unknown for many extant species, a taxonomical system based on the motile stages would exclude all fossil species from a unified classification and not consider the greater morphological variability in the cysts. On the other hand, a cyst-based classification that allows the same theca-type for different species or even genera would prevent an unambiguous correlation of a theca to a certain taxon. First molecular observations on calcareous cyst producing dinoflagellates held in culture by d'Onofrio et al. (1999), Montresor et al. (2003) and Gottschling & Plötner (2004) indicate that the morphological variability within the theca and our cysts is reflected in the ribosomal DNA

internal transcribed spacers ITS1 and ITS2. Results of molecular phylogeny studies of *Scrippsiella trochoidea* suggest the presence of "cryptic" species within this previously considered single (morpho-) species. Nevertheless, first results from the above cited studies and from ongoing molecular genetic investigations at the Free University of Berlin suggest the calcareous cyst forming dinoflagellates to be monophyletic (GOTTSCHLING pers comm.). By comparing morphological and genetic data it will be evaluated, which taxonomical characters of cysts and thecae are of phylogenetic value. This, in turn, might lead to a unified classification for both extant and fossil calcareous dinoflagellates.

(Palaeo-)ecological significance

The ecology of individual dinoflagellate species and, as such, the palaeo-ecological significance of their cysts is determined by biotic factors (e.g. inter- and intraspecific competition, predation, endogenous rhythms etc.) and a-biotic factors. The biotic factors characterising dinoflagellate ecology are investigated in rare cases only and are very difficult to estimate (e.g. ABRAHAMS & TOWNSEND 1993). In consequence, this chapter will focus on physical factors that can determine dinoflagellate cyst distributions. As mentioned in the previous chapter, several physical factors are known to be important for steering cyst production and germination. Of these factors, temperature, salinity, trophic conditions and stratification of the upper water column have been studied in more detail considering their effect on the geographical and temporal dinoflagellate cyst distribution. However, until now, detailed (palaeo-) ecological studies of calcareous cyst producing dinoflagellates are restricted to the open oceanic environments of the equatorial and South Atlantic Ocean, the Mediterranean Sea and the Arabian Sea (northwest Indian Ocean) (VINK et al. 2000; ZONNEVELD et al. 2000; MEIER & WILLEMS 2003; WENDLER et al. 2002a; VINK et al. 2002, 2003; VINK 2004.). In modern sediments of these regions, 12 calcareous dinoflagellate cyst species can be found regularly, whereas all other species listed within Tab. 1 are most probably restricted to coastal environments. Consequently, within the present chapter we will focus on the ecology of these 12 species; *Calciodinellum albatrosianum*, paratabulated form of *Calciodinellum albatrosianum*, *Calciodinellum elongatum*, *Calciodinellum levantinum*, *Caracomia arctica*, *Lebessphaera urania*, *Leonella granifera*, *Melodomuncula berlinensis*, *Pernambugia tuberosa*, *Scrippsiella regalis*, *Scrippsiella trochoidea* and *Thoracosphaera heimii*.

Temperature

Based on field and culture observations, it appears that several calcareous dinoflagellate cysts can be observed in modern sediments ranging from polar to tropical environments (Zonneveld et al. 1999, 2000; Esper et al. 2000; Wendler et al. 2002a; Meier & Willems 2003; Vink 2004.). The greatest diversity and abundance of cysts in sediments is, however, found in tropical and subtropical areas. Regarding the distribution patterns of individual species, several of them have a broad tolerance for temperature, whereas others show a more restricted range. Of those species with a large tolerance, the vegetative cyst forming *Thoracosphaera heimii* is the best studied species. Growth experiments on cultures showed that *T. heimii* has highest growth rates at temperatures ranging from 14°C to 26°C. Maximum growth rates were reached at temperatures around 27°C, but over a longer period of time greatest numbers of cysts were produced at lower temperatures around 16°C (Karwath et al. 2000a). These results are supported by field studies that show that the greatest numbers of cysts are produced at somewhat cooler subsurface depths. Furthermore highest concentrations of cysts of *T. heimii* can be observed in the relatively cooler regions of the equatorial and South Atlantic (South Atlantic Gyre and the Benguela upwelling region; Karwath et al. 2000b; Vink et al. 2000; Vink 2004.) and those areas of the Arabian Sea characterised by upwelling during the SW monsoon (Wendler et al. 2002a). However, a sediment trap study of the Somali upwelling region shows that increased production of cysts is observed when temperatures rise from approximately 22°C toward 25°C as the result of the passage of cold upwelling filaments at the mooring site (Wendler et al. 2002b) .
Several calcareous cyst forming species show a distribution related to a restricted temperature range:

(1) Warm/tropical species: *Leonella granifera*, *Calciodinellum albatrosianum* and the paratabulated form of *Calciodinellum albatrosianum*. Highest relative abundance of *L. granifera* can be observed in regions with sea surface temperatures (SST) between 25°C to 28°C (Zonneveld et al. 1999; Wendler et al. 2002a; Vink 2004.). Until now, *L. granifera* was not found in regions with mean annual temperatures below 14°C. In the Arabian Sea, the flux of *L. granifera* is reduced at times of active upwelling when temperatures are relatively low. *Calciodinellum albatrosianum* and its paratabulated form have highest abundance in modern sediments of the equatorial and South Atlantic Ocean in areas with mean annual SST ranging from 25°C to 28°C (Janofske & Karwath 2000; Zonneveld et al. 2000; Vink 2004). Although present throughout the Arabian Sea and the Mediterranean, highest abundance of this species is registered for the warmest areas of these regions (Wendler et al. 2002a; Meier & Willems 2003). In modern sediments, *C. albatrosianum* and its paratabulated form are not observed in regions with mean annual SST below 15°C. Also downcore studies of the South and Equatorial

Atlantic Ocean show that *C. albatrosianum* is correlated to time intervals of relatively warm SST (Esper et al. 2000).

(2) Cool-temperate species: *Calciodinellum levantinum*, *Scrippsiella regalis*. Highest relative abundance of *C. levantinum* can be related to SST between 13°C to 20 °C (Esper et al. 2000; Vink et al. 2000; Meier & Willems 2003; Vink 2004.). Similar observations were made on *Scrippsiella regalis*, which prefers a temperature range of 12° C to 21°C (Vink 2004.).

(3) Polar species: *Caracomia arctica*. The distribution of *C. arctica* is restricted to the (sub-) arctic regions south and north of the subtropical fronts in both hemispheres (Streng et al. 2002; Vink 2004.).

Stratification and nutrient availability

One of the first observations within ecological studies on calcareous dinoflagellate cysts was that enhanced calcareous cyst concentrations can be observed in regions and time intervals with relatively stratified and oligotrophic conditions of the upper water column (Höll et al. 1998, 1999; Zonneveld et al. 1999; Esper et al. 2000; Vink et al. 2000). Recent studies show, that the relationship between cyst distribution patterns and the trophic condition of the water column or the rate of stratification is species specific (Meier & Willems 2003; Vink et al 2002; Vink 2004.).

In a sediment trap study of the Somalia upwelling area, highest abundance of the vegetative cysts of *Thoracosphaera heimii* occured under stratified and mesotrophic to eutrophic surface water conditions, whereas lowest *T. heimii* fluxes are registered during times of active upwelling when surface waters are well mixed (Wendler et al. 2002b). In culture experiments the final yield of *T. heimii* cysts is higher in media with enhanced nutrient concentrations (Karwath et al. 2000a).

The limited amount of studies on resting cyst species characteristic for coastal environments, suggest that these species are most abundant in eutrophic environments. In a sediment trap located in the Gulf of Naples (Tyrrhenian Sea), highest productions of these cysts can be observed in autumn when nutrient concentrations are relatively high (Montresor et al. 1998). In a Swedish fjord, increased cyst production could be related to a deepening of the halocline, related to lower irradiance and lower temperatures of the upper water column (Godhe et al. 2001).

For the cyst species characteristic for open oceanic environments, both stratification and the trophic state of the water column, as well as the combination of these factors, which influence the presence and depth of the Deep Chlorophyll Maximum (DCM), form important

steering parameters. Several species show a restricted distribution in relation to these factors:

(1) Oligotrophic species: *Pernambugia tuberosa*, *Lebessphaera urania*, *Calciodinellum elongatum*. The distribution of *P. tuberosa* is so far known from the Atlantic Ocean only, where it is restricted to regions with oligotrophic conditions throughout the water column with relatively mixed subsurface conditions and low nitrate and phosphate concentrations (Vink 2004.). *L. urania* was until now only observed in the most oligotrophic parts of the Mediterranean Sea, especially in the most nitrate-depleted areas (Meier & Willems 2003). Although not restricted to these regions, *C. elongatum* is found in high abundance in the most oligotrophic parts of the South Atlantic Ocean and the Mediterranean Sea.

(2) Nutrient-enrichement: *Leonella granifera*, *Caracomia arctica*. High abundance of *L. granifera* can be found in regions that are characterised by river input such as the Gulf of Guinea in the Niger and Congo River discharge regions, in the western tropical Atlantic related to the Amazon and Orinoco river plumes (Vink 2004.), the Indus Fan region (Arabian Sea) (Wendler et al. 2002a) and at times with presumed enhanced Nile discharge into the eastern Mediterranean Sea (Meier et al. 2004). Increased production of *L. granifera* has been found in a sediment trap off Cap Blanc (off northwest Africa) at times of active coastal upwelling when the region is characterised by increased terrestrial dust input (Siggelkow et al. 2002). This led Vink (2004) to suggest that the distribution of this species might be largely influenced by the rate of the terrestrial derived nutrient input.

Until now, the distribution of *C. arctica* is restricted to regions with cold, eutrophic surface waters. However, it is yet unknown, to what extent nutrient availability influences its abundance. In the Mediterranean Sea, the distribution of *Scrippsiella regalis* and *Calciodinellum albatrosianum* can be significantly related to regions with enhanced but still oligotrophic nutrient concentrations (Meier & Willems 2003). *C. albatrosianum* is also found in the eutrophic Arabian Sea with enhanced production during the Southwest monsoon at times between periods of active upwelling (Wendler et al. 2002b). However, in the equatorial and South Atlantic Ocean these species are also found in considerable concentrations in modern sediments of oligotrophic regions suggesting a large tolerance to different nutrient concentrations (Vink 2004.).

Concerning stratification of the water column, *Scrippsiella regalis*, *Scrippsiella trochoidea* and *Pernambugia tuberosa* appear to be present in high abundance in regions with no permanent pycnocline is present and upper watermasses can be turbulent. On the contrary, high relative abundance of *Leonella granifera* and *Calciodinellum levantinum* are observed in regions where generally a pycnocline is present. The distribution of *C. levantinum* seems, however, to be related to the presence of a deep chlorophyll maximum just below the thermocline where temperatures are somewhat lower and nutrients are available in an otherwise

warm, oligotrophic area (Meier & Willems 2003; Vink 2004.).

Salinity

Dinoflagellates producing calcareous cysts have been reported from all marine salinity regimes, ranging from brackish waters present in the Baltic Sea and the Black Sea to the highly saline waters of the eastern Mediterranean and the Red Sea. Generally, only few species seem to be adapted to special salinity conditions.

In the open Atlantic Ocean and the Arabian Sea, only little variation occurs in salinity, and its influence on species distribution is considerably small (Wendler et al. 2002a; Vink 2004.). The only species related to lowered salinity is *Leonella granifera*, which reaches increased abundance in regions affected by substantial river input. However, Vink (2004) suggested land derived nutrients discharged by the rivers as the main factor increasing the abundance of *L. granifera*.

In the Mediterranean Sea, a prominent E-W directed salinity gradient is present, ranging from approximately 36.5 PSU at the Strait of Gibraltar to more than 39.0 PSU in the eastern Levantine Sea. The species *Lebessphaera urania* and *Calciodinellum elongatum* show increasing abundance towards the east and are probably best adapted to highly saline environments. The occurrence of *L. urania* seems to be even restricted to high salinity, as it was so far exclusively reported from the eastern Mediterranean Sea (Meier & Willems 2003).

Neritic species have so far not been reported to be adapted to high salinity. The most common species *Scrippsiella trochoidea* was even found in brackish to fully marine conditions (Janofske 2000). Cysts reported from brackish seas like the Baltic Sea, i.e. *Scrippsiella lachrymosa* (Nehring 1994a, b), or the Black Sea, i.e. *Calciodinellum operosum* (Wall et al. 1973), can also be found in other euhaline neritic regions. However, records are too scarce to estimate their rate of tolerance for different sea surface salinity levels.

Transport and preservation of calcareous dinoflagellate cysts

Regarding their size of about 10 to 50 µm, calcareous cysts of dinoflagellates behave like particles of the silt fraction while sinking to the seafloor. Sinking experiments carried out on *Scrippsiella trochoidea* show a settling velocity of 0.013 to 0.008 cm s-1 (Anderson et al. 1985). These sinking rates would require almost a year for a single cyst to reach the bottom of a 4000-m deep ocean. Results of sediment trap analyses off Cape Blanc (NW Africa) suggest a

much higher sinking velocity of ~1.62 cm s-1 (SIGGELKOW et al. 2002; VINK 2004.), possibly because the cysts are transported in form of faecal pellets, "marine snow" or through agglomeration and flocculation in the presence of structureless organic matter as has been described for organic-walled dinoflagellate cysts (MUDIE 1996). Recently, it has been shown that calcareous cysts of *Scrippsiella trochoidea* and *Scrippsiella ramonii* are less grazed by copepods than their thecate stages, and that those cysts ingested were not digested. Cysts of *S. trochoidea* could even be germinated after passage through the gut of some copepod species (MONTRESOR et al. 2002). On their way to the seafloor, the cysts could be transported laterally by ocean currents or can later be relocated by slumping, turbiditic transport or winnowing by bottom water currents. Although in most cases it is extremely difficult to quantify these processes, there are arguments against large-scale displacement of the cysts as the species' distribution patterns in surface sediments generally give a very detailed reflection of the overlying surface-water hydrography (e.g. VINK 2004; WENDLER et al., 2002a).

The primary ecological signal of the calcareous cyst association might also be altered by calcite dissolution while sinking through the water column or after sedimentation. There is growing evidence for substantial calcite dissolution in water depths well above the carbonate saturation horizon, apparently as a result of biological mediation (MILLIMAN et al. 1999). However, until now no evidence was found for dissolution of cysts during the sinking process (SIGGELKOW et al. 2002; WENDLER et al. 2002b, c). This might result from the fact that living dinoflagellate cysts are covered by a thin organic layer (JANOFSKE & KARWATH 2000), which protects them from dissolution but is rapidly destroyed after excystment. Accordingly, only empty cysts might be subject to dissolution.

Calcite dissolution at the sediment-water interface can be induced by several factors, such as undersaturation of sea water in [CO_3^{2-}] and aerobic decay of organic matter leading to a lower pH of the pore water (EMERSON & BENDER 1981; HALES et al. 1994). The latter, in turn, is dependent on supply and quality of organic matter, the carbonate to organic carbon rain ratio, oxygen availability in the bottom and pore waters, oxygen exposure time and penetration depth of oxygen related to sedimentation rate, bioturbation and sediment re-distribution. Calcareous dinoflagellate cysts are frequently found in high concentrations in sediments situated below the calcite lysocline, suggesting that they are quite resistant to depth-related dissolution (VINK et al. 2000; ZONNEVELD et al. 2000; VINK 2004.). In several regions, they can even be observed in sediments at the CCD (calcite compensation depth). However, in some sites several depth-related changes in cyst associations which can not be subscribed to environmental factors indicate that species selective dissolution can occur in sediments below the lysocline depth. Most sensitive to dissolution are the vegetative cysts of *Thoracosphaera heimii* with a reduction of 180 times for a depth transect of 3395 to 4638 m depth in the western equatorial Atlantic,

where the lysocline is positioned at 4200 m depth. *T. heimii* is followed by *Pernambugia tuberosa* with a reduction of 44 times, *Calciodinellum albatrosianum* (reduction of 8.5 times) and *C. levantinum* (reduction of 4 times; VINK 2004). A comparable species specific susceptibility of cysts to dissolution was documented for the north-western Arabian Sea based on a sediment trap study. Here, high cyst quantities including very fragile cysts (not fully calcified) were found in a trap sediments collected at 1032 m water depth. In the underlying surface sediments at 4035 m, which are positioned well below the lysocline, thin-walled cysts were nearly absent and a considerable decrease in cyst flux between the trap and the surface sediments could be calculated (between 81 – 96% reduction, WENDLER et al., 2002c). Again the small porous spheres of *T. heimii* appeared to be most prone to dissolution.

Species selective calcite dissolution above the lysocline and related to aerobic organic matter decay has been observed in the north-eastern Arabian Sea. In this region, the water is undersaturated in [CO_3^{2-}] below 3400 m (MILLERO et al., 1998), but a drastic drop of cyst accumulation rates in surface sediments can be observed between 1250 and 1550 m and is related to the lower boundary of the very stable and intense oxygen minimum zone (OMZ; WENDLER et al. 2002c; Fig. 5). Within the OMZ, cyst preservation is enhanced as organic matter is degraded via other oxidation paths like sulphate reduction, whereby the pore water alkalinity can even increase. Again, the small porous spheres of *T. heimii* are most prone to dissolution and there is also indication for sensitivity differences between the following cyst species (in the order of dissolution sensitive to more resistant cysts): *C. levantinum*, *C. albatrosianum*, and *L. granifera*. However, in other regions with a less stable OMZ, such as the western Arabian Sea and the Namibian upwelling area, preservation differences related to the position of the OMZ and enhanced preservation within the OMZ could not be observed so far.

Post-depositional aerobic organic matter decay, appears not to have an effect on the preservation of calcareous dinoflagellate cysts as indicated by results from the eastern Mediterranean S1 sapropel (ZONNEVELD et al. 2001; MEIER et al. 2004). More studies are therefore required to obtain a detailed insight in the preservation rates of calcareous cysts in various environments.

Palaeoceanographic reconstructions

Until now mainly inventory taking studies have been carried out on calcareous dinoflagellate cysts from Cretaceous to Tertiary sediments (e.g. BOLLI 1974, KEUPP 1981, 1991, 1995, KOHRING 1993; KIENEL 1994; ZÜGEL 1994). For the Quaternary time interval studies have

been focused on the palaeoenvironmental applicability of this phytoplankton group. As the work on Mesozoic and Cenozoic material was based mainly on the time consuming analysis of dinoflagellate cyst assemblages in the scanning electron microscope, the use of faster polarised light microscopic identification techniques were a first step to improve the applicability of the calcareous cysts in Quaternary studies (JANOFSKE 1996).

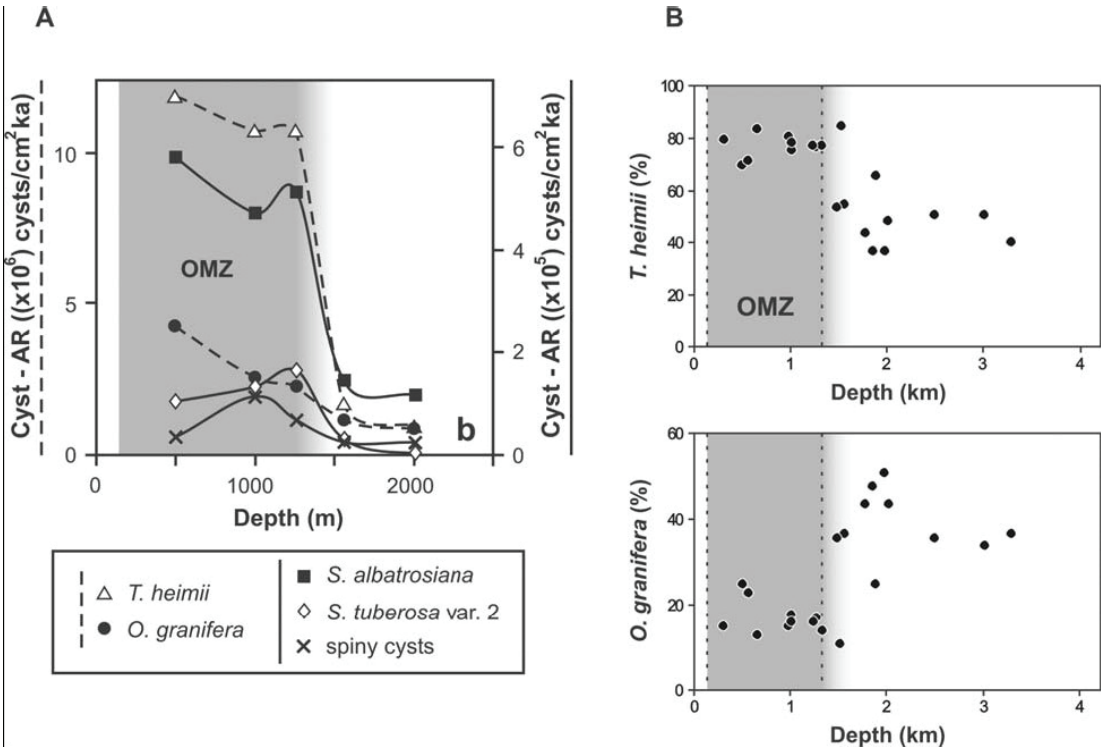

Fig. 5. – **A.** Cyst accumulation rates (AR) of different calcareous cyst producing dinoflagellate species versus water depth in the Indus Fan (north eastern Arbaian Sea). – **B**. Abundance of *Thoracosphaera heimii* and *Leonella granifera* relative to the total amount of calcareous cysts versus water depth in the Indus Fan. Grey area marks the depth interval where the Oxygen Minimum Zone (OMZ) intersects the slope (Wendler et al. 2002a)

First pilot studies on the palaeoecological affinity of calcareous dinoflagellates were carried out within several Late Quaternary time series of the Equatorial Atlantic Ocean. They showed that during times of low nutrient concentrations in the surface water and a stable, deep thermocline highest accumulation rates of *Thoracosphaera heimii* and five other calcareous cyst species could be observed the region characterised by equatorial divergence (HÖLL et al. 1998). Based on the statistical methods of detrended correspondence analysis and redundancy analysis, the distribution of calcareous cysts could be attributed to surface water nutrient concentrations and stratification of the water column. This assumption was supported by the comparison to a western equatorial time series within the Brazil Basin, where high numbers of calcareous dinoflagellate cysts coincide with low organic carbon accumulation rates during times of reduced palaeoproductivity (HÖLL et al. 1999). Within a first attempt for a synthesis of several

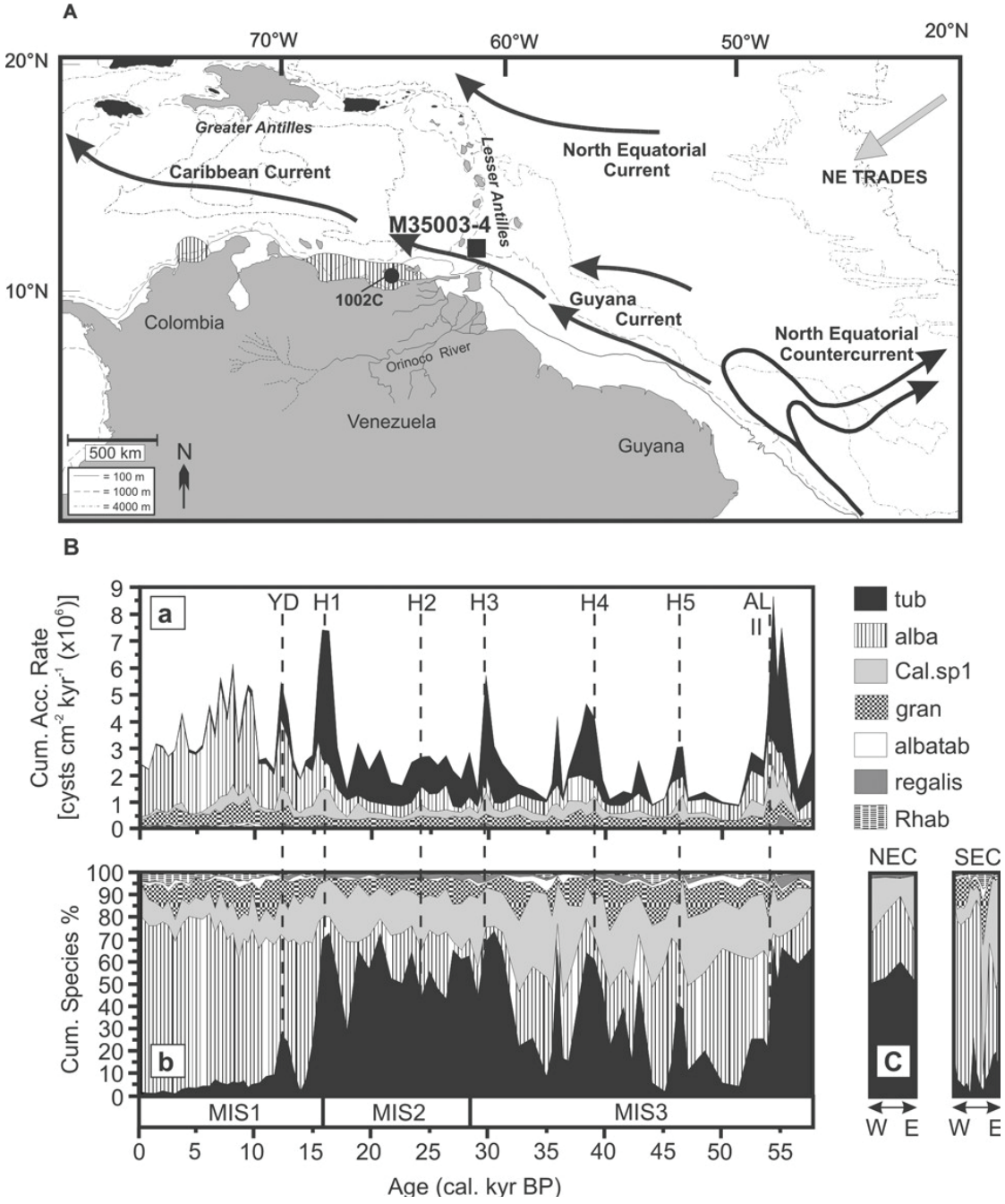

Fig. 6. – **A.** Map showing the position of M35003-4 and the surface water current system of the western tropical Atlantic Ocean. – **B.** Calcareous dinoflagellate cyst association in sediments of core M35003-4 (a) Cumulative dinocyst accumulation rate, (b) relative abundance of individual cyst species; tub = *Pernambugia tuberosa*, alba = *Calciodinellum albatrosianum*, Cal. Sp. 1 = *Calciodinellum levantinum*, gran = *Leonella granifera*, albatab = paratabulated form of *Calciodinellum albatrosianum*, regalis = *Scrippsiella regalis* and Rhab. *Rhabdothorax* spp. YD = Younger Dryas cooling event, H5-H1 = Heinrich events 1 - 5; Al II = Ash Layer II (c) present-day east to west relative abundance distributions of cyst species in the North Equatorial Current (NEC) and South Equatorial Current (SEC) after Vink et al. (2001)

regions of the South Atlantic Ocean Esper et al. (2000) pointed out a coincidence of high cyst production during less trophic, stable water conditions and excellent carbonate preservation to be responsible for the overwhelmingly high cyst numbers at the last two glacial Terminations. In addition, the high occurrence of *Calciodinellum albatrosianum* was attributed to warmer surface water conditions, whereas higher abundance of *Calciodinellum levantinum* was related to colder water conditions. A correlation of high SST with maximum accumulation rates of calcareous dinoflagellate cysts was also observed in a multiproxy study from an eastern Equatorial Atlantic Late Quaternary time series (Höll & Kemle-von Mücke 2000).

Increasing availability of information on modern distribution patterns of calcareous dinoflagellates, as well as more detailed palaeoenvironmental studies provides a more nuanced picture about the paleo-environmental applicability of calcareous dinoflagellate cysts (Vink et al. 2000, 2002; Vink 2004). As documented in chapter 5 calcareous dinoflagellate cyst species can not be considered as one uniform group but individual cyst species have different palaeoenvironmental significance. A high resolution study on calcareous dinoflagellate cyst distribution in the Caribbean Sea shows that this can have advantage over the traditionally used tools or proxies shows (Vink et al. 2001). This study documents that rapid and pronounced changes in the cyst associations reflect a significant southward shift in the position of the North Equatorial Current during the last glacial period and the Younger Dryas cold interval (Fig. 6). Furthermore, rapid changes in local productivity in marine isotopic stage 3 that are associated with variations in Orinoco River nutrient discharge and coastal upwelling strength are being reconstructed. It can be suggested that changes in the zonality of the low-latitude winds play an important role in modulating rapid interhemispheric climate variability. These signals could not be documented with traditionally used proxies in palaeoceanographic research and the study therefore provided new evidence for a coupled tropical/high-latitude climatic system during the last glacial and deglacial periods.

Linear response to orbital forcing could be revealed by frequency analysis of calcareous dinoflagellate cyst accumulation rates in a subtropical eastern South Atlantic Ocean core off South Africa (Esper et al. 2004). The accumulation rates for the last 160 kyr of *T. heimii*, *C. albatrosianum* and *C. levantinum* are positively correlated to the insolation intensity and show strong response to the precession and obliquity components of the mid-latitude southern hemisphere winter insolation. A combined study on Mediterranean calcareous dinoflagellate cysts assemblages and geochemical proxies focused on the time of the S1 sapropel, a time of high seasonal contrast, point out calcareous cysts to be useful in reconstructing variations in surface water productivity (Meier et al. 2004).

The successful application of calcareous dinoflagellate cysts in several marine environments and regions demonstrates the large potential of these marine fossils for

palaeoceanographic and palaeoclimatologic studies.

Future perspectives

In recent years, the information on dinoflagellate ecology has increased considerably, and in consequence, the detail of palaeoenvironmental and -oceanographic reconstructions has been greatly extended. Nevertheless, many ecological questions remain unsolved. For instance, information about where, when (seasonal?) and under which environmental conditions cysts are being produced in the water-column, and which biotic (next to a-biotic) factors influence cyst production and distribution is extremely limited. To solve some of these problems, studies will be and are being carried out (a) on sediment trap material, (b) on surface sediment samples, and (c) on dinoflagellate cultures held under different environmental conditions.

To use calcareous dinoflagellate cysts in palaeoceanographic research, it is essential to have information about the vulnerability of these cysts to dissolution. As documented in chapter 6, the rate of dissolution depends on the mechanisms of dissolution and is species specific. To determine the effect of dissolution by undersaturation of sea-water to calcium carbonate on different species, experiments have been carried out in cooperation with the Alfred Wegener Institute of Polar Research in Bremerhaven. A known amount of calcareous dinoflagellates have been incubated into sea-water solutions containing 120%, 90%, 70% and 50% $CaCO_2$. After one and two month's reaction time, the cysts were harvested. First results show that calcareous dinoflagellate cysts are extremely resistant to undersaturation of sea-water to $CaCO_2$. Dissolution effects could exclusively be determined for the 50% undersaturation solution. Future experiments will focus on the effect of eventual dissolution on the isotopic signal of calcareous cyst walls.

A complete new direction in dinoflagellate research is formed by the use of oxygen isotopes composition of shells of *Thoracosphaera heimii* to reconstruct palaeotemperatures of the sea water at thermocline and/or DCM depth. The use of stable oxygen isotopes composition of carbonate fossils is a standard tool in palaeoceanography to calculate palaeotemperatures. The vegetative cysts of *Thoracosphaera heimii* appear to be an extremely suitable tool for this way of temperature quantification, as (a) they have a widespread distribution, (b) they are formed throughout the year, therefore probably reflecting mean annual sea water conditions, (c) their preferred depth habitat is the deep part of the mixed layer of the upper water column with maximum abundance at thermocline depth with an estimated dial migration of a few meters only (Karwath et al. 2000b), and (d) they occur in high abundance in sediments well below the

lysocline, suggesting extreme resistance against dissolution. Recently it has been shown that *T. heimii* can relatively easily be isolated from sediment samples (Zonneveld 2004.). Until now, stable oxygen and carbon isotopes have been measured on *T. heimii* cysts from surface sediment samples from the equatorial Atlantic and South Atlantic Ocean. Calculated temperatures based on the palaeotemperature equation for inorganic calcite precipitation generally reflect mean annual temperatures at thermocline (Deep Chlorophyll Maximum) depths (Fig. 7). No indication can be found that the fractionation process of stable oxygen isotopes during calcite precipitation of *T. heimii* cysts is strongly affected by metabolic or kinetic processes. Although the results of this pilot study are promising, there are many uncertainties. First of all, future studies will concentrate on the establishment of a palaeotemperature equation for *T. heimii*. This will be done by culturing *T. heimii* under different temperatures. The second step will be to obtain insight in the possible effect of metabolic and kinetic effects on isotopic fractionation during calcite precipitation. For this culture experiments are planned where *T. heimii* will be cultured under different light regimes and medium conditions (with variable pH and carbon ion concentrations). Furthermore, the reliability and practicability of this new tool will be tested by studying fossil sediments and time series where detailed palaeotemperature reconstructions are available, based on other palaeotemperature proxies such as the Uk^{37} of coccolithophores or stable oxygen isotope records of planktic foraminifera.

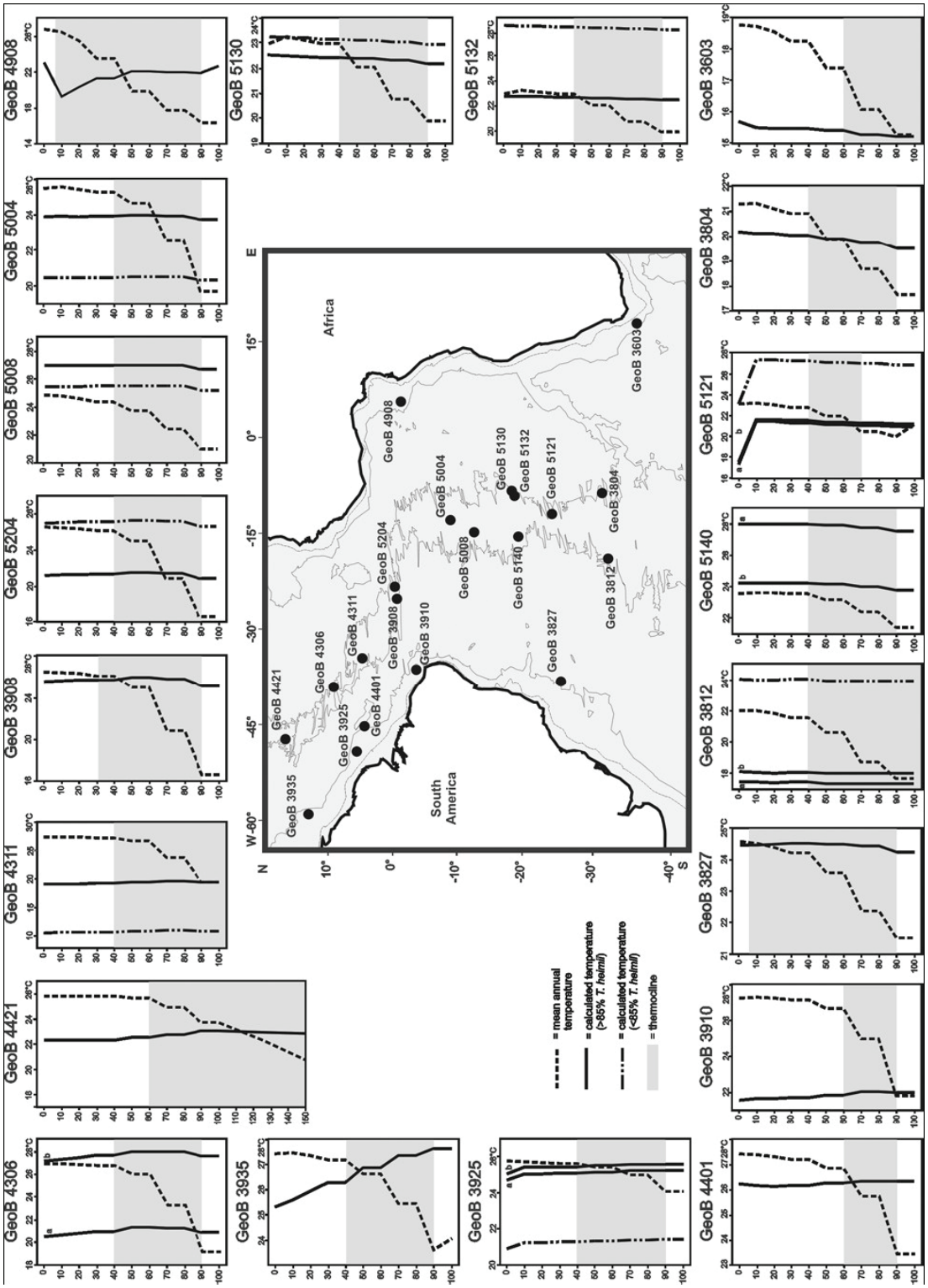

Fig. 7. Sample position and mean annual temperatures and calculated temperatures values based on the stable isotopic composition of *Thoracosphaera heimii* in the upper water column in the equatorial and south Atlantic Oceans. Solid lines a and b represent samples that have been analysed or processed twice (Zonneveld 2004).

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