Production and preservation of calcareous dinoflagellate cysts in the modern Arabian Sea

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Woher kommen die höchsten Berge? So fragte ich einst.
Da lernte ich, daß sie aus dem Meere kommen. -
Aus dem Tiefsten muß das Höchste zu seiner Höhe kommen.

Friedrich Nietzsche

Summary

Although numerous studies have focused on the taxonomy and biology of dinoflagellates, our knowledge of the environmental affinities of calcareous dinoflagellates and the secondary alteration of their cysts is still marginal. This information is, however, an essential prerequisite for the interpretation of the cyst signal left in the sediments, which is used to unravel the causes and effects of past climate change. Atmospheric impulses are normally transferred via upper ocean conditions and the biotic response to the marine sediments, where the environmental signal might be modified by biological and geochemical processes. Thus, geologic research should take the inverse path to reconstruct climatic conditions, as reconstructing is to go from the results back to the causes. This means that post-depositional alteration has to be studied first, before ecological interpretations can be made, which finally are used to reconstruct climate. With the main aim of improving the applicability of calcareous dinoflagellate cysts as (palaeo-) environmental proxy, the major objectives of this thesis are (1) to examine the preservation potential of the individual cyst species, and (2) to contribute to the knowledge on the ecology of calcareous dinoflagellates. For these purposes, surface sediment samples from different areas of the Arabian Sea and sediment trap material from the northern Somali Basin were quantitatively analysed for their calcareous dinoflagellate cyst content.

Upper ocean conditions in the Arabian Sea are strongly determined by climatic forcing of the SW and NE monsoon winds, which leads to considerable regional variations in environmental conditions. A permanent oxygen minimum zone from about 150 to 1200 m water depth creates different diagenetic regimes at the sediment/water interface. In the NE Arabian Sea, substantially higher cyst accumulation rates within this oxygen depleted zone in comparison to above and beneath it indicate that calcite preservation is enhanced under low-oxic bottom water conditions in this region, which can be explained by the lower production rate of metabolic CO_2. Cyst accumulation rates drop at the lower boundary of the oxygen minimum zone by 50 to 84%, depending on the cyst species. These data show that (1) considerable calcite dissolution occurs above the lysocline in the NE Arabian Sea, and (2) although all species are affected by dissolution, the preservation potential of the individual species is not equal, whereby the small and porous shells of *Thoracosphaera heimii* are affected most. This species-selective dissolution also manifests itself in a shift in the relative abundances of the individual species at the lower boundary of the oxygen minimum zone. Low concentrations of *T. heimii* in the NE Arabian Sea most probably result from enhanced dissolution in this region. The generally negative relationship between carbonate content and total organic carbon, which is commonly observed in sediment cores, appears to reverse as soon as the bottom water is oxygen depleted, as shown by the positive relationship between these two parameters in the surface sediments of the NE Arabian Sea. In the western Arabian Sea, cyst accumulation rates do not reveal a relationship with the oxygen minimum zone and are most likely dominated by horizontal differences in primary cyst production caused by coastal upwelling. Samples from below 3500 m depth are strongly influenced by calcite dissolution due to deep water undersaturation.

The basin-wide trends in cyst distribution patterns, that cannot be explained by early diagenetic processes, likely reflect differences in primary cyst production. The two dominating species in the Arabian Sea, *T. heimii* and *Leonella granifera*, have distributions opposite to each other. High absolute and relative abundances of *L. granifera* occur in the NE of the area and can be related to relatively high surface water temperatures, low seasonality and the influence of the Indus River. Other species which are frequently found in the Arabian Sea sediments are *Calciodinellum albatrosianum*, *Calciodinellum sp.* 1, *Calciodinellum operosum* and *Scrippsiella trochoidea*. With its high abundance in the open ocean, *C. albatrosianum* appears to prefer relatively warm surface water within a stable environment and is probably adapted to reduced nutrient concentrations. The shelfward distribution of *S. trochoidea* indicates that this species thrives in eutrophic, relatively cool and unpredictable environments. Generally low cyst concentrations and accumulation rates in the zones of active coastal upwelling encourage the belief that calcareous dinoflagellates are more successful under less agitated conditions.

Neither the data from the surface sediments nor the sediment trap cyst fluxes off Somalia indicate that cyst production is increased under more oligotrophic conditions, as was proposed in earlier studies. The trap recorded highest fluxes of calcareous dinoflagellate cysts and *T. heimii* at the end of the SW monsoon just after the period of coastal upwelling, and lowest fluxes during the following inter-monsoon when surface waters are strongly stratified and nutrient depleted. This indicates that the combination of beginning re-stratification and relatively high nutrient concentrations is most favourable for the studied calcareous dinoflagellate species. Although they appear to prefer a stratified water column, high to intermediate nutrient levels seem to be necessary to maintain high cyst production. Decreases in *L. granifera* fluxes could be linked to reduced surface water temperatures which is in accordance with the results from the surface sediments. Comparison of cyst fluxes at the trap and the seafloor at 4035 m below the trap shows that substantial calcite dissolution takes place at the studied site. With a loss of 96%, *T. heimii* is again the species which is most affected by dissolution. Accordingly, concentrations of this species can be expected to show the strongest variations with time in the sedimentary record as compared to the other species.

The results of this thesis imply that the studied calcareous dinoflagellate cysts can generally be applied as an indicator for stratified but not yet nutrient depleted surface waters, whereby the individual species may be used for the assessment of surface water temperatures or freshwater influence. However, the results also demonstrate that the primary signal in the sediments can be strongly modified by post-depositional processes, especially in highly productive oceanic regions. As it is difficult to discriminate between alteration and the environmental information contained in the calcareous dinoflagellate cyst associations, caution is needed in interpreting the geological record. Several proxies should be combined in a study, with special emphasis on examining the rate of organic matter decay which serves as the driving force for most diagenetic processes.

Zusammenfassung

Eine Vielzahl von Untersuchungen beschäftigt sich mit der Biologie und Taxonomie von Dinoflagellaten. Unser Wissen über die Ökologie dieser Organismen sowie die Erhaltung ihrer Zysten ist jedoch sehr beschränkt. Diese Kenntnisse stellen aber eine unerläßliche Voraussetzung für die Interpretation von Sedimentdaten und somit für Klimarekonstruktionen dar. Atmosphärische Impulse werden über die Verhältnisse in den oberen Wasserschichten und die Reaktion der sedimentbildenden Organismen ins marine Sediment übertragen, wo das ökologische Signal durch biologische und geochemische Prozesse überprägt werden kann. Für Klimarekonstruktionen sollten geologische Studien daher in umgekehrter Reihenfolge vorgehen, denn etwas zu rekonstruieren heißt, von den Ergebnissen auf die Ursachen zu schließen. Mit anderen Worten, die diagenetischen Prozesse müssen zuerst untersucht werden, bevor ökologische Interpretationen erfolgen können, die letztlich zur Rekonstruktion des Klimas dienen. Mit dem Hauptanliegen, die Anwendung kalkiger Dinoflagellatenzysten als Anzeiger für Umweltbedingungen zu verbessern, wurden in der vorliegenden Dissertation die folgenden Ziele verfolgt: (1) das Erhaltungspotential der verschiedenen Zystenarten zu erkunden und (2) unsere Kenntnisse über die ökologischen Ansprüche von kalkigen Dinoflagellaten zu erweitern. Zu diesem Zweck wurden Oberflächenproben aus unterschiedlichen Gebieten des Arabischen Meers sowie Proben einer Sedimentfalle aus dem nördlichen Somalia Becken auf ihren Gehalt an kalkigen Dinoflagellatenzysten quantitativ analysiert.

Die Oberflächenwasserverhältnisse im Arabischen Meer werden hauptsächlich durch die SW- und NE Monsunwinde gesteuert, die starke regionale Unterschiede in den Umweltbedingungen innerhalb des Beckens hervorrufen. Eine permanente Sauerstoffminimumzone erstreckt sich in Wassertiefen von etwa 150 bis 1200 m und schafft unterschiedliche diagenetische Verhältnisse an der Grenzschicht von Sediment und Bodenwasser. Im NE des Arabischen Meeres wurden innerhalb dieser sauerstoffarmen Zone erheblich höhere Akkumulationsraten von kalkigen Zysten beobachtet, was auf bessere Karbonaterhaltung unter geringem Sauerstoffgehalt im Bodenwasser in Zusammenhang mit reduzierter Bildung von metabolischem Kohlendioxid zurückgeführt werden kann. An der unteren Grenze der Sauerstoffminimumzone sinken die Zystenakkumulationsraten in Abhängigkeit der Arten um 50 bis 84%. Diese Daten zeigen, daß (1) die Sedimente im NE des Arabischen Meeres auch oberhalb der Lysokline von erheblicher Karbonatlösung betroffen sind, und (2) die einzelnen Arten unterschiedlich anfällig gegenüber Lösung sind, wobei sich die kleinen, porösen Schalen von *Thoracosphaera heimii* am leichtesten lösen. Diese selektive Lösung wirkt sich auch auf die Artenzusammensetzung aus und führt zu einer Verschiebung der relativen Häufigkeiten an der unteren Grenze der Sauerstoffminimumzone. Die niedrigen Konzentrationen von *T. heimii* im NE des Arabischen Meeres sind vermutlich überwiegend durch verstärkte Lösung in dieser Region bedingt. Die in Sedimentkernen häufig beobachtete negative Korrelation der Gehalte an Karbonat und organischem Kohlenstoff scheint sich unter sauerstoffarmen Verhältnissen im Bodenwasser umzukehren, wie die positive Korrelation dieser beiden Gehalte in den Oberflächenproben des nordöstlichen Arabischen Meeres zeigen. Im westlichen Teil des

Arabischen Meeres besteht keine Beziehung zwischen dem Verteilungsmuster der kalkigen Dinoflagellatenzysten und der Sauerstoffminimumzone. In diesem Gebiet scheint die Zystenverteilung zum großen Teil die Unterschiede in der primären Produktion in Zusammenhang mit Küstenauftrieb zu reflektieren, wobei Proben aus Wassertiefen von mehr als 3500 m bereits stark von Karbonatlösung auf Grund untersättigten Tiefenwassers betroffen sind.

Die beckenweiten Verteilungstrends der Zysten, die sich nicht durch frühdiagenetische Prozesse erklären lassen, spiegeln wahrscheinlich Unterschiede in der primären Zystenproduktion wider. Die beiden im Arabischen Meer dominierenden Arten *T. heimii* und *Leonella granifera* haben entgegengesetzte Verteilungsmuster. Erhöhte absolute und relative Häufigkeiten von *L. granifera* im NE des Arabischen Meeres können mit erhöhten Temperaturen des Oberflächenwassers, geringen jahreszeitlichen Schwankungen und dem Einfluß des Indus in Zusammenhang stehen. Weitere im Arabischen Meer relativ häufige Arten sind *Calciodinellum albatrosianum*, *Calciodinellum sp.* 1, *Calciodinellum operosum* und *Scrippsiella trochoidea*. Erhöhte Konzentrationen von *C. albatrosianum* im offenen Ozean deuten darauf hin, daß diese Art warmes Oberflächenwasser und stabile Umweltbedingungen bevorzugt und möglicherweise an reduzierte Nährstoffkonzentrationen angepaßt ist. Verstärktes Auftreten von *S. trochoidea* entlang der Schelfe zeigt an, daß diese Art unter eutrophen, relativ kühlen und wechselhaften Bedingungen gedeiht. Generell niedrige Zystenkonzentrationen und -akkumulationsraten in den Zonen des aktiven Küstenauftriebs bestätigen die Annahme von erhöhter Zystenproduktion unter weniger turbulenten Verhältnissen.

Die bisher bestehende Theorie bevorzugter Produktion von Zysten unter oligotrophen Bedingungen wird weder durch die Daten aus den Oberflächenproben noch durch die Flußraten in die Sedimentfalle bestätigt. In letzterer akkumulierten die meisten Zysten während des späten SW Monsuns nach dem Ausklingen des Küstenauftriebs, wenn das Oberflächenwasser noch nährstoffreich aber schon leicht stratifiziert ist. Die geringsten Zystenflüsse treten während des folgenden Intermonsuns unter nährstoffarmem, stark geschichteten Oberflächenwasser auf. Diese Daten zeigen, daß die Kombination von Wasserschichtung und relativ hohen Nährstoffkonzentrationen die besten Voraussetzungen für die untersuchten Dinoflagellaten bietet. Obwohl diese Organismen offenbar stärker stratifiziertes Wasser bevorzugen, scheint ein erhöhter Nährstoffgehalt für hohe Zystenproduktion notwendig zu sein. Geringe Flüsse von Zysten der Art *L. granifera* treten in Perioden reduzierter Temperaturen im Oberflächenwasser auf, was im Einklang mit den Ergebnissen aus den Oberflächenproben steht. Der Vergleich von Zystenflüssen in die Sedimentfalle und in das darunterliegende Oberflächensediment deutet auf erhebliche Karbonatlösung an dieser Stelle. Mit einem Verlust von 96% ist *T. heimii* erneut die am stärksten von Lösung betroffene Art. Folglich ist zu erwarten, daß diese Art in Sedimentkernen im Vergleich zu anderen Arten die größten Häufigkeitsschwankungen aufweist.

Die Ergebnisse der vorliegenden Dissertation zeigen, daß kalkige Dinoflagellatenzysten generell als Anzeiger für stratifiziertes, jedoch nicht nährstoffarmes Oberflächenwasser dienen können. Die einzelnen Arten können zur Abschätzung von Temperaturen im Oberflächenwasser bzw. den Einfluß von Süßwasser benutzt werden. Die Ergebnisse verdeutlichen aber auch, daß das primäre ökologische Signal in den Sedimenten durch sekundäre Umwandlungsprozesse stark verändert werden kann. Insbesondere Sedimentkerne aus Hochproduktionsgebieten müssen mit Vorsicht interpretiert werden. Da es meist schwierig ist, das sekundäre Signal von der primären ökologischen Information der Zystenassoziationen zu trennen, sollten immer mehrere Proxies miteinander kombiniert werden. Der Abbau organischer Substanz sollte besonders berücksichtigt werden, da er die treibende Kraft für die meisten diagenetischen Prozesse darstellt.

Contents

1. Introduction

1.1. Motivation and main objectives

One of the major concerns of modern civilisation is the impact of man-induced infringement of environmental processes on climate change, which can exert environmental stress on living creatures on Earth. To understand the climate system, it is helpful to unravel the causes and effects of climate changes in the past, using the geological record for reconstructions of palaeoenvironmental conditions. As most proxies applied currently are modified by pre- or post-depositional processes, it has become clear that multi-proxy analyses are necessary to avoid misleading interpretations. A relatively new tool for palaeoceanographic reconstructions are calcareous dinoflagellate cysts, which can provide information on environmental conditions in the photic zone of the oceans (e.g. Höll et al., 1999; Esper et al., 2000; Vink et al., 2001 a). The results of these first studies demonstrate that some basic questions pertaining detailed information on the ecology of calcareous dinoflagellates and preservation of their cysts still need to be clarified to allow for unequivocal and more reliable interpretations. Central problems hereby are (1) assessment of the relative importance of primary production and post-depositional alteration for the cyst distribution in the sedimentary record, (2) differentiation between covarying environmental parameters, such as oligotrophy and stratification (3) seasonal variations of upper ocean conditions to which the cyst distributions can be related.

The present study aims at contributing to the knowledge on the ecology of calcareous dinoflagellates and at testing the applicability of their cysts to reconstruct palaeoenvironment. Major emphasis has been placed on highly productive regions such as coastal upwelling zones, where diagenetic overprinting can severely modify the ecological signal in the sediments. The Arabian Sea provides a variety of environmental and sedimentary facies due to (1) the strong influence of the semi-annually reversing monsoon winds on climatic, oceanographic and biological processes and (2) the existence of an extensive permanent subsurface oxygen minimum zone which impinges on the continental slope of the surrounding land masses at water depths ranging from 150 to 1200 m (van der Weijden et al., 1999). In this study, surface sediment samples from different parts of the Arabian Sea and sediment trap material from the northern Somali Basin have been analysed. The results are presented and discussed in chapters 2 to 4.

- **Chapter 2** deals with the preservation of calcareous dinoflagellate cysts. Surface sediments with known sedimentation rates from the NE Arabian Sea and the northern Somali basin were selected, and the calcareous dinoflagellate cyst associations and accumulation rates from different diagenetic regimes were compared to answer the following research questions:
    - Are calcareous dinoflagellate cysts affected by dissolution?
    - Does calcite dissolution in the Arabian Sea occur above the lysocline?
    - Is there a relationship between cyst accumulation rates and bottom water oxygen concentrations?
    - What is the relationship between cyst accumulation rates and organic carbon fluxes?
    - Are there regional differences in early diagenetic calcite dissolution within the Arabian Sea?
    - Is there species-selective dissolution and if so, what is the preservation potential of each cyst species and how do cyst associations change under the influence of calcite dissolution?

- **Chapter 3** focuses on the ecology of calcareous dinoflagellates. The ecosystem of the Arabian Sea ranges from eutrophic to oligotrophic, which gives us the opportunity to compare cyst associations in surface sediments from various environmental settings within a relatively small ocean basin. The following questions arise:
    - Which recent calcareous dinoflagellate cyst species are found in the Arabian Sea?
    - How are the individual species distributed and do these patterns reflect the monsoon system?
    - What can be said about their ecology and are these results consistent with existing ideas about their environmental affinities?
    - To what extent are the distributions determined by regional differences in cyst preservation?

- A main characteristic of the Arabian Sea and many other oceanic regions is the seasonal variation of environmental parameters within the upper water layers. Since little is known on possible seasonal differences in cyst production, it is difficult to determine the exact conditions to which conditions the distribution of cysts in surface sediments should be related. **Chapter 4** represents a sediment trap study in which the influence of the monsoon system and the related seasonal changes of environmental parameters on cyst production are examined. In this chapter the following questions are discussed:

- Are there times of preferred cyst production of the individual species and is there a relation to the monsoon system?
- Which conditions are favourable for cyst production in general and which conditions are preferred by the individual species?
- Is enhanced cyst flux indicative for more oligotrophic conditions as proposed in earlier studies of sediment cores (e.g. Höll et al., 1998, 1999; Esper et al., 2000)?
- What is the relative importance of nutrient supply and stratification for cyst production?
- What can be said about cyst preservation by comparing cyst fluxes in the trap to those in the underlying surface sediments?

1.2. Dinoflagellates

Dinoflagellates are unicellular protists which inhabit almost all aquatic environments and represent one of the major phytoplankton groups in the oceans. During their cellulosic thecate life-stage they have two dissimilar flagella (one transverse and one longitudinal) which enable them to migrate with a typical spiral swimming movement. Nutritional strategies of dinoflagellates are extraordinary miscellaneous, including autotrophy, auxotrophy, heterotrophy and mixotrophy. Some species are parasitic or form a symbiotic relationship, e.g. with corals or foraminifera (Taylor, 1987). One of the most characteristic features of the theca is a tabulation pattern on the surface, which is species-specific and is therefore used as a basic taxonomic criterion.

Several species produce geologically preservable cysts as a part of their life cycle, which can consist of organic sporopollenin-like material, silica or calcite crystals that are species-specific in shape and crystallographic orientation. The tabulation pattern of the theca may be fully or partly reflected on the cysts, for which the term paratabulation is used. Dinoflagellates capable of producing calcareous stages are hereafter referred to as calcareous dinoflagellates. In the fossil record their cysts have been commonly described as "calcispheres" and were first ascribed to foraminifera (Kaufmann, 1865). Their taxonomic affinity remained under debate until Deflandre (1947) was able to prove an affinity to dinoflagellates, which was confirmed by later studies (e.g. Wall and Dale, 1968; Fütterer, 1976; Tangen et al., 1982). There is biogeochemical evidence for the existence of dinoflagellates as early as the Late Precambrian or Early Cambrian (Taylor, 1980; Moldowan and Talyzina, 1998), but the first abundant and relatively diverse occurrence of dinoflagellates has been registered from the Late Triassic (Goodman, 1987). Calcareous dinoflagellate cysts have formed a major component of marine sediments especially in the Cretaceous. Recent calcareous dinoflagellates are primarily phototrophic and live in the photic zone of the oceans. Their cysts are usually 20 to 45 µm in size. One exception is *Thoracosphaera heimii*, which forms smaller (9 to 25 µm), metabolically active calcareous spheres as a dominant vegetative-coccoid life stage (Inouye and Pienaar, 1983), thereby having a much greater turn-over rate with formation of a new sphere every 1-2 days (Tangen et al., 1982; Dale, 1992). In *Leonella granifera* the calcareous cyst stage also seems to be the dominant life stage (Janofske and Karwath, 2000).

It is generally believed that most dinoflagellate cysts found in the sediments represent resting cysts which are formed as a result of sexual fusion. These metabolically less active cysts sink to the seafloor and enable the organism to survive adverse conditions such as nutrient depletion following a bloom. After a certain period of dormancy (which may take several years), the protoplast hatches through an excystment aperture known as the archeopyle. Adaptation to a dormant, benthic existence appears apt in lacustrine or shallow marine environments, but is inappropriate in the open ocean where water depths of several km prevent the return of the motile cell to the photic zone. Nevertheless, a number of calcareous dinoflagellates inhabit pelagic environments and their cysts are very abundant in sediments of tropical and sub-tropical oceanic regions (Dale, 1992; Höll et al., 1998, 1999; Vink et al., 2000; Vink et al., 2001 a, b). It is a puzzle as to why dinoflagellates in the open ocean produce such heavily calcified cysts which they have to leave after a relatively short period of time, while the cyst is still within the upper water layers. Janofske and Karwath (2000) studied three of these pelagic species *(L. granifera, Calciodinellum albatrosianum* and *Pernambugia tuberosa*) in the laboratory and could not connect the encystment process to a sexual phase in the life cycle. They infer that these cysts may not be resting cysts. Their results also show that the cysts are produced constantly and may form 50% or more of the living specimens of a culture. A question sometimes referred to pertains to the fact that formation of resting cysts is often triggered by detrimental conditions: to what extent can increased cyst fluxes into the sediment be related to known ecological demands of a certain species? A regular formation of calcareous cysts in pelagic environments would mean that enhanced cyst production reflects a growing population under favourable environmental conditions, which makes these species especially valuable for palaeoenvironmental reconstructions provided the ecology of a taxon is known.

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2. Oxygen availability effects on early diagenetic calcite dissolution in the Arabian Sea as inferred from calcareous dinoflagellate cysts

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Abstract

In oceanic regions with high primary production, such as the Arabian Sea, the primary signals of proxies are often altered by diagenetic processes. The present study aims at assessing the effects of early diagenesis on calcareous dinoflagellate cysts, which represent a relatively new tool for reconstructing the palaeoenvironmental conditions within the photic zone. For this purpose, surface sediment samples from within and below the oxygen minimum zone (OMZ) of the north-eastern and south-western Arabian Sea have been analysed quantitatively for their calcareous dinoflagellate cyst content. The calculated cyst accumulation rates (ARs), the relative abundances and cyst fragmentation values were compared to bottom water oxygen (BWO) content and ARs of organic carbon at the sample positions. Different patterns were found in the north-eastern and south-western part of the Arabian Sea. In the SW, no relationship between cyst ARs and BWO is distinguishable, and the distribution of cyst ARs is thought to largely reflect primary cyst production. In the NE, much higher ARs of all species are found in samples from within the OMZ in comparison to samples from below it. This is interpreted to result from better calcite preservation within the OMZ, presumably due to reduced oxic degradation of organic matter. The differential drop of cyst ARs of the individual species at the lower boundary of the OMZ in the NE Arabian Sea, as well as the species-specific change in relative abundance and fragmentation, indicate different sensitivity to calcite dissolution of the different species. These results show that early diagenetic calcite dissolution can change both, relative and absolute abundances of calcareous dinoflagellate cysts, which has to be considered if using them for palaeoenvironmental reconstructions. Furthermore, it is shown that considerable calcite dissolution can occur above the carbonate saturation horizon in high productive areas. However, calcite preservation can be substantially increased, as soon as oxygen concentrations are too low for oxic degradation of OM. Under low oxic conditions (within and near the OMZ), the main factor controlling organic matter (OM) preservation appears to be BWO concentrations. Under higher oxygen levels (below ~1500 m depth in the NE Arabian Sea) there seems to be an increasing influence of bioturbation and sedimentation rate on the preservation of OM by controlling its oxygen exposure time. This study presents an example of a highly productive basin in which differences in early diagenetic processes can lead to the preservation of a signal that is either dominated by primary production (off Somalia) or by secondary alteration (off Pakistan), although in both areas an oxygen depleted zone is present. For estimating the effects of early diagenetic calcite dissolution in a sediment by metabolic CO_2 (and probably by H_2S oxidation), not only the content of organic carbon but also other geochemical proxies for palaeoredox-conditions have to be included for palaeoenvironmental reconstructions.

Introduction

Oceanic regions with high primary production are suitable sites for high resolution studies of variations in climatic and oceanic conditions in the past. However, in such environments the primary signals of proxies are often subjected to diagenetic overprinting related to organic matter (OM) degradation. In order to validate palaeoceanographic proxies in these regions, detailed information on their diagenetic alteration is first necessary. A region which is highly suited for such investigations is the Arabian Sea. Here, very high primary production and reduced mid-water ventilation lead to the formation of a pronounced permanent oxygen minimum zone (OMZ). Where the OMZ impinges on the continental slopes of the surrounding land masses, it creates suboxic to anoxic conditions at the sediment/water interface (e.g. Wyrtki, 1973; Quasim, 1982; You and Tomczak, 1993; Olson et al., 1993; Morrison et al., 1999). The amount of OM that can be degraded in the sediments at a given position is highly dependent on the export production of OM at that site and on the extension and intensity of the OMZ which, in turn, is influenced by the primary production in the surface waters. The latter is tightly coupled to atmospheric monsoon circulation, which controls the input of nutrients into the photic zone via (1) coastal and open ocean upwelling during summer, (2) convective mixing of surface and subsurface waters during winter, (3) eolian dust input and (4) the amount of fluvial sediments brought in by the Indus River (e.g. Kolla et al., 1981; Quraishee, 1988; Brock et al., 1992; Measures and Vink, 1999).

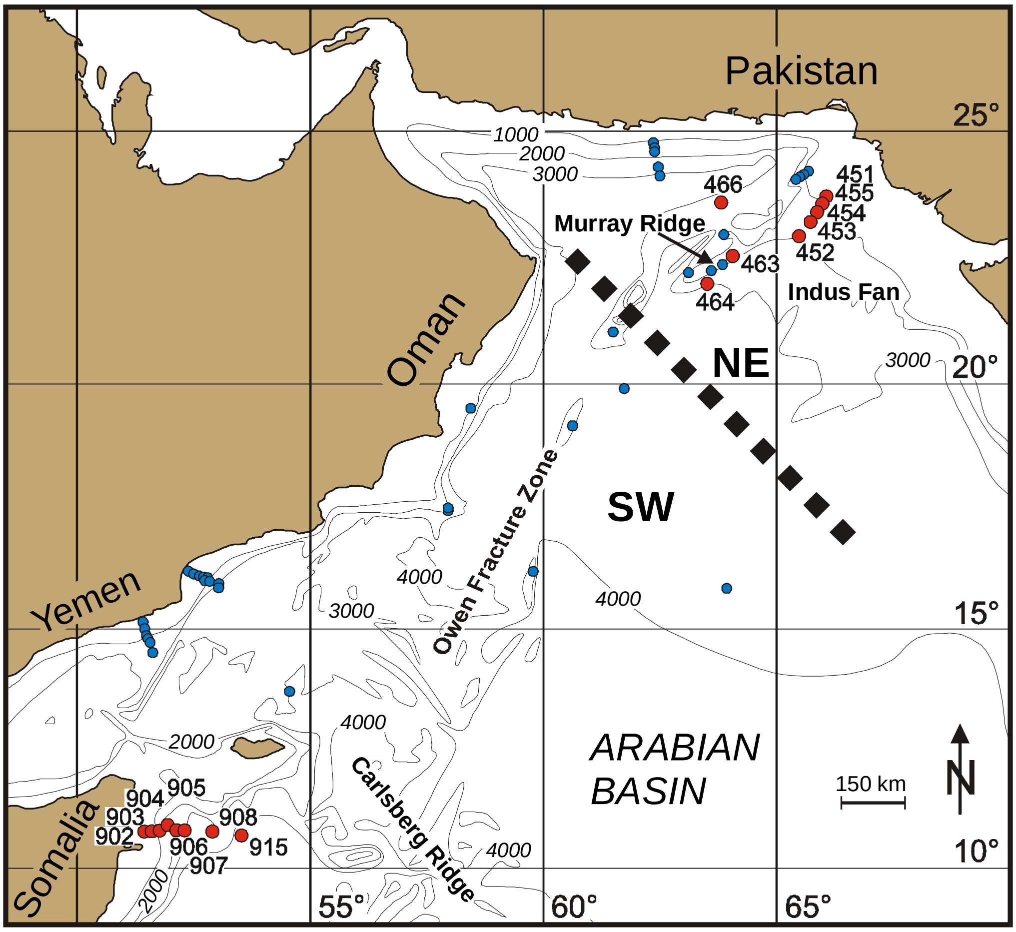

Fig. 1. Sample locations in the Arabian Sea. Red, numbered dots: sites with known sedimentation rates (where cyst accumulation rates would be calculated). Blue dots: additional sites without known sedimentation rates (only cysts per gram and relative abundance would be calculated). Dashed line divides the Arabian Sea into a north-eastern and a south-western part as used in this paper and is based on cyst associations and oceanographic parameters (see text).

In the present study, the contrasting levels of bottom water oxygen (BWO) within and outside the OMZ are used to examine the impact of aerobic and anaerobic diagenetic processes on calcareous dinoflagellate cyst preservation. These cysts are the fossilisable remains of photosynthetic living unicellular organisms and represent a relatively new proxy in palaeoceanography, that may be applied for the reconstruction of palaeoenvironmental conditions within the photic zone (Höll et al., 1998, 1999; Esper et al., 2000; Vink et al., 2001). The interpretation of the observed signals, however, is not always unambiguous as very little is known about the secondary alteration of the cysts' primary ecological information by diagenetic processes. The specific objectives of our research were to assess the importance of early diagenetic processes for cyst distribution patterns and to examine whether their effect on the cysts is species-specific. This information improves the use of calcareous dinoflagellate cysts as a palaeoenvironmental proxy, which will inherently contribute to a better understanding of past climatic and oceanic fluctuations.

Material and oceanography

To compare the effects of diagenesis on calcareous dinoflagellate cysts within different oceanographic settings, we selected surface sediment samples from two transects: (1) in the western Arabian Sea along the relatively steep slope of the Somali continental margin and (2) in the NE Arabian Sea on the more gently sloping Karachi continental margin; as well as three samples from the Murray Ridge area (black dots in Fig. 1; Table 1). For these 16 samples, sedimentation rates are known, from which cyst accumulation rates (AR) can be calculated. To test the relevance of the observed trends, additional samples (grey dots in Fig. 1) with unknown sedimentation rates were included in the present study, using their relative cyst abundance, percentage of cyst fragmentation and cysts per gram of dry sediment. All samples represent the upper centimetre of box-cores that were recovered during the Netherlands Indian Ocean Program cruise 1992-1993 (van Hinte et al., 1995).

The driving force for the upper ocean circulation in the Arabian Sea is the bi-annually reversing monsoon that is generated by differential heating over land and the Indian Ocean. During summer, the strong jet-like SW monsoon creates approximately clockwise surface currents (Wyrtki, 1971; Shetye et al., 1994) and induces open ocean and strong coastal upwelling along the Arabian and Somali coasts. The surface circulation is reversed during winter when the cool and dry NE monsoon blows from the Tibetan Plateau, leading to deep vertical mixing in the NE Arabian Sea and to repletion of the upper water layers with nutrients (Dickey et al., 1998; Smith et al., 1998; Weller et al., 1998).

The NE Arabian Sea is characterised by relatively high surface water nutrient concentrations throughout the year, causing high primary production over large areas as can be inferred from satellite images showing chlorophyll concentrations. Strong oxygen consumption by bacterial decay in combination with relatively weak aeration results in an intense and stable OMZ in this region, reaching from about 150 to 1200 m water depth

Table 1

Sample locations, water depth, linear sedimentation rates (LSR; for Indus Fan and Murray Ridge from van der Weijden et al., 1999; for Somalia from Ivanova, 2000), dry bulk densities (DBD; for Indus Fan and Murray Ridge from van der Weijden et al., 1999).

Region	Station	Latitude (°N)	Longitude (°E)	Depth (m)	LSR (cm/ka)	DBD (g/cm^3)
Somalia	902	10.46	51.34	459	48.0	0.70
	903	10.46	51.39	789	40.0 [a]	0.56
	904	10.47	51.46	1194	29.0 [a]	0.53
	905	10.54	51.56	1567	20.0	0.30
	906	10.48	52.07	2020	14.0 [a]	0.35
	907	10.48	52.14	2807	8.0	0.35
	908	10.46	52.54	3572	5.0 [a]	0.36
	915	10.41	53.31	4035	3.6	0.39
Indus Fan	451	23.41	66.02	495	25.5	0.96
	452	22.56	65.28	2001	5.0	1.33
	453	23.14	65.44	1555	8.1	1.24
	454	23.27	65.52	1254	10.1	1.12
	455	23.33	65.57	998	16.0	0.87
Murray Ridge	463	22.33	64.03	970	15.0	0.73
	464	22.15	63.35	1511	6.4	1.21
	466	23.36	63.48	1960	8.1	1.29

[a] interpolated values

(van der Weijden et al., 1999). Reduced ventilation arises from a combination of different factors, such as (1) the geographic position of the basin, which is land-locked in the north and thus reduces the circulation of intermediate waters, (2) lateral sub-thermocline advection of low-oxygen source waters, (3) high-salinity intermediate waters which originate from the Persian Gulf and contribute to the stratification of OMZ waters, and (4) the high surface water temperatures that reduce oxygen solubility (Swallow, 1984; Olson et al., 1993; You and Tomczak, 1993; Morrison et al., 1998). Convective winter mixing in the NE Arabian Sea extends to depths of about 100 m (Banse, 1984; Madhupratap et al., 1996) which is too shallow to introduce significant amounts of oxygen into the oxygen depleted zone. In contrary, mixing enhances primary production by introducing nutrients into the photic zone, thereby increasing oxygen consumption by the subsequent OM degradation. An overview of the basic characteristics of the OMZ is given in Morrison et al. (1999).

In the western Arabian Sea, primary production is largely controlled by coastal upwelling of cold, nutrient-rich water during the SW monsoon and has a seasonal, pulsating character. Primary production rates decrease strongly towards the open ocean. Composite satellite images show that, in the yearly mean, values of primary production are lower in the SW than in the NE Arabian Sea, except for a narrow zone along the Somali and Arabian coasts. The OMZ in the western part exhibits less thickness and intensity compared to the north-eastern region (Slater and Kroopnick, 1984; Paropkari et al., 1992).

Preparation and analysis

To analyse the samples for their content of calcareous dinoflagellate cysts, ca. 0.5 g of the dried sediment was weighted and disintegrated in tap water (containing a few drops of ammonia to prevent calcite dissolution) by ultrasound treatment for < 1 minute. The sediment was subsequently separated through 63 µm and 20 µm stainless steel sieves to concentrate 20 - 45 µm-sized cysts. The <20 µm and 20 - 63 µm fractions were concentrated to 100 ml and 15 ml of water, respectively. A split (50 or 100 µl) of homogenised material of each of the two fractions was separately placed on a cover slip, dried in an oven or on a heating plate and finally fixed with Spurr's resin (Spurr, 1969). For more detailed information on the preparation method see Vink et al. (2000).

The cysts were counted under a light microscope using polarised light (Janofske, 1996). We follow the taxonomy of Williams et al. (1998) for *Calciodinellum operosum* and *Thoracosphaera heimii*, of Janofske (2000) for *Scrippsiella trochoidea* and *Scrippsiella regalis*, and of Janofske and Karwath (2000) (synonyms used in earlier publications are given in brackets) for *Leonella granifera* (*Orthopithonella granifera*), *Calciodinellum albatrosianum* (*Sphaerodinella albatrosiana*), *Calciodinellum* sp. 1 (*Sphaerodinella tuberosa* var. 2). The morphological group of spiny cysts used here contains the species *S. regalis* and *Rhabdothorax* sp. 1 as used in Vink et al. (2000), which were not analysed separately since the characterising shape of the calcite crystals was often not recognisable due to organic matter between the spines. At least one slide per fraction and sample was scanned. If there were less than 200 specimens in one slide of each fraction, additional slides were analysed. Fragments were counted separately except for fragments of *L. granifera* which are very similar to fragmented single chambers of foraminifera. This species can only be clearly identified if unbroken. The absolute abundance (A) of each species/morphotype (in cysts per gram of dry sediment) was calculated using the counted number of cysts (C), the dry weight of the sediment used for preparation (W, in g), the volume of water the fraction was concentrated in (V, in µl) and the amount of split that was used for the slide (S, in µl):

$$A = [(C * V) / (W * S)]_{20\text{-}63\mu m} + [(C * V) / (W * S)]_{<20\mu m}$$

Data are given in App. 1. Cyst accumulation rates (cyst AR, in cysts/cm^2ka) were calculated using the absolute cyst abundances (A), the linear sedimentation rates (LSR, in cm/ka) and the dry bulk densities of the sediments (DBD, in g/cm^3):

$$\text{cyst AR} = A * LSR * DBD$$

The LSR and DBD of the samples from the Indus Fan and the Murray Ridge were taken from van der Weijden et al. (1999) and LSR for the stations off Somalia were from Ivanova (2000). The correction of absolute cyst abundances for sedimentation rates results in a landward shift of maximal values, although the principle distribution patterns do not change significantly.

In addition to cyst AR, the relative abundance of each species/morphotype was calculated. Two species, *T. heimii* and *L. granifera*, clearly dominate the association (forming together 88-97% of the association), and their relative abundance is given in percent of the whole association. For the less abundant species/morphotypes, the relative abundance is based on the association excluding the two dominating species which otherwise would conceal all trends. The relative abundance of the spiny cysts is rather low and therefore not used for examining trends in calcite dissolution of the individual species. Cyst AR and relative abundance have been plotted in relation to water depth at the stations giving the position relative to the OMZ and thus to the approximate BWO concentrations (Figs. 2 and 4). The division of the Arabian Sea into a north-eastern and a south-western region as used in this paper (Fig. 1) is based on calcareous dinoflagellate cyst associations and on oceanographic parameters such as the influence of upwelling processes which are characteristic for the SW. In the NE Arabian Sea fluvial input by the Indus River and convective winter mixing are important factors.

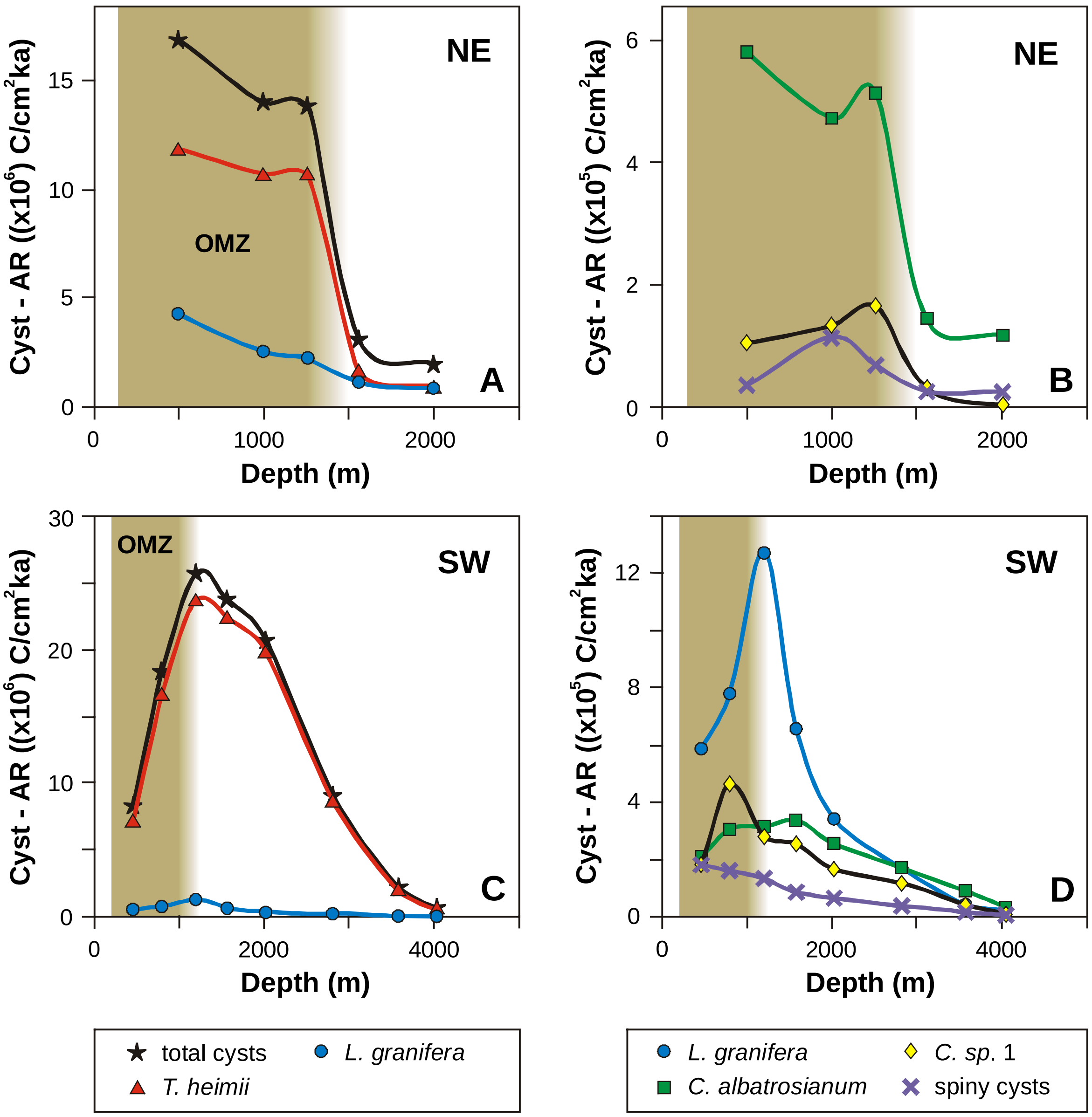

Fig. 2. Cyst accumulation rates (AR) of the different species versus water depth in the Indus Fan profile (A and B) and in the profile off Somalia (C and D). The brown area marks the OMZ. Note marked drop in ARs at the lower boundary of the OMZ in the Indus Fan profile.

Results

The five most commonly occurring species/morphotypes of calcareous dinoflagellate cysts are discussed in this paper. The dominating species is *T. heimii*, followed by *L. granifera*. Less abundant are *C. albatrosianum*, *C.* sp. 1 and the spiny cysts. The calculated cyst accumulation rates (AR) are generally higher in the SW than in the NE (Fig. 2) with a more pronounced dominance of *T. heimii* in the SW (Fig. 4).

NE Arabian Sea

In the NE Arabian Sea, a clear relation exists between the cyst ARs and sample positions relative to the OMZ (Fig. 2). All species show higher ARs in samples from the oxygen depleted zone compared to samples from above or below it. A very marked drop can be seen at the lower boundary of the OMZ (Fig. 2A, B). When we compare the ARs in the two samples covering the transition from OMZ to higher bottom water oxygen (BWO) concentrations (i.e. at 1254 and 1555 m water depth) and set the AR values of the upper sample to 100%, the largest drop in AR (over 80%) is found for *T. heimii* and *C. sp.* 1, followed by *C. albatrosianum* (72%), the spiny cysts (66%) and *L. granifera* (50%; Fig. 3A). Towards a depth of 2000 m, the AR of the first two species continue to strongly decrease in contrast to *C. albatrosianum*, the spiny cysts and *L. granifera*, which all remain at an almost constant level (Fig. 2A, B).

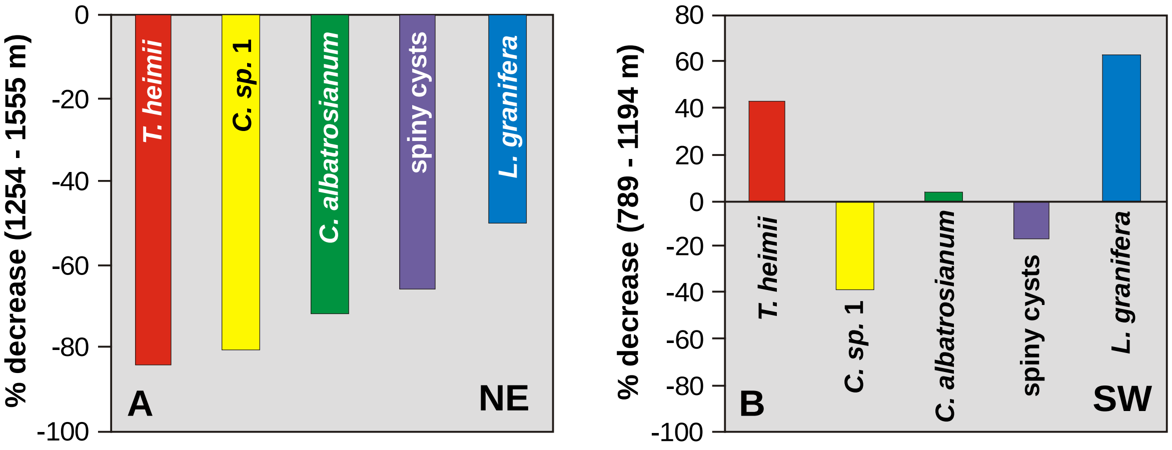

Fig. 3. Change in cyst accumulation rates as crossing the lower boundary of the OMZ (upper sample set to 100%). A: difference between the two samples at 1254 m and 1555m depth in the Indus Fan profile. B: difference between the two samples at 789 m and 1194 m depth in the profile off Somalia.

The different impact of high and low BWO concentrations on species distribution is also reflected by their relative abundance (Fig. 4, left side), showing a drop for *T. heimii* and *C. sp.* 1 over the transition, no change for *C. albatrosianum* and an increase for *L. granifera*. Furthermore, the percentage of fragmented specimens of *T. heimii* and *C. sp.* 1 is much higher in samples from below the OMZ, where indeed much lower cyst ARs are found compared to samples from within the OMZ (Fig. 5A, B). A similar relationship

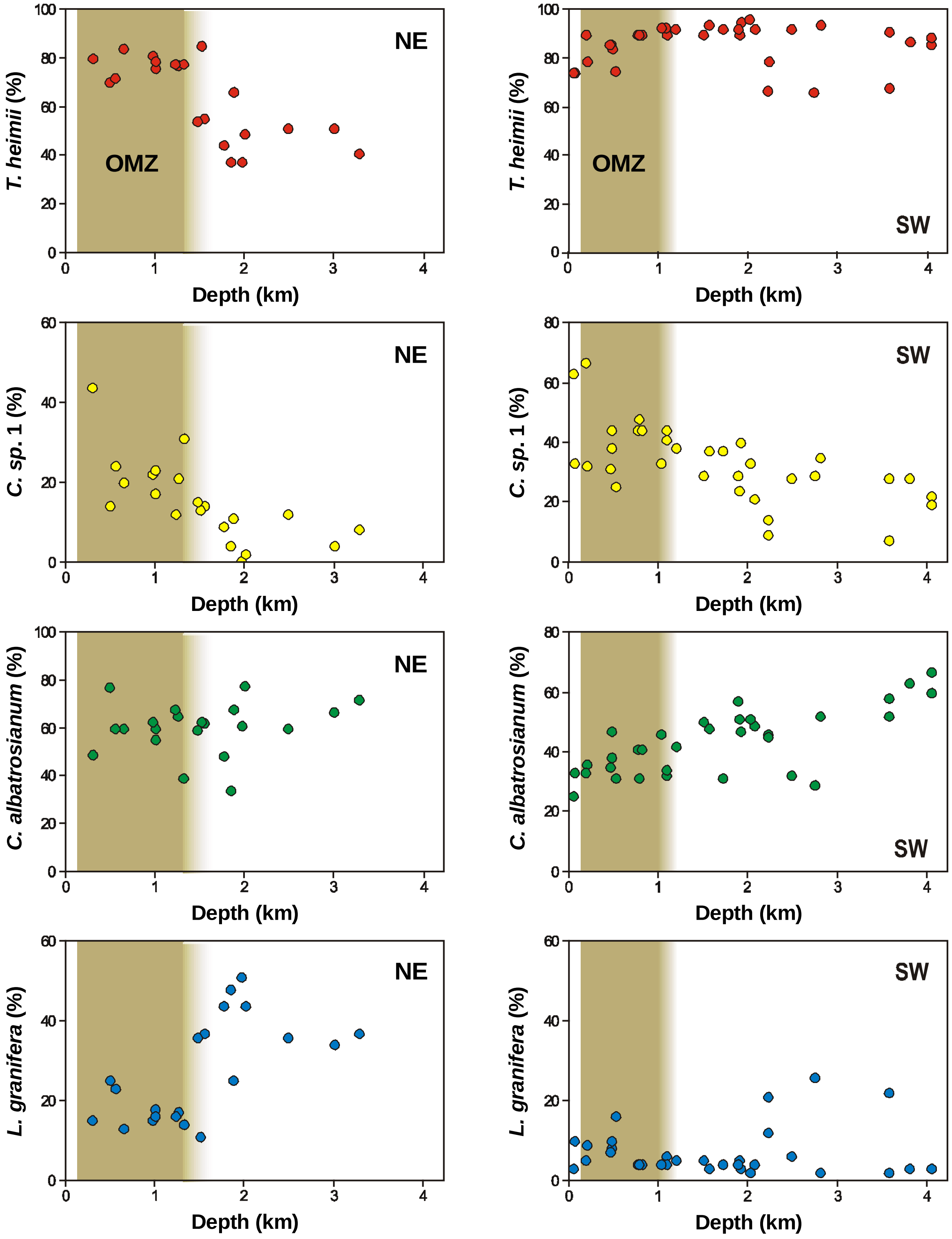

Fig. 4. Relative abundances of the four most common species versus water depth in the NE Arabian Sea (left) and SW Arabian Sea (right). Brown areas mark the OMZ. Note the drop in relative abundance of *T. heimii* and *C. sp.* 1 and the rise of relative abundance of *L. granifera* at the lower boundary of the OMZ in the NE Arabian Sea.

between *T. heimii* and fragments is observed when using the additional samples (grey dots in Fig. 1) and cyst per gram sediment (Fig. 6). *C. albatrosianum* shows comparable values of fragmentation within and below the OMZ (with the exception of one sample), although cyst ARs are higher within the OMZ (Fig. 5C).

The diagram in Fig. 7 illustrates the relation between cyst AR of the different species and the AR of organic carbon (C_{org}, values from van der Weijden et al., 1999). It shows that samples from within the OMZ (black) and those from below it (grey) cluster together: much lower cyst ARs are found in samples from below the OMZ with low C_{org} ARs compared to samples from within the OMZ with higher C_{org} ARs. This pattern is equally reflected by all species even though they show a differential decrease in cyst AR at the lower boundary of the OMZ (compare with Figs. 3A and 4).

SW Arabian Sea

The situation is different in the SW Arabian Sea where no clear relation between cyst AR and BWO can be recognised. Highest cyst ARs are observed below the OMZ, slightly decreasing down to 2000 m and then dropping to very low values at 4000 m (Fig. 2C, D). Only the AR of the spiny cysts decreases continuously with depth. No large drops of cyst ARs occur at the lower boundary of the OMZ and *T. heimii* even increases by 40% (Fig. 3B).

The relative abundances of *T. heimii* and *L. granifera* show no change with water depth (Fig. 4, right). Values for *C. albatrosianum* increase slowly with depth, whereas those for *C. sp.* 1 decrease with depth. However, no abrupt changes are visible at the OMZ boundary. Regarding the fragmentation of *T. heimii*, no relation to the OMZ is distinguishable (Fig. 5D).

Discussion and conclusions

In the NE Arabian Sea, large differences in primary production do not occur over short distances. Consequently, the higher cyst ARs and lower percentage of cyst fragmentation in the samples from within the OMZ (Figs. 2A, B, 5A-C, 6, 7) are interpreted as being the result of differentiated calcite dissolution. This process can take place in the water column and at the sediment/water interface. The NE Arabian Sea is undersaturated with respect to calcite below 3400 m (Millero et al., 1998). The deepest

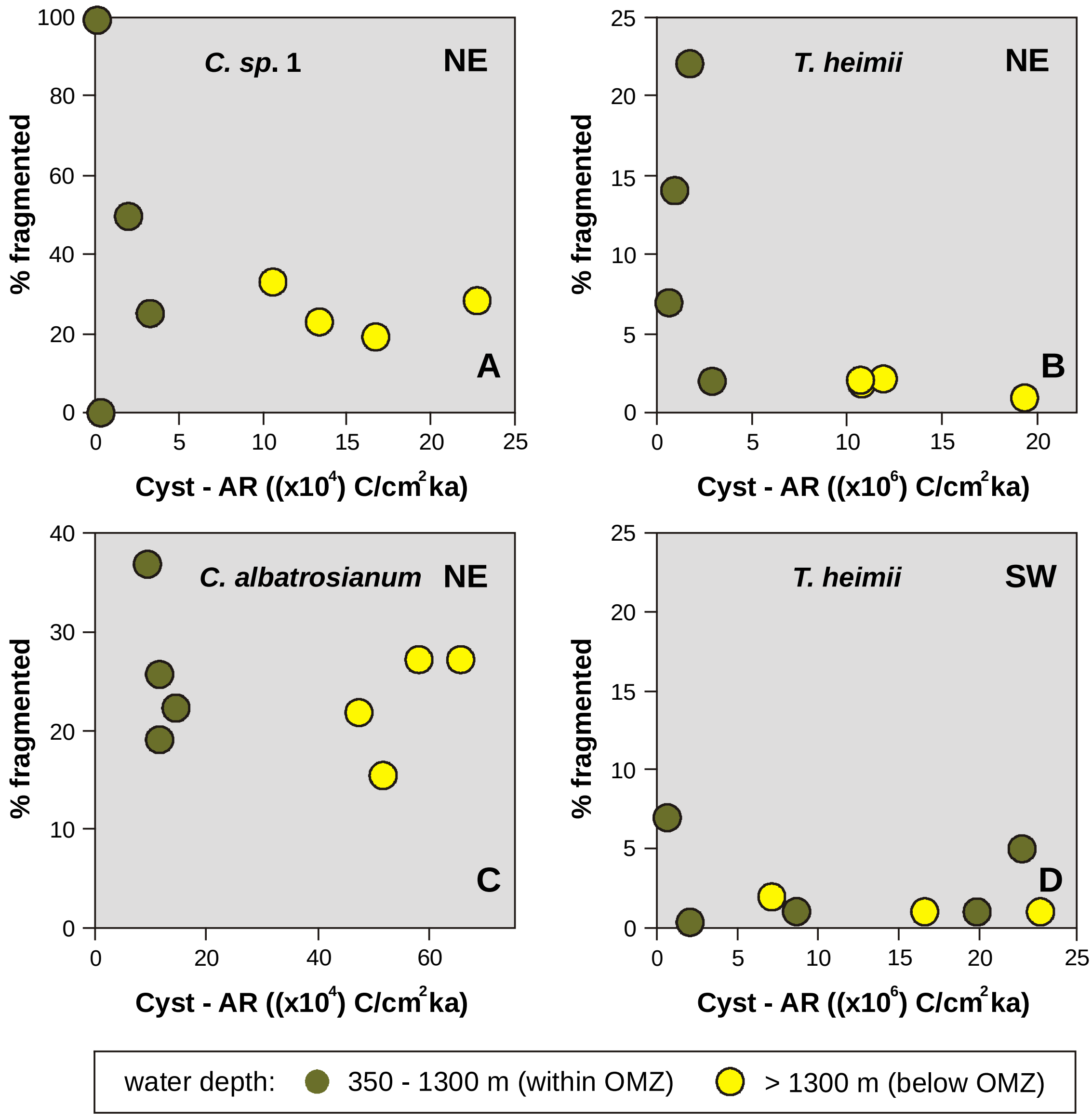

Fig. 5. Percent fragmented specimens versus cyst accumulation rates of different species in the NE Arabian Sea (A-C) and in the profile off Somalia (D).

station we investigated from this region is at 2001 m and thus lies above the carbonate saturation horizon. Calcite dissolution due to deep water undersaturation can therefore be excluded. However, this does not rule out calcite dissolution in the water column or at the seafloor by other means.

Dissolution in the water column

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). Recent studies on sediment traps in the Pacific Ocean show that as much as 80% of the particulate inorganic carbon can be redissolved in the upper 100 m of the water column (Hernes et al., in press).

One possible mechanism is calcite dissolution within faecal pellets or in gut-environments (e.g. Bishop et al., 1986; Harris, 1994; Milliman et al., 1999). One of the most important grazing zooplankton groups world-wide are calanoid copepods which usually make up 70% by mass or more of all net-collected zooplankton (Lalli and Parsons, 1993, p. 88). Dinoflagellates are a major component in the diets of copepods (Mauchline, 1998). Although it seems that copepods mainly feed on dinoflagellates which produce organic-walled cysts (Mauchline, 1998), it is not unlikely that their diets also includes the motile stages of dinoflagellates which produce calcareous cysts. It is, however, questionable whether calcareous cysts are consumed as they are more stable and larger than coccospheres. Based on model results by Jansen and Wolf-Gladrow (in press) dissolution of coccoliths in copepod guts is insignificant if one assumes continuous grazing. In a scenario that involves alternating grazing and non-grazing periods, however, their model yields dissolution of up to 25% of the ingested carbonate. In pre- or post-bloom situations, when grazing pressure is high, about 15% of the calcite standing stock can be dissolved, which leads Jansen and Wolf-Gladrow (in press) to conclude that calcite dissolution in copepod guts does not account for the majority of $CaCO_3$ dissolution in the upper water column (assessed at 60% by Milliman et al., 1999), but may contribute a significant portion.

A second mechanism, which seems to be important for calcite dissolution in the water column, is organic carbon remineralisation in marine snow aggregates (Jansen et al., submitted), whereby CO_2 locally rises, resulting in a decreased CO_3^{2-} concentration within the boundary layer of the sinking particle. To date, it is not known whether calcareous dinoflagellate cysts mainly sink as single particles or within marine snow aggregates. In the first case there would not be enough OM around the cysts to result in carbonate dissolution. (A hatching dinoflagellate leaves behind an empty cyst, which - with respect to dissolution - could be an important difference to the shells of other planktonic groups that can contain organic remains of the dead organism.) If the cysts are transported within marine snow aggregates, their dissolution depends on the OM availability, remineralisation rate and size of the aggregates. In view of the production of large amounts of OM in the NE Arabian Sea, dissolution of calcareous cysts in the water column cannot be excluded. Lee et al. (1998) investigated the particulate organic carbon flux in the Arabian Sea and report that "the largest rates of flux-decrease with depth occurred at the top and bottom boundaries of the water column. On an annual average, only 4.3 - 8.2 % of the carbon fixed by primary producers was exported to 100 m." In a recent study on calcification in the Arabian Sea, Balch et al. (2000) found that the turnover times of particulate inorganic carbon and particulate organic carbon in this region are not significantly different, which is suggesting that the processes responsible for their production and removal were similar. This could mean that there is substantial carbonate dissolution in the upper water column in the Arabian Sea. The results of Balch et al. (2000) indicate a 75% calcite loss in the upper water column in the Arabian Sea, which they attribute to dissolution of sinking coccoliths. Calcareous dinoflagellate cysts, however, are larger than coccoliths and thus sink faster which makes them less prone to dissolution. The living cysts are protected from dissolution by a thin organic layer (Janofske and Karwath, 2000) which is rapidly destroyed after excystment. Therefore, only empty cysts can be subject to dissolution. In the tropical and equatorial Atlantic Ocean the highest quantities of living *T. heimii* shells have been observed in water depths between 50 and 100 m (Karwath et al., 2000). Thus, it is not very likely that a large part of at least this species is dissolved or fractionated in the upper 100 m. Below 150 m, the marine snow aggregates (potentially carrying cysts) sink trough oxygen depleted waters, which precludes respiration and associated calcite dissolution in the aggregates on a substantial part (ca. 1000 m) of their way to the seafloor.

Even if assuming some cyst dissolution in the upper water column, this process cannot explain the observed cyst distributions since conditions in the upper 1200 m above "OMZ- and non-OMZ stations" are the same. The only difference is that the cysts that sink to depths below the OMZ additionally pass through oxygenated waters before they reach the seafloor. It is, however, very unlikely that the cysts experience strong dissolution on this part of their way to the seafloor as the largest drop in cyst ARs occurs between 1254 and 1555 m water depth, while a significant difference between 1555 and 2000 m is not notable. Compared to their exposure time at the seafloor, the sinking time of the cysts below the OMZ appears negligible short and should not greatly influence the cyst ARs. This assertion is supported by the results of Lee et al. (1998), who found that only little organic carbon is remineralised in the water column between 1000 and 3000 m, bracketing our studied depth interval below the OMZ.

Dissolution at the sediment/water interface

The lack of evidence for differentiated cyst dissolution in the water column leaves differences in early diagenetic processes at the sediment/water interface to explain the large discrepancy between cyst ARs within and below the OMZ. Lee et al. (1998) observed

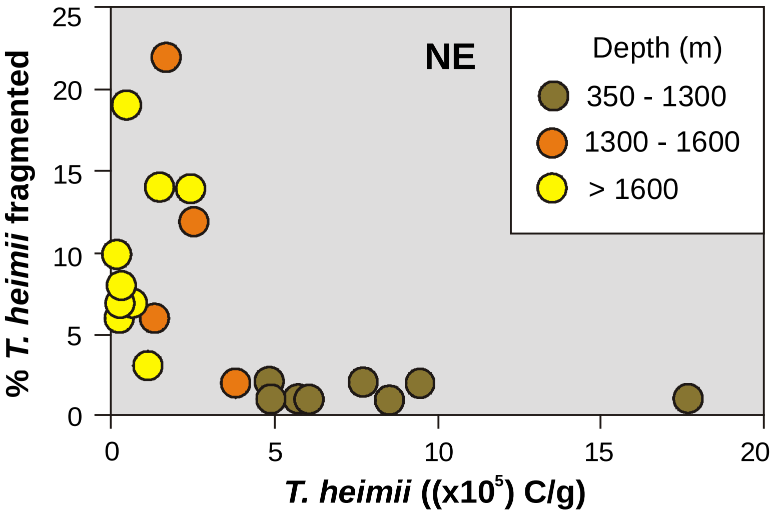

Fig. 6. Percent fragmented specimens versus cysts per gram of dry sediment of *T. heimii* in the SW Arabian Sea. Depth gives the position of the samples relative to the OMZ: dark green = very low bottom water oxygen within the OMZ; orange = relatively low bottom water oxygen below the OMZ; yellow = more oxygenated bottom water.

a much stronger offshore decrease in organic carbon accumulation than in primary production in a transect off Oman and state that "most of this preservation effect must be at the seafloor." Since OM degradation is a driving force for many diagenetic processes, including calcite dissolution, it is at first essential to understand the mechanisms leading to the pronounced mid-slope maximum in surficial sedimentary OM content in the NE Arabian Sea.

The reason for this characteristic distribution of OM has been intensively debated and discussed in the literature during the last years. On the one hand, it has been argued that preservation of OM is enhanced under low oxygen conditions due to decreased aerobic microbial decomposition and reduced or absent bioturbation (Slater and Kroopnick, 1984; Paropkari et al., 1992, 1993; Reichart, 1997; van der Weijden et al., 1999.) On the other hand, alternative factors were proposed to control the distribution of OM in this area. Such factors are hydrodynamic sorting and downslope reworking, depth-related settling fluxes of OM to the sea floor, dilution by other sedimentary components, variations in primary productivity and lateral advection of OM, sediment texture, OM-source and molecular-level composition (Calvert, 1987; Pedersen et al., 1992; Canfield, 1994; Hedges and Keil, 1995; Calvert et al., 1995; Cowie et al., 1999). There is no doubt that these factors exert an influence on the distribution of OM, but it is not clear whether they are more important than BWO concentrations.

Another parameter that was shown to be important for OM degradation is the protective role of OM adsorption on mineral surfaces (e.g. Mayer, 1994; Keil et al., 1994; Bergamashi et al., 1997). Keil and Cowie (1999) investigated this process in the NE Arabian Sea and observed a high ratio of organic carbon to mineral surface areas, indicating high OM preservation, only at stations with low BWO but not necessarily limited to laminated sediments. High OM accumulation below the OMZ (down to 1400 m depth) was also reported by other authors (e.g. Schulz et al., 1996; Cowie et al. 1999, Keil and Cowie, 1999) and was thought to result from downslope reworking (von Stackelberg, 1972; Pedersen et al., 1992; von Rad et al., 1995; Schulz et al., 1996). Keil and Cowie (1999), however, conclude that redistribution of organic-rich material cannot fully account for the observed distribution of OM. Another reason could be that the OMZ extends into deeper regions temporally, thereby increasing the preservation of OM below 1200 m. It should be pointed out that the marked drop of cyst ARs and the increase of fragmentation also occurs not exactly at the boundary of the OMZ but slightly below it. In contrast to the upper boundary of the OMZ, the lower boundary is not very sharply defined, with BWO concentrations rising gradually from ~0,1 ml/l within the OMZ to 1 ml/l at ~1500 m depth (Smith et al., 2000). Therefore, it is difficult to determine a specific depth to distinguish between different regimes of early diagenetic processes. Finally, there are biotic processes that can influence particle fluxes. Wishner et al. (1998) observed a clear relation between zooplankton biomass and oxygen in the NE Arabian Sea. Since zooplankton feeding is an

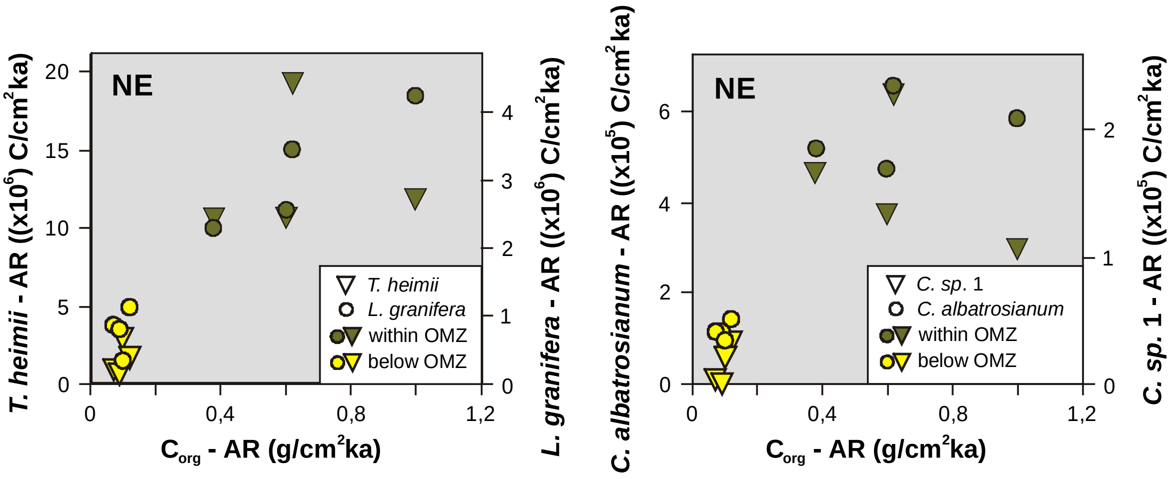

Fig. 7. Cyst accumulation rates of the four most common species versus accumulation rates of organic carbon (C$_{org}$-AR: from van der Weijden et al., 1999) in relation to the OMZ. Note the different scales.

important mechanism in repackaging particles, this is thought to be responsible for the apparently increased OM flux below the OMZ (Lee et al., 1998).

It seems likely that all or most of the aforementioned factors play a role in elevating the mid-slope OM accumulation in the NE Arabian Sea and most of them are interdependent on BWO, making their effects difficult to deconvolve. For example, higher primary production increases the intensity of the OMZ and processes such as downslope transport of sediment can compensate for the effect of longer exposure times of OM in open ocean sites relative to the shelf. The mean renewal time for the Arabian Sea OMZ is ~11 years for the entire layer (Olson et al., 1993). This means that, although the source water is oxygen-poor Indian Ocean Central Water [~1 ml/l (Olson et al., 1993)], a certain amount of oxygen is constantly brought into the OMZ and could be used for OM degradation. During oxic respiration CO_2 is produced, leading to a lower pH of the pore water which influences the preservation of calcium carbonate (Emerson and Bender, 1981; Hales et al., 1994). As mentioned above, even above the carbonate saturation horizon excess pore water CO_2 can force calcite dissolution in the upper sediment column (Emerson and Bender, 1981; Archer, 1991, 1994; Jahnke et al. 1994; Martin and Sayles, 1996). The protons produced from metabolic CO_2 are neutralised at the sediment/water interface by CO_3^{2-} in the seawater. Very old bottom water, as is present in the northern Indian Ocean, is depleted with respect to CO_3^{2-}, leading to less neutralisation and more corrosive pore water. If the high ARs of OM within the OMZ would be the result of factors other than enhanced OM preservation, no differences in cyst ARs would be expected within and below the OMZ. The observed elevated cyst ARs and reduced fragmentation within the OMZ (Figs. 2 and 5), however, could indicate that oxic respiration within the OMZ is strongly reduced, thereby enhancing OM preservation. This is expressed by the relationship between cyst AR and C_{org} AR within and below the OMZ (Fig. 7). However, there are other processes which lower the rate of calcite dissolution and could partly compensate for the effect of oxic respiration, such as (1) the occupation of surface sites by adsorbed Ca^{2+}, heavy metal ions or phosphate ions (Morse and Berner, 1979; Svensson and Dreybrodt, 1992), or (2) OM oxidation by sulfate reduction and anoxic methane oxidation, in which very few protons are produced compared to the oxic degradation of OM. Lückge et al. (1999) reported sulfate reduction to be an extremely efficient process in the uppermost part of the sediments within the OMZ of the NE Arabian Sea. It even takes place in the sediments of the deep Arabian Sea in depths below 12 cm (Böttcher et al., 2000). Bacterially-formed methane emanating from a variety of pockmarks and gas seepage structures are described by von Rad et al. (1996) from the Makran accretionary prism off Pakistan. The gas is partly oxidised to HCO_3^- in the bacterial sulphate reduction zone, resulting in precipitation of authigenic carbonates at these positions near the sediment/water interface within the OMZ.

During sulfate reduction and anoxic methane oxidation, alkalinity and the pH of the pore water can increase, shifting the carbonate system equilibrium towards increased CO_3^{2-} ion concentrations (Berner, 1971; Canfield and Raiswell, 1991). Accordingly, less calcite needs to be dissolved to maintain the equilibrium. However, it is not clear whether these processes are important for enhanced preservation of calcite compared to the large role played by metabolic CO_2 release due to oxic OM degradation. Jahnke et al. (1997) simulated the influence of SO_4^{2-} reduction and HS^- and NH_4^+ oxidation on calcite dissolution and conclude that there is a relatively minor impact. However, there is also an indirect influence on calcite preservation due to the re-oxidation of the products of sulphate reduction (and also of the other forms of OM degradation) when they diffuse upwards and come in contact with the seawater (Jørgensen, 1982). Oxygen is consumed which then is no longer available for oxic respiration. On the other hand, very effective calcite dissolution can be expected if BWO concentrations are high enough to oxidise large amounts of H_2S (depending on the availability of reactive iron) as shown by a study of Ku et al. (1999) on the South Florida Platform. Thus, sulfate reduction can have contrasting effects on calcite preservation under different BWO conditions: increased alkalinity and enhanced calcite preservation under low BWO levels, and acidic pore waters due to H_2S oxidation under high BWO levels leading to calcite dissolution. Accordingly, the dramatic drop of cyst ARs below the OMZ could be explained by geochemical processes related to OM degradation via oxic respiration and sulfate reduction under oxic and anoxic conditions. To what extent H_2S oxidation occurs in the NE Arabian Sea, however, is not clear as there seems to be no iron limitation for pyrite-formation (Lückge et al., 1999).

Apart from BWO concentrations, there are other factors that can influence OM degradation and carbonate dissolution and merit further discussion such as bioturbation and oxygen exposure time, which is dependent on penetration depth of oxygen and sedimentation rate (Hedges and Keil, 1995; Hartnett et al., 1998; Hedges et al, 1999). It could be suspected that the observed differences in cyst ARs and fragmentation are not caused by respiratory CO_2 but are a secondary effect of bioturbation and benthic life that is supported by higher BWO levels below the OMZ. A number of recent studies deal with bioturbation and related processes across the OMZ in the Arabian Sea (Levin et al., 2000; Meadows et al., 2000; Smith et al., 2000) and in the abyssal Arabian Sea (Kurbjeweit et al., 2000; Luff et al., 2000; Turnewitsch et al., 2000). In the NE Arabian Sea, shelf sediments and slope deposits below 1100 m are usually bioturbated and contain abundant epibenthos whereas distinctly laminated sediments without benthic macrofauna are restricted to the central part of the OMZ (300 - 900 m) (von Rad et al., 1995; Schulz et al., 1996; Parulekar et al., 1982). Clear evidence of benthic reworking near the base of the OMZ (~1000 m) is also reported by Smallwood and Wolff (2000), who studied molecular characteristics of OM. Accordingly, some bioturbation below 900 m has to be assumed, indicating that the abrupt drop in cyst ARs below 1254 m is probably not primarily caused by bioturbation. This is confirmed by the results of Meadows et al. (2000), who suggest that microbiological rather than macrobenthic activity is the main biological driving force for the geochemical processes on the Oman slope.

On the other hand, there was evidence of enhanced bioturbation at the OMZ boundary on the NE Pacific slope (Mullins et al., 1985). Smith et al. (2000) and Levin et al. (2000) expected a similar situation in the Arabian Sea at the lower boundary of the OMZ, where BWO concentrations just exceed the lower limits of burrowing and bioturbating fauna, and faunal densities could be enhanced by relatively undegraded organic matter sinking from the OMZ. However, the data of both studies did not support this hypothesis. Levin et al. (2000) observed an increasing proportion of subsurface-feeding and omnivorous taxa below 850 m, and dwelling-mode patterns shifted from tube or mudball builders at stations between 400 and 1000 m to burrowing forms at 1250 and 3400 m, but there was no clear enhancement of bioturbation (Smith et al., 2000). It seems plausible that increased burrowing activity below 1250 m catalyses cyst fragmentation and dissolution. However, a similar effect can be expected within guts of surface-feeding organisms within the OMZ. In fact, Levin et al. (2000) report elevated macrobenthos density and biomass at stations within the OMZ at the Oman Margin and a dominance of the low diverse assemblage by surface-feeding polychaetes. This feeding strategy does not produce particularly intense vertical mixing and could explain the substantially reduced mixed layer in the Arabian Sea OMZ as inferred from ^{210}Pb mixing (Smith et al., 2000). Hence, there could be a comparable effect of surface-deposit feeders within the OMZ and of increased bioturbation below the OMZ on the fragmentation and dissolution of calcite particles, which would indicate that benthic reworking may influence the preservation of cysts but is not the controlling factor for the observed cyst AR patterns.

Increased burrowing activity below the OMZ, however, influences the penetration depth of oxygen into the sediment pore waters which, together with sedimentation rates, determines oxygen exposure times for accumulating particles. Lee et al. (1998) studied sediment trap material from the NE and central Arabian Sea and conclude that the influence of processes at the sediment/water interface on the proportion of primary production preserved in the sediment increases offshore relative to upper water column processes. They regard sedimentation rate and sediment oxygen content to be the major factors that control carbon preservation in this region. Similar conclusions were drawn from the results of a study on amino acids in surface sediments from the Pakistan continental margin, which suggest that productivity-related OM input, bulk accumulation rate and BWO influence the alteration of sedimentary OM by controlling its oxygen exposure time (Suthof et al., 2000). The latter can be determined by dividing the depth of oxygen penetration by linear sedimentation rate (Hartnett et al., 1998).

At the studied sites very low oxygen penetration depths of only 1 to 5 mm were measured, even below the OMZ (W.J. Zachariasse, pers. comm.). A reason for this could be that the increased flux of labile OM from the OMZ enhances the sediment oxygen demand, thereby shoaling the oxygen penetration depth (Smith et al., 2000). The importance of sedimentation rates for OM preservation should be generally decreasing with decreasing BWO concentrations (in extreme the oxygen exposure time would be zero if BWO is zero, irrespective of sedimentation rate). Accordingly, OM degradation within and near the OMZ should be controlled by BWO levels rather than by sedimentation rates. With increasing water depth an increasing influence of oxygen exposure time can be expected because enhanced bioturbation and stronger oxygen gradients due to higher BWO levels result in larger oxygen penetration depths, combined with lower sedimentation rates.

The observed abrupt drop in cyst-ARs below the OMZ is in contrast to the continuously decreasing sedimentation rates along the transect and is therefore thought to be largely caused by decreased OM degradation under low BWO conditions. This conclusion is supported by pollen ARs of the same samples (unpublished data) which for some species show a similar drop at the same depth whereas ARs of other (presumably more labile) species decrease already at 1000 m depth. The data of pollen and dinoflagellate cyst ARs could indicate that there is a critical depth between 1200 and 1500 m, shifting the system of OM preservation from a mainly "BWO-control" within and near the OMZ to an increased "control by sedimentation rates" (reinforced by bioturbation) in greater water depths. This hypothesis is strengthened by the results of Suthof et al. (2000) who state that there is no overall control of oxygen exposure time on OM preservation, and that BWO appears to be the dominating factor especially in the central part of the OMZ.

Whatever the importance of the individual factors for OM preservation, the distribution of cyst ARs and cyst fragmentation suggest that processes are favouring calcite preservation within the OMZ of the NE Arabian Sea. That carbonate dissolution is a major process in the deep Arabian Sea was shown in a numerical model of benthic processes by Luff et al. (2000). Their model yields dissolution of 52-83% of the carbonate rain to the seafloor which is in good agreement with the 50% (*L. granifera*) to 84% (*T. heimii*) drop in cyst ARs below the OMZ, which also hints to strongly reduced carbonate dissolution within the OMZ.

SW Arabian Sea

When comparing the cyst ARs in the SW Arabian Sea with that of the NE Arabian Sea, the most obvious difference is the lack of an abrupt drop of cyst AR at the lower boundary of the OMZ in the Somali profile and the relatively low cyst AR within the OMZ (Figs. 2C, D, 3B). As the studied area off Somalia is characterised by coastal upwelling and by a steep continental slope, gradients of ecological parameters as well as horizontal transport in the water column or due to re-suspension of sediment have to be taken into account when interpreting the cyst AR patterns. The transect is overrun by large gyres such as the Great Whirl, which transport large quantities of coastal upwelled water offshore (Fischer et al., 1996; van Weering et al., 1997). Broerse et al. (2000) recorded a strong upwelling signal of coccolithophores in a sediment trap outside the zone of coastal upwelling (station 915) caused by offshore transport of upwelled water along the gyre margins. Zonneveld and Brummer (2000) studied organic-walled dinoflagellate cysts in sediment traps that were moored at stations 905 and 915 of the Somali transect. They found no evidence for considerable lateral relocation of these cysts during transport to the sea floor and suggested that mechanisms such as incorporation in faecal pellets or flocculation of sediment particles increased the sinking velocities of the cysts. These processes might also be assumed for the calcareous cysts, especially during high, pulse-like primary production in the summer. Conan and Brummer (2000) found remarkably similar species composition of foraminifers at station 905 in the core top and in a sediment trap, moored 268 m above the sea floor at the same station, and conclude that there is no alteration of the primary signal by carbonate dissolution or winnowing.

Comparing the two sediment traps at station 905 and 915, some transport is thought to have affected the trap at station 905 but not at 915 (van Weering et al., 1997; Zonneveld and Brummer, 2000). However, sediment cores from the investigated stations reveal undisturbed, relatively high sedimentation at the upper slope (down to station 905) although cores at 907-915 contain numerous turbidite intervals (van Weering, 1997). While sediment re-deposition seems to play only a minor role at the upper slope, it seems likely that at the deeper stations mass wasting derived from the lower slope and turbidites may be deposited occasionally, extending far into the Somali Basin. Evidence for such a mass transport is, however, not reflected in the sediment trap material or in the studied surface sediments.

As mentioned before, the continental slope off Somalia is relatively steep, so the two samples laying within the OMZ are situated close to the coast below the active zone of coastal upwelling. The related turbulence in the upper water column is unfavourable for the development of phytoplankton (including calcareous dinoflagellates) since it hampers the build up of a standing stock in the photic zone. This could be one reason for the lower cyst ARs in the upper samples, even though they are influenced by low-oxic conditions at the sediment/water interface. Another possibility would be that early diagenetic processes off Somalia differ from those in the NE Arabian Sea as a result of the higher rate of OM decay in the more aerated western Arabian Sea (Slater and Kroopnick, 1984; Paropkari et al., 1992). During the Netherlands Indian Ocean Program 1992-1993, nitrite maxima were not found associated with the oxygen minima off Somalia (van Weering et al., 1997) and oxygen concentrations never dropped low enough to allow for N_2O cycling by denitrification (de Wilde and Helder, 1997). This could indicate that OM degradation by oxic respiration plays a larger role in the western Arabian Sea compared to the north-eastern part. However, it is not clear whether oxic OM degradation really enhances calcite dissolution within the OMZ off Somalia since the efficiency of calcite dissolution by metabolic CO_2 depends not only on the oxidation rate of OM but also on the organic carbon to calcium carbonate rain ratio at the sediment surface and on the saturation state of bottom water with respect to calcite (Emerson and Bender, 1981; Milliman et al., 1999; Schneider et al., 2000). Both parameters are more favourable for calcite preservation off Somalia than in the NE Arabian Sea since the sediment flux in the Somali transect is strongly dominated by $CaCO_3$ (van Weering et al., 1997, Koning et al., 1997). Local bottom water, being younger than that in the NE Arabian Sea, should be less undersaturated with respect to CO_3^{2-}. This inference is strengthened by the fact that in the Somali profile, no relation of cyst fragmentation to BWO was found (Fig. 5D). So, while it is possible that some calcite dissolution occurs within the OMZ off Somalia, the most straightforward explanation for the observed distribution pattern is that lower cyst production within the zone of active upwelling is directly reflected in the underlying sediments.

Since too much turbulence can hamper the development of a standing stock of phototrophic organisms, the highest primary production can generally be expected slightly more offshore from the zone of active upwelling - in horizontally advected, upwelled water with lower turbulence. Primary production then decreases rapidly towards the open ocean as nutrient levels decrease. However, dinoflagellates that produce calcareous cysts also seem to be successful in low-nutrient environments, as shown by high cyst abundances in oligotrophic, open oceanic regions of the Atlantic Ocean (Zonneveld et al, 2000), and by the generally negative correlation of cyst abundance with proxies indicating high primary productivity in sediment cores (Höll et al., 1998, 1999; Esper et al., 2000; Vink et al., 2001). This relationship would cause a further offshore shift of maximal cyst production off Somalia and also could explain the high cyst ARs below the OMZ (and the lack of cyst AR drop at the lower OMZ boundary in this region), without invoking down-slope reworking. According to Troelstra et al. (1995), calcite dissolution off Somalia starts strongly below 3500 m depth. Consequently, the very low cyst ARs at the two deepest stations (3572 m and 4035 m; Fig. 2C, D), and the slightly elevated percentage of fragmentation of *T. heimii* (>5%) in the deepest sample (Fig. 5D), are thought to result largely from calcite dissolution due to deep water undersaturation, probably further enhanced by aerobic decay of OM. The latter can be expected to be very effective at these stations since they are sites with low sedimentation rates and thus long oxygen exposure times.

We conclude that the cyst ARs in the surface sediments of the Somali slope reflect horizontal gradients in primary cyst production caused by coastal upwelling, which seems to outweigh early diagenetic overprinting, whereas calcite dissolution becomes the dominating factor in the Somali Basin (below 3500 m).

Species-selective preservation

As discussed above, the large difference in cyst ARs within and below the OMZ in the NE Arabian Sea is mainly the result of differential calcite dissolution during early diagenetic processes. This gives us the opportunity to assess the impact of dissolution on cysts of the individual species. For this purpose, two samples from the Indus Fan profile are compared: one at 1254 m depth (base of the OMZ) just above the distinct drop of cyst AR and one at 1555 m depth, just below the cyst AR drop (Fig. 2A and B).

The large loss which is recorded for *T. heimii* and *C. sp.* 1 (Fig. 3A) could indicate that these two species are more sensitive to dissolution than the other species. If true, this should also be reflected in their relative abundance and percentage of fragmentation. From Fig. 4 (left) it can be inferred that *T. heimii* and *C. sp.* 1 indeed exhibit higher relative abundances in all samples from within the OMZ than from those below it. Strong sensitivity to dissolution of these two species can also be inferred from their fragmentation relative to BWO (Fig. 5A, B), with a high cyst AR and a low percentage of fragments in samples from within the OMZ (black dots), and a low cyst AR with a higher percentage of fragments in samples from below the OMZ (grey dots). The pattern for *T. heimii* is confirmed by the relationship between fragmentation and cyst per gram values in additional samples from the NE Arabian Sea (Fig. 6).

No significant changes of relative abundance and fragmentation with water depth occur for *C. albatrosianum* (Fig. 4, left and Fig. 5C). *L. granifera*, which shows the lowest loss at the OMZ boundary of the Indus Fan profile (Fig. 3A), has a lower relative abundance in all samples from within the OMZ (Fig. 4, left). This indicates that *L. granifera* is less sensitive to calcite dissolution than the other species. Thus, we conclude from the cyst ARs and relative abundances in the NE Arabian Sea that species-selective preservation of calcareous dinoflagellate cysts does occur, with *T. heimii* being most dissolution sensitive, followed by *C. sp.* 1, the spiny cysts, *C. albatrosianum* and finally by *L. granifera* which seems to be the most dissolution resistant.

Reasons for species-selective calcite dissolution can be differences in the chemical composition of the cysts and/or a different surface to volume ratio of calcite. This ratio is determined by the size and shape of the individual calcite crystals and by the size of the cyst itself. We found that the cysts of the species discussed in this paper are composed of low-magnesium calcite. However, slight differences in chemical composition such as different organic compounds between and/or within the crystals cannot be excluded and may have an influence on the dissolution sensitivity. Further work is needed to clarify this point. A clear difference between *T. heimii* and the other species is the much smaller size of *T. heimii* (about 10 - 20 µm compared to 20 - 45 µm of the other cysts), which could explain the higher dissolution sensitivity of this species. However, its percentage of fragmentation is generally much lower as compared to the other species (Fig. 5). This could be explained by the different wall structures. The crystals of *T. heimii* appear to be rather compact compared to the irregularly shaped crystals of *C. sp.* 1 and the spiny cysts, which are sometimes only loosely attached to each other or to an organic layer beneath. This makes them sensitive to mechanical destruction, especially after decomposition of the organic layer has occurred. The cysts of *C. albatrosianum*, with their net-like crystal structure arranged in rosettes also seem to be more susceptible to mechanical fragmentation than to dissolution. This difference could explain its relatively high percentage of fragmentation and the small difference between samples from within and below the OMZ (Fig. 5C). The comparably small susceptibility to dissolution of *L. granifera* is possibly due to its relatively thick and compact wall structure composed of small, tightly packed calcite crystals.

Summary

The data presented in this paper arise from the first investigation of calcareous dinoflagellate cysts and their preservation under different oxygen levels in the Arabian Sea. Distinct differences in the relation of cyst accumulation rates (ARs) and bottom water oxygen (BWO) were observed between the NE and SW of the studied area. In the NE Arabian Sea, higher cyst ARs within the OMZ indicate reduced calcite dissolution, most likely due to lower production rates of metabolic CO_2. Below the OMZ, increased bioturbation, longer oxygen exposure times and probably H_2S oxidation lead to enhanced calcite dissolution of 50-84% compared to the OMZ. All investigated species are affected by dissolution, though not to the same degree. The different percentages of AR decrease at the lower boundary of the OMZ of the individual species, and differences in relative abundance and fragmentation, point to species-selective preservation. This can be explained by differences in the size and wall structure of the cysts. *Thoracosphaera heimii* has the smallest size and seems to be most affected by calcite dissolution. In the SW Arabian Sea, the patterns of cyst AR reveal no relation to the OMZ and are most likely dominated by horizontal differences in primary cyst production caused by coastal upwelling. Samples from below 3500 m depth are strongly influenced by calcite dissolution due to deep water undersaturation.

The results show that within one basin such as the highly productive Arabian Sea, differences in early diagenetic processes can lead to the preservation of a signal that is either dominated by primary production or by secondary alteration, although in both areas an oxygen depleted zone is present. Further studies on well-dated sediments are necessary for the calculation of sediment flux rates, as are geochemical measurements to improve our understanding of the secondary alteration of primary ecological signals.

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Appendix 1: Absolute abundance (cysts/g)

sample	*T. heimii*	*L. granifera*	*C. albatrosianum*	*C. sp.* 1	spiny cysts
902	210943	17409	6104	5426	5426
903	743739	34974	13601	20725	7124
904	1549934	83297	20548	18559	8617
905	3693827	108473	55236	42239	13997
906	4044065	69415	51883	33404	13504
907	3078704	61728	61343	41281	12731
908	1158358	23636	50924	24495	10314
915	435524	16783	24336	6713	4196
451	485103	173955	23787	4325	1442
452	146951	133260	17707	548	3834
453	168002	114049	14423	3205	2404
454	945864	204359	45700	14764	6328
455	769420	186190	34032	9618	8138
463	1764779	317437	60358	20864	5961
464	378735	47423	12343	2599	2599
466	57218	77465	11092	0	6514

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3. Calcareous dinoflagellates - ecology and aspects of preservation in a highly productive oceanic region

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Abstract

Absolute and relative abundance of calcareous dinoflagellate cysts in surface sediment samples from the Arabian Sea are compared with environmental parameters of the upper 100 m of the water column to gain information on the largely unknown ecology of the individual species. Ten species/morphotypes were encountered of which four occurred only accessory. On the basis of the distribution patterns of the six more abundant species/morphotypes, the studied area is subdivided into three provinces, whereby a clear relation to monsoon-controlled upper ocean conditions is evident. The two dominating species *T. heimii* and *L. granifera* show opposite trends in distribution of absolute and relative abundance. In the NE Arabian Sea, low abundance of *T. heimii* is mainly attributed to enhanced dissolution of the small shells in this region, whereas elevated concentrations of *L. granifera* seem to be related to higher water temperatures and the influence of the Indus River. *C. albatrosianum* and *C. operosum* are most abundant in the open ocean, associated with lower nutrient levels, relatively high temperatures and low seasonality. Spiny cyst (mainly represented by *S. trochoidea*), in contrast, exhibit a more shelf-ward distribution and are most abundant in regions which are influenced by coastal upwelling, characterized by eutrophic and rather unstable conditions with seasonally lower temperatures and a shallow thermocline. A generally negative correlation of calcareous dinoflagellate cysts to primary productivity or high nutrient concentrations, as was proposed by other authors, cannot be confirmed. Cyst accumulation rates off Somalia show that strong turbulence and high current speeds are unfavourable for calcareous dinoflagellates which is encouraging the belief that these organisms are more successful under rather stratified conditions.

Introduction

Dinoflagellates represent one of the major phytoplankton groups in the oceans. Some species produce a fossilizable calcareous stage as part of their life cycle and are hereafter referred to as calcareous dinoflagellates. They are phototrophic and thus inhabit the photic zone. First studies on calcareous dinoflagellate cysts in sediment cores from the Atlantic Ocean revealed distinct changes in absolute and relative cyst abundance over time, and the comparison of these data with other proxies gave valuable information on the (palaeo)ecological significance of this organism group (Höll et al. 1998, 1999; Höll & Kemle-von Mücke 2000; Esper et al. 2000; Vink et al. 2001 a; Vink et al. 2001 b). The application of calcareous dinoflagellate cysts for the reconstruction of environmental changes requires knowledge on the ecological preferences of the individual species. However, detailed ecological information - particularly from high productive areas - is still sparse. In order to improve the use of calcareous dinoflagellate cysts as palaeo-environmental proxy we studied surface sediment samples from different parts of the Arabian Sea. This high productive oceanic region is characterized by strong seasonality in atmospheric and oceanic conditions and provides a wide spectrum of environmental settings which can be compared to cyst distribution patterns.

Climatic and oceanographic setting

The climatic and oceanographic processes in the Arabian Sea are largely determined by strong Monsoon winds which reverse semi-annually due to the shifting position of the Inter Tropical Convergence Zone (ITCZ), following the region of maximum solar heating. During summer, differential heating over the continents and the Indian Ocean creates a pressure gradient between Central Asia and the area of high atmospheric pressure over the relatively cool southern Indian Ocean. This gradient results in a strong, topographically steered south-westerly wind (SW Monsoon), which from May to September forms a strong low-level jet stream (also called the Findlater Jet; Findlater 1971) and extends across the Arabian Sea parallel to the coast of the Arabian Peninsula. The ocean reacts with the formation of approximately clockwise surface currents (Wyrtki 1971; Shetye et al. 1994; Shi et al. 1999) including the very strong Somali Boundary Current. A prominent feature of this current is the development of clockwise rotating eddies (Bruce 1979; Schott 1983) that move north to north-east at the end of the SW

Monsoon (Schott 1983; Fisher et al. 1996). The large 'prime' eddy is sometimes referred to as the "great whirl" (Swallow & Bruce 1966). Recent measurements based on acoustic Doppler current profiler and near-surface drifter tracks do not reveal a continuous flow pattern from the SW Monsoon current off Somalia into the northern Arabian Sea along the Arabian coast but an eastward transport of upper water masses south of 15°N and a strong dominance of upper ocean currents in the northern Arabian Sea by large eddies (Molinari et al. 1990; Flagg & Kim 1998; Elliot & Savidge 1990). The strong north-eastward alongshore current at the Arabian peninsula (East Arabian Current) leaves the coast as a jet at Ras al Hadd (Böhm et al. 1999) where it meets the warmer and saltier water which is carried southward out of the Gulf of Oman, forming a strong near-surface temperature-salinity front (Lee et al. 2000). Ekman dynamics lead to coastal upwelling along the Somali and Arabian coasts, introducing cold, nutrient rich water into the photic zone (e.g. Sastry & D'Souza 1972; Currie et al. 1973; Bruce 1974; Prell & Curry 1981; Prell & Streeter 1982) which raises primary productivity (e.g. Quraishee 1988; Brock et al. 1992; Smith et al. 1998). Coastal filaments, which are colder and fresher than their surroundings, carry nutrient-rich, highly productive waters into the central basin (Keen et al. 1997; Manghnani et al. 1998; Arnone et al. 1998; Lendt et al. 1999; Lee et al. 2000). Inshore of the wind-stress maximum (north-west of the Findlater Jet axis) open oceanic upwelling occurs (e.g. Smith & Bottero 1977; Brock et al. 1992). Both, offshore advection of coastally upwelled water and upward Ekman pumping counter the wind-driven entrainment and maintain upper ocean stratification in this region (Lee et al. 2000). Deepening of the mixed-layer in the central Arabian Sea (south-east of the Findlater Jet axis) is attributed to convergence in the Ekman layer caused by negative wind-stress curl (Rao et al. 1989; Bauer et al. 1991), and to wind-driven entrainment (Lee et al. 2000). The SW Monsoon drives strong evaporative salinity enhancement in the central basin, whereas the upwelling waters near the coasts are relatively fresh, resulting in a salinity gradient in the upper water layers. The mixed-layer waters cool and freshen during fall inter-monsoon. This period is characterized by variable to northward surface currents, shoaling of pycnoclines and very shallow mixed-layers (e.g. Dickey et al. 1998; Lee et al. 2000).

During winter, low solar insolation and increased albedo, due to the seasonal snow cover, cause high atmospheric pressure over Central Asia. The now reversed pressure gradient between Central Asia and the ITCZ at about 10°S force the dry and cold north-east (NE) Monsoon with generally lower wind stress magnitudes (2 dyne/cm^2) compared to the SW Monsoon (6 dyne/cm^2, Shetye et al. 1994). Also the mean basin-wide flow of surface currents reverse during the NE Monsoon to approximately anti-clockwise (Wyrtki 1971; Shetye et al. 1994; Shi et al. 1999). Lee et al. (2000) observed southward currents along the Omani coast and generally northward flowing mid-basin currents. The NE Monsoon leads to cooling of the surface waters, especially in the north-east of the basin, which results in deep vertical mixing and dramatic deepening of the mixed-layer with distance offshore (Bauer et al. 1991; Lee et al. 2000). Stratification is stronger at the base of the shallower mixed-layers near the coast than beneath deep mid-basin mixed-layers (Lee et al. 2000). Surface water salinity is enhanced in the central basin and in the northern Arabian Sea, due to evaporation driven by the NE Monsoon and advection of high saline Gulf of Oman water, respectively (Lee et al. 2000; Wiggert et al. 2000). The cool and salty surface water drives convective overturning which causes repletion of the upper layers

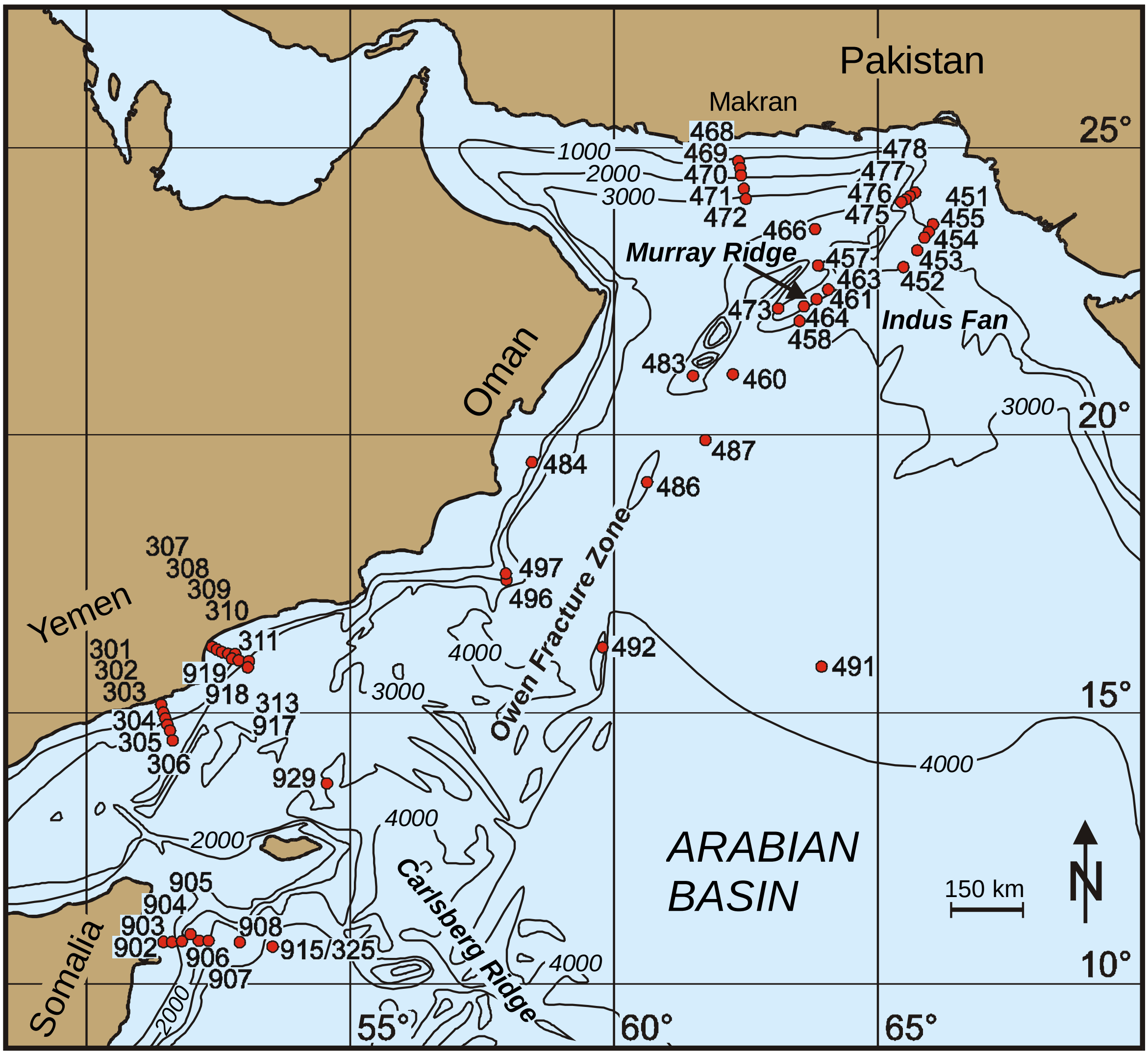

Fig. 1. Studied area and sample locations.

with nutrients and stimulates primary production especially in the north-eastern part of the Arabian Sea (Banse & McClain 1986; Madhupratap et al. 1996; Dickey et al. 1998; Smith et al. 1998; Weller et al. 1998). During spring inter-monsoon, weakened wind forcing and strong surface heating lead to warming and re-stratification of the upper water layers and to shoaling of the mixed-layer from depths of up to 120 m in February to about 20 m in April (Gardner et al. 1999; Lee et al. 2000). Small mixed-layer variations limit the mixing of nutrients into the surface layer, thus maintaining oligotrophic conditions and low primary production with a subsurface chlorophyll maximum during this period (Gardner et al. 1999).

Except for spring inter-monsoon, the surface waters in the Arabian Sea are very fertile, especially in the north-eastern part of the basin and off the Somali and Arabian coasts (Fig. 2), which makes the Arabian Sea one of the worlds most productive oceanic provinces (Ryther et al. 1966). Apart from upwelling processes and convective overturning, further sources of nutrients are the Indus River discharge and deposition of aerosols. Recycling of large amounts of organic matter in combination with reduced mid-water aeration create a permanent and intense oxygen minimum zone (OMZ) which is a characteristic feature of the Arabian Sea. The oxygen deficient zone impinges on the continental slopes of the surrounding landmasses at water depths ranging from 200 - 1200 m (e.g. von Rad et al. 1995), whereby the eastern Arabian Sea exhibits lower oxygen concentrations than the western region at the same latitude (Slater & Kroopnick 1984; Paropkari et al. 1992). In the cruise report of the Netherlands Indian Ocean Programme (NIOP) it is concluded "that the contrast between the two monsoon periods is very marked in the upper 100 m of the water column, and that there are hardly differences below 150 m depth" (van Hinte et al. 1995).

Material and methods

Fifty five surface sediment samples from the Arabian Sea (Fig. 1) were analysed for their content of calcareous dinoflagellate cysts. The samples represent the upper centimetre of box cores that were recovered during the Netherlands Indian Ocean Program 1992-1993. For details on positions and water depths see App. 2. Ca. 0,5 g of the dried sediment was weighted and disintegrated in water (containing a few drops of ammonia to prevent calcite dissolution) by ultrasound treatment of < 1 minute. The sediment was subsequently sieved over 63 µm- and 20 µm stainless steel sieves to concentrate the larger cysts. The <20 µm and 20 - 63 µm fractions were concentrated to 100 ml and 15 ml of water, respectively. A split (50 µl or 100 µl) of the homogenized material of the two fractions was separately placed on a cover slip, dried in an oven or on a heating plate and finally fixed with Spurr's resin. For more detailed information on the preparation method see Vink et al. (2000).

The cysts were counted under a light microscope using polarized light (Janofske 1996). At least one slide per fraction and sample was scanned. If there were less than 200 specimens in one slide of each fraction then additional slides were analysed. The species discussed in the present paper are illustrated in Plate 1, and a list of their new generic attribution is given in App. 1. The spiny cysts in the studied sediments show a large morphological variety regarding shape and size of the cyst as well as shape and number of calcite crystals and spines. Most spiny cysts in the studied material appeared to belong to *Scrippsiella trochoidea* but the group may also contain *Scrippsiella regalis* (and possibly other spiny cysts which are not described jet). A clear separation of the different species of spiny cysts under the light microscope was often not possible due to organic matter between the spines hiding the characteristic shape of the calcite crystals.

Absolute abundance (in cysts/g of dry sediment, App. 2) and cyst accumulation rates (cyst AR, in cysts/cm^{2}ka) were calculated as described in Chapter 2. Furthermore, the relative abundance of each species/morphotype was calculated. Two species, *Thoracosphaera heimii* and *Leonella granifera*, clearly dominate the association, and their relative abundance is given in percent of the whole association. For the less abundant species/morphotypes, the relative abundance is based on the association excluding the two dominating species. The geographic distributions of absolute and relative abundance of each species are illustrated in Figs. 3-8. The chosen limits for dot sizes are based on natural brakes. The distribution patterns of the individual species/morphotypes have been visually compared with physical parameters in the upper 100 m of the water column in five standard water depths:

0 m:	mean of values from 0 m - 5 m depth
25 m:	mean of values from 20 m - 30 m depth
50 m:	mean of values from 45 m - 55 m depth
75 m:	mean of values from 70 m - 80 m depth
100 m:	mean of values from 95 m - 105 m depth

during four different periods:

NE Monsoon: December - February
spring inter-monsoon: March - May
SW Monsoon: June - September
fall inter-monsoon: October - November

Mean temperature and salinity values for the last 92 years of one degree latitude and longitude square blocks are obtained from the National Oceanographic Data Center, Washington, DC. Density and Brunt-Väsälä frequency (as a measure of stratification) was calculated as in Vink et al. (2000). In the comparison of cyst distributions with environmental parameters we pay special attention to conditions in water depths between 50 and 100 m since field and laboratory studies indicate that *T. heimii* and possibly also the other species are adapted to low irradiance conditions and preferentially inhabit the lower part of the photic zone (Karwath et al. 2000 c; Janofske & Karwath 2000).

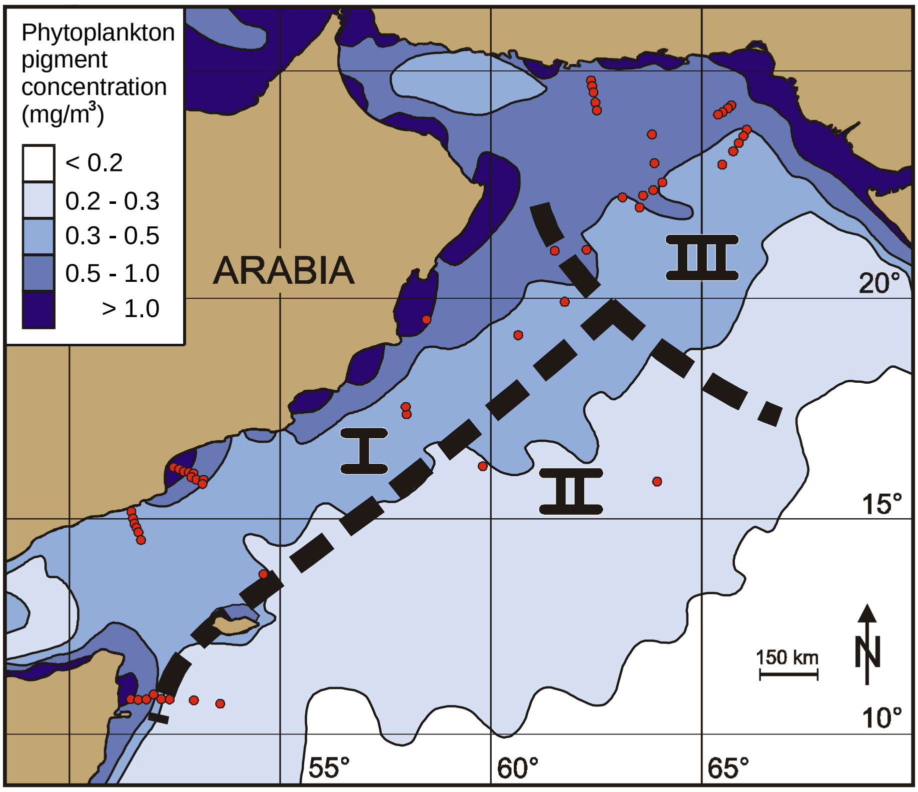

Fig. 2. Map showing sample locations in relation to phytoplankton pigment concentrations (mg/m^3; after composite satellite images over 8 years from NASA/GSFC) which reflect nutrient supply in surface waters. Black dashed line separates three provinces (I-III) based on distribution patterns of calcareous dinoflagellate cysts, and divides the Arabian Sea into a north-eastern (III) and a south-western part (I and II) as used in this paper.

Results

All of the investigated samples contained calcareous dinoflagellate cysts. Of the ten species recovered only six occurred in significant concentrations: *Thoracosphaera heimii, Leonella granifera*, *Calciodinellum albatrosianum*, *Calciodinellum sp.* 1, group of spiny cysts (mainly *Scrippsiella trochoidea*) and *Calciodinellum operosum*. These species were found throughout the whole Arabian Sea in varying concentrations. The four rare species (App. 3) do not have distinct distribution patterns, except for *Pernambugia tuberosa*, which was found only near the Gulf of Aden.

Highest total cyst concentrations of up to 4 million cysts/g were seen off Somalia and on the Murray Ridge, in water depths between 900 and 2000 m. Low cyst concentrations were observed in samples from the Makran Margin, in the shallowest samples off Yemen, Somalia and Oman and in samples below 1500 m in the NE Arabian Sea (Figs. 3-8). In most samples, the association is clearly dominated by *T. heimii* (Fig. 3B). The second most abundant species is *L. granifera* with maximal 51% (Fig. 4B). Together, these two species form 76-98% of the association.

Distribution of individual species

T. heimii

High absolute and relative abundance of *T. heimii* was found mainly in the SW Arabian Sea (Fig. 3). In the NE of the basin, some elevated values occur on the Murray Ridge and on the Indus Fan, in water depths shallower than 1300 m. Fragmentation of this species is high (up to 22% of total specimens) in those samples with low absolute and relative abundance, namely in the NE Arabian Sea except for samples from water depths shallower than 1300 m (Fig. 9). The percentage of fragments is low (mainly 1-3%, maximal 7%) in the SW of the area. The ratio other species : *T. heimii* in the SW Arabian Sea decreases from the shallow samples towards water depths of 1000 m and remains low down to 3000 m to slightly increase again below that depth (Fig. 10A). In the NE, this ratio is generally higher than in the SW and shows a drastic increase below 1500 m depth (Fig. 10B).

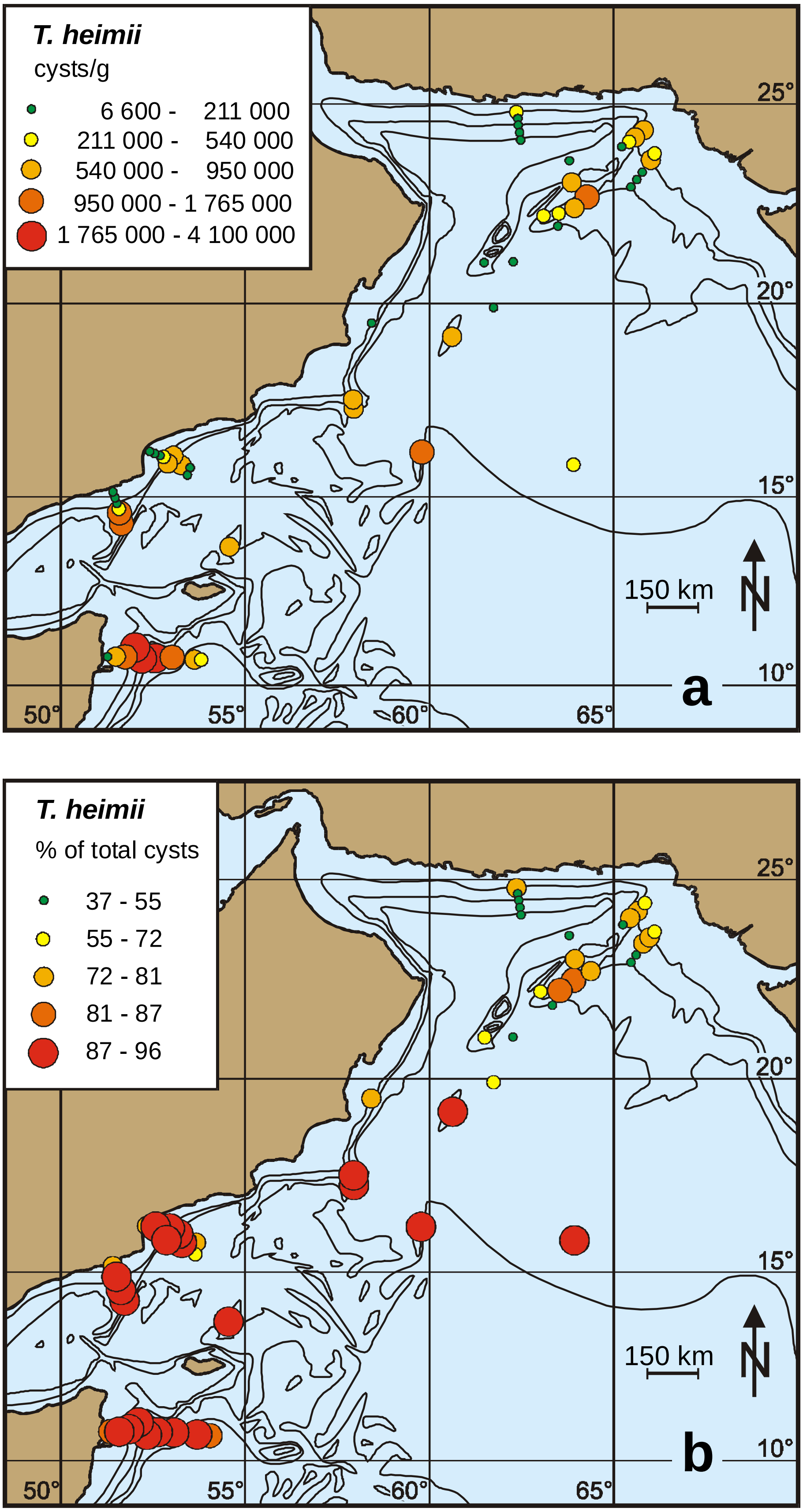

Fig. 3. Surface sediment distribution map of *Thoracosphaera heimii*. (a) absolute abundance, (b) relative abundance (percent of whole association).

L. granifera

In contrast to *T. heimii*, *L. granifera* has high absolute and relative abundance only in the NE Arabian Sea, with exception of the Makran Margin, where high relative but low absolute abundances are found (Fig. 4).

C. sp. 1

The distribution pattern of *C. sp.* 1 is comparable to that of *T. heimii*, with generally higher concentrations in the SW of the area (Fig. 5). It also shows elevated values in the samples from water depths shallower than 1300 m on the Murray Ridge and on the Indus Fan. High relative abundances are seen especially off Yemen and Somalia.

C. albatrosianum

C. albatrosianum is generally more abundant in the open ocean and in the NE of the Arabian Sea, whereas low concentrations and relative abundance can be observed close to the Somali and Arabian coasts (Fig. 6).

C. operosum

The distribution pattern of *C. operosum* is similar to that of *C. albatrosianum*, with higher absolute and relative abundances in the open ocean and in the NE Arabian Sea (Fig. 7).

Spiny cysts

In contrast to *C. albatrosianum*, the spiny cysts are less abundant in samples from the open ocean (Fig. 8). Their absolute and relative abundance is especially high offshore Oman (Owen Ridge area) and off Somalia and Yemen.

Cyst accumulation rate (AR)

The correction of cyst concentrations for sedimentation rates along the Indus Fan- and Somali profile results in a relative increase of values near the coast, a decrease at deeper stations and a slight shift of maximal concentrations towards shallower water depths, whereby the general shape of the curve does not change significantly (Fig. 11).

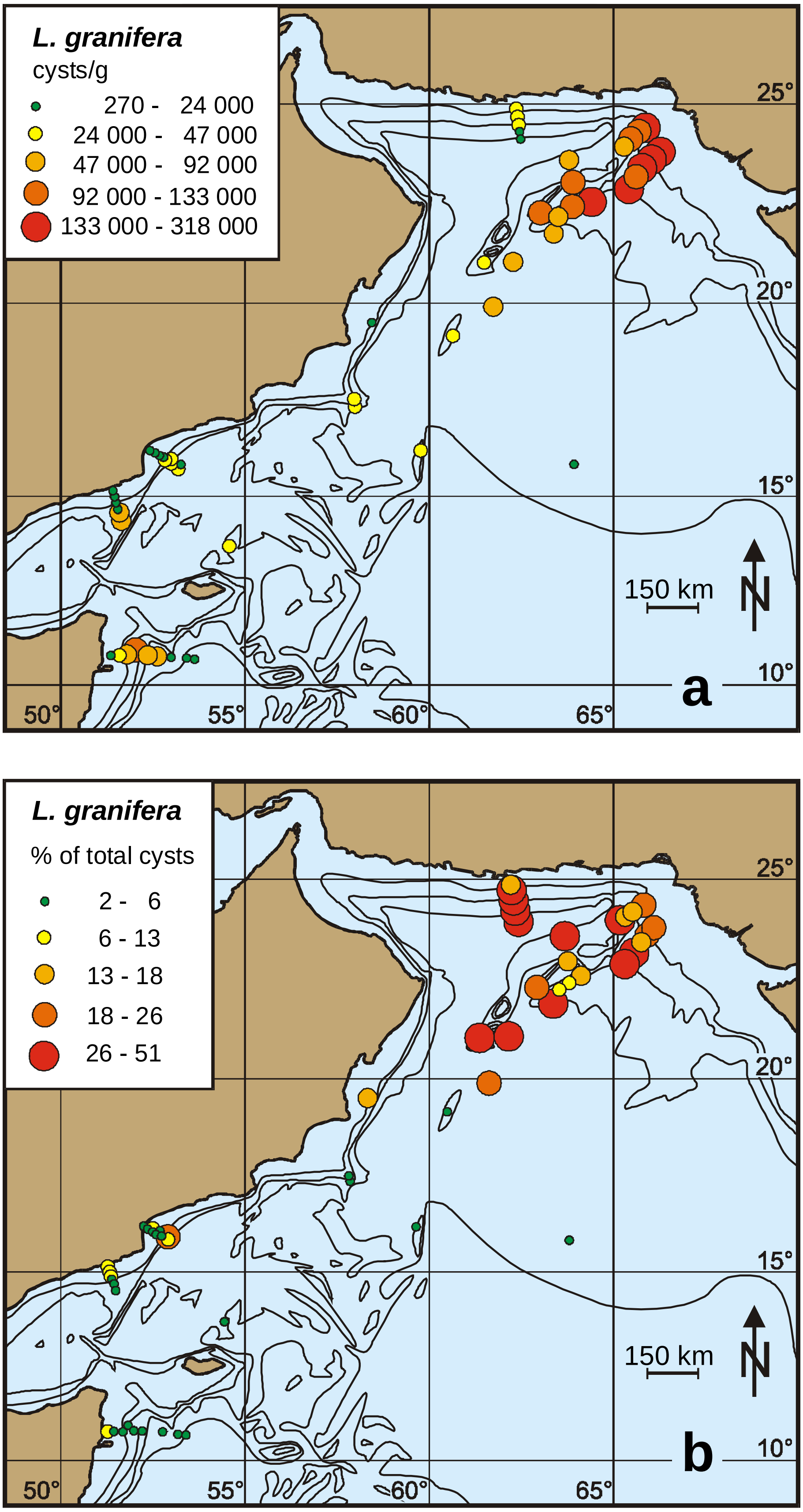

Fig. 4. Surface sediment distribution map of *Leonella granifera*. (a) absolute abundance, (b) relative abundance (percent of whole association).

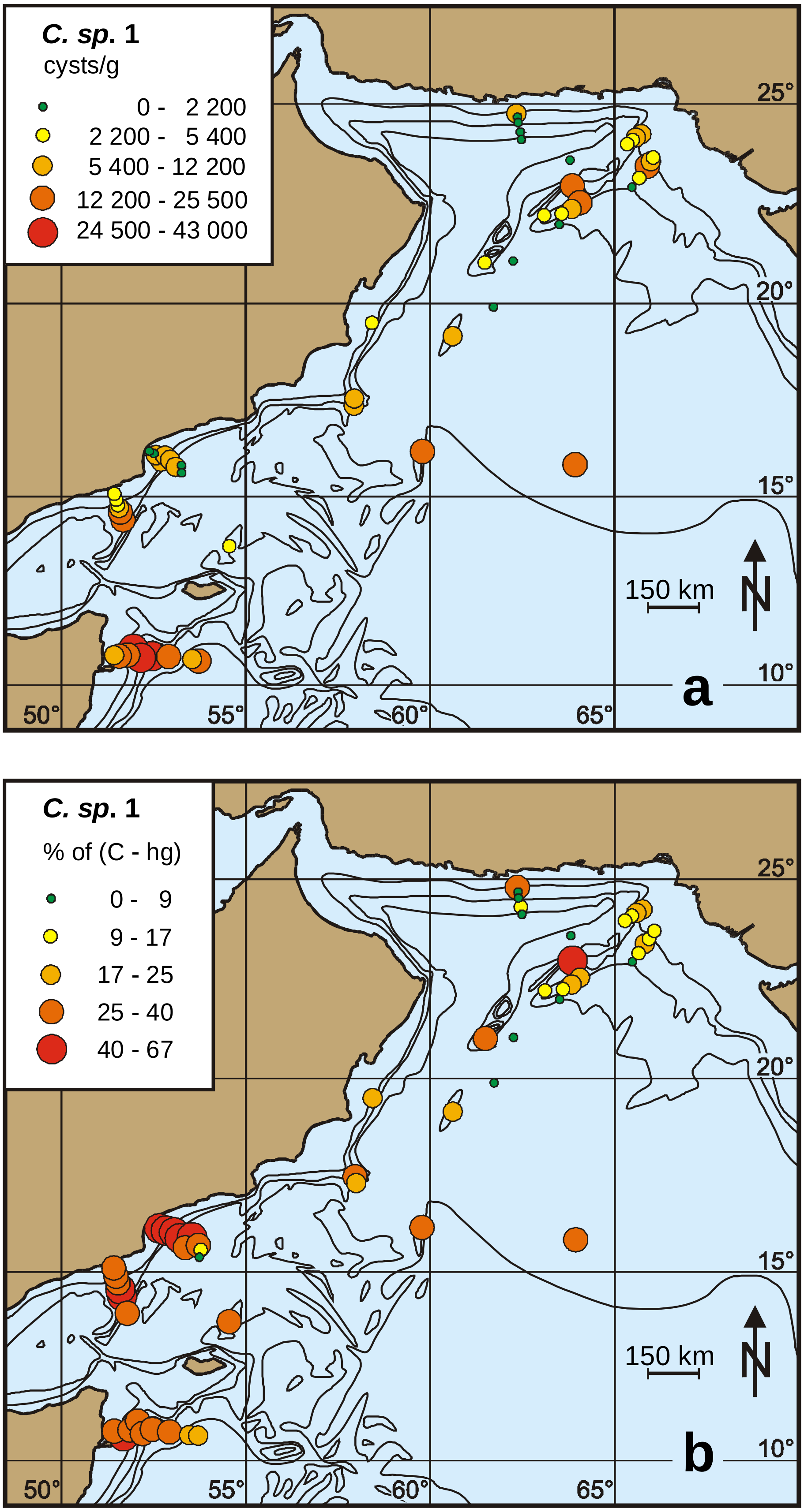

Fig. 5. Surface sediment distribution map of *Calciodinellum sp.* 1. (a) absolute abundance, (b) relative abundance (percent of association excluding *T. heimii* and *L. granifera*).

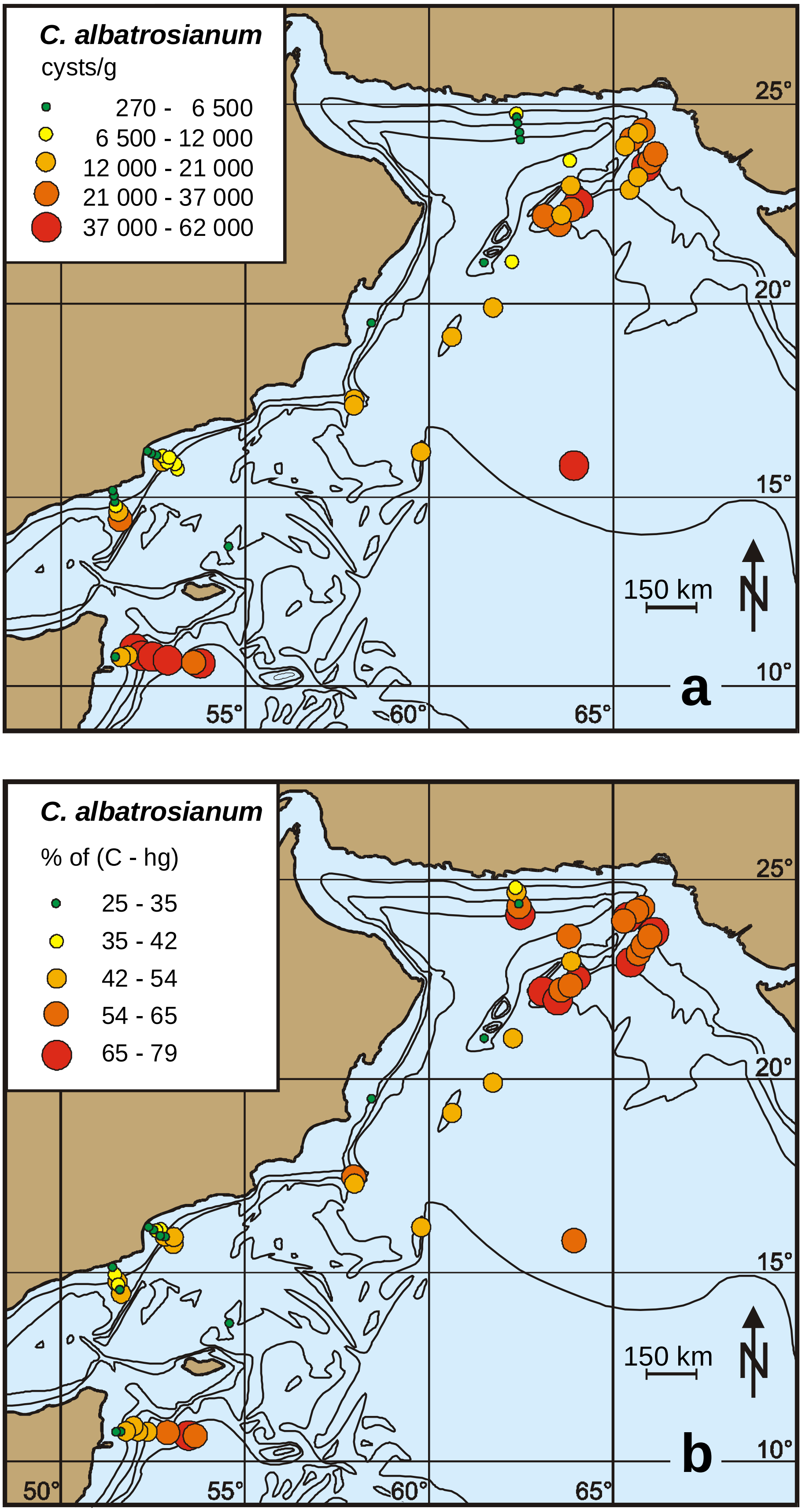

Fig. 6. Surface sediment distribution map of *Calciodinellum albatrosianum*. (a) absolute abundance, (b) relative abundance (percent of association excluding *T. heimii* and *L. granifera*).

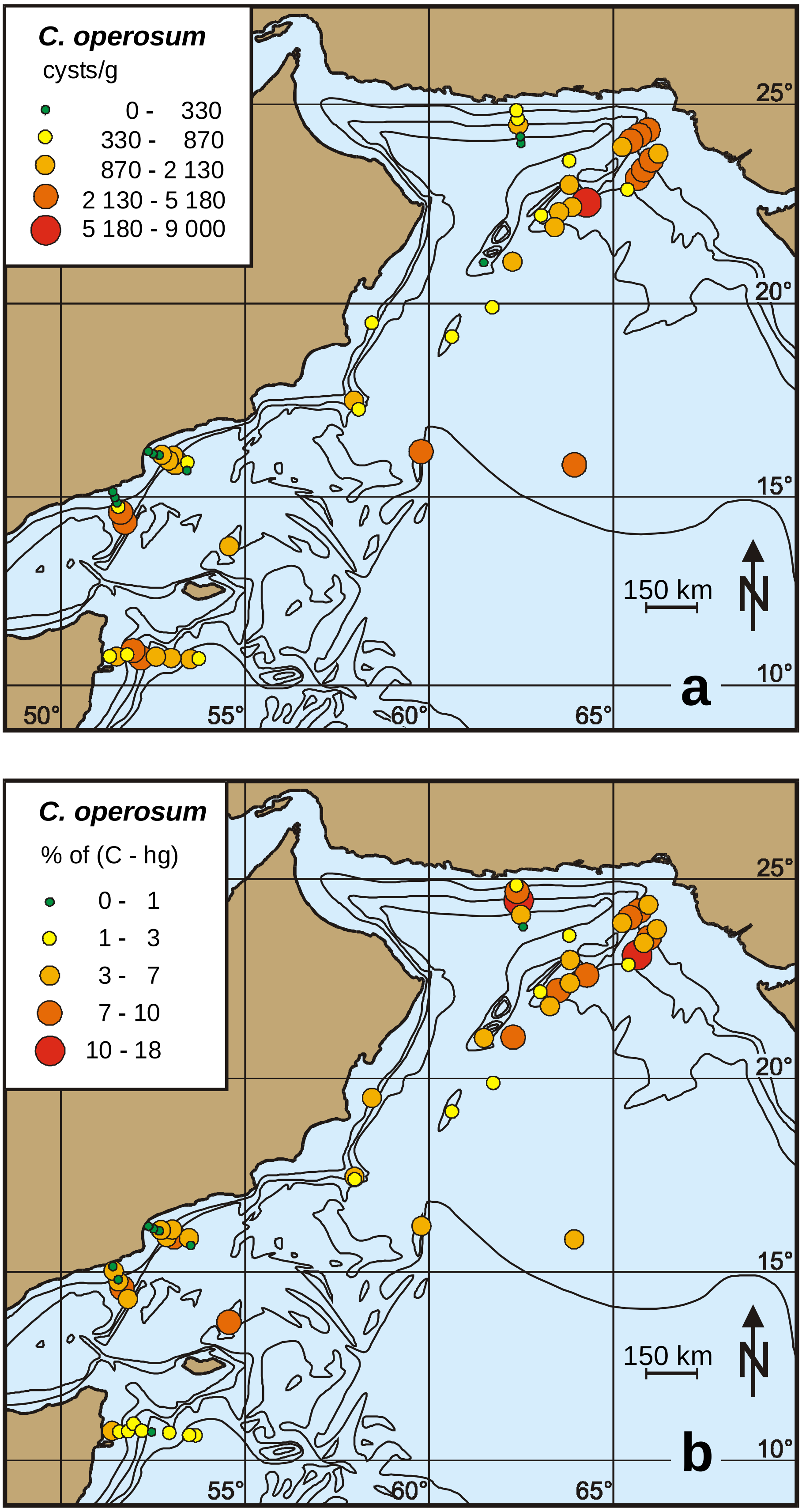

Fig. 7. Surface sediment distribution map of *Calciodinellum operosum*. (b) absolute abundance, (b) relative abundance (percent of association excluding *T. heimii* and *L. granifera*).

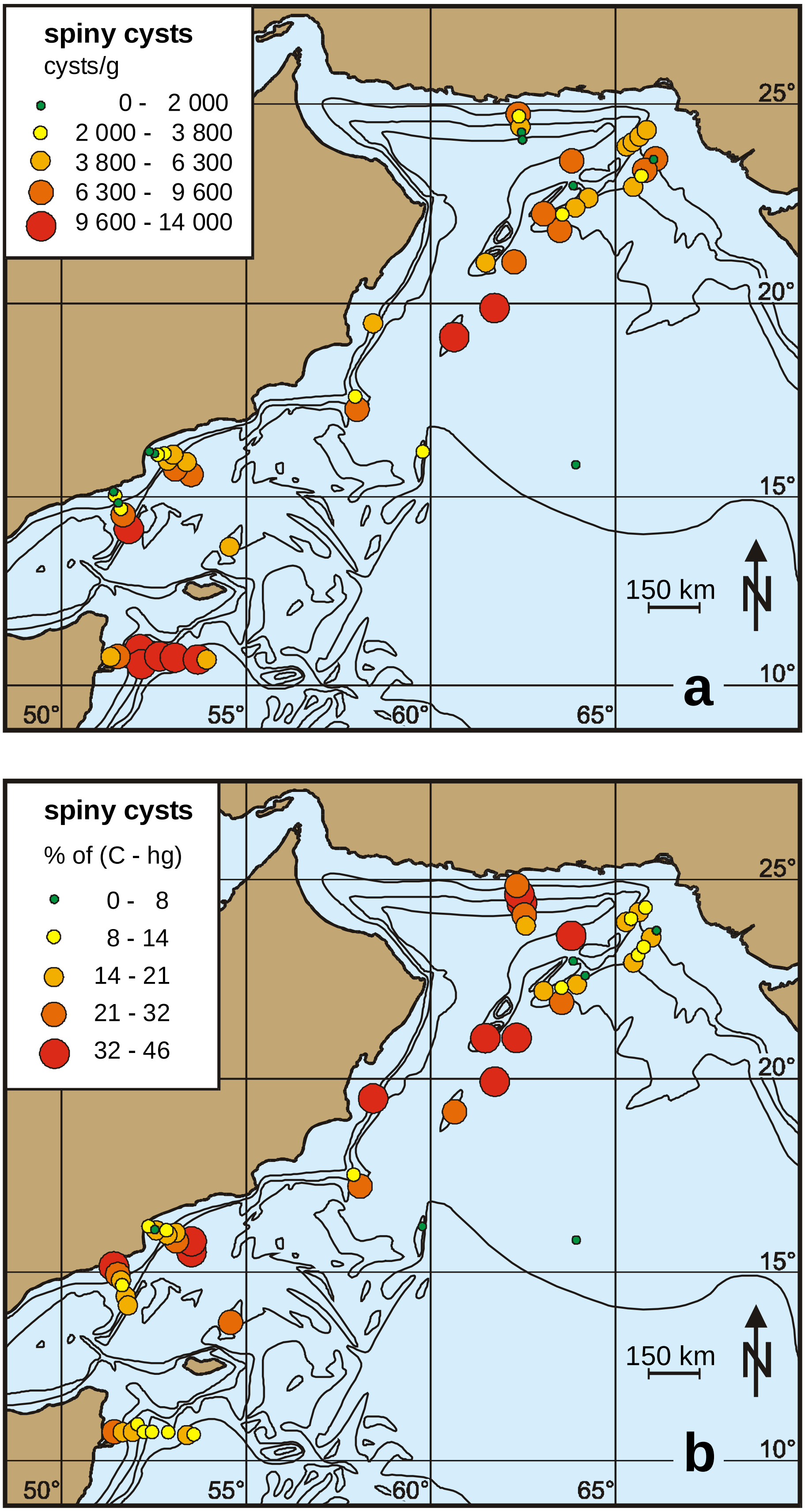

Fig. 8. Surface sediment distribution map of spiny cysts (mainly *S. trochoidea*). (a) absolute abundance, (b) relative abundance (percent of association excluding *T. heimii* and *L. granifera*).

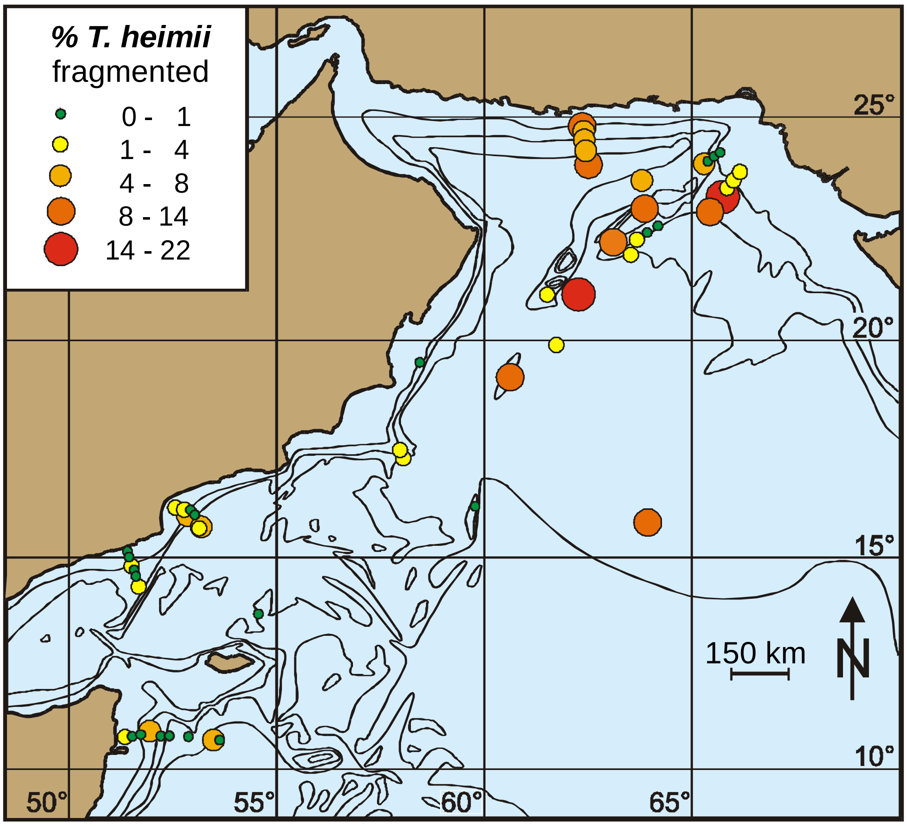

Fig. 9. Surface sediment distribution map showing fragmentation of *Thoracosphaera heimii*.

Cyst ARs in the profile off Somalia reach higher values than in the Indus Fan profile (Fig. 12). In the Somali transect, most species have maximum ARs between 1000 and 2000 m water depth (Fig. 12A). Exceptions are *C. sp.* 1 with a maximum that lies closer to the coast at about 800 m depth, and the spiny cysts which decrease continuously with distance from the coast. All species show strongly decreased ARs below 3000 m depth, whereby the AR curve of *T. heimii* exhibits the steepest slope. In the Indus Fan profile the cyst ARs are high in the upper samples and drop significantly between 1250 and 1500 m depth, at the lower boundary of the OMZ.

Cyst provinces

Combining the distribution patterns of absolute and relative abundance of all species, three provinces can be defined in the studied area (Fig. 2):

province I : NW Arabian Sea with upper Somali continental slope, shelf areas of Arabia and adjacent deeper parts north-west of the Owen Fracture Zone;

province II : open ocean with the central Arabian Basin, northern Somali Basin and adjacent lower slope;

province III: NE Arabian Sea including the Makran margin, Murray Ridge and the upper Indus Fan.

The characterizing species are listed in Table 1.

Table 1.

Provinces based on the distribution patterns of absolute and relative cyst abundances

Characteristic species	I	II	III
Thoracosphaera heimii	x	x	
Calciodinellum sp. 1	x	x	
spiny cysts	x		x
Calciodinellum operosum		x	x
Calciodinellum albatrosianum		x	x
Leonella granifera			x

Discussion

In the Arabian Sea, the same species of calcareous dinoflagellate cysts were observed as are reported from the tropical Atlantic Ocean and the Caribbean Sea (Höll et al. 1998, 1999; Vink et al. 2000; Zonneveld et al. 2000). The Arabian Sea differs in the low abundance of *P. tuberosa* and *C. sp.* 1 and the high abundance of *L. granifera* (Höll et al. 1999; Zonneveld et al. 2000; Vink et al. 2001 a). The mean ARs of *T. heimii* and *C. albatrosianum* are slightly higher than Höll et al. (1999) reported from the eastern and western equatorial Atlantic but considerably lower than in the Caribbean Sea (Vink et al. 2001 a). To understand to what part the variety in absolute and relative abundance within the Arabian Sea and the differences to other oceanic regions are ecologically controlled, it is necessary to assess the impact of factors that modify the primary signals such as transport, dilution and calcite dissolution.

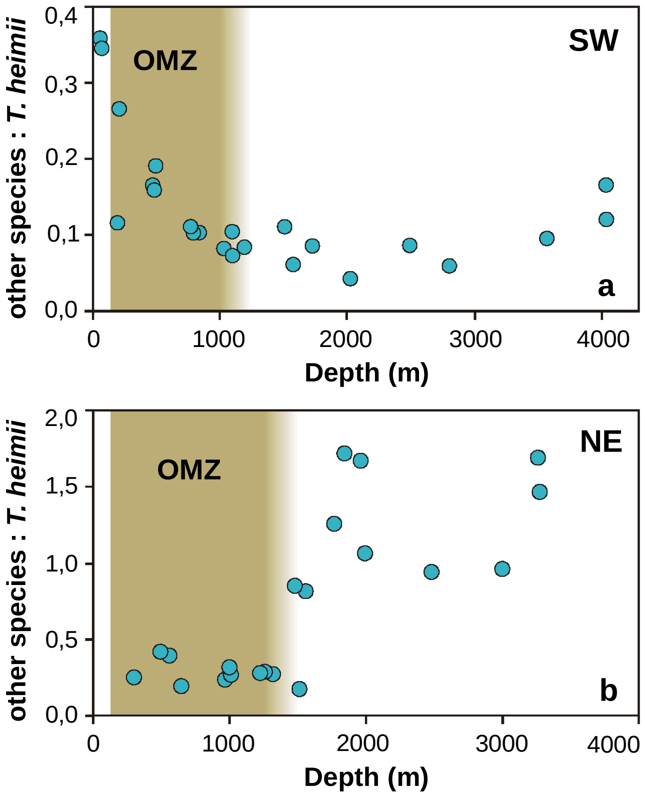

Fig. 10. Ratio of other species to *Thoracosphaera heimii* versus water depth in the SW (a) and NE (b) of the studied region (see Fig. 2 for separation of the two parts). Grey area marks the depth interval where the OMZ intersects the slope. Note the marked increase of values at the lower boundary of the OMZ in the NE and the generally much lower values in the SW.

Transport and dilution

Calcareous dinoflagellate cysts may be laterally transported in the water column or redistributed after settling. Lateral transport of the motile cells and cysts in the water column might occur via eddies and filaments, for example in the "great whirl" off Somalia (van Weering et al. 1997) and in offshore transporting eddies and topographically induced coastal squirts at the Oman shelf (e.g. Brock et al. 1992; Arnone et al. 1998; Latasa & Bidigare 1998; Manghnani et al. 1998; Lendt et al. 1999; Rixen et al. 2000). However, the very high primary production in the Arabian Sea (induced by seasonal upwelling) favours aggregation of smaller particles which leads to fast settling of the sediment and reduces horizontal transport in the water column. Furthermore, strong diel variations in mixed-layer depths is reported for the NE Arabian Sea during the NE Monsoon (Gardner et al. 1999), whereby re-stratification supports settlement of particles in deeper waters which are unaffected by mixing in surface layers (Gardner et al. 1995). Indeed, fast settling of particles especially during the SW Monsoon is documented from sediment trap studies off Oman (Honjo et al. 1999) and in the Somali region. Based on a sediment trap study of sites 905 and 915 Zonneveld & Brummer (2000) found no evidence for lateral relocation of organic-walled dinoflagellate cysts during transport to the seafloor. Horizontal transport of small particles in the water column might therefore be of minor importance there.

The second transport can result from turbidits, bottom water currents and bioturbation. The latter may play a role above and below the OMZ but is very reduced or lacking within it, as is evident from laminated sediments that are common within the OMZ (e.g. Schulz et al. 1996; van der Weijden et al. 1999; von Rad et al. 1999; Smith et al. 2000). Meadows et al. (2000) state that microbiological rather than macrobenthic activity is the driving force in the processes that lead to the typical geochemical characteristics of the NE Arabian Sea sediments.

Gundersen et al. (1998) observed a deep particle maximum below the mixed layer in the northern Arabian Sea during both, the SW and NE Monsoon which they interpret to result from advection of re-suspended sediment from the continental margin. Local winnowing by bottom water currents is known from some stations at the Oman margin, on the Owen Ridge and on the Murray Ridge (Prins et al. 1994). The winnowed sediments are enriched in foraminifers and depleted in the fine fraction. Three samples of the studied material (457, 461, 484) showed these characteristics and have to be interpreted with care. At station 457, the cyst association differs from the surrounding samples (higher percentage of *C. sp.* 1 and lower *C. albatrosianum* values) which could indicate that recent material was eroded.

Off Oman and Yemen, irregular seabed topography and frequently disturbed surface sediments, especially between 1000 and 1500 m water depth, were described (van Weering et al. 1997). Heier-Nielsen et al. (1995) report frequent reworking of the inner shelf surface sediments off Yemen by slumping, bioturbation and mechanical mixing due to wave action during the SW monsoon. They assume turbiditic flow processes to play an important role in transporting sediment from the upwelling zone off Yemen to the adjacent basin, and regard deposition of older, reworked organic matter as being the reason for the large discrepancies in 14C ages derived from organic matter and foraminifera. Episodic down-slope movement of sediment is also characteristic for the Makran margin, which is an active continental margin with high sedimentation rates (e.g. Prins et al. 1994).

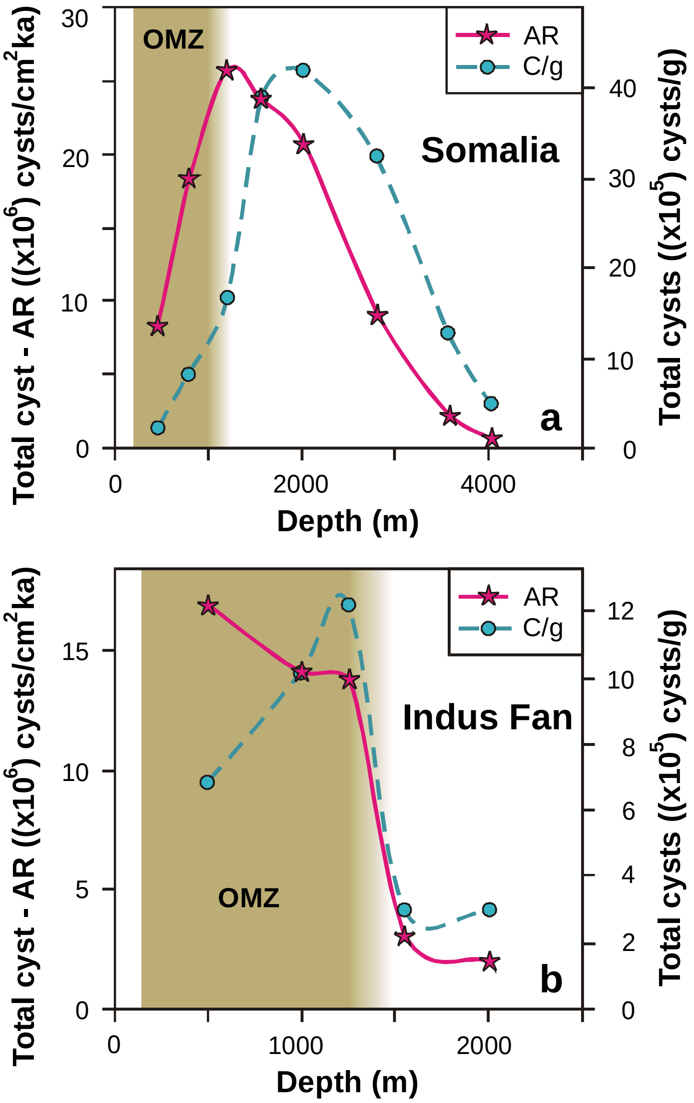

Fig. 11. Comparison of absolute abundance (dashed line, right scale) and accumulation rates (solid line, left scale) of total calcareous dinoflagellates versus water depth in the profile off Somalia (a) and the Indus Fan profile (b).

Accordingly, no reliable sedimentation rates are available for the Makran and the two Yemen profiles and cyst ARs could not be calculated for these samples. interpolation between the dated samples on the Murray Ridge and Owen Ridge or application of regional average sedimentation rates (e.g. given by Sirocko et al. 1991) would cause uncertainties which are larger than the variability in the data set of cyst concentrations. Because of the down-slope transport at the Makran and Yemen margins, any distribution trends within the profiles have to be considered with care. Nevertheless, these samples give information on the general cyst association in these regions. It should be noted, however, that low cyst contents especially in the shallow samples of these three profiles are at least partly caused by dilution due to high near-coast sedimentation rates, whereby terrigenous material plays an important role (Kolla et al. 1981; Sirocko & Lange 1991; Sirocko et al. 1991).

Reliable sedimentation rates were available for the Indus Fan profile, for some samples on the Murray Ridge and for the Somali transect. Although there are hints for some across-slope transport of re-suspended sediment at the Somali slope (Brummer 1995) most of the material is thought to be autochthonous, since the sedimentation rates in the profile decrease continuously with distance from the active upwelling zone, as would be expected. This assumption is also strengthened by studies with a long term deployed tripod lander at 1500 m depth in the transect, which measured low current speeds in the boundary layer implying that post-depositional removal of fine grained sediment is not likely to occur (van der Land & Stel 1995). A further argument comes from continuously decreasing ARs of spiny cysts with depth along this profile (Fig. 12) which is thought to reflect their original distribution in coastal waters (see discussion below). So, although some minor offshore transport may occur, the general trends in primary cyst production seem to be preserved in the Somali transect.

Although some small scale transport may change local cyst distribution patterns there is no indication for large scale transport, in the Arabian Sea. This supposition is supported by the results of Zonneveld (1997), who studied organic-walled dinoflagellate cysts in the same samples and found no relation of the variance in the association to the ocean current system in the Arabian Sea.

Calcite preservation

Carbonate dissolution in the northern Somali Basin starts strongly at 3500 m depth and below, but the Calcite Compensation Depth (CCD) is not reached with the deepest station of the studied transect (Troelstra et al. 1995). For the NE Arabian Sea, Millero et al. (1998) report undersaturation with respect to calcite below 3400 m. Two stations from the Somali transect (908, 915), the deepest station at the Makran Margin (472) and four stations on the abyssal plain of the Arabian Basin (458, 460, 487 and 491) were retrieved from water depths greater than 3000 m and could be affected by calcite dissolution due to deep water undersaturation. The two deepest samples from Somalia indeed exhibit very low cyst ARs compared to the shallower stations (Fig. 12). Also the four deep samples from the NE Arabian Sea show very low absolute abundances (e.g. Fig. 3A), especially for *T. heimii*

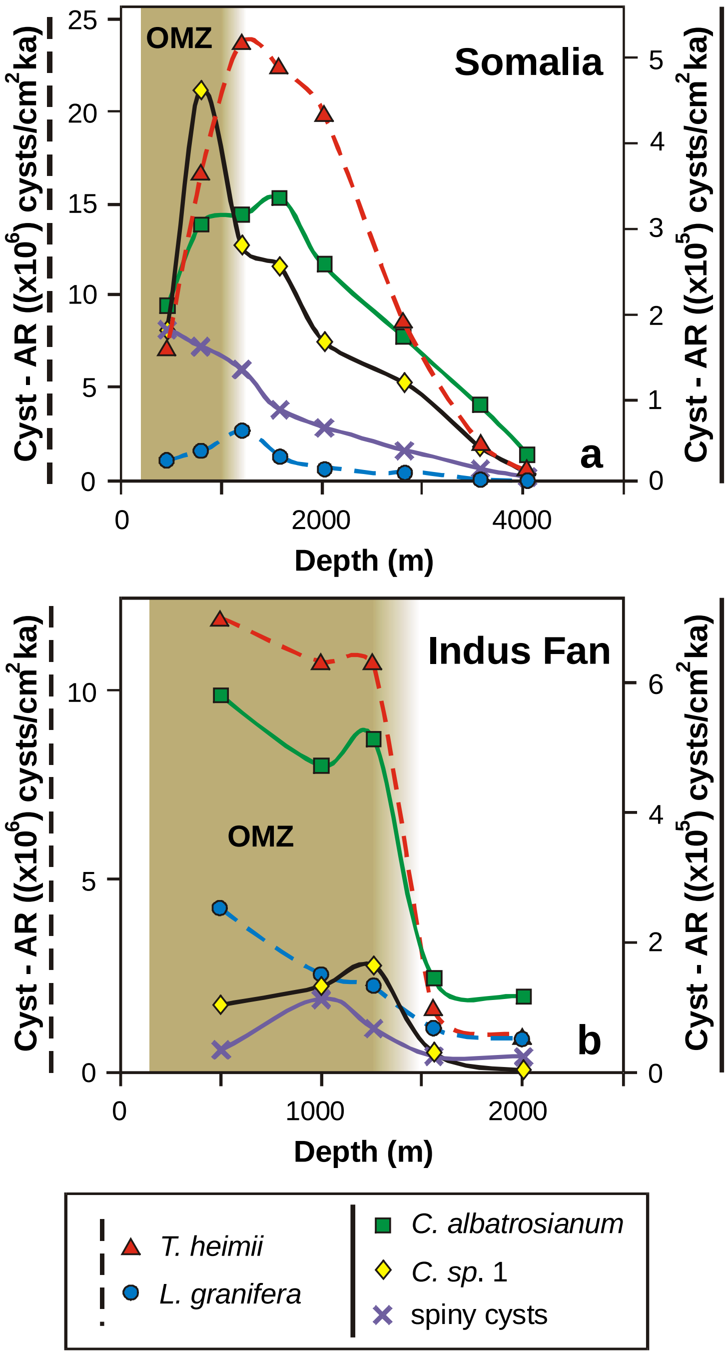

Fig. 12. Cyst accumulation rates (AR) of the different species versus water depth in the profile off Somalia (a) and in the *Indus Fan* profile (b). Brown area marks the depth interval where the OMZ intersects the slope. Left scale applies for the two dominating species *T. heimii* and *L. granifera*. Note the marked drop in ARs at the lower boundary of the OMZ in the *Indus Fan* profile. In the Somali section ARs of most species are lower near the coast at sites of active coastal upwelling.

which is regarded to be the most dissolution sensitive of the studied species (see Chapter 2). In the sample from the central Arabian Basin (491), however, relatively high cyst concentrations of *C. albatrosianum* and *C. sp.* 1 and intermediate abundance of *T. heimii* were found, although water depth at this station is almost 3800 m. This could be caused by increased cyst production, better calcite preservation and/or lower sedimentation rates in the central than in the NE Arabian Sea.

For the NE Arabian Sea (province III) it was shown that the preservation of calcareous dinoflagellate cysts is enhanced within the OMZ, most probably due to reduced rates of organic matter decay in this zone of very low-oxic bottom water (Chapter 2). Variations in absolute and relative cyst abundances within province III are therefore mainly caused by differences in early diagenetic calcite dissolution within and below the OMZ. These secondary processes are assumed to play only a minor role in the SW of the studied area (provinces I and II), because a relation of cyst abundances to the OMZ was not notable there (Chapter 2), possibly related to fast sedimentation due to particle aggregation and reduced thickness and intensity of the OMZ in this area. We assume that the variations in cyst abundances in provinces I and II largely reflect differences in primary cyst production, with the exception of the deepest stations where calcite dissolution due to deep water undersaturation has to be taken into account.

Ecology

The basin-wide presence of the six species discussed in this paper indicates that these species are tolerant to a relatively wide range of ecological conditions. The prevalence of *T. heimii* and *L. granifera* in the calcareous dinoflagellate associations in the studied sediments can be explained by the dominance of the shelled stage during the life cycles of both species, and especially for *T. heimii* by its ability to produce large numbers of calcareous spheres (representing a vegetative-coccoid life-stage) in a relatively short period of time (Tangen et al. 1982; Inouye & Pienaar 1983; Karwath et al. 2000 a; Janofske & Karwath 2000).

If comparing the three provinces based on the cyst abundances (Fig. 2) with the distribution of certain monsoon-controlled oceanic conditions it is most striking that the dividing line between provinces I and II coincides with the mean position of the Findlater Jet axis. Sites of province I are strongly influenced by coastal upwelling during the SW monsoon accompanied by low water temperatures, high nutrient concentrations, a shallow thermocline, low salinity and comparably high yearly temperature variations in 50 - 100 m water depth (up to 8°C). Sites of province II are characterized by open oceanic conditions with lower nutrient concentrations, higher water temperatures and salinity and a deep thermocline during most time of the year. Province III is effected by the influence of the Indus River discharge and by the NE monsoon deep winter mixing, accompanied by high nutrient concentrations, relatively warm temperatures down to 100 m depth and small seasonal temperature variations in 50 - 100 m depth (less than 2°C). Yearly mean temperatures in 50 - 100 m depth as well as the seasonal minimum and maximum temperatures are higher in province III (20 - 29°C) than in the other two provinces (15 - 26°C). Yearly mean values of Brunt-Väsälä frequency between 0 and 100 m water depth are higher in the SW (representing more stratified conditions) than in the NE of the area and reflect the conditions during the NE Monsoon and the two inter-monsoon periods.

T. heimii and C. sp. 1

Both species are characteristic for provinces I and II whereas they are less abundant in province III. It has been shown that these two species are more dissolution sensitive than the other species discussed here (Chapter 2), and the observed lower abundance in the NE Arabian Sea (except for samples from within the OMZ) may not reflect ecological conditions but could be the result of increased calcite dissolution under oxic bottom water conditions in this region. The increased ratio of other cysts : *T. heimii* below the OMZ in the NE and below 3000 m in the SW (Fig. 10) indicates that the shells of *T. heimii* (which are smaller than the cysts of the other species) are preferentially dissolved. To separate the primary signal from secondary alteration, samples from the SW are compared with samples from within the OMZ in the NE (Fig. 13), because these samples are assumed to be largely unaffected by early diagenetic calcite dissolution, which is also expressed in their low percentage of fragments of *T. heimii* (Fig. 9). Maximal ARs of *T. heimii* are higher off Somalia than within the OMZ on the Indus Fan and the Murray Ridge. This would mean that the reduced abundance of *T. heimii* (and possibly also of *C. sp.* 1) in the NE Arabian Sea reflects both, increased dissolution and lower production than in the SW.

The slightly lower surface water salinity in the SW Arabian Sea is not likely to have influenced the primary cyst production, since culturing experiments indicate that these organisms are rather tolerant to salinity: reproduction and cyst production of some species still continued under values as high as 50‰ (C. Höll and B. Karwath pers. comm. 2000).

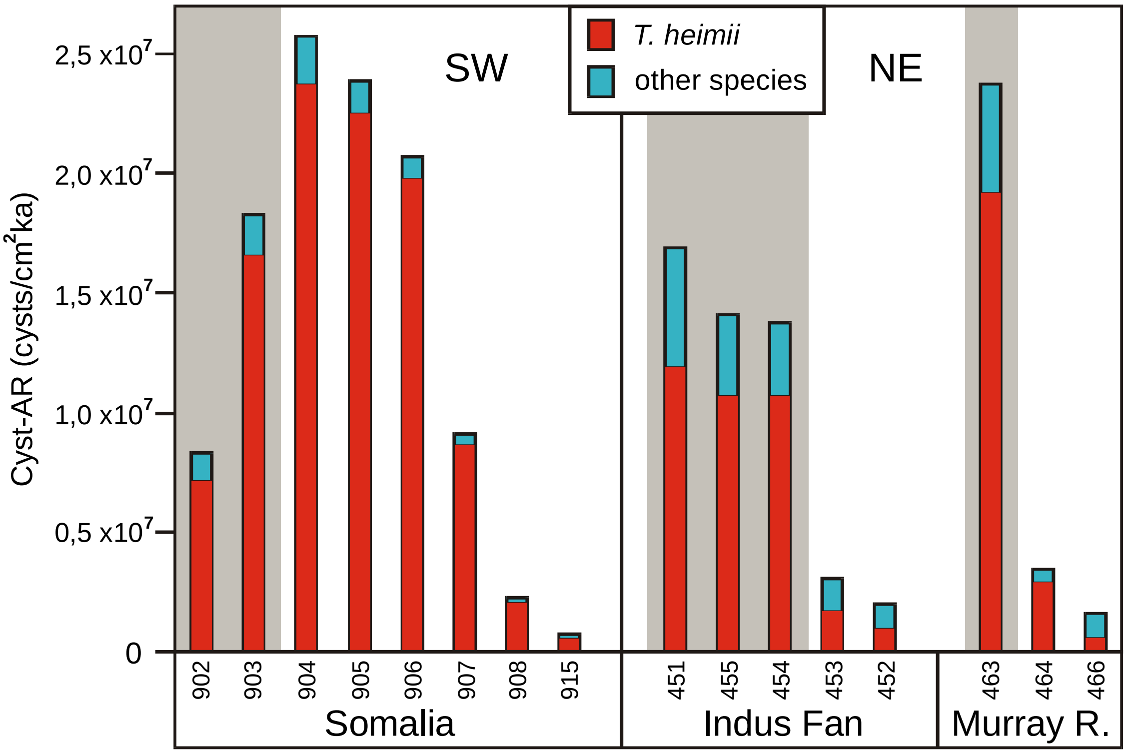

Fig. 13. Comparison of accumulation rates of *Thoracosphaera heimii* and other species in three regions in the Arabian Sea: in the SW a transect off Somalia, in the NE a profile on the *Indus Fan* and samples from the *Murray Ridge*. Grey background marks samples from within the OMZ.

Seasonal water temperatures during NE Monsoon and spring inter-monsoon are related positively, and temperatures during the SW Monsoon and fall inter-monsoon are related negatively to the distribution of the two species. To date, it is not known whether there is any seasonality in the production of the cysts and if so, in which time most cysts are formed. However, although the temperature gradients reverse biannually, the absolute temperatures (maximum and minimum values) as well as the yearly mean temperatures, especially in the lower photic zone, are lower in the SW. This would imply a larger tolerance of *T. heimii* and *C. sp.* 1 to cooler temperatures, which is in accordance with the results of other studies from the Atlantic Ocean (Vink et al. 2000; Karwath et al. 2000 b; Zonneveld et al. 2000). In culturing experiments under controlled laboratory conditions it was shown that *T. heimii* developed less efficient at high temperatures with the final yield about five times higher at 16°C compared to 27°C (Karwath et al. 2000 a). However, these experiments show that *T. heimii* grows in a wide temperature range (14 - 27°C), which indicates large temperature tolerance. This can be expected from species typical for province I where high temperature variations are caused by seasonal upwelling.

Stratification of the upper water column has been proposed to influence the calcareous dinoflagellates distribution (Höll et al. 1998, 1999; Vink et al. 2000; Vink et al. 2001 b). Well stratified water can hamper the vertical migration of motile cells or could act positively as a barrier for the calcareous cysts, preventing them to sink at depths where return to the photic zone is impossible. For several dinoflagellate species producing red tides, it is known that blooms occur in periods of calm weather and warm, stratified waters (e.g. Allen 1946; Marasović 1989). In the Arabian Sea, the yearly mean stratification is stronger in the SW of the basin, which means that this variable is positively related to the distributions of *T. heimii* and *C. sp.* 1. This relation suggests preference of both species to stratified conditions, which is consistent with the earlier findings. However, due to the strong seasonality especially of water temperatures in the Arabian Sea, stratification is generally very variable, and its role as controlling factor for the observed cyst distributions in the studied area is therefore not clear.

Within the SW Arabian Sea, where calcite dissolution in water depths above 3000 m seems to be neglectable (Chapter 2), the relative abundances of *T. heimii* and *C. sp.* 1 exhibit no large variations. Their absolute abundance, however, is very low near the coasts, in zones of active coastal upwelling. The same pattern can be seen in the ARs off Somalia (Fig. 12A), which is indicating that not only enhanced dilution by other particles near the coasts but also reduced cyst production is reflected in the sediments. The production rates could be lower under the turbulent conditions of coastal upwelling because too much turbulence can preclude the build up of a standing stock of phototrophic organisms. Veldhuis et al. (1997) observed high primary production during the upwelling season off Somalia only in more matured water, whereas productivity in freshly upwelled water was relatively low despite high nutrient concentrations. These authors consider high surface current speeds and deep vertical mixing to be the reason for this phenomenon. Various laboratory studies emphasize the sensitivity of dinoflagellates to water motion (Thomas & Gibson 1990; Thomas & Gibson 1992 and references therein). Cyst production of various species of calcareous dinoflagellates was considerably higher under non-agitated conditions (Höll pers. comm. 2001), which is in accordance with their adaptation to low irradiance conditions since with increasing water depth both, light and turbulence can be expected to decrease.

Based on Atlantic Ocean studies it has been suggested that calcareous dinoflagellates might be adapted to oligotrophic conditions (Höll et al. 1998, 1999; Vink et al. 2000; Esper et al. 2000). However, in these regions it is difficult to separate the effects of oligotrophy and stratification. In the Arabian Sea *T. heimii* and *C. sp.* 1 are characteristic for both, the relatively oligotrophic province II as well as the nutrient rich province I. From this it can be inferred that these species are tolerant to different nutrient levels, and that their distribution is not primarily controlled by differences in nutrient supply. This supposition is supported by results of culturing experiments with *T. heimii*, which did not show differences in growth rate and final yield under different nutrient levels and constant temperature (Karwath et al. 2000 a). A similar conclusion is drawn by Zonneveld et al. (2000) who compared surface sediments in the Atlantic Ocean and state that, if correcting for sedimentation rates, the differences in concentrations of *T. heimii* between the oligotrophic open ocean and the eutrophic Benguela area would largely be compensated.

The extremely low abundance of *P. tuberosa* in the Arabian Sea might be explained by the generally high trophy of this oceanic region since, as is evident from surface sediments of the Atlantic Ocean, this species appears to be adapted to rather oligotrophic conditions (Zonneveld et al. 2000; Vink et al. 2000; Vink pers. comm. 2001).

L. granifera

The absolute and relative abundance of *L. granifera* in the Arabian Sea is considerably higher than what is known from the Atlantic Ocean so far (Höll et al. 1998, 1999; Vink et al. 2000; Esper et al. 2000; Zonneveld et al. 2000). Concentrations are especially high in the NE Arabian Sea, where the species forms up to 51% of the association (Fig. 4B). The higher absolute and relative abundance in the NE cannot be explained by early diagenetic calcite dissolution, as it is stronger in the NE. The fact that the cysts of *L. granifera* appear to be least sensible to dissolution compared to the other species (Chapter 2) could be the reason for an increase of its relative abundance in the NE but would not explain the higher absolute abundances and ARs there (Fig. 4A). Accordingly, it is likely that variations in primary cyst production are reflected.

A possible relation of higher concentrations of *L. granifera* to relatively low salinity as observed by Vink et al. (2000) cannot be seen in the Arabian Sea using the available salinity data set, which shows higher salinity (up to 36,8‰) in the NE, although this area is influenced by the Indus River discharge. Obviously during the last decades, when most of the salinity measurements were done, the fresh water input was compensated by high evaporation rates. However, the mean annual water and suspended sediment discharge load has been much higher before 1950, when damming/channelling of the Indus River and utilisation for agriculture were lower (Milliman et al. 1984) and lower salinity values have to be assumed. Sedimentation rates near the Indus outlet indicate that the studied surface samples contain 43 to 213 years of deposition, so a large part of the signal reflects oceanographic conditions before 1950. Therefore, it is likely that also in the Arabian Sea *L. granifera* is related to lower salinity. On the other hand, Schulz et al. (1996) found no freshwater signal in the distribution of stabile isotopes in surface sediments from the Indus Fan. However, elevated *L. granifera* concentrations were also observed in the Atlantic Ocean in regions that are influenced by river outflow such as the Amazon or the Congo River (Vink et al. 2000; A. Vink pers. comm. 2000). It seems very likely that this species is adapted to conditions that are related to fluvial input, be it a lowered salinity and/or some other abiotic (e.g. specific nutrients) or biotic factors (competition or symbiosis).

Most areas which are characterized by river discharge are rather stratified due to the lower density of freshwater. In the NE Arabian Sea, however, the upper water masses are less stratified than in the SW of the basin most time of the year, which is mainly caused by convective turnover. This results in a negative correlation of yearly mean stratification and the distribution of *L. granifera* in the Arabian Sea. Presumably, the species is tolerant to various levels of stratification.

Beside the fluvial influence, generally high temperatures and low seasonality in the NE Arabian Sea might be favourable for *L. granifera*. This is supported by culturing experiments which have shown that the species grows better under relatively high temperatures (C. Höll pers. comm. 2000). In the oceans, *L. granifera* is so far reported exclusively from (sub)tropical regions, whereas the other species were also found in warm/temperate regions (Zonneveld et al. 1999). A positive correlation of *L. granifera* with temperatures has also been reported by Vink et al. (2000). However, in the SW Arabian Sea, where cold deep water wells up near the coasts during summer and temperatures in depths of 50 m to 100 m are about 15°C to 20°C, concentrations of the species are still higher than in most studied regions of the Atlantic Ocean. This shows that temperature cannot be the only controlling factor.

One of the main characteristics of the Arabian Sea is the extremely high primary production caused by high nutrient concentrations. Lowest concentrations of *L. granifera* were observed in province II, which is the most oligotrophic part of the studied area (Figs. 4 and 2). From this we glean that *L. granifera* is adapted to rather high nutrient concentrations.

C. albatrosianum and C. operosum

Both species show lower absolute and relative abundance in province I. This distribution pattern cannot be explained by calcite dissolution since, as mentioned before, more dissolution would be expected in the deep samples from the open ocean and in province III. Low concentrations in samples close to the Somali and Arabian coasts give a negative correlation with parameters that are typical for seasonal coastal upwelling, such as large seasonality, strong turbulence, high nutrient concentrations and low temperatures. Within the lower photic zone in the NE Arabian Sea and especially in the open ocean, seasonality is much smaller and yearly mean temperatures are relatively high due to downwelling-induced deepening of the mixed-layer, causing a relatively uniform vertical temperature distribution of about 20 - 24°C down to 100 m depth.

Though *C. albatrosianum* might be less successful in upwelling areas with very high nutrient concentrations, the species seems to be adapted to a relatively wide range of nutrient levels, since high cyst concentrations have been found in the eutrophic NE Arabian Sea as well as in the oligotrophic open ocean. A mainly open oceanic distribution of *C. albatrosianum* and a negative relation to nutrient concentrations has been reported by Vink et al. (2000) for the western equatorial Atlantic Ocean. Furthermore, Zonneveld et al. (2000) describe a trend to higher concentrations of *C. albatrosianum* from onshore to offshore areas in the Benguela region and observed a positive relation to water temperatures by comparing samples from different regions in the equatorial and south Atlantic Ocean. These observations subscribe the interpretation of *C. albatrosianum* as being typical for open oceanic, rather oligotrophic environments with low seasonality and relatively high temperatures. In view of the usually very low cyst concentrations of *C. operosum* it appears uncertain whether similar conclusions can be drawn for this species.

Spiny cysts

The low abundance of the spiny cysts (which in the studied material mainly belong to *S. trochoidea*) in samples from the open ocean of the Arabian Sea is in general agreement with observations from other studies, where *S. trochoidea* is reported only from neritic environments (Janofske 2000). However, in the studied area there is no restriction of the spiny cysts to coastal waters: relatively high concentrations were also found offshore Oman and in the westernmost samples from the Murray Ridge (Fig. 8). This could indicate that *S. trochoidea* is not restricted to coastal environments. On the other hand, as noted above, some basin-ward transport of cysts in the water column can be expected via eddies and filaments off Oman which move east to north-east. Furthermore, there might be some contribution of *S. regalis* to the group of spiny cysts. This species is described from the open ocean (Vink et al. 2000; Janofske et al. 2000 and references therein), so the distribution pattern of all spiny cysts could represent a combined oceanic and coastal signal.

The group of spiny cysts is the only morphotype which is abundant in areas of active upwelling and shows continuously decreasing ARs with depth (Fig. 12A). This suggests that the dominating species *S. trochoidea* is adapted to eutrophic and rather unstable environments (large seasonality) with seasonally lower temperatures and a shallow thermocline. The interpretation is subscribed by a study of surface sediments of the Benguela upwelling region, where high abundance of spiny cysts is related to high nutrient concentrations and strong seasonality (Zonneveld et al. 2000). In surface sediments from different parts of the worlds oceans, *S. trochoidea* is mainly reported from temperate regions (Zonneveld et al. 1999).

Spiny cysts found in the Arabian Sea show a large morphological variety and fragile cysts (consisting of calcite crystals loosely attached to an organic layer) are particularly well preserved within the OMZ. More work on the taxonomy of this type of cysts is necessary to clearly separate different species and to gain information on their ecology.

Conclusions

The distribution of calcareous dinoflagellate cysts in surface sediments of the Arabian Sea is controlled by a combination of ecology and early diagenetic calcite dissolution. Sediments in the SW of the studied area largely reflect ecologically controlled variations in dinoflagellate cyst production, in contrast to the NE where cyst accumulation rates (AR) are strongly related to bottom water oxygen concentrations and are thought to be determined by differences in calcite dissolution within and below the OMZ. Not all of the basin-wide trends within cyst distribution patterns can be explained by early diagenetic processes and are interpreted to result from different ecological conditions within the (lower) photic zone.

The two dominating species of calcareous dinoflagellates in surface sediments of the Arabian Sea are *T. heimii* and *L. granifera*, which show distribution patterns opposite to each other. Lower ARs and relative abundance of *T. heimii* in the NE might mainly result from increased dissolution, whereas high absolute and relative abundance of *L. granifera* in this region is related to higher water temperatures, low seasonality and the influence of the Indus River. *C. sp.* 1, which has a similar distribution as *T. heimii*, is negatively related to temperature and appears to be tolerant to a wide range of nutrient concentrations. However, the distribution of *C. sp.* 1 might also be affected by enhanced dissolution in the NE. Higher abundance of *C. albatrosianum* in the open ocean and NE of the basin can be related to higher temperatures and a deep thermocline. The species seems to be less successful under upwelling conditions and is probably adapted to rather oligotrophic and stable environments in the open ocean. Spiny cysts in the studied material mainly belong to *S. trochoidea* which is known from neritic environments and appears to be adapted to eutrophic and probably cool, rather unstable conditions. The extremely low abundance of *P. tuberosa* in the Arabian Sea is attributed to the species' preference of oligotrophic environments. However, a general relation of calcareous dinoflagellates to oligotrophic conditions, as was proposed earlier (e.g. Höll et al. 1998, 1999), cannot be confirmed. It should be carefully evaluated to what extend the observed negative correlation of calcareous dinoflagellate cysts with content of organic carbon in sediment cores might be caused by enhanced calcite dissolution, which is driven by metabolic CO_2 during times of high primary production and increased organic matter decay. Low cyst concentrations and ARs in zones of active coastal upwelling off Somalia and Yemen indicate that strong turbulence and high current speeds are unfavourable for calcareous dinoflagellates. This is encouraging the belief that these organisms are more successful under rather stratified conditions.

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Appendix 1: Taxonomic information

The calcareous dinoflagellate cyst species/morphotypes cited in the current paper are listed below and illustrated in Plate 1. We follow the taxonomy of Williams et al. (1998) for *Thoracosphaera heimii*, *Calciodinellum operosum, Calcigonellum infula, Calciperidinium asymmetricum* and *Melodomuncula berlinensis*, of Janofske (2000) for *Scrippsiella trochoidea and Scrippsiella regalis*, and of Janofske and Karwath (2000) (synonyms used in earlier publications are given in brackets) for *Leonella granifera* (*Orthopithonella granifera*), *Calciodinellum albatrosianum* (*Sphaerodinella albatrosiana*), *Calciodinellum sp.* (*Sphaerodinella tuberosa* var. 2) and *Pernambugia tuberosa* (*Sphaerodinella tuberosa* var. 1).

Most specimens of spiny cysts fall within the "*Scrippsiella trochoidea*-complex" described in D'Onofrio et al. (1999) and are comparable to *Rhabdothorax* sp. 1 in Vink et al. (2000). Only a few specimens were identified as *S. regalis.* The species *P. tuberosa* and *C. sp.* 1 were formerly both ascribed to *Sphaerodinella tuberosa* (Kamptner 1963) Hildebrand-Habel, Willems & Versteegh 1999, and separated as variant 1 and 2, respectively (e.g. Vink et al. 2000). The cysts of *P. tuberosa* are composed of relatively large, block-like individual crystals which do not inter-finger with each other, whereas those of *C. sp.* 1 consist of smaller, roughly triangular-shaped, inter-fingering crystals.

Thoracosphaera heimii (Lohman 1920) Kamptner 1944
Pernambugia tuberosa (Kamptner, 1963) Janofske & Karwath 2000
Calciodinellum sp. 1 (still informal for *S. tuberosa* var. 2)
Leonella granifera (Fütterer, 1977) Janofske & Karwath 2000
Calciodinellum albatrosianum (Kamptner, 1963) Janofske & Karwath 2000
Calciodinellum operosum (Deflandre 1947) emend. Montresor et al. 1997
Scrippsiella trochoidea (Stein 1883) Loeblich III 1965
Scrippsiella regalis (Gaarder 1954) Janofske 2000
Melodomuncula berlinensis Versteegh 1993
Calciperidinium asymmetricum Versteegh 1993
Calcigonellum infula (Deflandre 1947) Montresor 1999

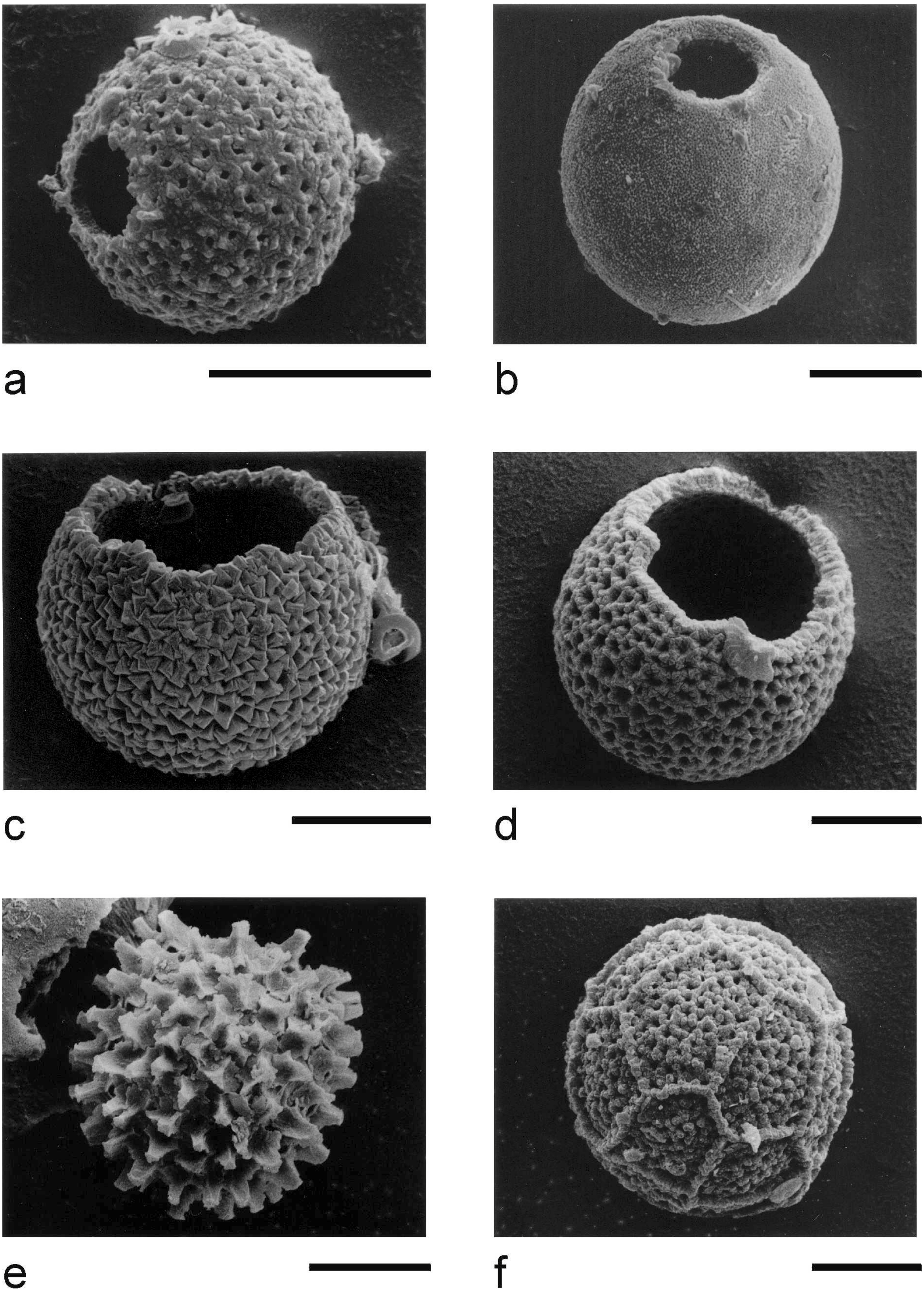

Plate 1

SEM photographs of the calcareous dinoflagellate cyst species; sample 457; Scale bars are 10 µm. (a) *Thoracosphaera heimii*; (b) *Leonella granifera*; (c) *Calciodinellum sp.* 1; (d) *Calciodinellum albatrosianum*; (e) *Scrippsiella trochoidea*; (f) *Calciodinellum operosum.*

Appendix 2: Position and water depth of surface samples and absolute cyst abundances

Sample No.	Depth (m)	Latitude N	Longitude E	Absolute abundance (cysts per gram of dry sediment)					
				T. heimii	*O. gran.*	*S. alba.*	*S. tub.* 2	*C. oper.*	spiny
301	74	15,08	51,25	38339	5021	2738	2738	0	2738
302	208	15,00	51,27	48255	5709	2585	2262	323	1939
303	474	14,51	51,29	173124	16909	5039	4031	0	1680
304	770	14,47	51,31	311999	14836	8122	8772	650	2274
305	1098	14,43	51,34	1234126	77242	17019	21602	3928	9164
306	1504	14,30	51,37	1246473	75246	31424	17956	3206	9619
307	50	16,11	52,23	6684	267	535	1337	0	267
308	196	16,08	52,30	13847	804	268	536	0	0
309	487	16,05	52,37	193671	22679	5380	6329	0	2532
310	810	16,04	52,42	356822	16158	8752	9425	1346	2020
311	1087	16,02	52,46	810395	30778	9582	12195	871	5226
313	2215	15,53	53,01	93159	29703	7201	1350	0	7201
325	4035	10,41	53,31	564115	17147	45477	16402	1491	12674
451	495	23,41	66,02	485103	173955	23787	4325	1442	1442
452	2001	22,56	65,28	146951	133260	17707	548	548	3834
453	1555	23,14	65,44	168002	114049	14423	3205	3205	2404
454	1254	23,27	65,52	945864	204359	45700	14764	3515	6328
455	998	23,33	65,57	769420	186190	34032	9618	5179	8138
457	301	22,58	63,51	600388	112850	20216	18139	1662	1662
458	3000	22,00	63,30	113176	74588	23294	1412	2118	7765
460	3262	21,43	62,55	46623	59814	10234	682	1365	6823
461	643	22,23	63,50	855004	128605	23404	7801	2128	5831
463	970	22,33	64,03	1764779	317437	60358	20864	8942	5961
464	1511	22,15	63,35	378735	47423	12343	2599	1949	2599
466	1960	23,36	63,48	57218	77465	11092	0	528	6514
468	1318	24,46	62,21	251785	46504	8969	7308	332	6643
469	1768	24,40	62,22	27477	27579	3371	613	613	2451
470	1840	24,36	62,22	26358	34288	3744	441	1909	4993
471	2482	24,18	62,27	32750	23172	4634	927	309	1854
472	3274	24,07	62,29	15816	14324	6416	671	0	1791
473	1877	22,13	63,06	245218	92007	23555	3624	604	6644
475	1472	24,05	65,27	133988	90390	13696	3424	1370	4793
476	1226	24,06	65,28	490909	98409	27955	4773	3409	4773
477	1000	24,08	65,31	575567	116709	19521	8186	2519	5038
478	556	24,13	65,40	605106	191277	27447	10851	2553	5106
483	2734	21,02	61,29	107338	42497	3943	3943	657	5257
484	527	19,30	58,26	78451	16386	3021	2472	549	3845
486	2070	19,09	60,37	737472	28825	17738	7539	665	10421
487	3566	19,54	61,43	184448	61081	14467	1808	603	10850
491	3797	15,50	63,55	539771	20949	37316	16694	3928	982
492	1917	16,11	59,46	1451045	39604	20902	17602	2750	3300
496	1900	17,26	57,57	683486	36927	17890	8257	688	8257
497	1890	17,28	57,57	646991	28472	13889	6944	1389	2083
902	459	10,46	51,34	210943	17409	6104	5426	678	5426
903	789	10,46	51,39	743739	34974	13601	20725	1295	7124
904	1194	10,47	51,46	1549934	83297	20548	18559	663	8617
905	1567	10,54	51,56	3693827	108473	55236	42239	2999	13997
906	2020	10,48	52,07	4044065	69415	51883	33404	2843	13504
907	2807	10,48	52,14	3078704	61728	61343	41281	1157	12731
908	3572	10,46	52,54	1158358	23636	50924	24495	1934	10314
915	4035	10,41	53,31	435524	16783	24336	6713	839	4196
917	2225	15,54	53,01	133435	20244	6530	1959	653	5224
918	1716	15,58	52,50	672260	26803	9806	11767	2615	7191
919	1030	16,00	52,44	758493	34556	12231	8736	1165	4659
929	2484	13,42	53,14	729687	46452	5447	4766	1362	5447

Appendix 3: Rare species - distribution (sample no.) and total number of occurrence

	Pernambugia tuberosa	*Melodomuncula berlinensis*	*Calcigonellum infula*	*Calciperidinium asymmetricum*
Somalia	903, 906, 907	902	915	-
Yemen	305, 306	-	313, 918, 919	307
Pakistan	-	476, 477, 455	452	-
Murray Ridge	-	457, 463	463	457
total number of occurrence	7	7	8	2

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4. Production of calcareous dinoflagellate cysts in response to monsoon forcing off somalia: a sediment trap study

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Abstract

To increase the knowledge on the so far poorly understood ecology of calcareous dinoflagellates we examined the impact of the SW and NE monsoons on cyst formation using sediment trap material collected at 1032 m water depth off Somalia from June 1992 to February 1993. The results do not confirm the hitherto applied theory of a negative relationship between cyst production and nutrient concentrations, as highest cyst fluxes were recorded during late SW monsoon under relatively nutrient-rich and less agitated conditions of mature upwelled water, and lowest fluxes were found under strongly stratified, nutrient-depleted surface waters during the inter-monsoon. Elevated fluxes of *Leonella granifera* occurred during periods of warm, stratified surface water, whereas for *Calciodinellum sp.* 1 a relation to changes in surface water conditions was not evident. Although all of the studied species seem to prefer a stratified water column, an elevated concentration of nutrients appears to be necessary to maintain high cyst production. Comparison of the mean cyst flux into the sediment trap with that into the underlying surface sediments reveals a 81 - 96% loss of cysts on their way to the seafloor, which can be attributed to calcite dissolution. The relatively small spheres of *Thoracosphaera heimii* are affected more than the cysts of the other species, which has to be kept in mind for interpreting the sediment record.

Introduction

Surface circulation in the Arabian Sea is driven by the regular and intense forcing of the seasonally reversing monsoon winds. The Somali Current develops in response to the onset of the Southwest (SW) monsoon in May and induces coastal upwelling off

Somalia during boreal summer. There, nutrient-rich surface water is transported offshore within the cold wedges of a two gyre system (Schott, 1983), leading to strongly enhanced primary production. The northern anticyclonic gyre, which is sometimes referred to as the great whirl (Swallow and Bruce, 1966), influences the sedimentation at the investigated sediment trap site. Coastal upwelling does not occur during boreal winter but primary production is enhanced through mixing caused by the Northeast (NE) monsoon (Banse and McClain, 1986). The inter-monsoon periods are characterised by weak winds, stratified and nutrient-depleted surface waters and hence a low primary production (Smith and Codispoti, 1980). A detailed description of the hydrographic setting during the 1992-1993 monsoons at the trap site is given in Broerse et al. (2000).

The vigorous response of the plankton community to the strong atmospheric forcing makes the Arabian Sea a suitable site for palaeo-climatic studies. Calcareous-cyst producing dinoflagellates (hereafter referred to as calcareous dinoflagellates) are phototrophic, unicellular organisms and form part of the phytoplankton. Their cysts are frequently found in marine sediments and represent a relatively new tool for palaeo-environmental reconstruction (Höll et al., 1998, 1999; Höll and Kemle-von Mücke, 2000; Esper et al., 2000; Vink et al., 2001 a, b). As opposed to the organic-walled dinoflagellates, information on the ecology of calcareous dinoflagellates is still sparse. During the last couple of years studies on surface sediments have been carried out, comparing the distribution and abundance of the different cyst species with recent conditions in the upper water column (Vink et al, 2000; Zonneveld et al., 2000; Chapter 3). These conditions, however, can have a considerable seasonal component. The objective of our investigation is to assess the seasonal variability in production of calcareous dinoflagellate cysts in relation to monsoon forcing and their export to the deep sea.

Material and methods

In the frame of the Netherlands Indian Ocean Programme (NIOP) 1992-1993 three sediment traps were deployed in the upwelling area off NE Somalia to study particle fluxes trough the individual Monsoon periods. The present paper reports on the sediment trap MST-9E at 10°43N and 53°34E with a bottom depth of 4047 m (Fig. 1). A sample of the underlying surface sediments was retrieved from 10°41N and 53°31E in 4035 m depth (upper cm of boxcore 915, representing about 270 years of sedimentation). The trap

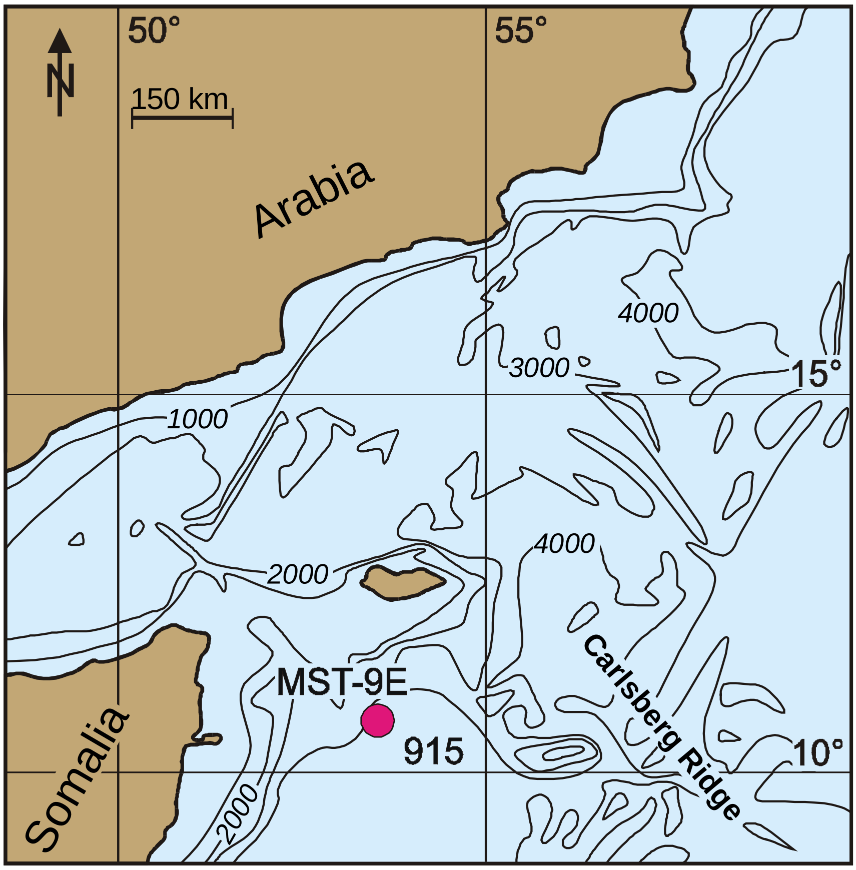

Fig. 1. Location of the Netherlands Indian Ocean Program (NIOP) sediment trap array MST-9E and underlying surface sediments at site 915

collected sediment at a water depth of 1032 m over a period of nine months (7 June to 21 February), covering the SW and NE monsoons and fall inter-monsoon. Sampling intervals were 7 or 14 days, except for sample 1 which collected only for 30 min and served as a semi-blank (App. 1). Due to a premature mooring release at the end of the sampling period, the trap collected just below the photic zone for 6 h, so the last sample (cup 24) does not present reliable fluxes and is excluded from the calculation of mean cyst fluxes. Detailed information on the mooring design, trap efficiency and current speed velocities are given in Brummer (1995) and Brummer et al. (2000).

To analyse the sediment trap samples for their content of calcareous dinoflagellate cysts, the dried sediment (about 5 to 28 mg) was weighted and disintegrated in 0.2 to 1.5 ml of water by ultrasound treatment of < 1 min. A split (25 to 50 µl) of the homogenised material was placed on a cover slip, dried on a heating plate and finally fixed with Spurr's resin. Preparation of the surface sediment is described in Chapter 2. The cysts were counted using a light microscope with polarised light. At least two slides per sample were scanned. We follow the taxonomy of Williams et al. (1998) for *Thoracosphaera heimii*, *Calciodinellum operosum* and *Melodomuncula berlinensis*, of Janofske (2000) for *Scrippsiella trochoidea*, and of Janofske and Karwath (2000) (synonyms used in earlier publications are given in brackets) for *Leonella granifera* (*Orthopithonella granifera*), *Calciodinellum albatrosianum* (*Sphaerodinella albatrosiana*), *Calciodinellum* sp. 1 (*Sphaerodinella tuberosa* var. 2) and *Pernambugia tuberosa* (*Sphaerodinella tuberosa* var. 1).

The absolute cyst abundance (A, in cysts/mg of dry sediment) was calculated as follows:

$$A = [(C * V) / (W * S)]$$

where C represents the counted number of cysts, V (in µl) the volume of water used to solve the dry sample, W (in mg) the dry weight of sediment and S (in µl) the volume of split that was used for the slides (App. 1). Relative abundance of the dominating species *T. heimii* is given in percent of the whole association whereas this species is excluded from the association for the calculation of relative abundances of the other species. Cyst fluxes (in cysts/m^2d) were calculated by multiplying the absolute cyst abundance (A) with the total mass flux (in mg/m^2d). To allow for the response of biota and sinking time of particles we apply a two weeks time lag between conditions at the sea surface and the arrival of the signal at the depth of the sediment trap, following Broerse et al. (2000).

Results

Eight calcareous dinoflagellate cyst species were identified in the sediment trap material. Most abundant species are *Thoracosphaera heimii*, *Leonella granifera*, *Calciodinellum albatrosianum* and *Calciodinellum sp.* 1. The rare species comprise *Calciodinellum operosum*, *Scrippsiella trochoidea*, *Pernambugia tuberosa* and *Melodomuncula berlinensis*. The fluxes are illustrated in Fig. 2 and compared with conditions in the upper water column.

With more than 90% of the association, *T. heimii* represents the dominating species throughout the whole sampling period (Fig. 3). Its relative abundance increases during the SW monsoon to reach 99% in sample 13 and then slowly decreases again. The *T. heimii* fluxes generally follow the total mass flux (Fig. 2C) and are comparable with the fluxes of coccoliths and coccospheres (Broerse et al., 2000), showing a first peak after the first gyre

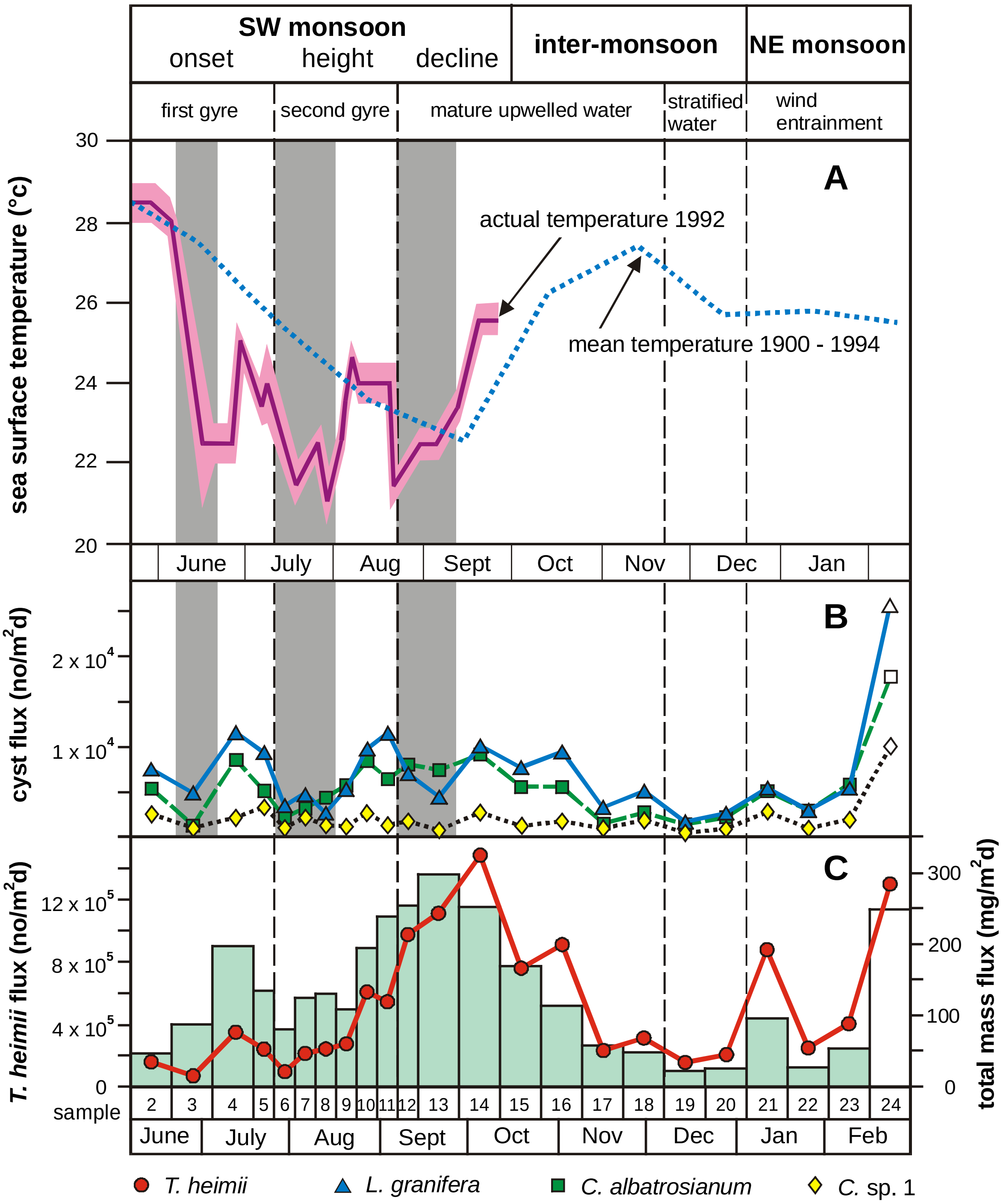

Fig. 2. Compilation of sea surface temperatures (A), calcareous dinoflagellate cyst fluxes (B and C) and total mass flux (bars in C). A two weeks time-lag is applied for the sediment trap data. Grey bars correlate low cyst fluxes (especially of *L. granifera*) with low sea surface temperatures. Actual temperatures are based on shipboard measurements and satellite imagery, mean annual temperatures are based on temperature measurements of one degree latitude/longitude squares between 1900 and 1994 (NOAA global ocean temperature and salinity data set; Boyer and Levitus, 1994). Sample 1 served as a semi-blank and is not depicted; sample 24 is contaminated with near-surface flux (white bar and symbols).

has passed the trap site (sample 4), increasing values during the height of the SW monsoon and a major peak during late SW monsoon. The highest flux of *T. heimii* was observed in sample 14, whereas the late SW monsoon peak of the total mass flux and flux of coccoliths and coccospheres occurs already in sample 13. An increase from sample 15 to 16 as for *T. heimii* flux is not seen in the total mass flux nor in the coccosphere flux but is also evident in the coccolith flux. The early NE monsoon peak (sample 21) is less pronounced for *T. heimii* than for the coccoliths and coccospheres, for which fluxes even exceed the late SW monsoon values.

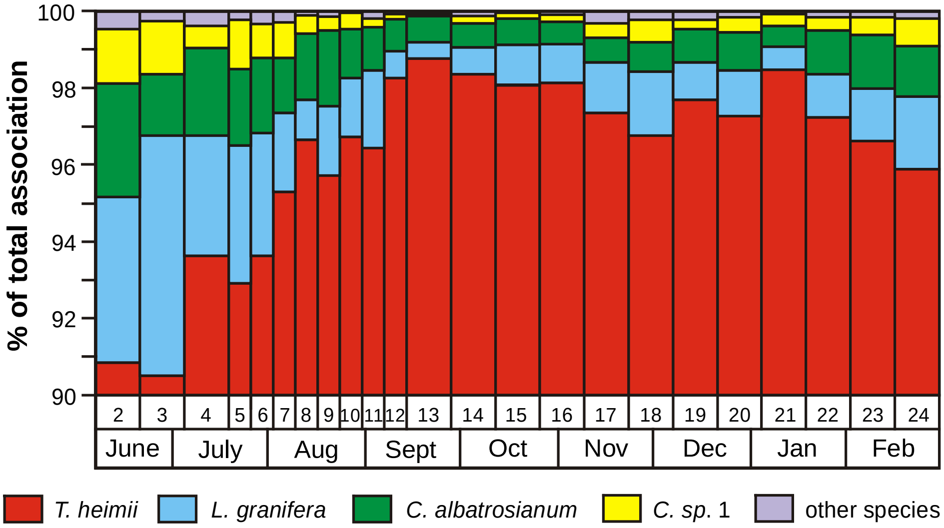

Fig. 3. Relative abundance of the calcareous dinoflagellate cysts. Note that scale starts at 90%.

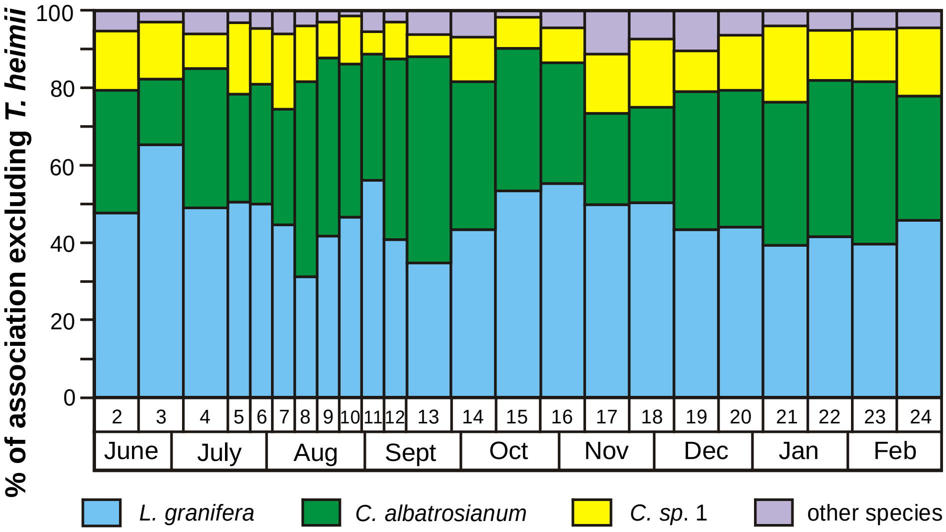

Fig. 4. Relative abundance of the calcareous dinoflagellate cysts if excluding the dominating species *T. heimii*.

L. granifera is the second most abundant species, accounting for 31 to 65% of the association without *T. heimii* (Fig. 4). Similar to *T. heimii* fluxes, the *L. granifera* fluxes show a first peak in sample 4, a decrease when the second gyre reaches the trap site and surface temperatures drop, and an increase again from sample 9 to 11. As opposed to the continuously increasing flux of *T. heimii* during late SW monsoon, there is a decrease in the *L. granifera* flux in sample 12 and 13, once again during times of decreased sea surface temperatures (grey bars in Fig. 2 A, B). The two pronounced drops in *L. granifera* fluxes (samples 6-8 and 12,13) are also expressed by a decrease in the relative abundance of this species (samples 8 and 13, Fig. 4). During fall inter-monsoon the *L. granifera* fluxes decrease until they reach very low values in December (samples 19 and 20), to slightly increase again with the beginning of the NE monsoon.

The development of the *C. albatrosianum* flux is comparable to that of *L. granifera* but lacks the drop during late SW monsoon, showing a broad maximum instead. Fluxes of *C. sp.* 1 do not change significantly over the studied period.

In the underlying surface sediments the same calcareous dinoflagellate cyst species are found as in the sediment trap material. However, cyst accumulation rates at the seafloor (4047 m depth) are considerably lower than the mean fluxes into the trap at 1032 m depth (Table 1). The largest loss with 96% is found for *T. heimii*, whereas surface sediment accumulation rates of the other species differ by 81 to 90% from the mean flux at the sediment trap. In other words, the mean *T. heimii* flux in the sediment trap is 28.5 times higher than at the seafloor; this factor is only 5.2 to 9.6 for the other species. This also manifests itself in a lower relative abundance of *T. heimii* in the surface sediments (89%) as compared to the sediment trap (mean 96%).

Table 1

Comparison of mean cyst flux in the trap (samples 2 to 23) with cyst accumulation rates at the seafloor.

Cyst flux (no./m^2d)	*T. heimii*	*L. gran.*	*C. alba.*	*C. sp.* 1
MST-9E mean	476458	6154	4824	1635
915	16705	644	933	257

Discussion

Maximal fluxes of calcareous dinoflagellate cysts during the late SW monsoon indicate that cyst production is favoured under conditions of mature upwelled water, which is characterised by relatively high nutrient concentrations and reduced turbulence (Fig. 2). In turn, increasing re-stratification of the upper water column and nutrient depletion during fall inter-monsoon lead to considerably decreasing cyst fluxes. Earlier work on core material and surface sediments suggested the opposite: higher production of calcareous dinoflagellate cysts during oligotrophic and more stratified conditions (Höll et al., 1998, 1999; Esper et al., 2000; Vink et al., 2000; Vink et al., 2001 a). So far, it has been difficult to separate the effects of nutrient concentrations and stratification on the cyst production. Vink et al. (2001 b) describe prominent increases in cyst accumulation rates in the equatorial Atlantic only at times of nutrient-enriched but more stratified conditions and propose that thermocline stratification is the more important factor. However, they still support the hypothesis of a relationship between cyst production and oligothrophy and thus contrast our results, showing enhanced formation of cysts during periods of increased nutrient supply.

The fact that cyst fluxes increase slightly later than the arrival of the colder, nutrient-rich water from the area of coastal upwelling, encourages the belief that calcareous dinoflagellates are more successful under less agitated conditions. Small-scale turbulence can be favourable for non-motile organisms such as diatoms, because it can (1) overcome diffusive transport limitations so that nutrient uptake is enhanced, and (2) create a more favourable light regime by mixing the organisms in and out the photic zone (Thomas and Gibson, 1990). Motile cells such as dinoflagellates are able to migrate, so that these positive effects of turbulence become less important and possible cell damage effects may play a role. Various laboratory studies emphasise the sensitivity of dinoflagellates to water motion (Thomas and Gibson, 1990; Thomas and Gibson, 1992 and references therein). Blooms of organic-walled dinoflagellates in upwelling regions were reported to be associated with the relaxation of upwelling and hence an increase in water column stability (Blasco, 1977; Estrada and Blasco, 1979; Goodman et al., 1984; Shannon and Pillar, 1986). But also cyst production of various species of calcareous dinoflagellates in laboratory experiments was observed to be considerably higher under non-agitated conditions (Höll, pers. commun. 2001).

However, during the second half of fall inter-monsoon, when stratification is strongest, we recorded minimal cyst fluxes, indicating that stratification may be important but an elevated concentration of nutrients appears to be necessary to maintain cyst production within a stratified water column. We therefore infer that all species discussed in this paper do benefit from increased nutrient supply in the same way as other organism groups, but are less tolerant to turbulence and appear to be able to survive also in lower trophic environments. This explains (1) the slight offset between the peak of calcareous dinoflagellate cysts and the late SW monsoon peak of both the total mass flux and the coccoliths, and (2) that generally in a plankton succession dinoflagellates follow after diatoms, foraminifers and coccolithophorids (Margalef, 1978; Taylor, 1987 and references therein). Our interpretation is in agreement with the results of Montresor et al. (1998), who studied dinoflagellate cysts in surface sediments and sediment trap material from the Gulf of Naples, and describe an association of calcareous dinoflagellates which mainly comprises neritic species. They observed highest cyst production rates from spring to late autumn, when stratified surface waters prevail whereby nutrient concentrations in those coastal waters can be expected to remain higher than in the oligotrophic surface waters off Somalia during late fall inter-monsoon.

The frequently observed inverse relationship between accumulation of calcareous cysts and nutrient levels (or proxies for primary productivity in sediment cores) is most probably the result of increased stratification rather than oligotrophy. As these environmental parameters are often covarying identification of this relationship is often difficult or impossible. In sediment cores, an anti-correlation of cyst accumulation rates and organic carbon content might also reflect enhanced preservation of calcite at times of reduced production and/or re-oxidation of organic matter, depending on oxygen availability and sedimentation rates (Chapter 2).

The stronger reaction on the changing environmental conditions of *T. heimii* as compared to the other species, and accordingly its increasing relative abundance during late SW monsoon can be explained by the ability of *T. heimii* to produce more spheres in the same period of time (Karwath et al., 2000a). Enhanced fluxes of *T. heimii* after the passage of cold gyres, when temperature is rising again, disagree with the results of culturing experiments and field studies, which show that this species is adapted to a wide range of temperatures and has its optimum at rather low temperatures around 16°C (Karwath et al., 2000a, b). We therefore infer that the production of *T. heimii* in the western Arabian Sea is controlled by water column stability and nutrient supply rather than by temperature.

A drop in cyst fluxes and relative abundance of *L. granifera* at times of reduced temperatures (grey bars in Fig. 2) and related decrease in stratification is in accordance with results from the Atlantic Ocean (Zonneveld et al., 1999; Vink et al., 2000; A. Vink pers. comm. 2001), the Arabian Sea (Chapter 3) and culturing experiments (C. Höll pers. comm. 2000) which suggest that *L. granifera* prefers warm and stratified surface waters. Although *C. albatrosianum* is also regarded to be a "warm water species" (Kerntopf, 1997; Esper et al., 2000; Zonneveld et al., 2000) its flux does not decrease during the temperature drop in late SW monsoon, indicating that *C. albatrosianum* is more tolerant to lower temperatures and/or reduced stratification than *L. granifera*. Paucity of a clear relation of the *C. sp.* 1 fluxes with any of the studied environmental parameters is consistent with the wide and uniform distribution of this species in various oceanic settings in the Atlantic Ocean (Vink et al., 2001 a; A. Vink pers. comm. 2001).

Comparison of mean cyst fluxes at the sediment trap with fluxes at the seafloor (station 915) points to substantial calcite dissolution at this site. Even if assuming that cyst production during the unsampled time of the year was zero, mean cyst fluxes into the trap would still be 4- to 22-fold higher than into the surface sediment below the trap. That the largest loss is found for *T. heimii* can be explained by the comparably small size of these spheres, making them more susceptible to calcite dissolution. These results are consistent with observations from the NE Arabian Sea, where *T. heimii* was shown to be the most dissolution sensitive calcareous dinoflagellate species (Chapter 2). For the interpretation of cyst fluxes in a sediment core this means that times of enhanced calcite preservation would lead to more pronounced peaks of *T. heimii* fluxes in the profile as comparred to the other species. The effect of a decrease in relative abundance of *T. heimii* due to species-selective dissolution would be even more dramatic if the species was less dominant, e.g. accounted only for 50% of the original association.

Conclusions

The study of calcareous dinoflagellate cyst fluxes in a sediment trap off Somalia reveals a positive relationship between cyst production and nutrient supply which is opposed to the hitherto applied hypothesis of increased formation of calcareous dinoflagellate cysts under more oligotrophic conditions. Highest cyst fluxes during the late

SW monsoon indicate that the combination of relatively high nutrient concentrations and beginning re-stratification within mature upwelled surface waters are favourable conditions for these organisms. Lower fluxes of *L. granifera* cysts could be linked to decreased surface water temperatures and reduced stratification.

We propose that the negative relationship between calcareous dinoflagellate cyst fluxes and primary production, which is often reported from the sediment record, reflects increased stability of the upper water column rather than lower nutrient levels. However, enhanced preservation of calcite at times of decreased organic matter decay would lead to the same pattern and must be considered if interpreting sediment core data.

Comparison of cyst fluxes at the trap and the seafloor below the trap shows that substantial dissolution of calcite takes place at the studied site. With a loss of 96% the small spheres of *Thoracoshphaera heimii* are affected most by this process. Due to the species' ability to produce a large number of spheres in a relatively short period and their high susceptibility to calcite dissolution, *T. heimii* concentrations in sediment cores can be expected to show the strongest variations with time in comparison to other species.

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Appendix 1 - Cyst counts and data used for the calculation of cyst fluxes

sample	starting	mass flux	sediment	water	split	counts						
MST-9E	date	(mg/m^{2}d)	(mg)	(ml)	(µl)	*T. hei.*	*L. gra.*	*C. alb.*	*C. sp.*1	spiny	*C. ope.*	other
2	07/06/92	47.58	4.39	1.0	100	1488	70	49	23	3	4	1
3	21/06/92	86.87	9.11	1.0	100	722	50	13	11	2	0	0
4	05/07/92	198.00	8.37	1.0	100	1468	49	36	9	2	3	1
5	19/07/92	134.19	3.40	0.5	100	1220	47	26	17	1	2	0
6	26/07/92	80.07	7.85	0.8	100	1232	42	26	12	2	2	0
7	02/08/92	123.85	27.95	1.5	50	1620	35	24	16	3	1	1
8	09/08/92	131.89	14.27	1.5	100	1768	19	31	9	0	1	1
9	16/08/92	107.96	9.44	1.0	100	2434	46	50	10	1	2	0
10	23/08/92	194.16	8.04	1.0	100	2532	40	34	11	0	1	0
11	30/08/92	238.86	28.24	1.5	60	2575	55	30	6	3	2	0
12	06/09/92	254.13	26.58	1.5	60	4092	29	33	7	2	0	0
13	13/09/92	297.60	1.30	0.2	125	2990	12	20	2	2	0	0
14	27/09/92	252.65	21.08	1.5	60	4951	34	30	9	5	0	1
15	11/10/92	169.00	18.03	1.5	60	3233	33	23	5	1	0	0
16	25/10/92	114.11	5.46	1.0	100	4350	45	26	8	3	1	0
17	08/11/92	57.34	13.19	1.0	60	3223	44	20	13	6	3	1
18	22/11/92	49.27	6.75	1.0	60	2563	42	21	15	4	2	0
19	06/12/92	22.32	8.47	1.5	70	2823	29	23	7	3	2	2
20	20/12/92	25.97	4.25	1.0	100	3416	42	34	14	2	3	1
21	03/01/93	96.32	8.95	1.5	100	5412	33	31	17	0	2	1
22	17/01/93	27.58	7.42	1.1	70	4303	51	49	16	2	3	1
23	31/01/93	54.23	8.13	1.0	60	3658	49	52	17	2	3	1
24	14/02/93	249.26	20.87	1.5	50	3618	72	49	28	4	3	0

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5. Conclusions and prospects for future research

Amongst the three processes that determine the content of biogenic particles in a sediment, that is, production, transport and diagenesis, the first and the last predominantly influence the calcareous dinoflagellate cyst associations in surface sediments of the Arabian Sea.

Diagenesis

The present thesis clearly demonstrates that calcareous dinoflagellate cysts can be subject to early diagenetic calcite dissolution. In the Recent, sediments under oxic bottom water conditions in the NE Arabian Sea appear to be much more affected by calcite dissolution than those in the western part of the studied area. In the NE Arabian Sea, this process takes place even above the lysocline, which is attributed to high rates of organic matter degradation. Paucity of oxygen within the bottom water leads to considerably enhanced calcite preservation in this region, as shown by the drastic increase of cyst accumulation rates in sediments from within the oxygen minimum zone. This leads to a positive correlation between accumulation rates of carbonate and total organic carbon in these sediments.

Dissolution of calcareous dinoflagellate cysts appears to be species-selective, and thus changes relative abundances of the individual species, thereby falsifying the environmental information contained in the sediments. *Thoracosphaera heimii* is most susceptible to dissolution as is indicated by the surface sediment composition as well as by the comparison of cyst fluxes in a sediment trap off Somalia with those in the underlying surface sediments. Decreasing dissolution sensitivity in the order *Calciodinellum sp.* 1, followed by *Calciodinellum albatrosianum*, thence *Leonella granifera*, is indicated by the surface sediment data, but could not be confirmed in the sediment trap study, whereby the latter represents only one site.

Ecology

Apart from diagenesis, the calcareous dinoflagellate cyst distribution also reflects primary cyst production and thus growth conditions within the studied area. In the Arabian Sea the same species are found as so far are known from the Atlantic Ocean (Höll et al., 1998, 1999; Vink et al., 2000, 2001 a, b; Esper et al., 2000), however, with a generally higher abundance of *L. granifera* and a much lower abundance of *Pernambugia tuberosa* and *Scrippsiella regalis*. The sediment trap data indicate a continuous cyst production of all investigated species, at least from June to February, with highest fluxes during September. This means that these species are able to survive a wide range of environmental conditions, but thrive best in relatively nutrient-rich, re-stratifying surface waters which dominate the trap site at the end of the SW monsoon, just after the upwelling period. Although it is obvious that nutrient concentrations and the degree of surface water stratification both influence the production of calcareous cysts, their relative importance has not been fully understood so far. The significant finding of the sediment trap study is that the combination of elevated nutrient supply and relatively stratified surface waters appears to be most favourable for high cyst production and that strongly stratified but nutrient depleted conditions result in very low cyst fluxes of the studied species. These results do not confirm the existing hypothesis of increased cyst production under stratified but oligotrophic conditions.

The surface sediments indicate that almost all encountered species occur basin-wide in the Arabian Sea, which again points to their relatively large environmental tolerance. However, distinct regional differences in absolute and relative cyst abundances and cyst accumulation rates of the individual species reflect their different ecological optima (after subtracting the dissolution effects), which can be used for palaeoenvironmental reconstructions. The two dominating species *T. heimii* and *L. granifera* have opposing distribution trends, which are - like the monsoon winds - NE/SW directed. Whereas the distribution of *T. heimii* in the surface sediments is most probably determined by species-selective dissolution (see above), higher abundance of *L. granifera* in the NE Arabian Sea can be related to relatively high surface water temperatures (about 25 to 30°C) and the influence of the Indus River. A preference of warm conditions by *L. granifera* is confirmed by the results of the sediment trap study. *C. albatrosianum* also seems to be a “warm water species”, whereas *Scrippsiella trochoidea* thrives along the coasts where seasonality is strongest and cool, nutrient-rich conditions prevail during the upwelling period.

Prospects

The results of this thesis show that calcareous dinoflagellate cysts can generally be applied for palaeoenvironmental reconstructions. However, calcite dissolution must be seriously considered for interpreting a sediment record, and should not be deemed inconsequential even when studying sediments from above the lysocline, especially within highly productive oceanic regions. The results furthermore emphasise the importance of bottom and pore water characteristics for the transformation of the sedimentary record. In most cases the primary signal is difficult to demarcate from post-depositional modification, and it is indispensable to apply a number of different proxies to the same material in order to avoid misleading interpretations. As a consequence, future projects should be planned such that sample sizes large enough to allow for multi-proxy analyses are taken.

Although species selective dissolution is evident from the data of the surface sediments and an approximation of the dissolution sensitivity of the studied species can be given, more data from other regions are necessary to obtain a better idea of the preservation potential of each species and to examine those species which are rare or do not occur in the Arabian Sea. It is, however, certain that the small shells of *T. heimii* are most easily dissolved. Accordingly, their concentrations can be expected to show the largest down-core variations. Low *T. heimii* concentrations and an unusually high ratio of other species to *T. heimii* in a sediment should be viewed as an indicator for calcite dissolution. To assess how much a calcareous dinoflagellate cyst association is changed by calcite dissolution, further investigations of sediment trap material and associated surface sediments are required. Additionally, dissolution experiments under controlled laboratory conditions can help to better define the dissolution sensitivity of the individual cyst species. Such experiments have already started for *T. heimii* (K. Zonneveld, pers. comm. 2001) but should be extended to the other species. Special attention should be paid to the change of the saturation state of the surrounding water through metabolic CO_2 from decaying organic matter.

As opposed to the studied surface sediments, most sediment cores exhibit an inverse relationship of accumulation rates of carbonate and total organic carbon. Likewise, an anti-correlation between concentrations of calcareous and organic-walled dinoflagellate cysts is frequently observed in core material and surface sediments. As long as enough oxygen in the surrounding seawater is available for organic matter decay, an increase in organic carbon fluxes should result in enhanced decay rates and thus enhanced calcite dissolution, which would explain the inverse relationship of calcareous cysts to organic carbon in general and also to organic-walled cysts. In this case, the inverse abundance patterns of calcareous dinoflagellates and dinoflagellates producing organic-walled cysts would not indicate that they occupy different surface water habitats, as proposed in Vink (2000). The idea that the observed anti-correlation of both cyst types is caused by preservation effects rather than different habitats is confirmed by their concomitant abundance peaks in the sediment trap MST-9E off Somalia (chapter 4; Zonneveld and Brummer, 2000) as well as in a sediment trap in the Gulf of Naples (Montresor et al., 1998). It is, however, also possible that calcareous dinoflagellates which inhabit pelagic environments are more tolerant to relatively low nutrient levels than species forming organic-walled cysts, which can lead to the formation of sediments rich in calcareous but poor in organic-walled cysts in nutrient-poor environments. More data from water samples and sediment trap material are needed to assess the habitat widths of both dinoflagellate groups. The problem of selective preservation of organic-walled cysts is often neglected in palaeoceanographic studies and should be focused on more intensely in the future (Zonneveld and Versteegh, subm.). Combination of paleontological and geochemical analyses will obviously help to better understand the interplay of production and alteration of calcareous and organic particles in the sedimentary record.

The inverse relationship between the contents of calcareous cysts and total organic carbon / organic-walled cysts served as the basis for the aforementioned hypothesis which relates high fluxes of calcareous cysts to oligotrophic conditions. Although this hypothesis is not confirmed by the observed seasonal cyst fluxes of the studied species it cannot be excluded that (1) over a longer time period, calcareous dinoflagellates are generally more successful under reduced nutrient levels than most other planktonic organisms, and (2) that some species (e.g. *P. tuberosa*) are less competitive for nutrients, and thus are found in meso- to oligotrophic environments. It has to be carefully evaluated to what extend the mentioned anti-correlation between calcareous cysts and organic carbon / organic-walled cysts reflects biology or diagenesis. More studies on sediment traps also outside the Arabian Sea should be carried out (1) to cover the un-sampled period from March to May, (2) to obtain information on species which are rare or missing in the Arabian Sea, and (3) to test whether the conclusions drawn from the Arabian Sea also hold for other regions and thus can be applied for palaeoceanographic reconstructions.

To further improve our knowledge on the ecological affinities of calcareous dinoflagellates, special emphasis should be placed on their distribution within the water column. Data from water samples of the Atlantic Ocean have shown that *T. heimii* thrives in the deeper parts of the photic zone (Karwath et al., 2000). Similar data should also be obtained for the other species since they are essential for detecting relations between cyst production and environment, including the interaction of different factors. Such studies could also provide more insight into the hitherto poorly understood processes of encystment of calcareous dinoflagellates. In first laboratory studies, carried out at the

University of Bremen, the growth of some calcareous dinoflagellate species was tested under variable temperature, salinity and light conditions (Karwath, 1999). These experiments should be continued with other species and extended to turbulence and nutrient conditions.

Successful application of calcareous dinoflagellate cysts for palaeoceanographic and -environmental reconstructions in the Atlantic Ocean (e.g. Vink et al., 2001 a, b) demonstrates that these cysts are a promising tool in climate research, although some basic questions still need to be resolved. The present study presents an example of a highly productive basin in which differences in early diagenetic processes can lead to the preservation of a signal that is either dominated by primary production (W Arabian Sea) or by diagenesis (NE Arabian Sea), although in both areas an oxygen depleted zone is present. First results from a pilot study on sediment core samples from the NE Arabian Sea

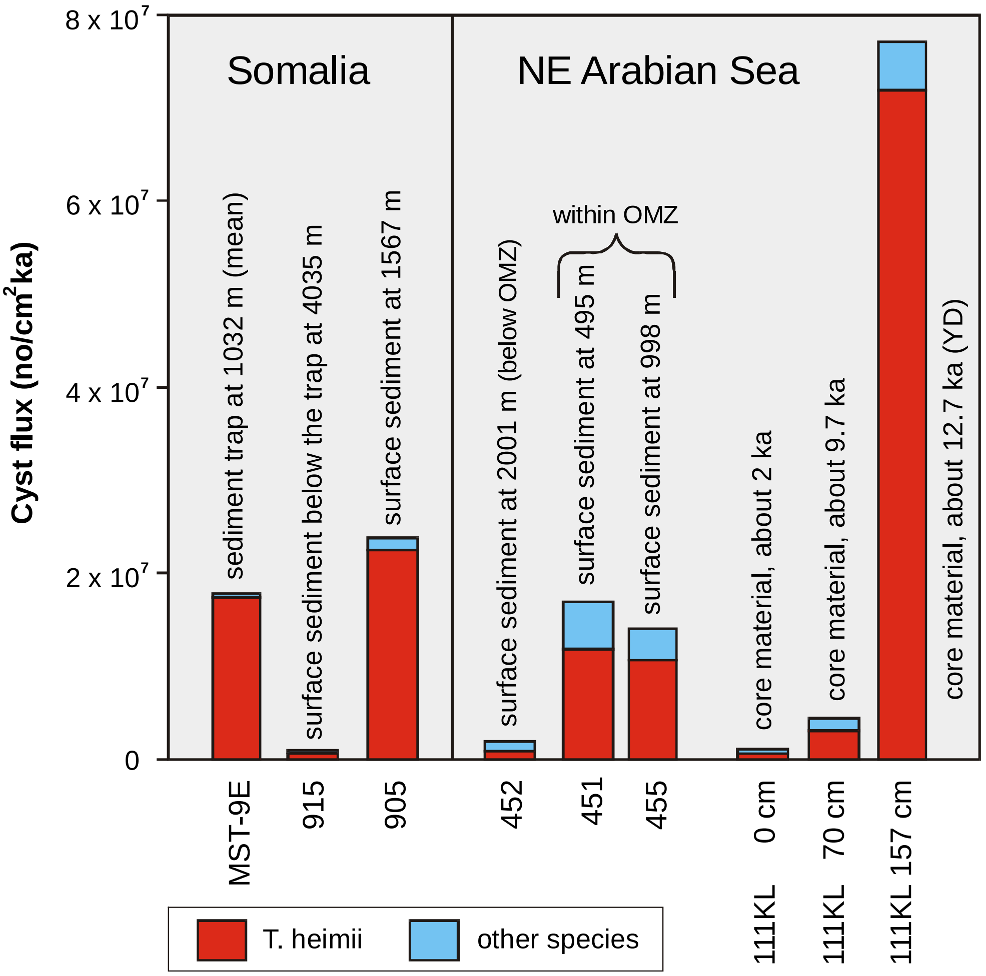

Fig. 1. Comparison of cyst fluxes in the Arabian Sea: mean of samples from the trap MST-9E off Somalia, surface sediments from the Somali continental slope and the NE Arabian Sea and three samples from the sediment core SO90-111KL (775 m water depth) off Pakistan

(SO90-111KL) show that the fluxes of calcareous cysts in this region have varied considerably with time (Fig. 1). Very high sedimentation rates enable a high resolution analysis of this core which allows for detailed reconstruction of changes in palaeoproductivity, intensity and position of the oxygen -minimum zone as well as variations in the strength of the monsoon winds, and which may help to untangle the many loose ends which still exist in our present understanding of the climate system.

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Curriculum vitae; presentation of this thesis

Ines Wendler was born in Dresden, Germany, on 15th of February 1973. In 1997 she finished her study in Geology at the TU Bergakademie Freiberg. Her Diploma thesis, under supervision of Prof. Dr. J. Schneider (Division of Paleontology and Stratigraphy), dealt with the investigation of sequence stratigraphy, sedimentology and micro-facies of Permian carbonates from the Southern Permian Basin and was part of an industrial research project of the Erdöl-Erdgas Gommern GmbH. In the frame of the Graduiertenkolleg "Stoff-Flüsse in Marinen Geosystemen" at the University of Bremen, she carried out studies on calcareous dinoflagellates in sediments from the Arabian Sea, under supervision of Prof. Dr. H. Willems (Division of Historical Geology and Paleontology) from 1997 to 2001, and wrote the present thesis. Results of this project were published as oral- and poster presentations at the following national and international conferences:

- 6th International Conference on Paleoceanography (ICP 6), Lisbon, Portugal, 1998
- Geo-Berlin ‘98, Berlin, Germany, 1998
- Workshop 'Arabian Sea-Benguela upwelling system: tracing climate dynamics across Africa', Schiermonnikoog, Netherlands, 1998
- NEBROC-Workshop, Texel, Netherlands, 1999
- 1st Meeting of German Dinoflagellate Researchers, Darmstadt, Germany, 1999
- 2nd Meeting of German Dinoflagellate Researchers, Kiel, Germany, 2000
- European Geophysical Society XXV General Assembly (EGS 2000), Nice, France, 2000 *(Chapter 2 of this thesis appears in a special publication on one session of this conference)*
- 8th International Nannoplankton Association Conference (INA 8), Bremen, Germany, 2000
- 3rd Meeting of German Dinoflagellate Researchers, Bremen, Germany, 2001
- Geological Society of London: Conference on the Geologic and Climatic Evolution of the Arabian Sea Region, London, England, 2001 *(Chapter 3 of this thesis appears in a special publication on this conference)*