

**Characterization of
West African upwelling areas
based on organic-walled dinoflagellate cysts
and their application in the fossil record**

**Dissertation zur Erlangung des Doktorgrades
der Naturwissenschaften
am Fachbereich Geowissenschaften
der Universität Bremen**

vorgelegt von Ulrike Holzwarth

Bremen, Mai 2009

Tag des Kolloquiums
13.11.2009

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παντα ρει

Alles fließt

All is flux

(Heraklit)

Acknowledgements

I sincerely thank Prof. Dr. Helmut Willems for giving me the opportunity to work out this doctoral thesis. I owe my gratitude to Dr. Oliver Esper and Dr. PD Karin Zonneveld for introducing me to the fascinating world of dinoflagellate cysts. Both of them supervised me in their own special manner and contributed with their permanent support, knowledge and encouragement to the evolution of my ideas. I am also grateful to Prof. Dr. Rüdiger Henrich for providing the second expertise

All members and former members of the Division of Historical Geology and Paleontology contributed to a positive atmosphere and are thanked for their general support: Angelika, Anne, Annemiek, Carmen, Dorit, Dorothee, Erna, Ewa, Frank, Gabie, Gerard, Hartmut, Helmut, Ilham, Ines, Jeanette, Jens, Kai-Uwe, Kara, Katarzyna, Karin, Liang, Marco, Maria, Matthias, Marion, Michl, Monika I, Monika II, Nicole, Oliver, Petra, Rehab, Sebastian, Sonja, Stefanie, Stijn, Tanja, Thomas, Vanessa.

Angelika Freseman, Anne Hübner, Monika Kirsch, Nicole Kniebel are thanked for their help with laboratory work, Michael Marhold and Christian Harnach for sample processing. Computer problems were always successfully solved by Oliver, Matthias Bork and Petra Witte. My office and floor mates Katarzyna Bison, Sonja Heinrich, Dorit Richter, Matthias, Marion Kohn, Vanessa Lürer and Stefanie Dekeyzer are thanked for sharing scientific ideas and also joy, fun and drama. Thank you, Marion, for your empathy and a heart of gold. Stijn de Schepper tried his best to correct my “charming” English mistakes. I thank Karin and Gerard for their unconventional ideas. They are especially acknowledged for the rental of their private microscope which enabled me to dino-homecounting during parental leave. Gerard is thanked for discussing scientific topics at the border to philosophy.

This work was funded by the DFG (Deutsche Forschungsgemeinschaft) through the DFG-Research Center / Excellence Cluster "The Ocean in the Earth System" formerly Research Center Ocean Margins (RCOM) of the University of Bremen. I greatly acknowledge the funding of the participation in several conferences, workshops and courses. The Dino7 conference in Nagasaki with giant spiders, domoic acid and karaoke will remain unforgettable.

The participants and crew members of Meteor Cruise M57/2 and Poseidon Cruise P339 are thanked for their support and the nice working atmosphere on board.

I appreciated scientific discussions with Astrid Eberwein, Martin Butzin, Oscar Romero, Peer Helmke, Holger Kuhlmann, Kenneth Mertens, Jeroen Warnaar, Merlijn Sprangers, Helge Meggers, Gesine Mollenhauer and Jan-Berend Stuut.

My rowing team “Dynamo Damen” is thanked for the great distracting time on the water. Practicing Yoga with Heidrun I, Renate, Anna and Karen helped me a lot in order to relax and see (also scientific) things clearer.

Daz did a good job in counterchecking parts of this thesis.

My brother Peter and my friends Alice, Anne I, Annette I, Annette II, Bärbel, Christine, Claudia, Fernando, Maik, Marc, Markus, Natascha, Philine, Robert, Sabine, Sonja, Salim and Vera are thanked for their friendship and for cheering me up, especially during the last months.

I am deeply grateful to my parents for teaching me important skills, for their neverending encouragement and financial support. Also my family members, particularly Anne II, HU, Doris, Keno (>Dinokakerlaken<), Heidrun II and Ingo are thanked for their interest and emotional support. My son Juro contributed with useful comments to Figure 6a in Chapter 4 (<das ist eine tolle Piratenschatzkarte<) and broadened my mind with his happiness and by separating the important from the unimportant.

Benno, words are not enough to thank you for your love, understanding, patience and the best recourse one can imagine.

Lieber Juro,

Du wächst in einer Zeit auf, in der kein Zweifel mehr besteht, daß wir Menschen einen Teil zum Klimawandel beitragen, was zu viel Unsicherheit und Angst führt.

Wenn Du später einmal lesen kannst und Englisch gelernt hast, wirst Du Dir vielleicht meine Doktorarbeit ansehen. Ich habe mich bemüht, in der Einleitung alles aufzuschreiben, was Du wissen musst, um nachzuvollziehen, woran ich geforscht habe und weshalb ich das getan habe. Mit diesem Wissen kannst Du auch Diskussionen und Szenarien über den Wandel des Weltklimas besser verstehen und einordnen. Das Klimageschehen befindet sich auch ohne den Einfluß der Menschen ständig im Wandel und hängt von so vielen Faktoren ab, die sich gegenseitig verstärken oder abschwächen, dass wir sie für Vorhersagen - zumindest bis heute - nicht alle berücksichtigen können. Und obwohl es schon sehr viele Untersuchungen über das Klima in der Vergangenheit (zB. der Saurierzeit oder der Zeit, in der die Mammuts, Säbelzahn tiger und Riesenfaultiere gelebt haben) gibt, wissen wir noch lange nicht alles über die Mechanismen und Ursachen der damaligen Klimaveränderungen. Auch meine Untersuchung über die Klimaveränderungen innerhalb der letzten 45.000 Jahren ist nur ein winzig kleines Puzzlestück in dem großen Bild der Weltklimageschichte, das von ForscherInnen auf der ganzen Welt zusammengesetzt wird. Obwohl es in der Geologie heißt "the past is the key to the future", kann ich Dir beim besten Willen nicht voraussagen, wie das Klima der Zukunft aussehen wird. Ich kann nur hoffen, dass der Wandel keine bedrohlichen Ausmaße annimmt und Du Dir Deine Lebensfreude trotz aller Schreckensmeldungen nicht nehmen läßt.

Deine Mama

Ulrike Holzwarth

28.5.2009

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-Erklärung-

Hiermit versichere ich, daß ich

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Preface

This work has been funded through DFG-Research Center / Excellence Cluster "The Ocean in the Earth System" as part of project A1 "Characterisation of high-productivity regions using microfossils and organic compounds". The work is submitted as a dissertation and has been supervised by Prof. Dr. Helmut Willems under the guidance of Dr. Oliver Esper and PD Dr. Karin Zonneveld.

The thesis is cumulative and includes three manuscripts which are preceded by a general introduction and followed by conclusions and scientific perspectives. Hereby, the introduction provides the scientific background of the thesis and builds the superstructure for the separate manuscripts. The three manuscripts are first-authorships and are either published, have been or will be submitted to peer-reviewed journals.

Appropriate to the journal requirements, different writings for "palaeo" or "paleo" have been used. References are given at the end of each chapter. All personally gathered data presented in this thesis are or will be online available from the public database Pangaea (<http://www.pangaea.de>) and are also either already included in the manuscripts or provided in the Appendix.

Additionally to the findings presented in the three manuscripts, the Appendix of this thesis includes two other published manuscripts which are closely related to but not focus of the main research topic. I contributed to these papers with sample material, data and extensive scientific discussions.

Addendum:

Since the submission of this thesis in May 2009, the second manuscript has been accepted for publication and is now in press and the third manuscript has been submitted in August 2009, so the most recent versions of these two papers have been included in the present thesis for online-publication.

Summary

Environmental and oceanographical dynamics in the world ocean are closely linked to shifts in global climate. Especially coastal upwelling systems are sensitively connected to atmospheric conditions. African continental climate and its adjacent eastern boundary current upwelling areas experienced substantial variations in the past. Hereby, a coupling of aridification in North Africa with Heinrich events in the North Atlantic is currently discussed.

The ongoing enlargement of the Saharan desert and recurrent droughts in the Sahel are attributed to anthropogenic induced climate change. Progressing desertification would force millions of inhabitants to leave their homes as climate refugees with various political and socioeconomic consequences. In order to estimate future climate development, a better understanding of past climatic processes in pre-industrial times is needed. This can be achieved by studying marine productivity records from upwelling regions which represent an archive for climate fluctuations. Organic-walled dinoflagellate cyst (dinocyst) associations in sediments at the sea floor reflect oceanographic conditions in the watercolumn. As such, they have become a valuable tool for paleoceanographic and paleoclimatic reconstructions. For optimal applicability, the dinocyst species have to be tuned to local conditions and small scale features. The present study is based on the analysis of dinocyst associations from coastal upwelling areas off NW Africa and Namibia covering different facets of upwelling patterns as well as regional terrestrial influences. Previous to this work, only limited information on dinocysts in nearshore sediments of the West African upwelling areas was available.

First, the relations between dinocyst associations in surface sediment samples and the present-day sea-surface parameters of the Benguela upwelling system were determined. The 58 investigated samples include in large part shelf sites which are influenced by active upwelling conditions. The dinocyst assemblages reflect gradients of the main oceanographical variables and allow the classification of six subregions: (1) coastal regions associated with turbulence and highest chlorophyll-*a* values, (2) the vicinity of active upwelling with eutrophic conditions, (3) river mouths with terrestrial nutrient supply, (4) more oligotrophic slope and offshore areas, (5) the southern part of the Benguela region and (6) the northern part of the Benguela region characterized by more permanent upwelling conditions. Multivariate ordination analyses reveal the

chlorophyll-*a* content as well as the salinity at the sea-surface as most significantly related to the dinocyst species composition.

Dinocyst associations from surface sediments of the NW African upwelling area have likewise been related to modern environmental conditions in the upper water column. As a new approach, the oceanographic parameters have been supplemented by grainsize-based proxies for fluvial and aeolian input. The dinocyst associations clearly reflect a latitudinal gradient in seasonality of upwelling conditions in combination with different sources of terrestrial input. Four hydrographic regimes are distinguished: (1) the area off Cape Ghir where the upwelling season is shortest and fluvial input highest, (2) the area off Cape Yubi with increasing permanent upwelling, (3) the more oligotrophic area between Cape Ghir and Cape Yubi and (4) the area off Cape Blanc where upwelling prevails perennially. By use of redundancy analysis, the parameters fluvial mud, sea surface temperature and the depth of the mixed layer are revealed to be most significantly related to the dinocyst species association. As second novation, accumulation rates of the dinocyst species were calculated in order to test their potential as productivity proxy. The dinocyst accumulation rates reflect the eutrophic conditions within upwelling filaments and are significantly related to the chlorophyll-*a* content at the sea surface. A combined interpretation of accumulation rates with relative abundance data leads to a better understanding of marine productivity patterns.

This basic knowledge gathered in the NW African upwelling region was applied in a glacial to interglacial reconstruction of paleoceanographic and paleoclimatic conditions off Cape Yubi covering the last 45,000 years. Relative abundances of dinocyst species indicative for the seasonality of upwelling suggest that upwelling conditions prevailed during glacial times and the Younger Dryas whereas stratification increased during the warm Bølling/Allerød and the Holocene. Upwelling coupled trade wind activity decreased during deglaciation while continental humidity increased resulting in fluvial input. Dinocyst accumulation rates suggest that marine productivity off Cape Yubi has not been enhanced during glacial times compared to today. This is most likely due to the local influence of the lowered glacial sea level on the coastal morphology and the shelf width leading to reduced filament formation and nutrient recirculation. On the other hand, highest dinocyst accumulation rates during the early Holocene African Humid Period (AHP) can be attributed to the regional nutrient supply via river input. The dinocyst association suggests changes in upwelling seasonality related to the position of

the ITCZ which was in its southernmost position during glacial times, moved northward during the AHP and again shifted southward from the mid Holocene on.

Finally, two new approaches to improve future reconstructions are presented. One proposes the use of accumulation rates of sensitive and resistant dinocysts and their selective degradation in order to quantitatively estimate primary productivity as well as the bottom water oxygen content. The second study evaluates morphological variabilities of the dinocyst species *Lingulodinium machaerophorum* as a proxy for temperature and salinity in the upper water column.

This thesis enlarged the knowledge about both, spatial and temporal variations in upwelling regions. Dinocysts accurately reflect oceanographic and terrestrial influences which forms the basis for their applications within further reconstructions in coastal areas.

Zusammenfassung

Ozeanographische und ökologische Prozesse im Ozean sind mit dem globalen Klima eng verbunden. Insbesondere Küstenauftriebsgebiete reagieren sensibel auf atmosphärische Veränderungen. Das Klima des afrikanischen Kontinents und seine strömungsabhängigen Auftriebsgebiete an der Westküste unterlagen in der geologischen Vergangenheit erheblichen Veränderungen. Hierbei wird eine Verbindung zwischen Wüstenbildung in Nordafrika und Heinrich-Ereignissen im Nordatlantik diskutiert.

Die Ausbreitung der Sahara sowie wiederkehrende Dürreperioden in der Sahelzone während der letzten Jahrzehnte werden dem anthropogen verursachten Klimawandel zugeschrieben. Fortschreitende Wüstenbildung würde Millionen von Bewohnern dazu zwingen, als Klimaflüchtlinge ihre Heimat zu verlassen - mit unterschiedlichen politischen und sozioökonomischen Folgen. Um zukünftige Klimaentwicklungen vorhersagen zu können, ist es notwendig, klimatische Prozesse zu verstehen, die weit in die vorindustrielle Zeit zurückgehen. Hierzu können marine Sedimentkerne aus Auftriebsgebieten als Klimaarchive genutzt werden. Artenvergesellschaftungen organisch-wandiger Dinoflagellatenzysten (Dinozysten) in Meeressedimenten spiegeln die ozeanographischen Bedingungen in der Wassersäule wider. Somit werden sie als wertvolles Hilfsmittel in detaillierten paleozeanographischen und paleoklimatischen Rekonstruktionen verwendet. Für ihre optimale Anwendbarkeit muß das Vorkommen bestimmter Dinozysten-Arten mit lokalen Bedingungen und kleinskaligen Besonderheiten abgeglichen werden. Die vorliegende Studie basiert auf der Analyse von Dinozysten-Assoziationen aus Auftriebsgebieten vor Nordwestafrika und Namibia wobei unterschiedlichste Facetten des Küstenauftriebs sowie terrestrische Einflüsse betrachtet werden. Bislang waren nur geringfügige Informationen über Dinozysten in küstennahen Sedimenten westafrikanischer Auftriebsgebiete vorhanden.

Zunächst wurden die Beziehungen zwischen den Dinozysten-Assoziationen in Oberflächensedimentproben mit den heutigen Umweltvariablen an der Meeresoberfläche im Benguela Auftriebssystem ermittelt. Die 58 untersuchten Proben stammen zum Großteil vom Kontinentalschelf und sind von aktivem Upwelling beeinflusst. Die Artengemeinschaften der Dinozysten spiegeln die Gradienten der Hauptparameter wider und ermöglichen die Klassifizierung von sechs Unterregionen: (1) küstennahe Regionen mit Turbulenz und höchsten Chlorophyll-*a* Messwerten, (2) eutrophe Gebiete in unmittelbarer Nähe von aktivem Upwelling, (3) Flussmündungen mit terrestrischem

Nährstoffeintrag, (4) oligotrophe Regionen über dem Kontinentalhang und im offenen Ozean, (5) der südliche Teil des Benguela Auftriebssystems und (6) der nördliche Teil des Benguela Auftriebssystems wo permanentes Upwelling herrscht. Multivariate statistische Analysen ergeben, dass der Chlorophyll-*a* Gehalt sowie die Salinität an der Meersoberfläche signifikant mit der Dinozysten Artenzusammensetzung korreliert.

Dinozysten-Assoziationen aus Oberflächensedimenten des Nordwestafrikanischen Auftriebsgebiets wurden gleichfalls zu den dortigen aktuellen Umweltparametern in der oberen Wassersäule in Beziehung gesetzt. Als neuartiger Ansatz wurden diese Parameter durch Proxis für Fluß- und Staubeintrag basierend auf Korngrößenanalysen ergänzt. In den Dinozysten-Assoziationen spiegeln sich deutlich Gradienten in Auftriebssaisonalität kombiniert mit unterschiedlichen Quellen terrestrischen Eintrags wider. Vier hydrographische Regionen können unterschieden werden: (1) das Gebiet vor Cape Ghir, wo die Auftriebssaison ist am kürzesten und Flusseintrag am höchsten (2) das Gebiet vor Cape Yubi, wo die Auftriebsaison länger ist, (3) die eher oligotrophe Region zwischen Cape Ghir und Cape Yubi und (4) das Gebiet vor Cape Blanc, wo konstanter Auftrieb herrscht. Eine Redundanzanalyse ergibt, dass die Parameter Flußeintrag, Meeresoberflächentemperatur und die Tiefe der durchmischten Oberflächenschicht signifikant mit der Dinozysten-Artenassoziation korreliert. Als zweite Neuerung wurden Akkumulationsraten der einzelnen Dinozysten-Arten berechnet, um ihr Potenzial als Produktivitätsproxy zu überprüfen. Die Dinozysten-Akkumulationsraten spiegeln die eutrophen Bedingungen in den Auftriebsfilamenten wider und korrelieren signifikant mit dem Chlorophyll-*a* Gehalt an der Meeresoberfläche. Eine kombinierte Interpretation von Akkumulationsraten und relativen Häufigkeiten ermöglicht ein besseres Verständnis der Produktivitätsmuster im Ozean.

Das im Nordwestafrikanischen Auftriebsgebiet gewonnene Basiswissen wurde daraufhin in einer glazial/interglazialen Rekonstruktion der paleozeanographischen und paleoklimatischen Bedingungen vor Cape Yubi während der letzten 45,000 Jahre angewendet. Relative Häufigkeiten der Dinozysten Arten, die Auftriebssaisonalität anzeigen, lassen darauf schliessen, dass während des Glazials sowie in der Jüngeren Dryas Auftriebsbedingungen herrschten, wohingegen während des warmen Bølling/Allerød sowie des Holozäns stratifizierte Bedingungen zunahmen. Die mit dem Auftriebsgeschehen gekoppelte Passatwindaktivität nahm während der Abschmelzphase ab, während eine Zunahme von Niederschlag zu verstärktem Flusseintrag führte.

Akkumulationsraten der Dinozysten weisen darauf hin, dass die marine Produktivität vor Cape Yubi im Vergleich zu heutigen Bedingungen während des Glazials nicht erhöht war. Dies könnte auf den lokalen Einfluß des niedrigeren glazialen Meeresspiegels auf die Küstenmorphologie und die Schelfbreite zurückzuführen sein, was wiederum eine Reduktion der Filamentbildung und Nährstoffrückführung zur Folge hatte. Demgegenüber stehen höchste Akkumulationsraten der Dinozysten während der Feuchteperiode in Afrika im frühen Holozän, die regionaler Nährstoffzufuhr durch Flußeintrag zuzuschreiben sein könnte. Die Dinozystenassoziation lässt auf Veränderungen der Auftriebsaisonalität schließen, die in engem Zusammenhang mit der Position der Innertropischen Konvergenzzone. Diese hatte ihre südlichste Position während des Glazials, wanderte nordwärts während der afrikanischen Feuchteperiode und bewegte sich wieder südwärts ab dem mittleren Holozän.

Schließlich werden zwei neuartige Ansätze zur Verbesserung zukünftiger Rekonstruktionen vorgestellt. Die eine Studie basiert auf Akkumulationsraten von selektiv erhaltenden sensitiven und resistenten Dinozystenarten, um sowohl die Primärproduktion des Ozeans zu quantifizieren also auch um den Sauerstoffgehalt des Bodenwassers zu rekonstruieren. In einer zweiten Methode werden morphologische Ausprägungen einer Dinozystenart für die Anwendung als Proxy für Salinität und Temperatur in der oberen Wassersäule bewertet.

Diese Dissertation hat das Wissen sowohl über geographische als auch zeitliche Variationen in Auftriebsgebieten erweitert. Dinozysten spiegeln detailliert die ozeanographischen und terrestrischen Einflüsse wider, was für zukünftige paleoklimatische Rekonstruktionen genutzt werden kann.

1. Introduction

1.1. Scientific context and objectives

Global climate is determined by a highly complex interplay of orbital to regional parameters. It is in a state of constant change and evidence for climatic variations can be found all over the Earth's history. The oceans and the atmosphere are tightly linked and together form the most dynamic component of the climate system. Ocean currents and circulation patterns play a crucial role within the process of heat transfer from the equator to the poles (e.g., Broecker, 1987, Weaver et al., 1999; Kuhlbrodt et al., 2007).

Since the last century, the climate system has been additionally affected by anthropogenic induced rapid increase of atmospheric carbon dioxide (CO₂). As a greenhouse gas, CO₂ traps heat within the surface-troposphere system. Elevated concentrations primarily lead to global warming involving a number of secondary effects like hydrological shifts, desertification, melting of the polar caps or an increase of storms and hurricanes. These consequences are of vast ecological and political importance.

CO₂ is part of the global carbon cycle within which the ocean represents the world's major carbon reservoir. Via marine bioproduction, CO₂ is withdrawn from the atmosphere and partly stored in the ocean - a process which recently gave the idea to fertilize parts of the ocean in order to increase the amount of CO₂ sequestration (e.g., Buesseler et al., 2008).

With regard to the ocean's connection to global climate, various studies have been conducted on reconstructions of oceanography and estimates of marine productivity during the last decades (e.g., Fischer et al., 1999 and references therein; Hebbeln et al., 2002; Berger, 2007; Shannon et al., 2009). Although geochemical proxies can provide reliable information on paleoproductivity, they reach their limits when the paleoecological background as an explanation for changes in paleoproductivity is required. Organic-walled dinoflagellate cyst (dinocyst) associations accurately reflect environmental parameters and productivity conditions which in turn are influenced by climate.

In the first part of the study, relationships between the dinocyst community in modern sea floor sediments and the productivity conditions in the upper water column are determined. Hereby, two different high productive upwelling regions have been investigated. In **Manuscript 1** (Chapter 2), dinocyst species associations from sediments

of the Benguela upwelling area off SW Africa are related to environmental parameters. **Manuscript 2** (Chapter 3) relates dinocyst assemblages from sediments of the NW African upwelling area with the conditions at the sea surface. Supplementary, proxies for dust and fluvial input as well as dinocyst accumulation rates are included in the dataset.

Within the second part, this knowledge is applied in a paleostudy where detailed regional information is needed. In **Manuscript 3** (Chapter 4), the oceanographic and climatologic history of the past 45,000 years off and of NW-Africa is reconstructed. Special focus is directed to variations in marine productivity.

1.2. Factors controlling marine productivity and plankton community

Biological processes in the ocean play an important role in terms of carbon exchange between the atmosphere and the ocean (Siegenthaler and Sarmiento, 1993). During photosynthesis, CO₂ is absorbed and converted into carbohydrates. Productivity is the amount of living tissue produced per unit time, often expressed as g C m⁻² d⁻¹. The basis of marine productivity is constituted by marine primary producers, mainly by single-celled photoautotrophic phytoplankton. Biogenic particles are partly exported from the euphotic zone to the deep ocean and buried in the sediment (Berger and Keir, 1984). Together with physicochemical processes, this biological pump allows the world ocean to act as the Earth's largest CO₂ sink (Raven and Falkowski, 1999). Current estimates of carbon fixation by marine phytoplankton amount to about 46 gigatons of carbon per year (Falkowski et al., 2000) of which 16 gigatons are transported to the oceans interior (Falkowski et al., 1998). There are numerous environmental factors which influence ocean primary production which have been reviewed by Levinton, (2001). As photosynthesis is dependent on light, marine phytoplankton are restricted to the photic zone where, in turn, nutrients as well as trace elements are the limiting factors for growth. Major nutrients include nitrogen, phosphorus and silicon. Nitrogen is required for protein synthesis and is taken up by phytoplankton in the form of ammonium, nitrite and nitrate (the latter occurs most abundantly in the ocean). Only cyanobacteria are able to incorporate gaseous nitrogen. Phosphorus is found in sea water mainly as phosphate and is required as an energy source for all enzymatic reactions in the cell. Silicon is present in the ocean as silicic acid and is essential for the skeletal growth of diatoms. Trace elements such as iron, copper or vanadium as well as organic nutrients including vitamins are required in small amounts but can have a severe limiting effect on phytoplankton

growth (Morel et al., 1991). Iron limits the photosynthetic potential as it is the central atom in several proteins which are parts of the electron transport chain. Although iron is most abundant in its oxidized form, phytoplankton may synthesize and release chelating substances into the water to make iron available for absorption.

The amount of primary production attributable to nutrient supply from deeper waters or other external sources is known as new production. The supply of major and trace elements is linked to remineralization of organic matter within the benthic boundary layer (Thomsen, 1999; 2003). Nutrients are carried to the euphotic zone mainly by upwelling and storm-induced turbulence as well as by terrestrial input by rivers and wind. Ocean margins therefore play an important role for the global new production. Recycling within the water-column also takes place and is known as regenerated production.

In addition, other environmental parameters such as temperature, salinity and water turbulence determine the phytoplankton community and distribution as many species are adapted to a specific range of each of these parameters. Water movement, finally, is an important factor as it not only has impact on all the other parameters, but also directly influences the planktic organisms. Turbulence can push the organisms down to a critical depth below which photosynthesis is inhibited. Contrarily, mixing is important for those species which otherwise would sink to the bottom. Finally, horizontal water movements and ocean currents can effectively disperse planktic organisms which enables them to expand their habitats.

Grazing is an important top down process which removes the product of primary production. Within the food web, most heterotrophic planktic organisms are directly dependent on the primary producers. As a result, a succession of prey and predator species occurs.

The species composition and productivity of planktic organisms in the ocean depends on a variety of factors and can change rapidly, especially in highly variable environments like coastal areas. Detecting the relationships between the distribution of these organisms and the controlling factors is of fundamental importance in order to use them for reconstructions of oceanic conditions.

1.3. Dinoflagellates

1.3.1. Biology and life strategies of dinoflagellates

Dinoflagellates (Dinoflagellata Bütschli 1885) are unicellular eukaryotic protists being globally dispersed in aquatic environments (e.g., Evitt et al., 1985; Fensome et al., 1996) with about 2000 known species (Taylor and Pollinger, 1987). This highly diverse group includes planktic, benthic, parasitic and symbiotic forms embarking on photoautotrophic, auxotrophic, heterotrophic or mixotrophic feeding strategies (Schnepf and Elbrächter, 1992). About one half of the dinoflagellate species is heterotrophic feeding on particulate food like diatoms, other dinoflagellates, ciliates or organic matter, while the other half is photoautotrophic possessing chloroplasts.

The major part (~90%) of dinoflagellate species lives planktic in marine surface watermasses exhibiting the greatest diversity in the tropics and in neritic temperate waters (e.g., Stover et al., 1996). They range commonly in size from 20 to 200µm and are capable of vertical migration through the water column with the aid of two flagellae (Taylor and Pollinger, 1987). Dinoflagellates contribute together with diatoms and coccolithophorids to a significant proportion to the marine primary production (Parsons 1984). They generally thrive in matured waters when nutrients are still available, but turbulence decreased (Smayda, 2002). Some species are able to form extensive blooms with millions of cells per liter. Many of the bloom-forming species release toxins into the water. These toxic blooms (so called red tides) sometimes cause massive fish and invertebrate kills (e.g., Heil et al., 2001; Backer et al., 2003). The toxins can also suppress other phytoplankton species allowing the toxic dinoflagellates to dominate the association (Paerl, 1988).

Dinoflagellates feature a multi-stage life cycle which can be very complex. The generally haploid, motile dinoflagellate cells are covered by a cellulosic theca which is non-fossilisable. During periods favoured by rapid growth and population expansion vegetative division dominates (Evitt et al., 1985). Within the life cycle of several species, metabolically inactive resting cysts are produced (Fig. 1). These fossilisable stages are surrounded by a continuous cell wall which consists of highly resistant organic material (Kokinos et al., 1998) or, in much fewer cases, of calcite or silica (e.g., Head, 1996). The diploid resting cysts are thought to be the result of sexual fusion of haploid gametes which are produced by the parent dinoflagellates (Fig. 1; Taylor and Pollinger, 1987). Resting cysts sink to the ocean floor where they are able to survive unfavorable

conditions like anoxia, low temperatures or darkness and remain viable for many years (Dale, 1983). After a certain period of dormancy which can be very variable (Pfiester and Anderson, 1987) during which meiotic division occurs, the protoplast hatches and builds a new vegetative cell. There are additional factors like temperature or light which initiate excystment (e.g., Kremp and Anderson, 2000; Blackburn and Parker, 2005).

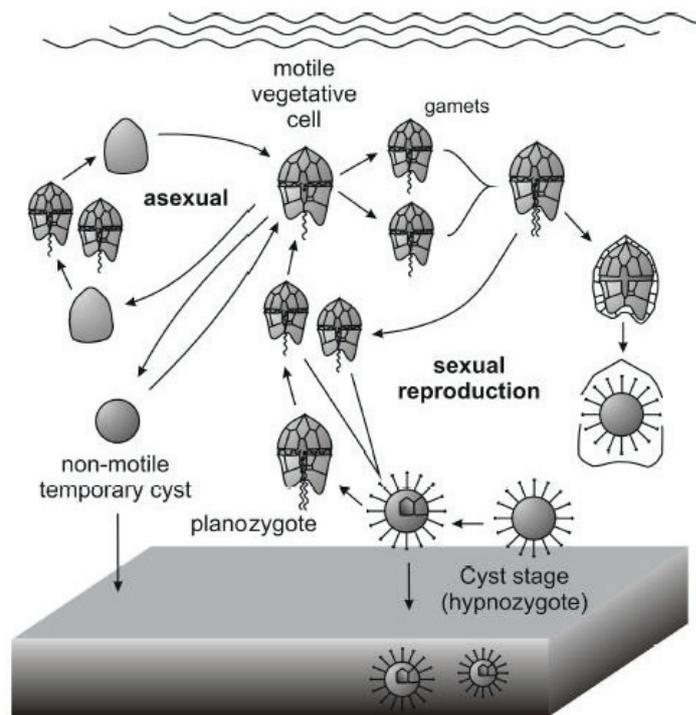


Figure 1. Simplified life cycle of cyst-producing dinoflagellates (from Bockelmann, 2007; after Dale (1983)).

Cyst production often seems to succeed exponential growth of a population and commonly occurs after blooms. Cell density is discussed to cause the release of pheromone-like substances which enable the dinoflagellates to tune their gamete formation (Wyatt and Jenkinson, 1997; Blackburn and Parker, 2005). Triggers like changes in temperature, salinity, light and nutrients also can determine the onset of cyst production. Although encystment is associated with sexual reproduction, it has an important ecological function as a means of surviving adverse conditions (Sarjeant et al., 1987) and seeding new populations when conditions are favorable (Dale, 1983).

About 260 (adequate to ~16%) of the known living dinoflagellates produce resting cysts (Fensome et al., 1993; Head, 1996). Each cyst forming dinoflagellate species produces a cyst which is morphologically specific for that species which is called

cyst-theca relation (Head, 1996). Figure 2 shows a selection of organic-walled dinocyst species which were observed (among others) in this study

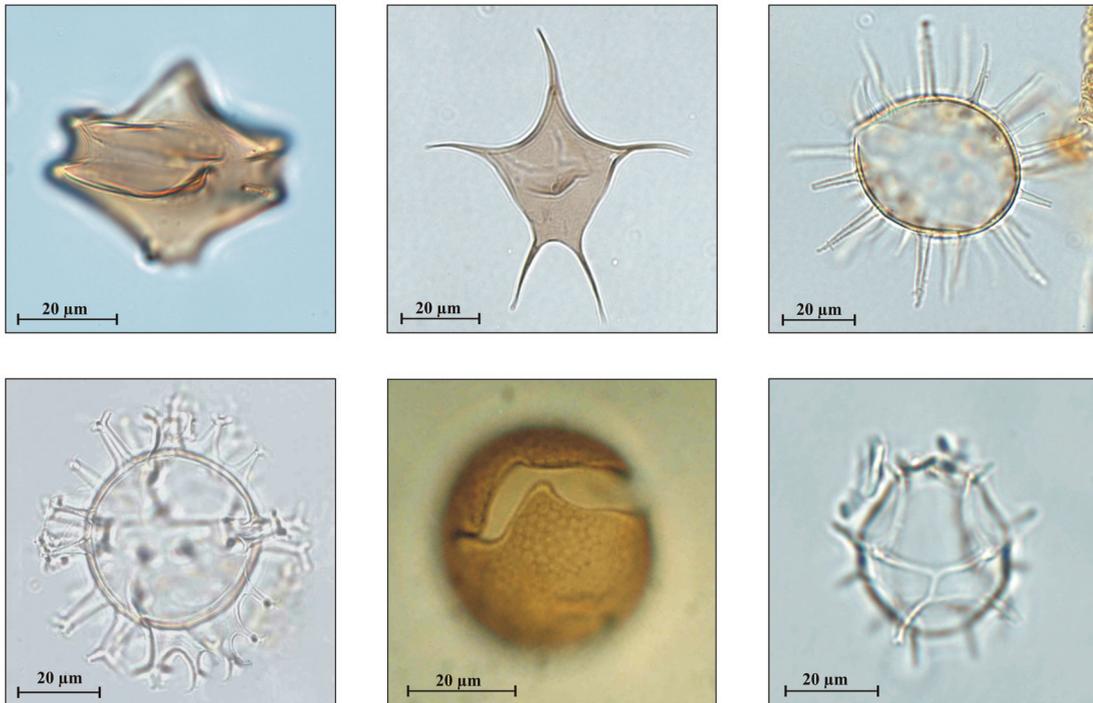


Figure 2. Selection of organic-walled dinoflagellate cyst species. From left to right: *Selenopemphix quanta*, cyst of *Protoperidinium stellatum*, *Lingulodinium machaerophorum*, *Spiniferites mirabilis*, cyst of *Gymnodinium catenatum*, *Impagidinium aculeatum*.

(Photos: Oliver Esper, Ulrike Holzwarth, Jeroen Warnaar and Karin Zonneveld)

The record of dinoflagellate cysts with similar morphological characteristics like those of today goes back to the Early Triassic. Diversity maxima occur in the Late Triassic and Early Jurassic which have been linked to higher ecological variance within shelf environments during sea level highstand (MacRae et al., 1996). Because of their long geological history and high biostratigraphic resolution, the cyst record of dinoflagellates is increasingly used in paleoecologic reconstructions and hydrocarbon exploration (e.g., Pross and Brinkhuis, 2005).

1.3.2. Application of organic walled dinoflagellate cysts in paleoceanographic reconstructions

Assemblages of dinocyst species preserved in sediments correspond to the association of their motile stages in the upper water column and therefore reflect the prevailing conditions there. The first studies on the modern distribution of dinoflagellate cysts and their ecological affinities were carried out by e.g. Wall and Dale (1967) and Wall et al. (1977). Since then, an increasing number of studies proves organic-walled dinoflagellate cysts to be useful proxies for environmental and hydrographic changes (e.g., Harland, 1994; Marret, 1994; Dale, 1996; Rochon et al., 1999; Zonneveld and Brummer, 2000; de Vernal et al., 2001; Dale et al., 2002; Marret and Zonneveld, 2003; Pospelova et al., 2006, Esper and Zonneveld, 2007; Pospelova et al., 2008). Several studies have recognised regionally restricted distributions or provinces where terrestrial input and stratification exert a more important influence on the dinocyst assemblage than sea surface temperature or salinity (e.g., Vink et al., 2000; Radi and de Vernal, 2004; Pospelova et al., 2005; Bouimetarhan et al., 2009; Zonneveld et al., 2009). Dinocyst-based paleostudies include reconstruction of sea-surface temperature or salinity, sea ice cover, bottom water ventilation or marine productivity (e.g., Lewis et al., 1990; de Vernal et al., 1994; Rochon et al., 1998; Mudie et al., 2002, Esper et al., 2004; Bockelmann, 2007; Radi and de Vernal, 2008).

However, the application of fossil organic-walled dinocysts as a proxy for abiotic conditions has to be exercised with caution due to various reasons. Firstly, depending on the sedimentation rate, associations in the sediment represent a longer time interval than the known corresponding conditions in the water column. Secondly, little is known about the frequency of reproduction and encystment. The resulting cyst flux can be species-specific and might depend on other factors than physical water characteristics (Persson et al., 2008). Thirdly, like all particles in the ocean, dinocysts can be dislocated from their site of production resulting in a spatial shift of the original association. Finally, organic-walled dinocysts are species-specifically sensitive to oxidation. This has been suggested during laboratory sample processing (Dale, 1976; Marret, 1993; M. Bork, pers. comm.) and documented in natural environments (Zonneveld et al., 1997; Zonneveld et al., 2001; Kodrans-Nsiah et al., 2008). Selective degradation effects can considerably alter the primary dinocyst assemblage which could lead to severe misinterpretations. However, selective preservation could be a promising tool to quantify past primary production and

to reconstruct bottom water oxygen concentrations (Versteegh and Zonneveld, 2002; Zonneveld et al., 2007; Bockelmann, 2007).

1.4. Areas of investigation

1.4.1. Features of coastal upwelling regions

Within eastern boundary current systems, the phenomenon of coastal upwelling provokes extraordinary high marine productivity (e.g., Longhurst et al., 1995; Carr, 2002). Two major examples, the Benguela upwelling system off SW Africa and the NW African upwelling area are focus of this study. The mechanism of coastal upwelling is physically driven by the longshore blowing SE or NE trade winds and Coriolis-force induced Ekman transport which causes an offshore movement of surface waters. As a consequence, central water masses well up on the shelf and are then transported at the surface within a divergent horizontal flow (Fig. 3).

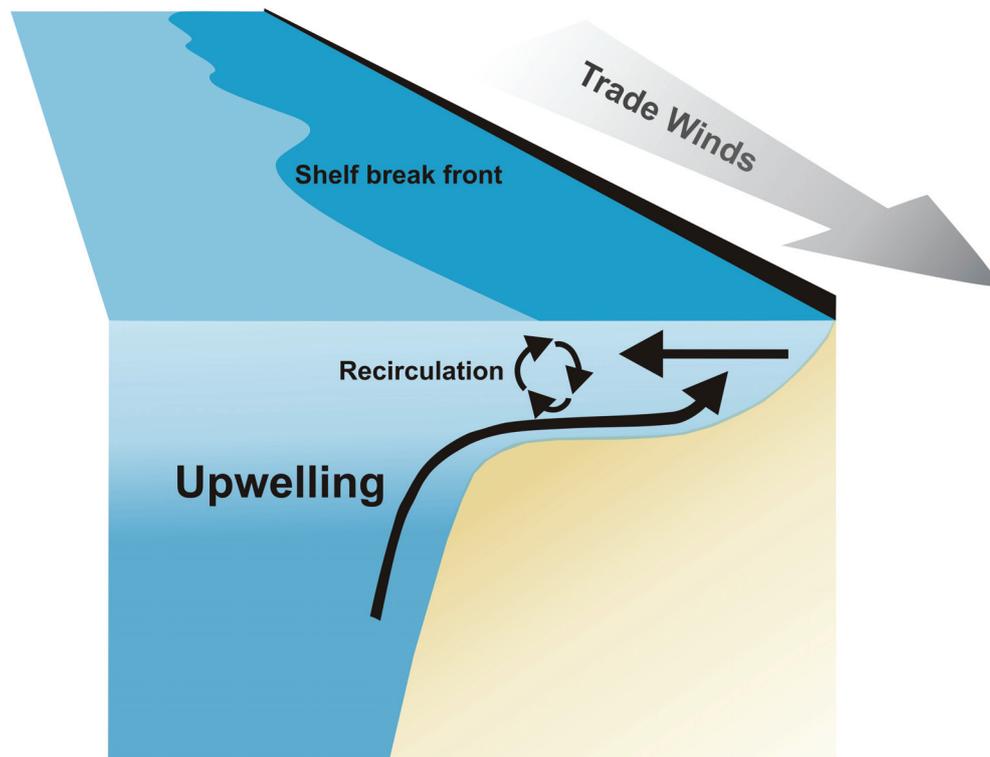


Figure 3. Conceptual model of coastal upwelling (simplified after Summerhayes et al., 1995a).

Central waters are characterised by low temperatures and relatively high nutrient contents. The shelf edge usually forms the border between cold and nutrient rich upwelled water masses and the warmer oligotrophic oceanic waters (Barange and Pillar, 1992; Hagen, 2001). However, depending on the coast morphology, eddies and filaments can develop at prominent capes which then export the upwelled waters from the shelf far offshore (Lutjeharms et al., 1991; Hagen, 2001). These filaments show a high variability in time, offshore expansion and width. The strength and duration of coastal upwelling is coupled with the intensity and presence of the trade winds. Trade wind forcing, in turn, varies with the position of the intertropical convergence zone (ITCZ), a band of low pressure where the SE and NE trade winds converge.

A key feature of bioproductivity in upwelling systems is that it is mainly based on new production fuelled by large amounts of remineralized nitrate. High rates of new production and the nutrient transfer to higher trophic levels are fundamental to sustain productive fisheries (Croll et al., 2004). It is estimated that the world's upwelling regions account for 5% in total for the global primary production (Pauly and Christensen, 1995) although covering only 1% of the ocean's surface (Berger and Wefer, 2002).

The reconstruction of upwelling patterns is an essential part of paleoceanography as upwelling is linked to major oceanic processes such as current patterns, mixing of water masses, wind stress and biogeography (Summerhayes et al., 1995b; Berger and Wefer, 2002 and references therein) but also to the global heat budget (e.g., Wefer et al., 1996; Lutjeharms et al., 2001).

1.4.2. Comparison of the Benguela upwelling system with the NW African upwelling region

The Benguela upwelling system and the NW African upwelling region have much in common, but there are also notable differences. The Benguela upwelling system (BS) is located between 35 and 15°S off the SW African coast (Fig. 4).

It is named after the SE trade wind driven Benguela Current which flows northward along the coast as part of the South Atlantic Subtropical Gyre (Fig. 5). The NW African upwelling region (NWU) extends from 12 to about 32°N. The NE wind driven Canary Current flows southward between the Canary islands and the coasts of Morocco, West Sahara and Mauritania and is part of the North Atlantic Subtropical Gyre (Fig. 5).

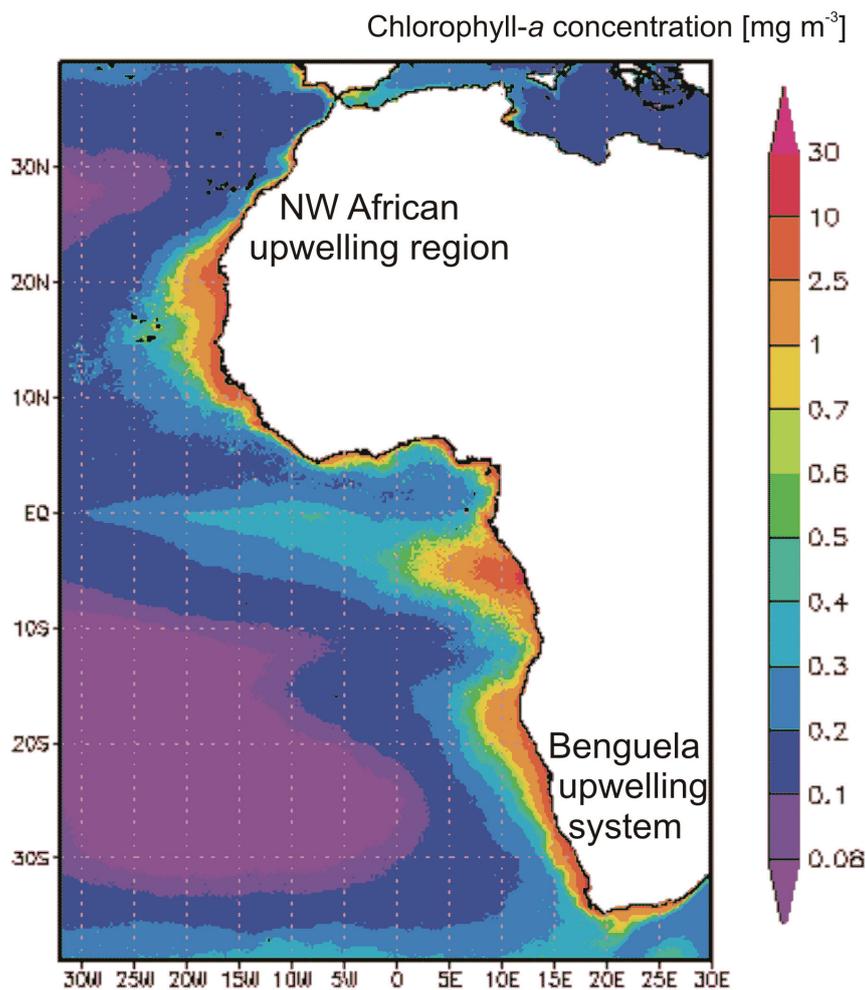


Figure 4. Chlorophyll-*a* concentrations at the Sea surface averaged over monthly values from September 1997 to January 2009 (Source: Ocean Biology Processing Group SeaWiFS Monthly Global 9-km Products; <http://reason.gsfc.nasa.gov/OPS/Giovanni/ocean.seawifs.shtml>)

Chapters 2.2., 3.2 and 4.2 provide detailed descriptions of the oceanographic and climatologic features of the BS and the NWU. Here, we concentrate on the characteristic differences between the two investigated upwelling areas.

Mean primary productivity rates are estimated to be slightly higher in the BS ($2.49 \text{ g C m}^{-2} \text{ d}^{-1}$) compared to the NWU ($1.71 \text{ g C m}^{-2} \text{ d}^{-1}$) (Carr, 2002). In contrast, latitudinal productivity variations are higher in the NWU where chlorophyll-*a* based productivity estimations decrease rapidly to the North (Carr (2002); Fig. 4).

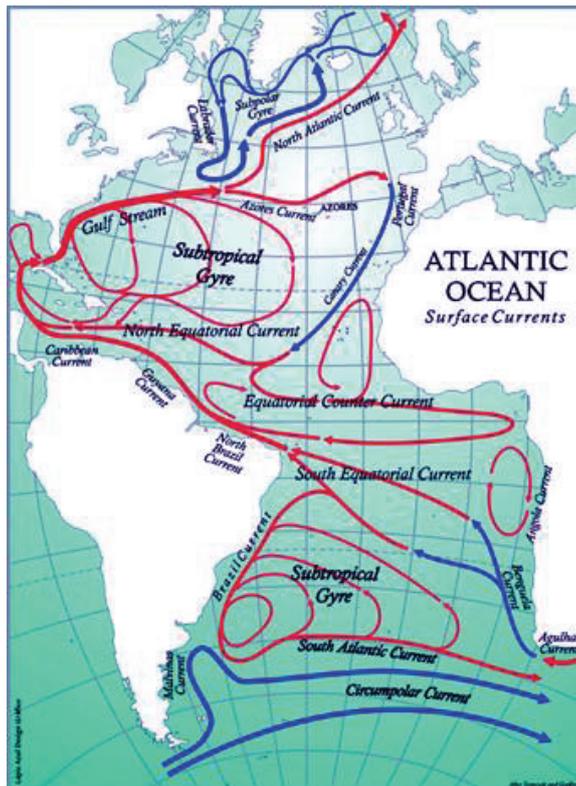


Figure 5. Surface Currents of the Atlantic (after Tomczac and Godfrey, 1994).

Because of seasonal changes in insolation and local air pressure, the position of the ITCZ is located more northward in boreal summer and more southward in boreal winter (Fig. 6a and b). This also leads to latitudinal shifts of the trade wind belts (Fig. 6a and b). As a result, the duration of the annual upwelling period changes with latitude (Fig. 6c) which causes the latitudinal productivity differences in upwelling regions. Within the BS, SE trade winds exhibit their maximum strength at 25°S (Shannon and Nelson, 1996). In the Southern Benguela Region (SBR), between 25-35°S, upwelling occurs seasonally in austral spring and summer (Lutjeharms and Meeuwis, 1987; Shannon and Nelson, 1996) whereas in the Northern Benguela Region (NBR), between 15-25°S, permanent upwelling is observed (Shannon, 1985; Lutjeharms and Meeuwis, 1987). Upwelling activity is sharply confined by the Angola Benguela Front between 14 and 17°S. In the NWU, upwelling occurs seasonally in summer to early autumn from 25-32°N whereas from 20-25°N perennial upwelling prevails (Mittelstaedt, 1991; Hernández-Guerra and Nykjær, 1997). From 12-20°N, seasonal upwelling is observed in boreal winter (Nykjær and Van Camp, 1994; Santos et al., 2005).

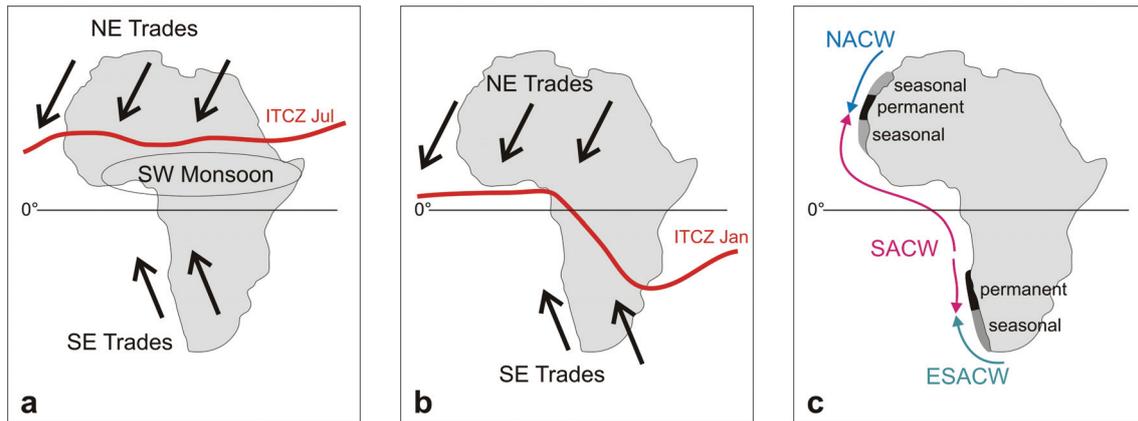


Figure 6. Position of ITCZ over the African continent in July (a) and January (b). Resulting latitudinal differences in the seasonality of upwelling conditions within the NW African upwelling region and the Benguela upwelling system (c). The central water masses as upwelling source are also displayed. For references, see text.

The southwest coastline of Africa runs relatively straight and is incised only with a few capes and embayments. Off these capes, about seven major upwelling filaments expand from the coast (Shannon, 1985; Lutjeharms and Meeuwis, 1987). The NW African coastline in contrast, is more irregular and features prominent capes, one of which is the so called giant filament off Cape Blanc which spreads over 450km offshore (Van Camp et al., 1991).

The nutrient properties of the upwelled source waters also govern productivity. Within both upwelling system, the central water masses vary latitudinally (Fig. 6c). Within the BS, relatively nutrient-poor East Atlantic Central Water (ESACW) enters from the South (Mohrholz et al., 2001) and flows northward. Contrarily, South Atlantic Central Water (SACW), featuring a relatively high nutrient content, flows southward in the BS and generally reaches up to 25-29°S (Shannon and Nelson, 1996, Zabel et al., 2003). SACW originates in the area of the Angola gyre and is also transported into the Northern Hemisphere (Chapman and Shannon, 1987). It is upwelled in the southern part of the NWU with decreasing proportions to the North. From the North, Northern Atlantic Central Water (NACW) enters the NWU. NACW is characterized by lower nutrient contents than SACW (Pastor et al., 2008). Minimum sea surface temperatures of upwelled waters are lower in the BS in relation to the NWU.

The BS is characterized by large areas where bottom waters are oxygen-depleted (Chapman and Shannon, 1985). The intense primary production leads to remineralisation of organic matter by bacteria. During this process, dissolved oxygen is consumed. When

oxygen is depleted, nitrates and ammonium are used to anaerobically decompose the organic matter. If nitrates are completely consumed, sulphates are reduced and hydrogen sulphide is released which is a striking phenomenon in the BS. Within the NWU, only the high productive region off Cape Blanc at about 20°S features low bottom water oxygen concentrations (Sarnthein et al., 1982).

Climatic conditions on land influence the amount of terrestrial input into the ocean. In turn, continental climate is influenced by the cold upwelled coastal waters. The dry Saharan climate is mainly caused by the subtropical high-pressure cell centred over the tropic of Cancer (Nicholson, 2000). The aridity of the Namib desert in SW Africa is determined by the descent of dry, warm air from the east that is cooled by the cold Benguela current (Van Zinderen Bakker, 1975). The upper layer of warm, dry air prevents the cool, humid air from rising and forming clouds. As a result of these arid conditions, only two major rivers discharge perennially into the BS: the Orange River at 29°S and the Kunene River 17°S. Within the NWU, considerable terrestrial input by the Senegal river system at 17°N contrasts absent fluvial input further north - apart from input by the Souss river at about 30°N.



Figure 7. Satellite image of Africa showing the Saharan desert belt in the North and the Namib and Kalahari deserts in the South (Source: NASA).

Because of the aridity of the mainland of both upwelling regions, terrestrial input via aeolian dust plays an important role. Within the BS, dust from the Namib and Kalahari desert is transported by the SE trade winds and the periodically bergwinds into the ocean, especially in the SBR (Shannon and Nelson, 1996). In the northern area of the NWU, Saharan aeolian dust is introduced by the NE trade winds into the NW African margin (Pye, 1987). To a lesser degree, the Saharan Air layer transports dust from the Sahara and the Sahel into the ocean at midtropospheric levels (Prospero et al., 2002). The dust input is considered to add micronutrients into the ocean but can also act as a carrier accelerating the downward transport of particles (Fischer et al., 2009).

Sediments of the NW-African upwelling region are carbonate-dominated whereas sediments from the Benguela upwelling system are comparatively rich in biogenic opal. This is why the region off NW Africa is considered as a carbonate system whereas the BS is regarded as a silicate system (e.g., Fischer et al., 2003; Fischer and Karakas, 2009). One of the reasons for this difference is most likely the silica content of the central water masses. Depletion of silicon in the sea water can limit diatom populations and may direct the course of succession toward phytoplankton lacking a silicous test (Levinton, 2001). SACW is enriched in silica in relation to NACW (Barton, 1998; Pastor et al., 2008). Combined with perennial upwelling in the NBR, this most likely leads to high productivity of diatoms.

To sum up, the environmental parameters influencing the upwelling processes are more seasonal and variable in the NWU than in the BS. Within the NW African margin, this results in higher latitudinal productivity variations.

1.5. Paleoclimate and paleoceanography

Changes in the Earth's climate have been caused primarily by cyclical alterations of the magnitude and seasonality of solar radiation received on Earth. Differences in the amplitude of the Earth's eccentricity, axial tilt, and precession comprise three dominant cycles, collectively known as the Milankovitch Cycles (e.g., Ruddiman, 2001). Taken in unison, variations in these three cycles cause recurrent insolation fluctuations resulting in alternating glacial and interglacial periods. Although insolation plays a key role, many other factors such as atmospheric chemistry, geography or volcanic activity determine the Earth's climate. Climatic and oceanographic conditions influence each other and are connected within a very complex system via positive and negative feedback mechanisms.

1.5.1. Late Quaternary climate fluctuations

Superimposed on the Milankovitch cycles, continental ice cores as well as deep sea sediments provide evidence for the occurrence of rapid climate oscillations at millennial scales (Fig. 8; Heinrich, 1988; Bond et al., 1992; Broecker et al., 1992; Dansgaard et al., 1993). Periods of rapid temperature decrease are known as Heinrich events (HE) whereas Dansgaard-Oeschger oscillations are characterized by rapid warming and gradual cooling over several centuries (Bond et al., 1999). HEs are documented in the North Atlantic as anomalous occurrences of ice-rafted debris layers every 7-10ka (Hemming, 2004). They are thought to be triggered by the Laurentide ice sheet instability and to be related to changes in the thermohaline circulation (MacAyeal, 1993; Sarnthein, 2000; Rahmstorf, 2002). It is supposed that the melting of icebergs during HEs lowered the salinity and density of the high latitude surface waters. Thus, these waters could not sink anymore and as a result, the Atlantic meridional overturning circulation (AMOC) and therefore the heat transport from the equator to the Northpole were interrupted (e.g., Broecker et al., 1986; Shackleton et al., 2000; McManus et al., 2004).

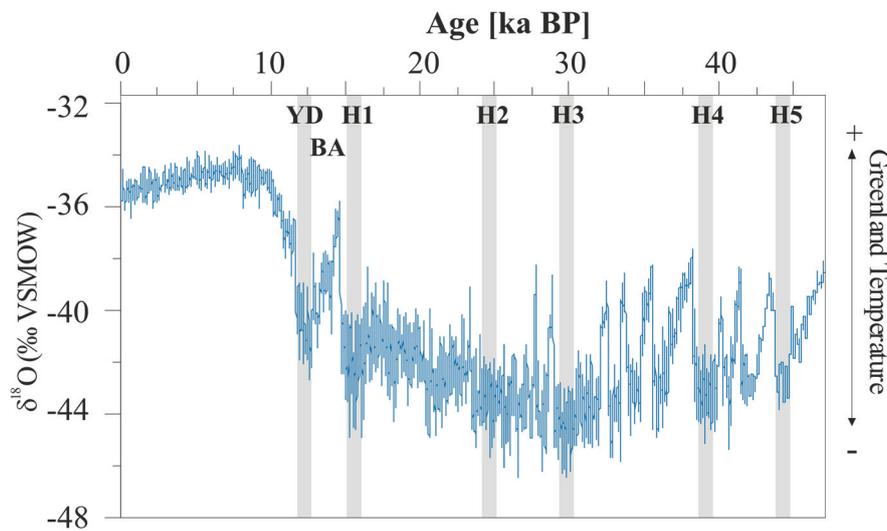


Figure 8. Stable isotope stratigraphy over the last 55ka of the North Greenland Ice Core Project (NGRIP-members, 2004) showing Heinrich events (H), the Bølling/Allerød warm event (BA) and the Younger Dryas (YD).

Numerous authors identified millennial scale variability in hydrological and climatological patterns from subtropical to tropical records to be synchronous with HEs (e.g., Zhao et al., 1995; Arz et al., 1998; Leuschner and Sirocko, 2000; Wang et al., 2001;

Dupont and Behling, 2006; Jullien et al., 2007; González et al., 2008; Mulitza et al., 2008; Tjallingii et al., 2008). Shifting of the ITCZ and its associated monsoon system to the south, has been proposed to be strongly linked to cold HEs in high latitudes (Schulz et al., 1998; Wang et al., 2001; Broecker, 2003; Tjallingii et al., 2008).

A southward shift of the ITCZ is thought to be the cause for phases of desertification in North Africa during glacial times (Mulitza et al., 2008; Tjallingii et al., 2008; Itambi et al., 2009). A shift of the ITCZ to the North, in contrast, is suggested to have led to an increase in precipitation over northern Africa in the early Holocene known as the African Humid Period (AHP) (deMenocal, 2000) with lush vegetation in the recent Saharan desert (e.g., Dupont, 1993; Jolly et al., 1998;).

Climate projections in the frame of anthropogenic climate warming propose a repeated shutdown of the AMOC in consequence of Arctic ice sheet melting (Intergovernmental Panel on Climate Change, 2007). To predict possible consequences of this high latitude process for low latitude climate, it is crucial to have a better understanding the past climatic processes.

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2. Distribution of organic-walled dinoflagellate cysts in shelf surface sediments of the Benguela upwelling system in relationship to environmental conditions

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Marine Micropaleontology (2007), 64(1-2): 91-119. doi:10.1016/j.marmicro.2007.04.001
(received 28.11.2006; received in revised form 28.3.2007; accepted 2.4.2007)

Abstract

To obtain insight in the relationship between the spatial distribution of organic-walled dinoflagellate cysts (dinocysts) and local environmental conditions, fifty-eight surface sediment samples from the coastal shelf off SW Africa were investigated on their dinocyst content with special focus on the two main river systems and the active upwelling that characterise this region. To avoid possible overprint by species-selective preservation, samples have been selected mainly from shelf sites where high sedimentation rates and/or low bottom water oxygen concentrations prevail.

Multivariate ordination analyses have been carried out to investigate the relationship between the distribution patterns of individual species to environmental parameters of the upper water column and sediment transport processes.

The main oceanographical variables at the surface (temperature, salinity, nutrients chlorophyll-*a*) in the region show onshore-offshore gradients. This pattern is reflected in the dinocyst associations with high relative abundances of heterotrophic dinocyst species in neritic regions characterised by high chlorophyll-*a* and low salinity conditions in surface waters. Phototrophic dinocyst species, notably *Operculodinium centrocarpum*,

dominate in the more oceanic area. Differences in the distribution of phototrophic dinocyst species can be related to sea surface salinity and sea surface temperature gradients and to a lesser extent to chlorophyll-*a* concentrations.

Apart from longitudinal gradients the dinocyst distribution clearly reflects regional environmental features. Six groups of species can be distinguished, characteristic for (1) coastal regions (cysts of *Polykrikos kofoidii* and *Selenopemphix quanta*), (2) the vicinity of active upwelling (*Brigantedinium* spp., *Echinidinium aculeatum*, *Echinidinium* spp. and *Echinidinium transparentum*), (3) river mouths (*Lejeunecysta oliva*, cysts of *Protoperidinium americanum*, *Selenopemphix nephroides* and *Votadinium calvum*), (4) slope and open ocean sediments (*Dalella chathamense*, *Impagidinium patulum* and *Operculodinium centrocarpum*), (5) the southern Benguela region (south of 24°S) (*Spiniferites ramosus*) and (6) the northern Benguela region (north of 24°S) (*Nematosphaeropsis labyrinthus* and *Pyxidinosia reticulata*).

No indication of overprint of the palaeo-ecological signal by lateral transport of allochthonous species could be observed.

Keywords: organic-walled dinoflagellate cysts; upwelling; Benguela-System; productivity; chlorophyll-*a*; river mouths

2.1. Introduction

The Benguela upwelling system (BS) along the west coast of Southern Africa is one of the most productive areas of the world ocean (e.g., Shannon, 1985). This is not only important for the fishing industry but also for the accumulation of organic carbon which is a factor of major importance in relation to the global carbon cycle and consequently to global climate change. The high productivity in the region is induced by high input of marine and terrestrial nutrients and trace metals into the photic zone. This supply results from the presence of permanent upwelling as well as aeolian and riverine sources. The temporal dynamics of the carbon production, transport and storage in the BS are not sufficiently understood. To learn more about the reasons of its variability, it is essential to perform detailed reconstructions of the conditions in the past.

Together with diatoms and coccolithophores, dinoflagellates represent a major part of the eukaryotic primary production in marine environments (e.g., Parsons et al., 1984). During their life cycle dinoflagellates produce hypnozygotes during sexual

reproduction for a resting phase of variable duration. Hypnozygotes of several species are protected by an organic-walled cyst (e.g., Dale, 1976; Head, 1996) which can be fossilized in the sediment. More than 80 species of marine dinoflagellates are now known to produce these cysts (Matsuoka and Fukuyo, 2000).

The quantitative analysis of organic-walled dinoflagellate cysts (dinocysts) has become a valuable tool for palaeoclimatic and palaeoceanographic reconstructions, especially in coastal high productive environments where proxies based on calcareous plankton are often problematic (Dale, 1996; Versteegh, 1997; Zonneveld et al., 1997; Rochon et al., 1998; Santarelli et al., 1998; de Vernal et al., 2001; Esper et al., 2004). In regions with high marine productivity the microbial degradation of organic matter in the sediments causes carbonate dissolution (Berger et al., 1982).

The relationship between modern assemblages in the sediment and the environmental conditions in the upper water column is the basis for the use of dinocysts as a proxy for oceanographic conditions.

Studies from quaternary open oceanic environments (e.g., Harland, 1983; Turon, 1984; Mudie and Short, 1985; de Vernal and Giroux, 1991; Edwards and Andrieu, 1992; Matthiessen, 1995; Marret and de Vernal, 1997; Rochon et al., 1998; Marret and Zonneveld, 2003) suggest that it is basically nutrient concentration, turbulence, sea surface temperature and sea surface salinity which are related to the composition of the dinocyst assemblage. Though the general knowledge about modern dinocyst distribution in coastal areas increased considerably (Davey and Rogers, 1975; Lewis et al., 1990; Powell et al. 1990; Dale and Fjellså, 1994; Biebow, 1996; Thorsen and Dale, 1997; Rochon et al., 1999; Zonneveld and Brummer, 2000; Radi et al., 2001; Dale et al., 2002; Matsuoka et al., 2003; Pospelova et al., 2002, 2004, 2005; Kawamura, 2004; Radi and de Vernal, 2004), the understanding of dinocyst assemblages in upwelling systems is still limited. Especially the recognition of the differential effects of upwelling and river discharge on the composition and distribution of the dinocyst association in bottom sediments has not yet been studied in detail. Another complicating factor is the recent discovery that species-selective aerobic degradation can severely alter the dinocyst association in bottom sediments where high oxygen concentrations in bottom/pore waters and low sedimentation rates prevail (Zonneveld et al., 1997; 2001b; 2007). Consequently, previous concepts concerning the ecological relationship of several species have to be revised. Detailed studies in regions where aerobic diagenesis does not overprint the ecological signal are required.

In the present study, we therefore relate the spatial distribution of dinocyst species to the environmental parameters in the upper water column at the sample sites. To avoid possible overprint of the ecological signal by species-selective aerobic degradation, we focussed on shelf samples of sites that are characterised by high sedimentation rates and/or low bottom water oxygen concentrations. Our study complements the work of Zonneveld et al. (2001a) and Bockelmann et al. (2007), where mostly offshore locations and locations along bottom water oxygen gradients were examined. It extends the work of Davey and Rogers (1975) by examining the continental shelf of the Benguela System (BS) in detail.

2.2. Regional setting

The oceanography of the BS has been reviewed by several authors (e.g., Nelson and Hutchings, 1983; Lutjeharms and Meeuwis, 1987; Peterson and Stramma, 1991; Shannon and Nelson, 1996; Shillington, 1998). Fig. 1 shows the main oceanographic features.

The highly productive BS is situated along the south-west coast of Africa and characterised by wind-driven coastal upwelling. The oceanic circulation of this region is controlled by the semi-permanent high pressure system over the subtropical South Atlantic Ocean and a low pressure system that develops over Southern Africa during the austral summer. These atmospheric conditions lead to prevailing winds from the south and southeast. The southeast trade winds are blowing longshore and provide the driving force for upwelling processes in the northward flowing cold Benguela Current (BC). This current is the eastern boundary current of the South Atlantic subtropical gyre and can be distinguished into two branches. The stronger Benguela Coastal Current (BCC) is flowing inshore along the coast, whereas the weaker Benguela Oceanic-Current (BOC) is branching northwestward at about 28°S.

The Benguela System is the only upwelling system which is bounded by warm water currents: the Agulhas Current (AgC) in the south and the Angola Current (AC) in the north. The influence of the AgC is of mesoscale variability. The southwestward flowing AgC collides at the Agulhas Retroflexion south of Southern Africa with the Antarctic Circumpolar Current and the BC (Gordon, 1986). Within this collision zone, rings and eddies of warm and saline AgC water are shed into the South Atlantic Ocean and filaments of AgC-water enter the BCC.

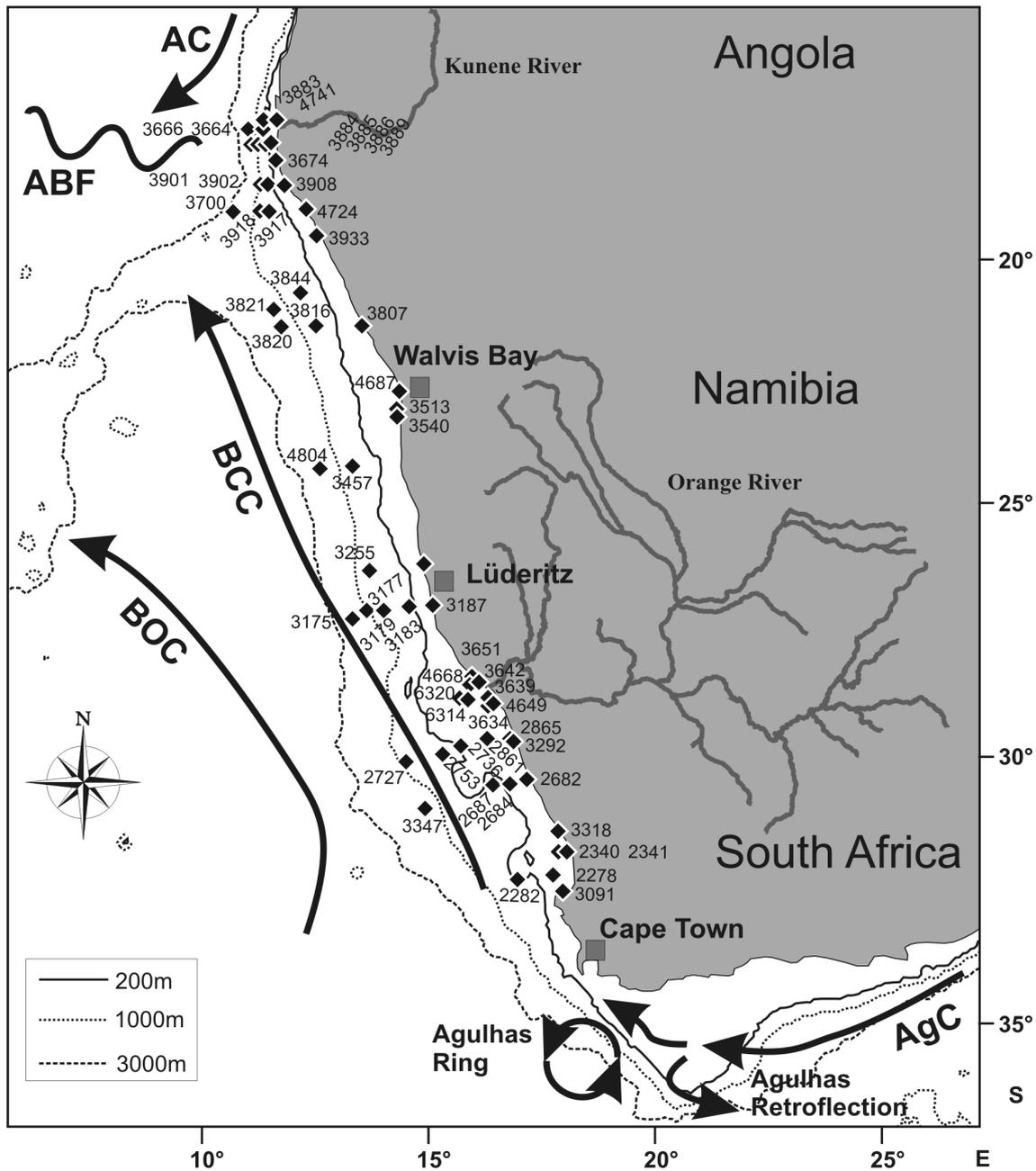


Figure 1. Oceanographic setting of the Benguela System with station numbers of the surface sediment samples (black diamonds).

In the north, at about 16°S, the BCC encounters the poleward flowing AC and forms with a convergence zone the Angola-Benguela Front (ABF) (Shannon et al., 1987; Meeuwis and Lutjeharms, 1990). This front is a permanent feature within the upper 50 m and represents the northern boundary of the BS. A temperature gradient up to 4°C per 1° latitude can be reached. The ABF extends from about 16°S to 14°S and from the coast up to 1000 km offshore during austral spring and summer. The average position of the ABF

shifts seasonally up to two latitudinal degrees in both directions (Meeuwis and Lutjeharms, 1990). In austral winter, the position of the ABF shifts to the north and in austral summer it is situated farthest south.

The depth of the BCC varies from a few meters nearest to the coast to about 120 m depth along the outer shelf. Below, there is a poleward undercurrent which is positioned permanently south of 33°S while the northward boundary changes seasonally. Farther offshore, in the deeper water layers of the BS, water masses of the South Atlantic are common. The thermocline waters (100-500 m) consist of South Atlantic Central Water (SACW). Water is upwelled from a depth of 50-300 m. As there are two different central water masses in the BS, the source of the upwelled water is regionally different. In the northern part of the BS, SACW is flowing polewards with the AC, but in the southern part the Eastern South Atlantic Central Water (ESACW) is flowing northwards with the BC and the poleward undercurrent (Lass and Mohrholz, 2005). SACW is formed in the Angola Gyre and is oxygen depleted, saline and nutrient enriched. ESACW is formed in the Agulhas Rings and is oxygen enriched, less saline and relatively poor in nutrients. Antarctic Intermediate Water (AAIW) occurs between about 500 to 1200 m and flows northwards. At depths between 1000 and 3500 m, the oxygen-rich North Atlantic Deep Water (NADW) is found to flow southwards. Antarctic Bottom Water (AABW) flows northwards below 3800m.

Along the West African Coast, from about 17°S to 35°S, Ekman-driven upwelling of cold and nutrient-rich water occurs. The strength and continuity of the longshore blowing SE trade winds controls the upwelling intensity. In the southern Benguela region (SBR) these trade winds appear highly seasonal with their maximum in austral spring and summer (Shannon and Nelson, 1996). Seasonality is weaker north of 31°S. In the northern Benguela region (NBR) north of 25°S, upwelling persists almost perennial but with its maximum in late austral winter to spring. The warmer oligotrophic subtropical surface water and the cold upwelled water is separated by the upwelling front (Barange and Pillar, 1992). This seaward limit of the active upwelling region is also determined by the topographic change at the shelf break. The westward extent of the upwelling zone is typically between 150 and 250 km offshore, depending on the position of the shelf break front and the intensity of the Ekman transport. In the NBR, the shelf is much narrower and the continental slope is steeper compared to the SBR. As a result, the shelf break front and upwelling region in the NBR are located closer to the coast. With the formation of perpendicular to the coast orientated filaments, plumes and eddies the coastal waters

can be transported across the upwelling front into the open ocean. In extreme cases, these filaments may reach up to 1000 km offshore (Lutjeharms et al., 1991). The life span of such a filament ranges from a few days to several weeks.

The intensity of the Benguela upwelling can vary on an interannual timescale. Hagen et al. (2001) distinguished between weak and strong upwelling years. When the South East Trade winds weaken, Ekman offshore transport ceases and equatorial water intrudes into the NBR (Shannon et al., 1986). The neritic water is then warm and saline. Such events are described as Benguela Niños. During these events the ABF can reach up to 24°S.

The upwelling process strongly influences all oceanographic properties of the water column, such as sea surface temperature (SST), sea surface salinity (SSS), nutrients and the stratification of the upper water column. A longitudinal gradient can be observed and, due to the above mentioned warm water influence of the AC, also a latitudinal gradient. SST for example is much higher in the North (>20°C) compared to the South where SST can be below 14°C near the coast. In general, the values for SST show a strong seasonality (see Fig. 2). Regional differences between austral summer and austral winter amount up to 5°C.

According to the data of the LEVITUS World Ocean Atlas 1994 (<http://ingrid.ldeo.columbia.edu/SOURCES/.LEVITUS94/>), the depth of the mixed layer in the BS shows a coast to ocean gradient with increasing values from 10 to 70 m. The lowest values of the mixed layer depth are found in austral spring and summer. In austral winter it deepens and latitudinal gradients can be observed.

SSS ranges from 34.9 to 35.7 and is lowest in the upwelling area around Lüderitz (Fig. 3). Within the upwelling area, SSS values change from austral summer to winter by only 0.1. North of 20°S, SSS increases within latitudinal gradients with highest maxima in austral summer. Two major rivers discharge perennially from the arid hinterland into the investigation area: the Orange River in the South at 29°S and the Kunene River in the North at 17°S. With a discharge of 6.8 km³/year and 11 km³/year of respectively on the Kunene and Orange rivers (Milliman et al., 1995), they only have limited influence SSS.

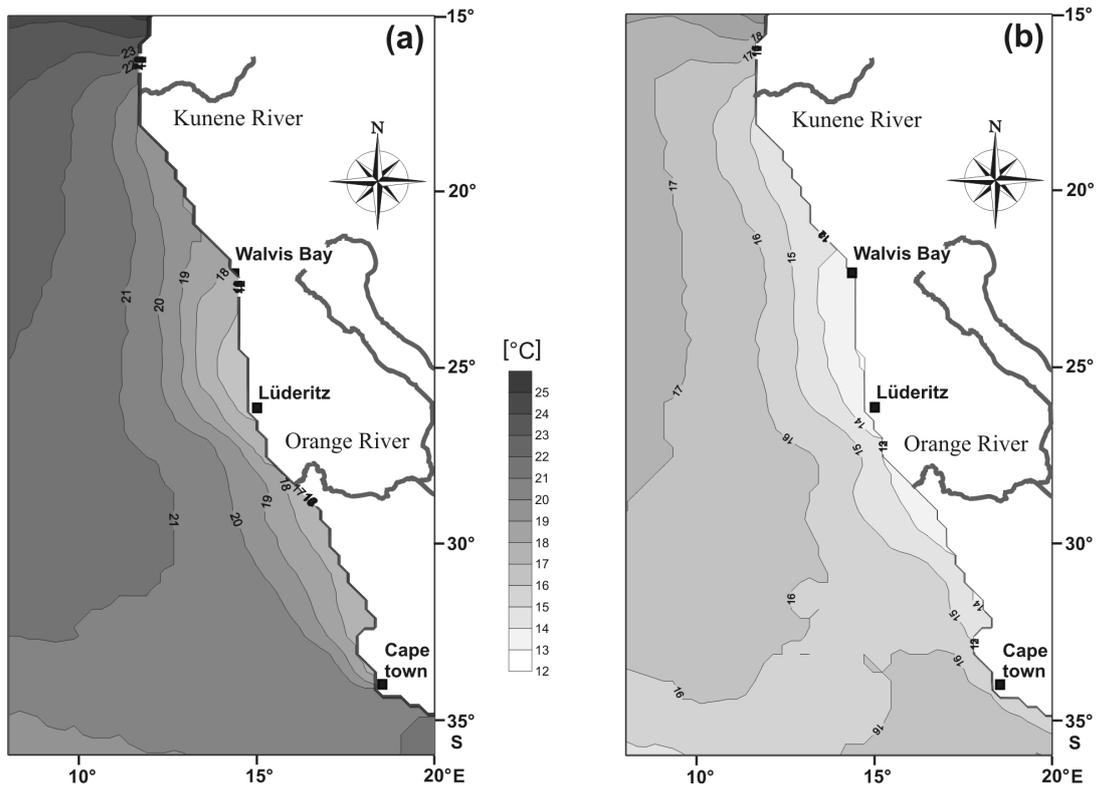


Figure 2. Sea surface temperature in austral summer (a) and austral winter (b). Source: <http://seawifs.gsfc.nasa.gov>.

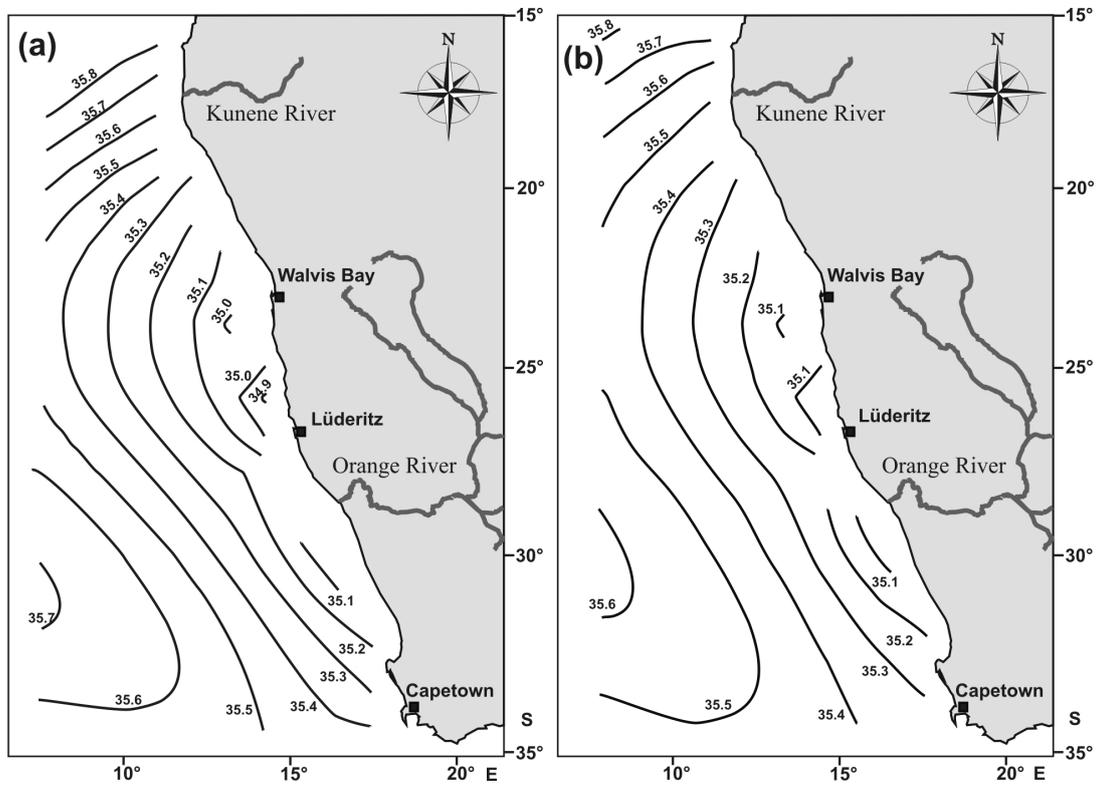


Figure 3. Sea surface salinity in austral summer (a) and austral winter (b). Source: <http://ingrid.ldeo.columbia.edu/SOURCES/.LEVITUS94/>.

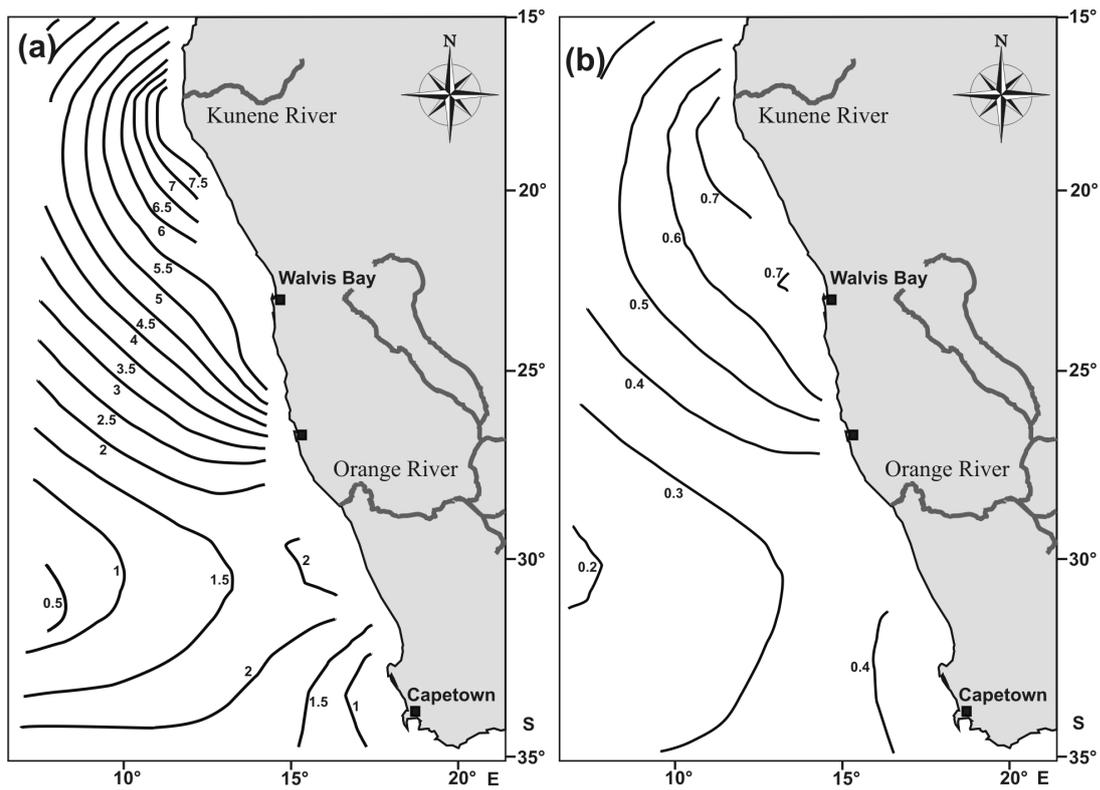


Figure 4. Yearly values (micromolar) for nitrate (a) and phosphate (b). Source: <http://ingrid.ldeo.columbia.edu/SOURCES/.LEVITUS94/>.

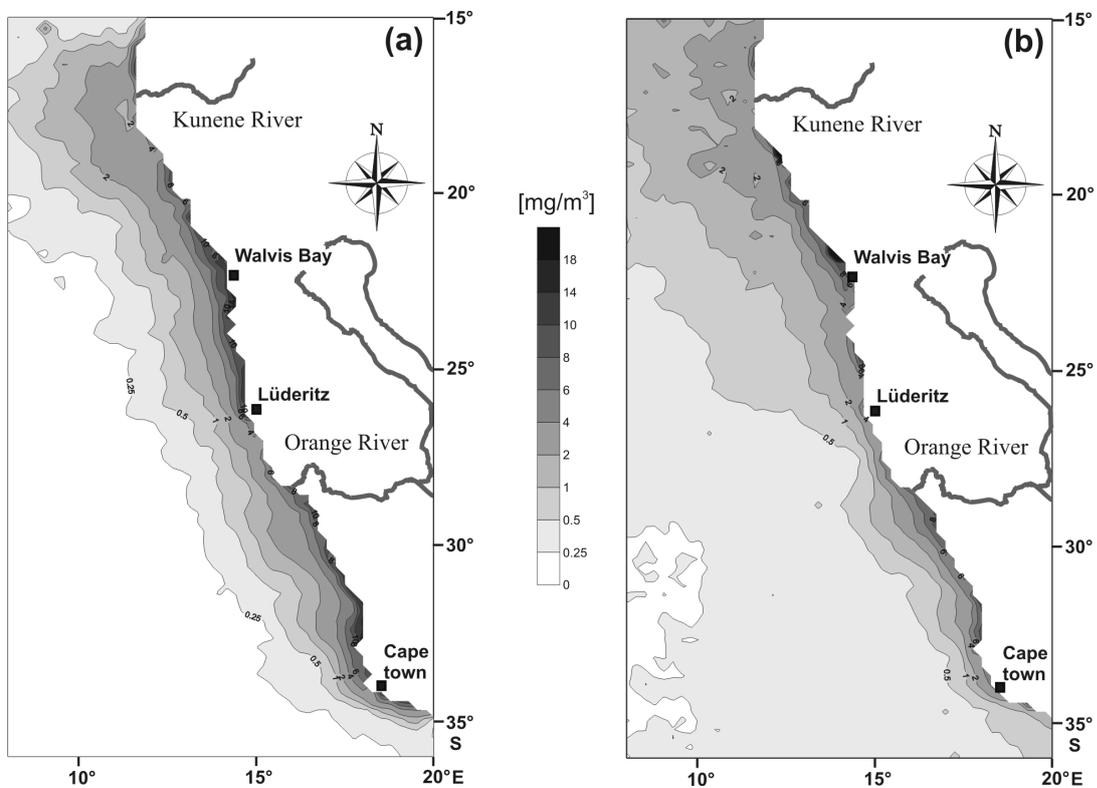


Figure 5. Chlorophyll-a concentrations at the surface in austral summer (a) and austral winter (b). Source: <http://seawifs.gsfc.nasa.gov>.

Aeolian dust from the Kalahari and Namib deserts is transported by two wind systems into the ocean: the south east trade winds and the periodically blowing north east Bergwinds (Shannon and Nelson, 1996). This terrestrial input could be a considerable source of iron, which plays an important role in world oceans as a limiting factor for primary production (e.g., Martin, 1992; Pittman, 2002).

According to the LEVITUS World Ocean Atlas 1994 (<http://ingrid.ldeo.columbia.edu/SOURCES/.LEVITUS94/>), nitrate and phosphate concentrations at the surface are lower in the SBR (Fig. 4). This could be due to the limited nutrients of the ESACW, which is upwelled there.

Satellite images of the chlorophyll-*a* pigment concentration of the sea surface show a general maximum of about 4 to 10 mg per m³ on the shelf (<http://seawifs.gsfc.nasa.gov>). Latitudinal differences are not very pronounced. In austral summer, highest values (about 30 mg per m³) of chlorophyll-*a* have been measured. In this season the gradient between the highly productive coastal waters and the more oligotrophic open ocean is steepest, while during the austral winter the values are more dispersed (Fig. 5).

The Benguela upwelling region is characterised by large areas where very low contents of dissolved oxygen are found (Chapman and Shannon, 1985). Concentrations are much higher above the thermocline because of surface mixing and primary production (Nelson and Hutchings, 1983). Oxygen-deficient bottom water (<2ml/l) is found on the entire continental shelf between the Kunene River and the city of Lüderitz (Dingle and Nelson, 1993). Similarly, also Kristmannsson (1999) concluded that low bottom concentrations of dissolved oxygen occur almost perennially in the BS. Chapman and Shannon (1985) recognise two different sources of low oxygen water. The first is SACW, an oxygen-depleted water mass at about 300 m depth in the Angola region which is transported by a poleward flowing subsurface current. SACW ranges from 25°S to maximal 29°S (Zabel et al., 2003) and often upwells on the shelf. The second source is the local biochemical production of oxygen-depleted water on the shelf because of the decay of organic matter. The main area of production is between Lüderitz and the Kunene River. Other regions with oxygen depleted bottom water are the Orange River mouth (28.5°S) and St. Helena Bay (33°S) (Visser, 1969). In the NBR, transport and production of oxygen-depleted water can combine. Increased upwelling would then lead to decreased oxygen content because of enhanced productivity leading to higher

degradation rates on the one hand and because of upwelling of already oxygen-depleted water on the other hand.

2.3. Materials and methods

2.3.1. Material

The 58 samples investigated in this study were obtained from the uppermost centimetre of the sediment. Samples have been taken with a box- or gravity corer of the South African research vessel Thomas B. Davie during cruises TBD 236, 239, 257, 261, 268, 273, 279, 283, 300 and 398 (Birch, 1975; Rogers, 1977; Bremner, 1981). For sample numbers, sampling dates and geographic positions see Fig. 1 and Table 1. The water depth ranges from 9 m to 2090 m. Sedimentation rates in the investigated area are at least 2 cm/kyr with a maximum of over 16 cm/kyr (Mollenhauer et al., 2004). Thus, most of the studied sediments are much younger than 1000yr. Furthermore, radiocarbon dates of sediment in vicinity of our sample sites reveal that the studied material is of modern age (Mollenhauer et al., 2002; Inthorn et al., 2006b).

2.3.2. Methods

2.3.2.1. Laboratory preparation and taxonomy

About 1 cm³ of sediment was dried at 70°C for at least 24 h. After being weighed, each sample was treated with 10% hydrochloric acid (HCl) to dissolve the carbonates. Shortly after, the suspension was neutralised with 10% potassium hydroxide solution (KOH). After 24h, the liquid was decanted over a 20 µm mesh sieve and washed twice with demineralised water. Hydrofluoric acid (HF, 38%) was added to dissolve the silicious content. Two hours of agitation were followed by two days HF-treatment without agitation. Subsequently, the solution was neutralised by 40% KOH and after another 24 h decanted and washed twice with demineralised water. Each sample was treated with ultrasound for about 1-2 h to clear the dinocysts from organic debris and separate the particles from each other. Samples were washed over a 20 µm precision sieve (Storck-Veco) (equivalent to a 10µm sieving cloth) and concentrated by centrifugation (8 minutes at 3500 revolutions per minute) to 500-1500 µl depending on the particle content.

Dinocysts in the Benguela Upwelling System

Table 1. Geographic sample positions, water depth and count data of the individual species.

Station	Lon	Lat	depth	Cruise	sampling date	cysts/g	total dinocysts	B spp	D cha	E acu	E del	E mon	E spp
2278	17.90	-32.40	105	TBD236	17.06.1970	2700.00	270	22	0	1	0	0	2
2282	17.10	-32.49	295	TBD236	18.06.1970	3718.84	373	55	0	4	0	0	25
2340	18.02	-31.93	116	TBD239	01.08.1970	14190.00	473	207	0	0	0	0	88
2341	18.21	-31.93	84	TBD239	01.08.1970	28020.00	934	528	0	12	2	0	121
2682	17.31	-30.46	56	TBD257	18.02.1971	2020.00	202	66	0	0	0	0	66
2684	16.93	-30.55	180	TBD257	19.02.1971	7280.00	364	16	0	2	0	0	14
2687	16.55	-30.57	224	TBD257	19.02.1971	4666.00	468	6	0	0	0	0	0
2727	14.60	-30.10	530	TBD257	22.02.1971	7200.00	288	9	0	0	0	0	3
2736	15.42	-29.95	205	TBD257	23.02.1971	2102.16	214	7	0	0	0	0	0
2753	15.83	-29.78	191	TBD257	24.02.1971	4116.77	275	13	0	0	0	0	5
2861	16.42	-29.63	165	TBD261	14.05.1971	5384.62	539	34	0	0	0	0	6
2865	16.93	-29.63	102	TBD261	14.05.1971	3952.10	264	122	0	1	0	0	12
3091	18.12	-32.73	9	TBD268	10.11.1971	1862.55	374	58	0	7	0	0	13
3175	13.40	-27.20	2060	TBD268	21.11.1971	21400.00	535	65	0	1	0	0	13
3177	13.72	-27.03	1000	TBD268	21.11.1971	24320.00	608	15	0	0	0	0	13
3179	14.10	-27.03	437	TBD268	21.11.1971	16254.98	544	22	0	3	0	0	12
3183	14.67	-26.95	270	TBD268	21.11.1971	3031.81	305	185	0	19	0	0	26
3187	15.18	-26.96	36	TBD268	22.11.1971	0	0	0	0	0	0	0	0
3255	13.78	-26.22	390	TBD268	28.11.1971	9960.00	332	34	0	0	0	0	18
3265	14.93	-26.05	31	TBD268	29.11.1971	0	0	0	0	0	0	0	0
3292	17.01	-29.69	80	TBD268	01.12.1971	2870.00	287	110	0	1	0	0	7
3318	18.01	-31.51	62	TBD268	02.12.1971	508.47	204	60	0	0	0	0	24
3347	15.03	-31.05	2035	TBD273	10.05.1972	6140.00	307	12	1	0	0	0	0
3457	13.40	-24.10	304	TBD273	10.05.1972	5060.00	253	26	0	0	0	0	6
3513	14.39	-22.94	40	TBD273	20.05.1972	38580.00	643	161	0	16	0	0	109
3540	14.40	-23.10	38	TBD273	21.05.1972	26640.00	222	54	0	0	0	0	8
3634	16.44	-28.97	123	TBD279	29.11.1972	339.17	271	83	0	3	0	0	9
3639	16.44	-28.80	50	TBD279	29.11.1972	139.86	224	184	0	0	0	0	0
3642	16.23	-28.50	27	TBD279	29.11.1972	0	0	0	0	0	0	0	0
3651	16.08	-28.37	43	TBD279	29.11.1972	521.25	278	94	0	2	0	0	6
3664	11.39	-17.26	198	TBD279	03.12.1972	1096.67	329	69	0	4	0	0	22
3666	11.06	-17.26	1485	TBD279	03.12.1972	2800.00	280	87	0	1	0	0	31
3674	11.70	-17.94	108	TBD279	04.12.1972	6380.00	319	0	0	0	0	0	77
3700	10.72	-18.92	1455	TBD279	05.12.1972	5778.44	193	0	0	0	0	0	28
3807	13.61	-21.25	29	TBD283	20.03.1973	258.45	221	85	0	17	0	0	17
3816	12.58	-21.25	390	TBD283	21.03.1973	6460.62	216	20	0	1	0	0	5
3820	11.80	-21.27	1502	TBD283	21.03.1973	3730.00	373	84	3	0	0	0	17
3821	11.63	-20.92	1525	TBD283	21.03.1973	3016.98	302	20	0	1	0	0	15
3844	12.23	-20.58	339	TBD283	22.03.1973	10290.00	343	43	0	2	0	0	18
3883	11.40	-17.07	140	TBD283	28.03.1973	905.00	362	86	0	4	0	2	52
3884	11.12	-17.57	1502	TBD283	28.03.1973	4770.00	477	62	0	7	0	0	47
3885	11.28	-17.57	776	TBD283	28.03.1973	2584.83	259	109	0	0	0	0	46
3886	11.45	-17.57	222	TBD283	28.03.1973	1290.00	258	12	1	1	0	0	3
3889	11.57	-17.53	130	TBD283	28.03.1973	2110.00	211	11	0	0	0	0	27
3901	11.33	-18.38	620	TBD283	28.03.1973	4633.92	250	101	1	12	0	0	21
3902	11.50	-18.38	249	TBD283	28.03.1973	460.00	184	40	0	0	0	0	16
3908	11.87	-18.40	98	TBD283	29.03.1973	836.67	251	77	0	10	0	0	25
3917	11.53	-18.93	285	TBD283	29.03.1973	701.88	211	68	0	5	0	0	20
3918	11.32	-18.92	468	TBD283	29.03.1973	1648.35	220	100	0	0	0	0	32
3933	12.60	-19.25	36	TBD283	30.03.1973	0	0	0	0	0	0	0	0
4649	16.56	-28.92	77	TBD300	17.05.1974	3133.73	314	137	0	3	0	0	12
4668	16.03	-28.54	100	TBD300	17.05.1974	492.84	296	112	0	16	0	0	36
4687	14.45	-22.58	25	TBD300	19.05.1974	1185.48	356	24	0	0	0	0	0
4724	12.36	-18.88	50	TBD300	21.05.1974	2085.40	210	35	0	3	0	0	60
4741	11.70	-17.07	48	TBD300	22.05.1974	711.20	214	22	0	8	0	0	44
4804	12.67	-24.15	2090	TBD300	30.05.1974	16020.00	533	448	0	0	0	0	13
6314	15.99	-28.84	152	TBD398	18.11.1979	3390.00	226	152	0	1	0	0	29
6320	15.80	-28.81	177	TBD398	18.11.1979	3060.00	204	37	0	0	0	0	8

Table 1. (continued)

Station	E tra	I acu	I par	I pat	I pli	I sph	I spp	I str	I var	L oli	N lab	O cen	O isr	O jan	P ame	P dal	P kof	P zoh	Py re
2278	0	0	0	0	0	0	0	0	0	0	0	113	2	1	0	0	4	2	0
2282	0	0	0	0	0	0	0	0	0	0	0	78	0	0	0	0	7	0	0
2340	0	0	0	0	0	0	0	0	0	0	2	88	0	0	0	0	10	0	0
2341	2	0	0	0	0	0	0	0	0	0		17	1	0	0	1	110	0	0
2682	2	0	0	0	0	0	0	0	0	0	1	7	0	0	0	0	1	2	0
2684	0	0	0	0	0	0	3	0	0	0		169	1	0	0	0	6	0	1
2687	0	0	0	0	0	0		0	0	0	5	141	0	0	0	3	0	0	0
2727	0	0	0	0	0	0	1	0	0	0	4	230	3	0	0	0	0	0	0
2736	0	0	0	0	0	0	1	0	0	0	2	162	4	0	0	0	0	0	0
2753	2	0	0	0	0	0	1	0	0	0	1	145	7	0	0	0	0	2	0
2861	0	1	2	1	0	0	3	0	0	0	2	210	10	0	0	1	4	4	0
2865	0	0	0	0	0	0	0	0	0	23	1	12	0	0	0	0	5	0	0
3091	0	0	0	0	0	0	0	0	0	0	0	216	0	0	0	1	31	0	0
3175	0	1	0	0	1	0	4	0	0	0	48	329	2	1	0	0	0	0	0
3177	0	0	0	0	0	0	0	0	0	0	20	486	5	3	0	1	0	3	0
3179	0	0	0	0	0	0	1	1	0	0	15	422	3	7	0	1	0	2	0
3183	0	0	0	0	0	0	1	0	1	1	6	14	0	0	0	0	0	1	0
3187	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
3255	0	0	0	0	0	0	0	0	0	0	14	222	4	0	2	0	0	0	2
3265	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
3292	3	0	0	0	0	0	0	0	0	6	0	9	0	0	22	0	2	1	0
3318	0	0	0	0	0	0	0	0	0	8	0	32	0	0	0	0	8	0	0
3347	0	0	0	2	0	0	2	0	0	0	10	233	0	0	0	1	1	2	3
3457	1	0	0	0	0	0	0	0	0	0	8	191	0	0	0	0	0	7	7
3513	0	0	0	0	0	0	3	0	0	2	21	88	7	3	0	6	37	0	2
3540	1	0	0	0	0	0	0	0	0	0	3	89	0	0	0	0	10	0	0
3634	1	0	0	0	0	0	4	0	0	0	4	18	0	0	0	2	3	0	0
3639	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
3642	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
3651	8	0	0	0	0	0	0	0	0	0	0	2	0	0	6	0	40	0	0
3664	7	0	0	0	0	0	0	0	0	0	20	109	1	0	2	0	4	0	0
3666	1	0	0	0	0	0	0	0	0	0	0	47	0	0	0	0	15	1	0
3674	0	0	0	0	0	0	0	0	0	0	20	57	0	0	0	0	74	0	0
3700	0	0	0	0	0	0	0	0	0	0	10	34	0	0	0	0	98	0	0
3807	0	0	0	0	0	0	0	0	0	0	17	34	0	0	0	0	0	0	0
3816	0	0	0	0	0	0	0	0	0	0	8	152	1	0	0	0	0	5	1
3820	0	2	1	2	0	4	13	0	0	0	65	143	3	1	0	0	1	0	2
3821	0	6	0	4	0	8	8	0	0	0	50	162	0	0	0	0	0	0	1
3844	1	0	0	0	0	1	2	0	0	0	21	212	3	2	0	1	0	3	2
3883	0	0	2	0	0	0	2	0	0	0	40	64	2	0	0	0	10	0	0
3884	0	0	0	0	3	0	0	0	0	0	11	106	0	0	0	0	1	0	4
3885	0	0	0	0	0	0	2	0	0	0	5	56	0	0	0	0	5	0	0
3886	0	0	1	0	0	0	0	0	0	0	67	87	3	0	0	2	8	3	2
3889	0	0	0	0	0	0	0	0	0	0	20	62	0	0	0	0	8	2	1
3901	1	0	0	0	0	0	0	0	0	0	17	39	2	0	0	0	3	1	5
3902	0	0	0	0	0	0	0	0	0	0	8	32	0	0	0	0	8	0	0
3908	6	0	0	0	0	0	0	0	0	0	7	25	0	0	0	0	15	0	1
3917	2	0	0	0	0	0	0	0	0	0	13	50	0	0	0	0	3	2	1
3918	4	0	0	0	0	0	4	0	0	0	4	48	0	0	0	0	0	0	0
3933	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
4649	0	0	0	0	0	0	1	0	0	0	0	3	0	0	0	0	1	0	0
4668	4	0	0	0	0	0	0	0	0	0	0	16	0	0	6	0	2	0	0
4687	0	0	0	0	0	0	4	0	0	0	0	232	0	4	0	0	4	2	4
4724	0	1	0	0	0	0	2	0	0	1	7	40	2	0	0	1	20	0	0
4741	0	0	0	0	0	0	0	0	0	2	2	66	0	0	0	0	16	0	2
4804	0	0	0	0	0	0	2	0	0	0	13	4	0	0	0	0	35	1	0
6314	0	0	0	0	0	0	0	0	0	0	0	25	0	0	0	0	0	0	0
6320	1	0	0	0	0	0	0	0	0	0	0	85	1	0	0	0	0	0	1

Table 1. (continued)

Station	S nep	S qua	S ben	S bul	S del	S mem	S mir	S ram	S sp.1	S spp	S ste	T app	V cal	reworked
2278	0	4	0	0	0	3	2	30	15	65	0	4	0	0
2282	0	1	0	0	1	0	0	27	1	154	0	20	0	0
2340	0	7	0	0	1	0	0	16	0	49	0	5	0	0
2341	1	116	0	0	0	0	1	5	0	11	0	4	2	0
2682	6	44	0	0	0	0	0	0	0	3	0	1	3	0
2684	0	3	0	0	0	0	1	111	0	35	0	0	2	0
2687	0	0	0	0	0	0	0	100	0	200	0	0	13	2
2727	0	0	0	0	0	0	0	18	0	18	0	2	0	0
2736	0	0	0	0	0	0	0	19	0	18	0	1	0	0
2753	0	1	0	0	0	1	2	41	4	46	0	4	0	0
2861	1	8	0	0	0	3	1	151	0	82	0	15	0	0
2865	8	48	0	0	0	0	0	11	0	6	0	2	13	0
3091	0	28	0	0	0	0	1	9	0	9	0	0	1	0
3175	0	10	0	0	0	0	1	22	0	21	5	11	0	0
3177	0	8	0	0	0	3	3	26	0	14	0	7	1	0
3179	0	7	0	0	0	1	3	30	0	10	0	4	0	0
3183	0	26	0	0	0	0	0	13	0	11	0	0	1	0
3187	0	0	0	0	0	0	0	0	0	0	0	0	0	0
3255	0	14	0	0	0	0	0	10	0	6	0	6	0	0
3265	0	0	0	0	0	0	0	0	0	0	0	0	0	0
3292	4	70	0	0	0	0	0	7	0	4	0	0	41	0
3318	0	64	0	0	0	0	4	0	0	4	0	0	0	0
3347	0	0	0	0	1	0	1	20	0	12	0	6	0	0
3457	0	1	0	0	0	0	0	0	0	3	0	3	0	0
3513	1	97	2	0	0	6	1	12	0	66	0	3	0	0
3540	0	34	0	0	0	0	0	10	0	13	0	0	0	1
3634	0	73	0	0	0	0	0	13	0	49	0	3	7	1
3639	0	8	0	0	0	0	0	0	0	8	0	0	24	0
3642	0	0	0	0	0	0	0	0	0	0	0	0	0	0
3651	0	112	0	0	0	0	0	0	0	6	0	0	2	2
3664	0	18	0	0	0	0	1	2	3	57	0	9	1	0
3666	1	20	0	0	0	1	2	0	22	40	0	9	2	0
3674	0	2	0	0	0	0	0	34	0	50	0	5	0	0
3700	0	2	0	0	0	0	0	1	0	13	0	7	0	0
3807	0	0	0	0	0	0	0	0	0	51	0	0	0	0
3816	0	13	0	0	0	1	0	0	0	3	0	6	0	0
3820	0	9	0	0	0	1	0	0	0	8	0	14	0	0
3821	0	8	0	0	0	0	0	1	0	6	0	12	0	0
3844	0	23	0	0	0	0	0	1	0	5	0	3	0	0
3883	0	42	0	0	0	0	2	2	0	48	0	4	0	0
3884	0	26	0	0	0	3	0	3	128	47	0	29	0	0
3885	0	1	0	0	1	0	0	6	0	27	0	1	0	0
3886	0	7	0	0	0	2	0	4	2	45	0	8	0	0
3889	0	17	0	0	0	2	0	4	0	55	0	2	0	0
3901	0	25	0	0	0	1	0	1	1	14	0	5	0	0
3902	0	40	0	0	0	0	0	0	0	20	0	20	0	4
3908	4	51	0	0	0	0	0	5	2	17	0	6	0	0
3917	0	24	0	0	0	2	0	4	0	8	0	9	0	0
3918	0	24	0	0	0	0	0	0	0	4	0	0	0	0
3933	0	0	0	0	0	0	0	0	0	0	0	0	0	0
4649	9	137	0	0	0	0	0	2	0	2	0	0	7	0
4668	2	54	0	2	0	0	0	12	0	30	0	0	4	0
4687	0	16	0	0	0	4	0	2	0	60	0	0	0	0
4724	0	14	0	0	0	0	1	5	0	10	0	7	1	0
4741	0	24	0	0	0	2	0	4	0	16	0	4	2	0
4804	0	2	0	0	0	0	0	0	0	15	0	0	0	0
6314	1	5	0	0	0	0	0	3	0	8	0	2	0	0
6320	0	3	0	0	0	0	0	44	0	24	0	0	0	0

Notes to Table 1:

B spp = *Brigantedinium* spp.; D cha = *Dalella chatamensis*; E acu = *Echinidinium aculeatum*; E del = *Echinidinium delicatum*; E mon = *Echinidinium monospinum*; E spp = *Echinidinium* spp.; E tra = *Echinidinium transparentum*; I acu = *Impagidinium aculeatum*; I par = *Impagidinium paradoxum*; I pat = *Impagidinium patulum*; I pli = *Impagidinium plicatum*; I sph = *Impagidinium sphaericum*; I spp = *Impagidinium* spp.; I str = *Impagidinium striatum*; I var = *Impagidinium variseptum*; L oli = *Lejeunecysta oliva*; N lab = *Nematosphaeropsis labyrinthus*; O cen = *Operculodinium centrocarpum*; O isr = *Operculodinium israelianum*; O jan = *Operculodinium janduchenei*; P ame = cyst of *Protoperidinium americanum*; P dal = cyst of *Pentapharsodinium dalei*; P kof = cyst of *Polykrikos kofoidii*; P zoh = *Polysphaeridium zoharyi*; Py re = *Pyxidinosia reticulata*; S nep = *Selenopemphix nephroides*; S qua = *Selenopemphix quanta*; S ben = *Spiniferites bentorii*; S bul = *Spiniferites bulloides*; S mem = *Spiniferites membranaceus*; S mir = *Spiniferites mirabilis*; S ram = *Spiniferites ramosus*; S spp = *Spiniferites* spp.; S sp. 1 = *Spiniferites* sp. 1; S ste = *Stelladinium stellatum*; T app = *Trinovantedinium applanatum*; V cal = *Votadinium calvum*

An aliquot of 50 μ l was brought onto a slide, embedded in glycerine jelly and sealed with paraffin wax. The dinocysts were then counted with a light microscope at 400x magnification. Whenever a slide contained less than 200 dinocysts, additional slides were counted. Table 1 shows count data of all identified dinocysts. The taxonomy for the fossil dinoflagellates was used. The nomenclature of the identified dinocysts follows Fensome et al. (1993), Zonneveld (1997) and Fensome and Williams (2004). *Spiniferites*-like cysts with a granulate cell wall are included in *Spiniferites* sp.1. *Brigantedinium* spp. includes all spherical brown cysts.

2.3.2.2. Statistical methods

To compare environmental variables in the water column with relative abundances of dinocyst species, the multivariate ordination techniques Detrended Correspondence Analysis (DCA) and Canonical Correspondence Analysis (CCA) (ter Braak and Smilauer, 1998) have been used. These calculations were performed with the program CANOCO version 4. Tests carried out previous to the analyses showed that the studied system has an unimodal character, therefore validating the use of unimodal ordination programs. Using DCA assumes that the major environmental gradient causes the largest variation within the dataset. The direction of this variation is calculated by a two way weighted averaging algorithm, which is represented by the first DCA-axis. The second DCA-axis then represents the second-most important direction of variation and so on. In order to avoid a quadratic relation between the first and higher axes, the method of detrending (by segments) has been applied (Hill and Gauch, 1980). The variation represented by a DCA-axis is interpreted as caused by one or more environmental parameters. A perpendicular projection of a species or sample point to an

Table 2. Environmental data used in the CCA.

Station	D	T1	T2	T3	T4	S1	S2	S3	S4
	[E]	[U]	[U]	[U]	[U]				
2278	105	17.59	15.15	13.99	15.88	35.18	35.15	35.21	35.21
2282	295	18.54	16.63	15.51	16.84	35.18	35.15	35.21	35.21
2340	116	17.59	15.15	13.99	15.89	35.08	35.07	35.17	35.13
2341	84	17.63	15.15	13.96	15.90	35.08	35.07	35.17	35.13
2682	56	17.61	14.96	14.01	16.18	35.03	35.02	35.13	35.07
2684	180	17.85	15.27	14.23	16.30	35.03	35.02	35.13	35.07
2687	224	18.44	16.04	14.92	16.67	35.03	35.02	35.13	35.07
2727	530	20.11	17.89	15.68	17.44	35.29	35.28	35.31	35.28
2736	205	19.18	16.57	14.94	16.97	35.04	35.08	35.14	35.08
2753	191	18.61	15.94	14.53	16.60	35.04	35.08	35.14	35.08
2861	165	17.70	15.08	13.81	16.11	34.87	34.91	35.02	34.94
2865	102	17.38	14.70	13.53	16.03	34.87	34.91	35.02	34.94
3091	9	17.45	15.15	14.12	15.80	35.18	35.15	35.21	35.21
3175	2060	20.28	18.22	15.86	17.22	35.18	35.29	35.22	35.16
3177	1000	19.76	17.81	15.71	17.02	35.18	35.29	35.22	35.16
3179	437	19.27	17.15	15.43	16.84	35.11	35.24	35.20	35.13
3183	270	17.61	15.98	14.27	15.81	34.96	35.09	35.03	34.95
3255	390	18.07	16.21	14.62	15.69	35.09	35.22	35.14	35.07
3292	80	17.39	14.74	13.55	16.07	34.87	34.91	35.02	34.94
3318	62	17.60	15.13	13.90	15.93	35.08	35.07	35.17	35.13
3347	2035	20.18	18.13	15.76	17.43	35.27	35.24	35.29	35.27
3457	304	17.89	15.99	14.23	15.72	35.05	35.18	35.09	34.99
3513	40	17.18	14.70	13.20	14.72	35.08	35.22	35.13	35.01
3540	38	17.10	14.62	13.20	14.70	35.00	35.13	35.04	34.94
3634	123	17.51	14.91	13.58	15.97	34.93	35.02	35.06	34.99
3639	50	17.51	14.93	13.58	15.96	34.93	35.02	35.06	34.99
3651	43	17.78	15.50	13.68	15.90	34.93	35.02	35.06	34.99
3664	198	20.92	19.37	15.54	17.64	35.65	35.55	35.45	35.50
3666	1485	21.24	19.43	15.88	18.01	35.65	35.55	35.45	35.50
3674	108	20.22	18.72	14.93	17.00	35.65	35.55	35.45	35.50
3700	1455	21.21	19.19	15.84	17.84	35.62	35.58	35.46	35.47
3807	29	18.93	16.13	14.15	16.19	35.08	35.24	35.14	35.02
3816	390	19.68	17.44	15.03	17.01	35.17	35.31	35.21	35.11
3820	1502	20.73	18.61	15.89	17.64	35.26	35.38	35.29	35.19
3821	1525	21.11	18.97	16.06	17.87	35.32	35.42	35.31	35.24
3844	339	19.92	17.69	15.16	17.08	35.21	35.35	35.24	35.15
3883	140	21.44	19.61	16.01	18.24	35.65	35.55	35.45	35.50
3884	1502	20.85	19.08	15.53	17.56	35.65	35.55	35.45	35.50
3885	776	20.76	19.05	15.42	17.45	35.65	35.55	35.45	35.50
3886	222	20.58	18.99	15.23	17.27	35.65	35.55	35.45	35.50
3889	130	20.62	19.14	15.22	17.26	35.65	35.55	35.45	35.50
3901	620	20.27	18.65	15.15	17.13	35.55	35.55	35.42	35.42
3902	249	20.02	18.47	14.94	16.94	35.55	35.55	35.42	35.42
3908	98	19.81	18.23	14.67	16.67	35.55	35.55	35.42	35.42
3917	285	20.08	18.36	15.08	17.10	35.55	35.55	35.42	35.42
3918	468	20.33	18.56	15.24	17.26	35.55	35.55	35.42	35.42
4649	77	17.47	14.90	13.56	15.95	34.93	35.02	35.06	34.99
4668	100	17.78	15.41	13.70	15.97	34.93	35.02	35.06	34.99
4687	25	17.52	14.98	13.30	15.00	35.08	35.22	35.13	35.01
4724	50	19.65	17.38	14.33	16.33	35.55	35.55	35.42	35.42
4741	48	20.96	19.49	15.59	17.78	35.65	35.55	35.45	35.50
4804	2090	19.44	17.12	15.14	16.69	35.13	35.26	35.17	35.07
6314	152	17.92	15.35	13.76	16.08	34.93	35.02	35.06	34.99
6320	177	18.24	15.62	13.92	16.25	34.93	35.02	35.06	34.99

Table 2. (continued)

Station	Zm1	Zm2	Zm3	Zm4	C1	C2	C3	C4	N1a	PHa	Corg	Ox
	[μm]	[μm]	[μm]	[μm]	[mg/m^3]	[mg/m^3]	[mg/m^3]	[mg/m^3]	[$\mu\text{g}/\text{l}$]	[$\mu\text{g}/\text{l}$]	[weight%]	[ml/l]
2278	14.80	31.75	78.46	25.74	21.13	16.14	22.74	15.30	3.12	0.48	0.65	0.390
2282	14.80	31.75	78.46	25.74	3.26	2.20	1.32	2.43	3.12	0.48	0.45	0.522
2340	14.80	31.75	78.46	25.74	12.52	11.36	7.88	10.94	2.49	0.50	4.85	0.759
2341	14.80	31.75	78.46	25.74	15.79	15.58	12.13	15.46	2.49	0.50	1.28	1.369
2682	15.35	33.31	71.20	24.07	11.75	7.14	8.15	10.85	1.29	0.37	0.64	0.742
2684	15.35	33.31	71.20	24.07	5.65	3.93	3.43	5.04	1.29	0.37	0.92	0.058
2687	15.35	33.31	71.20	24.07	2.79	2.24	1.34	2.42	1.29	0.37	0.66	0.121
2727	10.50	24.17	34.80	17.99	0.48	0.56	0.41	0.45	1.56	0.32	0.79	0.906
2736	7.92	19.93	23.02	15.63	1.65	1.32	0.88	1.41	1.45	0.33	0.35	0.746
2753	7.92	19.93	23.02	15.63	2.54	2.37	1.48	2.73	1.45	0.33	0.75	0.056
2861	15.18	35.71	81.66	25.93	4.34	3.84	4.98	5.32	1.00	0.34	0.98	0.334
2865	15.18	35.71	81.66	25.93	14.99	11.40	18.87	16.60	1.00	0.34	1.88	0.011
3091	14.80	31.75	78.46	25.74	17.45	16.82	9.86	14.46	3.12	0.48	0.33	2.547
3175	11.60	34.28	85.41	36.07	0.49	0.42	0.39	0.50	2.39	0.37	0.81	4.982
3177	11.60	34.28	85.41	36.07	0.63	0.46	0.47	0.67	2.39	0.37	1.66	2.640
3179	9.40	24.08	32.00	20.14	0.98	0.54	0.54	1.04	2.12	0.35	1.27	0.188
3183	13.82	35.00	82.37	35.15	2.98	1.29	1.59	2.98	3.61	0.46	0.75	0.045
3255	12.67	29.65	77.52	39.91	1.20	1.08	0.89	1.30	3.35	0.44	3.46	0.276
3292	15.18	35.71	81.66	25.93	6.45	6.47	6.33	7.68	1.00	0.34	1.71	0.295
3318	14.80	31.75	78.46	25.74	20.38	20.70	23.33	22.65	2.49	0.50	0.14	0.476
3347	11.02	23.46	33.92	17.77	0.45	0.40	0.37	0.37	1.86	0.36	0.82	4.422
3457	13.09	27.21	35.49	25.87	1.83	1.95	1.47	1.14	5.19	0.60	1.80	0.111
3513	13.93	32.99	51.80	26.00	15.04	9.99	7.38	10.92	5.62	0.72	5.13	0.202
3540	13.55	24.94	34.71	21.56	23.20	7.86	4.28	11.08	5.51	0.62	4.15	1.464
3634	9.95	25.34	40.21	19.60	13.67	5.92	14.18	16.89	1.68	0.31	1.00	0.174
3639	9.95	25.34	40.21	19.60	15.22	7.28	15.11	18.38	1.68	0.31	0.51	2.308
3651	9.95	25.34	40.21	19.60	13.61	16.74	17.13	19.17	1.68	0.31	0.45	2.047
3664	13.41	29.18	65.08	22.93	3.11	1.72	2.95	2.89	7.89	0.71	1.11	0.012
3666	13.41	29.18	65.08	22.93	2.19	1.99	1.93	2.31	7.89	0.71	1.36	4.296
3674	13.41	29.18	65.08	22.93	3.90	3.10	3.23	2.73	7.89	0.71	1.20	0.506
3700	15.55	31.72	58.60	26.47	2.93	2.06	2.53	2.24	6.16	0.62	4.90	4.379
3807	11.25	27.37	52.68	17.53	15.75	9.27	8.10	16.39	5.92	0.67	0.19	1.529
3816	12.44	29.63	45.68	20.11	2.56	2.71	1.76	2.67	5.98	0.67	2.70	0.147
3820	14.58	33.00	52.45	24.64	1.16	1.72	2.06	1.31	5.63	0.63	4.00	3.434
3821	13.45	31.41	48.34	22.56	0.60	1.50	1.64	1.07	6.24	0.67	4.30	3.213
3844	11.17	27.01	32.71	16.59	2.26	2.32	2.00	1.60	6.86	0.71	1.92	0.670
3883	13.41	29.18	65.08	22.93	2.25	1.80	2.04	2.42	7.89	0.71	0.66	0.130
3884	13.41	29.18	65.08	22.93	1.92	2.07	2.48	1.81	7.89	0.71	1.46	4.261
3885	13.41	29.18	65.08	22.93	1.97	2.08	2.60	1.84	7.89	0.71	1.49	1.408
3886	13.41	29.18	65.08	22.93	2.96	2.00	2.75	2.47	7.89	0.71	0.80	0.183
3889	13.41	29.18	65.08	22.93	5.74	2.11	2.78	3.51	7.89	0.71	0.93	0.078
3901	13.34	33.64	71.67	25.00	2.30	2.76	2.94	2.26	7.78	0.79	1.00	0.578
3902	13.34	33.64	71.67	25.00	2.43	2.63	3.49	2.33	7.78	0.79	2.40	0.485
3908	13.34	33.64	71.67	25.00	8.52	11.28	13.71	10.92	7.78	0.79	0.50	0.390
3917	13.34	33.64	71.67	25.00	2.79	2.77	2.19	2.15	7.78	0.79	2.38	0.347
3918	13.34	33.64	71.67	25.00	2.77	2.82	2.39	2.23	7.78	0.79	3.60	0.059
4649	9.95	25.34	40.21	19.60	17.71	8.08	17.94	21.07	1.68	0.31	0.76	0.039
4668	9.95	25.34	40.21	19.60	5.90	6.75	5.51	9.67	1.68	0.31	0.28	0.207
4687	13.93	32.99	51.80	26.00	10.71	14.21	9.90	10.64	5.62	0.72	1.23	3.954
4724	13.34	33.64	71.67	25.00	14.51	6.75	15.86	8.70	7.78	0.79	0.79	2.860
4741	13.41	29.18	65.08	22.93	4.00	2.25	3.23	3.83	7.89	0.71	0.43	3.329
4804	15.62	30.73	47.69	27.70	0.92	1.18	0.89	0.70	4.43	0.54	5.76	4.947
6314	9.95	25.34	40.21	19.60	4.25	2.79	3.96	6.35	1.68	0.31	1.57	0.533
6320	9.95	25.34	40.21	19.60	3.30	2.10	2.99	4.64	1.68	0.31	1.68	0.557

Notes to Table 2:

C = chlorophyll-*a* content at the surface; D = waterdepth; Ni = nitrate concentration at the surface; Ox = bottom water oxygen content; Ph = phosphate concentration at the surface; S = sea surface salinity; T = sea surface temperature; TOC = total organic carbon content of the sediment; Zm = mixed layer depth; 1 = austral summer; 2 = austral autumn; 3 = austral winter; 4 = austral spring

axis gives the respective optimum of abundance. This position is given in units of standard deviations (sd). Species that plot more than 4 sd apart do not occur in the same sample. If the length of the first axis is more than 2 sd, it can be assumed that there is a unimodal response of species abundance to environmental parameters.

With a CCA, the species optima can be determined directly along gradients of inferred environmental variables. The length of an arrow represents the length of the gradient. The nearer a species is situated to the tip of an environmental parameter arrow, the stronger it is correlated with this parameter. The optimum of that species can be found by the perpendicular projection on the variable arrow.

So far, the nutrient content in the upper water column has generally been used as a sign for productivity. But nutrients in the water column are laborious to measure and data are not available in a high spatial resolution data set. Also, the measured nutrient values do not represent the nutrient supply but the in situ concentration which is much lower than the nutrient availability because of permanent consumption. In the present study, chlorophyll-*a* concentrations in surface waters have been chosen as unambiguous indicators of actual sea surface productivity.

The following parameters have been used for the calculations (Table 2): seasonal values for SST (T), chlorophyll-*a* (C), SSS (S), mixed layer depth (Zm); annual values for bottom water oxygen content (Ox) nitrate at the surface (NI) and phosphate at the surface (PH) as well as waterdepth (D) and the total organic carbon content of the sediment (Corg).

Seasonal SST data were calculated from monthly values of the years 1985-1997 which were obtained from the NASA Physical Oceanography Distributed Active Archive Center at the Jet Propulsion Laboratory, California Institute of Technology. Seasonal chlorophyll-*a* data were derived from the SeaWiFS-Project of the Goddard Space Flight Center (<http://seawifs.gsfc.nasa.gov>) and were calculated from monthly values of the years 1997-2003. The months January to March are referred to as austral summer (1), April to June as austral autumn (2), July to September as austral winter (3) and October to December as austral spring (4). The grid for the chlorophyll-*a* and SST data is 9x9 km.

To exclude extreme local deviations, especially in the near shore regions, we averaged over the data point nearest to the respective sample and its eight surrounding data points.

The depth of the mixed layer is constructed based on density variation determined from temperature, salinity, pressure and the corresponding temperature change.

Values for annual mean bottom water oxygen concentrations were obtained from the LAS Server of the Leibniz Institute of Baltic Sea Research, which provides a regional ecosystem model of the South-East Atlantic (<http://las.io-warnemuende.de>). Seasonal data for the mixed layer depth and SSS, as well as data for annual mean concentrations of nitrate and phosphate were obtained from the LEVITUS World Ocean Atlas 1994 (<http://ingrid.ldeo.columbia.edu/SOURCES/.LEVITUS94/>). Here, the grid dimension is 1° latitude and longitude.

Values for Corg have been measured on the examined samples by Guerrero (2002).

Species that occurred in only one of the investigated samples or never occurred in numbers higher than one per sample have either been grouped or excluded from the analyses. *Spiniferites bentorii*, *Spiniferites delicatus* and *Spiniferites bulloides* have been grouped into *Spiniferites* spp.; *Impagidinium variaseptum* and *Impagidinium striatum* have been grouped into *Impagidinium* spp.; *Echinidinium delicatum* and *Echinidinium monospinum* have been grouped into *Echinidinium* spp.; *Stelladinium stellatum* has been excluded.

In the statistical analyses *Spiniferites* sp. 1 caused a strong bias. Since this morphotype includes most probably cysts formed by species with different ecologies we have grouped them with *Spiniferites* spp., prior to the statistical treatment.

Dinocyst concentrations (dinocysts/g dry sediment) range from 140 to 38 580 in the studied region (Fig. 6). Four samples (TBD 3187, 3265, 3642 and 3933) did not contain any dinocysts. In most of the nearshore samples concentrations are lower than in more neritic sites. Within the studied region, a large variation in sedimentation rates can be observed (Mollenhauer et al., 2004). This implies that concentrations of dinocysts (cysts/g) can not be interpreted in terms of accumulation rates. We therefore focus in this study on the relative abundances.

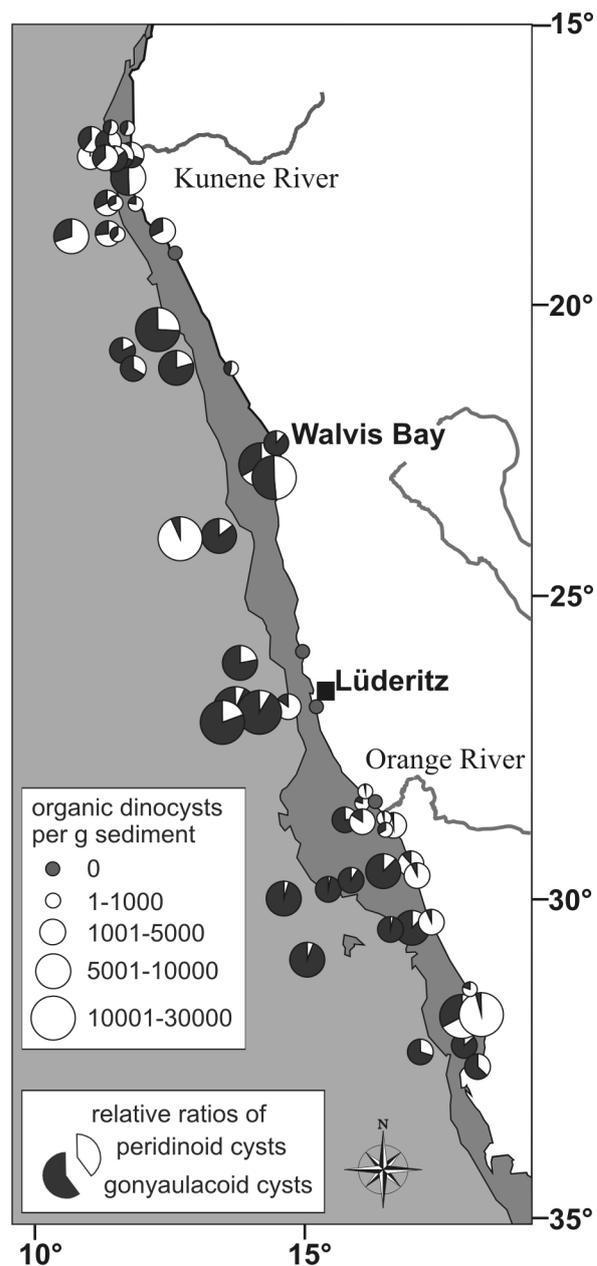


Figure 6. Organic walled dinoflagellate cyst concentrations in the Benguela upwelling system.

2.4. Results

2.4.1. Geographic distribution of organic-walled dinocysts from the present study

Most of the samples are either dominated by *Brigantedinium* spp. (Fig. 7c), *Spiniferites* spp. (Fig. 11e) or *Operculodinium centrocarpum* (Fig. 9a) with maximum relative abundances of 84%, 43% and 80%, respectively.

By visual classification the following groups with comparable geographical distribution patterns can be recognized:

Group 1: Coastal regions

Cysts of *Polykrikos kofoidii* and *Selenopemphix quanta* (Fig. 7a,b) show their highest relative abundances at sites very close to the coast.

Group 2: Vicinity of active upwelling

The relative abundances of *Brigantedinium* spp., *Echinidinium aculeatum*, *Echinidinium* spp. and *Echinidinium transparentum* (Fig. 7c-f) are highest on the shelf.

Group 3: Restricted to river mouths

Lejeunecysta oliva, cysts of *Protoperidinium americanum*, *Selenopemphix nephroides* and *Votadinium calvum* (Fig. 8a-d) occur exclusively in sites influenced by river outflow.

Group 4: Slope to open ocean

Dalella chathamense, *Impagidinium patulum* and *O. centrocarpum* (Fig. 8e,f and 9a) show their highest relative abundances at sites on the slope and open ocean.

Group 5: Southern Benguela region

Spiniferites ramosus (Fig. 9b) is relatively more abundant in sites of the SBR.

Group 6: Northern Benguela region

Nematosphaeropsis labyrinthus and *Pyxidinoopsis reticulata* (Fig. 9c,d) are found in higher relative abundances in the NBR.

Species with random distributions (Fig. 9-11)

Impagidinium aculeatum, *Impagidinium paradoxum*, *Impagidinium plicatum*, *Impagidinium sphaericum*, *Impagidinium* spp., *Operculodinium israelianum*, *Operculodinium janduchenei*, cysts of *Pentapharsodinium dalei*, *Polysphaeridium zoharyi*, *Spiniferites membranaceus*, *Spiniferites mirabilis*, *Spiniferites* sp. 1, *Spiniferites* spp. and *Trinovantedinium applanatum* do not show defined distribution patterns, so they were not associated to any group.

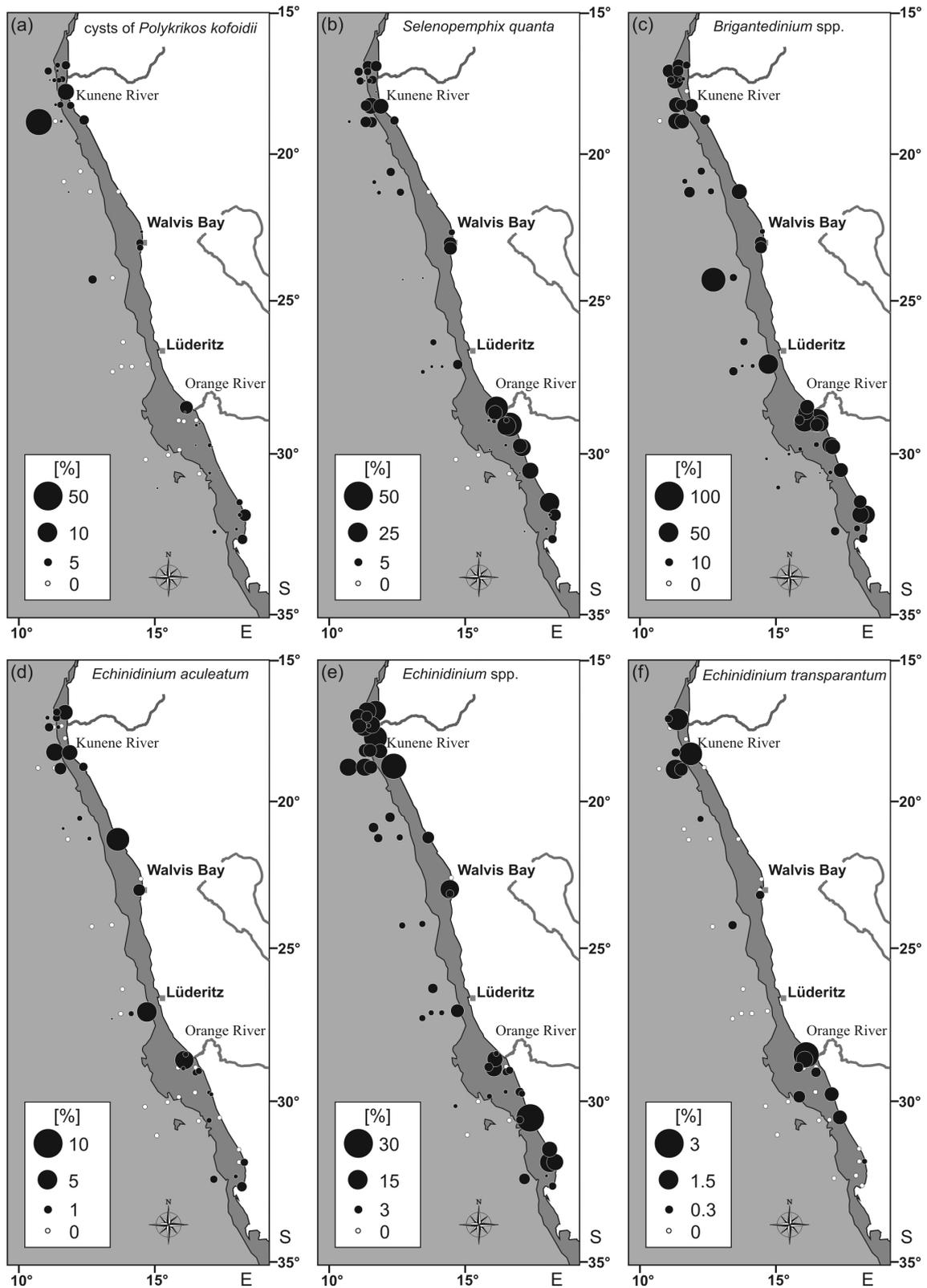


Figure 7. Relative abundances (note different scales) of cysts of *Polykrikos kofoidii* (a), *Selenopemphix quanta* (b), *Brigantedinium* spp. (c), *Echinidinium aculeatum* (d), *Echinidinium aculeatum* (e) and *Echinidinium transparantum* (f).

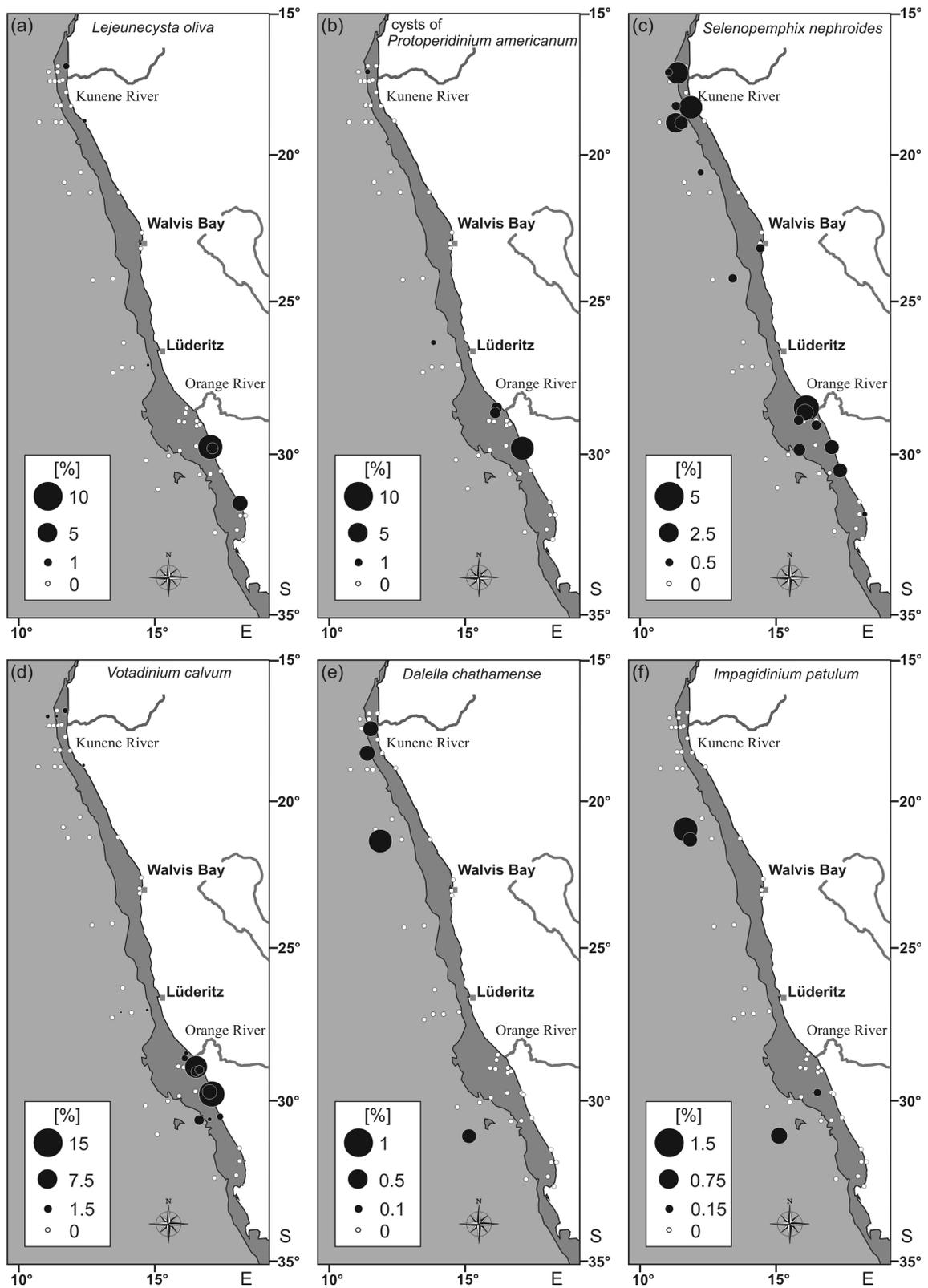


Figure 8. Relative abundances (note different scales) of *Lejeunecysta oliva* (a), cysts of *Protoperidinium americanum* (b), *Selenopemphix nephroides* (c), *Votadinium calvum* (d), *Dalella chathamense* (e) and *Impagidinium patulum* (f).

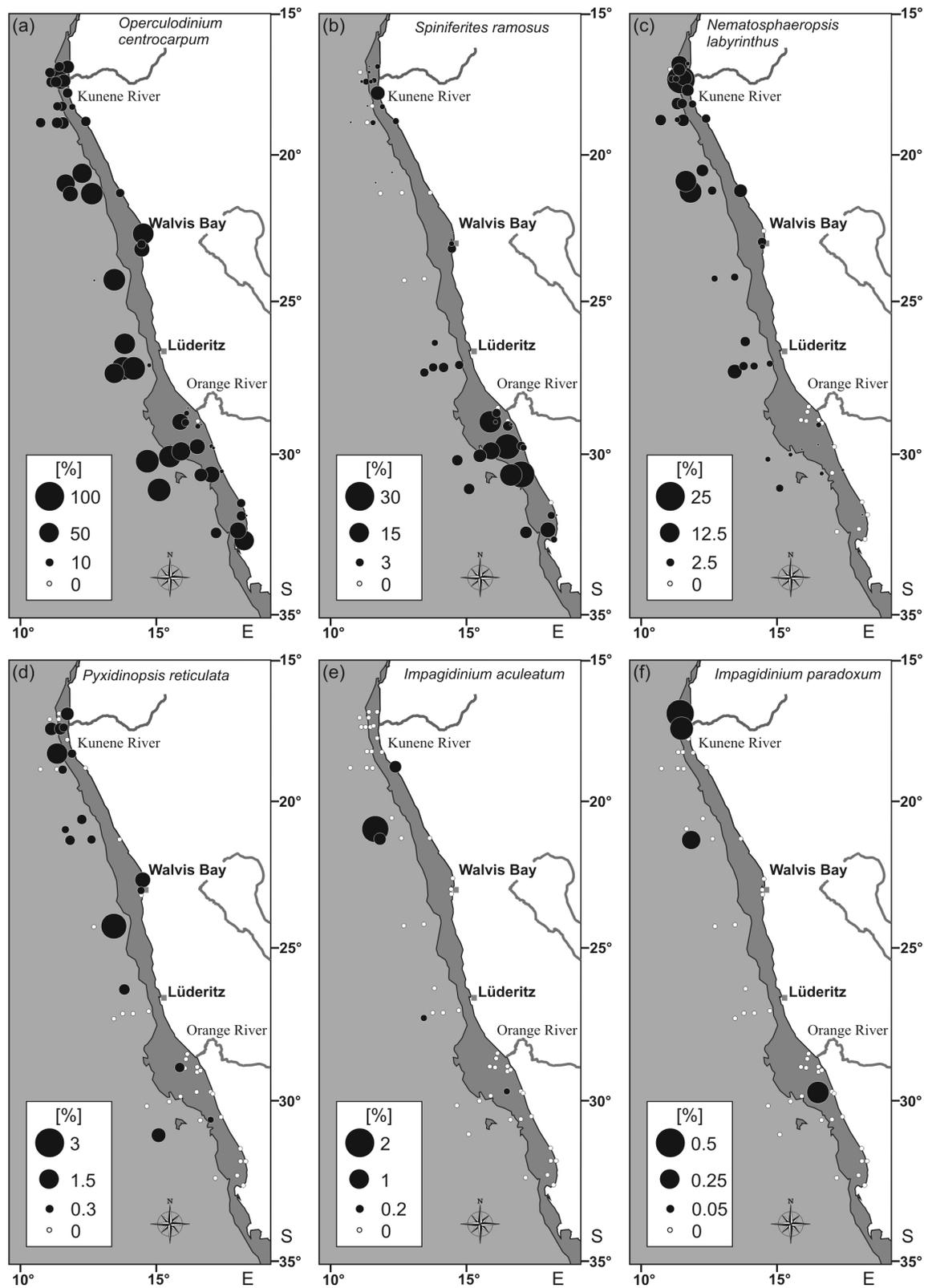


Figure 9. Relative abundances (note different scales) of *Operculodinium centrocarpum* (a), *Spiniferites ramosus* (b), *Nemosphaeropsis labyrinthus* (c), *Pyxidiniopsis reticulata* (d), *Impagidinium aculeatum* (e) and *Impagidinium paradoxum* (a).

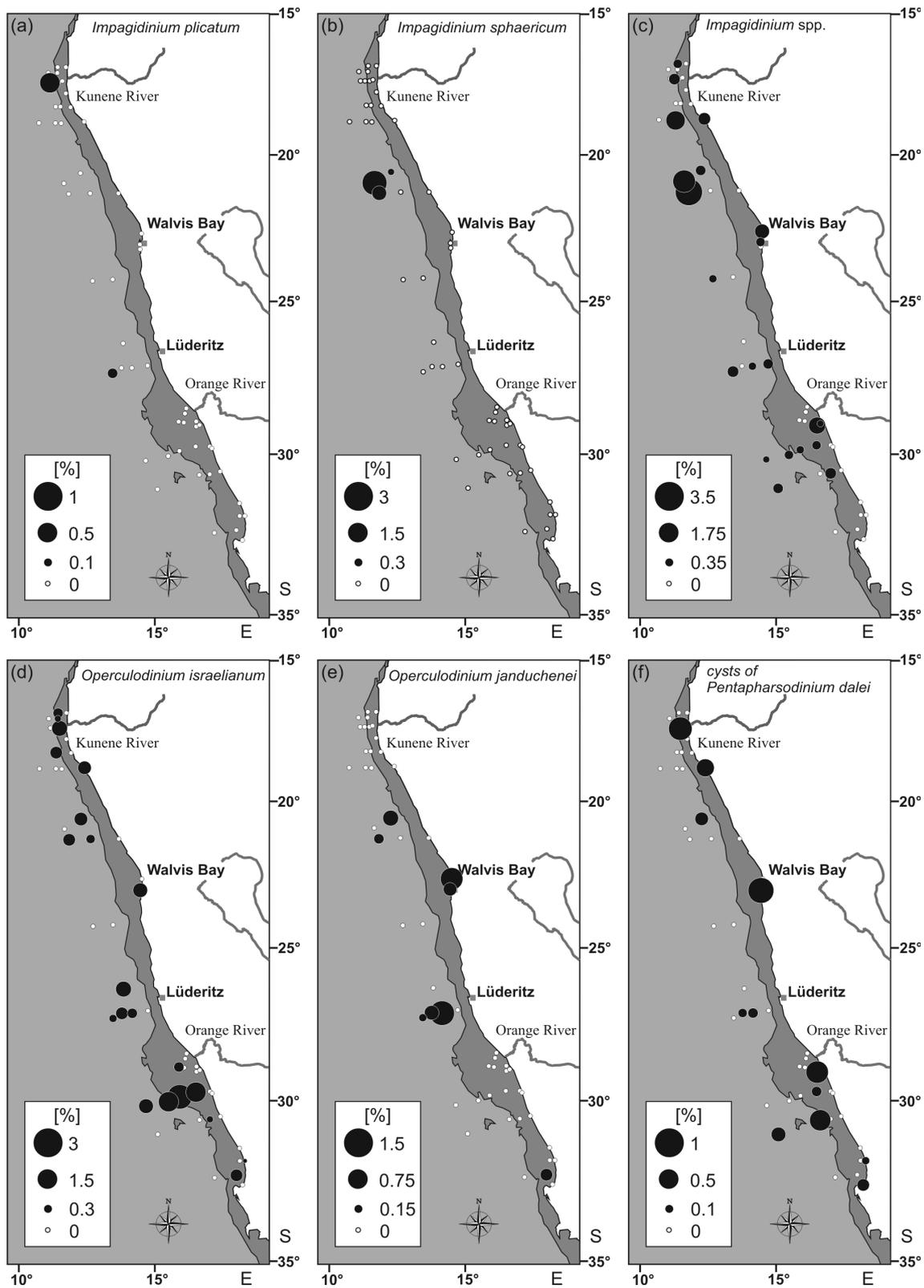


Figure 10. Relative abundances (note different scales) of *Impagidinium plicatum* (a), *Impagidinium sphaericum* (b), *Impagidinium* spp. (c), *Operculodinium israelianum* (d), *Operculodinium janduchenei* (e) and cysts of *Pentapharsodinium dalei* (f).

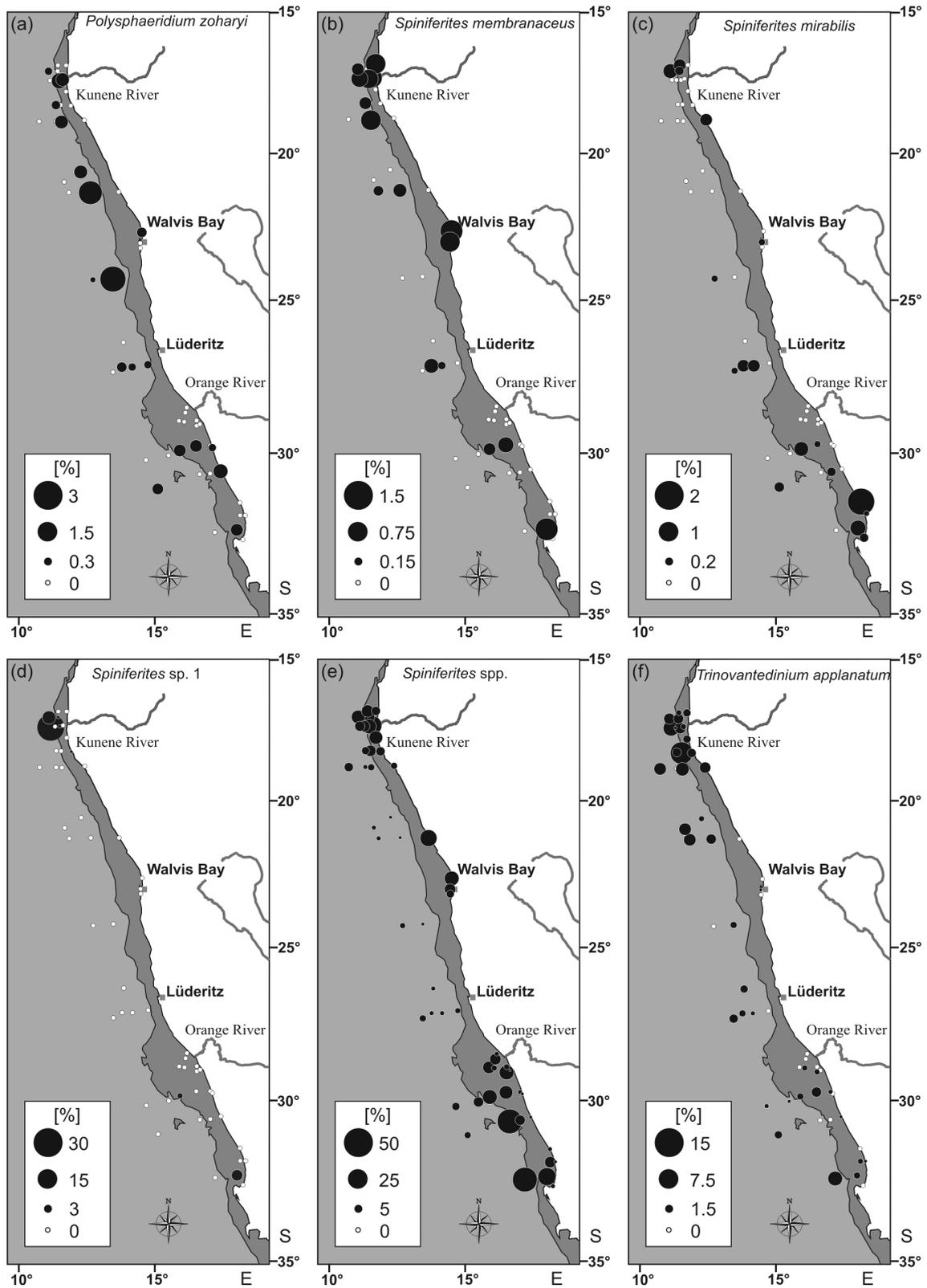


Figure 11. Relative abundances (note different scales) of *Polysphaeridium zoharyi* (a), *Spiniferites membranaceus* (b), *Spiniferites mirabilis* (c), *Spiniferites* sp. 1 (d), *Spiniferites* spp. (e) and *Trinovantedinium* (f).

2.4.2. Detrended Correspondence Analysis (Fig. 12 and 13)

The DCA reveals a gradient with a length of 2.345, indicating a unimodal distribution of the dinocyst species. The first and second DCA axis respectively represent 42.3% and 14.7% of the variance in the data set. Higher axes explain less than 8.7% and were not taken into account.

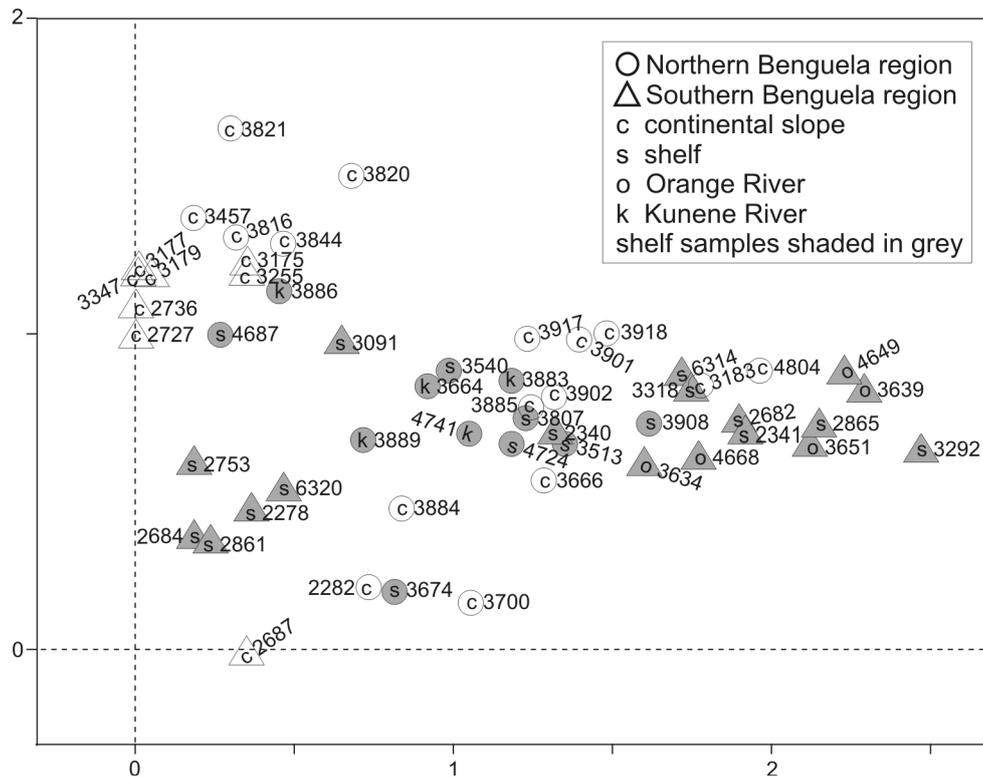


Figure 12. DCA plot of the variation between sampling sites. Values along the axes are given in standard deviations.

Samples near the Orange River mouth are ordinated on the right side of the first DCA-axis, whereas samples from the Kunene River mouth area are ordinated in the centre (Fig. 12). Samples from the NBR are randomly spread, whereas samples from the SBR form two clusters on both extremes of the first axis. The right cluster only contains samples from the SBR-shelf and Orange River. The left cluster includes samples from the SBR-continental slope and some SBR-shelf samples. Phototrophic species (gonyaulacoid dinocysts) can clearly be distinguished from heterotrophic taxa (peridinoid dinocysts). *L. oliva*, cysts of *P. americanum*, *S. nephroides* and *V. calvum* are ordinated at the most positive site of the first axis, corresponding to the position of the Orange River samples. *I. aculeatum*, *I. patulum*, *I. sphaericum*, *O. centrocarpum*, *O. israelianum*, *O. janduchenei* and *S. ramosus* are ordinated at the negative side of the first axis. The

Echinidinium species group together with *Brigantedinium* spp., cysts of *P. kofoidii* and *S. quanta* in the centre more or less conform to the ordination of the Kunene River samples. *D. chathamense*, *I. aculeatum*, *I. patulum* and *I. sphaericum* are ordinated at the most positive side of the second DCA axis whereas *S. ramosus* is ordinated at the negative side of this axis.

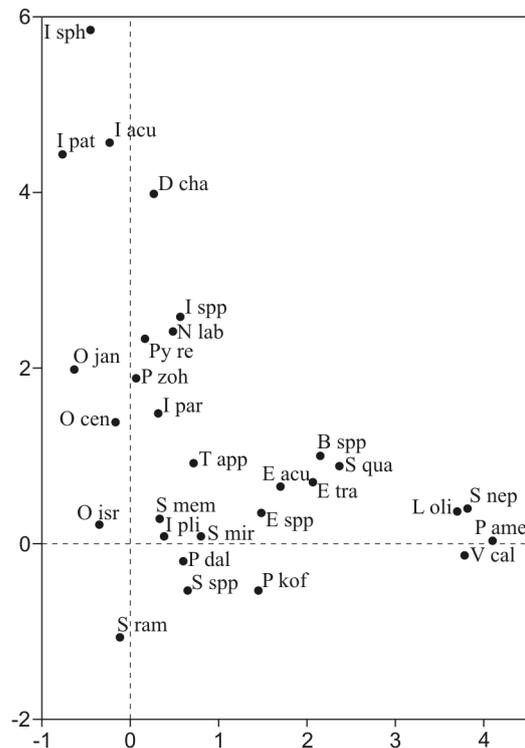


Figure 13. Results of the DCA analysis showing the variation within the species distribution. Values along the axes are given in standard deviations.

B spp = *Brigantedinium* spp.; D cha = *Dalella chatamensis*; E acu = *Echinidinium aculeatum*; E spp = *Echinidinium* spp.; E tra = *Echinidinium transparentum*; I acu = *Impagidinium aculeatum*; I par = *Impagidinium paradoxum*; I pat = *Impagidinium patulum*; I pli = *Impagidinium plicatum*; I sph = *Impagidinium sphaericum*; I spp = *Impagidinium* spp.; L oli = *Lejeunecysta oliva*; N lab = *Nematosphaeropsis labyrinthus*; O cen = *Operculodinium centrocarpum*; O isr = *Operculodinium israelianum*; O jan = *Operculodinium janduchenei*; P ame = cyst of *Protoperidinium americanum*; P dal = cyst of *Pentapharsodinium dalei*; P kof = cyst of *Polykrikos kofoidii*; P zoh = *Polysphaeridium zoharyi*; Py re = *Pyxidinosopsis reticulata*; S nep = *Selenopemphix nephroides*; S qua = *Selenopemphix quanta*; S mem = *Spiniferites membranaceus*; S mir = *Spiniferites mirabilis*; S ram = *Spiniferites ramosus*; S spp = *Spiniferites* spp.; T app = *Trinovantedinium appplanatum*; V cal = *Votadinium calvum*

2.4.3. Canonical Correspondence Analysis

The parameters chlorophyll-*a* (spring, summer and winter), SST (summer, autumn and winter) and SSS (summer, autumn and winter) significantly relate to the dinocyst distribution on the 95% confidence limit (Table 3). After correcting for co-

variance only the parameters austral spring chlorophyll-*a* content, austral summer and austral autumn SSS significantly relate to the dinocyst species distribution on the 95% confidence limit (Table 3).

Table 3. Percentage of variance explained by the environmental variables used in the CCA. Bold variables are significant at the 5% significance level ($P \leq 0.05$).

Marginal Effects uncorrected for covariance		Conditional Effects corrected for covariance		
Variable	Variance	Variable	Variance	P-value
C4	0.16	C4	0.16	0.005
C3	0.13	S2	0.11	0.005
T3	0.12	S1	0.06	0.005
S2	0.11	Corg	0.05	0.040
C1	0.10	C1	0.05	0.040
T1	0.10	S3	0.05	0.040
T2	0.10	NIa	0.02	0.165
S3	0.10	C2	0.03	0.120
S1	0.10	Zm2	0.03	0.120
C2	0.09	T2	0.02	0.270
S4	0.09	T3	0.03	0.275
NIa	0.09	Zm1	0.02	0.505
PHa	0.08	D	0.01	0.500
T4	0.07	T1	0.02	0.330
D	0.06	T4	0.03	0.105
Ox	0.04	C3	0.02	0.310
Zm1	0.04	S4	0.02	0.605
Corg	0.04	Zm4	0.02	0.365
Zm3	0.03	Zm3	0.02	0.415
Zm2	0.03	Ox	0.01	0.440
Zm4	0.01	PHa	0.02	0.865

C = chlorophyll-*a* content at the surface; D = waterdepth; NI = nitrate concentration at the surface; Ox = bottom water oxygen content; PH = phosphate concentration at the surface; S = sea surface salinity; T = sea surface temperature; Corg = total organic carbon content of the sediment; Zm = mixed layer depth; 1 = austral summer; 2 = austral autumn; 3 = austral winter; 4 = austral spring

L. oliva, cysts of *P. americanum*, *S. nephroides* and *V. calvum* are ordinated at the most positive part of the chlorophyll-*a* gradient and on the most negative part of the SSS and SST gradients. *I. aculeatum* and *I. sphaericum* are most anti-correlated to the chlorophyll-*a* content (Fig. 14).

The variance of *D. chathamense*, *I. aculeatum*, *I. patulum*, *I. sphaericum* and cysts of *P. kofoidii* relates positively to SSS in austral summer and autumn and SST.

The distribution of *S. ramosus* is ordinated together with *L. oliva*, cysts of *P. americanum*, *S. nephroides* and *V. calvum* at the negative side of the SSS gradient but its

sedimentation area is 300 km for the smallest size (64 μm). Several dinocyst species are even smaller and might be transported even further. In experiments with individual dinocysts Anderson and Lively (1985) observed sinking rates between 0,011 and 0,013 cm/s. To reach the shelf at 200 m depth it would then take about 9 days for a single dinocyst. In the BCC area, current velocities of 10-75 cm/s are recorded (Shannon and Nelson, 1996). Theoretically this could displace a single sinking dinocyst by 80 - 600 km. However, there are biological and physical processes that can accelerate the settlement of dinocysts such as aggregation in faecal pellets or coagulation by collision (Alldredge and Jackson, 1995; Zonneveld and Brummer, 2000; Susek and Zonneveld, subm). Repacked particles, known as marine snow (Fowler and Knauer, 1986) are characteristic for high productive areas. Since the water depth in the investigated area is relatively low, the distance to the seafloor is comparably short, especially on the shelf. We therefore expect little lateral displacement of dinocysts during their transport to the ocean floor.

However, several currents have the potential to transport dinocysts into the study area; (1) from the north by the AC, SACW or NADW, (2) from the Indian Ocean by the AgC and AAIW and (3) from the south by ESACW and AABW.

(1) North of the BS, Dale et al. (2002) and Marret (1994) found *Lingulodinium machaerophorum* in relatively high abundances. In case of poleward transport by the AC (a current which reaches occasionally up to 24°S), SACW or NADW, this species would be expected at least in the northernmost parts of the BS. However, the results show that this dinocyst species is completely absent there. This is consistent with earlier findings by Zonneveld et al. (2001a) who recorded *L. machaerophorum* in only a few samples in very low abundances at the Kunene River and off Walvis Bay.

(2) Species specific for the warm and nutrient poor waters in the southwestern Indian Ocean have not been detected in the studied material. However, sediments along the east African Coast have not been investigated on dinocysts up to today. Nine by the authors investigated pilote samples off the city of Durban (30°S) did not contain a single dinocyst, probably due to fast currents flowing over the shelf and a very steep slope in this region. Davey (1971) investigated dinocysts in surface sediments on the shelf between Cape Town and Cape Agulhas. In this geographically small area, he found *O. centrocarpum* associated with the AgC and *Spiniferites ramosus* related to the BC. Our results show that *O. centrocarpum* is abundant in the entire BS (Fig. 9a), but more abundant in the warmer waters offshore. Esper et al. (2004) proposed amongst other species *O. centrocarpum*, *O. israelianum*, *S. mirabilis* and *S. membranaceus* as indicators

for the AgC inflow. Marret and de Vernal (1997) also found *O. centrocarpum* and several *Spiniferites* species as part of a subtropical assemblage in their study on dinocysts from surface sediments of the southern Indian Ocean. We find only slightly higher abundances of *S. mirabilis* in the south, whereas *S. membranaceus* and *O. israelianum* do not show this trend. We therefore assume that these species have not been transported into the BS.

(3) In the present study, not a single specimen of characteristic subpolar or polar species such as *Selenopemphix antarctica* and *Impagidinium pallidum* (Marret and Zonneveld, 2003) are recorded. We therefore assume that no large scale transport from the south has influenced our association.

Apart from lateral displacement by ocean currents, particles can also be transported secondarily by turbidites, debris flows, winnowing or sliding processes. Reworked dinocyst species can be an indicator for the rearrangement of sediments. Within the investigated sediment samples reworked dinocysts are extremely rare and occur in very low abundances (see Table 1). We cannot exclude sliding of sediments in the BS but assume that as a result of the mostly shallow position of the sites on the continental shelf this potential effect on the association may be ignored. No indication of winnowing can be detected within the research area with exception of four samples from extreme shallow water depths that contained pure sand particles and were barren of dinocysts (see Fig. 6).

Particles also can be displaced within nepheloid layers. Bottom nepheloid layers (BNLs) at the seafloor are maintained by turbulent mixing in the bottom boundary layer (e.g., Bacon and Ruettgers van der Loeff, 1989; McCave, 1986). Sediments can permanently be disaggregated, resuspended, transported within the bottom nepheloid layer (BNL) by bottom water currents and then redeposited (Thomsen and van Weering, 1998; Hensen et al. 2000). Intermediate nepheloid layers (INLs) develop near continental margins by detachment of the BNL and seaward advection along an isopycnal surface (e.g., McCave et al., 2001). They are considered to be very important for transporting organic matter from the ocean margin to the deeper regions (Murray, 1987). McPhee-Shaw et al. (2004) showed that INLs off Northern California contribute considerably to cross-margin transport. Studies of Giraudeau et al. (2000), Mollenhauer et al. (2003) and Inthorn et al. (2006a,b) indicate a notable transport of resuspended material from the outer shelf to the upper continental slope off Namibia. BNL intensity is highest at the outer shelf near the shelf break. Between 24°S and 26.5°S a depocenter with as much as

9% organic carbon content is observed on the slope between 400 and 1500 m water depth (Rogers and Bremner, 1991; Mollenhauer et al., 2002; Inthorn et al., 2006b). The ^{14}C ages of surface sediments collected across this depocenter by Inthorn et al. (2006b) decrease downslope from 3100 yrs to about 1900 yrs. Sample 4804 from the continental slope at about 24°S shows a completely different dinocyst association than the surrounding samples. This sample with very high relative abundances of cysts of *Brigantedinium* spp. and highest values for Corg (Guerrero, 2002) is positioned at the deepest position of the depocenter. Giraudeau et al. (2000) propose a conceptual model of the flow field off Walvis Bay in the NBR. Due to Ekman transport the bottom currents are deflected. East of the upwelling front (equatorward flow over the bottom) onshore transport takes place, whereas west of the front (poleward flow over the seafloor) offshore transport occurs.

According to the flow direction of the prevailing ocean currents there would be an onshore bottom transport at depths which are influenced by equatorward flowing ESACW and NADW and an offshore bottom transport at depths which are influenced by poleward flowing SACW and AAIW. The distribution of the dinocyst species does not support this bottom transport hypothesis. It is conceivable that the direction of transport varies with time depending on changing influence areas of the bottom currents. The signal in the sediment would then rather be random.

2.5.2. Preservation

Recently it has been shown that organic-walled dinocysts associations may be altered pre- and post-depositionally as a result of species-selective degradation (Zonneveld et al., 1997). The rate of degradation appears to be related to the bottom water oxygen concentration (Zonneveld et al., 2007). According to the CCA (Fig. 14 and table 3), bottom water oxygen does not form a significant factor related to the dinocyst distribution in the studied area. At most sites sedimentation rates are relatively high and bottom waters are oxygen-depleted. We consequently assume that aerobic degradation did not severely affect the dinocyst association.

2.5.3. Ecological borders

Within the BS fronts may act as a physical barrier to the movement and exchange of the organisms in the water column. The distributions of shoals, commercial catches

and larvae of pelagic fish species in the Benguela ecosystem suggest that a well-defined ecological boundary at 24°30' S exists which is caused by changes in wind stress, turbulence and stratification (Agenbag and Shannon, 1988). This environment is unsuitable for the consistent passage of pelagic organisms. Water mass analyses performed by Duncombe Rae (2005) suggest an oceanographical discontinuity at about the latitude of Lüderitz. A closed meshed zooplankton study on euphausiid species by Barange et al. (1992) revealed the shelf break zone, the Lüderitz upwelling cell (24-25°S) and the ABF as biogeographical borders. Also the distribution of planktic foraminifera tests in the sediment reflect the Lüderitz boundary as shown by Giraudeau (1993). Little et al. (1997) concluded that the diverse environmental conditions in the SBR and NBR cause these faunal differences.

The dinocyst distribution does not reflect a sharp discontinuity at the Lüderitz boundary but some species do show preferences. The distribution of *S. ramosus* (Fig. 9b) reveals a south to north gradient, whereas *N. labyrinthus* is found rarely in the SBR (Fig. 9c).

According to Marret and Zonneveld (2003) *N. labyrinthus* is a cosmopolitan and tolerant species which reflects regional conditions. This is supported by the achieved results where it can be assumed that its motile takes some advantage of the instable conditions caused by the merging ABF.

The shelf break front as a longitudinal boundary is not sharply mirrored by any of the dinocyst species.

2.5.4. Distribution of organic-walled dinocysts related to environmental factors

Both, visual observation and the statistical analyses show that the dinocyst distribution is mainly related to onshore-offshore trends. Thereby, the relative ratio of peridinoid to gonyaulacoid cysts in Fig. 6 is lower near the coast. Coastal samples are plotted on the most positive side of the first DCA axis (Fig. 12).

Regarding the ordination of the samples from the SBR or NBR (Fig. 12), it can be concluded that the second DCA-axis represents a gradient from North to South, whereas mostly the continental slope samples are mainly influenced by this gradient. The oceanographic features of the BS show strong gradients in the shelf region influenced by upwelling whereas farther offshore the latitudinal climatic gradients have more effect.

The CCA shows that chlorophyll-*a*, SST and SSS are related significantly to the distribution of the dinocyst species. However, after correcting for co-variance only chlorophyll-*a* and SSS remain.

Cysts formed by heterotrophic species have their highest relative abundances at sites with relatively high chlorophyll-*a* concentrations whereas phototrophic species plot on the negative side of the CCA. This does, however, not necessarily imply that phototrophic species produce more cysts at sites with relatively low chlorophyll-*a* concentrations. Recently, Zonneveld et al. (2007) showed that in regions without diagenetic overprint both, phototrophic and heterotrophic dinoflagellates increased their cyst production in linear relationship to increasing chlorophyll-*a* concentrations. Heterotrophic dinoflagellates increased their cyst production about 70 times more than phototrophic dinoflagellates, thereby resulting in lower relative abundances of cysts of phototrophic dinoflagellates in regions with relatively low chlorophyll-*a* concentrations. Within the studied area the relative abundances of heterotrophic dinoflagellate cysts form, however, a good proxy for productivity reconstructions. This conforms earlier studies by Zonneveld et al. (2001b) and Reichart and Brinkhuis (2003) which show that only in case of perfect preservation, cysts of heterotrophic species can be used as productivity indicators.

Based on visual examination of the dataset, six groups of species have been determined.

The first group consists of two species whose distribution is restricted to the most coastal sites. These species cysts of *P. kofoidii* and *S. quanta* do not plot closely together in the DCA or CCA. This is most likely due to two samples on the slope where cysts of *P. kofoidii* occur in exceptional high concentrations. Nevertheless, the two species of group 1 occur in samples characterised by extremely high chlorophyll-*a* concentrations. Both species are known to occur in upwelling regions (Marret and Zonneveld, 2003). Within these areas wave generated mixing enhances nutrient concentrations in the upper water rather than wind induced upwelling which can be observed in the studied region along the shelf break front. The high productivity close to the coast might also be enhanced by aeolian input of trace elements and iron. Since *P. kofoidii* and *S. quanta* occur in high relative abundances along the whole coast they are not specifically influenced by the rivers.

Cysts of *Zygabikodinium lenticulatum*, a species common in coastal areas of was not found in the BS samples studied here, nor by Zonneveld et al. (2001). Joyce and Pitcher (2004) and Joyce et al. (2005) found cysts of *Z. lenticulatum* dominating the dinocyst associations off Lambert's Bay (32°S) and in Saldanha Bay (33°S). This could be the result of the occurrence of locally restricted blooms of *Z. lenticulatum*. Within the

semi-enclosed embayment of Saldanha Bay this seems very plausible. Pitcher and Calder (2000) report frequent occurrences of red tides in the Lambert's Bay region.

The dinocyst species of group 2 (*Brigantedinium* spp., *E. aculeatum*, *Echinidinium* spp. and *E. transparantum*) form a cluster as well in the DCA as in the CCA where they plot in the middle of the chlorophyll-*a* gradient. Several studies suggest a relationship between high productivity and high relative abundances of *Brigantedinium* spp., including mostly “round browns” (Marret and Zonneveld, 2003). In our investigated region we can also determine such a relationship since they occur in samples with intermediate to high chlorophyll-*a* concentrations. Exceptions can be caused by local lateral transport as already discussed. *Echinidinium* species have been recorded to be characteristic for upwelling regions (Marret and Zonneveld, 2003). In the active upwelling region it is turbulence, however, which prevents primary producers to build up a standing stock. Once upwelling ceases, the nutrient-rich water is ideal for phytoplankton growth and, as the thermocline develops through solar warming of the euphotic layer, plankton biomass increases (Chapman and Shannon, 1985). As *Echinidinium* species are thought to be heterotrophic, the high amount of prey in the vicinity of the region of active upwelling might be the cause of the high cyst concentrations of these species in the studied region.

Group 3 consists of the heterotrophic species *L. oliva*, cysts of *P. americanum*, *S. nephroides* and *V. calvum* whose distribution separates distinctly from the other species. Their maximal abundance is found in sites at the river mouths characterised by high chlorophyll-*a* and low salinity concentrations in the upper waters.

However, SSS are low at most nearshore sites in the BS. Chlorophyll-*a* values are likewise high along the whole coast, not especially at the river mouths. There must therefore be other river-specific factors which influence the dinocyst distribution at the two river mouths in the BS. The motiles of the species of group 3 might prefer particular prey organisms which grow in river discharge plumes. Rivers introduce land-derived solutes which influence the nutrient composition of the sea water. Birch (1975) showed that increased concentrations of Fe and Mn on the shelf at 29°S most likely derive from the Orange River. Anthropogenic input of nutrients or heavy metals into the Orange River is relatively high because of mining, urbanisation and substantial agriculture, which also accelerate erosion (Orange River system overarching strategies, 2004). The Kunene River is less eutrophied, because as the drainage area is sparsely populated and agriculture is extensive. Considering the enormous load of material transported by the

river sedimentation rates at the river mouths are expected to be as high enough to end up with anthropogenic influenced surface sediments in these regions.

There are numerous studies that focus on dinocyst records in regions influenced by fluvial input (e.g., McMinn, 1991; Thorsen and Dale, 1997; Matsuoka, 1999; Mudie and Rochon, 2001; Dale et al., 2002; Pospelova et al., 2002, 2004, 2005; Sangiorgi and Donders, 2004). They show that generally *L. machaerophorum*, *O. centrocarpum*, *O. israelianum*, *P. schwartzii* and cysts of *S. quanta* can reach high concentrations in these sediments. However, these studies all focus on estuaries in non-upwelling regions and found higher relative abundances of mainly *L. machaerophorum* and *S. quanta* related to pollution.

Studies on the distribution of *L. oliva*, cysts of *P. americanum*, *S. nephroides* and *V. calvum* in other regions show that their occurrence is not restricted to river estuaries or even to coastal environments (Marret and Zonneveld, 2003; Biebow, 1996; Kawamura, 2004). Even in the BS cysts of *P. americanum* and *S. nephroides* were present in outer neritic sites along the entire coast. Nevertheless, within our shelf samples there is a clear relationship to the river mouths and as such they can be used as proxy for fluvial influences in local palaeoenvironmental studies.

Conform to worldwide records, *D. chathamense*, *I. patulum* and *O. centrocarpum* (group 4) have their highest relative abundances on the slope to open ocean where oligotrophic conditions prevail (Marret and Zonneveld, 2003). However, the conditions at our investigated sites are not oligotrophic but meso- to eutrophic. The abundant occurrence of these species in the BS can therefore be refined as reflecting mesotrophic to eutrophic conditions at the border of the upwelling.

S. ramosus (group 5) shows higher relative abundances in the south of the BS where temperatures are lower. Regarding the SBR there is a relation to higher chlorophyll-*a* concentrations for this species. This supports the recorded affinity to eutrophic upwelling conditions of *S. ramosus* by Marret and Zonneveld (2003).

N. labyrinthus and *O. centrocarpum* (group 6) are relatively more abundant in the NBR where values for SSS and SST are higher compared to the SBR. Both species show no particular relationship to the chlorophyll-*a* concentrations. *N. labyrinthus* has also been found more abundantly in the NBR by Zonneveld et al. (2001a). Within the worldwide dataset of Marret and Zonneveld (2003) this species shows no global preferences but clear regional relationships to environmental parameters.

The spatial distribution of species of group 5 and 6 could also be influenced by the Lüderitz Boundary as explained in 5.3..

Most of the species showing random distributions are likewise not related to any of the environmental parameter in the CCA. Nevertheless, the spatial distribution of *Impagidinium* species in Fig. 8-10 reveals, that they are present, although in low relative abundances, on the highly productive shelf in the BS. According to former studies, most species of the genus *Impagidinium* were considered to be restricted to open oceanic sediments (e.g., Wall et al., 1977; Harland, 1983; Edwards and Andrieu, 1992). This could be due to the former small sample coverage in upwelling regions and to transport. Our results also show, however, that cyst forming heterotrophic dinoflagellates can not be considered as one uniform group but that different species give different signals.

2.6. Conclusions

The composition of organic-walled dinoflagellate cyst species in the surface sediments of the Benguela upwelling region differs remarkably within relatively small regions. The assemblages reflect the highly variable environmental conditions of the surface waters.

Six associations were identified as characteristic for certain regions within the Benguela system:

1. *S. quanta* and cysts of *P. kofoidii* occur in highest relative abundances in sediments close to the coast.
2. *Brigantedinium* spp., *E. aculeatum*, *Echinidinium* spp. and *E. transparentum* are found in highest relative abundances on the shelf in the vicinity of active upwelling.
3. *L. oliva*, cysts of *P. americanum*, *S. nephroides* and *V. calvum* occur restricted to the river mouths most likely related to the input of trace metals.
4. *D. chathamense*, *I. patulum* and *O. centrocarpum* are found in highest relative abundances in sediments on the slope and open ocean.

5. *S. ramosus* is found with increasing relative abundances in the southern Benguela region (south of 24°S).

6. *N. labyrinthus* and *P. reticulata* occur in highest relative abundances in the northern Benguela region (north of 24°S).

The composition of the dinocyst assemblages is significantly related to the chlorophyll-*a* content at the sea surface and to sea surface salinity. Bottom water oxygen values are low at most sites and do not show a significant relationship to the dinocyst species distribution. No indications of large scale transport were found and lateral sediment displacement only seems to influence the dinocyst community in the sediments to a small amount.

Organic walled dinoflagellate cysts seem to be a useful tool to reconstruct past productivity in the Benguela system.

2.7. Acknowledgements

We are grateful to John Rogers for collaboration and provision of sediment samples. Michael Marhold is acknowledged for his support in the laboratory. Henk Brinkhuis and one anonymous reviewer provided constructive comments that improved the manuscript. We thank Peer Helmke and Martin Butzin for advice in environmental data procession. Fernando Guerrero kindly provided his data for the content of total organic carbon. This work was funded by the Deutsche Forschungsgemeinschaft as part of the Research Center “Ocean Margins” (RCOM) of the University of Bremen, contribution RCOM No. 0491.

All data presented in this study are available from the public database Pangaea (www.pangaea.de).

doi:10.1594/PANGAEA.714259

doi:10.1594/PANGAEA.693973

doi:10.1594/PANGAEA.693946

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3. Organic-walled dinoflagellate cysts as indicators of oceanographic conditions and terrigenous input in the NW African upwelling region

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Review of Palaeobotany and Palynology, in press. doi: 10.1016/j.revpalbo.2009.10.005

(Received 1 May 2009; revised 25 September 2009; accepted 15 October 2009)

Abstract

In order to examine the spatial distribution of organic-walled dinoflagellate cysts (dinocysts) in recent sediments related to environmental conditions in the water column, thirty-two surface sediment samples from the NW African upwelling region (20-32°N) were investigated.

Relative abundances of the dinocyst species show distinct regional differences allowing the separation of four hydrographic regimes. (1) In the area off Cape Ghir, which is characterized by most seasonal upwelling and river discharge, *Lingulodinium machaerophorum* strongly dominates the associations which are additionally characterized by cysts of *Gymnodinium nolleri*, cysts of *Polykrikos kofoidii* and cysts of *Polykrikos schwartzii*. (2) Off Cape Yubi, a region with increasing perennial upwelling, *L. machaerophorum*, *Brigantedinium* spp., species of the genus *Impagidinium* and cysts of *Protoperidinium stellatum* occur in highest relative abundances. (3) In coastal samples between Cape Ghir and Cape Yubi, *Gymnodinium catenatum*, species of the genus *Impagidinium*, *Nematosphaeropsis labyrinthus*, *Operculodinium centrocarpum*, cysts of *P. stellatum* and *Selenopemphix nephroides* determine the species composition. (4) Off

Cape Blanc, where upwelling prevails perennially, and at offshore sites, heterotrophic dinocyst species show highest relative abundances. A Redundancy Analysis reveals fluvial mud, sea surface temperature and the depth of the mixed layer in boreal spring (spring) as the most important parameters relating to the dinocyst species association.

Dinocyst accumulation rates were calculated for a subset of samples using well-constrained sedimentation rates. Highest accumulation rates with up to almost 80.000 cysts $\text{cm}^{-2} \text{ky}^{-1}$ were found off Cape Ghir and Cape Yubi reflecting their eutrophic upwelling filaments. A Redundancy Analysis gives evidence that primary productivity and the input of fluvial mud are mostly related to the dinocyst association.

By means of accumulation rate data, quantitative cyst production of individual species can be considered independently from the rest of the association, allowing autecological interpretations. We show that a combined interpretation of relative abundances and accumulation rates of dinocysts can lead to a better understanding of the productivity conditions off NW Africa.

Keywords: organic-walled dinocysts, accumulation rates, aeolian dust, river discharge, upwelling, Cape Ghir, Cape Yubi, Cape Blanc

3.1. Introduction

Upwelling areas are among the most productive regions of the modern oceans (e.g. Longhurst et al., 1995; Carr, 2002). Oceanographic changes in these systems are connected with global climate (Berger and Wefer, 2002) and are discussed as having a major impact on the global carbon budget (e.g. Lampitt et al., 1995). Therefore, upwelling systems have become of increasing interest in palaeoclimatic studies during recent years (e.g. Summerhayes et al., 1995; Berger and Wefer, 2002; Zhao et al., 2006; Mohtadi et al., 2008).

The NW African coastal upwelling is one of the four large Eastern boundary current systems within the trade wind belts of the subtropics. A number of studies have dealt with the marine hydrographic and productivity conditions off NW Africa (e.g. Meggers et al., 2002a; Eberwein and Mackensen, 2006 and Richter et al., 2007), showing a high regional complexity. Gradients in environmental parameters influencing marine productivity are

documented in the underlying sediments. However, the productivity patterns are not yet fully understood.

The study of organic-walled dinoflagellate cyst (dinocyst) assemblages preserved in marine sediments has proved to be useful for reconstructing past changes in oceanographic conditions and primary productivity in highly productive areas (Zonneveld et al., in press; de Vernal et al., 2005; Pospelova et al., 2006; Marret et al., 2008). Dinocyst associations in marine sediments reflect the environmental conditions of upper waters in detail (e.g. Rochon et al., 1999; de Vernal et al., 2001; Marret and Zonneveld, 2003; de Vernal et al., 2005; Pospelova et al., 2006; Esper and Zonneveld, 2007; Radi et al., 2007; Pospelova et al., 2008). The increasing number of studies on the present day geographic distribution of dinocysts in upwelling systems shows that, although there are some generalities, every system has its own characteristic associations (Lewis et al., 1990; Marret, 1994; Biebow, 1996; Zonneveld et al., 1997a; Marret et al., 2001; Zonneveld et al., 2001a; Radi and de Vernal, 2004; Sprangers et al., 2004; Patterson et al., 2005; Holzwarth et al., 2007; Radi et al., 2007; Bouimetarhan et al., 2009). Consequently, to establish an area-specific palaeoceanographic reconstruction based on fossil dinoflagellate cyst assemblages it is essential to obtain regionally focused information about the relationship between cyst distribution in recent sediments and the according environmental conditions in the upper water column.

Until now, only one study has been carried out on organic-walled dinocysts in the NW African upwelling area (Targarona et al., 1999). This study concentrates on only three dominant dinocyst species and lacks their correlation to environmental data. Furthermore, it dates from before it became widely known that post-depositional aerobic degradation can change the cyst association considerably (Zonneveld et al., 1997b; Zonneveld et al., 2001b; Hopkins and McCarthy, 2002; Kodrans-Nsiah et al., 2008; Zonneveld et al., 2008). As a result, the environmental characterization of the dinoflagellate cyst associations in this region needs revising in order to perform detailed oceanographic and climatic reconstructions. To obtain this basic information we studied the modern cyst associations of 32 surface sediment samples located along onshore-offshore transects between 20°N and 32°N where a latitudinal change from perennial to seasonal upwelling is observed (Mittelstaedt, 1991; Hernández-Guerra and Nykjær, 1997; Fig. 1). The input of dust aerosols and fluvial compounds also shows regional differences. This terrigenous supply can enrich the surface waters with trace elements

such as iron, resulting in enhanced marine productivity (e.g. Middleton and Goudie, 2001; Pittman, 2002).

The dinoflagellate cyst associations were related to upper ocean environmental conditions. Well-assessed sedimentation rates at 14 sites enable the calculation of accumulation rates of individual cyst species which can be assumed to reflect cyst production rates for at least those species resistant to aerobic degradation. Comparing dinocyst composition and production with the gradational changes in the upper-oceanic environment, namely temperature, salinity, chlorophyll-*a* content, nitrate and phosphate concentrations as well as the amount of aeolian and fluvial input, allows us to adapt and refine the ecological characterization of selected cyst species.

3.2. Oceanographic and climatological setting

The investigated area is located in the eastern part of the subtropical North Atlantic gyre off Morocco, Western Sahara and Mauritania. Fig. 1 shows the most important oceanographical features.

The southward flowing Canary Current (CC) transports subtropical water which reaches down to 100 m depth (Knoll et al., 2002). It is underlain by North Atlantic Central Water (NACW) and/or South Atlantic Central Water (SACW). SACW is characterized by high nutrient concentrations relative to low-salinity NACW, and flows northward between 200 and 400 m depth. NACW features lower nutrient concentrations and flows southward between 100 and 600 m. Proportions of SACW decrease to the north until about 23°N in favour of NACW. Beneath these water layers, Mediterranean Outflow Water (MOW) flows southward down to a depth of 1700 m. Antarctic Intermediate Water (AAIW) enters the region from the south between 800 and 1000 m. It is underlain by the southward flowing North Atlantic Deep Water (NADW) (Knoll et al., 2002; Llinas et al., 2002).

The NE trade winds blowing parallel to the coast lead to Ekman transport which results in upwelling of cool and nutrient-rich central water. The intensity and occurrence of upwelling depends on the meridional shift of the Intertropical Convergence Zone. The cold upwelling zone on the continental shelf is separated by the shelf break front from warmer offshore waters (Hagen, 2001). As the trade wind belt moves seasonally (Fig. 1), the upwelling conditions change within a seasonal cycle (Wooster et al., 1976; Mittelstaedt, 1991; Nykjær and Van Camp, 1994).

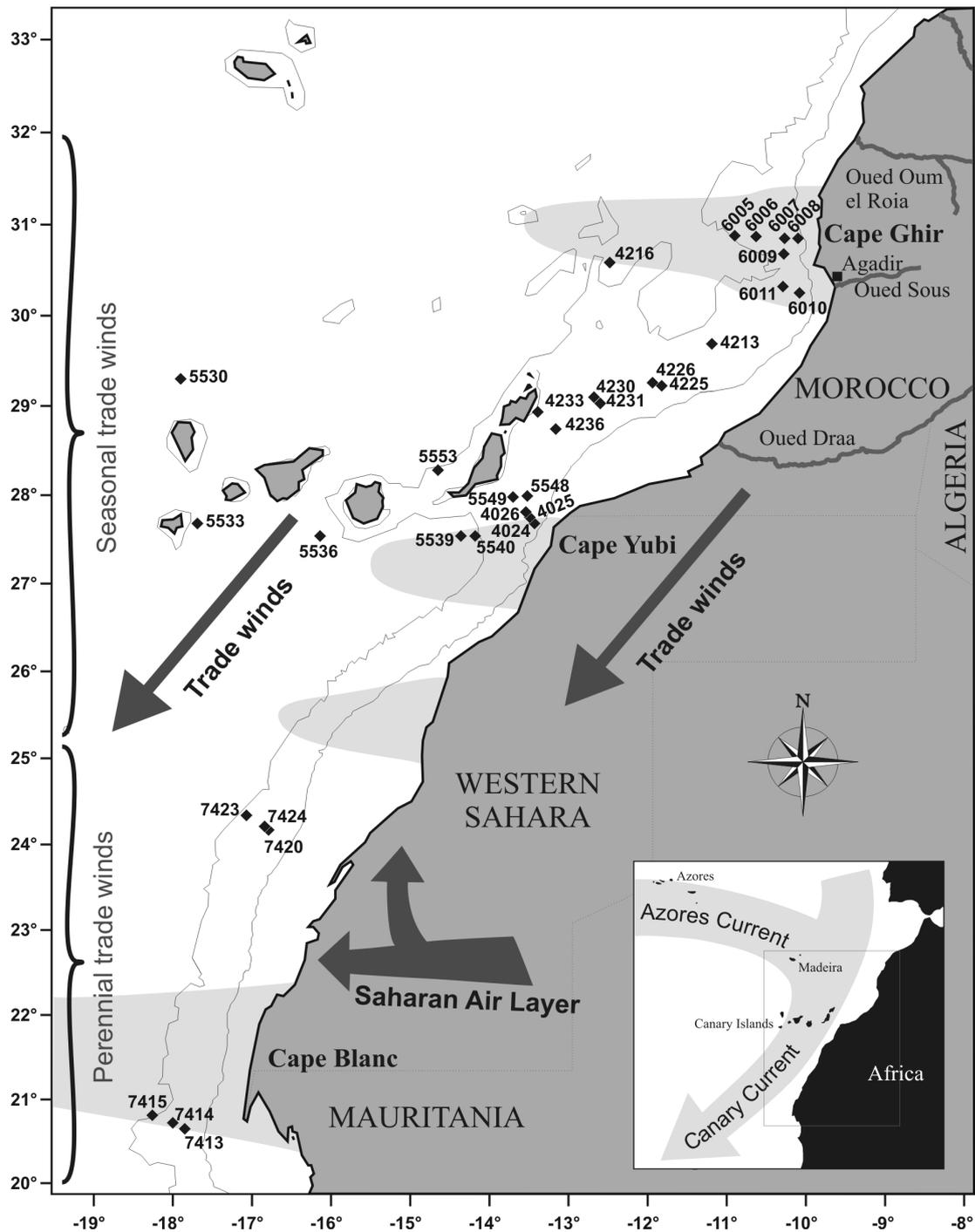


Fig. 1 Map of the study area off NW-Africa with main surface ocean currents, wind field, bathymetry and location of 32 surface sediment samples. Isobaths indicate 200 and 2000 m water depth. Numbers represent GeoB sample numbers. Shaded areas depict main filaments of upwelled waters (see section 3.2.).

Between 20°N and 25°N, upwelling persists throughout the year whereas north of 25°N coastal upwelling is predominant in boreal summer (summer) and early boreal fall (fall) (Mittelstaedt, 1991; Hernández-Guerra and Nykjær, 1997). At pronounced capes (Cape Ghir, Cape Yubi and Cape Blanc), filaments of upwelled water spread for

hundreds of kilometers offshore (Van Camp et al., 1991; Nykjær and Van Camp, 1994; Hernández-Guerra and Nykjær, 1997; Hagen, 2001). These filaments are generated by the interaction of the current system with the coastal cape morphology (Hagen et al., 1996; Stevens and Johnson, 2003). The upwelling signal off Cape Ghir and Cape Yubi is strongest in summer and early fall (Hernández-Guerra and Nykjær, 1997). Productivity off Cape Blanc, characterized by perennial upwelling, is highest in boreal winter (winter) and spring (Mittelstaedt, 1991) when nutrient-rich SACW is the source of the upwelled water (Hagen, 2001).

The oceanographical parameters are affected by the upwelling processes but also directly by latitudinal and seasonal climatic variations. In general, upwelled water is characterized by low temperature, low salinity, high nutrient concentrations and a shallow mixed layer. According to the World Ocean Atlas 2005 Data Set (WOA 2005), National Oceanographic Data Centre, Washington D.C. (http://www.nodc.noaa.gov/OC5/WOA05/pr_woa05.html), yearly sea surface temperatures (SST) at the sampling locations vary within about 18 to 21 °C, being lowest off Cape Ghir and Cape Blanc and highest at offshore sites (Fig. 2). Additionally, SST values show a latitudinal gradient at offshore sites with higher temperatures in the south.

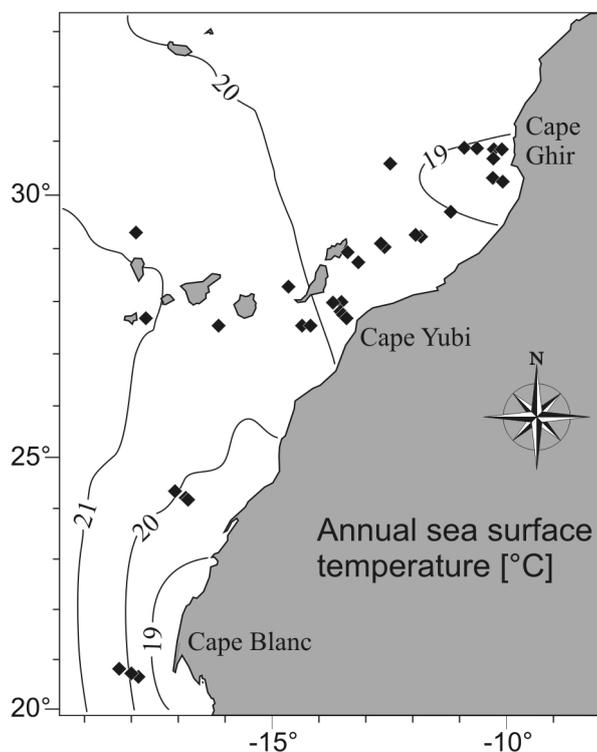


Fig. 2. Annual sea surface temperature [°C] off NW-Africa

Yearly salinity data at the sea surface at the sampling locations range from about 36.2 psu off Cape Blanc (indicating SACW as the source of the upwelled water) to about 36.8 psu off Cape Yubi (WOA 2005). Yearly sea-surface nitrate concentrations at the sampling locations are highest off Cape Blanc (up to about $5 \mu\text{mol l}^{-1}$), whereas in other regions including Cape Ghir and Cape Yubi values from 0 to $1 \mu\text{mol l}^{-1}$ are common (WOA 2005). A similar pattern is shown by yearly sea-surface phosphate concentrations at the sampling locations where high values of about $0.4 \mu\text{mol l}^{-1}$ off Cape Blanc contrast with low values of about 0 to $0.15 \mu\text{mol l}^{-1}$ within the rest of the investigated area (WOA 2005). Yearly sea-surface silicate concentrations at the sampling locations do not show this extreme variation. They vary from about 1.5 to $3.6 \mu\text{mol l}^{-1}$ with highest values off Cape Blanc and Cape Yubi and lowest values off Cape Ghir (WOA 2005). Satellite-derived yearly sea-surface chlorophyll-*a* concentrations (<http://seawifs.gsfc.nasa.gov/SEAWIFS.html>) at the sampling locations mirror the coastal upwelling band with maximum values of 2 to 6 mg m^{-3} off the capes and within the filaments. At offshore sites, values from 0 to 1 mg m^{-3} of chlorophyll-*a* are common. As another indicator of productivity, Meggers et al. (2002a) reported highest values for total organic carbon of about 1.5 to 1.8 % in the sediments off Cape Ghir and Cape Yubi (Cape Blanc was not included in their study). The mixed layer depth (MLD) (Fig. 3; Monterey and Levitus, 1997) at the sampling locations is generally deeper in offshore areas (down to 150 m), most likely as a result of stronger stratification compared to turbulent upwelling regions. MLDs also show a strong seasonal variation with deepest values in spring and shallowest values in fall. Off Cape Blanc, this variation is lowest and MLDs are relatively shallow throughout the year, probably due to perennial upwelling activity at this site. Bottom waters in the investigated area show relatively high values of dissolved oxygen (Sarnthein et al., 1982; WOA 2005). Only south of 25°N is an oxygen minimum layer with values below 2 ml l^{-1} observed at the upper continental slope. The oxygen consumption is due to bacterial decomposition of organic material. Terrigenous compounds from land are introduced either by aeolian dust or river discharge. The region off NW Africa is influenced by frequent Saharan dust storms. Aeolian dust is transported from the Sahara and the Sahel deserts offshore by three wind systems: the NE trade winds, the Harmattan and the Saharan Air Layer (details are reviewed by Stuut et al. (2005). Holz et al. (2004) used grain size data along the continental margin off NW Africa to calculate end members (EM) representing different sediment sources. The most widespread EM reflecting fine grained aeolian dust

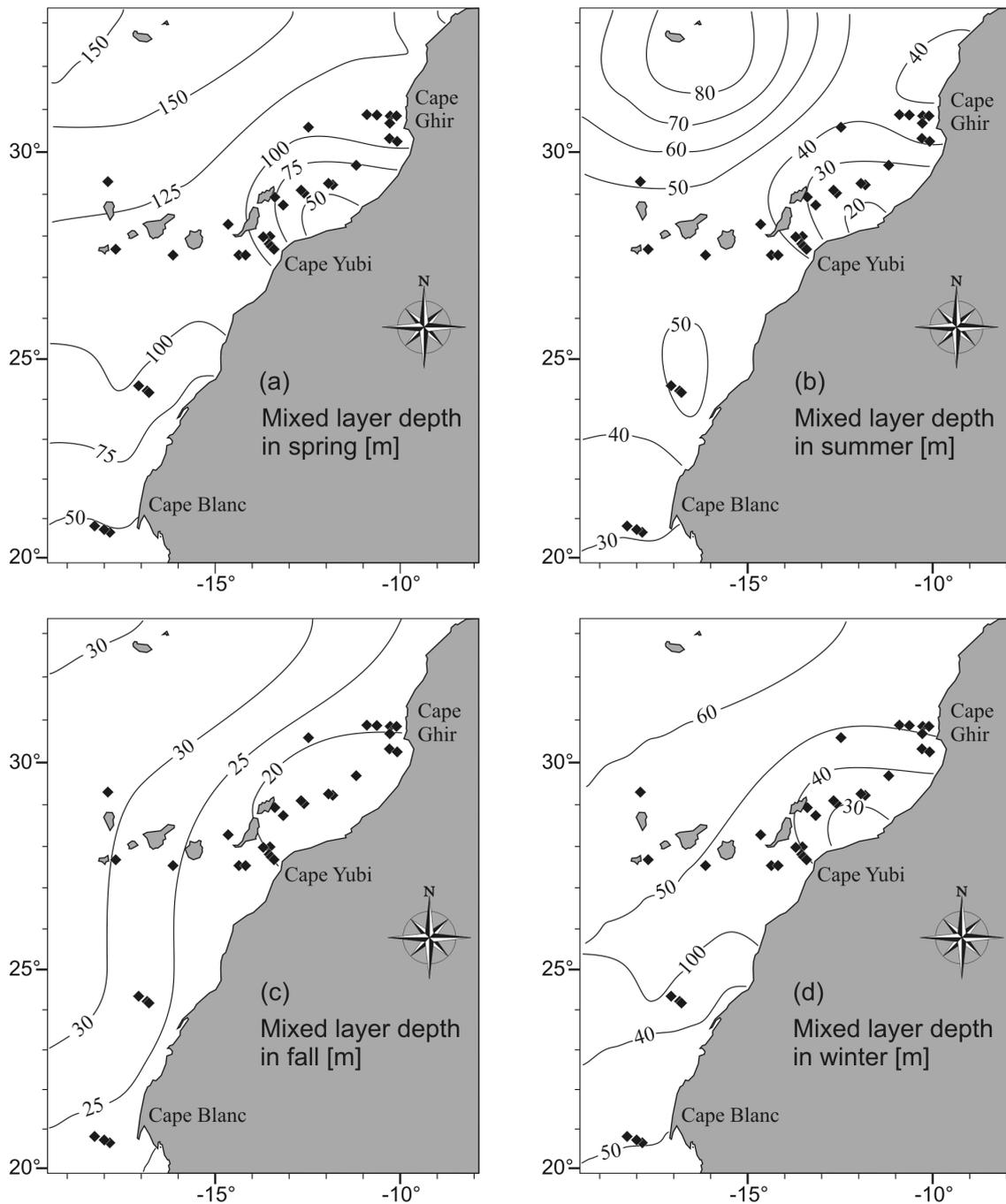


Fig. 3. Seasonal mixed layer depth [m] off NW-Africa in boreal spring (a), boreal summer (b), boreal fall (c) and boreal winter (d).

dominates in samples around the Canary Islands and generally in most samples south of Cape Ghir. In a few samples off Cape Blanc the EM representing coarse grained aeolian dust predominates. The most fine grained EM reflecting fluviially discharged mud is confined to the area off Cape Ghir most likely provided by the Sous River draining the Atlas Mountains (Fig. 1) which reaches the ocean at 30.3°N, south of Cape Ghir.

According to Elmouden et al. (2005), the runoff varies extremely (seasonally and interannually) and has an annual average water discharge of 0.3km^3 which is relatively low. During times of flash flood, water flow is fast and soil erosion is considerable, with total suspended solid of about $1.6 \cdot 10^6 \text{ t y}^{-1}$ (Elmouden et al., 2005). This high suspended sediment yield relative to the proportion of runoff is caused by the rock erodibility (Probst and Amiottes-Suchet, 1992). South of 30°N , arid conditions prevail and fluvial input into the research area only sporadically occurs where active small wadi systems are connected to the ocean.

3.3. Materials and methods

3.3.1. Materials

The 32 samples investigated in this study were taken with a boxcorer device during the Victor Hensen 96/1 cruise (Neuer et al., 1997a) and with a multicorer during Poseidon 272 (Meggers and participants, 2002b), Meteor M37/1 (Wefer et al., 1997), M42/4 (Wefer et al., 1999) and M45/5 (Neuer et al., 2000) cruises and were obtained from the uppermost centimetre of the sediment. Water depths range from 95 to 3985 m. For sample positions and other details see Fig. 1 and Table 1. Sedimentation rates in the investigated area vary between 2 cm ky^{-1} further offshore and 10 cm ky^{-1} off Cape Yubi (Table 1; Kuhlmann et al., 2004). We therefore assume that sediments of all samples are of late Holocene to modern age. Dating is based on the stratigraphy of gravity cores from the same sites (Kuhlmann et al., 2004).

3.3.2. Methods

3.3.2.1. Laboratory preparation and taxonomy

About 1 cm^3 of the sediment was dried for at least 24 h at 70°C . After being weighed the sample was treated with cold 10 % hydrochloric acid (HCl) in order to dissolve the carbonates. Shortly after, the suspension was neutralized with 10 % potassium hydroxide solution (KOH). After 24 h the liquid was decanted and washed twice with demineralised water. Cold 38 % hydrofluoric acid (HF) was then added to dissolve the silicates. Two hours of agitation were followed by two days HF-treatment without agitation.

Table 1. Sample positions and other details. Lat = latitude; Lon = longitude; VH = Victor Hensen; M = Meteor; P = Poseidon; BC = box corer; MUC = multicorer; SR = sedimentation rate; DBD = dry bulk density. Values for SR and DBD are mean values for the Holocene from Kuhlmann et al. (2004).

Sample GeoB	Lat	Lon	Depth [m]	Cruise	Device	SR [cm ka ⁻¹]	DBD [g cm ⁻³]
4024-1	27.678	-13.432	95	VH96/1	BC		
4025-2	27.748	-13.488	504	VH96/1	BC		
4026-1	27.808	-13.543	990	VH96/1	BC		
4213-1	29.697	-11.078	1547	M37/1	MUC	2.92	0.84
4216-2	30.632	-12.397	2325	M37/1	MUC	3.83	0.78
4225-3	29.275	-11.782	1281	M37/1	MUC	4.25	0.89
4226-1	29.320	-11.833	1400	M37/1	MUC	4.17	0.86
4230-1	29.128	-12.597	1316	M37/1	MUC	5.50	0.85
4231-2	29.088	-12.555	1207	M37/1	MUC	7.75	0.88
4233-2	28.975	-13.330	1303	M37/1	MUC	6.00	0.88
4236-2	28.783	-13.095	1030	M37/1	MUC	6.83	0.93
5530-3	29.303	-17.897	3985	M42/4	MUC		
5533-1	27.682	-17.693	3251	M42/4	MUC		
5536-3	27.537	-16.135	3456	M42/4	MUC	6.50	0.80
5539-2	27.537	-14.355	2202	M42/4	MUC		
5540-3	27.535	-14.175	2035	M42/4	MUC	9.92	0.88
5548-3	27.992	-13.518	1162	M42/4	MUC	8.83	0.93
5549-2	27.978	-13.695	1454	M42/4	MUC	11.25	0.87
5553-2	28.277	-14.645	3397	M45/5	MUC		
6005-1	30.880	-10.897	1781	M45/5	MUC		
6006-2	30.868	-10.630	1282	M45/5	MUC	5.92	0.99
6007-1	30.852	-10.267	899	M45/5	MUC		
6008-2	30.845	-10.098	355	M45/5	MUC		
6009-1	30.682	-10.275	579	M45/5	MUC		
6010-1	30.250	-10.083	406	M45/5	MUC		
6011-2	30.315	-10.288	993	M45/5	MUC	6.83	0.98
7413-2	20.647	-17.845	508	P272	MUC		
7414-1	20.718	-18.000	1014	P272	MUC		
7415-1	20.805	-18.262	1911	P272	MUC		
7420-1	24.165	-16.788	676	P272	MUC		
7423-2	24.338	-17.070	1624	P272	MUC		
7424-1	24.210	-16.843	1063	P272	MUC		

Subsequently the solution was carefully neutralised using 40 % KOH, ensuring that it did not become alkaline. After another 24 h the solution was decanted and washed twice with demineralised water. Each sample was treated with ultrasound to clear the dinocysts and to separate the particles from each other. Then the samples were washed over a 20 µm mesh steel precision sieve and concentrated by centrifuge (8 min at 3500 revolutions per minute) to 500-1500 µl depending on the particle content. A fraction of 50 µl was brought onto a slide, embedded in glycerine jelly and sealed with paraffin wax. The dinocyst content of the slides was counted with a light microscope at 400 x magnification. Whenever a slide contained less than 200 dinocysts additional slides were counted. The nomenclature for the dinoflagellate cyst species was used and follows Fensome et al., (1993), Zonneveld (1997), Head et al. (2001) and Fensome and

Williams (2004). We grouped spherical brown cysts without spines (“round browns”) as *Brigantedinium* spp. Morphological criteria given in Bolch et al. (1999) were used to distinguish between cysts of *Gymnodinium catenatum* and cysts of *Gymnodinium nolleri*. Table 2 lists all dinocyst taxa which were observed in this study. Count data of all identified dinocysts are available on www.pangaea.de. Taxonomic information on the dinocyst species encountered in this study is provided in Appendix A.

Table 2. List of the identified dinoflagellate cyst taxa and their according cyst-theca relationship (following Head, 1996 and Marret and Zonnveld, 2003). For details on nomenclature, grouping and taxonomy see section 3.3.2.1 and Appendix A.

Dinoyst species	Motile affinity	Abbreviation	Figure No.
<i>Brigantedinium</i> spp.	<i>Protopteridinium</i> spp.	B spp	5a and 5b
<i>Echinidinium aculeatum</i>	unknown	E acu	5c and 5d
<i>Echinidinium delicatum</i>	unknown	E del	5e and 5f
<i>Echinidinium transparantum</i>	unknown	E tra	
<i>Echinidinium</i> spp.	unknown	E spp	5g and 5h
Cyst of <i>Gymnodinium catenatum</i>	<i>Gymnodinium catenatum</i>	G cat	6a and 6b
Cyst of <i>Gymnodinium nolleri</i>	<i>Gymnodinium nolleri</i>	G nol	6c and 6d
<i>Impagidinium aculeatum</i>	<i>Gonyaulax</i> sp.	I acu	6e and 6f
<i>Impagidinium patulum</i>	<i>Gonyaulax</i> sp.	I pat	6e and 6f
<i>Impagidinium sphaericum</i>	<i>Gonyaulax</i> sp.	I sph	6e and 6f
<i>Impagidinium</i> spp.	<i>Gonyaulax</i> spp.	I spp	6e and 6f
<i>Lejeunecysta oliva</i>	<i>Protopteridinium</i> sp.	L oli	
<i>Lingulodinium machaerophorum</i>	<i>Lingulodinium polyedra</i>	L mac	6g and 6h
<i>Nematosphaeropsis labyrinthus</i>	<i>Gonyaulax spinifera</i>	N lab	7a and 7b
<i>Operculodinium centrocarpum</i>	<i>Protoceratium reticulatum</i>	O cen	7c and 7d
<i>Operculodinium israelianum</i>	? <i>Protoceratium</i> sp.	O isr	
<i>Operculodinium janduchenei</i>	unknown	O jan	
Cyst of <i>Pentapharsodinium dalei</i>	<i>Pentapharsodinium dalei</i>	P dal	
Cyst of <i>Polykrikos kofoidii</i>	<i>Polykrikos kofoidii</i>	P kof	7e and 7f
Cyst of <i>Polykrikos schwartzii</i>	<i>Polykrikos schwartzii</i>	P sch	7g and 7h
<i>Polysphaeridium zoharyi</i>	unknown	P zoh	
Cyst of <i>Protopteridinium americanum</i>	<i>Protopteridinium americanum</i>	P ame	8a and 8b
Cyst of <i>Protopteridinium monospinum</i>	<i>Protopteridinium monospinum</i>	P mon	8c and 8d
Cyst of <i>Protopteridinium stellatum</i>	<i>Protopteridinium stellatum</i>	P ste	8e and 8f
<i>Pyxidinospis reticulata</i>	<i>Pyrodinium bahamense</i>	Py re	
<i>Selenopemphix nephroides</i>	<i>Protopteridinium subinermis</i>	S nep	8g and 8h
<i>Selenopemphix quanta</i>	<i>Protopteridinium conicum</i>	S qua	9a and 9b
<i>Spiniferites membranaceus</i>	<i>Gonyaulax</i> sp.	S mem	
<i>Spiniferites mirabilis</i>	<i>Gonyaulax spinifera</i>	S mir	
<i>Spiniferites pachydermus</i>	<i>Gonyaulax</i> sp.	S pac	
<i>Spiniferites ramosus</i>	<i>Gonyaulax</i> sp.	S ram	
<i>Spiniferites</i> spp.	<i>Gonyaulax</i> spp.	S spp	9c and 9d
<i>Trinovantedinium applanatum</i>	<i>Protopteridinium pentagonum</i>	T app	9e and 9f
<i>Votadinium calvum</i>	<i>Protopteridinium oblongum</i>	V cal	

3.3.2.2. Data processing

On the basis of the dinocyst count data, relative abundances and accumulation rates (AR) were calculated. AR were calculated for 14 of the 32 sites based on sedimentation rates and dry bulk density (DBD) measurements (see Table 1) according to Kuhlmann et al. (2004) using the following equation:

$$\text{dinocyst AR [cysts cm}^{-2} \text{ ky}^{-1}] = \text{sedimentation rate [cm ky}^{-1}] * \text{DBD [g cm}^{-3}] * \text{dinocysts g}^{-1}$$

Environmental parameters chosen for the calculations are listed in Table 3. Annual mean values at the sea surface were used for the chlorophyll-*a* content (Chl*a*), temperature (SST), salinity (SSS), nitrate (NO₃), phosphate (PO₄) and silicate (Si). Although these parameters do show seasonal differences, seasonal values of each parameter strongly co-variated when performing a first RDA so we chose annual mean values in RDA rel and RDA acc to ease the analysis. The correlation matrix of RDA rel illustrates the co-variation of the above mentioned parameters (Appendix B).

As the depth of the mixed layer (MLD) shows strong regional variations during the year, seasonal values for MLD were used. To check for selective preservation, the bottom water oxygen content was also included in the analyses. As a measure for the form of terrigenous input, we used end members for coarse grained aeolian dust (ADc), fine grained aeolian dust (ADf) and fluvially induced mud (FM) calculated by Holz et al. (2004). Seasonal values for MLD were obtained from Monterey and Levitus (1997) and were interpolated with Ocean Data View. The months January to March are referred to as winter (wi), April to June as spring (sp), July to September as summer (su) and October to December as fall (fa). Chl*a* values were derived from the SeaWiFS Project from the NASA Goddard Space Flight Center (<http://seawifs.gsfc.nasa.gov/SEAWIFS.html>). The grid for the Chl*a* data is 9 x 9 km. To exclude extreme local deviations, we averaged the data point nearest to the respective site with the 8 surrounding data points. All other environmental data were obtained from the World Ocean Atlas 2005 Data Set (WOA 2005), National Oceanographic Data Centre, Washington D.C. (http://www.nodc.noaa.gov/OC5/WOA05/pr_woa05.html). The bottom water oxygen data were completed by data from Sarnthein et al. (1982). Values for SSS, SST, NO₃, PO₄ and Si were interpolated with Ocean Data View, Version 3.4.0 (Schlitzer, 2008).

Because endmember calculations of grain size classes were not available for samples GeoB 4024-1, 4026-1, 4216-2, 4231-2, 5539-2 and 7415-1, these sites were not included in the statistical calculations.

Table 3. Environmental parameters used in the RDAs. Chl*a* = annual chlorophyll-*a* content at the sea-surface; NO₃ = annual nitrate concentration at the sea-surface; Ox = bottom water oxygen content; MLD = mixed layer depth in sp = boreal spring, su = boreal summer, au = boreal autumn and wi = boreal winter; PO₄ = annual phosphate concentration at the sea-surface; Si = annual silicate concentration at the sea-surface; SSS = annual sea-surface salinity; SST = annual sea-surface temperature. For values for ADF = aeolian dust fine grained; ADC = aeolian dust coarse grained and FM = fluvial mud see Holz et al. (2004) and www.pangaea.de.

Sample	Chl <i>a</i>	MLD sp	MLD su	MLD fa	MLD wi	NO ₃	Ox	PO ₄	Si	SSS	SST
GeoB	[mg m ⁻³]	[m]	[m]	[m]	[m]	[μmol l ⁻¹]	psu	[°C]			
4024-1	3.13	47.25	21.86	46.08	106.91	0.74	4.91	0.15	2.69	36.47	19.84
4025-2	2.43	46.21	21.58	45.60	105.39	0.74	2.50	0.15	2.69	36.48	19.85
4026-1	1.39	45.04	21.26	45.07	103.73	0.73	3.20	0.15	2.69	36.49	19.87
4213-1	0.30	23.59	13.96	34.36	58.89	1.09	4.53	0.16	2.00	36.45	18.90
4216-2	0.22	37.86	20.22	47.40	106.34	0.85	5.25	0.13	1.91	36.51	19.29
4225-3	0.27	22.41	13.88	33.32	54.23	1.02	4.13	0.17	2.26	36.45	19.18
4226-1	0.24	22.44	13.94	33.39	54.33	1.02	4.54	0.17	2.25	36.45	19.19
4230-1	0.23	20.06	13.36	29.25	44.91	0.89	4.29	0.16	2.42	36.43	19.46
4231-2	0.23	19.26	12.96	27.97	41.71	0.89	4.11	0.16	2.42	36.43	19.45
4233-2	0.21	29.70	17.22	38.22	83.36	0.80	4.28	0.15	2.58	36.47	19.70
4236-2	0.27	24.22	14.74	31.45	60.98	0.84	3.54	0.16	2.59	36.44	19.65
5530-3	0.13	50.58	31.06	57.08	133.81	0.18	5.38	0.09	2.01	36.81	20.90
5533-1	0.18	45.59	28.84	51.08	116.27	0.20	5.43	0.08	1.79	36.79	21.04
5536-3	0.20	44.80	25.64	49.45	114.32	0.29	5.39	0.09	2.02	36.70	20.63
5539-2	0.29	44.57	22.44	46.43	109.17	0.44	5.08	0.12	2.49	36.59	20.12
5540-3	0.33	45.21	22.41	46.49	109.18	0.47	5.08	0.12	2.52	36.58	20.08
5548-3	0.58	39.73	19.77	42.48	95.50	0.76	3.80	0.15	2.71	36.47	19.84
5549-2	0.34	40.51	20.09	43.08	97.50	0.70	4.50	0.15	2.69	36.50	19.90
5553-2	0.20	40.05	21.66	45.40	107.55	0.46	5.40	0.12	2.60	36.58	20.15
6005-1	0.46	45.08	19.99	51.77	123.05	1.03	4.99	0.14	1.51	36.42	18.78
6006-2	0.63	47.91	20.05	53.21	129.08	1.05	4.30	0.14	1.47	36.40	18.71
6007-1	1.37	49.45	20.08	53.98	132.48	1.07	3.70	0.14	1.42	36.39	18.63
6008-2	2.85	49.77	20.09	54.13	133.24	1.08	4.33	0.14	1.41	36.38	18.60
6009-1	1.39	51.93	20.06	54.99	138.85	1.07	3.98	0.15	1.46	36.38	18.56
6010-1	1.29	49.39	19.29	52.86	131.38	1.08	4.33	0.16	1.51	36.38	18.45
6011-2	0.72	50.60	19.59	53.78	134.94	1.08	3.80	0.16	1.52	36.38	18.50
7413-2	3.42	30.74	23.10	30.62	46.04	5.58	1.70	0.45	3.15	36.17	19.38
7414-1	2.65	30.54	23.12	30.59	45.77	5.15	2.89	0.42	3.03	36.20	19.62
7415-1	2.32	30.13	23.14	30.43	44.70	4.48	4.95	0.37	2.84	36.24	20.00
7420-1	0.86	57.93	25.90	47.57	95.89	1.10	2.66	0.09	2.10	36.58	19.82
7423-2	0.54	52.25	27.69	46.53	104.24	1.08	4.65	0.10	2.05	36.61	20.04
7424-1	0.77	57.29	26.10	47.74	97.74	1.09	3.27	0.09	2.09	36.58	19.87

3.3.2.3. Statistical methods

To determine the relationship between the distribution of dinocyst species in the sediment and the environmental variables in the water column, a Principal Component Analysis (PCA) and Redundancy Analyses (RDA) were carried out with CANOCO for Windows version 4.02 (Jongman et al., 1987; ter Braak and Smilauer, 1998). Both

analyses were performed with the relative dinocyst abundances as well as with the accumulation rates of the dinocyst species. The data were not transformed. An initial Detrended Correspondence analysis (also performed with CANOCO 4.02) indicated that each dataset is characterized by a linear relationship between the dinoflagellate cyst distribution and the environmental gradients.

For details on the interpretation of RDA diagrams we refer to e.g. Jongman et al. (1987) and Richter et al. (2007). The principle of forward selection allows the detection of covariance between the environmental parameters and their importance in significantly influencing the distribution of the species. Marginal effects represent the amount of variance explained by the variable uncorrected for possible covariance. Conditional effects represent the amount of variance after the elimination of covariance (explained by that particular variable only). The significance of each environmental variable was calculated by a Monte Carlo permutation test with 199 permutations at a significance level of $P \leq 0.05$.

3.4. Results

3.4.1. Relative abundances

3.4.1.1. Geographical distribution of organic-walled dinocyst species

The spatial distribution of dinocysts in the investigated surface sediments off NW Africa shows distinct regional patterns. Based on visual examination of the dataset, four regions with characteristic dinocyst associations can be observed. PCA analysis illustrating the variation of species associations between the sampling sites reveals different groups separating the samples from regions with seasonal upwelling from samples derived from regions with perennial upwelling and oceanic sites (PCA rel; Fig. 4). Overall, we divide the investigation area into four regions: 1. the Cape Ghir region, 2. the Cape Yubi region, 3. the coastal area between Cape Ghir and Cape Yubi and 4. offshore regions together with sites south of Cape Yubi.

1. Cape Ghir region. Sediment samples off Cape Ghir, where seasonal upwelling prevails, are characterized by the dominance of *Lingulodinium machaerophorum* at relative abundances of up to 83 % (Fig. 6g). Cysts of *Gymnodinium nolleri* (Fig. 6c), cysts of *Polykrikos kofoidii* (Fig. 7e) and cysts of *Polykrikos schwartzii* (Fig. 7g) also occur in highest relative abundances off Cape Ghir.

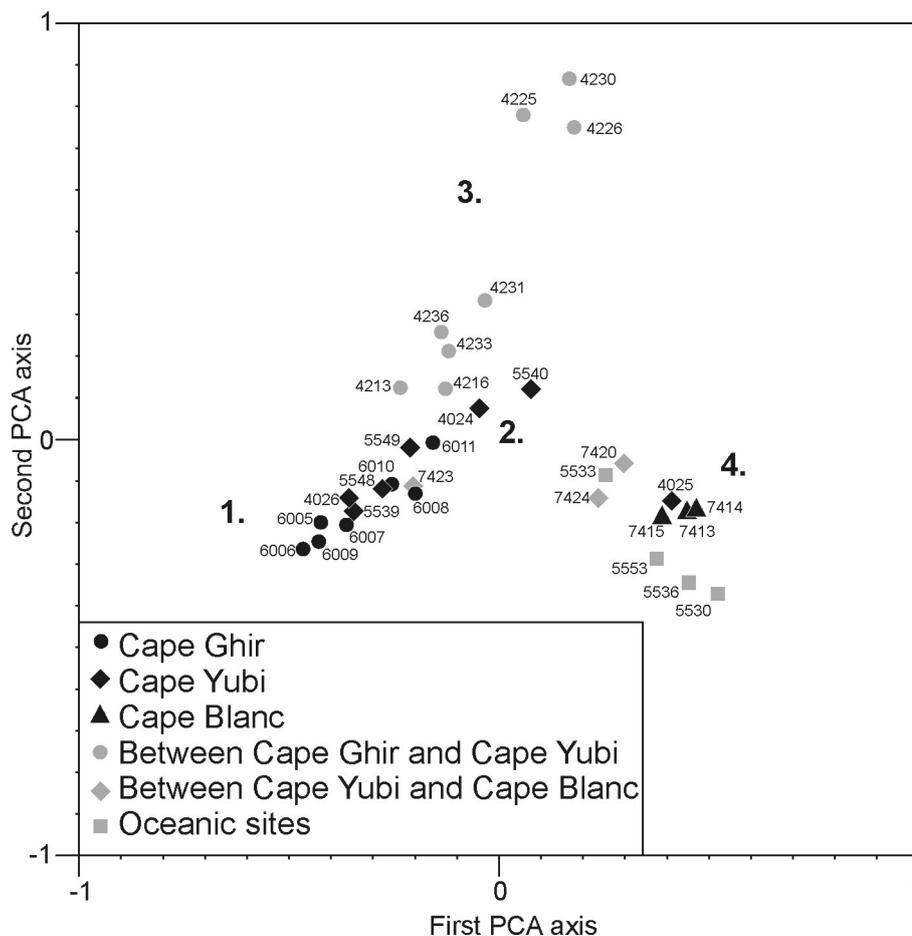


Figure 4. Principal Component Analysis (PCA) based on the relative abundances of the dinocyst species in 32 surface sediment samples (GeoB sample numbers). Stations located in the cape regions in black; stations between the capes and in oceanic regions in grey. Bold numbers represent 1. the Cape Ghir region, 2. the Cape Yubi region, 3. the coastal area between Cape Ghir and Cape Yubi and 4. offshore regions and sites south of Cape Yubi.

2. Cape Yubi region. In samples off Cape Yubi, that are influenced by a longer upwelling season, *L. machaerophorum* is also the dominant cyst species. The remaining association is different from that off Cape Ghir and is characterized by high relative abundances of *Brigantedinium* spp. (Fig. 5a), species of the genus *Impagidinium* (Fig. 6e) and cysts of *Protoperidinium stellatum* (Fig. 8e). In PCA rel, samples of the Cape Yubi region are ordinated in the vicinity of the Cape Ghir samples indicating that the cyst associations of these two regions are related (Fig. 4).

3. Coastal area between Cape Ghir and Cape Yubi. In the coastal region between Cape Ghir and Cape Yubi, which is not influenced by active upwelling, highest relative abundances of *Gymnodinium catenatum* (Fig. 6a), species of the genus *Impagidinium*,

Nematosphaeropsis labyrinthus (Fig. 7a), *Operculodinium centrocarpum* (Fig. 7c), cysts of *Protoperidinium stellatum* and *Selenopemphix nephroides* (Fig. 8g) can be observed.

4. Offshore regions and sites south of Cape Yubi. Despite the differing upper ocean environmental characteristics of offshore regions that are not influenced by upwelling and the research area south off Cape Yubi (including the area off Cape Blanc), dinocyst assemblages are comparable. The species *Brigantedinium* spp., *Echinidinium aculeatum* (Fig. 5c), *Echinidinium delicatum* (Fig. 5e), *Echinidinium* spp. (Fig. 5g), cysts of *Protoperidinium americanum* (Fig. 8a), cysts of *Protoperidinium monospinum* (with highest values off Cape Blanc) (Fig. 8c), *Selenopemphix quanta* (Fig. 9a) and *Trinovantedinium applanatum* (Fig. 9e) show their highest relative abundances in these regions. Samples of these regions are ordinated as a conspicuously isolated cluster indicating that the dinocyst association of these sites has little similarity with associations of the previously discussed regions (Fig. 4).

Relative abundances of other dinocyst species do not display particular distribution patterns. show their highest relative abundances in these regions. Samples of these regions are ordinated as a conspicuously isolated cluster indicating that the dinocyst association of these sites has little similarity with associations of the previously discussed regions (Fig. 4).

Relative abundances of other dinocyst species do not display particular distribution patterns.

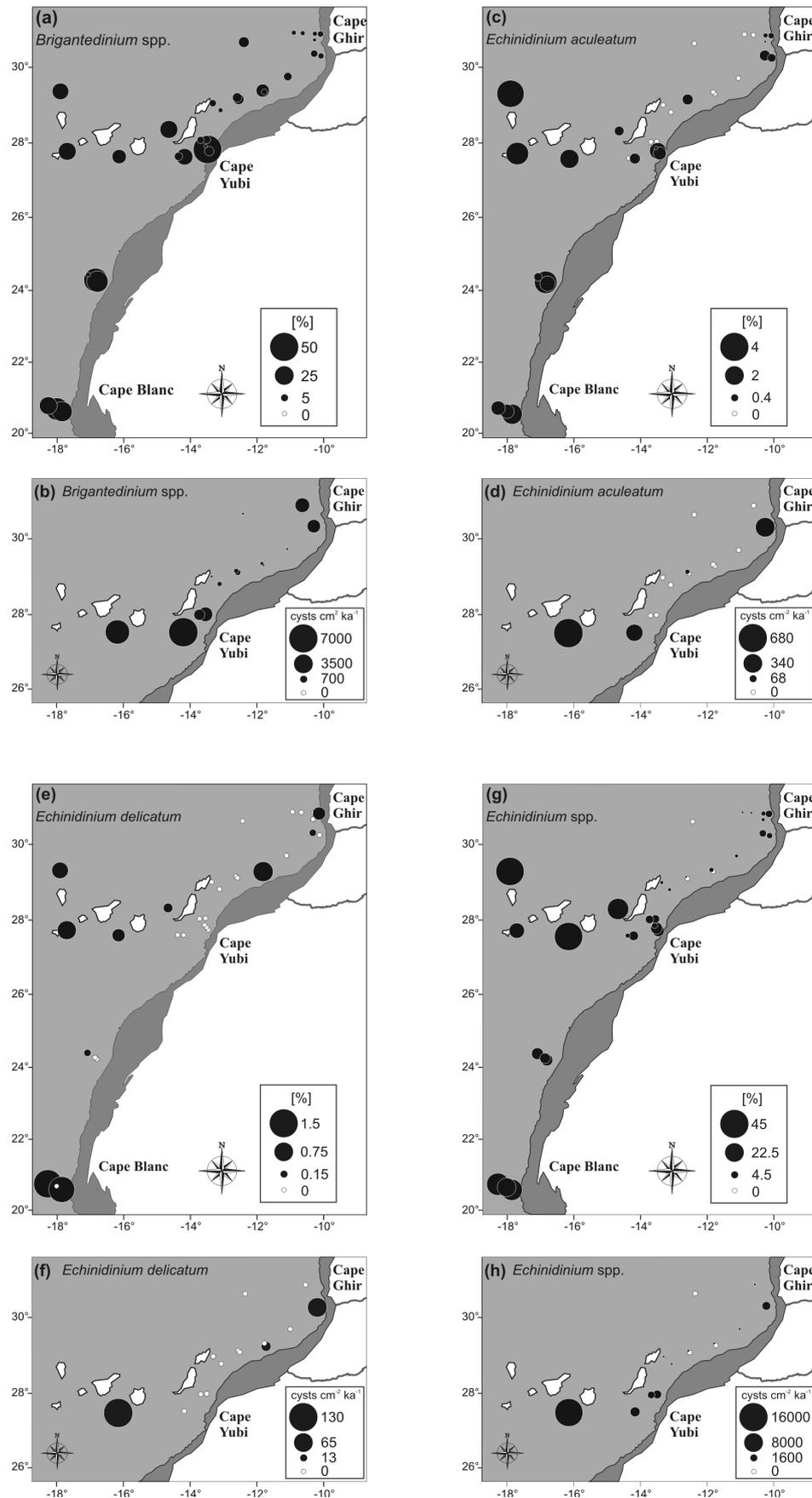


Figure 5: Relative abundances and accumulation rates of *Brigantedinium* spp. (a) and (b), *Echinidinium aculeatum* (c) and (d), *Echinidinium delicatum* (e) and (f) and *Echinidinium* spp. (g) and (h). The continental shelf is shaded in grey.

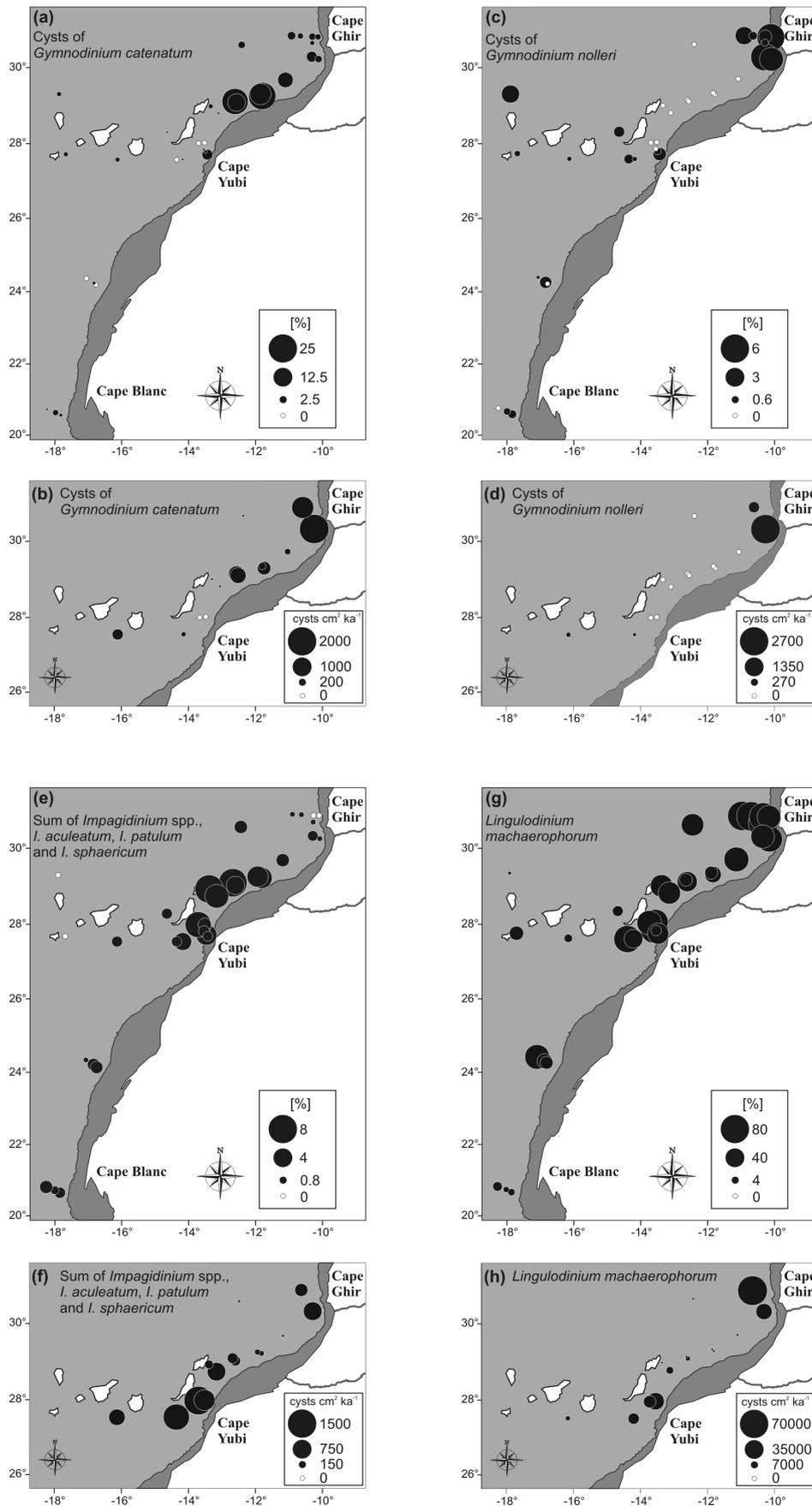


Figure 6. Relative abundances and accumulation rates of cysts of *Gymnodinium catenatum* (a) and (b), cysts of *Gymnodinium nolleri* (c) and (d), *Impagidinium* (e) and (f) and *Lingulodinium machaerophorum* (g) and (h). The continental shelf is shaded in grey.

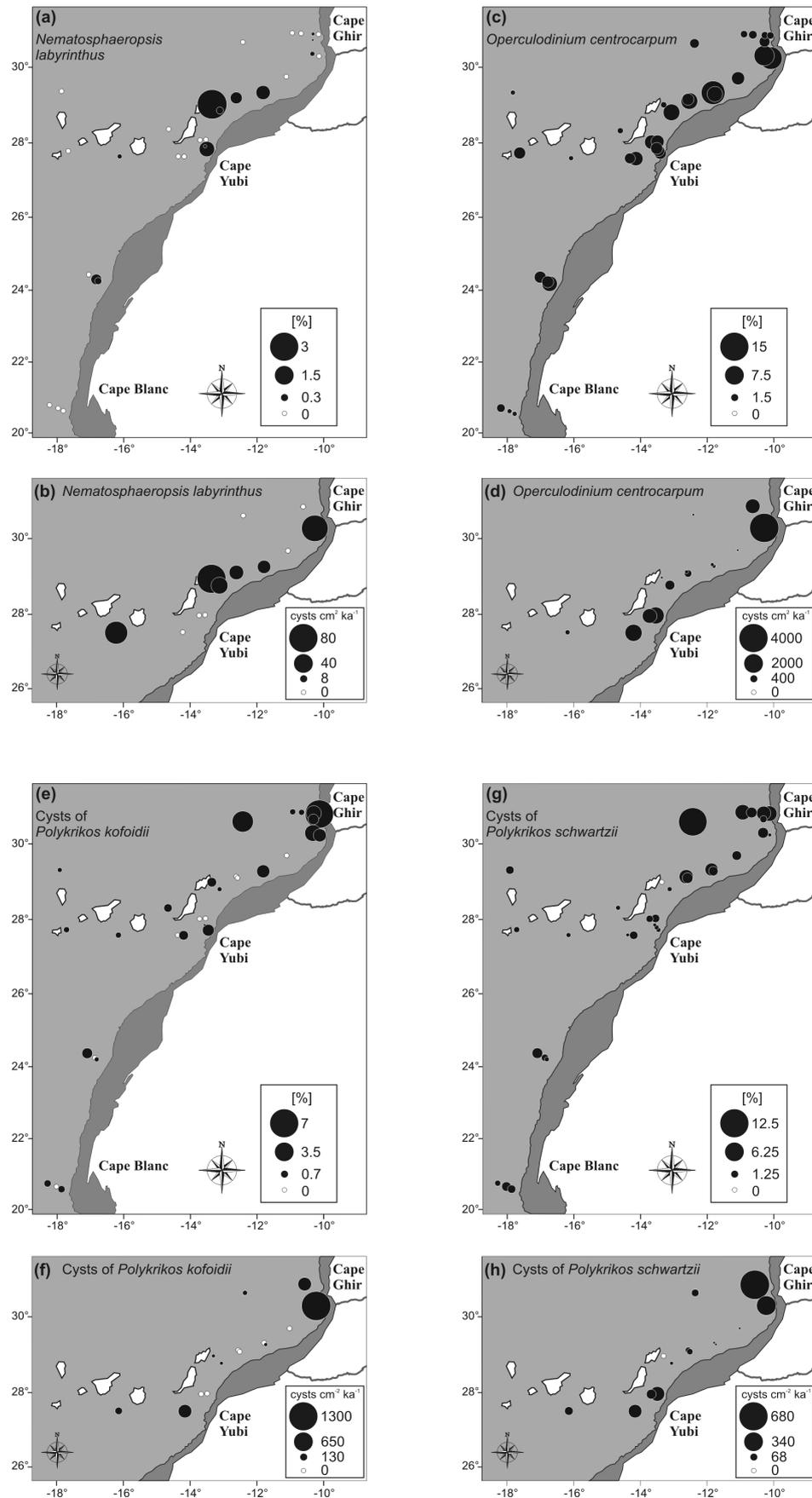


Figure 7. Relative abundances and accumulation rates of *Nematosphaeropsis labyrinthus* (a) and (b), *Operculodinium centrocarpum* (c) and (d), cysts of *Polykrikos kofoidii* (e) and (f) and cysts of *Polykrikos schwartzii* (g) and (h). The continental shelf is shaded in grey.

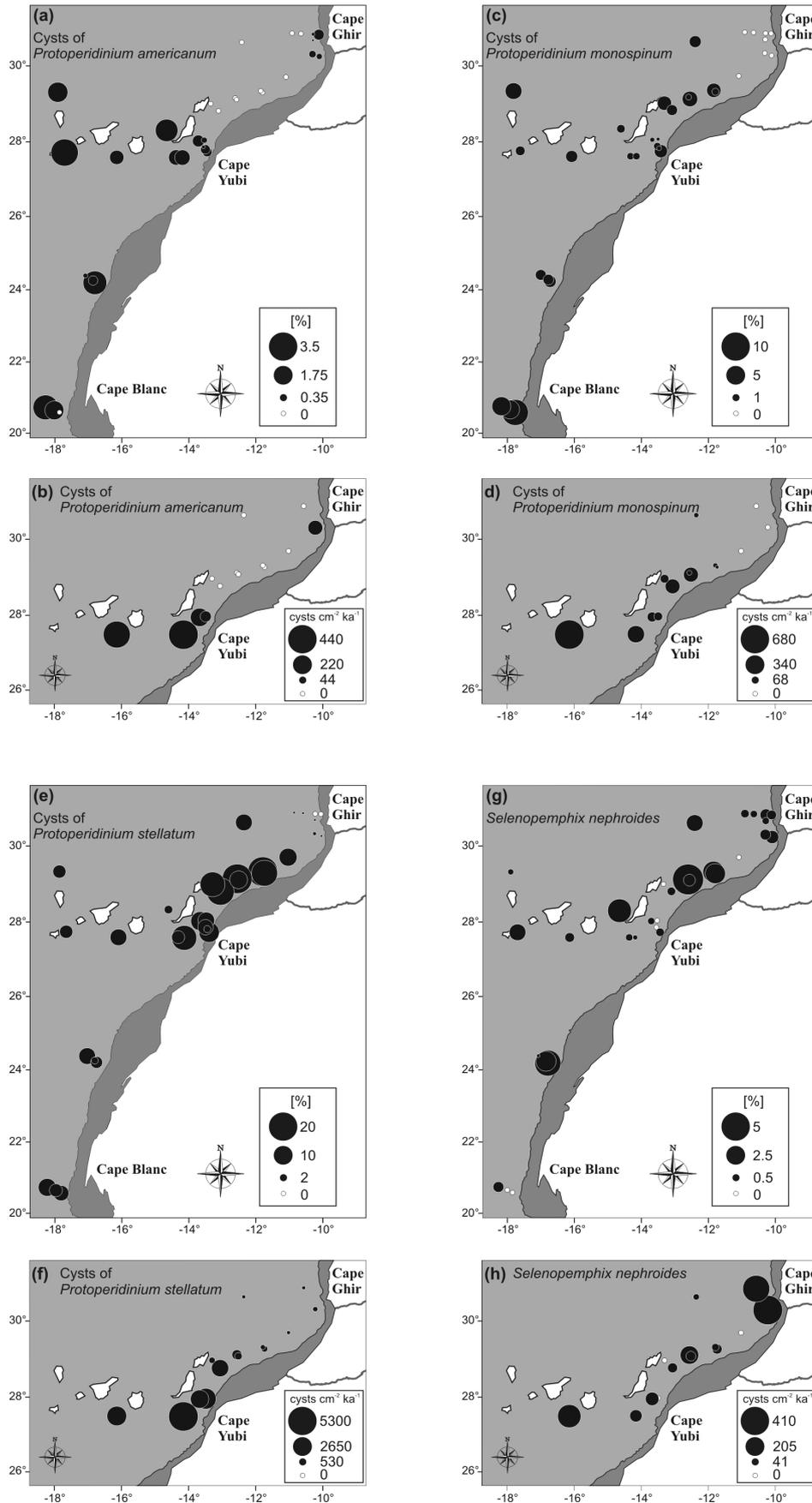


Figure 8. Relative abundances and accumulation rates of cysts of *Protoperidinium americanum* (a) and (b), cysts of *Protoperidinium monospinum* (c) and (d), cysts of *Protoperidinium stellatum* (e) and (f) and *Selenopemphix nephroides* (g) and (h). The continental shelf is shaded in grey.

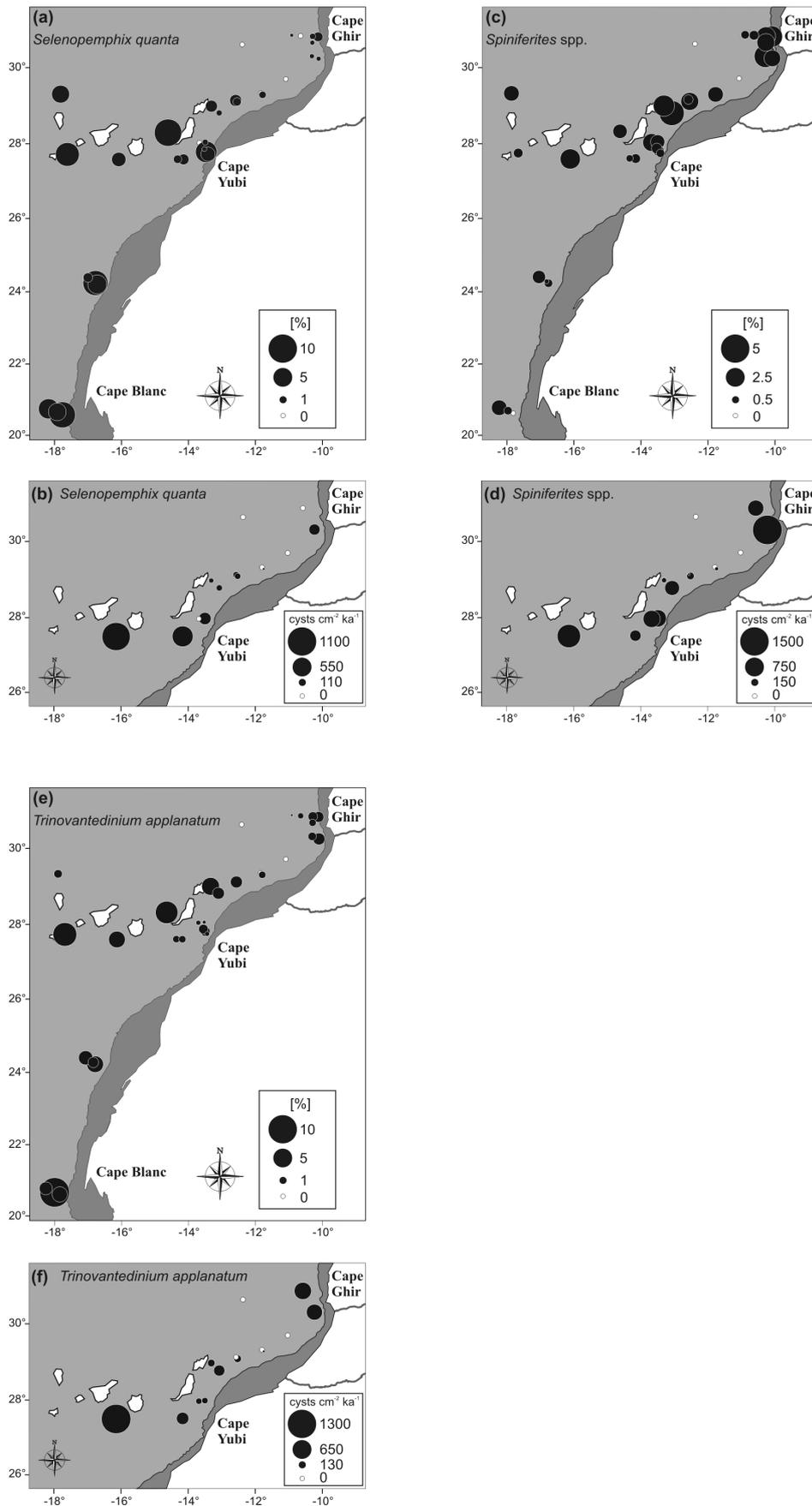


Figure 9. Relative abundances and accumulation rates of *Selenopemphix quanta* (a) and (b), *Spiniferites* spp. (c) and (d) and *Trinovantedinium applanatum* (e) and (f). The continental shelf is shaded in grey.

3.4.1.2. Redundancy analysis of relative abundance data

The RDA analysis reveals that the gradients FM, ADf, SST, Si and MLDwi relate to more than 15 % of the variance in the dinocyst association (Fig. 11 and Table 4; marginal effects). After correcting for covariance (Table 4; conditional effects) FM, SST and MLDsp explain the species variance significantly. *Lingulodinium machaerophorum* and cysts of *Polykrikos schwartzii* show a positive correlation with FM while correlating negatively with ADf, Si and SST. *Gymnodinium catenatum*, species of the genus *Impagidinium*, cysts of *P. stellatum* and *S. nephroides* correlate negatively with MLDwi and MLDsp whereas *G. nolleri* correlates positively with these parameters. Most of the heterotrophic cyst species correlate with ADf, Si and SST while correlating negatively with FM.

Table 4. Percentage of variance explained by environmental variables used in RDA rel. Bold variables are significant at the 5% significance level ($P \leq 0.05$). For abbreviations see Table 3.

Marginal Effects		Conditional Effects		
Uncorrected for covariance		Corrected for covariance		
Variable	Variance	Variable	Variance	P-value
FM	0.33	FM	0.33	0.005
ADf	0.33	SST	0.13	0.01
SST	0.26	MLD sp	0.09	0.025
Si	0.2	Si	0.03	0.175
MLD wi	0.17	Chla	0.03	0.13
MLD fa	0.13	SSS	0.01	0.32
MLD su	0.13	NO3	0.03	0.21
NO3	0.11	MLD su	0.01	0.22
ADc	0.1	MLD fa	0.03	0.185
PO4	0.08	MLD wi	0.02	0.21
MLD sp	0.08	PO4	0.01	0.38
Chla	0.04	Ox	0.01	0.465
Ox	0.03	ADc	0.01	0.39
SSS	0.02	ADf	0.01	0.92

3.4.2. Accumulation rates

3.4.2.1. Geographical distribution of organic-walled dinocyst species

Highest accumulation rates of dinocysts can be observed in the regions off Cape Yubi and Cape Ghir with a maximum of almost 80,000 cysts $\text{cm}^{-2} \text{ky}^{-1}$ (Fig. 10). The accumulation rates of cysts of heterotrophic species increases southward from about 600 to 28,000 cysts $\text{cm}^{-2} \text{ky}^{-1}$. Between these two capes, accumulation rates of all dinocyst species are generally much lower.

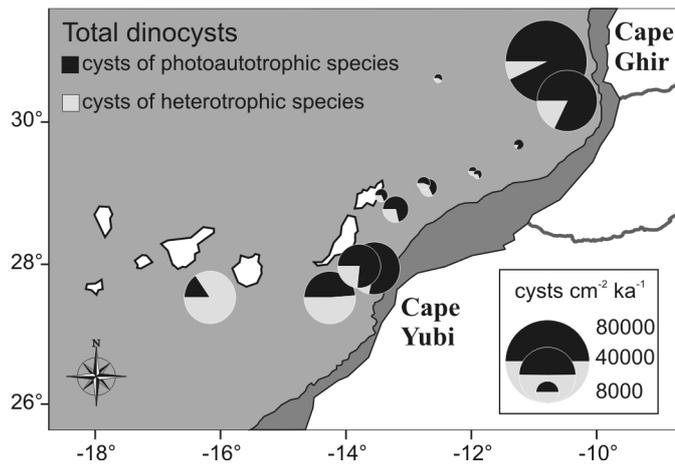


Figure 10. Organic-walled dinoflagellate cyst accumulation rates in the NW-African upwelling region. The continental shelf is shaded in grey.

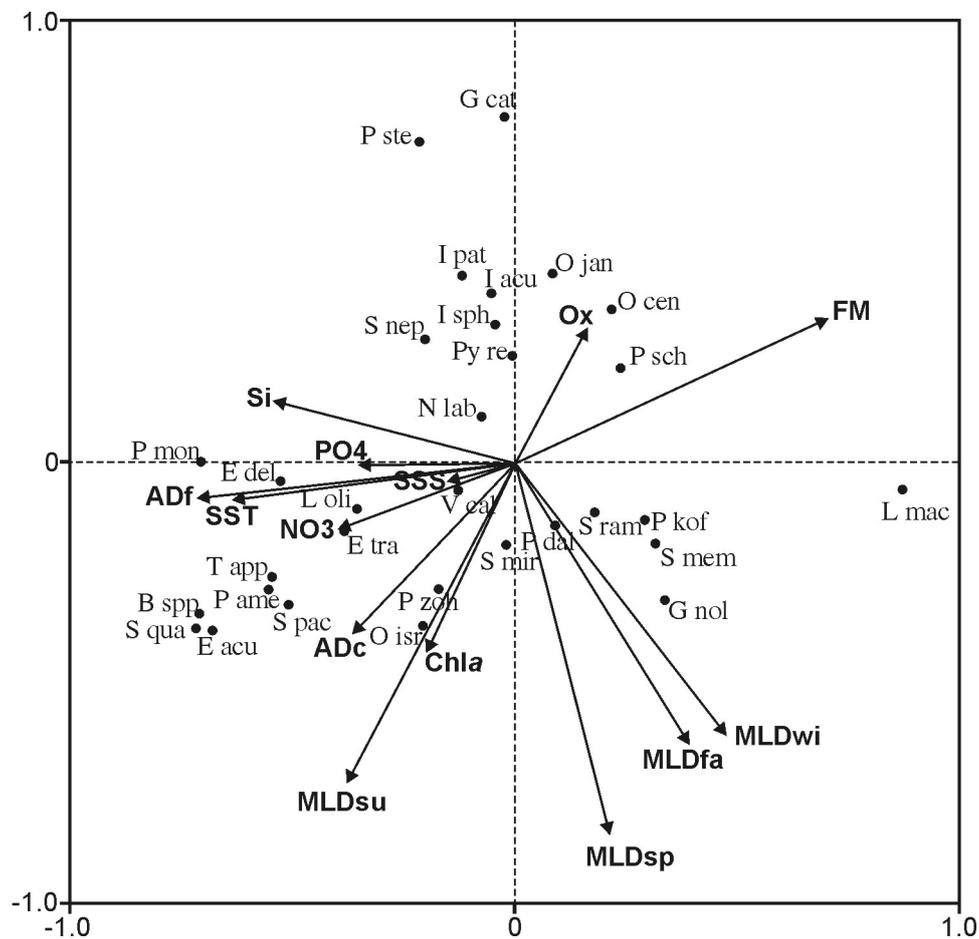


Figure 11. Results of the Redundancy Analysis using relative abundances of organic-walled dinoflagellate cysts (RDA rel). For abbreviations see Tables 2 and 3.

In samples off Cape Ghir, highest accumulation rates for *L. machaerophorum* reach nearly 70,000 cysts $\text{cm}^{-2} \text{ky}^{-1}$ at site GeoB 6006-2 (Fig. 6h). Likewise, cysts of *G.*

catenatum (Fig. 6b), cysts of *G. nolleri* (Fig. 6d), cysts of *P. kofoidii* (Fig. 7f), cysts of *P. schwartzii* (Fig. 7h) and *S. nephroides* (Fig. 8h) are found with highest accumulation rates in sediments in this region.

Off Cape Yubi, *Brigantedinium* spp. (Fig. 5b), *E. aculeatum* (Fig. 5d), *Echinidinium* spp. (Fig. 5h), species of the genus *Impagidinium* (Fig. 6f), cysts of *P. americanum* (Fig. 8b), *Spiniferites* spp. (Fig. 9d) and *S. quanta* (Fig. 9b) all have their highest accumulation rates.

Cysts of *P. monospinum* (Fig. 8d) and cysts of *Protoperidinium stellatum*, (Fig. 8f) are found more abundantly in the south (and not only off Cape Yubi).

There are no species whose accumulation rates are higher between the capes.

3.4.2.2. Redundancy analysis of accumulation rate data

Fig. 12 and Table 5 show the results of the RDA based on accumulation rates of the dinocysts (RDA acc). The following environmental variables each explain the species variance to more than 15 %: *Chla*, FM, MLDsp, MLDwi, MLDau, ADf and Si (Table 5; marginal effects). After correcting for covariance, *Chla* and FM remain as gradients that significantly relate to the variance in dinocyst accumulation rates (Table 5; conditional effects). *L. machaerophorum* and cysts of *P. schwartzii* correlate strongest with *Chla* and FM while correlating negatively with ADf and Si. To a smaller extent, this is

Table 5. Percentage of variance explained by environmental variables used in RDA acc. Bold variables are significant at the 5 % significance level ($P \leq 0.05$). For abbreviations see Table 3.

Marginal Effects		Conditional Effects		
Uncorrected for covariance		Corrected for covariance		
Variable	Variance	Variable	Variance	P-value
<i>Chla</i>	0.65	<i>Chla</i>	0.65	0.005
FM	0.44	FM	0.16	0.02
MLD sp	0.4	SST	0.06	0.055
MLD wi	0.39	Ox	0.03	0.17
MLD fa	0.38	PO4	0.02	0.19
ADf	0.28	SSS	0.02	0.16
Si	0.21	NO3	0.01	0.215
MLD su	0.14	ADc	0.02	0.175
SST	0.12	ADf	0.01	0.275
SSS	0.09	MLD su	0	0.44
Ox	0.05	MLD wi	0.01	0.17
NO3	0.05	Si	0.01	0.525
ADc	0.04	MLD sp	0	0.83
PO4	0.02	MLD fa	0.01	1

also true for *G. catenatum*, *G. nolleri*, and *S. nephroides*. Most heterotrophic cyst species form a cluster but do not correlate significantly with any of the environmental parameters.

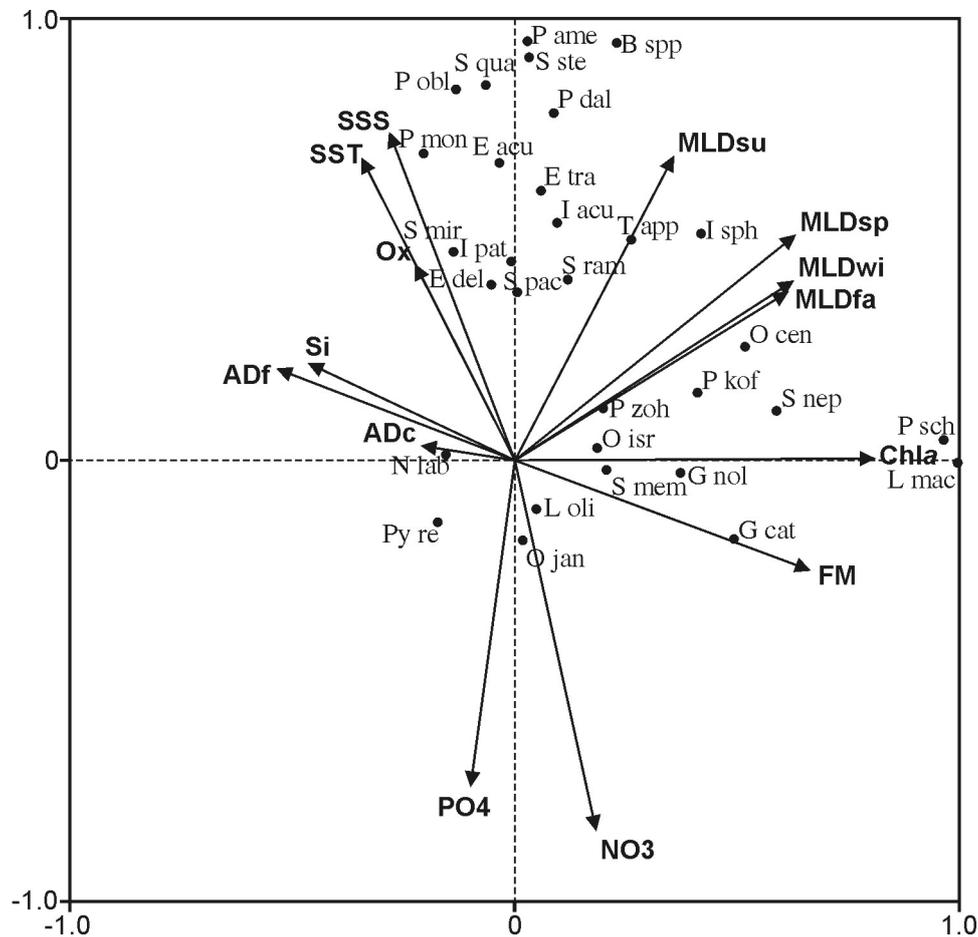


Figure 12. Results of the Redundancy Analysis using accumulation rates of organic-walled dinoflagellate cysts (RDA acc). For abbreviations see Tables 2 and 3.

3.5. Discussion

Before interpreting the dinocyst signal in the sediment, it is necessary to discuss the effect of mechanisms possibly altering the original assemblage.

3.5.1. Transport

On their way from the upper water column to the sediment, dinocysts might be affected by transport processes. It is therefore important to consider whether

allochthonous dinocyst species are found in the sediment samples and alter the autochthonous dinocyst species association.

One of the transport processes is the offshore spreading of upwelling filaments (see 3.2) within which originally neritic organisms bloom (Gabric et al., 1993; Rodríguez et al., 1999). While these organisms grow in situ (and, in the case of dinoflagellates, form cysts) they can be dislocated hundreds of kilometers from the coast. As the oceanographic parameters are conveyed also within the filaments, this transport mechanism is not problematic in terms of linking results with the conditions in the upper water column. The Cape Ghir filament in particular is reflected by similar compositions of the dinocyst species in the sediment samples.

If transport takes place during or after the sinking process and/or after resuspension by winnowing or slumping, dinocysts can be carried far away from their site of production. Lateral transport in the Canary Islands region is suggested by e.g. (Fütterer, 1983; Neuer et al., 1997b; Freudenthal et al., 2001; Neuer et al., 2002). In contrast, Nave et al. (2001) found benthic diatoms (which only live in shallow depths) only in very low abundances on the continental slope and offshore sites of the Canary basin and consequently exclude lateral transport from the shelf. Off Cape Blanc, lateral particle transport does not seem to play an important role (e.g. Fischer and Wefer, 1996; Ratmeyer et al., 1999; Helmke, 2004; Nowald et al., 2006).

As sample positions in this study do not include the shelf, it is difficult to discuss whether offshore transport has taken place. Typical shelf species such as *Spiniferites ramosus* (Marret and Zonneveld, 2003 and references therein) are found in low relative abundances in all samples and their patterns do not indicate lateral transport. *Brigantedinium* spp. and *Echinidinium* species, cysts of *P. monospinum*, *S. quanta* and *T. applanatum* can be produced in high amounts in coastal environments (Marret and Zonneveld, 2003 and references therein). These species show increased relative abundances in offshore samples but higher accumulation rates at coastal sites. If transport was the reason for their higher relative abundances offshore, these species would have been transported selectively compared to other species, which is unlikely.

Reworked dinocyst species were found in very low numbers (see table on www.pangaea.de) in a random pattern throughout the research area. They therefore do not indicate possible sediment slumping activities.

3.5.2. Selective degradation

Indications for post depositional species selective degradation within our research area come from the sediment trap studies of Susek (2005). Whereas heterotrophic (sensitive) taxa form about 96-99 % of the dinocyst association in the trap samples they form only 71 % of the association at the sediment surface in favour of species known to be more resistant to degradation. Similar indications are found by Zonneveld et al. (2007) who document a strong degradation of the group of sensitive dinocyst species in relationship to high bottom water oxygen concentrations in the study region.

Bottom-water oxygen concentrations are uniformly relatively high in the studied sites with exception of site GeoB 7413 where bottom water oxygen is depleted (Table 3) We therefore have to assume that species selective degradation has affected our dinocyst association. For example, we find high relative abundances of species of the genus *Impagidinium*, these being extremely resistant to aerobic decay. This can be interpreted as enrichment in favour of resistant dinocyst species. It might well be possible that aerobic degradation processes largely overprint the primary productivity signal within the relative abundance data. Hence, the amount of especially sensitive dinocysts might be a considerable underestimation whereas that of the species known to be resistant against aerobic degradation might reflect their initial production in upper waters.

However, bottom water oxygen concentrations do not significantly relate to the variation within the dinocyst association (see 3.4.1.2., Fig. 11, Table 4, 3.4.2.2., Fig. 12 and Table 5) which is most likely due to the small gradient within the bottom water oxygen concentration data.

We conclude that the effect of selective degradation on the different samples should be similar and we consequently are able to compare the results among one another.

3.5.3. Distributon of dinocysts related to environmental parameters

The distribution signals of dinocyst species in the sediments show connections to the regional oceanographic conditions. Based on both visual and statistical analysis, we distinguish four different marine provinces within the investigated area. In the following, relative abundance patterns are compared with those of absolute abundances.

1. Cape Ghir region

Off Cape Ghir, high relative abundances of cysts of *Gymnodinium nolleri* (Fig. 6c), *Lingulodinium machaerophorum* (Fig. 6g), cysts of *Polykrikos kofoidii* (Fig. 7e) and cysts of *Polykrikos schwartzii* (Fig. 7g) match the high accumulation rates of these species. Within our studied area, the Cape Ghir region is characterized by lowest SST (Fig. 2), highest seasonal variation in MLD (Fig. 3), highest input of FM and high upper ocean production reflected by high Chla values.

A positive relationship between accumulation rates of *L. machaerophorum* and *P. schwartzii* with Chla and FM is clearly confirmed by RDA acc (Fig. 12). Studies on the geographic distribution of dinocysts in regions where upper waters are influenced by fluvial input often show that high relative abundances of *L. machaerophorum*, *P. kofoidii*, and *P. schwartzii* are observed in the surface sediments (McMinn, 1991; Thorsen and Dale, 1997; Matsuoka, 1999; Mudie and Rochon, 2001; Dale et al., 2002; Pospelova et al., 2002; Sangiorgi and Donders, 2004; Pospelova et al., 2004; Pospelova et al., 2005). *L. machaerophorum* is the cyst of the autotrophic toxic bloom-forming dinoflagellate *Lingulodinium polyedrum* (e.g. Shimizu, 1987; Kokinos and Anderson, 1995). It is well known that blooms of *L. polyedrum* occur preferably during periods with a stratified water column (Lewis and Hallett, 1997). *L. polyedrum* is able to perform vertical migration in order to assimilate nutrients at the nutricline (Lewis and Hallett, 1997). Gibson and Thomas (1995) showed in laboratory experiments that it is extremely sensitive to the intermittency, duration and strength of turbulence events. *L. polyedrum* was allocated to the group of Upwelling Relaxation Taxa by Smayda and Reynolds (2001). Investigations on the distribution of *L. machaerophorum* in sediments strongly support these findings. Targarona et al. (1999) concluded from their study of dinocyst species distributions in the North Canary Basin that the dominance of *L. machaerophorum* is related to the lack of turbulence in nutrient-rich filament waters. The results compiled by Marret and Zonneveld (2003) suggest that high abundances of *L. machaerophorum* are related to eutrophication and seasonally stratified waters. For the NW Iberian margin, Sprangers et al. (2004) found *L. machaerophorum* in abundances of up to 60 % in sediments related to seasonal upwelling. Bouimetarhan et al. (2009) recorded high relative abundances *L. machaerophorum* off West Africa in relation to seasonal upwelling. In contrast, *L. machaerophorum* has rarely been encountered in areas with perennial upwelling. For instance, it was found in extreme low abundances in the Peruvian upwelling area (Biebow, 1996; Lewis et al., 1990) as well as in the Benguela

upwelling region (Zonneveld et al., 2001a; Dale et al., 2002; Bockelmann et al., 2007; Holzwarth et al., 2007). This rareness has been related to the more turbulent and perennial character of the upwelling in these areas (Lewis and Hallett, 1987; Marret and Zonneveld, 2003). Our study supports this theory as we observe very low relative abundances of *L. machaerophorum* in the upwelling area off Cape Blanc, where permanent upwelling conditions prevail.

Within the region off Cape Ghir we find a combination of relatively high fluvial input and seasonal upwelling and we assume that these conditions form an optimal environment for *L. polyedrum* resulting in the extreme high relative abundances and accumulation rates of its cysts. Fluvial input and upwelling relaxation occur in the same season (boreal winter). The Riverine input of humic rich waters could favour the cyst production of *L. polyedrum* by adding vitamins, auxins and other essential micronutrients (Prakash and Rashid, 1968; Graneli and Moreira, 1990; Doblin et al., 1999).

Looking at the accumulation rates, we observe strikingly similar distribution patterns of cysts of *G. catenatum*, cysts of *Gymnodinium nolleri*, *L. machaerophorum*, cysts of *P. kofoidii* and cysts of *P. schwartzii*. In plankton surveys, a co-occurrence of *Polykrikos* cyst species and toxic dinoflagellate blooms has been reported by Matsuyama et al. (1999). Culture experiments reveal that maximum growth rates of *P. kofoidii* can be obtained when *P. kofoidii* is fed with *G. catenatum* and *L. polyedrum* (Jeong et al., 2001). *P. kofoidii* even selects *L. polyedrum* over other species in prey mixtures. The observed relationship off Cape Ghir might therefore reflect a predator-prey relationship with high abundances of cysts of *P. kofoidii* and *P. schwartzii* related to high abundances of cysts of their potential prey organisms *G. catenatum* and *L. polyedrum*.

2. Cape Yubi region

None of the dinocyst species occurring off Cape Yubi shows characteristically highest relative abundances there, although *L. machaerophorum* dominates most samples. Given the discussion of its distribution off Cape Ghir, this pattern can be interpreted in the way that off Cape Yubi the periods of upwelling relaxation are still favourable for the cyst production of *L. polyedrum*. *Brigantedinium* spp. (Fig. 5a) and cysts of *Protoperidinium stellatum* (Fig. 8e) are commonly registered in high relative abundances in upwelling regions (e.g. Lewis et al., 1990; Dale and Fjellså, 1994; Biebow, 1996; Targarona et al., 1999; Zonneveld et al., 2001a; Holzwarth et al., 2007). With regard to the whole investigated area, where the relative abundances of cysts of *P.*

stellatum increase further to the south, their distribution off Cape Yubi could be related to the increase in permanence of the upwelling conditions. This is supported by highest accumulation rates of *Brigantedinium* spp. (Fig. 5b) and cysts of *P. stellatum* (Fig. 8f) off Cape Yubi. Highest absolute abundances of *Echidinium aculeatum* (Fig. 5d), *Echinidinium* spp. (Fig. 5h), species of the genus *Impagidinium* (Fig. 6f), cysts of *Protoperidinium americanum* (Fig. 8b), *Spiniferites* spp. (Fig. 8d) and *S. quanta* (Fig. 8b) could also be due to the longer upwelling season off Cape Yubi compared to Cape Ghir. When we assume that degradation has affected the dinocyst association by more or less a similar rate in all studied samples (see 3.5.2.), the accumulation patterns might represent the primary cyst production signal even though the total accumulation values of the sensitive dinocyst species is lower than the export flux. If this is the case, it can be concluded that the cyst production of all these species is enhanced when upwelling conditions become more perennial. However, RDA acc does not show significant relationships between the above listed dinocyst species and any of the environmental parameters analyzed. The oceanographic conditions off Cape Yubi might be too complex to be comprised by the commonly used environmental parameters.

For species of the genus *Impagidinium*, a relationship with eutrophic waters contradicts the current concepts of their ecology, where these species have been associated with oligotrophic oceanic areas. However, these findings are based on relative abundance data only, which might suffer from a closed sum effect and diagenetic overprint (Zonneveld et al., in press). Furthermore, sediment trap studies in the Somali and NW African upwelling areas report highest cyst production at times of active upwelling (Zonneveld and Brummer, 2000; Susek, 2005). Consequently we suggest that cyst production of the observed *Impagidinium* species might be positively related to enhanced nutrient availability

3. Coastal area between Cape Ghir and Cape Yubi.

In the region between Cape Ghir and Cape Yubi, there is no export of eutrophic upwelling-influenced waters from the shelf by filaments. While a number of species show their highest relative abundances between these two capes, accumulation rates of all species are low within this region.

Cysts of *Gymnodinium catenatum* show highest relative abundances up to almost 25 % at slope sites between Cape Ghir and Cape Yubi (Fig. 6a). RDA rel shows a negative correlation to the mixed layer depth in winter and spring to which *G. nolleri* is

positively correlated. In surface sediments of the North Canary Basin, Targarona et al. (1999) did not distinguish between cysts of *G. nolleri* and cysts of *G. catenatum*. They reported highest relative abundances (up to 49 %) of cysts of *Gymnodinium* spp. in the region between Cape Ghir and Cape Yubi. Susek (2005) did not record *Gymnodinium* species in a trap study off Cape Blanc. Both studies conform to our findings. *Gymnodinium catenatum* is a photoautotrophic bloom forming toxic dinoflagellate which is widely distributed in coastal regions around the world (Bolch and Reynolds, 2002). It is able to form chains with a length of up to 64 cells (Blackburn et al., 1989) which enable the organism to perform effective vertical migration and to benefit from nutrients in depths beyond the photic zone (Doblin et al., 2006). In contrast to *G. catenatum*, *G. nolleri* is a non-bloom forming species and not able to form chains (Bolch and Reynolds, 2002). This could explain the oppositional correlation of their cysts to MLDsp in RDA rel (Fig. 11). Figueiras et al. (1996) found blooms of *G. catenatum* associated with downwelling and advection of warmer waters. Perhaps the reason for this is the ability to survive downwelling better than *G. nolleri*, rather than having a preference for these conditions. Gomez (2003) concluded that *G. catenatum* is able to adapt to varying trophic conditions. In contrast to the relative abundances, absolute abundances of cysts of *G. catenatum* show a totally different pattern (Fig. 6b). Its accumulation rates are highest off Cape Ghir where sediments indicate an input of FM. A relationship between blooms of *G. catenatum* to river runoff and influx of dissolved organic matter is reported by Doblin et al. (1999). Additionally, accumulation rates of cysts of *G. nolleri* are likewise highest off Cape Ghir. Hence, regarding their absolute abundances, the distribution patterns of both dinocyst species suggest similar ecological preferences for their motile cells, such as riverine input and seasonal upwelling (which is supported by RDA acc). This implies that relative abundances of cysts of *Gymnodinium* species are not suitable to draw ecological conclusions.

Although *Nematosphaeropsis labyrinthus* does show some patterns in the Northern North Atlantic Ocean (e.g. Rochon et al., 1999), it can be characterized as a cosmopolitan and tolerant species (Marret and Zonneveld, 2003). With regard to its non specific accumulation rates (Fig. 7b), conclusions about its preferences within the investigated area cannot be drawn.

Operculodinium centrocarpum occurs in highest absolute abundances off Cape Ghir and Cape Yubi (Fig. 7d). This suggests that its motile stage does take advantage of

the eutrophic conditions even though they are classified as cosmopolitan species with regard to the worldwide record.

Accumulation rates of cysts of *P. stellatum* are higher off Cape Yubi (Fig. 7f). Regarding the world dinocyst record, this cyst species has been found in high relative abundances in upwelling regions with a seasonally well-mixed upper water column (Marret and Zonneveld (2003) and references therein), which is generally the case for the NW African upwelling margin. Our results show rather a preference (or tolerance) for a longer upwelling season.

Marret and Zonneveld (2003) concluded that *Selenopemphix nephroides* is common in neritic as well as oceanic areas. Its high absolute abundances off Cape Ghir, however, point to an affinity for eutrophic conditions.

4. Offshore regions and sites south of Cape Yubi

Most heterotrophic species are found in highest relative abundances in offshore samples and south of Cape Yubi. There are no species that show highest relative abundances exclusively in offshore samples. Cysts of *Protoperidinium monospinum* is the only dinocyst species with highest relative abundances off Cape Blanc. *Brigantedinium* spp., *Echinidinium aculeatum*, *Echinidinium delicatum*, *Echinidinium* spp., cysts of *Protoperidinium americanum*, cysts of *P. monospinum*, *Selenopemphix quanta* and *Trinovantedinium applanatum* form a cluster in RDA rel and correlate to fine-grained aeolian dust and higher SST. Several studies compiled in Marret and Zonneveld (2003) as well as more recent studies (e.g. Radi and de Vernal, 2004; Holzwarth et al., 2007; Pospelova et al., 2008) suggest a relationship between relative abundances of these dinocyst species and high productivity (with the exception of *T. applanatum*). In sediment trap studies off Cape Blanc by Susek (2005) and Susek et al. (2005), highest fluxes of *Brigantedinium* spp., species of the genus *Echinidinium*, cysts of *P. americanum*, cysts of *P. monospinum*, cysts of *P. stellatum* and *S. quanta* were related to aeolian dust input. No clear relationship between SST and upwelling intensity could be determined by the authors. Additionally, they found flux patterns of *Brigantedinium* spp. and total diatoms (from Romero et al., 2002) to be very similar, pointing out that the supply of prey organisms is strongly related to the cyst production of heterotrophic dinoflagellates. We interpret the relationship of heterotrophic dinocysts to aeolian dust as a relationship to the occurrence of diatoms which are most likely influenced positively by iron contained in the dust particles (see 3.1.)

Nevertheless, the question remains why offshore samples and samples off Cape Blanc have similar assemblages. SST is the only tested environmental parameter which is similar at these sites. Off Cape Blanc, upwelling intensity and consequently SST can be extremely variable on daily to weekly scales (e.g. Nykjær and Van Camp, 1994; [Barton, 1998; Susek, 2005) but this is not reflected in averaged values. Although our investigated sites off Cape Blanc are often influenced by cold filaments, high SST during filament-free periods balance colder SST values. Considering the whole investigated area, this difference in SST is larger off Cape Blanc because of comparatively higher temperatures in non-filament influenced surface waters.

The similarly high relative abundances of heterotrophic cyst species we found off Cape Blanc and in offshore sites might have other reasons or could be due to the similarly low relative abundances of *L. machaerophorum* at these sites. An examination of accumulation rates off Cape Blanc and in offshore regions would help to clarify the situation.

Overall, in the studied region, relative abundances of dinocyst species are greatly influenced by cysts of blooming species such as *L. machaerophorum*. Their mass occurrence off Cape Ghir and Cape Yubi inevitably suppresses the relative abundances of the other dinocyst species. As a result, only the filament off Cape Blanc is mirrored by the relative abundances of heterotrophic species in contrast to the likewise productive filaments off Cape Ghir and Cape Yubi. At the highly productive San Francisco Bay, Pospelova et al. (2008) also recorded very low relative abundances of heterotrophic cyst species in favour of the dominating species *L. machaerophorum*. Accumulation rates of all species, however, do reflect high filamental productivity off the Cape Ghir and Cape Yubi. The accumulation rates of heterotrophic cyst species which latitudinally increase (Fig. 10) regarding Cape Ghir and Cape Yubi might reflect the gradient of the upwelling conditions from seasonal to perennial. We therefore would expect a continuation of this increase to the south which could be confirmed by accumulation rate data off Cape Blanc.

3.6. Conclusions

Organic-walled dinoflagellate cyst associations in 32 marine sediment samples off NW Africa reflect an interaction between upwelling conditions and additional terrestrial

supply of micronutrients. Between the northern two capes where seasonal upwelling prevails and the perennial upwelling region off Cape Blanc, a large difference in the dinocyst species composition is visible.

High relative abundances of *Lingulodinium machaerophorum* can be related to fluvial supply of micronutrients combined with seasonally stratified water conditions occurring particularly off Cape Ghir. Off Cape Blanc, where perennial upwelling of mainly nutrient-rich SACW occurs, heterotrophic cyst species dominate as indicators for the abundant supply of prey organisms. It becomes apparent that high relative abundances of *L. machaerophorum* and cysts of *Polykrikos schwartzii* are related to riverine input eventually based on micronutrients. Most heterotrophic cyst species can be related to aeolian dust input which benefits their prey organisms by the supply of trace metals. Cysts of bloom forming species such as *Gymnodinium catenatum* and *Lingulodinium polyedrum* strongly affect the relative abundances of dinocyst species off Cape Ghir and Cape Yubi where low relative abundances of cysts of heterotrophic taxa do not reflect the high productivity.

Accumulation rates partly give a different picture. Off Cape Ghir and Cape Yubi, high absolute abundances of heterotrophic cyst species do reflect large-scale primary productivity.

None of the dinocyst species shows higher cyst production in oligotrophic waters. The preference of *Impagidinium* species for oligotrophic conditions, which has often been documented in literature, is consequently questioned.

The comparison between relative abundances and accumulation rates gives evidence that the relative abundances are useful to distinguish regions with different oceanographic regimes whereas absolute abundances allow conclusions to be drawn about the actual cyst productivity. Our results show that accumulation rates of dinocysts provide reliable information about ecological coherences between absolute cyst production and environmental conditions. In conclusion, accumulation rates of dinocysts can be used as a proxy for palaeoproductivity in the studied region north and south of the Canary Islands.

3.7. Acknowledgements

Michael Marhold is acknowledged for his support in the laboratory. We thank Martin Head for accurate revision of an earlier version of this article. Three anonymous reviewer also contributed constructive remarks. This work was funded through the Deutsche Forschungsgemeinschaft as part of the Research Center / Excellence Cluster “The Ocean in the Earth System” of the University of Bremen.

Appendix A: Taxonomic information

Taxonomy follows Fensome and Williams (2004) and Head et al. (2001).

Division: Dinoflagellata (Bütschli 1885) Fensome et al. 1993

Subdivision: Dinokaryota Fensome et al. 1993

Class Dinophyceae Pascher 1914

Subclass Peridiniphycidae Fensome et al. 1993

Order Gonyaulacales Taylor 1980

Impagidinium aculeatum (Wall 1967) Lentin & Williams 1981

Impagidinium patulum (Wall 1967) Stover & Evitt 1978

Impagidinium sphaericum (Wall 1967) Lentin & Williams 1981

Impagidinium spp. Stover and Evitt 1978

Lingulodinium machaerophorum (Deflandre et Cookson 1955) Wall 1967

Nematosphaeropsis labyrinthus (Ostenfeld 1903) Reid 1974

Operculodinium centrocarpum (Deflandre & Cookson) Wall & Dale, 1966

Operculodinium israelianum (Rossignol 1962) Wall 1967

Operculodinium janduchenei Head et al. 1989

Cyst of *Pentapharsodinium dalei* Indelicato & Loeblich III 1986

Polysphaeridium zoharyi (Rossignol, 1962) Bujak et al., 1980

Pyxidinosia reticulata (McMinn & Sun 1994) Marret & de Vernal 1997

Spiniferites membranaceus (Rossignol 1964) Sarjeant 1970

Spiniferites mirabilis (Rossignol 1964) Sarjeant 1970

Spiniferites pachydermus (Rossignol 1964) Reid 1974

Spiniferites ramosus (Ehrenberg 1838) Mantell 1854

Spiniferites spp.

Order Gymnodiniales Apstein 1909

Cyst of *Gymnodinium catenatum* (Graham 1943) Anderson et al. 1988

Cyst of *Gymnodinium nolleri* Ellegaard et Moestrup 1999

Cyst of *Polykrikos kofoidii* Chatton 1914

Cyst of *Polykrikos schwartzii* Bütschli 1873

Order Peridinales Haeckel 1894

Brigantedinium spp. (Reid 1977)

Echinidinium aculeatum Zonneveld 1997

Echinidinium delicatum Zonneveld 1997 ex Head 2003

Echinidinium transparantum Zonneveld 1997

Echinidinium spp. Zonneveld 1997 ex Head et al. 2001

Lejeunecysta oliva (Reid 1977) Turon & Londeix 1988

Cyst of *Protoperidinium americanum* (Gran et Braarud) Balech 1974

Cyst of *Protoperidinium monospinum* (Paulsen 1907) Zonneveld et Dale 1994

Cyst of *Protoperidinium stellatum* (Wall 1968) Balech 1994

Selenopemphix nephroides (Benedek 1972) Benedek et Sarjeant 1981

Selenopemphix quanta (Bradford 1975) Matsuoka 1985

Trinovantedinium applanatum (Bradford 1977) Bujak et Davies 1983

Votadinium calvum Reid 1977

Appendix B: Correlation matrix of RDA rel

The correlation matrix of RDA rel can be found, in the online version, at [doi:10.1016/j.revpalbo.2009.10.005](https://doi.org/10.1016/j.revpalbo.2009.10.005).

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4. NW African climate variations during the last 47,000 years indicated by organic-walled dinoflagellate cysts

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(Submitted to *Palaeogeography, Palaeoclimatology, Palaeoecology*, 11 August 2009)

Abstract

NW African climate shows orbital and millennial-scale variations, which are tightly connected to changes in marine productivity. We present organic-walled dinoflagellate cyst (dinocyst) record from a sediment core off Cape Yubi at about 27°N in the Canary Basin covering the time period from 47 to 3ka before present (BP). The dinocyst record reflects differences in upwelling intensity and seasonality as well as the influence of fluvial input. Sea-level changes play an important role for the upwelling pattern and productivity signals at the core site. Within the studied time interval, four main phases were distinguished. (1) From 45 to 24ka BP, when sea-level was 75m lower than today, high relative abundances of cysts of heterotrophic taxa point to enhanced upwelling activity, especially during HEs, while relatively low dinocyst accumulation rates indicate that filament activity at the core location was strongly reduced. (2) At sea-level lowstand during the LGM to H1, dinocyst accumulation rates suggest that local filament formation was even more inhibited. (3) From the early Holocene to about 8ka

BP, extraordinary high accumulation rates of most dinocyst species, especially of *Lingulodinium machaerophorum*, suggest that nutrient supply via fluvial input increased and rising sea-level promoted filament formation. At the same time, the upwelling season prolonged. (4) A relative increase in cysts of photoautotrophic taxa from about 8ka BP on indicates more stratified conditions while fluvial input decreased. Our study shows that productivity records can be very sensitive to regional features. From the dinocyst data we infer that marine surface productivity off Cape Yubi during glacial times was within the scale of modern times but extremely enhanced during deglaciation.

Keywords: NW Africa, dinoflagellate cysts, fluvial input, sea-level, productivity, upwelling

4.1. Introduction

The Sahara is the largest desert in the world covering the main part of North Africa. Around four million inhabitants depend on the Saharan precipitation budget, which is subject to abrupt climate variations (Nicholson, 2000). In turn, the Sahara also affects regional and global climate with its high albedo (Knorr et al., 2001). Since the Pliocene, changes in aridity frequently affected the region of the Sahara (Leroy and Dupont, 1994; deMenocal, 1995). The early Holocene African Humid Period (AHP) from 14.8 to 5.5ka BP, characterized by extensive grasslands and numerous lakes in N Africa, was followed by the present-day arid conditions (Claussen et al. 1999; Gasse, 2000; deMenocal et al., 2000b). To estimate future climate fluctuations in North Africa, it is important to understand the mechanisms behind these former climatic changes.

Marine sediment records off NW Africa have been linked to climate variations by numerous authors (e.g., Sarnthein et al., 1981; Sarnthein et al., 1988; Berger and Wefer, 1991; Abrantes, 2000). Hereby, the upwelling pattern and its associated marine productivity are given particular attention. Coastal upwelling is driven by the trade winds whose range is determined by the position of the Intertropical Convergence Zone (ITCZ). The ITCZ is a rain-bearing low pressure zone generated by solar forcing at low latitudes. Its influence on N African climate as well as on upwelling conditions is considerable as its position moves latitudinally depending on seasonal insolation changes.

Reconstructions of upwelling activity off NW Africa are manifold and partly contradictory. Previous palaeoproductivity studies considered the upwelling region off NW Africa as a type example for glacial high productivity (e.g., Sarnthein et al., 1982; Sarnthein et al., 1988). Hooghiemstra et al. (1987) suggested a strengthening of NE trade winds during glacials, which led to intensified upwelling conditions (Sarnthein et al., 1981; Sarnthein et al., 1988; Berger and Wefer, 1991). This is supported by other studies that reconstruct enhanced productivity during glacial times using micropalaeontological and various geochemical proxies (e.g., Müller et al., 1983; Marret and Turon, 1994; Abrantes, 2000;). In contrast, high productivity off NW Africa during interglacial times was reported by , . These authors suggest local differences in hydrography and wind stress as well as sea-level impact as explanation for lower glacial productivity.

Aridification in N Africa has recently been linked to high latitude ocean cooling during Heinrich Events (HE) by several authors (e.g., deMenocal et al., 2000a; Mulitza et al., 2008;). They propose that a decrease in Atlantic meridional overturning circulation (AMOC) shifted the ITCZ and its associated rainbelt southward resulting in N African aridity. Climatic and productivity signals off NW Africa that occur synchronously with HEs have also been identified by other authors (e.g., Nave et al., 2003; ; Bouimetarhan, 2009; Itambi et al., 2009). Most of these records derive from regions off the southern boundary of the Sahara where perennial upwelling prevails. We aim to investigate oceanographical and climatological changes where present-day upwelling seasonality is more pronounced. Our sediment core site is located at the upper continental slope at about 27°N, the northernmost palaeoborder of the monsoonal system suggested by Kuhlmann et al. (2004b). By use of organic-walled dinoflagellate cysts (dinocysts) the importance of regional influences / low latitude variations is disentangled from high latitude induced climate changes. We discuss our dinocyst record in combination with geochemical data.

Dinocysts have proved to be a useful tool in palaeoenvironmental reconstructions as their distribution patterns correlate sensitively to distinct physical water properties. Studies on the spatial distribution of dinocysts in surface sediments off NW Africa and their relation to environmental conditions in the upper water column reveal, that species associations are indicative for regional gradients in upwelling conditions as well as fluvial input (Targarona et al., 1999, Holzwarth et al., in press).

4.2. Modern oceanographic and climatic setting off NW Africa

The NW African margin is one of the major eastern boundary current systems of the World where trade wind driven coastal upwelling favours marine productivity. Fig. 1 shows the main oceanographic and atmospheric features. The NE trade winds blow parallel to the coast and induce an offshore water movement due to Coriolis-force driven Ekman transport. As a compensation, nutrient-rich central water masses are brought up to the surface. The shelf break front separates cold eutrophic coastal waters from warmer oligotrophic oceanic waters (Hagen, 2001). Thus, upwelling occurs within a band of about 30-100km from the coast, depending on the shelf width (Mittelstaedt, 1991). At cape locations, large upwelling filaments can develop, exporting highly productive surface waters far offshore (Van Camp et al., 1991; Nykjær and Van Camp, 1994; Hernández-Guerra and Nykjær, 1997; Hagen, 2001). The formation of these filaments depends on a combination of local current patterns, the morphology of the sea floor and the coastline (Nykjær and Van Camp, 1994). Our working area is located on the slope off Cape Yubi (Fig. 1) where the filament expands hundreds of km offshore (Barton et al., 1998). Coastal upwelling is mainly a function of the intensity and seasonality of the trade winds. Due to the seasonally migrating ITCZ, there is a latitudinal gradient in duration and intensity of the upwelling season. In boreal summer, when the ITCZ is in its northernmost position at about 19°N, the NW African margin from 20° to 32°N is influenced by upwelling (e.g., Nicholson, 2000; Mittelstaedt, 1991). In boreal winter, the ITCZ and its associated trade wind belt is located at its southernmost position at about 5°S and upwelling does not occur north of 25°N (Mittelstaedt, 1991; Hernández-Guerra and Nykjær, 1997). Off Cape Yubi, upwelling occurs predominantly in summer and early autumn (Mittelstaedt, 1991; Hernández-Guerra and Nykjær, 1997).

As part of the subtropical North Atlantic Gyre, the Canary Current flows southward along the NW African continental margin (Mittelstaedt, 1991). Below this subtropical water, North Atlantic Central Water (NACW) flows southward at a depth of 100 to 600m and constitutes the main source of the upwelled water (Siedler and Onken, 1996). NACW can be mixed with northward bound South Atlantic Central Water (SACW) whose proportions increase to the south (Hagen, 2001). The investigated core is located at a depth of 1070m where Mediterranean Outflow Water (MOW) flows southward between 600 and 1700m (Knoll et al., 2002). In some cases, a derivative of Antarctic Intermediate Water was observed north of the Canary Islands flowing polewards between 500 and 1000m (Müller et al., 1983; Mittelstaedt, 1991; Knoll et al.,

2002). Between 1700 and 3500m, North Atlantic Deep Water (NADW) flows southward (Knoll et al., 2002; Llinas et al., 2002).

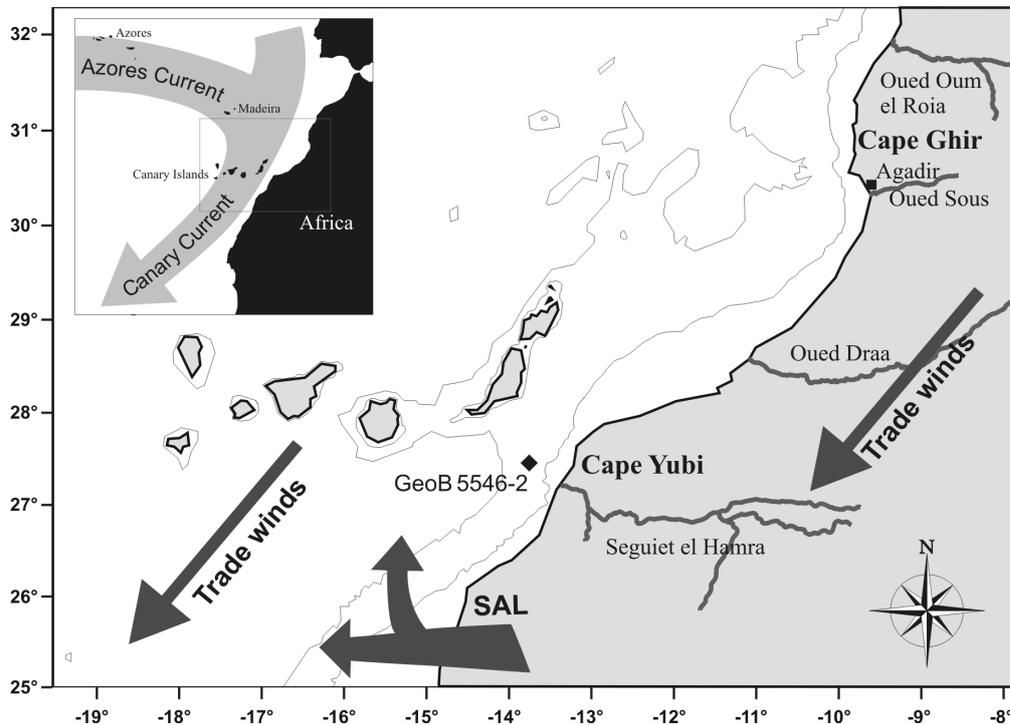


Figure 1. Oceanographic setting of core site GeoB 5546-2 (black diamond) off NW-Africa with major currents, wind field and bathymetry. Isobaths indicate 200m and 2000m waterdepth.

The Saharan desert belt extends from about 17 to 32°N (Schiffers, 1971). Modern climatic conditions in the Sahara are arid with less than 50mm annual precipitation in most areas (Nicholson, 2000). Fluvial input by the river Seguiet el Hamra nearshore the core site (Fig. 1) is very low and not permanent. The Saharan desert is the source region of considerable amounts of aeolian dust, which are transported into the Atlantic ocean off NW Africa by two main wind systems (Wilson, 1971; Pye, 1987). The NE trade winds transport dust from the northern Sahara parallel to the coastline. The African Easterly Jet is directed westward and carries Saharan and Sahelian dust over very long distances at mid-tropospheric levels within the Saharan Air Layer (SAL) (e.g., Prospero et al., 2002). By far, the largest amount of dust is transported to the ocean by the NE trades, whereas the contribution of SAL transported dust is relatively small (Swap et al, 1996; Stuut et al., 2005).

4.3. Materials and Methods

Piston core GeoB 5546-2 (27°32'2N, 13°44'2W; Fig. 1) with a length of 851cm was recovered during RV Meteor cruise M42/4 in 1998 (Wefer et al., 1999) at 1070m water depth. It covers the time interval of 3 to 47ka BP. The sediment consists mainly of foraminifera bearing nannofossil mud (Wefer et al., 1999).

4.3.1. Age model

The age model is based on a peak to peak correlation of the $\delta^{18}\text{O}$ record of the planktic foraminifera *Globigerina bulloides* to the $\delta^{18}\text{O}$ record of the NGRIP ice core and Accelerator Mass Spectrometry radiocarbon dating (Kuhlmann et al., 2004a; Mollenhauer et al., 2005; Plewa et al., 2006) using Analyseries 2.0.4.2 (Paillard et al., 1996). Figure 2 shows the tiepoints in an age versus depth profile. A detailed age model will be published in Meggers et al., subm.

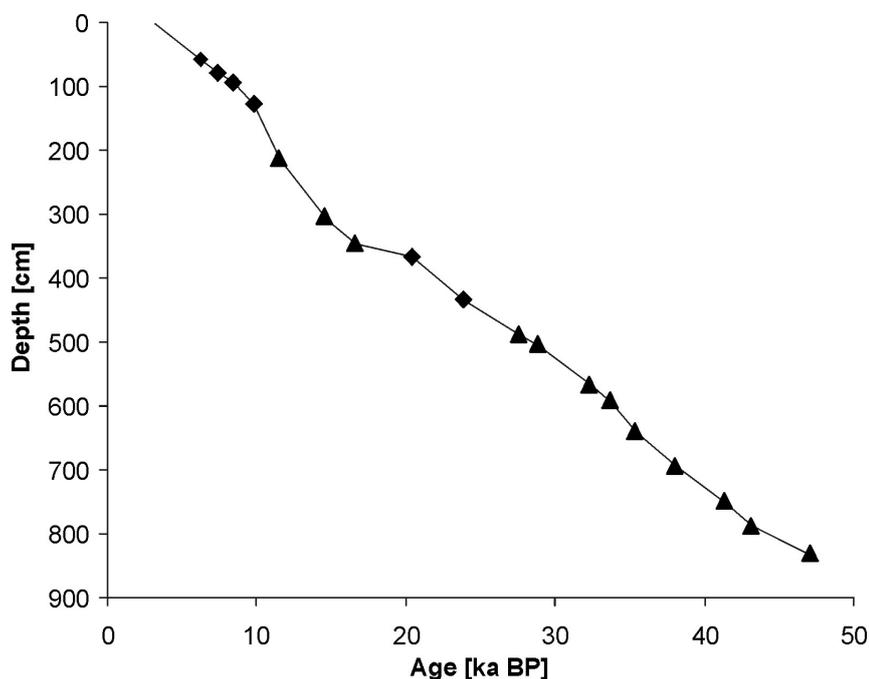


Figure 2. Age versus depth profile of sediment core GeoB 5546-2 including radiocarbon dated tiepoints (black diamonds) and tiepoints based on peak to peak correlation between the $\delta^{18}\text{O}$ record of the planktic foraminifera *Globigerina bulloides* and the $\delta^{18}\text{O}$ record of the NGRIP ice core (black triangles). The age model was performed with Analyseries 2.0.4.2 (Paillard et al., 1996).

The timing of geological periods and other events with the according references we used in this article can be gathered from Table 1. We refer to HEs as ages of Heinrich layers (Hemming, 2004 and references therein).

Table 1. Timing of geological periods and climatological events with according references.

Period name	Abbreviation	Time period [ka BP]	Most recent reference
African Humid Period	AHP	14.8 - 5.5	deMenocal et al. (2000b)
Bølling/Allerød	B/A	14.7 - 12.7	Broecker (1992)
Younger Dryas	YD	12.8 - 11.5	Muscheler et al. (2008)
Heinrich event 1	HE1	16.8	Hemming (2004) and references therein
Last Glacial Maximum	LGM	23 - 19	Mix et al. (2001)
Heinrich event 2	HE2	24	Hemming (2004) and references therein
Heinrich event 3	HE3	31	Hemming (2004) and references therein
Heinrich event 4	HE4	38	Hemming (2004) and references therein
Heinrich event 5	HE5	45	Hemming (2004) and references therein
Marine isotope stage 1	MIS1	14 - 0	Lisiecki and Raymo (2005)
Marine isotope stage 2	MIS2	29 - 14	Lisiecki and Raymo (2005)
Marine isotope stage 3	MIS3	57 - 29	Lisiecki and Raymo (2005)

4.3.2. Geochemical parameters

Potassium intensities were measured with the X-Ray Fluorescence (XRF) Core Scanner at MARUM, University of Bremen, which enables non-destructive logging of the major elemental composition. XRF data used in this study were collected in 1cm resolution on split sediment cores. Each measurement is carried out over an 1cm² area using 30 seconds count time, 10kV X-ray voltage and an X-ray current of 250µA. The resulting data are element intensities.

Prior to further geochemical analyses, sediment samples were freeze dried and homogenized. Total organic carbon (TOC) was determined on acidified samples using a CHN-Haereus Analyzer which measures the primary elements carbon (C), hydrogen (H) and nitrogen (N). Analytical standard deviation calculated for repeated measurements was 1.6%. TOC accumulation rates (AR) based on sedimentation rates (SR) and dry bulk density (DBD) were calculated using the following equation:

$$\text{TOC AR [g cm}^{-2} \text{ ka}^{-1}] = \text{SR [cm ka}^{-1}] * \text{DBD [g cm}^{-3}] * \text{TOC [g kg}^{-1}]$$

The method for density measurement is described in Kuhlmann et al. (2004a).

For bulk solid phase analysis, 50mg of ground sediment was processed in a microwave system with a mixture of concentrated nitric (3ml), hydrofluoric (2ml) and hydrochloric (2ml) acids of supra-pure quality. The concentrations of aluminium (Al) and titanium (Ti) in the digestion solutions were measured by Inductively Coupled Plasma Atomic Emission Spectroscopy (ICP-AES). For a detailed description we refer to Plewa et al. (2006).

Table 2. List of identified organic-walled dinoflagellate cyst taxa and their cyst-theka-relationship (following Head et al. (1996) and Marret and Zonneveld (2003)) from core GeoB 5546-2.

Dinocyst species/taxon	Motile affinity
<i>Bitectatodinium spongium</i>	Unknown
<i>Brigantedinium</i> spp.	<i>Protoperidinium</i> spp.
<i>Echinidinium aculeatum</i>	Unknown
<i>Echinidinium delicatum</i>	Unknown
<i>Echinidinium</i> spp.	Unknown
<i>Echinidinium transparentum</i>	Unknown
Cyst of <i>Gymnodinium catenatum</i>	<i>Gymnodinium catenatum</i>
Cyst of <i>Gymnodinium nolleri</i>	<i>Gymnodinium nolleri</i>
<i>Impagidinium aculeatum</i>	<i>Gonyaulax</i> sp.
<i>Impagidinium paradoxum</i>	<i>Gonyaulax</i> sp.
<i>Impagidinium patulum</i>	<i>Gonyaulax</i> sp.
<i>Impagidinium plicatum</i>	<i>Gonyaulax</i> sp.
<i>Impagidinium sphaericum</i>	<i>Gonyaulax</i> sp.
<i>Impagidinium strialatum</i>	<i>Gonyaulax</i> sp.
<i>Lejeunecysta oliva</i>	<i>Protoperidinium</i> sp.
<i>Lingulodinium machaerophorum</i>	<i>Lingulodinium polyedra</i>
<i>Nematosphaeropsis labyrinthus</i>	<i>Gonyaulax spinifera</i>
<i>Operculodinium centrocarpum</i>	<i>Protoceratium reticulatum</i>
<i>Operculodinium israelianum</i>	? <i>Protoceratium</i> sp.
<i>Operculodinium janduchenei</i>	Unknown
Cyst of <i>Pentapharsodinium dalei</i>	<i>Pentapharsodinium dalei</i>
Cyst of <i>Polykrikos kofoidii</i>	<i>Polykrikos kofoidii</i>
Cyst of <i>Polykrikos schwartzii</i>	<i>Polykrikos schwartzii</i>
<i>Polysphaeridium zoharyi</i>	Unknown
Cyst of <i>Protoperidinium americanum</i>	<i>Protoperidinium americanum</i>
Cyst of <i>Protoperidinium leonis</i>	<i>Protoperidinium leonis</i>
Cyst of <i>Protoperidinium monospinum</i>	<i>Protoperidinium monospinum</i>
Cyst of <i>Protoperidinium stellatum</i>	<i>Protoperidinium stellatum</i>
<i>Pyxidinospis reticulata</i>	<i>Pyrodinium bahamense</i>
<i>Selenopemphix nephroides</i>	<i>Protoperidinium subinermis</i>
<i>Selenopemphix quanta</i>	<i>Protoperidinium conicum</i>
<i>Spiniferites delicatus</i>	<i>Gonyaulax</i> sp.
<i>Spiniferites membranaceus</i>	<i>Gonyaulax</i> sp.
<i>Spiniferites mirabilis</i>	<i>Gonyaulax spinifera</i>
<i>Spiniferites pachydermus</i>	<i>Gonyaulax</i> sp.
<i>Spiniferites ramosus</i>	<i>Gonyaulax</i> sp.
<i>Spiniferites</i> spp.	<i>Gonyaulax</i> spp.
<i>Trinovantedinium applanatum</i>	<i>Protoperidinium pentagonum</i>
<i>Tuberculodinium vancampoeae</i>	<i>Pyrophacus steinii</i>
<i>Votadinium calvum</i>	<i>Protoperidinium oblongum</i>
<i>Votadinium spinosum</i>	<i>Protoperidinium claudicans</i>
<i>Xandarodinium xanthum</i>	<i>Protoperidinium divaricatum</i>

4.3.3. Organic-walled dinoflagellate cysts

For the study of dinocysts the core was sampled with 10cm³ syringes (with 10mm internal diameter). Sample resolution over core length is 15cm from 3 to 378cm, 5cm from 373 to 783cm and again 15cm from 783 to 833cm. Samples (102 in total) were prepared using the method described in Holzwarth et al. (2007). The dinocysts were counted with a light microscope at 400x magnification. Total slides were counted. When a slide contained less than 200 dinocysts, additional slides were prepared and counted. The nomenclature for the dinocyst species was used and follows Fensome et al. (1993), Zonneveld (1997), Head et al. (2001) and Fensome and Williams (2004). We denote spherical brown cysts without spines (“round browns”) as *Brigantedinium* spp. Morphological criteria given in Bolch et al. (1999) were used to distinguish between cysts of *Gymnodinium catenatum* and cysts of *Gymnodinium nolleri*. Cysts of the genus *Polykrikos* were determined conform to Matsuoka et al. (2009).

We identified 42 dinocyst taxa which are listed in Table 2.

Dinocyst accumulation rates based on SR and DBD were calculated using the following equation:

$$\text{dinocyst AR [cysts cm}^{-2} \text{ ka}^{-1}] = \text{SR [cm ka}^{-1}] * \text{DBD [g cm}^{-3}] * \text{dinocysts g}^{-1}$$

According to their congruent signals in relative and absolute abundances, we grouped all species of the genus *Spiniferites* as *Spiniferites* spp., all protoperidinioid cyst species except cysts of *Protoperidinium stellatum* as protoperidinioid cysts, all species of the genus *Echinidinium* as *Echinidinium* spp., cysts of *Gymnodinium catenatum* and cysts of *Gymnodinium nolleri* as cysts of *Gymnodinium* spp., cysts of *Polykrikos kofoidii* and *Polykrikos schwartzii* as cysts of *Polykrikos* spp., all species of the genus *Impagidinium* as *Impagidinium* spp. and gonyaulacoid cyst species except *Spiniferites* spp., *Impagidinium* spp. and *L. machaerophorum* as gonyaulacoid cysts. For an overview, see Table 3.

Table 3. Groups of organic-walled dinoflagellate cyst taxa with grouped dinocyst species from core GeoB 5546-2.

Dinocyst group / taxon	Included dinocyst species	Order	Fig.
<i>Spiniferites</i> spp.	<i>Spiniferites delicatus</i> <i>Spiniferites membranaceus</i> <i>Spiniferites mirabilis</i> <i>Spiniferites pachydermus</i> <i>Spiniferites ramosus</i> <i>Spiniferites</i> spp.	Gonyaulacales	3a and 4a
Proto-peridinioid cysts	<i>Brigantedinium</i> spp. <i>Lejeunecysta oliva</i> Cyst of <i>Proto-peridinium americanum</i> Cyst of <i>Proto-peridinium leonis</i> Cyst of <i>Proto-peridinium monospinum</i> <i>Selenopemphix nephroides</i> <i>Selenopemphix quanta</i> <i>Trinovantedinium applanatum</i> <i>Votadinium spinosum</i> <i>Votadinium calvum</i> <i>Xandarodinium xanthum</i>	Peridinales	3b and 4b
<i>Echinidinium</i> spp.	<i>Echinidinium aculeatum</i> <i>Echinidinium delicatum</i> <i>Echinidinium transparentum</i> <i>Echinidinium</i> spp.	Peridinales	3c and 4c
Cysts of <i>Gymnodinium</i> spp.	Cyst of <i>Gymnodinium catenatum</i> Cyst of <i>Gymnodinium nolleri</i>	Gymnodinales	3d and 4d
Cysts of <i>Polykrikos</i> spp.	Cyst of <i>Polykrikos kofoidii</i> Cyst of <i>Polykrikos schwartzii</i>	Gymnodinales	3e and 4e
<i>Impagidinium</i> spp.	<i>Impagidinium aculeatum</i> <i>Impagidinium paradoxum</i> <i>Impagidinium patulum</i> <i>Impagidinium plicatum</i> <i>Impagidinium sphaericum</i> <i>Impagidinium striatum</i>	Gonyaulacales	3f and 4f
Gonyaulacoid cysts	<i>Bitectatodinium spongium</i> <i>Nematosphaeropsis labyrinthus</i> <i>Operculodinium centrocarpum</i> <i>Operculodinium israelianum</i> <i>Operculodinium janduchenei</i> Cyst of <i>Pentapharsodinium dalei</i> <i>Polysphaeridium zoharyi</i> <i>Pyxidinospis reticulata</i> <i>Tuberculodinium vancampoeae</i>	Gonyaulacales	3g and 4g
<i>Lingulodinium machaerophorum</i>	<i>Lingulodinium machaerophorum</i>	Gonyaulacales	3h and 4h
Cyst of <i>Proto-peridinium stellatum</i>	Cyst of <i>Proto-peridinium stellatum</i>	Peridinales	3i and 4i

4.4. Results

4.4.1. Variations in relative abundances of dinocyst species

Generally, the relative abundance patterns of different dinocyst taxa are characteristic for distinct time intervals (Fig. 3). The time period between H5 and H4 is characterized by a steady increase of the *Spiniferites* species from 30% to up to more than 80% (Fig. 3a) while all other species show a decrease in their relative abundances.

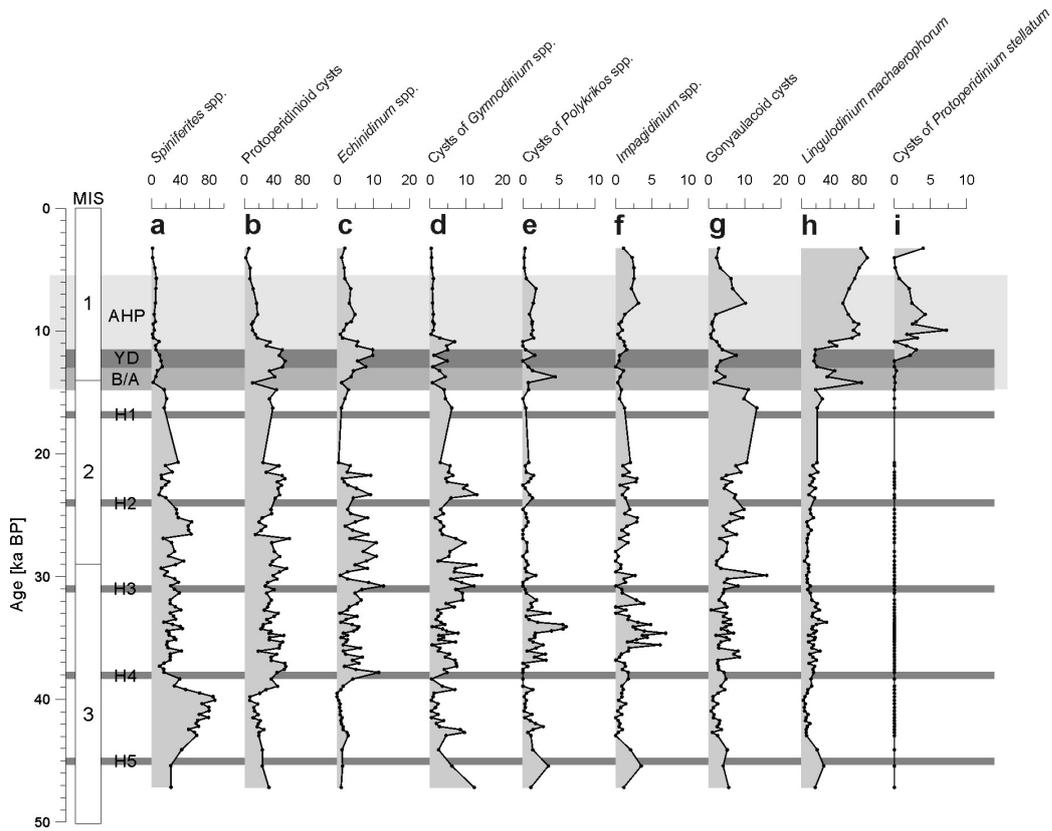


Figure 3. Relative abundances of organic-walled dinoflagellate cyst taxa expressed in percentages of total cysts from core GeoB 5546-2. Note three different scales.

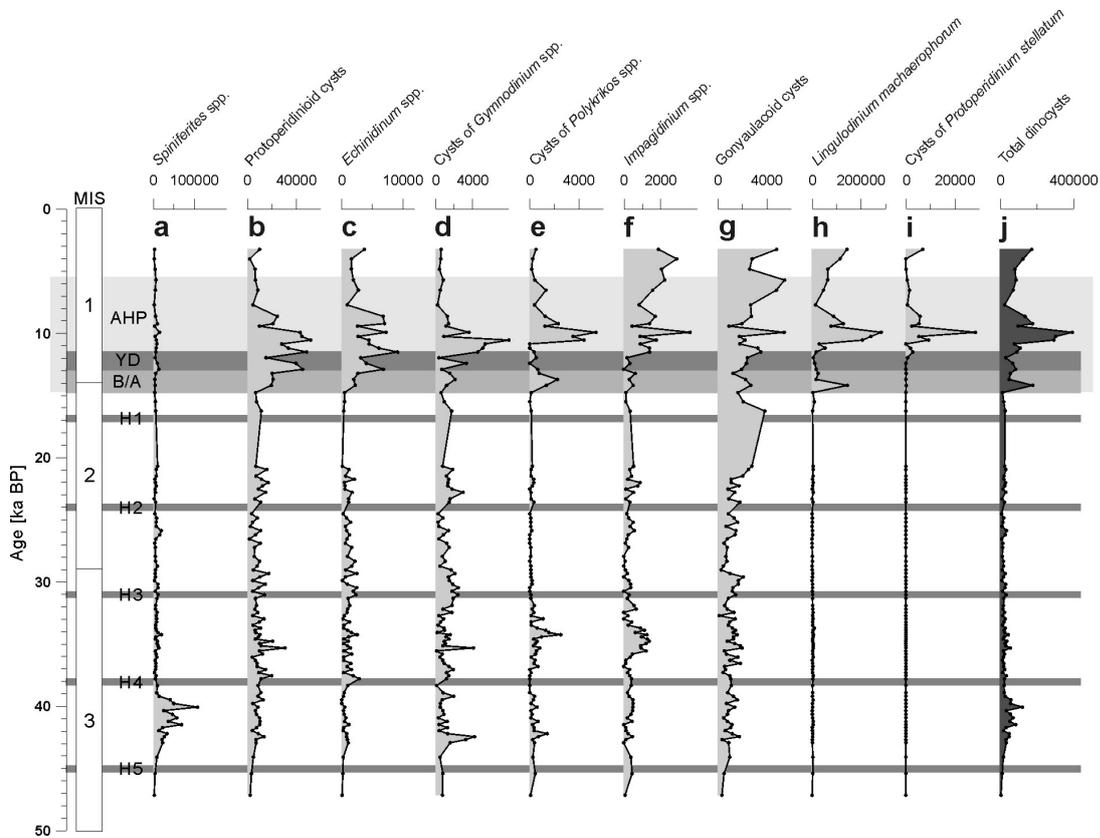


Figure 4. Accumulation rates of organic-walled dinoflagellate cyst taxa from core GeoB 5546-2 given in [cysts $\text{cm}^{-2} \text{ka}^{-1}$].

Notes to Figure 3 and 4:

Bars indicate in dark grey Heinrich events (H) and the Younger Dryas (YD), in lighter grey the Bølling/Allerød (B/A) and in light grey the African Humid Period (AHP). MIS is marine isotopic stage. For grouping of dinocyst taxa see Table 3.

Relative abundances of protoperidinioid cysts dominate the assemblage from H4 to the Younger Dryas (YD) with values around 40% before they decline considerably at the beginning of the Holocene to about 10% (Fig. 3b). *Echinidinium* spp. display peaks at H4, H3 and H2 (Fig. 3c). Cysts of *Gymnodinium* spp. show highest relative abundances around H3 and H2 (Fig. 3d). Relative abundances of cysts of *Polykrikos* spp. and *Impagidinium* spp. peak between H4 and H3 (Fig. 3e and f). Gonyaulacoid cysts display a continuous rise in their relative abundances until the end of MIS2 (Fig. 3g). At the beginning of the Bølling/Allerød (B/A) and with the onset of the AHP, most species sharply drop in their relative abundances while *L. machaerophorum* (Fig. 3h) and cysts of *Polykrikos* spp. (Fig. 3e) show distinct peaks. After a decline of relative abundances of *L. machaerophorum* during the YD, it becomes the most abundant species during the whole investigated interval of the Holocene with relative abundances of more than 80%. Cysts of *Protoperidinium stellatum* occur for the first time during the B/A and show rapidly increasing relative abundances at the beginning of MIS1 (Fig. 3i).

4.4.2. Variations in accumulation rates of organic-walled dinocyst species

Total dinocyst accumulation rates exhibit three distinct peaks over time (Fig. 4j). The first maximum at about 40ka BP is followed by a long period of lower fluxes with small variations. After a second peak during the B/A and a decline during the YD, total dinocyst accumulation rates reach their maximum of nearly 400,000 cysts cm⁻² ka⁻¹ in the early Holocene (Fig. 4j).

Accumulation rates of *Spiniferites* spp. (Fig. 4a) reach their highest values at 40ka BP before they sharply drop down. During upper MIS3 and MIS2, accumulation rates of protoperidinioid cysts (Fig. 4b), *Echinidinium* spp. (Fig. 4c) and other gonyaulacoid cysts (Fig. 4g) show relatively low values. Accumulation rates of cysts of *Gymnodinium* spp. (Fig. 4d), cysts of *Polykrikos* spp. (Fig. 4e) and *Impagidinium* spp. (Fig. 4f) show some congruent peaks during MIS3. During the B/A, with the onset of the AHP, all species exhibit distinct peaks in their accumulation rates. Hereby, *L. machaerophorum* (Fig. 4h) shows the most intense increase, which coincides with the first occurrence of cysts of *P.*

stellatum (Fig. 4i). After a short drop during the YD, accumulation rates of all dinocyst species except *Spiniferites* spp. increase rapidly with the beginning of the Holocene. At about 8ka BP, accumulation rates of all species strongly decline and only accumulation rates of *Impagidinium* spp., gonyaulacoid cysts and *L. machaerophorum* increase again afterwards.

4.4.3. Variations in geochemical parameters

Within MIS3, TOC accumulation rates (Fig. 5d) display increased values of up to about $0.4\text{g cm}^{-2}\text{ ka}^{-1}$ in periods between HEs. From H3 to H1, TOC accumulation rates stay constantly low. During the B/A and the early Holocene, accumulation rate values for TOC show distinct peaks of up to about $0.5\text{g cm}^{-2}\text{ ka}^{-1}$ before declining again from 8ka BP on.

The Ti/Al ratio displays relatively constant values throughout MIS3 and 2 between 0.055 and 0.06. During the B/A, values for Ti/Al decline to 0.05, are again enhanced during the YD and then sharply drop down to about 0.045 after the YD.

K intensities show an inverted pattern. Lower intensities throughout MIS3 and 2 are followed by highest intensities after the YD, which then decline at the end of the AHP.

4.5. Discussion

Before relating the dinocyst record to palaeoenvironmental conditions, processes possibly influencing the primary dinocyst assemblage in the sediment have to be discussed.

4.5.1. Transport

Transport processes, which might displace dinocysts after their production in the upper water column have been discussed in Holzwarth et al. (2007) and in a regional context in Holzwarth et al. (in press). Filaments in particular can be important carriers of neritic productivity, which is further promoted while the filament spreads further offshore. Lateral advection of particles in the NW-African margin has been inferred from a number of studies (e.g., Neuer et al., 1997; Freudenthal et al., 2001; Neuer et al., 2002; Karakas et al., 2006; Alonso-González et al., 2009). Dinocysts in core GeoB 5546-2

might therefore be of shelf origin to some extent. As the investigated core is located close to the shelf break (Fig. 1 and Fig. 6) and thus influenced by neritic conditions we assume that the dinocyst assemblage reflects the conditions in the water column from over the shelf and upper slope.

4.5.2. Aerobic degradation

Within the last years it has become evident that early diagenetic aerobic degradation can affect sensitive dinocyst species like *Brigantedinium* spp. and *Echinidinium* spp. in well oxygenated waters (e.g., Zonneveld et al., 2007; Zonneveld et al., 2008; Kodrans-Nsiah et al., 2008). However, fast burial in the sediment can protect organic material from oxidation. It was suggested that preservation of non-refractory organic carbon is improbable when sedimentation rates are lower than about 1-2cm ka⁻¹ (Jung et al., 1997; Kasten et al., 2003). Sedimentation rates in GeoB 5546-2 are relatively high and range with 11 to 48cm ka⁻¹ (Fig. 5j) and an average of 22.5cm ka⁻¹ well above this value. We therefore assume that aerobic degradation did not severely alter our cyst association post-depositionally. This is supported by Plewa et al. (2006) who propose total organic carbon (TOC) in GeoB 5546-2 as diagenetically unaltered because of a good correlation to alkenone concentrations.

Bockelmann (2007) suggested that changes in dinocyst associations in a sediment core off Cape Ghir (located about 3 degrees north of our core location, but further offshore) reflect differences in deep water ventilation of the North Atlantic Basin. High accumulation rates of sensitive dinocysts were linked to an oxygen depletion in bottom water (NADW) during periods of AMOC shutdown. Our studied site at 1070m depth is nowadays located in MOW, which is characterized by an intermediate oxygen content of between 3 and 4ml l⁻¹ off Cape Yubi (Sarnthein et al., 1982). Eberwein and Mackensen (2008) reconstructed MOW off NW Africa during the Last Glacial Maximum (LGM) to be situated between 800m and 1900m. We therefore assume that our core site was bathed in MOW throughout the studied time interval. Despite fluctuations in MOW through time (e.g., Sierro et al., 2005; Voelker et al., 2006; Millot, 2008) there is no indication for oxygen depletion of MOW in the past. We therefore can assume that oxygen concentrations of bottom waters at the core site have been relatively constant during the studied time interval. In fact, any possible degradative effect of the bottom water on sensitive dinocyst species, would have been constant over time.

We therefore interpret the dinocyst record excluding degradation effects.

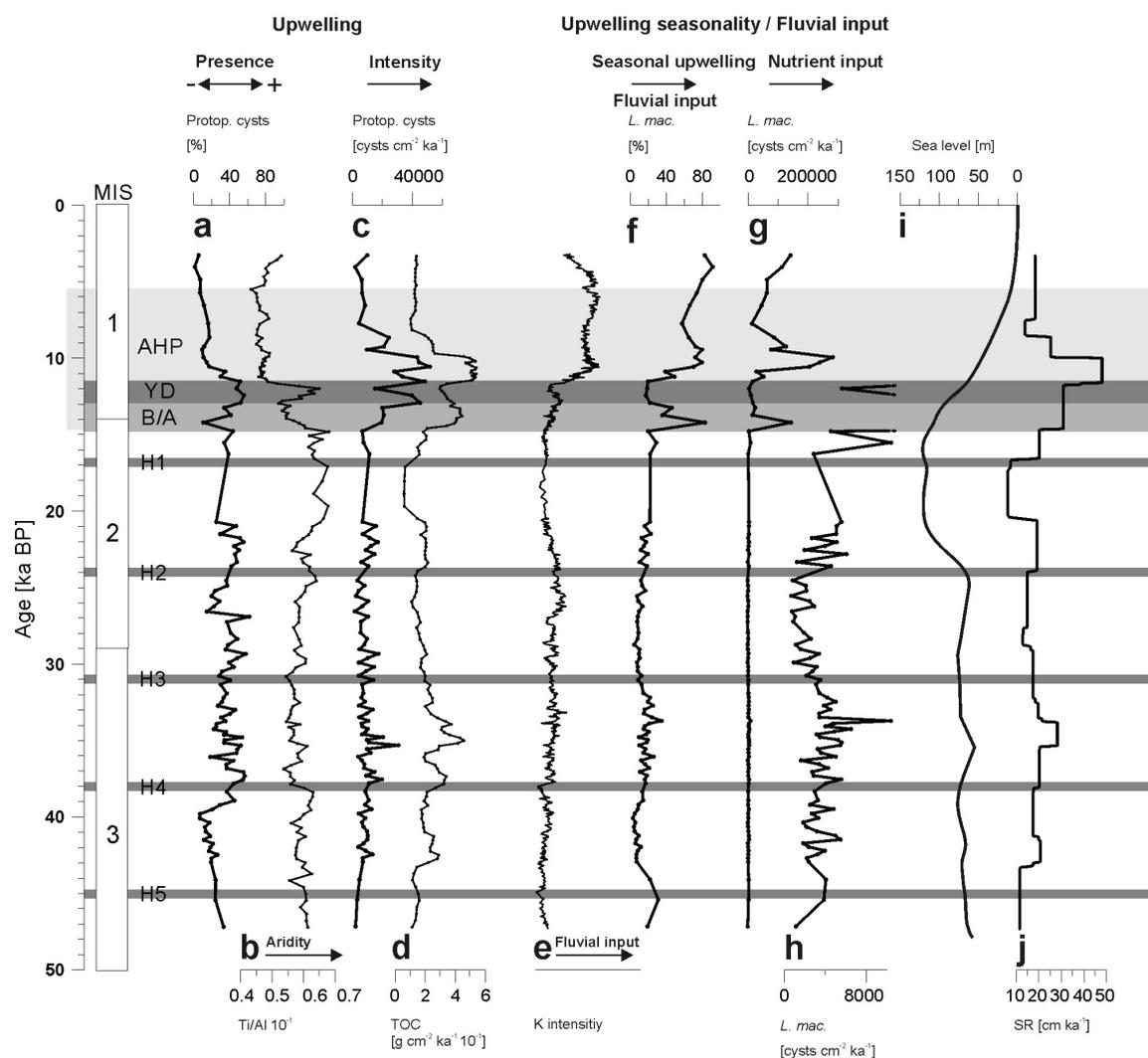


Figure 5. Downcore variations in GeoB 5546-2 of (a) percentages of protoperidinioid cysts (b) titanium/aluminium ratio, (c) accumulation rates of protoperidinioid cysts, (d) total organic carbon accumulation rates, (e) potassium intensities, (f) percentages of *Lingulodinium machaerophorum*, (g) accumulation rates of *L. machaerophorum* (h), accumulation rates of *L. machaerophorum* with enlarged scale, and (j) bulk sedimentation rates. (i) shows the relative sea-level reconstruction from Peltier and Fairbanks (2006). Bars indicate in dark grey Heinrich events (H) and the Younger Dryas (YD), in lighter grey the Bølling/Allerød (B/A) and in light grey the African Humid Period (AHP). MIS is marine isotopic stage.

4.5.3. Dinocyst variations in relation to palaeoenvironmental and palaeoclimatological changes

The modern dinocyst distribution in surface sediments off NW-Africa has been shown to be correlated to the chlorophyll-*a* content at the sea surface, seasonality and offshore range of coastal seasonal upwelling as well as river input (Holzwarth et al., in

press). Hereby, relative abundances of dinocysts rather point to the quality of environmental conditions whereas dinocyst accumulation rate data are more related to the quantity of marine productivity. According to these results, we are using certain dinocyst taxa as indicative for distinct conditions.

4.5.3.1. Upwelling and trade winds

High relative abundances of proteroperidinioid cysts (Fig. 3b) and *Echinidinium* spp. (Fig. 3c) as indicators for more perennial upwelling suggest that coastal upwelling prevailed throughout the last glacial with peaks at HEs 5-2 and the YD at the core site. Ti/Al ratio as a proxy for aridity (e.g., Shimmiel, 1992; Itambi et al., 2009) also point to more windy conditions from H5 until the end of the YD (Fig. 5b). High relative abundances of proteroperidinioid cysts and *Echinidinium* spp. could also be related to dust via supply of micronutrients as proposed by Susek (2005) and Susek et al. (2005) off NW Africa. It is suggested that trade wind activity off NW Africa increased during colder and drier HEs, the YD and the LGM (e.g., Sarnthein et al., 1982; Hooghiemstra, 1987; Moreno et al., 2001; Bozzano et al., 2002; Romero et al., 2008).

Variations in accumulation rates of proteroperidinioid cysts (Fig. 4b) and *Echinidinium* spp. (Fig. 4c) indicate an increase in upwelling strength during periods between HEs in MIS3, during the B/A, at the end of the YD and at the early Holocene. This is contradictory considering the relative abundances of these species which point to perennial upwelling throughout the last glacial with peaks at HEs 5-2 and the YD. However, accumulation rates of proteroperidinioid cysts are congruent to the TOC accumulation rate record (Fig. 5c, and 5d), which suggests this taxa to be a general proxy for productivity. Eventually, nutrient input has additionally been enhanced during times of increased accumulation rates of proteroperidinioid cysts and *Echinidinium* spp.

4.5.3.2. Seasonal upwelling and stratification

L. machaerophorum has been associated with seasonal upwelling conditions (i.e. periods of upwelling relaxation (Marret and Zonneveld, 2003 and references therein; Targarona et al., 1999; Holzwarth et al., in press). Its low relative abundances during MIS3 and 2 and the YD (Fig. 5f) suggest that permanent upwelling conditions prevailed during these times. During periods between HEs in MIS3, slightly increased relative abundances of *L. machaerophorum* point to a decrease in upwelling permanence. High relative abundances of *L. machaerophorum* during the B/A and the Holocene suggest increased upwelling seasonality.

Spiniferites ramosus can be indicative for more stratified conditions (Wall et al., 1977; Marret and Zonneveld, 2003 and references therein). It constitutes the main component of *Spiniferites* spp. in our study. High relative abundances of *Spiniferites* spp. in periods between HE5, HE4 and HE3 (Fig. 3a) could therefore be interpreted as a signal for stratified conditions.

Within the NW African upwelling region, relative abundances of cysts of *P. stellatum* have also been related to seasonal upwelling conditions (Targarona et al., 1999; Holzwarth et al., in press). In core 5546-2, an increase in relative abundances cysts of *P. stellatum* (Fig. 3i) from the YD on points to more seasonal upwelling conditions which is somewhat later than the above mentioned increase of *L. machaerophorum*. This suggests that additional factors have influenced the cyst record of *L. machaerophorum* at the beginning of the Holocene.

Accumulation rates of *L. machaerophorum* with two distinct peaks, one during the B/A and the other during the early Holocene could be related to elevated nutrient supply during upwelling relaxation. The upper part of the Holocene is characterized by high accumulation rates of *Impagidinium* spp. and gonyaulacoid cysts, which suggest further increased stratification.

4.5.3.3. Fluvial input

Apart from its relation to seasonal upwelling conditions, *L. machaerophorum*, has also been characterized as an indicator for river input in the NW-African margin (Holzwarth et al., in press). Its relative abundance pattern suggests drier conditions during MIS3 and 2, a first humid phase during the B/A and constantly higher river input from the beginning of the Holocene on (Fig. 5f). Marret and Turon 1994 also deduce enhanced river input during the B/A and the early Holocene from high percentages of *L. machaerophorum* in a sediment core off Morocco at about 34°N.

K intensities of GeoB 5546-2 have already been applied by Kuhlmann et al. (2004b) as an indicator for river input within the Holocene time interval. In our study, K intensity variations point to dry conditions during glacial times and the YD followed by more humid conditions during the early to mid Holocene until the end of the AHP (Fig. 5e).

Accumulation rates of *L. machaerophorum* also suggest dry conditions during the glacial period followed by an increase of nutrient input due to more humid conditions during the B/A and the early Holocene but decline after 10ka BP (Fig. 5g). Maximum

accumulation rates of *L. machaerophorum* in core GeoB 5546-2 are with more than 200,000 cysts $\text{cm}^{-2} \text{ka}^{-1}$ much higher than recent values off Cape Yubi (about 20,000 cysts $\text{cm}^{-2} \text{ka}^{-1}$ and still higher than recent accumulation rates of river-influenced samples off Cape Ghir (about 70,000 cysts $\text{cm}^{-2} \text{ka}^{-1}$) (Holzwarth et al., in press). This indicates enhanced river discharge throughout the AHP combined with further increased nutrient input and/or additional productivity enhancing factors during the B/A and the early Holocene until about 8ka BP. This could be due to the input of waters rich in humic substances which favour the growth of dinoflagellates by adding vitamins, auxins and other micronutrients which are essential for most dinoflagellate species (Doblin et al., 1999; Graneli and Moreira, 1990; Prakash and Rashid, 1968). The positive growth response could also be due to the chelating action of humic acids, which increase the availability of trace metals like iron (Doblin et al., 1999; Prakash and Rashid, 1968). A vegetation cover simulation by Tjallingii et al. (2008) illustrates most intense Saharan vegetation between 12 to 8ka BP. This supports our suggestion that high accumulation rates of *L. machaerophorum* in the early Holocene could point to vegetation-related river discharge. Cysts of *Gymnodinium* spp. and cysts of *Polykrikos* spp. have also been found to be indicative of fluvial input in the NW-African area (Holzwarth et al., in press). In core GeoB 5546-2, cysts of *Gymnodinium* spp. and cysts of *Polykrikos* spp. are found with increased accumulation rates during the B/A and at the beginning of the Holocene but also in periods between HEs in MIS3 (Fig. 4d and 4e). A closer view on the accumulation rates of *L. machaerophorum* (Fig. 5h) reveals that this species also shows enhanced values in periods between HEs in MIS3. This would suggest additional humid phases during MIS3. Tjallingii et al. (2008) simulated past vegetation cover of the Sahara and calculated a humidity index over time. Both parameters suggest a phase with enhanced continental precipitation during MIS3 which confirms our suggestion.

4.5.3.4. Comparison with other productivity records

Extraordinary high dinocyst accumulation rates in core GeoB 5546-2 during the B/A and the early Holocene in relation to lower values during glacial times would suggest “lower glacial productivity”. However, when comparing the mid to late Holocene dinocyst accumulation rates with glacial values, no significant difference in productivity can be suggested. Modern accumulation rates of total dinocysts off Cape Yubi are with about 40,000 cysts $\text{cm}^{-2} \text{ka}^{-1}$ in the same order of magnitude as values in core 5546-2 during MIS2 (Holzwarth et al., in press; Fig. 4j). We therefore can agree with Eberwein

and Mackensen (2008) who reconstructed organic carbon fluxes off Cape Yubi during the LGM as high as recent fluxes. Based on a dinocyst downcore record in the North Atlantic, Radi and de Vernal (2008) reconstructed enhanced palaeoproductivity during the early Holocene and lower during the glacial stage, the YD and HEs, which also is in line with our findings.

Partly in contrast to our data, Kuhlmann et al. (2004a) present higher bulk sedimentation rates off NW Africa as indicators for enhanced marine productivity during the last glacial period with highest values during the deglaciation. This could be attributed to local productivity variations. Freudenthal et al. (2002) report changes in productivity within small spatial scales of the Canary Basin and relate this to differences in the upwelling pattern depending on the sea-level.

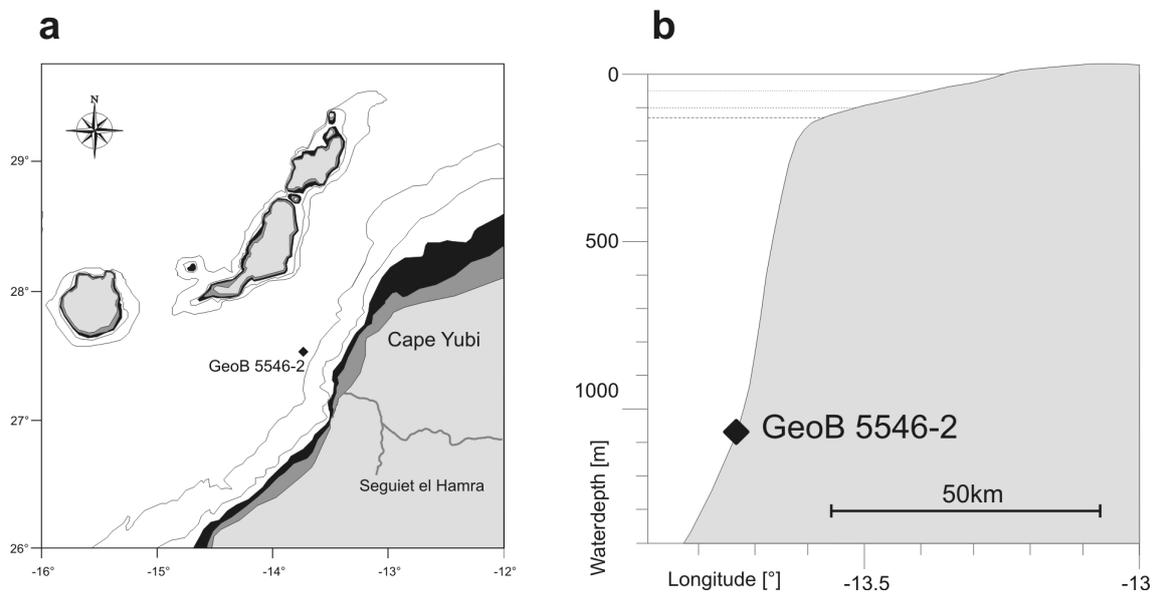


Figure 6. NW African coast morphology and bathymetry at different sea-levels (see also Fig. 5i). (a) Bathymetric map off Cape Yubi with core location GeoB 5546-2 and 50, 100, 200 and 1000m waterdepth isobaths. Dark grey area represents additional mainland when sea-level was 50m lower than today. Black area represents additional mainland when sea-level was 100m lower than today. Note that during times of low sea-level the cape morphology is shifted to the North and only a narrow shelf is shaped at the core site. (b) Cross section at latitude of core site GeoB 5546-2 (27°32'N). Dashed lines represent sea-level values bottom-up of 130m (sea-level lowstand), 100m and 50m below today. During times of low sea-level only a narrow shelf was shaped. Note that waterdepth is not to scale to longitude.

4.5.3.4. Impact of sea-level changes and synthesis

Relatively low accumulation rates of upwelling related dinocyst species during glacial times in contrast to peaks in accumulation rate of most dinocyst species at the beginning of the Holocene suggest additional productivity promoting factors for the latter time interval. Regarding the coastal morphology and the vertical profile off Cape Yubi during times of different sea-levels in detail (Fig. 5i and Fig. 6), several implications of relative sea-level fluctuations arise for the upwelling pattern at this site. In the following, we discuss this influence while establishing a chronological synthesis.

In times when sea-level was about 75m below today from 45 to 24ka BP, filament formation at 27°N was reduced because the cape profile was located farther north (Fig. 7a). The shelf area was downsized compared to modern conditions (Fig. 5i and Fig. 6), which most likely decreased the amount of export production to the slope as well as nutrient recirculation on the shelf (Thomsen, 2003). High relative abundances of upwelling related dinocyst taxa and Ti/Al values suggesting upwelling favourable dry and windy conditions face low dinocyst accumulation rates of upwelling related dinocyst taxa. This could be attributed to the narrower shelf as well as to reduced filament formation at the core location, which hampered the absolute cyst production. Enhanced accumulation rates of dinocyst species related to river input during periods between HEs of MIS3 point to an enhanced nutrient input. This could be due to increased continental humidity during these times. Fluvial input of nutrients could also be an explanation for enhanced accumulation rates of upwelling related dinocyst taxa during periods between HEs of MIS3.

At sea-level lowstand during the LGM and H1 (Fig. 7b), coast morphology was even more unfavourable for filament formation at the core site (Fig. 5i and Fig. 6a). Nutrient recycling above the very narrow shelf (Fig. 5i and Fig. 6b) near the core site as well as downslope export were also further reduced. Lowest accumulation rates of most dinocyst species during times of lowest sea-level suggest a relation to a most narrow shelf as well as still reduced filament formation. At the same time, relative abundances of upwelling related dinocyst taxa point to prevailing trade wind activity. It is generally thought that during times of sea-level lowstand, bare shelf sediments are subject to erosion by rivers and wind and as such redistributed far into the ocean basins (McCave, 2003). In our study, SR are lowest during the LGM (Fig. 5j) pointing to the fact that possibly eroded shelf sediments have been transported beyond the core site. Low SR

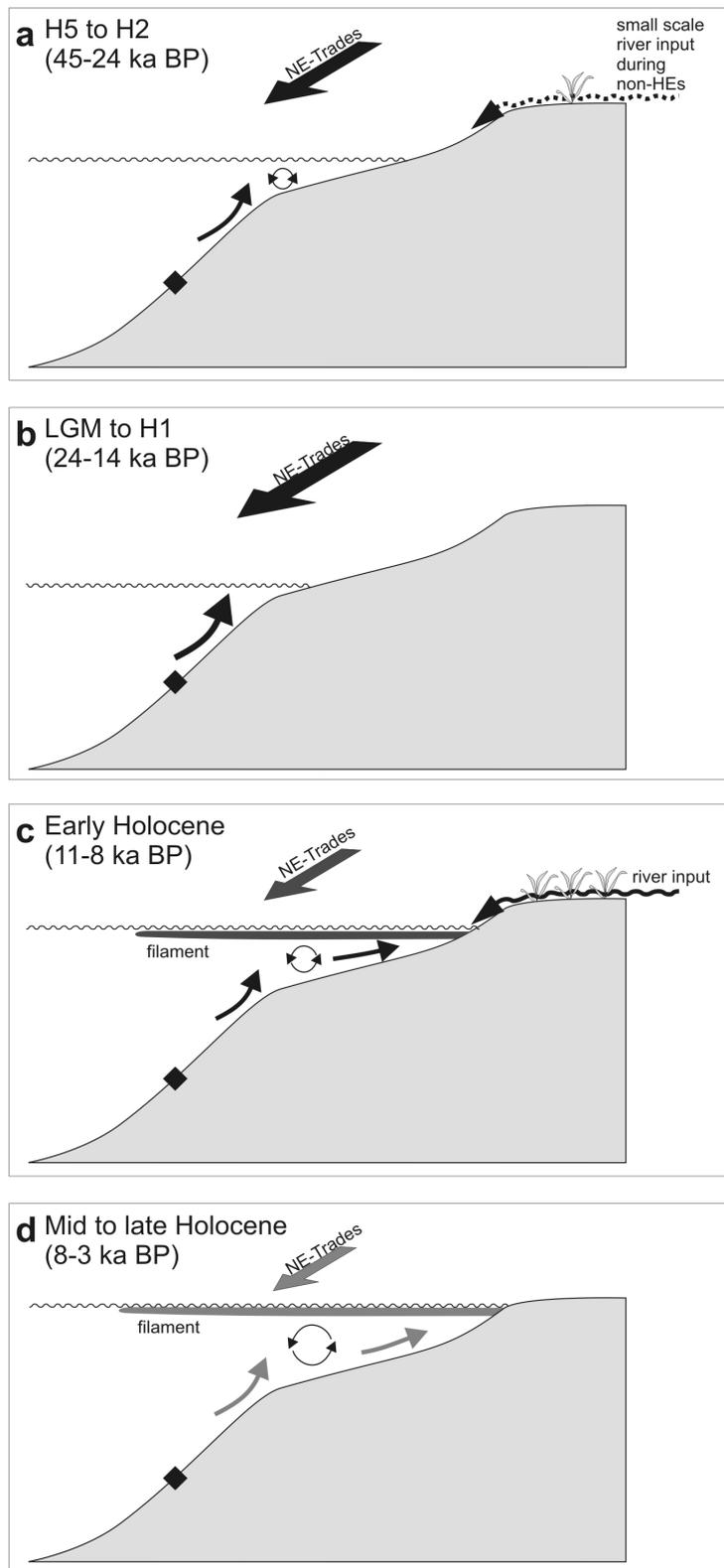


Figure 7. Schematic illustration of different sea-levels and the main environmental features off Cape Yubi (Morocco) inferred by the dinocyst record and geochemical parameters at different time intervals (a) 45 to 24ka BP, (b) 24 to 14ka BP, (c) 11 to 8ka BP and (d) 8 to 3ka BP. The black diamond represents core position GeoB 5546-2. Differences in arrow size represent the strength of contribution. Black colour represents more perennial upwelling and light grey colour stands for more seasonal upwelling. Note that horizontal and vertical proportions are not true to scale.

could also be due to a comparatively narrow shelf off Cape Yubi and thus a limited area where erosion could have taken place (Fig. 6 and 7).

Relative abundances of upwelling related dinocyst taxa suggest increased upwelling activity at HEs 5-2 and the YD. This agrees with the suggestion that African aridity during HEs and the YD is induced by a southward shift of the ITCZ associated with AMOC slowdown (Mulitza et al., 2008; Tjallingii et al., 2008). However, as upwelling off Cape Yubi is already seasonal today, a more southward position of the ITCZ during HEs and the YD should increase the upwelling seasonality at this site even more. Since our data suggest that upwelling was enhanced during glacial times, we can conclude that a southward shift of the ITCZ did not displace the northernmost border of the trade wind belt.

From the early Holocene to about 8ka BP (Fig. 7c), during sea-level rise, the Cape Yubi filament pathway gradually shifted to the core site. Nutrient recycling above the shelf and downslope productivity export were increased due to the enlarging shelf area. Bertrand et al. (2000) also suggested increased nutrient recycling during transgressions. Accumulation rate peaks of most dinocyst taxa at the early Holocene can be attributed to these factors. Additionally to these oceanic processes, an extraordinary increase of accumulation rates of *L. machaerophorum* suggests continental humidity and subsequent river input. This coincides with the period of most extensive vegetation cover during the AHP at about 9ka BP as simulated by Tjallingii et al. (2008) for the Sahara. The rising sea-level could also have led to nutrient input by erosion of soil as proposed by Scourse et al. (2005) off the Congo fan for the last deglaciation. A northward shift of the ITCZ at the onset of the AHP due to locally increased boreal summer insolation is proposed by e.g. deMenocal et al. (2000b) and Timm et al. (2008). High accumulation rates of upwelling related dinocyst taxa point to a prolongation of the upwelling season during the early Holocene. From this, we can conclude that the movement of the ITCZ to the North also shifted its associated trade wind belt further to the north.

Between about 8 to 3ka BP (Fig. 7d), the higher sea-level further favoured filament formation while nutrient recycling and downslope export of shelf productivity increased. Seasonal upwelling and stratification related dinocyst taxa point to a decrease in upwelling permanence which suggests that the winter position of the ITCZ shifted back southward. Moreover, low proportions of upwelling related dinocyst taxa point to a decrease in trade wind intensity.

4.6. Conclusions

Our record of dinocysts supported by geochemical proxies documents atmospheric and hydrographical changes during the last 45ka BP. Hereby, the local influence of sea-level induced upwelling variability could be disentangled from solar-forcing related humidity and high latitude controlled climatic changes related to HEs.

A combined interpretation of relative abundance data and accumulation rates of dinocysts enabled us to detect several interacting factors. Enhanced relative abundances of protoperidinioid cysts and *Echinidinium* spp. point to prevailing upwelling conditions during HEs of MIS3. A combination of seasonal upwelling conditions and river input is indicated by increased relative abundances of *L. machaerophorum*, especially during the B/A and the early Holocene. Accumulation rates suggest that both, upwelling conditions and fluvial input, were favourable at the same time during the B/A and the early Holocene.

The relative sea-level strongly influences the upwelling pattern off Cape Yubi. During intermediate to low sea-level in MIS3 and 2, low dinocyst accumulation rates can be explained by the coast morphology at the investigated site, which is unfavourable for filament formation and nutrient recycling on the uncovered shelf. The dinocyst accumulation rate maximum in the early Holocene can be partly attributed to rising sea-level, which leads to filament formation and enhanced nutrient recycling on the broadening shelf.

Arid conditions prevailed at Cape Yubi due to the ITCZ shifting southward during the last glacial, especially during HEs. Humid conditions occurred when the ITCZ shifted northward during the AHP. An increase in stratified conditions as suggested by our data from the mid Holocene indicates that the ITCZ then shifted back southward.

Our conclusion that marine productivity in glacial times has been as high as today although the promoting factors have been different is in agreement with other productivity studies. We conclude that records that are strongly influenced by neritic conditions have to be interpreted with respect to regional features, which in turn gives the chance to a better understanding of the mechanisms affecting palaeoproductivity.

4.7. Acknowledgements

We thank Christian Harnach for sample processing. Kenneth Mertens and Jan-Berend Stuut are acknowledged for useful and enthusiastic discussions. All data presented in this study will be available through the database PANGAEA (www.pangaea.de). This work was funded through DFG Research Center / Excellence Cluster “The Ocean in the Earth System” and is MARUM contribution No. xxx.

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5. Conclusions and perspectives

5.1. General conclusions

The dinocyst assemblages from sediments of the Benguela upwelling system (BS) and the NW African upwelling region (NWU) reflect similarities as well as remarkable ecological differences. From the results, a much broader spectrum of environmental conditions can be suggested for the NWU compared to the BS. In both regions, high relative abundances of protoperidinioid cyst species indicate perennial upwelling conditions whereas more stratified conditions are reflected by *Spiniferites* species. In the NWU, *Lingulodinium machaerophorum* is related to seasonal upwelling conditions - a species which is completely absent in the BS. Other dinocyst species which were not detected in the BS are *Gymnodinium spp.* and cysts of *Protoperidinium stellatum*, both also associated with seasonal upwelling in the NWU. Comparatively lower sea surface temperatures in the BS could be the reason for the absence of these species. Additionally, the Angola-Benguela front and the broad region of perennial upwelling in the BS might represent an ecological border for these species preventing their dispersion to the southern part of the BS (where upwelling is more seasonal). A more likely explanation is the high seasonality and variability in upwelling conditions in the northern part of the NWU. The motiles of especially *L. machaerophorum* presumably react opportunistically and develop blooms as soon as conditions are favourable.

Small scale regional factors such as river input and filament formation are resolved by the dinocyst assemblages within both regions. The importance of this sensitive reflection within the application in paleoreconstructions in upwelling regions is twofold. Environmental changes are accurately reflected and will allow detailed reconstructions. On the other hand, it is important to keep in mind that these changes could be overinterpreted when working with low resolution in time.

The use of dinocyst accumulation rate data has been shown to offer the opportunity to interpret the signals of single species independently from each other. Accumulation rate data were gathered for the northern part of the NWU where high productivity conditions off the cape locations are well reflected which makes them a reliable proxy for marine productivity. Moreover, a combined interpretation of accumulation rates and relative abundances of different cyst species help to unravel various factors which promote cyst productivity. This has been applied in a paleoreconstruction of core GeoB 5546-2 off Cape Yubi. The results show that in

addition to varying upwelling conditions, marine productivity in ocean margins can be considerably influenced by regional factors like fluvial input. These factors, in turn, are very sensitive to climatological changes. During the last 45,000ka BP, the environmental conditions off Cape Yubi varied considerably. Dry and windy conditions during glacial times were followed by more humid conditions during the African Humid Period. Productivity as suggested by TOC and dinocyst accumulation rates has been in the order of magnitude of modern times. This can be attributed to the local impact of different sea-levels on the upwelling pattern.

5.2. Future perspectives

To consolidate the newly acquired findings and to continue to improve dinoflagellate cysts as a paleoreconstruction-tool, further research within the following issues is recommended.

5.2.1. Studies on recent material

Dinocyst associations in surface sediments from the Benguela upwelling system reflect the shelf conditions. To test if this is also true for the NW African margin, the investigation of shelf-derived samples from the NW African upwelling region is needed. This is especially important for the Cape Blanc area where little is known about the differences between active upwelling and the area influenced by the giant filament. Dinocyst data from sediment traps deployed at more inshore sites or along a longitudinal gradient (like ESTOC) could additionally provide information about the preferences of upwelling related cyst species. With these results, further conclusions could be drawn about the amount of offshore and downslope transport which is a crucial aspect of paleostudies.

To obtain further insights into the factors which trigger encystment, sediment trap surveys or net studies encompassing both, cyst and motile stages of dinoflagellates are required.

About the most important recommendation which arises from this study is the dating of surface sediment samples in order to calculate dinocyst accumulation rates. As already explicated in Chapter 3, information on dinocyst accumulation rates off Cape Blanc is urgently needed to compare that region to the northern part in terms of productivity and to differentiate areas with different upwelling season lengths. As such,

dinocyst accumulation rates could also be used to quantitatively estimate and compare primary productivity within several upwelling areas on a global scale.

5.2.2. Studies on core material

Particularly the Holocene time interval of core GeoB 5546-2 comprises interesting climatic and oceanographic changes and needs extending to the present days. A dinocyst based study of a high resolution sediment record focusing on the Holocene could provide detailed information about variations in terrestrial input. For example, a combined interpretation with results of piston core GeoB 6007 with a temporal resolution between 15 and 120 years where proxies for fluvial input reflect an influence of the Mediterranean climate system (Holz et al., 2007) could be promising (for core location see Chapter 3, Fig. 1).

Data on process length variations of *Lingulodinium machaerophorum* which can be used as a proxy for sea-surface salinity and temperature (see Appendix 4) are already collected for core GeoB 5546-2 and will be applied within a comparative study in the nearer future.

Continuing insights could also be expected by the investigation of a core covering a longer time span of the last glacial period where several humid periods have been suggested by Tjallingii et al. (2008). Here, variations of the dinocyst species composition could add supplemental information about fluctuations in the amount of fluvial input compared to continental aridity.

A novel method to reconstruct bottom water oxygen contents by use of a degradation index based on dinocyst accumulation rates is presented in Appendix 3. This index allows reconstructions of the oxygen content of bottom waters which could improve the quality of estimates of carbon burial in the ocean as well as deep water ventilation changes.

5.2.3. Combination with additional proxies

In the present study, the potential of dinocyst data has been advanced by a combined discussion with sedimentological and geochemical proxies. However, information about the spatial distribution of these proxies in recent sediments is scarce. In the future, a systematic investigation of surface samples on TOC, sedimentological proxies for terrestrial input or element ratios could help to fill this gap and also to calibrate these proxies among another.

Palynological surveys on pollen provide information on continental climate. A number of joint studies of pollen and dinocysts has already been successfully applied in paleoreconstructions (e.g., Marret and Turron, 1994; Marret et al., 2008; González et al., 2008; Bouimetarhan, 2009). Off NW Africa, pollen downcore records could refine the knowledge on vegetation shifts and on - in combination with dinocyst data - the variations in hydrographical conditions.

5.3. References

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Appendix 1. Count data of organic-walled dinoflagellate cysts from surface sediments samples of the NW African upwelling region (for abbreviations see Chapter 3).

GeoB	Lon	Lat	depth	cruise	device	total dinocysts	total cysts/g	B spp	E acu	E del	E spp	E tra
4024-1	27.678	-13.432	95	VH96/1	boxcorer	197	490.78	13	2	0	23	4
4025-2	27.748	-13.488	504	VH96/1	boxcorer	204	2025.82	104	3	0	20	3
4026-1	27.808	-13.543	990	VH96/1	boxcorer	1015	10150.00	17	1	0	42	9
4213-1	29.697	-11.078	1547	M37/1	MUC	208	520.00	12	0	0	2	2
4216-2	30.632	-12.397	2325	M37/1	MUC	196	489.51	16	0	0	0	4
4225-3	29.275	-11.782	1281	M37/1	MUC	220	550.00	8	0	2	0	0
4226-1	29.320	-11.833	1400	M37/1	MUC	252	315.00	32	0	0	4	0
4230-1	29.128	-12.597	1316	M37/1	MUC	282	714.29	22	2	0	2	2
4231-2	29.088	-12.555	1207	M37/1	MUC	261	823.86	24	0	0	0	6
4233-2	28.975	-13.330	1303	M37/1	MUC	288	480.00	12	0	0	3	0
4236-2	28.783	-13.095	1030	M37/1	MUC	349	1743.26	8	0	0	5	3
5530-3	29.303	-17.897	3985	M42/4	MUC	313	1565.00	60	12	2	150	14
5533-1	27.682	-17.693	3251	M42/4	MUC	255	1428.41	57	7	2	42	4
5536-3	27.537	-16.135	3456	M42/4	MUC	1316	6580.00	199	26	5	606	44
5539-2	27.537	-14.355	2202	M42/4	MUC	240	2392.82	14	0	0	6	0
5540-3	27.535	-14.175	2035	M42/4	MUC	393	3926.07	80	3	0	28	3
5548-3	27.992	-13.518	1162	M42/4	MUC	462	4610.78	26	0	0	23	1
5549-2	27.978	-13.695	1454	M42/4	MUC	260	2597.40	12	0	0	14	3
5553-2	28.277	-14.645	3397	M45/5	MUC	479	2395.00	108	3	1	140	6
6005-1	30.880	-10.897	1781	M45/5	MUC	1262	12620.00	22	0	0	6	5
6006-2	30.868	-10.630	1282	M45/5	MUC	450	13500.00	11	0	0	1	1
6007-1	30.852	-10.267	899	M45/5	MUC	1928	19280.00	44	4	0	38	6
6008-2	30.845	-10.098	355	M45/5	MUC	751	15020.00	25	2	3	31	20
6009-1	30.682	-10.275	579	M45/5	MUC	2803	28030.00	47	2	0	26	11
6010-1	30.250	-10.083	406	M45/5	MUC	414	4140.00	14	2	0	11	3
6011-2	30.315	-10.288	993	M45/5	MUC	677	6770.00	28	5	1	25	5
7413-2	20.647	-17.845	508	P272	MUC	284	710.00	74	6	4	102	2
7414-1	20.718	-18.000	1014	P272	MUC	177	885.00	60	2	0	51	4
7415-1	20.805	-18.262	1911	P272	MUC	451	4510.00	100	5	7	153	1
7420-1	24.165	-16.788	676	P272	MUC	348	3480.00	110	5	0	45	9
7423-2	24.338	-17.070	1624	P272	MUC	726	7238.29	14	3	1	80	16
7424-1	24.210	-16.843	1063	P272	MUC	395	1969.09	141	11	0	38	3

Dinocyst count data NW Africa

Appendix 1. (continued)

GeoB	G cat	G noll	I acu	I pat	I sph	I spp	L mac	L oli	N lab	O cen	O isr	O jan	P ame	P dal	P kof	P mon	P sch
4024-1	9	3	0	0	1	1	93	2	0	6	0	0	1	0	3	0	1
4025-2	1	1	8	0	0	1	27	0	2	7	0	0	1	0	0	0	1
4026-1	1	0	6	4	0	3	786	0	1	33	4	0	1	2	1	0	3
4213-1	18	0	0	2	0	2	134	0	0	8	0	6	0	0	0	0	4
4216-2	4	0	0	4	0	0	104	0	0	4	0	0	0	0	8	4	24
4225-3	52	0	8	0	2	0	70	0	2	12	0	2	0	0	4	2	4
4226-1	40	0	8	0	0	4	56	0	0	28	0	0	0	0	0	8	8
4230-1	62	0	20	2	0	0	62	0	2	10	0	0	0	0	0	2	10
4231-2	30	0	0	6	3	0	114	3	0	15	0	0	0	0	0	9	6
4233-2	3	0	12	3	6	0	150	0	9	3	0	0	0	0	3	9	0
4236-2	1	0	9	7	3	0	185	0	1	20	0	1	0	0	1	6	2
5530-3	4	8	0	0	1	0	6	2	0	0	2	0	6	0	1	0	4
5533-1	3	1	0	2	0	1	57	1	0	8	1	0	8	0	1	0	2
5536-3	15	4	3	12	1	1	107	0	2	8	2	0	14	0	5	0	8
5539-2	0	2	3	0	0	0	185	0	0	6	0	0	3	1	0	0	1
5540-3	1	1	9	1	3	1	149	0	0	18	0	0	5	3	4	0	6
5548-3	0	0	6	2	0	1	327	0	0	18	0	0	1	1	0	0	7
5549-2	0	0	11	0	0	4	164	0	0	12	0	0	2	0	0	0	3
5553-2	1	5	1	3	1	0	66	1	0	5	1	0	11	0	4	0	3
6005-1	40	33	1	0	0	3	1052	1	0	17	0	1	0	0	5	0	56
6006-2	7	3	0	0	1	1	396	0	0	7	0	0	0	0	2	0	11
6007-1	38	29	0	0	0	2	1489	2	2	28	2	0	2	0	48	0	73
6008-2	11	42	0	0	0	0	453	3	0	11	1	0	5	0	51	0	31
6009-1	24	13	4	4	0	1	2354	7	1	72	7	9	1	0	33	0	34
6010-1	9	18	0	0	0	1	275	0	0	40	1	2	1	0	7	0	1
6011-2	29	39	3	4	0	2	378	1	1	59	6	1	2	0	19	0	15
7413-2	2	2	2	0	0	2	20	2	0	0	2	0	0	0	2	0	4
7414-1	3	1	1	0	0	0	10	1	0	1	0	0	3	0	0	0	3
7415-1	1	0	2	6	0	1	54	0	0	8	1	0	12	0	3	0	3
7420-1	0	0	4	2	0	1	68	4	1	17	0	0	9	0	1	0	2
7423-2	0	1	1	1	0	0	455	0	0	25	0	1	1	0	10	0	16
7424-1	3	5	3	1	2	1	105	1	2	12	2	0	2	1	0	0	4

Appendix 1. (continued)

GeoB	P zoh	Py re	S mem	S mir	S nep	S pac	S qua	S ram	S spp	S ste	T app	V cal	reworked
4024-1	0	3	0	1	1	0	6	0	1	21	1	1	1
4025-2	1	0	0	0	0	0	12	3	2	4	3	0	0
4026-1	0	0	1	1	0	0	4	2	9	69	14	1	0
4213-1	0	0	0	0	0	0	0	0	0	18	0	0	2
4216-2	0	0	0	0	4	0	0	0	0	16	0	4	0
4225-3	0	0	0	0	6	0	2	0	4	38	2	0	0
4226-1	0	0	0	0	8	0	0	0	0	56	0	0	4
4230-1	0	0	0	0	16	0	6	0	2	62	0	0	0
4231-2	0	3	0	0	3	0	3	0	6	24	6	0	0
4233-2	0	0	0	0	0	0	6	3	9	45	12	0	0
4236-2	0	1	1	0	2	0	2	6	14	63	7	1	0
5530-3	0	1	0	0	1	1	13	0	5	16	4	0	1
5533-1	0	0	0	1	5	1	18	0	2	12	18	1	1
5536-3	0	0	0	1	10	11	40	0	37	103	50	2	0
5539-2	0	0	0	0	1	0	3	0	1	12	2	0	0
5540-3	0	0	0	0	1	0	7	3	3	60	3	1	0
5548-3	1	0	0	0	0	0	3	0	7	37	1	0	0
5549-2	1	0	0	1	1	0	0	0	6	25	1	0	0
5553-2	0	0	0	0	17	1	44	3	7	12	32	3	0
6005-1	0	0	0	0	7	0	3	0	7	2	1	0	0
6006-2	0	0	0	0	2	0	0	0	3	1	3	0	0
6007-1	0	2	2	2	20	2	14	7	45	0	27	0	1
6008-2	2	0	1	0	5	1	12	4	23	0	13	1	3
6009-1	0	3	4	7	14	3	14	9	64	7	26	2	0
6010-1	0	0	0	2	5	0	2	2	8	1	9	0	0
6011-2	0	0	0	4	6	3	3	5	22	4	7	0	0
7413-2	2	0	0	0	0	2	24	0	0	20	10	0	0
7414-1	0	0	0	0	0	0	8	0	1	9	19	0	0
7415-1	0	0	0	0	4	6	24	0	8	40	11	0	0
7420-1	0	0	1	0	15	2	18	0	2	15	14	3	2
7423-2	0	0	0	1	1	0	10	0	9	56	23	1	1
7424-1	0	0	0	0	11	2	30	0	1	6	7	1	0

Appendix 2. Count data of organic-walled dinoflagellate cysts from samples of core GeoB 5546-2 off Cape Yubi (Chapter 4).

depth [cm]	sample weight [g]	sample vol [l]	slide vol [ml]	total dinos	E spp	E spp	E acu	E del	E tra	L oli	P kof	P sch	P ame	P cla
3	1.000	0.0005	0.1	2393	33	25	5	2	19	11	7			
17	1.000	0.0005	0.1	1613		6		1	13		3			
32	0.997	0.0005	0.1	1100	40	14			6		2			
48	1.003	0.0005	0.1	1164	35	9	1		13		5			
63	0.998	0.0005	0.1	1003	52	11			22		13	3		
83	1.004	0.0005	0.1	579	40	4	1	1	8		5	1		
98	1.000	0.0005	0.1	1393	128	31	4		24	11	9	2	4	
113	1.002	0.0005	0.1	1754	98	29	4	4	23		18	2		
118	1.000	0.0005	0.1	1115	45	13	2		8	9	6	5	3	1
133	1.001	0.0005	0.05	1140	56	6	1		9		10	2		1
149	1.003	0.0005	0.05	985	35	1	2		3		7	1		
163	1.004	0.0005	0.05	990	52	5	1		4	6	10			
178	1.004	0.0005	0.1	708	68	10		4	6					
194	1.004	0.0005	0.05	626	33	6			7	6				
209	1.003	0.0005	0.05	683	53	14	2		10	10		1		2
224	1.000	0.0005	0.2	814	84	18	4		14	4	2	4		2
238	1.003	0.0005	0.05	687	79	11		1					1	
253	1.002	0.0005	0.05	771	73	15			6	8	1	1		
263	1.001	0.0005	0.1	901	61	10			7	7	4	1		
278	1.005	0.0005	0.1	890	67	7			6	9	13	2		
293	1.000	0.0005	0.1	1649	33	6		2	5	3	5	3		
308	1.001	0.0005	0.2	872	80	4			4		2			
323	1.003	0.0005	0.2	1016	102	4			4					
338	1.001	0.0005	0.1	924	88	2			1		1			
373	1.001	0.0005	0.1	992	53				1		1	1		
378	1.004	0.0005	0.1	1061	131	7	1		3		1			
388	1.003	0.0005	0.1	989	49	6					1		1	
393	1.000	0.0005	0.1	990	87	13			6		2	1		
398	1.000	0.0005	0.1	1070	140	3			1		3			
403	1.000	0.0005	0.1	1056	101	4			1	1	2			
408	1.000	0.0005	0.2	1148	130	6	2		2					2
413	1.002	0.0005	0.1	1126	115	13	3					1	2	1
423	1.002	0.0005	0.2	1062	70	20				2	2			
428	1.004	0.0005	0.1	1080	81	6	3	1			3		2	
443	1.000	0.0005	0.2	1090	68	4	2							
448	1.008	0.0005	0.1	1138	77	2	3	1	3		1			
453	1.000	0.0005	0.1	1107	40	9	5	1	2			1		
458	1.000	0.0005	0.2	1190	42	10			4		2			
463	1.003	0.0005	0.1	1372	99	7	1		2	1	2			
468	1.000	0.0005	0.1	1281	62	8	3		4	1				1
473	1.001	0.0005	0.2	1180	16	6		2	12					
478	1.008	0.0005	0.2	1348	212	6	2	2	4				2	
483	1.002	0.0005	0.2	1316	90	26		4	8		2			
493	1.002	0.0005	0.2	1346	90	20			6	2	2			
498	1.004	0.0005	0.1	1262	102	23	3		3	2				1
503	1.000	0.0005	0.1	1227	61	11	2		5		1			
508	1.000	0.0005	0.2	1298	60	8	4		2		2			
513	1.000	0.0005	0.1	1325	141	18			7		1			
518	1.000	0.0005	0.1	1244	84	4	1		1			1		
523	1.003	0.0005	0.2	1270	72	2					4			
528	1.000	0.0005	0.1	1404	124	5	1		4	1	2			1

Appendix 2. (continued)

depth [cm]	P leo	P mon	S nep	S qua	P ste	T app	V cal	X xan	B spo	G cat	G nol	I acu	I par	I pat	I pli	I sph
3	1	2	14	18	95	40	3	13		8		13			9	
17		3		7		9		2		7		22	1	1	7	5
32		4	7	8	1	17		1		5		11		10	2	3
48		2	5	12	7	19		4		7	3	3		12	3	9
63		3	10	9	18	12	5	10		6		2		10		7
83	2		6	3	10	14	2			3		3		4	1	5
98	5		9	15	51	19	3	17	2	11		1		10	4	
113	4	6	6	24	46	9	1	30		11	1	2		7		3
118	1		3	4	22	4	5	9		10		2	1		1	
133	6	2	7	7	63	12		4		8		2		6		
149	20	1	5	20	12	2		17		2		1		1		
163	4	2	6	17	21	7		22		16	2	2		2		
178			4	22		8	2	20		24			2	2		
194	1	1	8	12	4	4	1	5		11			1	2		
209	2	3	10	17	8	3		37		13		3		1		
224			4	4	8	4		72		4			2			
238			3	22		4		9		10		1				
253	1	2	5	21		3		25		2						
263			5	14	1	3	2	36		10		4				
278			4	22		1	3	32		14		1		1		
293		1	9	28	1	4	1	35	1	7		3				
308			4	14		2		12		8	2					2
323				18		4		2		16		2				
338			2	4		2				10	5	2		1		
373		1	3	4				1		5	2	1		3	1	
378	1		5	5		1	1		1	12	5			3		
388	1		4	7		1				8	3	1		2		1
393		1	6	8		1		2		8	5	1		1		
398	2	1	4	5						9	3	3		5		
403	1	1	1	5		1	1			5	7	2		4		1
408	2	4	4	22		2		2	2	22	12			2		
413		6	1	5		3		5		23	5	2		3		
423		6	4	16		6				28				2		
428		2	2	6		1				11	2			3		
443			2	2				2	2	4	2	2		2		
448	1	3	3	2				4		8	1			3		
453	2	3	1			2			2	2	1	1		3		
458	2	4	2	4						6	2	2		6		
463		6	6	15		1				12	5	1		5		1
468			1	10		3				8	2			2		1
473		2	2	8		2		4		6	2	2		2		
478		12	6	8				2		28				2		
483	4		6	26		2		2		30	4	2		2		2
493	2	4	6	10			2	32		14	6					
498	2	6	5	3		1		7		10	4					1
503		14	2	4		1		3		3	2					
508	2	4	2	18				14		34	2					
513	3	3	7	5		3		11		19	2	1				1
518		1		9		3		3		11	3					
523		4		8		2		2		24	8					6
528	1	1	6	18		3				18	2	1		3		

Appendix 2. (continued)

depth [cm]	I str	L mac	N lab	O cen	O isr	O jan	P dal	P zoh	Py re	S spp	S del	S mem	S mir	S pac	S ram	T van	reworked
3	4	1968	1	64				1		27		1	1		2		
17		1440	3	30		2				17							
32		827	2	29		2				35		1	1		8		
48		785	1	61		2		2		56	4	4	2		2		
63		576	3	49		3		3		41	1	7	1				
83		236		42						22							
98		775	2	18		1				37		2		1		1	
113		1104		12		3		1	1	71		5			3		
118		698		7					1	15			2	1	1		
133		628		10		2				26					6		
149		545		2		2				8							
163		465	1	3		1				12		1			2		
178		136		6		2				30		2			4		
194		116	1	6						11					2		
209		51	3	7						14					1		
224		68	6	22						18		2		6	14		
238		36		5				2		25				2			
253		57		4				1	1	37				2			
263		172		8						21				2	7		
278		118	2	13						19							
293		881		10		5				17					3		
308		50	4	22					2	34					10		
323		106		32					4	66		4			6		2
338		54	1	27	3	2				36			1		6		1
373		53	2	18	2	1			3	72	2			1	15		
378		48		20	1			1		53	1	2			2		
388		48		19						51	1	1		1	7		
393		25		5	3	2				27							
398		47		8	1	1				36	1	1					
403		37	1	10	1	1			3	49			1		9		
408		38	2	10			2			50	4	2			8		
413		58	1	9	1	1			1	31	4			2	4		
423		22		10				4		18	4						2
428		41		11	1		2		1	37		3			4		1
443		24		12			6			62		2			6		
448		31		7	2	1	2	3		78	2	1			3		
453	2	33	1	5	3		1	2	5	64	5	2		1	2		
458		20		14	2					136	2		2	2	10		
463		39		9	3		2	2	2	197	2	5	4	2	15		
468		46		9	3				5	162	1	4		5	4		
473		22		12	2				4	122					6		
478		32		6	4			2		50		4		2	6		
483		26		12	2	4				74		4			18		
493		32		8	2	2		2	4	104	4	2			4		
498		21		7				3		56	1	1	2	1	1		
503		9		4	1					92	3	3					
508	2	28		6						82	6	2			4		
513		28		8	1	1				37	1	1					
518		21	2	19						43		2					
523		16		30		2			4	40							
528		28		16	1		1			99	4	3	1		4		

Appendix 2. (continued)

depth [cm]	sample weight [g]	sample vol [l]	slide vol [ml]	total dinos	B spp	E spp	E acu	E del	E tra	L oli	P kof	P sch	P anne	P cla
533	0.997	0.0005	0.1	1363	73	25			1					
538	0.998	0.0005	0.2	1372	64	32	2		4					
543	1.000	0.0005	0.1	1436	109	17	2		5		1			
548	1.000	0.0005	0.1	1318	43	3	3		5		1			
558	1.000	0.0005	0.1	1326	46	6	6		2		4			
563	0.989	0.0005	0.2	1486	72	12	4		4		4			
568	0.998	0.0005	0.1	1374	51	5	2		1	2	3			
573	1.003	0.0005	0.2	1428	48	4			4		2			
578	1.005	0.0005	0.1	1422	103	1			1	2	10			
583	1.000	0.0005	0.1	1383	59	7	3		2		1			
588	0.999	0.0005	0.2	1412	40				6		2			
593	1.002	0.0005	0.1	1383	44	1	1				4			
598	1.000	0.0005	0.2	1486	48	4	2		6		16			
603	1.003	0.0005	0.2	1540	58	14	2		4		18	2		
608	1.000	0.0005	0.2	1504	40	12			4		16			
613	1.002	0.0005	0.2	1530	84	8			6		12			
618	1.000	0.0005	0.2	1468	34	2			2		4			
623	1.005	0.0005	0.1	1491	86	6			1	1	3	1		
628	1.002	0.0005	0.2	1624	56	2			2		4	2		
633	1.006	0.0005	0.1	1475	26	2	1		3		2			
638	1.006	0.0005	0.1	1771	161	6			6	5	6	1		
643	1.007	0.0005	0.2	1644	84		2		4	2	6	4		
648	0.999	0.0005	0.1	1513	73	11	2		1		4			
653	0.999	0.0005	0.2	1650	50	2			4		2			
658	1.000	0.0005	0.2	1574	84	2	4				8			
663	1.009	0.0005	0.2	1700	88	14	2	4	6		6			
668	0.998	0.0005	0.2	1712	70	6	2	4	4		12			
673	0.989	0.0005	0.1	1595	104	6	5		4					1
678	0.994	0.0005	0.2	1652	110	4	2			2	2			
683	1.009	0.0005	0.1	1693	112	6	10		1					
688	1.000	0.0005	0.1	1610	61	16	8	1	2					
698	0.998	0.0005	0.1	1625	61	3	3		4					
708	0.997	0.0005	0.1	1652	86	1	1		2					
713	1.000	0.0005	0.1	1716	70	3					2	2	1	
718	1.001	0.0005	0.1	2050	101					1	2	1		
723	1.002	0.0005	0.1	2019	32						1			
728	1.000	0.0005	0.1	2695	55	2			3		6			
733	1.000	0.0005	0.1	1826	43	1			2		1			
738	0.999	0.0005	0.1	2060	47	2	2				2			
743	1.003	0.0005	0.1	2221	81	2	3	1	1		1			
748	1.003	0.0005	0.1	1979	59	2	1		1		6			
753	1.000	0.0005	0.1	2254	60	4	1		5	1	2			
758	1.004	0.0005	0.1	1809	36	2	1				3			
763	0.998	0.0005	0.2	1868	48	4					6			
768	1.003	0.0005	0.1	1961	61	3			4		10	2		
773	1.003	0.0005	0.1	1974	60	4	2		1		6			
778	0.996	0.0005	0.1	1849	38	4	2		2	4	2			
783	1.002	0.0005	0.1	1926	49	3	5		3			4		
798	0.999	0.0005	0.1	1887	40	4					2	2		
813	1.001	0.0005	0.2	2022	48	6					14			
833	1.000	0.0005	0.4	2026	68	4				8	4			

Dinocyst count data core GeoB 5546-2

Appendix 2. (continued)

depth [cm]	P leo	P mon	S nep	S qua	P ste	T app	V cal	X xan	B spo	G cat	G nol	I acu	I par	I pat	I pli	I sph
533		1	4	13		1	2			21	5	1		3		
538		2	2	6		8	2			32	4					
543	5	7	9	11			1			23	2			3		
548	2	1	1	17		2		1		16	4			1		
558	1	3	4	16		2		5		18	1			6		
563	4			32		2		10		16		2		10		2
568	3		5	10		1	3			14	2					
573		2	2	20				4		6		2		2		
578	1	1	4	10		1	1			8						
583	1	1	3	19		2	1	2		4	1	1		2		1
588		4	4	14			2	8		4				4		
593	2	2	3	12		2	3	2		6				6		
598		4	4	8		4	2	4		10	2	2		8		4
603		2	6	14		2	2			2				8		
608		2	2	20						10				8		
613		2	6	14		2	2			12	2			12		
618			2	28			10	4		18				14		2
623	2	1	8	27			3	4		6				9		
628		2	4	56				8		14		2		14		
633		1	6	29		2	1	6		1	4	1		5		
638	1	1	16	67		3		5		25	10	4			3	
643	4		30	40		2	10	2		2				18		2
648		3	8	12		1	2	4		6		1		3		
653		12	2							8				4		2
658		4	6	18		2				12	2			2		
663	2	2	8	32		2		2		14	2			2		
668	2	6	22	30		4	2	2		24	2					
673	1	1	9	13			6	3		17	1			2		1
678	2		10	32		4	6	2		14	8			2		2
683	3	1	11	41		2	4	5		12	1	1		1		1
688		3	6	18		8	4	4		10	1			2		2
698		1	1	14			1	6		1				3		1
708		1	2	16		1	1			7	1	1		1		
713			3	10		1				20					3	
718	1		4	8		7	4	1		7		1		3		1
723			3	5		1				5				5		
728		2	5	18		2	2	1		3	2			4		1
733	1	1	2	14		1	2			7	1			5		
738		1	6	10		5	4			9				4		
743		1	10	7		1				1	2			2		
748	2	1	6	7		3	8	3		11				4		
753	1	2	4	14			3			2	1					
758		1	11	7			6	2		9	2			1		
763	2	2				2	6	4		6				2		
768	1	1	4	3			1	2		7	4			2		
773	4	1	8	23		4	13			23	13			3		1
778			2	12				2		19	9					1
783	1	1	1	5		4	5	4		13	3					
798	2		9	12		1	6	1		6	1	1		5		
813	2		10	20			12	4		22	2		2	10		2
833			4	28		4		8		44					4	

Appendix 2. (continued)

depth [cm]	I str	L mac	N lab	O cen	O isr	O jan	P dal	P zoh	Py re	S spp	S del	S mem	S mir	S pac	S ram	T van	reworked
533		24		11		1		1		99	2	3	1		5		
538		36		20	2	2				74		2			2		
543		30	1	14						103		1		1	5		
548	1	27		8				1		66	2	2	1		14		1
558		30		5	1					42		3	2		7		
563		78		14				2		74	4	2	2		10		
568		46		9				3		70		2	1	1	4		
573		70		2						94		4	4		12		
578		42	1	12						57			3	2	6		
583		32		7				2		54	1		1	4	6		
588		56		14						74					4		
593		68		8						23	1	1			8		
598		60		14	2	2				70	2			2	10		
603		52		10		2		4		116	4	6			6		
608		42		10						100	10		2		10		
613		62		16						48	6				10		
618		40		10				4		50	2				4	2	
623		23		5						49	6	1	1		2		
628		70		18						84	6	6			18		
633		37		11		1				59	2		2		7		
638	1	49	4	13						78		9	2		19		
643	2	60		10						58	2	2			12		
648		31		6						35	2	2	1		9		
653		88		24				2	2	120	6	2	4	6	4		
658		30		12	2		4			56		2			8		
663		60		28	2		2			82	4	2			8		
668		78	2	8						82		2	2	2	8		
673		26		3		1		2		37	1			1	4		
678		54		8						20	2	2			8		
683		52		7				1		43	3	1		1	6	1	
688		39		10						26	5		2		6		
698		30		9		1		1		75	1	3	1	1	8		
708		33		8						65		2			7		
713		26		13						104		3		1	28		
718		49	2	11	1		1	1		385	6	5	1		10		
723		27		6				1		467	8	3			9		
728		34		13				1		1028	19	10	9		19		
733		19		8				1		234	4	4	2	1	6		
738		22		8						435	8	6	5	1	7		
743		33		4				1		575	3	1	5				
748		44		7						305	4	4	1		4		
753		48		9				1		566	7	3	3	1	10		
758		16		8				1		174	1	4	1		7		
763		40		10						198		4	2		6		
768		34		6		2		1		263	5	3			5	1	
773		28		8		4		1	2	199		7	1	1	11		1
778		19		2	1					159	2	5			8		
783		25		8		1				196		5	3		21		
798		63		15						117					4		
813		122	2	14						84	2	2	2		14		
833		68		20						92					4		

Appendix 3

Selective preservation of organic-walled dinoflagellate cysts as a tool to quantify past net primary production and bottom water oxygen concentrations

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Marine Geology (2007), 237(3-4): 109-126

doi: 10.101016/j.margeo.2006.10.023

(received 18.11.2005, received in revised form 5.9.2006; accepted 1.10.2006)

Abstract

To understand the role of the ocean within the global carbon cycle, detailed information is required on key-processes within the marine carbon cycle; bio-production in the upper ocean, export of the produced material to the deep ocean and the storage of carbon in oceanic sediments. Quantification of these processes requires the separation of signals of net primary production and the rate of organic matter decay as reflected in fossil sediments. This study examines the large differences in degradation rates of organic-walled dinoflagellate cyst species to separate these degradation and productivity signals. For this, accumulation rates of cyst species known to be resistant (R-cysts) or sensitive (S-cysts) to aerobic degradation of 62 sites are compared to mean annual chlorophyll-*a*, sea-surface temperature, sea-surface salinity, nitrate and phosphate concentrations of the upper waters and deep-water oxygen concentrations. Furthermore, the degradation of sensitive cysts, as expressed by the degradation constant k and reaction time t , has been related to bottom water $[O_2]$. The studied sediments were taken from the Arabian Sea, north-western African Margin (North Atlantic), western-equatorial Atlantic

Ocean/Caraibic, south-western African margin (South Atlantic) and Southern Ocean (Atlantic sector).

Significant relationships are observed between (a) accumulation rates of R-cysts and upper water chlorophyll-*a* concentrations, (b) accumulation rates of S-cysts and bottom water [O₂] and (c) degradation rates of S-cysts (*kt*) and bottom water [O₂].

Relationships that are extremely weak or are clearly insignificant on all confidence intervals are between (1) S-cyst accumulation rates and chlorophyll-*a* concentrations, sea-surface temperature (SST), sea-surface salinity (SSS), phosphate concentrations (P) and nitrate concentrations (N), (2) between R-cyst accumulation rates and bottom water [O₂], SST, SSS, P and N, and between (3) *kt* and water depth. Co-variance is present between the parameters N and P, N, P and chlorophyll-*a*, oxygen and water depth. Correcting for this co-variance does not influence the significance of the relationship given above.

The possible applicability of dinoflagellate cyst degradation to estimate past net primary production and deep ocean ventilation is discussed.

Keywords: dinoflagellate cysts, early diagenesis, organic matter, preservation, oxygen

1. Introduction

The fate of organic matter (OM) in the ocean has intrigued scientists over years. Especially in the last decades the role of the ocean within the global carbon cycle has been subject of intense focus as the concern grows about the possible effects of industrial-induced atmospheric *p*CO₂ increase on global climate. To understand the role of the oceans, detailed information is needed on key-processes within the marine carbon cycle such as bio-production in the upper ocean, especially primary production, the export of the produced material to the deep-ocean, the storage of carbon in sediments and the redistribution of carbon from the ocean to the atmosphere. The present-day marine net global production of phytoplankton has been estimated to be more or less comparable to the production of land plants (ocean ~ 45-50 Gt C year⁻¹, land plants about 45-68 Gt C year⁻¹; Longhurst *et al.*, 1995; Cao *et al.*, 2005). Although estimates of the above mentioned processes are thought to give more or less adequate results for the modern environments, quantification of these processes in the past is largely hampered by the

difficulty to separate past bio-productivity signals from those induced by (early-) diagenetic processes. As results, separating “export productivity from diagenesis” forms a key-target of world-wide operating research programs (e.g., IMAGES, JGOFS and WCRP).

Degradation of OM in surficial sediments occurs by either aerobic or anaerobic pathways. After oxygen is consumed, a series of electron acceptors are used by bacteria to decompose organic compounds in a sequence that depends on the yield of metabolic free energy (e.g., Jørgensen, 2000; Sun et al., 2002). Studies on natural diffusion-limited, oxidation phenomena, often referred to as “burn-down” events as well as laboratory experiments, reveal that early aerobic diagenesis is highly selective and that the rate of degradation with respect to the concentration of labile organic matter seems to be a typically first-order process. (e.g., Hedges and Prahl, 1993 and references therein; Cowie et al., 1995; de Lange, 1998; Prahl et al., 2003). The rate of degradation of a given concentration of labile organic matter component (G) can be expressed as $dG/dt = -kG$ where t is the reaction time and k is the first-order decay constant (Hedges and Prahl, 1993). This equation can be integrated between the boundary conditions $t = 0, G = G_0$ and $t \rightarrow \infty$ to obtain $G_t = G_0 \exp^{-kt}$. Hence, degradation depends on the lability of the OM expressed by the constant k , and the reaction time t .

Recently, Versteegh and Zonneveld (2002) suggested a method to separate production and preservation signals as archived in fossil sediments by using the different lability of OM components in relation to aerobic degradation. Their studies of post-depositional aerobic OM degradation at natural oxidation fronts in late Quaternary sediments of the Madeira Abyssal Plain f-turbidite, the mid-Holocene Eastern Mediterranean S1 sapropel and the modern Arabian Sea Oxygen Minimum Zone (OMZ) and surrounding sediments, show that the ranking of different OM components, with respect to their degree of degradation, is similar in all studied regions and time intervals. End-members on this scale of lability are groups of organic-walled dinoflagellate cyst (dinocysts) species (Zonneveld et al., 1997, 2001). Versteegh and Zonneveld (2002) concluded that concentrations of components resistant against degradation within (fossil) sediments are a reflection of the initial export production (with export production being the amount of material exported from the photic zone prior to degradation) of the component whereas the final concentrations of more labile components are the result of their export production and the aerobic degradation process within the water column and the sediments. Variability in accumulation rates of resistant components can therefore be

used as proxy to reconstruct past component production by assuming minimal degradation within the water column. The rate of (post-depositional) decay (kt) can be calculated using the stable ranking of the components with respect to their lability.

Here we aim to develop this method further and discuss if this method can be used to quantify past productivity and the rate of degradation. For this, we concentrate on dinocyst species which form the end members of the “lability ranking”. Dinoflagellates are a diverse group of eukaryotic, primarily unicellular organisms with two distinctive flagella which give the organisms a (species-) characteristic spiral motion. Many planktonic dinoflagellates show diel vertical migration as result of endogenous rhythms and their geotactic and phototactic (e.g., Anderson and Stolzenbach, 1985; Lieberman et al., 1994; Kamykowski et al., 1998). Although species dependent, their migration ability is limited to several meters only, as result of their small size (the majority of species have sizes between 10-60 μ m). Together with diatoms and coccolithophorids, dinoflagellates constitute the majority of marine eukaryotic phytoplankton and are, therefore, important primary producers. Fossilizable dinocysts are thought to be formed during the sexual life-cycle of dinoflagellates. During formation they lose their flagella and sink through the water column most probably as part of faecal pellets, aggregates and/or marine snow (Mudie, 1996). Field studies reveal that maximal cyst formation occurs during, or just after periods of maximal vegetative cell division (e.g., Ishikawa and Taniguchi, 1996; Montresor et al., 1998; Kremp and Heiskanen, 1999; Godhe et al., 2001; Matsuoka, 2001). The cyst species that have been classified as resistant against aerobic decay by Versteegh and Zonneveld (2002; R-cysts) are all able to photosynthesize although most, if not all of them are thought to be mixotrophic (Schnepf and Elbrächter, 1992). It is assumed that their vegetative production is positively influenced by enhanced availability of nutrients and/or trace elements when other biologic and a-biotic factors remain constant. Dinocysts that are extremely sensitive for aerobic decay (S-cysts) are found, or thought, to be heterotrophic. Their vegetative growth is likely enhanced as more prey is available when other factors being equal. To investigate if cyst production of both groups of dinocysts can be related to net primary production or other environmental parameters we correlated cyst accumulation rates of S-cysts and R-cysts with mean annual chlorophyll *a* concentrations, mean annual sea-surface temperature (SST), mean annual sea-surface salinity (SSS), mean annual nitrate concentrations [NO₃], and mean annual phosphate concentrations [PO₄] of the upper waters at the sampling sites (Fig. 1).

To investigate if the rate of decay of S-cysts might be useful to reconstruct ventilation of the deep-ocean, we correlated their accumulation rates as well as the degradation of S-cysts expressed by the “ kt ”-value with bottom water oxygen concentration [O_2] at the above mentioned sites.

2.2. Materials and methods

Surface sediments derived from 62 samples of well-dated multi-cores from the western-equatorial Atlantic Ocean, the northwest African margin (North Atlantic), southwest African margin (South Atlantic), the Southern Ocean (Atlantic sector) and the Arabian Sea, have been collected from box- and multicores during cruises of the R/V *Meteor* and R/V *Tyro* (Fig. 1, Table 1). Sediment samples have been processed using standard palynological techniques according to the aliquot method described in Marret and Zonneveld (2003). Accumulation rates are calculated by multiplying the numbers of dinocysts per gram of dry sediment with the dry bulk density and the sedimentation rate at the sample sites. Sedimentation rates have been estimated based on linear interpolation between the ^{14}C -AMS dates of the studied multi cores (Table 1). Accumulation rates of both R-cysts and S-cysts (Table 2) have been compared to chlorophyll a , SST, SSS, NO_3 , and PO_4 concentrations of the upper waters at the sampling sites and bottom water oxygen concentrations. Chlorophyll a values have been extracted from the SEAWIFS satellite images that depict mean annual chlorophyll a data compiled from 30 October, 1978-1 June, 2005 using the program NCSA JHV 2.7. Bottom water [O_2], SST, SSS, [NO_3], and [PO_4] have been derived from the NOAA, 1998 dataset (Appendix A1).

The degradation of S-cysts expressed by “ kt ” has been calculated assuming a first-order decay process: $kt = \ln(X_i / X_f)$, with X_f = final dinocyst concentration (cysts $cm^{-2} kyr^{-1}$), and X_i = initial cyst concentration (cysts $cm^{-2} kyr^{-1}$). We assume that in regions with minimal aerobic degradation surface sediments, such as oxygen-minimum zones (OMZ), the accumulation rate (AR) of R-cysts and S-cysts reflect their initial export production. Material from the surface samples of OMZs of the Arabian Sea and the Namibian shelf (SE-Atlantic) as well as sediment traps (western Arabian Sea) indicate that the ARs of R-cysts and S-cysts relate to the equation:

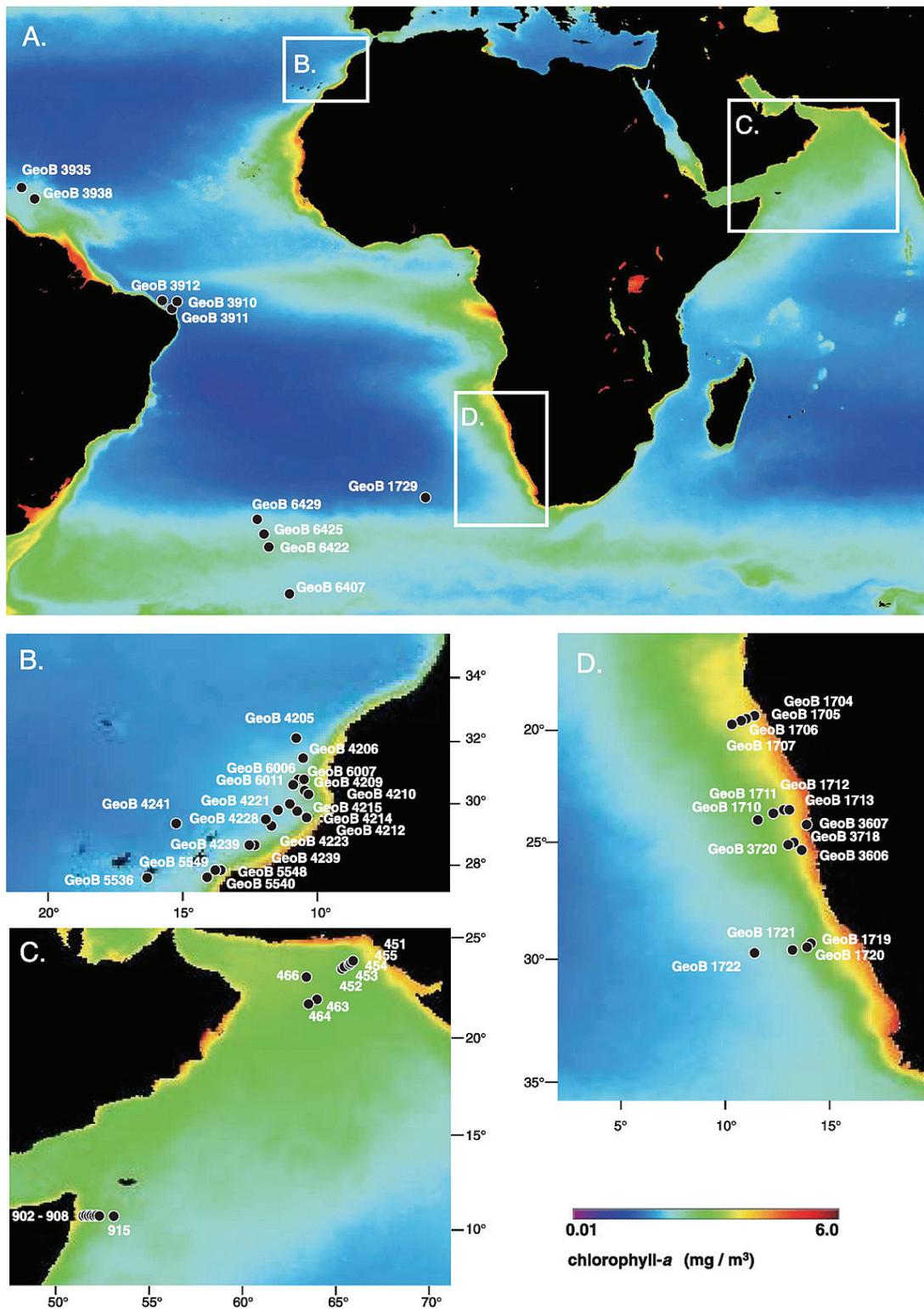


Figure 1. Maps of the Atlantic Ocean and Indian Ocean showing mean annual chlorophyll a concentrations of surface waters and sample positions of surface sediment samples. (A) Overview map of the studied regions, (B) Detailed map of the NW-African margin (C) Detailed map of the Arabian Sea, (D) Detailed map of the studied region off SW Africa.

$AR_{S-cysts} = 68 \times AR_{R-cyst}$ (Appendix A1, Zonneveld and Brummer, 2000). Based on this relationship initial concentrations of S-cysts can be calculated by multiplying the AR of R-cysts in the surface sediments by 68 and by using the above mentioned first-order decay function to determine the degradation index (kt). The kt values of the studied samples have been compared to mean annual bottom water oxygen values.

Table 1. List of samples with information about the sample position, water depth, sedimentation rates, and stratigraphy.

Sample	Lat. (N)	Long. (E)	Depth (m)	SR (cm/ky)	Stratigraphy after	Sample	Lat. (N)	Long. (E)	Depth (m)	SR (cm/ky)	Stratigraphy after
Geob4205	32.182	-11.648	272	1.83	Kuhlmann et al. (2002)	ARZE906	10.48	52.07	2020	20	Ivanova (2000)
Geob4206	31.498	-11.015	1855	4.67	Kuhlmann et al. (2002)	ARZE907	10.48	52.14	2807	14	Ivanova (2000)
Geob4209	30.357	-11.083	2150	4.17	Kuhlmann et al. (2002)	ARZE908	10.46	52.54	3572	8	Ivanova (2000)
Geob4211	30.193	-10.821	1173	3.83	Kuhlmann et al. (2002)	ARZE915	10.41	53.31	4035	5	Ivanova (2000)
Geob4212	29.603	-10.95	1256	4.42	Kuhlmann et al. (2002)	Geob1704	-19.4	11.62	395	3.6	Mollenhauer (2002)
Geob4214	29.781	-11.198	1788	3.08	Kuhlmann et al. (2002)	Geob1705	-19.5	11.38	647	13.1	Mollenhauer (2002)
Geob4215	30.036	-11.553	2106	3	Kuhlmann et al. (2002)	Geob1706	-19.57	11.18	980	9	Mollenhauer (2002)
Geob4221	29.775	-12.338	1826	3.08	Kuhlmann et al. (2002)	Geob1707	-19.7	10.65	1234	9.4	Mollenhauer (2002)
Geob4223	29.018	-12.467	777	11.17	Kuhlmann et al. (2002)	Geob1710	-23.43	11.68	2995	5.3	Mollenhauer (2002)
Geob4228	29.47	-12.99	1633	6.67	Kuhlmann et al. (2002)	Geob1711	-23.32	12.37	1975	10	Mollenhauer (2002)
Geob4237	28.493	-13.18	800	6.5	Kuhlmann et al. (2002)	Geob1712	-23.25	12.80	1004	8	Mollenhauer (2002)
Geob4239	28.493	-13.18	881	10.75	Kuhlmann et al. (2002)	Geob1713	-23.22	13.020	600	7.7	Mollenhauer (2002)
Geob4241	29.167	-15.453	3610	3.08	Kuhlmann et al. (2002)	Geob1719	-28.93	14.17	1023	6.5	Mollenhauer (2002)
Geob5536	27.537	-16.135	3456	6.5	Kuhlmann et al. (2002)	Geob1720	-29.	13.8	2011	4	Mollenhauer (2002)
Geob5540	27.535	-14.175	2035	9.92	Kuhlmann et al. (2002)	Geob1721	-29.18	13.08	3079	2.9	Mollenhauer (2002)
Geob5548	27.992	-13.518	1162	8.83	Kuhlmann et al. (2002)	Geob1722	-29.45	11.75	3971	1.9	Mollenhauer (2002)
Geob5549	27.978	-13.695	1454	11.25	Kuhlmann et al. (2002)	Geob1729	-28.9	01.0	4401	1.45	Thießen (1993)
Geob6006	30.868	-10.63	1282	5.92	Kuhlmann et al. (2002)	Geob3606	-25.46	13.08	1793	7.38	Mollenhauer (2002)
Geob6007	30.852	-10.267	899	86.75	Kuhlmann et al. (2002)	Geob3607	-23.88	14.33	97	60	Mollenhauer (2002)
Geob6011	30.315	-10.288	993	6.83	Kuhlmann et al. (2002)	Geob3718	-24.9	13.17	1313	7.7	Mollenhauer (2002)
ARZ451	23.41	66.02	495	25.5	van der Weijden et al. (1999)	Geob3720	-25.07	12.67	2517	10.5	Mollenhauer (2002)
ARZ452	22.56	65.28	2001	5	van der Weijden et al. (1999)	Geob3910	-04.245	-36.347	2359	3.56	Mollenhauer (2002)
ARZ453	23.14	65.44	1555	8.1	van der Weijden et al. (1999)	Geob3911	-04.613	-36.635	825	14.29	Mollenhauer (2002)
ARZ455	23.33	65.57	998	10.1	van der Weijden et al. (1999)	Geob3912	-03.665	-37.718	773	3.45	Mollenhauer (2002)
ARZ463	22.33	64.03	970	16	van der Weijden et al. (1999)	Geob3935	12.613	-59.388	1556	2.63	Mollenhauer (2002)
ARZ464	22.15	63.35	1511	15	van der Weijden et al. (1999)	Geob3938	12.257	-58.33	1972	1.32	Mollenhauer (2002)
ARZ466	23.36	63.48	1960	6.4	van der Weijden et al. (1999)	Geob6407	-42.05	-19.5	3354	1.76	Franke et al. (2004)
ARZ902	10.46	51.34	459	8.1	Ivanova (2000)	Geob6422	-35.71	-22.44	3972	1.77	Franke et al. (2004)
ARZ903	10.46	51.39	789	48	Ivanova (2000)	Geob6425	-33.83	-23.59	4352	1.05	Franke et al. (2004)
ARZE904	10.47	51.46	1194	40	Ivanova (2000)	Geob6429	-31.95	-24.25	4335	2	Schmieder (2004)
ARZE905	10.54	51.56	1567	29	Ivanova (2000)						

Sample Geob 1711 has been excluded from the analyses since accumulation rates of the cysts appeared a factor 10 higher than the surrounding samples. ARZE showed a remarkable difference in association as samples in its close vicinity and is excluded as well. Since both sites are not characterized by exceptional sedimentation regimes or

deviant environmental conditions in the water column we ascribe these discrepancies to “errors” during the counting process.

Accumulation rates of R-cysts, S-cysts and the degradation index (kt) have been compared with oxygen concentrations of bottom waters, and upper water mean annual chlorophyll a , SST, SSS, NO_3 and PO_4 concentrations using the multivariate ordination methods Redundancy Analysis (RDA) using the CANOCO for Windows software package (Jongman et al., 1987; ter Braak and Smilauer, 1998). Seasonal values of SST and SSS at the investigated sites strongly co-vary to each other (Fig. 2). As a result seasonal differences can be considered as of minor importance and annual values have been included within our analyses. As seasonal data of $[\text{PO}_4]$ and $[\text{NO}_3]$ are available for a few sites only, we have included annual data. Nitrate and phosphate values co-vary strongly (Fig 3, Table 3). Slight co-variation between chlorophyll a and NO_3 , PO_4 concentrations and between bottom water $[\text{O}_2]$ and water depth occurs. For this co-variance is corrected in the RDA analysis.

The preformed analyses are based on the assumption of a linear response of the species in relation to environmental variables. A detrended correspondence analysis carried out before the analysis confirmed such a linear response model.

Table 2. List of cyst-species included within the S-cyst and R-cyst groups.

R-cysts	S-cysts
<i>Dalella chathamensis</i>	<i>Brigantedinium</i> spp.
<i>Impagidinium aculeatum</i>	cyst of <i>Diplopelta parva</i>
<i>Impagidinium pallidum</i>	cyst of <i>Diplopelta symmetrica</i>
<i>Impagidinium paradoxum</i>	cyst of <i>Protoperidinium avellanum</i>
<i>Impagidinium patulum</i>	cyst of <i>Protoperidinium americanum</i>
<i>Impagidinium plicatum</i>	cyst of <i>Protoperidinium monospinum</i>
<i>Impagidinium sphaericum</i>	cyst of <i>Protoperidinium nudum</i>
<i>Impagidinium strialatum</i>	cyst of <i>Protoperidinium stellatum</i>
<i>Impagidinium variaseptum</i>	<i>Echinidinium aculeatum</i>
<i>Impagidinium velorum</i>	<i>Echinidinium granulatum</i>
<i>Impagidinium</i> spp.	<i>Echinidinium transparentum</i>
<i>Nematosphaeropsis labyrinthus</i>	<i>Echinidinium delicatum</i>
<i>Operculodinium israelianum</i>	<i>Echinidinium</i> spp.
<i>Pentapharsodinium dalei</i>	<i>Lejeunecysta oliva</i>
<i>Polysphaeridium zoharyi</i>	<i>Lejeunecysta sabrina</i>
	<i>Quinquecuspis concreta</i>
	<i>Selenopemphix antarctica</i>
	<i>Selenopemphix nephroides</i>
	<i>Selenopemphix quanta</i>
	<i>Stelladinium robustum</i>
	<i>Trinovantedinium applanatum</i>
	<i>Votadinium calvum</i>
	<i>Votadinium spinosum</i>
	<i>Xandarodinium xanthum</i>

2.3. Results

Accumulation rates of S-cysts (s) show an exponential decrease with oxygen concentrations (y_{O_2}) in bottom water that is significant on all significance levels (Fig. 4, Table 4) according to:

$$y_{O_2} = 4.3374 e^{-0.00001s}, \text{ with } R^2 = 0.73 \quad (1)$$

R-cyst accumulation rates and bottom water oxygen concentrations show an insignificant correlation ($R^2 = 0.23$; Fig. 5, Table 4).

Accumulation rates of R-cysts (r) show a significant linear relationship with chlorophyll a concentrations (y_{Chla}) in the upper water column (Fig. 6, Table 4) according to the equation:

$$y_{Chla} = 0,0002r + 0.2271, \text{ with } R^2 = 0.70 \quad (2)$$

Table 3. Correlation matrix of the environmental variables depicting the rate of co-variance.

Correlation matrix	O ₂	chl a	SST	SSS	PO ₄	NO ₃	water depth	A	B
O ₂ (ml l ⁻¹)	1							51%	51%
chl a (mg m ⁻³)	-0.409	1						19%	3%
SST (°C)	-0.389	-0.206	1					7%	0%
SSS (psu)	-0.150	0.020	0.130	1				1%	0%
PO ₄ (mM)	-0.331	0.448	-0.045	-0.075	1			14%	2%
NO ₃ (mM)	-0.171	0.441	-0.281	-0.034	0.829	1		5%	1%
water depth (m)	0.495	-0.363	-0.013	-0.243	-0.146	-0.195	1	19%	1%

Amount of variance in the dataset explained by the environmental variables.

A = without co-variance correction, B = with co-variance correction.

Site GeoB 3607 is located at the edge of an active upwelling cell along the Namibian coast (Fig. 1) and is characterized by extreme high chlorophyll a values that are a factor 100 higher than the other studied samples. This sample has been excluded from the establishment of equation no. 2.

Although by visual examination a positive relationship between accumulation rates of S-cyst with chlorophyll *a* concentrations seems to be present, this trend is extremely weak and not significant (Fig. 7, Table 4). The *kt*-values show a clear relationship with bottom water [O₂] according to the equation (Fig. 8A, Table 4):

$$[\text{O}_2] = 5.184 = 1 / e^{-1.131(kt-1.98)}, \text{ with } R^2 = 0.73 \quad (3)$$

When samples GeoB 5540 (NW-African margin) and GeoB 1704 (SW-African margin) are excluded from the dataset a relationship between oxygen concentration and the degradation index (*kt*) according to the following equation can be observed (Fig. 8B, Table 4):

$$[\text{O}_2] = 5.17 = 1 / e^{-1.23(kt-2.058)}, \text{ with } R^2 = 0.846 \quad (4)$$

A weak relationship ($R^2 = 0.42$) can be observed between water depth and *kt* (Fig. 9, Table 4). The *kt*-values decrease with increasing sedimentation rates (Fig. 10, Table 4). Mean annual SST, SSS, [PO₄], and [NO₃] show no significant or only a weak relationship between with R-cysts and S-cyst accumulation rates (Fig. 11, Table 3). By correcting for this co-variation the variables water depth, SST, SSS, [PO₄], and [NO₃] did not account for variation within the dataset (Table 3).

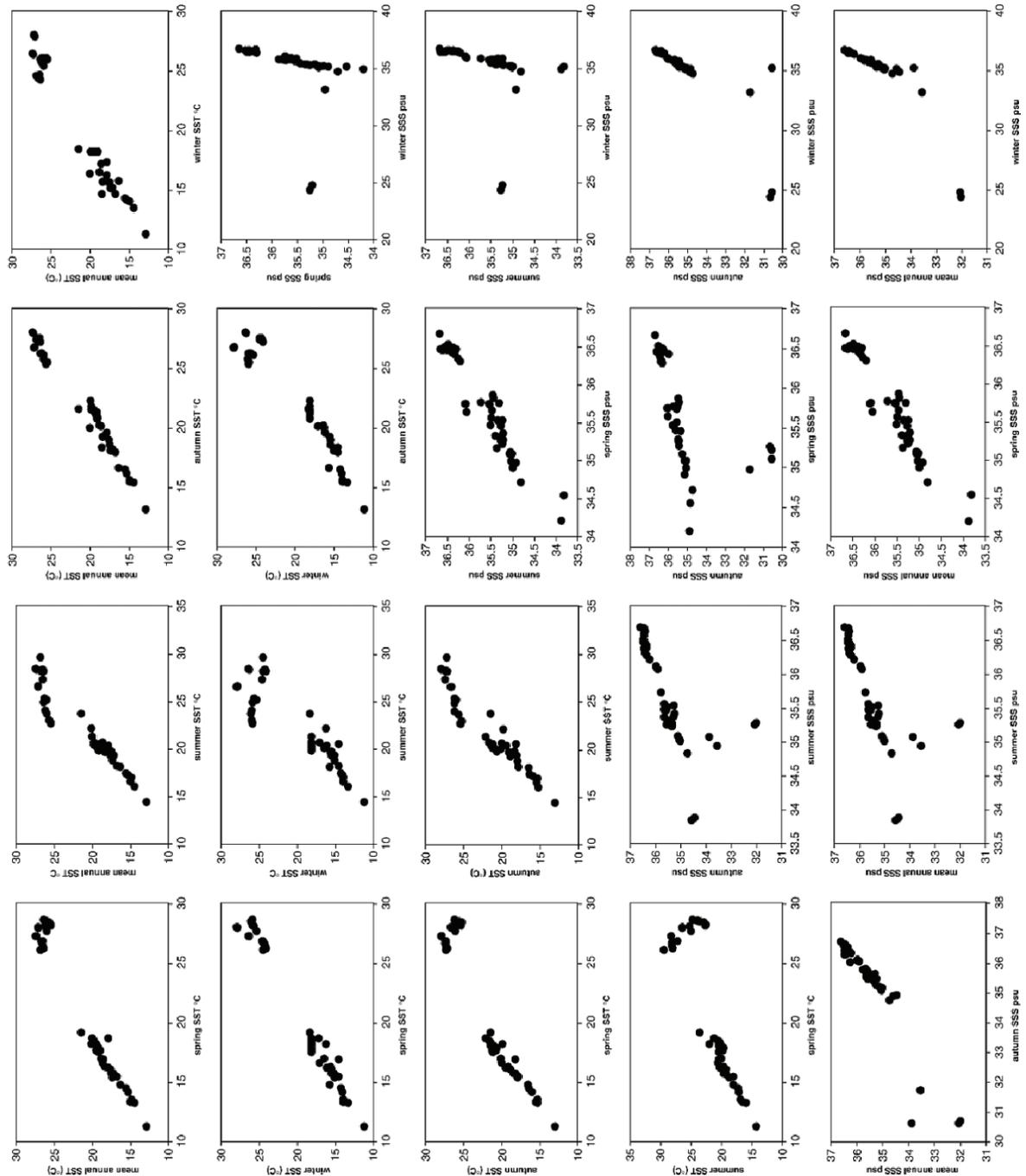


Figure 2. Draftman's plots of the seasonal variables of SST and SSS

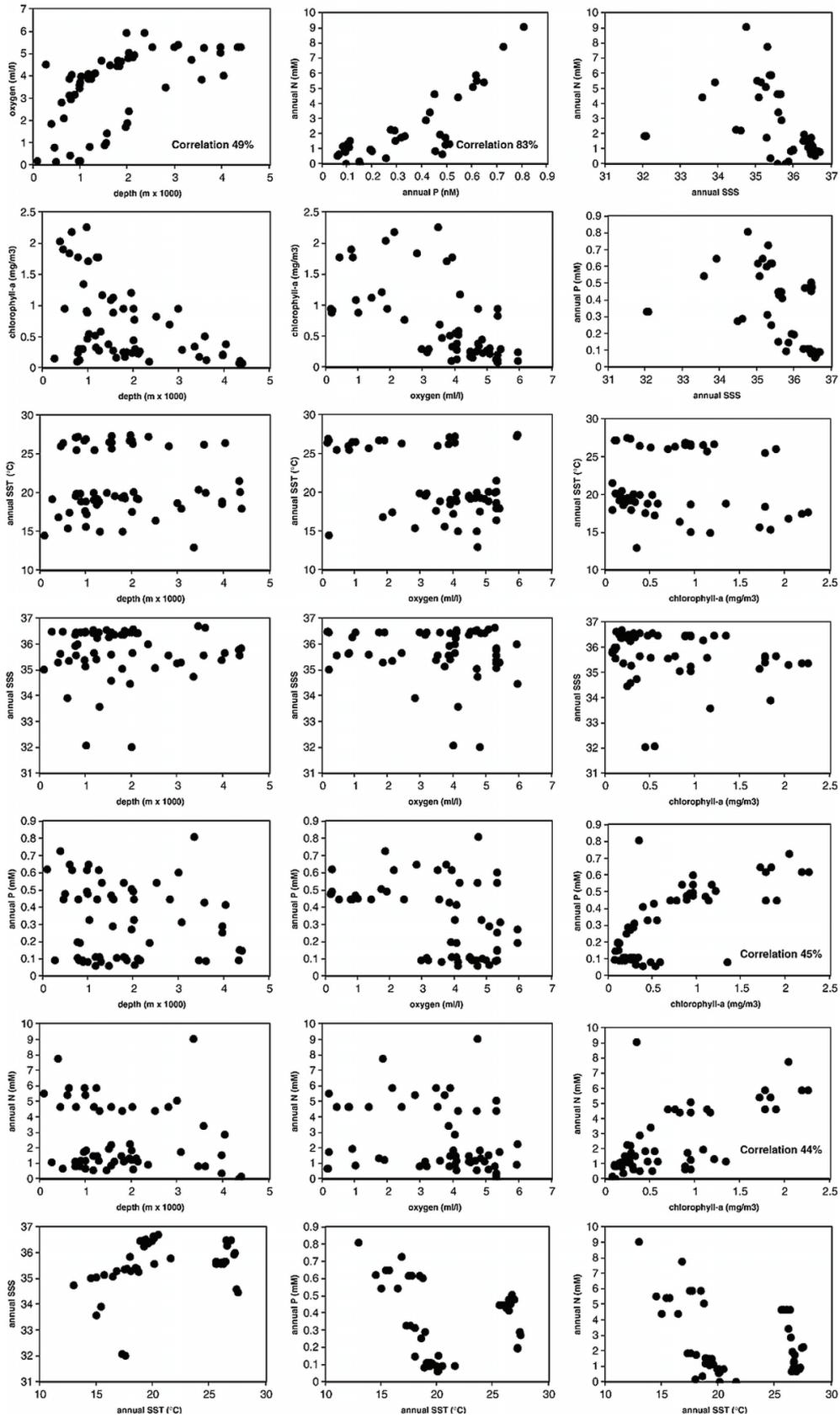


Figure 3. Draftman's plot of the analysed variables.

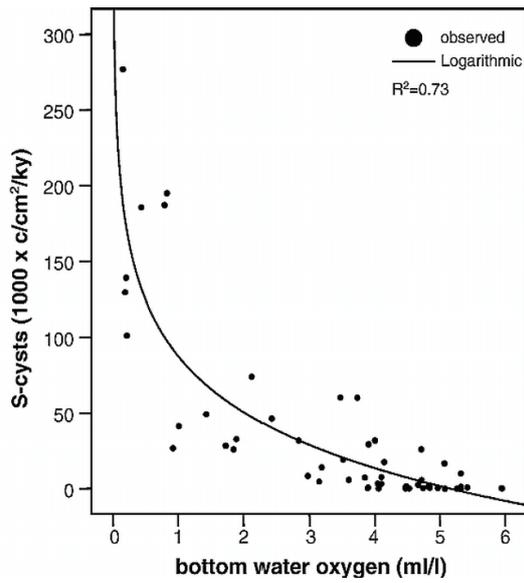


Figure 4. Relationship between accumulation rates of S-cysts and bottom water oxygen.

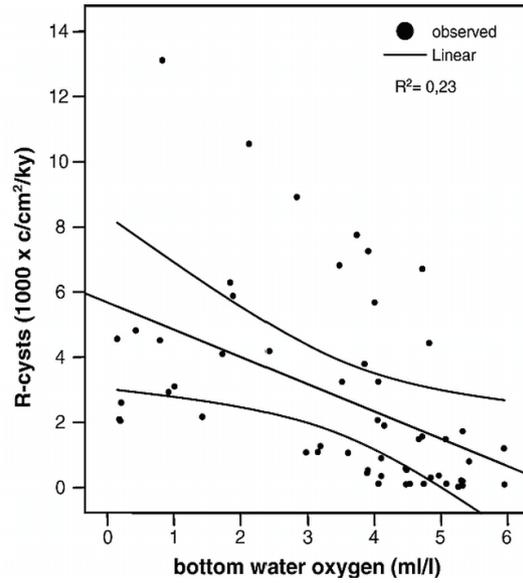


Figure 5. Relationship between accumulation rates of R-cysts and bottom water oxygen. Estimated relationship with 99.9% confidence limit of mean.

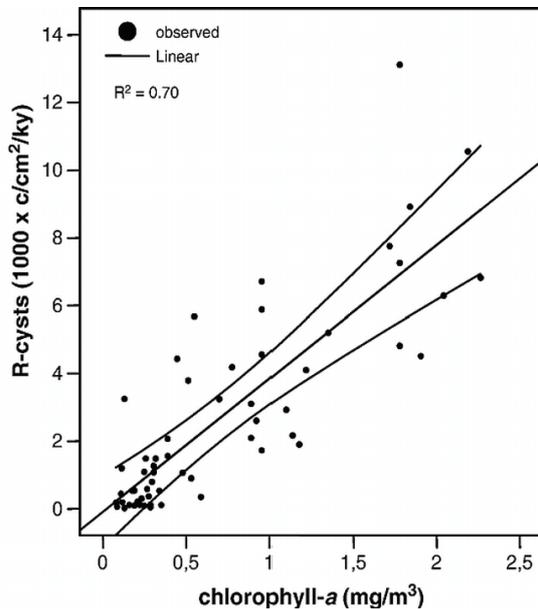


Figure 6. Relationship between accumulation rates of R-cysts and mean annual upper water chlorophyll a concentrations. Estimated linear relationship with 99.9% confidence limit of mean.

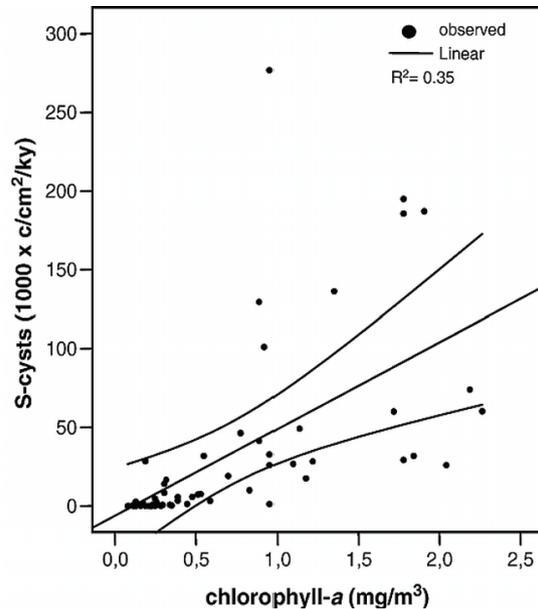


Figure 7. Relationship between accumulation rates of S-cysts and mean annual upper water chlorophyll a concentrations. Estimated linear relationship with 99.9% confidence limit of mean.

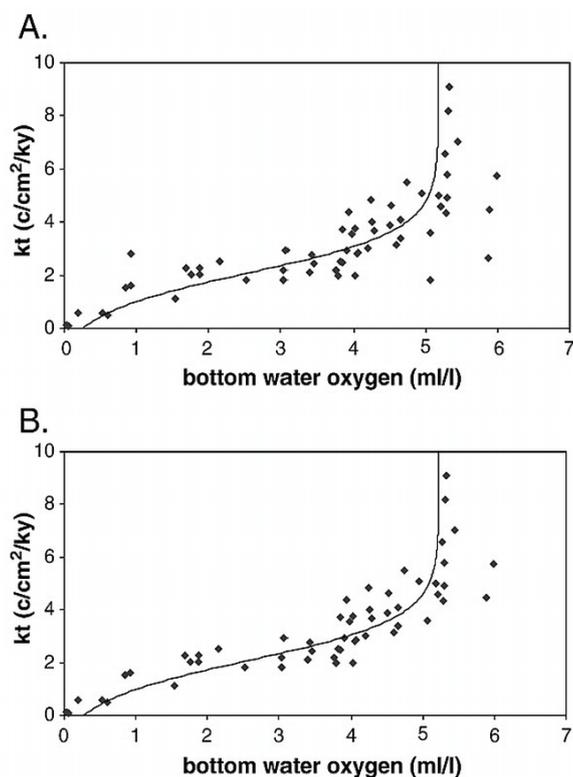


Figure 8. Relationship between the degradation expressed of S-cysts by kt and bottom water $[O_2]$. (A) with outliers, (B) without outliers.

4. Discussion

Our results document marked difference in relationship of accumulation rates of R-cysts and S-cysts to environmental gradients in upper water masses and bottom waters. The final recovery of dinocysts depends on numerous factors such as initial dinocyst production, degradation within the water column and sediment as result of bacterial activity and chemical processes, and lateral translocation during downward transport through the water column or post-depositional due to sediment winnowing. The following chapters discuss how these processes are related to our results.

4.1. Cyst production

The initiation of dinoflagellate sexuality and, as a result, cyst production is influenced by environmental conditions in surface waters such as nutrient availability, temperature, irradiance, turbulence and by endogenic encystment rhythms. (e.g., Pfiester and Anderson, 1987). Although salinity is an important parameter influencing the geographic distribution of dinoflagellates, it is not known to trigger or influence their

sexuality and dinocyst production. Laboratory experiments show that cyst production can often be induced when phototrophic dinoflagellates are grown under nitrogen or phosphate limitation and when cultures of heterotrophic dinoflagellates are exposed to food limitation (e.g., Anderson and Lindquist, 1985; Ishikawa and Taniguchi, 1996; Montresor et al., 1998; Sgroso et al., 2001; Olli and Anderson, 2002). However, studies in natural environments show that maximal cyst production occurs during or just after dinoflagellate cyst blooms, when nutrients in the water column are not limiting (Ishikawa and Taniguchi, 1996; Montresor et al., 1998; Kremp and Heiskanen, 1999; Godhe et al., 2001). Results of a long-term sediment trap study from just outside the upwelling region off NW-Africa covering a time interval of 5 years show that dinocyst export production of phototrophic dinoflagellates increases when more nutrients are available in the upper water column. Thereby, dinocyst production of some heterotrophic dinoflagellates is positively related to the export production of diatoms. In turn, export production of diatoms, the main food source of heterotrophic dinoflagellates, follows nutrient availability in upper waters (Susek et al., 2005). As a possible explanation for this paradox it is suggested that at maximal vegetative growth, nutrient depletion can occur within individual cells or their microhabitat and as such triggering enhanced sexuality.

Table 4. Regression table of the factors compared. Dependent variables: S-cyst ($1000 \times$ cysts cm^{-2} kyr $^{-1}$), R-cyst ($1000 \times$ cysts cm^{-2} kyr $^{-1}$), kt (cysts cm^{-2} kyr $^{-1}$).

Regression variables	Model	R	R^2	df_{regr}	df_{res}	F-value
S-cysts – O_2	logarithmic	0.85	0.73	1	55	145.53
S-cysts – chlorophyll <i>a</i>	linear	0.59	0.35	1	57	30.36
S-cysts – SST	linear	0.26	0.07	1	58	4.35
S-cysts – SSS	linear	0.04	0.002	1	57	0.11
S-cysts – PO_4	linear	0.37	0.13	1	58	9
S-cysts – NO_3	linear	0.23	0.05	1	58	3.14
R-cysts – O_2	linear	0.48	0.23	1	54	16.17
R-cysts – chlorophyll <i>a</i>	linear	0.84	0.7	1	56	128.98
R-cysts – SST	linear	0.0048	0.00002	1	57	0.0013
R-cysts – SSS	linear	0.31	0.1	1	56	6.13
R-cysts – PO_4	linear	0.62	0.38	1	57	35.58
R-cysts – NO_3	linear	0.56	0.31	1	57	25.42
kt – O_2	logistic	0.92	0.85	3	54	55.8
kt – water depth	linear	0.64	0.42	1	58	41.26
kt – sedimentation rate	linear	0.75	0.56	1	58	74.96

Independent variables: O_2 (ml l^{-1}), chlorophyll *a* (mg m^{-3}), SST ($^{\circ}\text{C}$), SSS (psu), PO_4 (mM), NO_3 (mM), water depth (m), and sedimentation rate (cm kyr^{-1}). df_{regr} = degrees of freedom for regression, df_{res} = degrees of freedom of residuals. F-value is the measurement of the distance between individual distributions. As F goes up, *p*-value goes down (i.e., more confidence in the difference between two means).

The amount of gametes produced is therefore related to the amount of motile cells but individual specimens are triggered to produce gametes by nutrient or food depletion. Nevertheless, independent of the question if this hypothesis is true or not, in natural environments, for both groups of dinocysts (R-cysts and S-cysts) increased production is related to enhanced production of motile cells, which in turn is observed when nutrient, trace element or food conditions are favourable.

Numerous studies show that dinoflagellates have complex ecologies with the cyst production of every species dependent on biotic and a-biotic factors (e.g., Marret and Zonneveld, 2003; Rochon and Marret, 2004; Harland et al., 2004). Within this study we have grouped cysts with different ecologies. By doing so, we expect that environmental factors that influence the cyst production, transport and preservation of all species in the group in a similar way, will have a strong relationship with the total dinocyst accumulation of that group. On the contrary, a damped effect is expected for factors that influence only part of the species within the group, or influence individual species of the group in different ways. We have correlated the a-biotic environmental factors; bottom water [O₂], water depth, mean annual chlorophyll *a*, SST, SSS, nitrate and phosphate concentrations, with total accumulation rates of R-cysts and S-cysts. The multivariate ordination analysis shows that mean annual SST, SSS, nitrate and phosphate concentrations do not show a significant relationship to the variation in accumulation rates of R-cysts or S-cysts (Fig. 11, Table 4). We therefore suggest that they had differential effects on the production of individual cyst species within the groups. Only the factors bottom water [O₂], chlorophyll *a* and water depth showed a significant relationship with accumulation rates of R-cysts and S-cysts. With exception of chlorophyll *a* these factors can not directly influence dinocyst production in upper water masses.

To date, satellite measurements routinely provide global chlorophyll *a* biomass. Since the remote sensing determination of phytoplankton carbon has been proven to be elusive, net primary production estimates use chlorophyll *a* as an index of phytoplankton biomass (e.g., Campbell et al., 2002). Although the above mentioned method has constraints and it is assumed that about 30% of daily water column photosynthesis is missed by satellite based estimates (e.g., Behrenfeld et al., 2005; Mouw and Yoder, 2005), we can safely assume that mean annual chlorophyll *a* is a qualitative reflection of mean annual net primary production.

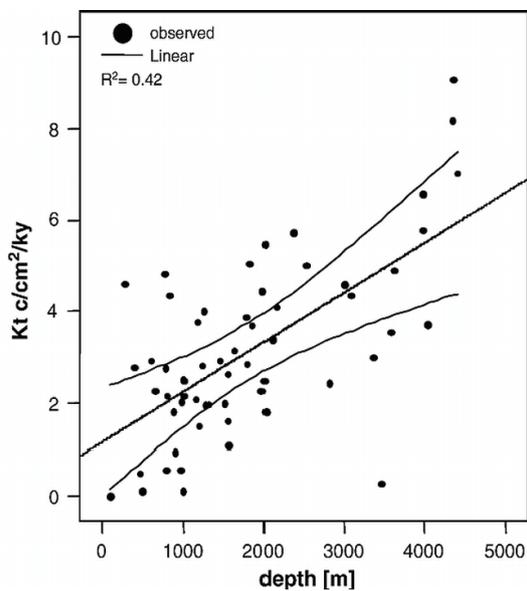


Figure 9. Relationship between the degradation of S-cysts expressed by *kt* and water depth at the sample sites. Estimated linear relationship with 99.9% confidence limits of mean.

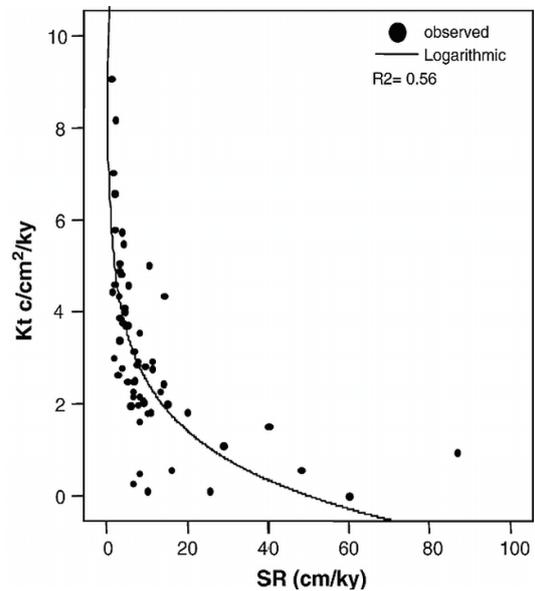


Figure 10. Relationship between the degradation of S-cysts expressed by *kt* and sedimentation rate.

Assuming that more cysts of heterotrophic dinoflagellates might be produced when more food is available we could expect to find a positive causal relationship between mean annual chlorophyll *a* concentration and S-cyst accumulation rates. However, although a trend is visible the relationship is weak ($R^2 = 0.35$, F-value = 30.36, df= 57; Fig.7, Table 4). A possible explanation for could be that production of S-cysts relates to the presence of individual phytoplankton prey species rather than to the phytoplankton community as a whole.

The positive relationship between R-cysts and upper water mean annual chlorophyll *a* concentrations suggests that the accumulation of R-cysts is somehow related to the total phytoplankton production in upper waters (Fig. 5). We do not think this relationship to be causal but assume that chlorophyll *a* and R-cyst accumulation rates react on similar factors, although we can not exclude a causal relationship completely, given the fact that many, if not all, dinoflagellates that are capable of photosynthesis, are capable of heterotrophy (Schnepf and Elbrächter, 1999; Smayda and Reynolds, 2003 and references therein). However, within our database we find one exception at site GeoB 3607. At this site chlorophyll *a* values are a factor 100 higher than at the other studied sites whereas accumulation rates of R-cysts have intermediate values. This sample is located at the edge of an active upwelling cell along the Namibian coast.

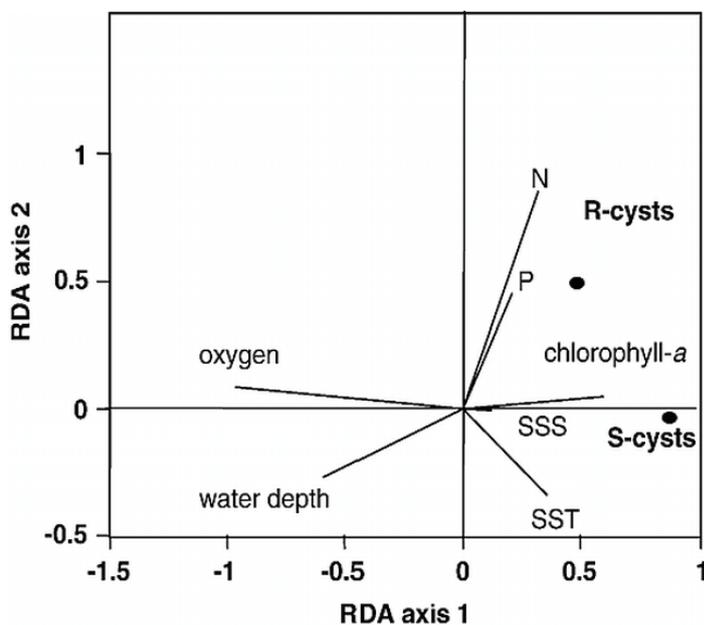


Figure 11. RDA diagram of R-cyst and S-cyst accumulation rates with environmental variables.

In contrast to all other studied sites, considerable mixing of waters takes place in the upper water column at this site. Field and laboratory studies show that dinoflagellate growth and cyst production can be strongly (negatively) influenced by turbulence intensity and the duration of turbulent phases (e.g., Thomas et al., 1995; Gibson and Thomas, 1995; Gibson, 2000; Smayda and Reynolds, 2001). They appear to be much more sensible for turbulence than other groups of primary producers such as diatoms. In high productivity areas such as upwelling regions it is often observed that dinoflagellates become abundant in the phytoplankton at times of upwelling relaxation when the water column becomes more stratified or in the more stratified upwelling filaments (e.g., Shannon and Pillar, 1986; Mitchell-Innes and Walker, 1991; Pitcher et al., 1991; Veldhuis et al., 1997; Smayda and Reynolds, 2003). At site GeoB 3607 turbulence might therefore be the limiting factor for cyst production.

4.2. Transport

Apart from reflecting differences in initial production and preservation processes at the sediment-water interface, accumulation rates can be affected by processes of winnowing or focusing. Winnowing or focusing result in an underestimation or overestimation of the accumulation rates compared to the real influx of cysts into the sediments. Regarding the fact that the size and cyst-outlines of the grouped species are comparable indicates that the processes of winnowing/focusing will have a similar effect on both groups. The marked differences in relationship of R- and S-cysts with upper water and bottom water conditions can, therefore, not be the result of winnowing or focusing.

Several authors have suggested that lateral transportation of cysts during downward migration within the water column or after deposition might form an important factor affecting the cyst distribution (e.g., Dale and Dale, 1992; Harland and Pudsey, 1999). However, except for mass transport (e.g., turbidites) studies on the distribution pattern of dinocysts in modern, undisturbed sediments as well as sediment trap studies document small scale transport only (e.g., Zonneveld and Brummer, 2000; Marret and Zonneveld, 2003; Susek et al., 2005). As far as we know no evidence is found that species selective cyst transport occurs in natural environments. We therefore assume that transport of dinocysts does not cause the observed differences in relationship between R-cysts and S-cysts and bottom water [O₂], water depth and upper water chlorophyll *a*.

4.3. Preservation

We observe a significant exponential relationship between S-cysts accumulation rates and bottom water $[O_2]$ (Fig. 4, Table 4). As discussed above, this relationship can not be explained by differential production related to upper water conditions and selective transport. Our results are consistent to earlier studies that conclude S-cysts to be extremely sensitive for degradation based on similar relationships and comparison with chemical data (Zonneveld and Brummer, 2000; Zonneveld et al., 2001; Versteegh and Zonneveld, 2002; Hopkins and McCarthy, 2002; Reichart and Brinkhuis, 2003). Again consistent with earlier studies we find no clear relationship between R-cysts accumulation rates and bottom water $[O_2]$ subscribing the assumption that they are minimally affected by aerobic degradation (Fig. 5, Table 4). We assume that the difference in relationship between R-cysts and S-cysts with bottom water $[O_2]$ can be subscribed to a fundamental difference in the chemistry of the cyst walls of both groups. Such a difference has previously been evidenced by differences in fluorescence, vulnerability to staining or oxidative laboratory treatments by various authors (e.g., Dale, 1976; Marret, 1993; Elbrächter, 1994 and references therein). To date, chemical data of dinoflagellate cyst walls are limited but indicate that they are composed of complex biomolecules (Kokinos et al., 1998; Versteegh and Blokker, 2004; de Leeuw et al., 2006). Nuclear magnetic resonance (NMR) analysis of the fossilizable organic inner-wall of *Scrippsiella* sp. (a peridinioid) cysts that are included into the species *Brigantedinium* spp. By palynologists, suggests that the macromolecules contain a substantial aliphatic component (Hemsley et al., 1994). A comparable aliphatic component is absent in the dinoflagellate cyst walls of *Lingulodinium polyedrum* (gonyaulacoid) in contrast to the presence of condensed and predominantly aromatic components (Kokinos et al., 1998). Furthermore, laboratory experiments based on dinocyst cultures and sediments suggest that gonyaulacoid cyst walls consists to a high proportion of carbon and ether-linked macromolecular building blocks, whereas the macromolecular building blocks of peridinioid cyst walls are much more ester linked (for an overview see Versteegh and Blokker, 2004). Versteegh and Blokker (2004) suggested that there are two variables influencing cyst wall composition, (i) the proportion of aliphatic versus aromatic moieties and (ii) the proportion of ether- and carbon-bonds versus ester-bonds.

Sediment trap studies have so far revealed no evidence that organic-walled dinoflagellate cysts are prone to degradation during their transport within the water column (Zonneveld and Brummer, 2000; Susek et al., 2005). This might be the result of

the fact that cyst accumulation is thought to be a rather fast process resulting in a relatively short reaction time. Within this study we observe a weak negative relationship between S-cysts accumulation rates and water depth that might suggest a degradation of these cysts within the water column. However, water depth co-varies with bottom water [O₂] and after correction for co-variance, no significant relationship can be found (Table 3).

4.4. Cyst accumulation rates as a tool to estimate past net primary productivity

One of the aims of this study is to discuss if we can use accumulation rates of R-cysts to estimate past net primary productivity. We observe a significant positive relationship between accumulation rates of R-cysts and chlorophyll *a*, according to equation no. 2 (Fig. 6, Table 4). Given the discussion above we can assume that this equation has the potential to be used as a past productivity proxy. We realize that this suggestion will cause controversy within the palynological community given the discussions about the attempts to digitalize past environmental conditions using dinoflagellate cyst associations (e.g., Dale et al., 2002; de Vernal et al., 2005). However, we suggest this relationship to be tested in paleo-studies to obtain insight into potentials and limitations. We already pointed out that this relationship cannot be used in environments that are characterized by strong or long-lasting turbulence or in regions where environmental factors influence dinoflagellate growth and dinocyst production differently compared with the production of other phytoplankton groups. Nevertheless, the empirical relationship appears to be clear in a large variety of environments.

4.5. Degradation rates of dinocysts as a tool to estimate past deep-ocean oxygen

The calculation of the degradation index (expressed by *kt*) of S-cyst assumes that the initial production is related to the production of R-cysts in all studied environments. This is based on the relationship we found in various regions, in sediment trap samples and samples from anoxic environments, where selective degradation can be expected to be minimal and where cyst accumulation rates of both groups can be assumed to reflect changes in their initial production (e.g., Reichart and Brinkhuis, 2003). As far as we know, there is no evidence from the literature that our assumption does not hold. Furthermore, if our assumption is wrong we would expect to find a random signal between *kt* and environmental gradients (such as bottom water [O₂]; Fig. 8).

A logical question arises; how causal is the relationship between kt and bottom water $[O_2]$. As explained in the Introduction part, individual OM components typically show a first order decay (e.g., Middelburg, 1989; Hartnett et al., 1998; Hedges et al., 1999). The cyst wall degradation can be considered to depend on the degradability of its biomolecules (expressed by their degradation constants k) and the oxygen exposure time (t). Other factors that are known to influence the rate of aerobic decay of organic matter such as bioturbation and sedimentation rates, oxygen concentration and water depth, are considered to actually modulate the effects of the oxygen exposure time (e.g., Hartnett et al., 1998; Sun et al., 2002; Keil et al., 2004). A decrease in rate of aerobic decay of organic matter with reaction time has often been observed and several mechanisms have been proposed to explain this phenomenon such as organic recalcitrance and biotic exclusion (e.g., Tegelaar et al., 1989; Derenne and Largeau, 2001; Mayer, 2004). For instance, complex biomolecules vary in their ease to disassembly, at monomer, polymer or supra-molecular scales of organization. In the case of dinocysts it is therefore possible that for S-cysts the degradation constant “ k ” is not completely constant with the most labile species degrading first, therefore increasing the relative amount of the less sensitive species through time. Through biotic exclusion, some organisms, or their digestive agents, are excluded or inhibited from access to organic matter, for instance through the accumulation of harmful metabolites or by transporting material to anoxic environments through bioturbation processes. Indeed kt shows a decreasing relationship to increasing sedimentation rates (Fig. 10) which suggests that the degradation processes might take place in the upper sediments or at the sediment-water interface.

If dinocyst degradation is a first-order process there should be a constant or decreasing relationship between kt and all the factors reflecting oxygen exposure time. The relationship between kt and bottom water $[O_2]$ is however more complex, suggesting a high-order degradation process. At low bottom water $[O_2]$ there is a strong increase in the degradation with increasing bottom water $[O_2]$ that becomes less intense at intermediate bottom water $[O_2]$. Above a bottom water $[O_2]$ at 4ml l^{-1} there is an exponential increase. This pattern can be explained when cysts are being degraded through a process with oxygen concentration being the limiting factor inhibiting the growth rate of degrading organisms (Jorge and Livingston, 1999; Guerra-García and García-Gómez, 2005). With the degrading organisms increasing in numbers with increasing oxygen concentration the rate of degradation will also increase. However, at a

certain threshold oxygen concentration the population of the degrader increases to a point where all S-cysts are being consumed and kt -values increase exponentially to infinity.

There are several methods to estimate past deep-ocean ventilation based on the sediment structure and the (bio-)chemical content of sediments including, numerical models, as well as the chemical and isotopic composition of microfossils (e.g., Francois et al., 1997; Toggweiler, 1999; Ninnemann and Charles, 2002; Matear and Hirst, 2003; McManus et al., 2004; Ivanochko and Pedersen, 2004). However, the estimation of past bottom oxygen concentrations is still problematic. The relationship documented here might form the basis of a new method that makes quantitative estimations of past deep-ocean oxygen concentrations possible. First applications of this method in sediments deposited during the last deglaciation, last 140 kyr and between 3.2 and 2.5 Ma years BP imply ventilation changes of the deep Equatorial Atlantic, South Atlantic and Southern Ocean (Atlantic Sector; Versteegh and Zonneveld, 2002). Further studies are required to determine the accuracy and restrictions of the method.

4.6. General remarks

Our results are in opposition to the strong traditional belief within the dinoflagellate research community, that cyst forming dinoflagellates with a heterotrophic life strategy prefer high productivity regions characterized by eutrophic conditions, whereas phototrophic cyst-forming dinoflagellates prefer low productivity, oligotrophic environments. This belief finds its basis in the results of the first pioneering studies on the geographic distribution of dinoflagellate cysts in modern environments carried out in the 60's and 70's of the last century. A strong dominance of cysts of photosynthetic species in the central oceanic basins was documented whereas the cyst associations of most coastal sediments appeared to be dominated by cyst of heterotrophic species (see overviews in Wall et al., 1977; Harland, 1983 and references therein). However, the lack of good dating methods prevented the calculation of accumulation rates in these studies. The recent compilation of large worldwide datasets show, that there are many sites from “low productivity, oligotrophic” regions that are dominated by heterotrophic taxa and vice versa (de Vernal et al., 2001; Marret and Zonneveld, 2003). Furthermore, several photosynthetic R-cyst species have their highest abundances in regions where eutrophic conditions prevail. For instance *Dalella chathamensis* can dominate assemblages in sediments of the eutrophic Southern Ocean frontal zones (Marret and Zonneveld, 2003). *Nematosphaeropsis labyrinthus*, *Pentapharsodinium dalei* and *Pyxidinosia reticulata*

can dominate cyst associations in regions characterized by eutrophic upper water conditions whereas the distribution of *Impagidinium pallidum*, is even restricted to these environments (Marret and Zonneveld, 2003). Several heterotrophic dinoflagellates have their highest abundances in “oligotrophic regions”. For instance *Polykrikos* species (such as *Polykrikos kofoidii* and *Polykrikos schwartzii*) and *Votadinium spinosum* have high or even their highest relative abundances in the oligotrophic part of the China Sea. These datasets indicate therefore, that the environmental “preferences” of cyst forming dinoflagellate species should not be generalized but have to be considered on an aut-ecological level and that the initial concept is due for revision.

Also in recent years many studies document that the cyst association of high productivity areas is dominated by heterotrophic species and conclude that dominance of heterotrophic species are characteristic for these regions (e.g., Hamel et al., 2002; Radi and de Vernal, 2004). These studies do, however, not consider the possible effect of selective preservation on the relative abundances of cysts and do not correct for differences in sedimentation rates in the studied region. Hence, although the conclusions that eutrophic regions are often characterized by a dinoflagellate association dominated by dinocysts of heterotrophic species while oligotrophic regions are characterized by a dominance of dinocysts of photosynthetic species are valid, the conclusion that cysts of both groups are produced in higher amounts in the respective regions can not be drawn. These studies give no support to the idea that heterotrophic dinoflagellates or phototrophic species “prefer” eutrophic or oligotrophic regions respectively. Our results indicate that cyst production has to be considered at an aut-ecologic scale and that only in case of excellent preservation (as can occur in regions characterized by oxygen minimum zones) cyst accumulation rates of S-cysts reflect their export production. It can be expected that in these extreme conditions their accumulation rates co-vary with changes in total export productivity (Reichart and Brinkhuis, 2003). Consequently, the results of this study clearly demonstrate that the traditional view about the ecology of cyst forming dinoflagellates has to be evaluated.

5. Conclusions

Accumulation rates of dinoflagellate cyst species known to be resistant against (post-depositional) aerobic decay show a significant positive relationship with upper water chlorophyll *a* concentrations (equation no. 2). No relationship with bottom water oxygen concentrations, annual sea-surface temperature, salinity, nitrate and phosphate

concentrations can be observed. This is in contrast to the general opinion that species producing these cysts are being produced in higher amounts in oligotrophic environments. The reason for this seemingly paradox is that previous studies considered relative abundances of cysts in sediments, did not correct for differential sedimentation rates or did not consider the possible effect of species selective preservation. Our study suggests that R-cyst accumulation rates might be a useful proxy to estimate net primary production in the past. Exception is found in regions with environments that are characterized by strong or long-lasting turbulence or in case other environmental factors influence dinoflagellate growth and cyst production differently from production of other phytoplankton groups.

Accumulation rates of dinocysts known to be sensitive for aerobic degradation show an exponential decrease in relation to bottom water oxygen concentration (equation no. 1; Fig. 4). Only a weak correlation can be found with upper water chlorophyll *a* concentrations (Fig. 5). This suggests that aerobic degradations might strongly overprint the initial production signal. Only in case of excellent preservation (as can occur in regions characterized by oxygen minimum zones) cyst accumulation rates of S-cysts reflect their export production.

The observed relationships between *kt*, water depth and sedimentation rates suggest that processes of organic recalcitrance and biotic exclusion might take place in the upper sediments rather than within the water column.

The positive relationship between degradation rate of S-cysts and bottom water [O₂] (equation no. 4; Fig. 8) suggests that S-cysts are being degraded according to a higher order decay process. This relationship forms the basis for a proxy that can be used to estimate past bottom water oxygen concentration.

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Appendix 4

Process length variation in cysts of a dinoflagellate, *Lingulodinium machaerophorum*, in surface sediments: Investigating its potential use as a salinity proxy

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Marine Micropaleontology (2009), 70: 54-69

doi: 10.101016/j.margeo.2006.10.023

(received 30.07.2008; received in revised form 10.10.2008; accepted 17.10.2009)

Abstract

A biometrical analysis of the dinoflagellate cyst *Lingulodinium machaerophorum* (Deflandre and Cookson 1955) Wall, 1967 in 144 globally distributed surface sediment samples reveals that the average process length is related to summer salinity and temperature at a water depth of 30 m by the equation $\text{salinity/temperature} = 0.078 * \text{average process length} + 0.534$ with $R^2 = 0.69$. This relationship can be used to reconstruct paleosalinities, albeit with caution. This particular ecological window can be associated

with known distributions of the corresponding motile stage *Lingulodinium polyedrum* (Stein) Dodge, 1989 that forms the *L. machaerophorum* cysts. Confocal laser microscopy shows that the average process length is positively related to the average distance between process bases ($R^2=0.78$), and negatively related to the number of processes ($R^2=0.65$). These results document the existence of two end members in cyst formation: one with many short, densely distributed processes and one with a few, long, widely spaced processes, which can be respectively related to low and high salinity/temperature ratios. Obstruction during formation of the cysts causes anomalous distributions of the processes.

Keywords: *Lingulodinium machaerophorum*, processes, *Lingulodinium polyedrum*, biometry, salinity, temperature, palaeosalinity, dinoflagellate cysts

1. Introduction

Salinity contributes significantly to the density of seawater, and is an important parameter for tracking changes in ocean circulation and climate variation. Palaeosalinity reconstructions are of critical importance for better understanding of global climate change, since they can be linked to changes of the thermohaline circulation (Schmidt et al., 2004). Quantitative salinity reconstructions have been proposed on the basis of several approaches that use for example foraminiferal oxygen isotopes (e.g. Wang et al., 1995), $\delta^{18}\text{O}_{\text{seawater}}$ based on foraminiferal Mg/Ca ratios and $\delta^{18}\text{O}$ (e.g. Schmidt et al., 2004; Nürnberg and Groeneveld, 2006), alkenones (e.g. Rostek et al., 1993), the modern analogue technique applied to dinoflagellate cyst assemblages (e.g. de Vernal and Hillaire-Marcel, 2000) or δD in alkenones (e.g. Schouten et al., 2006; van der Meer et al., 2007 en 2008). However, none of these approaches is unequivocal (e.g. alkenones; Bendle et al. 2005).

Some planktonic organisms are well-known to show morphological variability depending on salinity, e.g. variable nodding in the ostracod *Cyprideis torosa*, van Harten (2000) and morphological variation in the coccoliths of *Emiliana huxleyi* (Bollman and Herrle, 2007). A similar dependence has been reported for *Lingulodinium machaerophorum* (Deflandre and Cookson, 1955) Wall, 1967, the cyst of the autotrophic dinoflagellate *Lingulodinium polyedrum* (Stein) Dodge, 1989 which forms extensive harmful algal blooms reported from coasts of California (Sweeney, 1975), Scotland

(Lewis et al., 1985), British Columbia (Mudie et al., 2002), Morocco (Bennouna et al., 2002), West Iberia (Amorim et al., 2001) and other coastal areas. This species can be considered as a model dinoflagellate since it is easily cultured and has been the subject of numerous investigations. An extensive review of these studies is given by Lewis and Hallett (1997). Process length variation of *Lingulodinium machaerophorum* was initially related to salinity variations in the Black Sea by Wall et al. (1973), and subsequently investigated by others for other regions (Turon, 1984; Dale, 1996; Matthiessen and Brenner, 1996; Nehring, 1994, 1997; Ellegaard, 2000; Mudie et al., 2001; Brenner, 2005; Sorrel et al., 2006; Marret et al., 2007). Kokinos and Anderson (1995) were the first to demonstrate the occurrence of different biometrical groups in culture experiments. Later culture experiments (Hallett, 1999) discovered a linear relationship between average process length and salinity, but also with temperature.

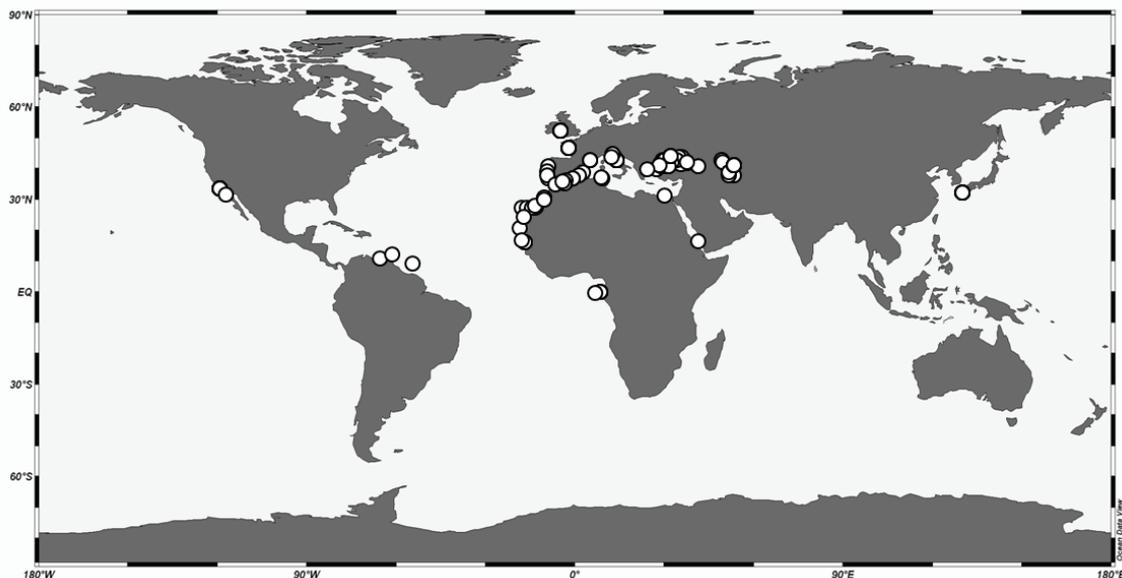


Figure 1. Distribution of the 144 surface samples where *Lingulodinium machaerophorum* process length were studied.

The process length of *L. machaerophorum* as a salinity proxy represents a large potential for palaeoenvironmental studies, since this species currently occurs in a wide range of marine conditions (Marret and Zonneveld, 2003), and can be traced back to the Late Paleocene (Head et al., 1996). The aim of the present study was to evaluate whether the average process length shows a linear relationship to salinity and/or temperature, and to assess its validity for palaeosalinity reconstruction. To achieve this goal, *L. machaerophorum* cysts were studied from surface sediments from numerous coastal

areas. Confocal laser microscopy was used for the reconstruction of the complete distribution of the processes on the cyst wall, which has important implications for cyst formation.

2. Material and Methods

2.1. Sample preparation and light microscopy

A total of 144 surface sediment samples were studied for biometric measurements of *L. machaerophorum* cysts from the Kattegat-Skagerrak, Celtic Sea, Brittany, Portuguese coast, Etang de Berre (France), Mediterranean Sea, Marmara Sea, Black Sea, Caspian and Aral Seas, northwest African coast, Canary Islands, coast of Dakar, Gulf of Guinea, Caribbean Sea, Santa Monica Bay (California), Todos Santos Bay (Mexico) and Isahaya Bay (Japan) (Figure 1). Most samples were core top samples from areas with relatively high sedimentation rates, and ages can be considered recent, i.e. a few centuries (see supplementary data). Five samples have a maximum age of a few thousand years, but since process lengths are as long as processes of recent, nearby samples, these samples can also be considered representative. In general, the cysts studied will give us a global view of the biometric variation of cysts formed during the last few centuries by *L. polyedrum*. It is assumed here that the environmental conditions steering the morphological changes within the cyst are similar to recent environmental conditions.

All the cysts were extracted according to different maceration methods described in the literature (see references in Table 1). Most methods use standard maceration techniques involving hydrochloric acid and hydrofluoric acid, sieving and/or ultrasonication. Regardless of the method used, the cysts all appeared similar in terms of preservation (Plates I-IV).

Almost all measurements were made using a Zeiss Axioskop 2 and Olympus BH-2 light microscope, equipped with a 100x oil immersion objective, and an AxioCam RC5 digital camera (Axiovision v.4.6 software) and Color View II (Cell F Software Imaging System) respectively. The absolute error on a single measurement was 0.5 μm . All measurements were done by Kenneth Neil Mertens, except for the samples from Portugal, which were measured by Sofia Ribeiro. Observer bias did not influence the measurements.

For each sample, the length of the three longest visible processes was measured together with the largest body diameter of 50 cysts for each sample. Measuring 50 cysts gave reproducible results: in sample GeoB7625-2 from the Black Sea, three process lengths. Results are stored by short to long process length per cyst for 50 cysts were measured, and the measurements were then repeated on 50 different cysts, showing no significant differences ($\bar{x}=13.50 \mu\text{m} \pm 2.99 \mu\text{m}$ and $\bar{x}=13.21 \mu\text{m} \pm 2.62 \mu\text{m}$, t-test: $p=0.37$). The length of each process was measured from the middle of the process base to the process tip. The absolute error in process measurement is $0.4 \mu\text{m}$. Within each cyst, three processes could always be found within the focal plane of the light microscope, and for this reason this number seemed a reasonable choice.

Three reasons can be advanced for choosing the longest processes. Firstly, the longest processes reflect unobstructed growth of the cyst (see below). Secondly, the longest processes enabled us to document the largest variation, and this enhanced the accuracy of the proxy. Thirdly, since only a few processes were parallel to the focal plane of the microscope, it was imperative to make a consistent choice. Sometimes fewer than 50 cysts were measured, if more were not available. Fragments representing less than half of a cyst were not measured, nor were cysts with mostly broken processes.

2.2. Salinity and temperature data

The biometric measurements on cysts from the different study areas were compared to both seasonal and annual temperature and salinity at different depths - henceforth noted as T_{0m} , T_{10m}, \dots and S_{0m} , S_{10m}, \dots , using the gridded $\frac{1}{4}$ degree World Ocean Atlas 2001 (Stephens et al. 2002; Boyer et al., 2002) and the Ocean Data View software (Schlitzer, R., <http://odv.awi.de>, 2008). For the Scandinavian Fjords, in situ data were available from the Water Quality Association of the Bohus Coast (<http://www.bvvf.com>).

2.3. Confocal laser microscopy

Confocal microscopy was performed using a Nikon C1 confocal microscope with a laser wavelength of 488 nm and laser intensity of 10.3%. No colouring was necessary since the cysts were sufficiently autofluorescent. The Z-stack step size was $0.25 \mu\text{m}$ with a Pixel dwell time of $10.8 \mu\text{s}$. The objective used was a 60x/1.40/0.13 Plan-Apochromat lens with oil immersion. After correcting the z-axis for differences in refractive index

between the immersion oil and glycerine jelly (here a factor of 78% of correction was used), images were rendered to triangulated surfaces (.stl files) with Volume Graphics VGStudioMax© software. These were imported in Autodesk 3DsMax©, where XYZ coordinates of the base and top of the processes were recorded. From these coordinates Euclidean distances were calculated, enabling the calculation of the process length and the distances between the processes. Distances to the two closest processes of each process were calculated, and by averaging these numbers, the average distance between processes was calculated. A more detailed description of the methodology is given at <http://www.paleo.ugent.be/Confocal.htm>.

Table 1. Average of process length from LM measurements, standard deviation, body diameter and standard deviation, average summer temperature and salinity at 30m water depth, ratio between both and density calculated from both.

Region	# samples	Processes measured	Average process length (μm)	Stdev (μm)	Average body diameter (μm)	Stdev (μm)	Average Summer T_{30m}	Average Summer S_{30m}	Density ($\text{kg}\cdot\text{m}^{-3}$)	Preservation	Reference
Caspian Sea-Aral Sea	13	1320	5.6	3.4	48.1	6.1	15.72	12.72	1008.87	Bad to good	Mamet <i>et al.</i> (2004), Sorrell <i>et al.</i> (2006), Leroy <i>et al.</i> (2006) and Leroy (unpublished data), Leroy <i>et al.</i> (2007)
Etang de Berre	2	300	7.5	2.5	44.9	4.5	19.91	26.10	1018.14	Average	Leroy (2001) & Robert <i>et al.</i> (2006)
Japan	5	755	8.0	1.9	45.3	5.7	24.54	33.72	1022.64	Good	Matsuoka (unpublished data)
Caribbean – West Equatorial Atlantic	6	306	13.0	4.4	44.1	6.4	26.19	36.08	1023.92	Average	Vink <i>et al.</i> (2000), Merrens <i>et al.</i> (2008) and Vink <i>et al.</i> (2001)
Scandinavian Fjords – Kattegat-Skagerrak	26	2271	13.2	4.2	47.9	6.4	16.55*	24.14*	1017.43	Bad to good	Grossfeld & Harland (2001), Gundersen (1988), Ellegaard (2000), Christensen <i>et al.</i> (2004) and Persson <i>et al.</i> (2000)
East Equatorial Atlantic – Dakar Coast	7	903	13.2	3.4	46.6	6.2	22.88	35.52	1024.49	Bad to good	Mamet <i>et al.</i> (1994) and Boumetthan <i>et al.</i> (unpublished data).
Black Sea and Marmara Sea	35	5196	15.0	4.1	46.3	4.6	12.22	20.08	1015.14	Good	Verleye <i>et al.</i> (2008), Cauer & Algan (2002), Cauer (unpublished data), Cagatay <i>et al.</i> (2000), Naudts (unpublished data), Popescu <i>et al.</i> (unpublished), Mudde <i>et al.</i> (2007) and van der Meer <i>et al.</i> (2008)
Portugal - Brittany	9	1350	16.8	3.6	45.3	5.5	16.53	35.22	1025.93	Good	Ribeiro <i>et al.</i> (unpublished data), Goubert (unpublished data)
NW Africa	12	1749	18.4	3.8	48.1	6.3	19.47	36.56	1026.07	Average to good	Holzwarth <i>et al.</i> (unpublished data), Kuhlmann <i>et al.</i> (2004), Richter <i>et al.</i> (2007)
Mediterranean – Red Sea	36	3507	19.6	4.4	45.6	6.1	18.39	37.57	1027.28	Average to good	Singiorgi <i>et al.</i> (2005), Londeix (unpublished data), Comboutien-Nebout <i>et al.</i> (1999), Pilet (unpublished data), Schoel (1974) and Kolhoff <i>et al.</i> (2008)
Pacific	9	1224	21.2	4.3	47.7	6.1	14.39	33.45	1025.04	Good	Pospelova <i>et al.</i> (2008) and Peña-Maunjarrez <i>et al.</i> (2005)
Celtic Sea	6	750	21.8	4.1	47.8	5.7	13.50	34.30	1025.88	Good	Mamet & Scurce (2002)

*For this region data from 0m water depth is used

3. Results

3.1. Preservation issue

To establish the validity of the measurements, preservation needs to be taken into account. Two types of degradation were considered: mechanical and chemical. Three categories were used to describe the mechanical degradation of the cysts: bad (most cysts were fragmented or torn, and processes were broken), average (about half of the cysts were fragmented or torn, and few processes were broken, and good (few cysts were torn or fragmented, and were often still encysted) (see Table 1).

The differences in mechanical breakdown were, from our experience, largely caused by post-processing treatments such as sonication. Prolonged sonication, however, does not significantly change the process length variation. The sample from Gullmar Fjord (average process length 14.6 μ m, st. dev. 4.0) was sonicated in an ultrasonic bath for two minutes and the results were not significantly different from samples that were not sonicated (average process length 14.3 μ m, st. dev. 4.1) (t-test: $p=0.38$).

Chemical breakdown could be caused by oxidation or acid treatment. *L. machaerophorum* is moderately sensitive to changes in oxygen availability (Zonneveld et al., 2001). Cysts from samples treated with acetolysis were clearly swollen (Plate 2.8). Most interestingly, both processes and cyst body swell proportionately. These samples were not used for analysis. Similar results were noted after treatment with KOH. These maceration methods should not be used in biometric studies. Cysts extracted using warm HF showed traces of degradation (see Plate III.23, III.24), but process length did not change.

3.2. Overall cyst biometrics for the multi-regional dataset

The 19,611 process length measurements resulted in a global average of 15.5 μ m with a standard deviation of 5.8 μ m, and a range from 0 to 41 μ m (Figure 2). Most cysts encountered were comparable to the forms described by Kokinos and Anderson (1995), and bald cysts were rare. The range we found is clearly broader than the 2 to 21 μ m range postulated by Reid in 1974. The skewness of the distribution was -0.12, since there is some tailing at the left side of the size frequency curve (Figure 2). The asymmetric distribution was due to a standard deviation that increased synchronously

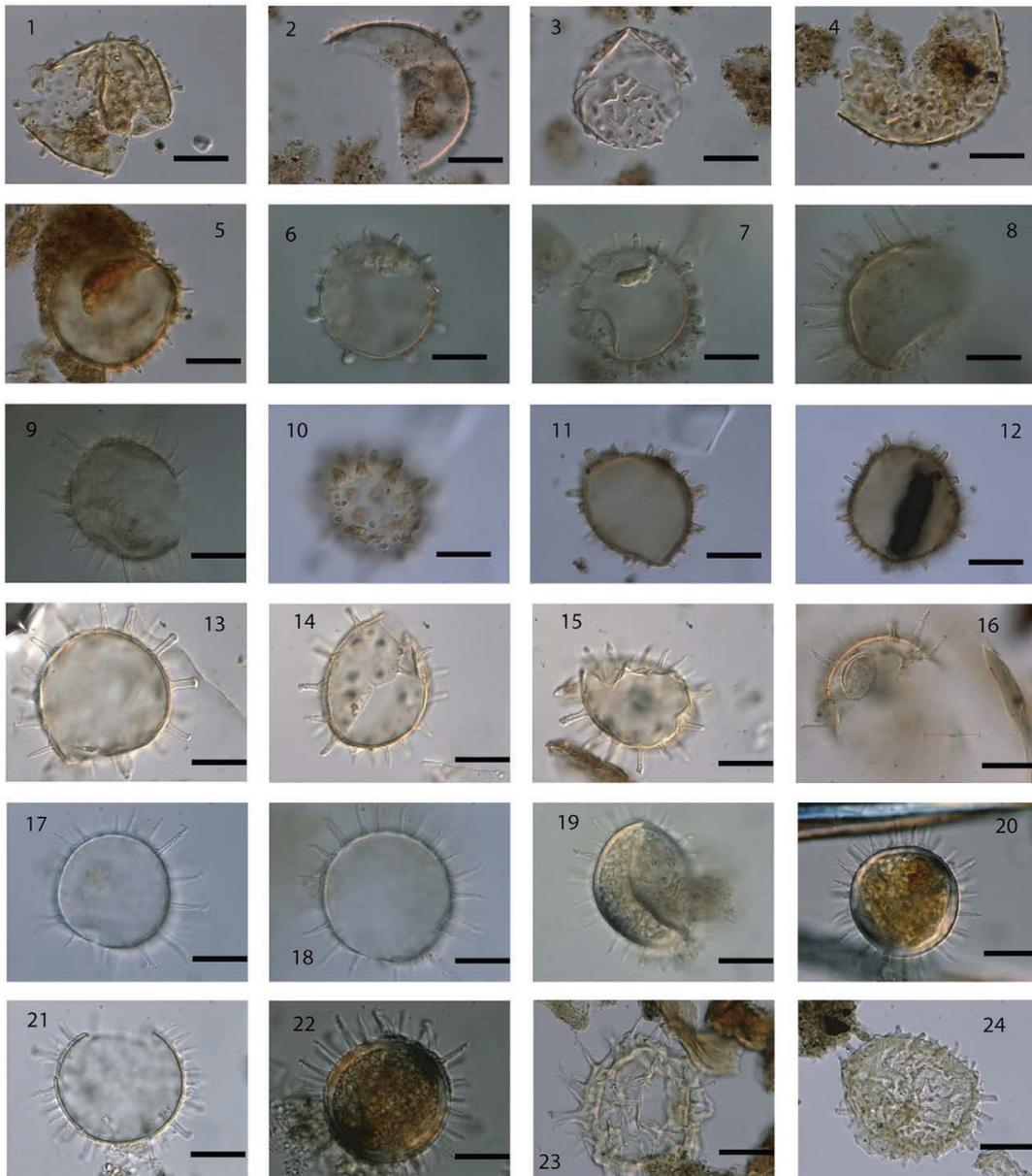


Plate I. *Lingulodinium machaerophorum* cyst from Caspian Sea (1-5), Aral Sea (6-9), Etang de Berre (10-12), Baltic Sea (13-15) and Scandinavian Fjords (16-24). Specific sample names are 1-4. CPO4.5.US02. 6-7.AR23. 8-9. AR17. 10-12. Etang de Berre (19). 13.NG6.14.NG.7.15. NG.9.16. Limfjord. Note inclusion of *Nannobarbophora* acritarch. 17. Havstenfjorden 18-19. Guumar Fjord 20-21. G2.22.K2. 23-24. Risor Site. All scale bars are 20 μ m.

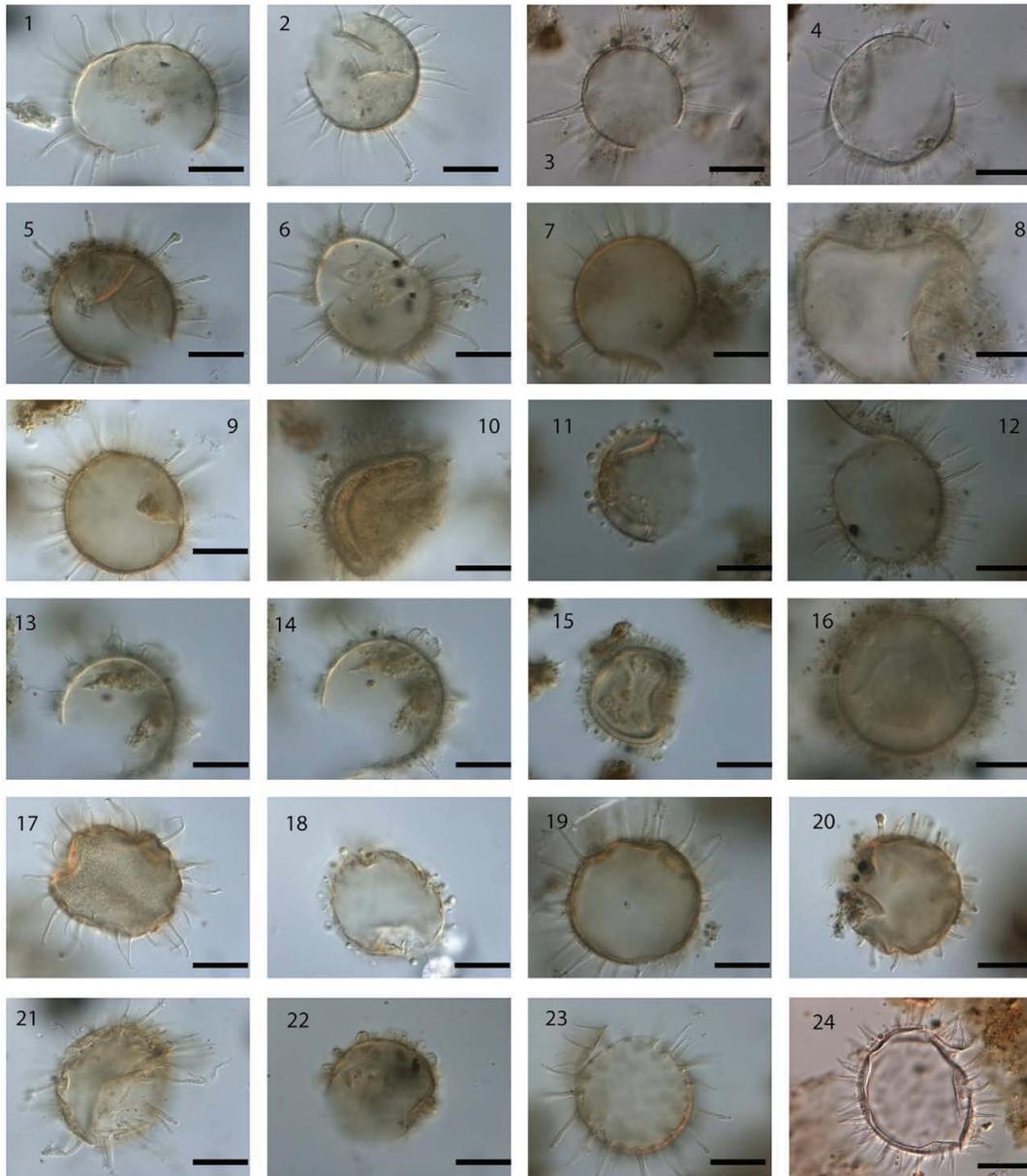


Plate II. *Lingulodinium machaerophorum* cyst from Marmara Sea (1-5) and Black Sea (5-24), Note the wide range of morphotypes occurring in these samples. Specific sample names are: 1-2.Dm 13 3-4. Dm5 5-6. Knorr 134.72.7. Knorr 134.51.8. GGC18 Swollen cyst due to use of acetolysis. 9-10. Knorr 134.35.11-12. Knorr134.2. 13-15. B2KS33 0-1. Note merged process in 13 and 14. 16.B2 KS 01 0-1. Note globules at basis of processes. 17-18. All 1443.20-21. All 1438.22. All 434. Note merged processes. 23. All 145.1.24. GeoB7625. coloured with safranin-O. All scale bars are 20µm.

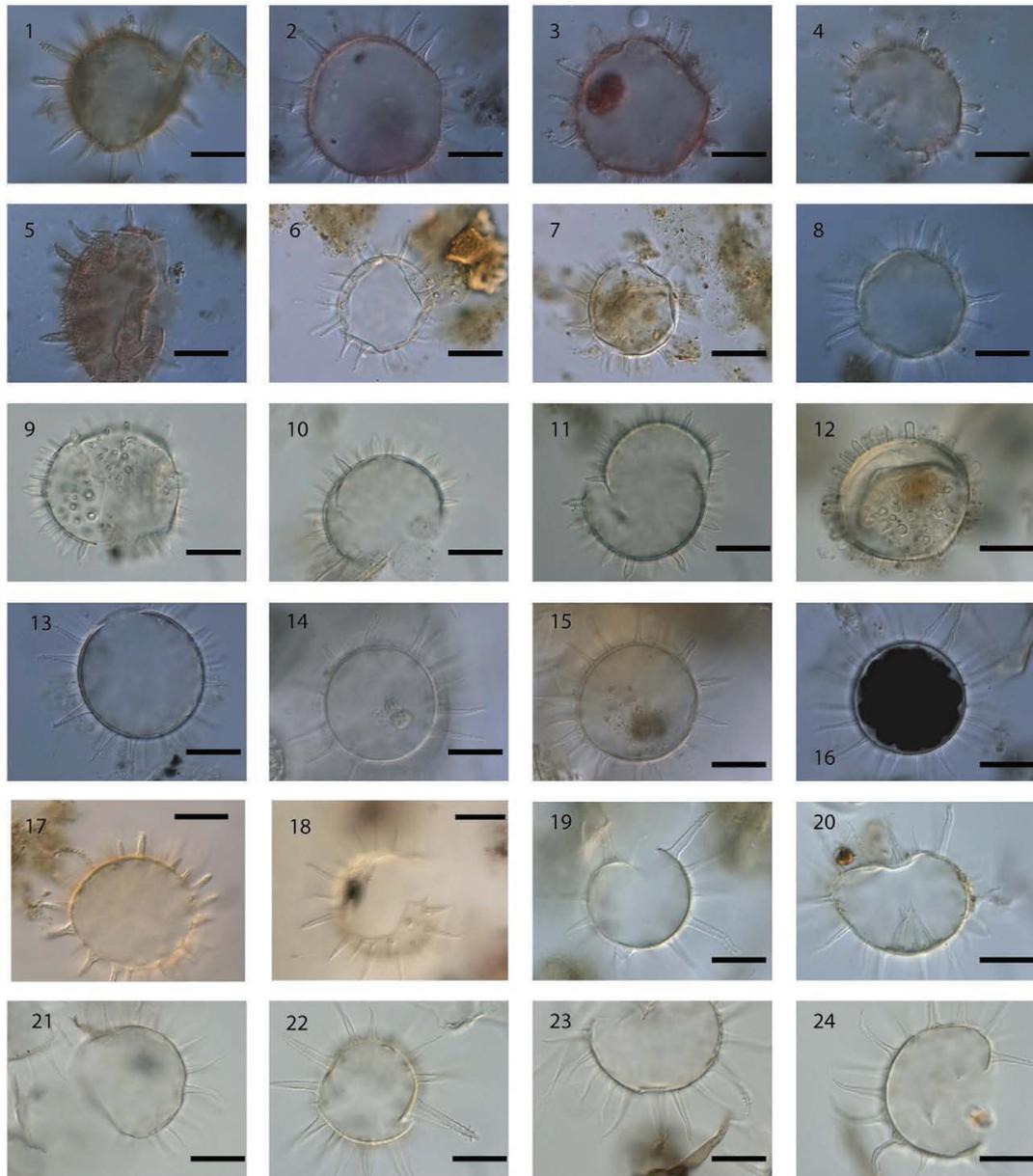


Plate III. *Lingulodinium machaerophorum* cyst from East Equatorial Atlantic (1-7), West Equatorial Atlantic (8), Japan (9-12), Britany (13-16), Portugal (17-18) and NW Africa (19-24). Specific sample names are: 1. 6437-1.2-3.6847-2. 4-5.6875-1.6-7. GeoB9503 Dakar.8.M35003-4. 9-10. AB22. 11. AB40.12.ISA2.13.BV1. 14-15. BV3.16.BV5.17-18. Tejo. 19-20. GeoB4024-121. GeoB5539-2.22-24. GeoB5548. All scale bars are 20µm.

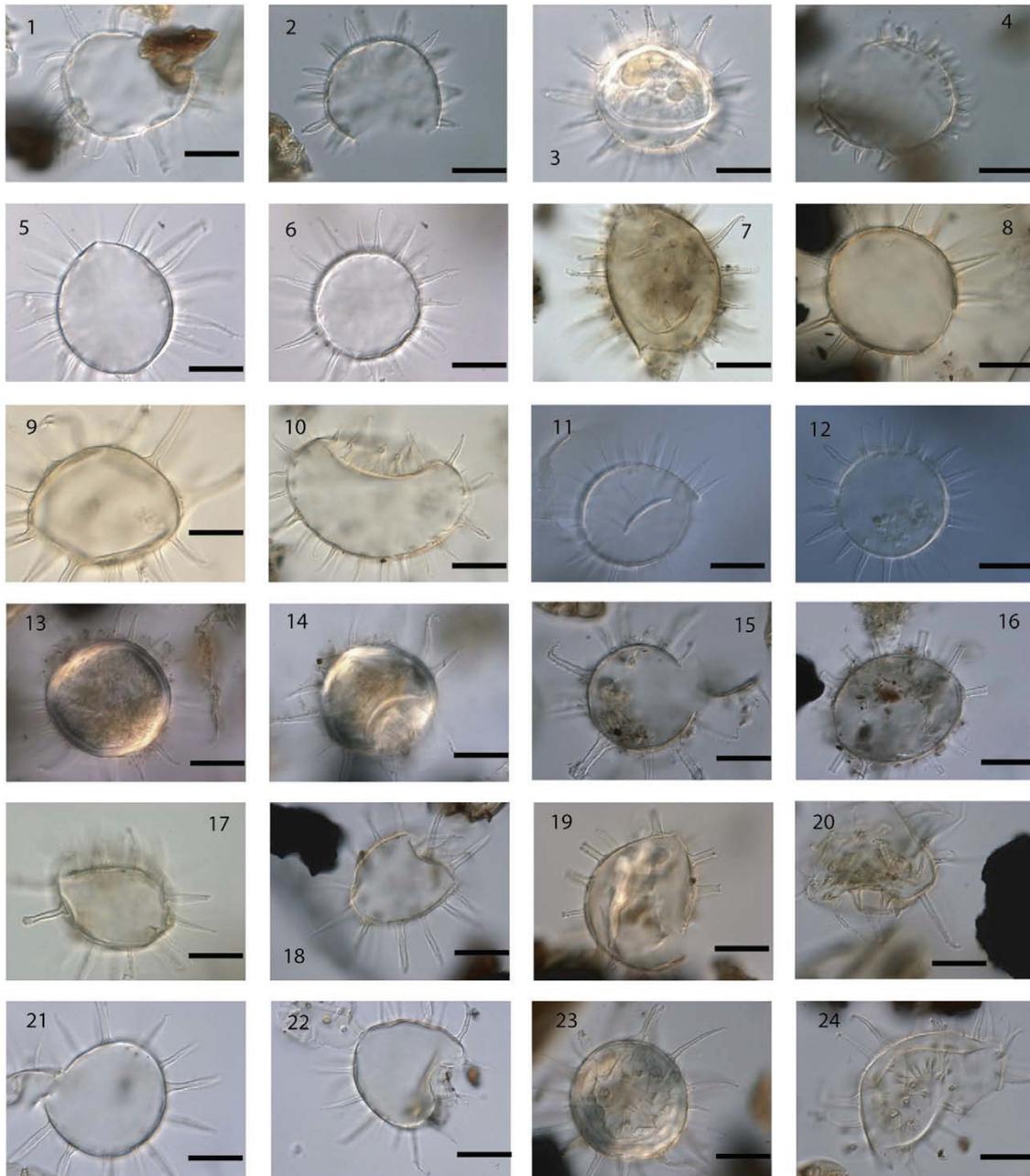


Plate IV. *Lingulodinium machaerophorum* cyst from Mediterranean (1–11), Red Sea (12) Celtic Sea (13–16) and Pacific Ocean (17–24). Note the widely distributed very long processes in Celtic Sea and Pacific Ocean samples. Specific samples are: (1) North Adriatic AN71. (2–4) North Adriatic AN71. (5–6) Nile Delta. (7) 273.4. (8) 5153. (9) 516.6. (10) 521.3. (11–12) Red Sea VA01-200P. (13–14) Station9 6.99. (15) Station 9 5.00 (16) Station 9 2.99 with truncated processes. (17) Todos Santos Bay (Mexico). (18–19) Santa Monica Bay, UVic07-89618 with truncated processes. (20) UVic07-897. (21–22) UVic07-898.22 with truncated processes. (23–24) UVic07-902. All scale bars are 20 μ m.

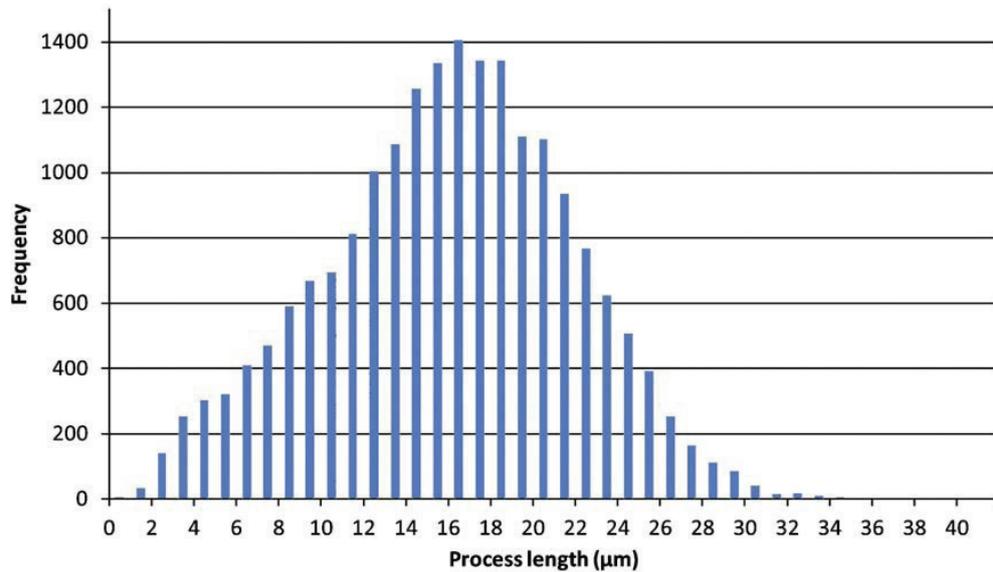


Figure 2. Size-frequency spectrum of 19,611 process measurements.

with the average process length. This could be explained partly by the methodological approach - errors on the larger measurements were larger, since larger processes were more often curved or tilted - and by the more common occurrence of cysts with relatively shorter processes in samples that mostly contain cysts with longer processes (also evident in regional size-spectra, Figure 4).

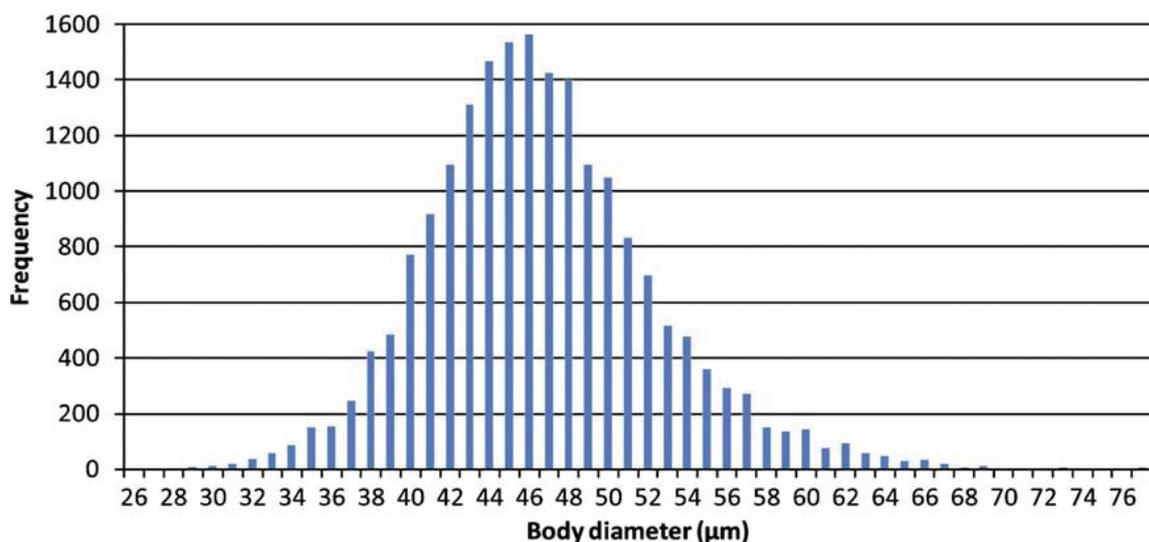


Figure 3. Size-frequency spectrum of 6211 body diameter measurements.

The 6,537 body diameter measurements resulted in an average body diameter of 46.6µm with a standard deviation of 5.8µm. The range was from 26 to 75µm. This was again a broader range than the 31 to 54µm given by Deflandre and Cookson (1955) and Wall and

Dale (1968). This discrepancy could be explained partly by cysts sometimes being compressed or torn, yielding an anomalously long body diameter. This mechanical deformation of the cyst explains also a positive skewness of the size-frequency spectrum (Figure 3).

The averaged data of *L. machaerophorum* cysts in every region is given in Table 1, sorted from low to high average process length. The individual size-frequency spectra are shown in Figure 4 and the cysts are shown in Plate I-IV. All measurements are available as supplementary data.

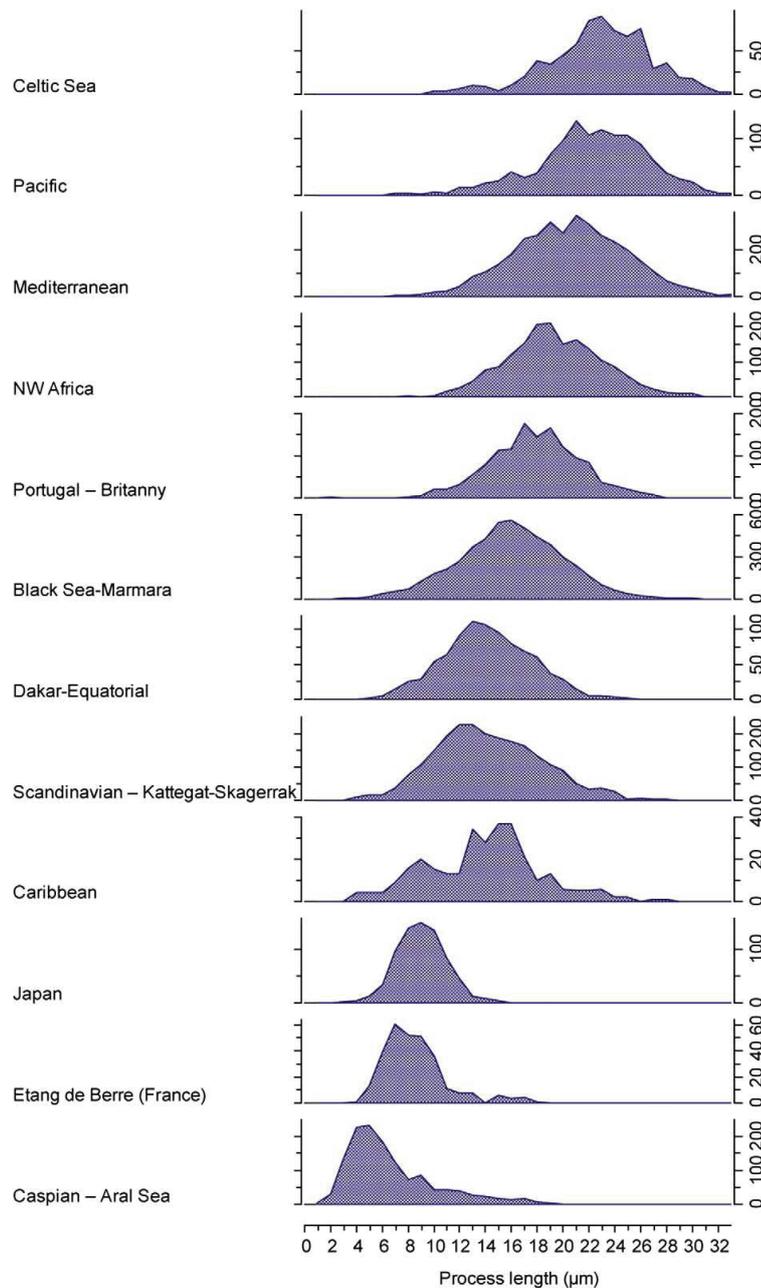


Figure 4. Size-frequency spectra of regional process measurements, sorted from top (long average processes) to bottom (short average processes).

3.3. Comparison of process length with salinity and temperature

Firstly, data from the Scandinavian Fjords and the Kattegat-Skagerrak were excluded from all relations since they significantly increased the scatter on all regressions. The reason is given below in the Discussion.

The relation of the average process length of *L. machaerophorum* with only the salinity data, fits best with the winter S_{0m} ($R^2=0.54$). When compared to temperature data alone, the best relationship is with the winter T_{50m} ($R^2=0.06$).

A much better relationship can be found with salinity divided by temperature at a water depth of 30 m from July to September (summer). This relationship is expressed as $S_{30m}/T_{30m} = 0.078 \cdot \text{average process length} + 0.534$, and has an $R^2=0.69$ (Figure 5) and a standard error is $0.31 \text{ psu}/^\circ\text{C}$. Since seawater density is dependent on salinity and temperature, one could expect that density would have a similar relationship with process length. However, the regression with water density at 30m water depth shows a stronger relation to process length ($R^2=0.50$) than with salinity alone ($R^2=0.42$ with summer S_{30m}), but not better than with S_{30m}/T_{30m} .

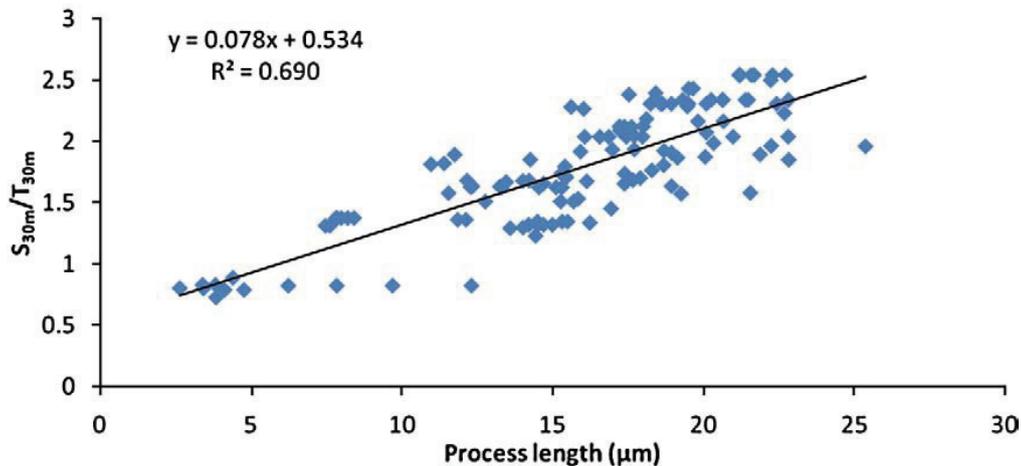


Figure 5. Regression between average process length and summer S_{30m}/T_{30m} for the 144 surface samples.

An overview of the results in the studied areas is given in Table 1. Next to average process length, salinity, temperature, and S_{30m}/T_{30m} , seawater density data are given, and illustrate that this parameter does not show a better fit than the S_{30m}/T_{30m} ratio. The regression between this averaged data from each region is $S_{30m}/T_{30m} = 0.085 \cdot \text{average process length} + 0.468$, $R^2=0.89$ (Figure 6).

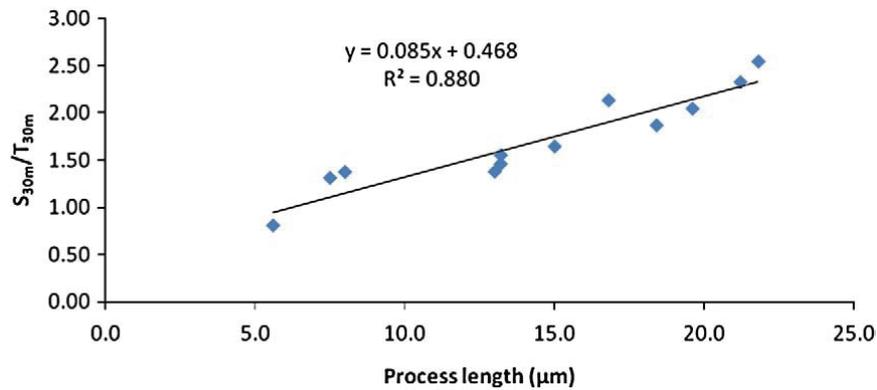


Figure 6. Regression between average process length and summer $S_{30\text{ m}}/T_{30\text{ m}}$ for every region separately.

3.4. Process length in relation to body diameter

No relation between the process length and cyst body diameter was found ($R^2=0.002$). This was expected since culture experiments also revealed no relation between the body diameter and the salinity (Hallet, 1999). Furthermore, no significant relation was found between body diameter with the ratio between salinity and temperature at different depths. Variations in cyst body diameter are probably caused mainly by germination of the cyst or compression.

3.5. Process length in relation to relative cyst abundance

Mudie et al. (2001) found a correlation of $R^2 = 0.71$ between the relative abundance of *L. machaerophorum* (all forms) and increasing salinity between 16 and 21.5psu for Holocene assemblages in Marmara Sea core M9. To check this relation in our dataset, the relative abundances of *L. machaerophorum* were determined in 92 surface samples. No significant linear relation between relative abundances in the assemblages and either the process length or the cyst body diameter was found. No significant relationship between relative abundance and temperature or salinity data was found. This is not surprising since the relationship between relative abundances and environmental parameters is not linear, but unimodal (Dale, 1996), and several other factors play a role in determining the relative abundances on such a global scale, mostly relative abundances of other species (closed-sum problems).

3.6. Confocal laser microscopy

All processes on 20 cysts from the North Adriatic Sea (samples AN71 and AN6b) and one from the Gulf of Cadiz (sample GeoB9064) were measured, resulting in 1460 process measurements. The average distances between the processes were also calculated from these measurements. A summary of the results is given in Table 2. Process length ranged from 0 to 31 μ m, which differs from the 1,983 process lengths from the North Adriatic Sea samples measured with transmitted light microscopy (6 to 34 μ m). The shift in the frequency size spectra was obviously due to the fact that only the longest processes were measured (Figure 7). Most remarkable was the large peak around 3 μ m in the confocal measurements. Apparently, a large number of shorter processes were present on most of these cysts.

Table 2. Average process length, stdev, number of processes measured and average distance between processes from CLSM in full measurements.

Cyst number	Sample	Average length (μ m)	Stdev length (μ m)	# Processes measured	Body diameter (μ m)	Average distance (μ m)
2	AN71	9.82	5.78	79	44.53	4.35
4	AN71	7.26	5.72	89	39.84	3.76
5	AN71	15.87	5.06	50	56.89	5.79
7	AN71	9.80	6.36	72	45.11	4.68
9	AN71	17.79	6.41	62	43.25	6.78
10	AN71	10.32	6.49	67	39.95	4.55
11	AN71	12.25	1.90	56	43.26	6.21
12	AN71	6.85	4.82	107	39.34	3.98
13	AN71	11.50	7.26	89	43.32	4.76
14	AN71	15.88	7.27	61	51.76	6.90
15	AN71	13.20	6.19	28*	40.54	5.67
16	AN71	15.43	4.19	59	41.93	5.61
17	AN71	12.44	5.43	71	44.69	4.95
2	AN6B	11.79	6.09	71	36.38	4.40
4	AN6B	9.86	5.47	103	45.60	4.88
5	AN6B	9.14	7.13	102	42.87	4.05
6	AN6B	12.17	4.72	76	47.13	4.71
8	AN6B	12.53	4.53	58	57.84	5.66
9	AN6B	13.07	3.50	51	40.77	5.40
10	AN6B	10.30	4.68	76	41.20	4.44
1	GeoB9064	18.16	6.76	33	36.10	6.24
Average		12.16	5.51	69.52	43.92	5.13
Stdev		3.11	1.33	21.06	5.68	0.91

* This number was not used in the regression with process length, since less than half of this cyst was preserved.

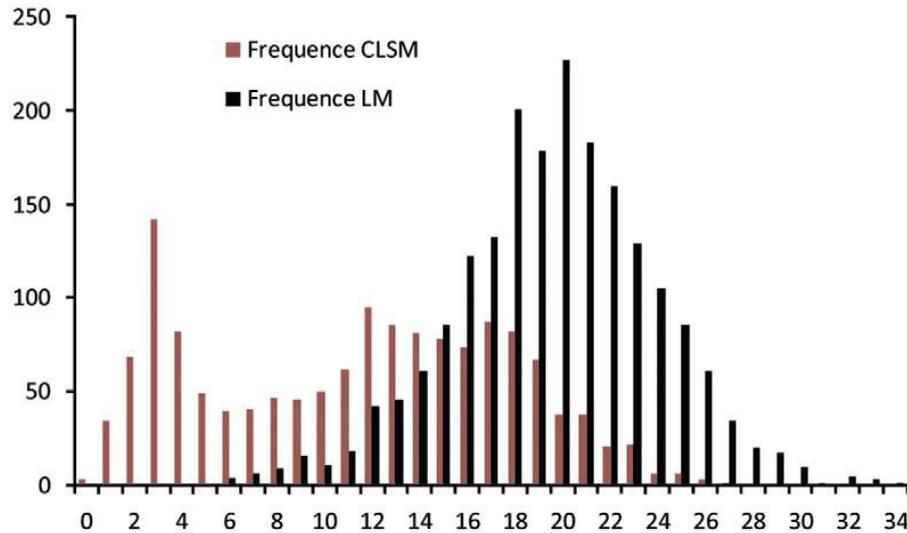


Figure 7. Comparison between the size-frequency spectra from 1460 confocal measurements (CLSM) from the North Atlantic Sea (samples AN71 and AN6b) and from the Gulf of Cadiz and 1983 light microscope (LM) measurements from the North Adriatic.

It is noteworthy that the average process length was significantly related to the average distance between the processes ($R^2=0.78$) (Figure 9), and that the number of processes is significantly inversely related to the average process length ($R^2=0.65$) (Figure 8). This lower R^2 can be explained by the incompleteness of the cysts: all cysts were germinated and thus lacking opercular plates, which can number between one and five or indeed more in the case of epicystal archeopyles (Evitt, 1985). This implies that a large number of processes can be missing, and it would be subjective to attempt a correction for the missing processes. It was not possible to use encysted specimens since the strong autofluorescence of the endospore of these specimens obscured many of the least autofluorescent processes. No significant relation was found between the body diameter and the average process length ($R^2=0.04$), which confirms the observation with transmitted light microscopy.

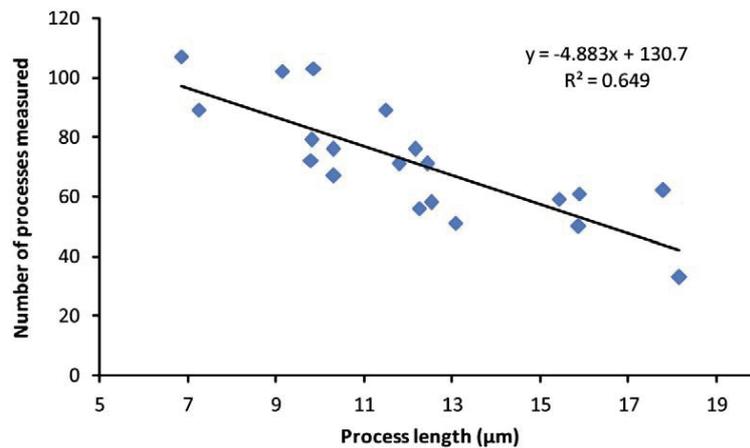


Figure 8. Regression between average process length and the number of processes for the cysts measured with conofocal microscopy.

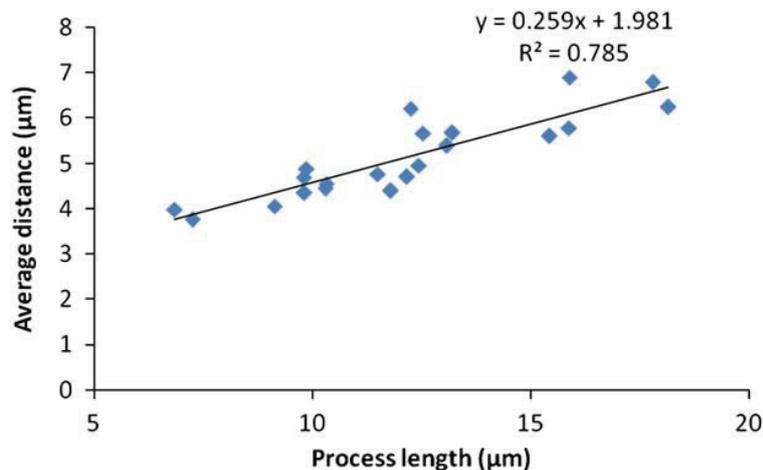


Figure 9. Regression between average process length and the average distance between process bases for the cysts measured with conofocal microscopy.

4. Discussion

4.1. Process length correlated to summer S30m/T30m: is it realistic?

The quasi unimodal size frequency spectrum of both process length and cyst body diameter (Figure 2-3), plus the correlation between the average process length and the summer S30m/T30m, strongly confirm that all recorded cysts are ecophenotypes of a single species. It is furthermore not surprising that the most significant relation was found with the summer S30m/T30m depth. These three extra parameters - seasonality, temperature and depth - are discussed below.

Late summer-early autumn is generally the time of maximum stratification of the surface waters. Reduced salinity would enhance the water column stability with the generation of a pycnocline, and lowered water column turbulence, conditions that favour growth of *Lingulodinium polyedrum* (Thomas and Gibson, 1990). In most upwelling regions, this would coincide with periods of upwelling relaxation (Blasco, 1977). Late summer-early autumn is the time of the exponential growth phase of *Lingulodinium polyedrum*, which coincides with peak production of *Lingulodinium machaerophorum* cysts, at least in Loch Creran northwest Scotland (Lewis et al., 1985) and Todos Santos Bay, Mexico (Peña-Manjarrez et al., 2005). Culturing suggests that the cyst production is triggered by nutrient depletion, and influenced by temperature (Lewis and Hallett, 1997). A relation between process length and both temperature and salinity is indeed not surprising since the formation of processes can be considered a biochemical process (Hallett, 1999), dependent on both temperature and salinity. The culture experiments by Hallett (1999) confirm a positive relation to salinity and a negative relation to temperature. Moreover, the cysts are probably formed deeper in the water column, which would explain the fit to a 30 meter depth. It is well known that *Lingulodinium polyedrum* migrates deep in the water column (Lewis and Hallett, 1997). A similar vertically migrating dinoflagellate, *Peridiniella catenata*, also forms its cysts deeper in the water column, mostly at 30-40 m depth (Spilling et al., 2006). These cysts are probably formed within a range of water depths, and 30 m depth reflects an average depth.

The ranges of temperature (9-31°C) and salinity (12.4-42.1psu) at 30 meter depth represent the window in which cyst formation takes place. Cultures show that *Lingulodinium polyedrum* forms cysts at salinities ranging from 10 to 40psu (Hallett, 1999), and this fits well with the results obtained in this study. The direct link between process length and both salinity and temperature is proven by culture data (Hallett, 1999), and the relation to deeper salinity and temperature data suggests that cyst formation more often than not takes place deeper in the water column, where salinities are higher and temperatures lower, which suggests that caution is needed before linking *Lingulodinium machaerophorum* cyst abundances directly to surface data. This could explain the occurrence of cysts of *Lingulodinium polyedrum* in regions with surface salinities as low as 5psu (e.g. McMinn, 1990, 1991; Dale, 1996; Persson et al., 2000).

No better relation was found with density despite its dependence on salinity and temperature. Apparently, density as calculated from salinity and temperature, and pressure (water depth) by Fofonoff and Millard (1983) is much more determined by salinity, and less by temperature, than the measured average process length.

4.2. Transport issues

Lingulodinium machaerophorum occurs in estuaries, coastal embayments and the neritic environments of temperate to subtropical regions (Lewis and Hallett, 1997). However, transport of the cysts into other areas by currents must be considered, and the records of *L. machaerophorum* in oceanic environments must be attributed to reworking or long-distance transport (Wall et al., 1977). A classic example is the upwelling area off northwest Africa where the cyst has been recorded over a much wider area than the thecate stage (Dodge and Harland, 1991). In this study, it was assumed that long-distance transport was not an important factor, since the transported cysts would be transported from areas with minor salinity and temperature differences, which would, according to the equation (see above), be reflected in negligible changes in process length.

4.3. The Problematic Kattegat–Skagerrak and Scandinavian Fjord samples

It is noteworthy that the inclusion of the Kattegat-Skagerrak and Scandinavian samples increased the scatter of the regression significantly. Two causes can be suggested. Firstly, since most samples plot above the regression line, the average process length could be too short. Most probably this is not linked to a preservation issue, since the average preservation is average to good (except for the Risør site), and broken processes are rare. All recovered cysts are from the uppermost section of box cores, and are thus recently formed. One possible explanation could be that these specimens are genetically different which could result in slightly different morphologies, although there is no *a priori* reason why this should be so, and conflicts with the unimodal size-frequency distribution of process length.

Secondly, summer S_{30m}/T_{30m} could be incorrect, and this can be attributed to several causes. On one hand, the cyst production could have taken place at different water depths. When included in the global dataset of summer S_{30m}/T_{30m} , the relation between average process length is more significant ($R^2=0.61$) when surface data is used for the

Kattegat-Skagerrak and Scandinavian samples. On the other hand, the timing of cyst production might be different. *L. polyedrum* blooms in fjords probably occur very quickly and are short-lived, followed by a long resting period (Godhe and McQuoid, 2003). As for the Kattegat-Skagerrak, the salinity-driven stratification, with higher salinity bottom waters and low salinity surface waters, could result in a very particular environment. In this way, they are formed probably under specific salinity and temperature, and which could explain the scatter increase.

4.4. Confocal measurements and implications for cyst formation

First, a short description of cyst formation is given as described by Lewis and Hallett (1997) and Kokinos and Anderson (1995). The motile planozygote ceases swimming, ejects the flagella, and the outer membrane swells. The thecal plates of the planozygote dissociate and are pulled away from the cytoplasm by the ballooning of the outer membrane and underneath this, the formation of the cyst wall occurs. A layer of globules (each $\sim 5 \mu\text{m}$ across) surround the cytoplasm and the spines grow outwards taking the globules with them. These terminal globules collapse to form spine tips and variations in this process confer the variable process morphology observed in *L. machaerophorum*. Probably, membrane expansion is activated by osmosis (Kokinos, 1994), which causes a pressure gradient. According to Hallett (1999) the outer membrane always reaches full expansion, both for short and long process bearing individuals. The measurements with the confocal laser microscope clearly show that a positive relation exists between the process length and the distance between processes, and a negative relation between the processes length and the number of processes. These findings lead towards three implications. Firstly, the amount of dinosporin necessary for construction the processes would be constant, at least for the studied cysts from the Mediterranean Sea. However, one needs to assume that the amount of dinosporin is proportionate to the number of processes, multiplied by the average process length. This entails that one supposes that the amount of dinosporin needed for formation of the periphragm is constant, which is reasonable since the body diameter is independent of process length. Secondly, the good correlation between the average distance and the process length, together with the observation that globules are all forming simultaneously (Hallett, pers. comm.), suggests that the process length is predetermined. Thirdly, these observations suggest the existence of two end members: one with many closely spaced short processes,

and one with a few, more widely spaced, long processes (Figure 10). This gradient in biometrical groups can also be visually observed in transmitted light (Plates I to IV).

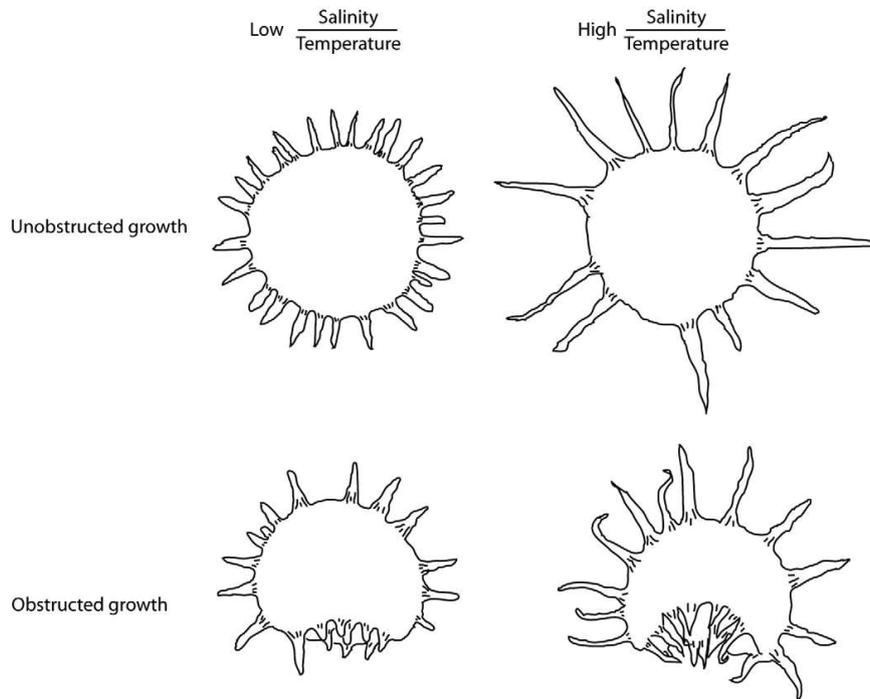


Figure 10. Conceptual model for process formation.

In order to reconcile these observations with observations from cultures, the physico-chemical properties of dinosporin have to be considered. According to Kokinos (1994), dinosporin consists of a complex aromatic biopolymer, possibly made of tocopherols. However, upon re-analysis, De Leeuw et al. (2005) showed the tocopherol link to be untrue. It can now be speculated that a certain fixed amount of this precursor monomer (probably a sugar, Versteegh, pers. comm.) for dinosporin is distributed across the sphere, in such a way that a minimum of energy is necessary for this process. This can happen through a process of flocculation (as proposed by Hemsley et al. (2004), and is dependent on both temperature and salinity. Fewer but larger colloids of the monomer will be formed when S_{30m}/T_{30m} is higher and these will coalesce on the cytoplasmic membrane. When many small colloids are formed, there is a chance that two or more colloids are merged, and form one larger process (Plate 2, 13-15 and 22). This theory can also explain the rare occurrence of crests on such cyst species as *Operculodinium centrocarpum*, where crests are formed when processes are closely spaced. In the next step, the visco-elastic dinosporin is synthesized on the globules, and stretches out in a radial direction. This stretching is clearly visible in the striations at the base of the

processes. Another result of this stretching is the formation of tiny spinules at the distal tip. These are more apparent on the longer processes, and could be the result of a fractal process: what happens at a larger scale, namely the stretching of the processes, is repeated here at a smaller scale, the stretching of the spinules. However, it is unlikely that the stretching is solely caused by membrane expansion. Hallett (1999) indicated that the outer membrane expansion is independent of the definitive process length. Thus the stretching is most probably caused by the combination of outer membrane expansion and a chemical process, similar to the swelling of cysts caused by acetolysis or KOH (see below).

Two types of cysts deserve special attention. Clavate or bulbous process bearing cysts (Plate 1, 13; Plate 2, 11, 20) were frequently encountered in surface sediments from low salinity environments (Black Sea, Caspian Sea, Aral Sea and the Kattegat-Skagerrak). They were frequently encountered in culture by Kokinos and Anderson (1995), but rarely by Hallett (1999). They only seem to differ from normal processes, in that globules were not able to detach from these processes. This is supported by the fact that the length of normal processes on cysts bearing clavate bearing processes is the same as for clavate processes.

The second type of cyst deserving attention is the bald or spheromorphic cyst. Lewis and Hallett (1997) observed that these cysts are not artifacts of laboratory culturing, since cysts devoid of processes occur in the natural environment of Loch Creran in northwest Scotland. Moreover, as noted by Persson from culturing experiments, these cysts are still viable, and thus cannot be regarded as malformations. Apart from the Aral Sea, very few bald cysts were recorded in surface sediments. It appears that on these cysts, process development did not take place. It can be speculated that this could be caused by a very early rupture of the outer membrane or the inability of the precursor monomer to flocculate at a very low S_{30m}/T_{30m} .

4.5. Process distribution

The process distribution on *Lingulodinium machaerophorum* was considered to be intratabular to non-tabular (Wall and Dale, 1968), although some authors noted alignment in the cingular area (Evitt and Davidson, 1964, Wall et al., 1973). Marret et al. (2004) showed a remarkable reticulate pattern in the ventral area on cysts with very short processes from the Caspian Sea, suggestive of a tabular distribution. Our findings

indicate a regular and equidistant distribution of the processes, with evidence of a tabulation pattern lacking.

The process length distribution is not uniform. In cultures, cysts are formed at the bottom of the observation chambers, and this results in an asymmetrical distribution of the processes on the cysts, where shorter processes are formed at the obstructed side, and longer processes at the unobstructed side (Kokinos and Anderson, 1995; Hallett, 1999). When it is assumed that a constant amount of dinosporin is distributed over the body, aberrantly long processes would form at the unobstructed side, and aberrantly short processes at the obstructed side. Our observations confirm this phenomenon: cysts from shallow areas show a similar asymmetry. The frequent occurrence of short processes on cysts from shallow areas in the Mediterranean Sea can be explained in a similar way (Figure 7). If one measures the longest processes on these cysts, values will be slightly larger than would be expected from our equation.

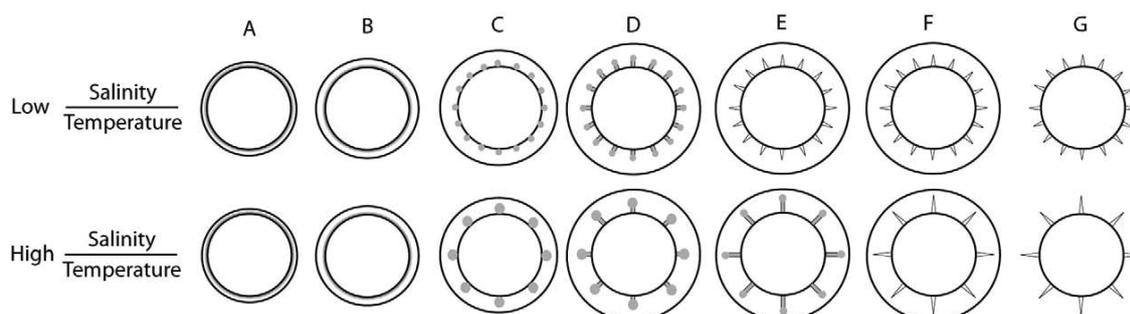


Figure 11. Suggested formation process for the two end members based on observation and documentation by Kokinos and Anderson (1995) and Hallett (1999), and theoretical consideration by Hamsley et al. (2004). Monomer is shown in grey, membranes and polymerised coat in black. (A-B) The outer membrane starts to expand, a fixed amount of monomer is formed and starts to coalesce on the cytoplasmic membrane. (C) depending on environmental parameters (salinity and temperature), a lot of small or few large colloids of the monomer are formed. (D) Visco-elastic dinosporin is synthesized on the globules and stretches in a radial direction. (E) Membrane expansion often comes to a stop before radial stretching ends. (F) Formation of longer process takes longer than shorter process formation. (G) Membrane rupture occurs.

This obstruction factor needs thus to be incorporated into our conceptual model (Figure 10). It is furthermore noticeable that a lot of the non-shallow cysts show this asymmetry to a certain degree (Plate 1-7). So, to a certain extent, this obstruction could be occurring more generally. The frequent occurrence of short processes along the

cingulum could also be explained in a similar way, if the cysts were to be formed in a preferred orientation, with the obstructed side along the archeopyle.

4.6. Biological function of morphological changes?

The final consideration deals with the biological function of the processes. Possible functions of spines on resting stages are proposed by Belmonte et al. (1997), and include flotation, clustering and enhanced sinking, passive defence, sensory activity and/or chemical exchanges and dispersal. Since the link between process length and S_{30m}/T_{30m} exists and density is also dependent on S_{30m}/T_{30m} , it is obvious that either flotation or clustering and enhanced sinking will be the most important biological function of morphological changes of the processes. Longer processes increase the drag coefficient of the cyst and thus increase floating ability according to Stokes' law, but also increase cluster ability. However, the longest processes occur in high density (high S_{30m}/T_{30m}) environments, where flotation would be easier, which is counterintuitive. It seems more logical, then, that longer processes are developed to facilitate sinking (through clustering) in high density environments.

5. Conclusions

- A total of 19,611 measurements of *Lingulodinium machaerophorum* from 144 surface samples show a relationship between process length and both summer salinity and temperature at 30m water depth, as given by the following equation: $S_{30m}/T_{30m} = 0.078 * \text{average process length} + 0.534$ with $R^2=0.69$. For salinity the range covered is at least 12.5 to 42psu, and for temperature 9-31°C. To establish the accuracy of this salinity proxy, future culture studies will hopefully further constrain this relationship.
- Confocal microscopy shows that distances between processes are strongly related to average process length, and that the number of processes is inversely related to average process length. This suggests a two end-member model, one with numerous short, closely spaced processes and one with relatively few, widely spaced, long processes.
- Processes of *Lingulodinium machaerophorum* are hypothesized to biologically function mainly as a clustering device.

Acknowledgements

Warner Brückmann and Silke Schenk (IFM Geomar), Rusty Lotti Bond (Lamont Doherty Earth observatory), Chad Broyles and Walter Hale (IODP), Jim Broda and Liviu Giosan (WHOI), Gilles Lericolais (IFREMER, France), Katrien Heirman and Hans Pirlet (RCMG), Jean-Pierre Arrondeau (IAV) and Rex Harland are kindly acknowledged for providing samples.

Marie-Thérèse Morzadec-Kerfourn is kindly thanked for providing detailed information on sampling locations from Brittany and Philippe Picon (GIPREB) for providing salinity data from Etang de Berre. We are grateful to Zoë Verlaak for helping out with the confocal measurements and Richard Hallett for stimulating discussions on *Lingulodinium machaerophorum* process development.

We express gratitude to Martin Head and one anonymous reviewer for detailed reviews of an earlier version of this manuscript.

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