

**ENVIRONMENTAL FACTORS INFLUENCING CYST FORMATION  
AND PRESERVATION OF ORGANIC-WALLED  
DINOFLAGELLATES: AN ENVIRONMENTAL AND LABORATORY  
STUDY**

Dissertation for the doctorate degree  
of the Department of Geosciences  
at the University of Bremen

submitted by

Ewa Justyna Susek

Bremen, 2005



**Tag des Kolloquiums:**

30.09.2005

**Gutachter:**

Prof. Dr. H. Willems

Prof. Dr. J. Peckmann

**Prüfer:**

Prof. Dr. J. Kuss

PD. Dr. K.A.F. Zonneveld



---

## Zusammenfassung

---

Organischwandige Dinoflagellatenzysten werden häufig für die Rekonstruktion der Paläoumwelt angewandt, obwohl die Faktoren, die die Zystenbildung und die Einbettung der Zysten im Sediment auslösen, noch nicht ausreichend erkannt sind. Diese Information ist wesentlich, wenn wir uns das Potenzial von Dinoflagellaten als Werkzeug für die Paläozeanographie voll und ganz zu Nutze machen wollen, d.h. zuverlässige Rekonstruktionen vergangener Bedingungen der marinen Umwelt erstellen. Deshalb befassen sich wesentliche Teile dieser Arbeit mit dem Prozess, der von der Zystenbildung bis zum Eingraben der Zysten führt. Sedimentfallen aus dem Auftriebsgebiet vor der Küste von NW Afrika wurden auf ihren Gehalt an organischwandigen Dinoflagellatenzysten untersucht. Die Bedingungen im (sub)tropischen Atlantik vor der Küste von Cape Blanc sind weitgehend bestimmt von fast ständigem Auftrieb im Zusammenhang mit den NE Passatwinden. Der Auftrieb führt an der Oberfläche zu einer hohen Produktivität bei niedrigeren Temperaturen. Außerdem wird die Produktivität vom äolischen Staub aus der Sahara beeinflusst, der Spurenelemente in die obere Wassersäule einbringt. Jahreszeitliche Variationen in der Staubzufuhr, Auftriebsintensität und in den Meeresoberflächentemperaturen beeinflussen die Produktion von organischwandigen Dinoflagellatenzysten. Insbesondere ein hoher Nährstoffgehalt ruft hohe Zystendurchflussmengen organischwandiger Dinoflagellaten hervor. Analysen der Zystenassoziationen, die in einem Zeitraum von vier Jahren gesammelt wurden, weisen darauf hin, dass der wichtigste Einflussfaktor in diesem Gebiet für die Zystenbildung die Zufuhr von Spurenelementen ist, z.B. Eisen durch äolischen Staub. Die Zystenproduktion von *Protoperidinium monospinum* und *P. americanum* kann eindeutig mit dem lithogenen Beitrag korreliert werden. Vor der Küste von Cape Blanc kann das Auftriebswasser unterschiedliche Beimischungen von relativ nährstoffreichem Wasser aus dem zentralen Südatlantik enthalten (South Atlantic Central Water, SACW). In Zeiten, in denen SACW den Transport von Auftriebswasser an die Küste speist, wird eine erhöhte Produktion von *Lingulodinium machaerophorum* beobachtet. Die Durchflussmengen von *Brigantedinium* spp. variieren ähnlich wie die gesamte Durchflussmenge der Diatomeen. Obwohl der Auftrieb ein wichtiger Einflussfaktor für die biologische Produktion vor der Küste NW Afrikas ist, wurde während der Langzeitbeobachtungen keine klare Beziehung zwischen Oberflächentemperaturen (Surface Temperatures, SST), Auftriebsintensität und Zystenproduktion festgestellt. *Brigantedinium* spp. gemeinsam mit dem heterotrophen Taxon *Protoperidinium monospinum* repräsentieren die dominierenden Taxa der Fallenassoziationen. Autotrophe Taxa machen nur ein bis vier Prozent der Vergesellschaftungen aus.

Die unterhalb der Sedimentfallen gesammelten Oberflächensedimente sind ebenfalls von heterotrophen Taxa dominiert, mit ähnlichen Werten von *Brigantedinium* spp. und *Protoperidinium monospinum*. Jedoch hat der Anteil der heterotrophen Taxa in Folge der Arten selektierenden aeroben Degradation abgenommen.

Obwohl *Protoperidinium monospinum* ein wichtiges Element der analysierten Assoziationen darstellt, wird diese Art hier zum ersten Mal aus einem Auftriebsgebiet dokumentiert. Wahrscheinlich führt die Morphologie dieser Art häufig dazu, dass sie für eine Art von *Echinidinium* oder *Islandinium* gehalten wird.

Obwohl die palökologische Forschung normalerweise mit den Veränderungen in der Zusammensetzung der Zystenassoziationen arbeitet, variieren viele Arten auch erheblich in ihrer Zystenmorphologie. Beobachtungen in der natürlichen Umgebung zeigen, dass einige dieser Variationen durch die Umwelt ausgelöst werden können. Um dieses Problem direkt zu untersuchen, wurden Zuchtexperimente mit *Tuberculodinium vancampoe* (motile Affinität *Pyrophacus steinii*) durchgeführt. Die Kulturen wurden hergestellt, indem einzelne Zysten aus Oberflächensedimenten ausgekeimt wurden. Die Art wurde bei unterschiedlichen Temperaturen, Lichtintensitäten und Salinitäten gezüchtet. Die Beobachtungen zeigen, dass die Zystenbildung von *T. vancampoe* in einem weiten Bereich von Umweltbedingungen stattfindet. Die maximale Zystenbildung wurde bei 27°C festgestellt, ähnlich wie im Ocean. Die Temperatur scheint den größten Einfluss auf die Morphologie zu haben. Bei extremen Temperaturen wird eine Reduzierung des Prozesses beobachtet. Auch Salinität beeinflusst die Morphologie von *T. vancampoe*. Das Längenverhältnis von Zyste zu Tuberkel nimmt mit steigender Salinität zwischen 20 und 40 psu zu. Obwohl frühere Beobachtungen darauf hinweisen, dass diese Art heterothallisch ist, legen unsere Ergebnisse nahe, dass Homothallie bei dieser Art auch vorkommt.

Ein ähnliches Experiment mit *Gonyaulax* sp. wurde vorbereitet. Jedoch hörte die Zystenproduktion während des Experiments auf und die Zystenbildung konnte nicht wieder hergestellt werden.

Alle während dieser Arbeit untersuchten Aspekte weisen darauf hin, dass es eine Verbindung zwischen Zystenproduktion und Umwelt gibt. Die Ergebnisse zeigen, dass die Zystenbildung mit der erhöhten Verfügbarkeit von Nährstoffen zusammenfällt. Trotz dieser Tatsache bleibt jedoch noch eine Menge Forschungsarbeit zu leisten, um die Faktoren vollständig zu verstehen, welche die Zystenbildung auslösen, wie man deutlich an der Laborarbeit mit *Gonyaulax* sp. sieht. Die Untersuchung zeigt auch ganz deutlich, dass das primäre Signal sehr stark durch sekundäre Prozesse modifiziert werden kann. Deshalb müssen bis zur erfolgreichen Anwendung von organischwandigen Dinoflagellatenzysten in der Klimarekonstruktion noch viele detaillierte Antworten zu den Prozessen, gegeben werden, die die Zystenassoziationen in den Sedimenten bestimmen.

---

## Summary

---

Organic-walled dinoflagellate cysts are often applied to reconstruct palaeoenvironments, notwithstanding the fact that the factors triggering encystment and cyst burial in sediments are only poorly understood. This information is essential if we want to fully exploit the dinoflagellate toolbox for palaeoceanography; i.e. to obtain reliable reconstructions of bygone conditions of the marine environment. Therefore, a large part of this thesis is devoted to the processes leading from cyst formation to cyst burial. Sediment trap samples from the upwelling area off NW Africa were analysed for their organic-walled dinoflagellate cyst content. Upper ocean conditions in the (sub)tropical Atlantic Ocean off Cape Blanc are strongly determined by almost permanent upwelling related to NE trade winds. Upwelling results on the surface in high productivity and lower temperatures. Additionally productivity is influenced by eolian dust from the Sahara, which provides the upper water column with trace elements. Seasonal variations in dust input, upwelling intensity and sea surface temperatures influence the production of organic-walled dinoflagellate cysts. High nutrient content particularly induces high cyst fluxes of organic-walled dinoflagellates. Analyses of cyst associations collected over a period of 4 years indicate that in this region the most important factor affecting encystment is trace elements supply e.g. iron by eolian dust. Cyst production of *Protoperidinium monospinum* and *P. americanum* can be positively correlated to the lithogenic input. Off Cape Blanc upwelled water can contain varying admixtures of relatively nutrient rich South Atlantic Central Water (SACW). During periods when SACW feeds the onshore transport of upwelled water, increased production of *Lingulodinium machaerophorum* is observed. The fluxes of *Brigantedinium* spp. vary similar to the total diatom flux. Although upwelling is important factor influencing biological production off NW Africa no clear relationship between surface temperatures (SST), upwelling intensity and cyst production is found in the long-term observations. *Brigantedinium* spp. together with another heterotrophic taxa *Protoperidinium monospinum* represent the dominating taxa of trap associations. Autotrophic taxa constitute 1 to 4% of the assemblages only.

The surface sediments collected under sediment traps are also dominated by heterotrophic taxa with co-domination of *Brigantedinium* spp. and *Protoperidinium monospinum*. However, the proportion of heterotrophic taxa decreased, which is a result of species selective aerobic degradation.

Although *Protoperidinium monospinum* constitutes an important element of analysed associations this species is documented for the first time from an upwelling area. Probably because the morphology of this species is such that it might often be mistaken for a species of *Echinidinium* or *Islandinium*.

Although, paleoecological research usually uses the changes in the composition of cyst associations, many species also vary considerably in their cyst morphology. Observations from natural environment indicate that some of these variations may be induced environmentally. To investigate this problem directly, *Tuberculodinium vancampoae* (motile affinity *Pyrophacus steinii*) culture experiments were carried out. Cultures were established by germinating of single cysts from surface sediments. The species was cultured at different temperatures, light intensities and salinities. Observations indicate that encystment of *T. vancampoae* occurs in a wide range of environmental conditions. Maximal encystment is observed at 27°C, similar to what is known from the field. Temperature seems to have the largest effect on morphology. In extreme temperatures a reduction of processes is observed. Also salinity affects *T. vancampoae* morphology. The cyst-to-tubercule length ratio increases with increasing salinity between 20 and 40psu. Although earlier observations indicate that this species is heterothallic, our results suggest that homothally occurs in this species as well.

A similar experiment on *Gonyaulax* sp. was prepared. However, cyst production halted during the experiment run and encystment could not be restored.

All of the aspects investigated during this work indicate that there is a link between cyst production and environment. Obtained results indicate that encystment coincides with elevated nutrient availability. Despite this fact a lot of research remains to be done to completely understand factors triggering encystment as is clearly illustrated by the laboratory work on *Gonyaulax* sp. The study also clearly demonstrates that the primary signal can be strongly modified by secondary processes. Therefore, the successful application of organic-walled dinoflagellate cysts for climate reconstruction, still awaits more detailed answers on the processes determining the cyst associations in sediments.

---

## Contents

---

<b>1. Introduction</b> .....	1
1.1. Motivation and main objectives .....	1
1.2. Dinoflagellates and their life cycle .....	2
1.3. Organic-walled dinoflagellate cyst: state of art .....	4
1.3.1. Variations in cyst morphology .....	5
1.4. Results .....	6
1.5. Material and methods .....	7
1.5.1. Environmental study (trap material) .....	7
1.5.2. Experimental study .....	7
1.5.2.1. Set up of dinoflagellate cultures .....	7
1.5.2.2. Equipment .....	8
1.5.2.3. Growth phases .....	9
1.5.2.4. <i>Tuberculodinium vancampoae</i> measurements .....	9
<b>2. Organic-walled dinoflagellate cyst production in relation to upwelling intensity and lithogenic influx in the Cape Blanc region (off north-west Africa).</b>	
<i>Ewa Susek, Karin A. F. Zonneveld, Gerhard Fischer, Gerard J. M. Versteegh and Helmut Willems.</i>	
<i>Phycological Research</i> 2005; <b>53</b> : 97-112 .....	17
<b>3. Interannual and seasonal variability of the organic-walled dinoflagellate cyst production in the northeast (sub)tropical Atlantic with emphasis on transport and preservation processes.</b>	
<i>Ewa Susek and Karin A. F. Zonneveld</i>	
<i>Submitted to Deep-Sea Research</i> .....	41
<b>4. Effect of temperature, light and salinity on cyst production and morphology of <i>Tuberculodinium vancampoae</i> (Rossignol 1962) Wall 1967 (<i>Pyrophacus steinii</i> (Schiller 1935) Wall et Dale 1971).</b>	
<i>Ewa Susek and Karin A. F. Zonneveld</i>	
<i>In preparation</i> .....	79
<b>5. Temperature, light and nutrient effect on growth of <i>Gonyaulax</i> sp.</b>	
<i>Ewa Susek and Karin Zonneveld</i> .....	97

<b>6. Conclusions and further perspectives .....</b>	<b>109</b>
<b>7. Acknowledgements .....</b>	<b>113</b>

## Introduction

### *1.1. Motivation and main objectives*

To better understand the changing Earth, it is necessary to reconstruct the Earth's history. This reconstruction requires good, credible tools, or 'proxies'. Palaeoenvironmental research have a large toolbox, consisting of a.o. isotopes, pollen, dinoflagellate cysts, foraminifera or diatoms in sediments to reconstruct climate and environment. With science progressing, the demands on the quality of the tools increase. In this thesis, the focus is on a better understanding of the tool of organic walled dinoflagellate cysts. Several dinoflagellate species produce cysts as a part of their life cycle. The cysts are made of highly resistant organic polymers which resulted in a rich fossil record. To establish palaeoenvironmental reconstructions, it is essential to know which environmental factors influence the cyst production. Most information about the relationship between variations in physical parameters and cyst production is available from temperate to arctic regions whereas from the (sub)tropics information is rare and e.g. not available from the Atlantic Ocean.

The present study, therefore, concentrates on the organic-walled dinoflagellate cyst fluxes in the (sub)tropical Atlantic area, off Cape Blanc, in relation to environmental factors. The data provides more insight into the relation between encystment of individual species and the environment. The region off NW Africa is characterised by relatively permanent upwelling resulting in high bioproductivity on the shelf (Hagen, 2001). Primary production is also enhanced when Saharan dust aerosol brings trace elements to the ocean surface (Sarhou et al., 2003). This work also deals with possible secondary factors effecting cysts assemblages observed in surface sediments since earlier results indicate that selective degradation may overprint the environmental signal delivered by the surface waters (Zonneveld et al., 1997). Furthermore, this study focuses on the relation between cyst morphology and environment. Environmental influence on cyst morphology has been proposed from field studies but, it needs further confirmation since a correlation is no proof of causality. Major emphasis has been placed on the following research questions:

- Dinoflagellates are known to be sensitive to water turbulence (Thomas et al., 1994; Gibson and Thomas, 1995). Can they live in areas of permanent upwelling? Do their fluxes coincide with periods of upwelling intensification or perhaps, rather with upwelling relaxation?
- Laboratory and environmental studies suggest two mechanisms triggering cyst production: environmental stress (e.g. culture starvation, temperature) and conditions optimal for vegetative cell growth. Is an increase in cyst fluxes to the sediment associated with relatively low or with enhanced nutrient availability? Is there any convergence between the fluxes of cysts of heterotrophic taxa and their food source fluxes?

- *Impagidinium* species are often considered to be characteristic for oligotrophic regions such as the open ocean. Do their fluxes coincide with periods of depreciate nutrient content in the upper water column?
- Can we consider the cyst assemblages in sediments to mirror of encystment in the upper water column? How can transport through the water column affect the assemblages? Has species selective oxygen decay any influence on observed assemblages?
- In the region off NW Africa seasonal and interannual differences are observed (e.g. Romero et al., 2002). Are these changes also reflected in the production of dinoflagellate cysts with respect to their total flux and/or species composition?
- In paleoecological reconstruction usually cyst associations are used. However, several species indicate ecophenotypism. Laboratory experiments showed morphological cyst variation in relation to varying environmental parameters for *Gonyaulax baltica* and *Lingulodinium machaerophorum*. Are these morphological changes observed also in other species? Which factors influence them?

### ***1.2. Dinoflagellates and their life cycle***

Dinoflagellates (Dinoflagellata (Bütschli 1885)) are a major group of marine phytoplankton but are also known from freshwater ecosystems. Approximately 2000 living species have been described. The group is very heterogeneous and there is no single feature that may unite all dinoflagellates (Taylor, 1987). Within this group there are photosynthetic as well as non-photosynthetic members and in the past these two groups were investigated separately – by botanists and zoologists respectively. Usually dinoflagellates are unicellular. In the motile (mastigote) phase a large number of species possesses a *theca* which lies internal to the cell membrane and is predominantly made of cellulose platelets. Cell size varies between 30-100µm. In the mastigote stage they possess two flagella which uniquely allow the motile cells to simultaneously swim forward and turn around (Levandowsky and Kaneta, 1987). Typically dinoflagellates possess a dinokaryon which occurs in dinoflagellates only and which implies that the chromosomes stay condensed, even during interphase (Taylor, 1987). The nutritional diversity in this group is very high – they can be photosynthetic, heterotrophic or mixotrophic (Schnepf and Elbrachter, 1992). Phototrophic species usually have a brownish pigment – peridinin. They are able to accommodate to changing light conditions. At low light levels cell pigmentation increases. *In situ* measurements indicate that to maximize daily rates of photosynthesis dinoflagellate migrate within the water column (Prézelin, 1987). Dinoflagellates are also known to cause very spectacular water fluorescence (e.g. Herring, 1998). Besides free-living there are symbiotic taxa as well as extra- and intracellular parasites (Cachon and Cachon, 1987; Rowan et al., 1997; Baker et al., 2004). Symbiotic taxa that live in coral reefs may enable coral communities to survive in warming waters (Baker et al., 2004). Parasitic species have

ecological and economical repercussions. Toxic dinoflagellates may cause mass mortality of sea mammals, fish and birds (Harwood, 1998; Hernández et al., 1998). For many people dinoflagellates are known for their “red tides” that cause poisoning of ecosystems and may be also fatal for humans (e.g. Dale and Yentsch, 1978; Burkholder et al., 1992; Hallegraeff, 1993). Although scientifically red tides were recognised as such since 1850, they were known as an oceanic phenomenon much earlier. In Japan the earliest historical “red tide” was recorded in 731 A.D. (Okaichi, 2003) when “seawater changed to blood”. The dinoflagellate fossil record is much longer. The earliest accepted dinoflagellate fossil is found in the Late Silurian material in North Africa (Goodman, 1980) and is about 400-410 Ma old. This group is well known from Mesozoic and Cainozoic sediments and at present over 2200 fossil species have been described and this number is growing. Fossil motile stages occur rarely. Usually the fossil dinoflagellates relate to the non-motile forms: spores or cysts (Goodman, 1980). The majority of fossil cysts is composed of an organic material: dinosporin - resembling sporopollenin occurring in spores and pollen grains (Goodman, 1980; Taylor, 1987; Falkowski et al., 2004).

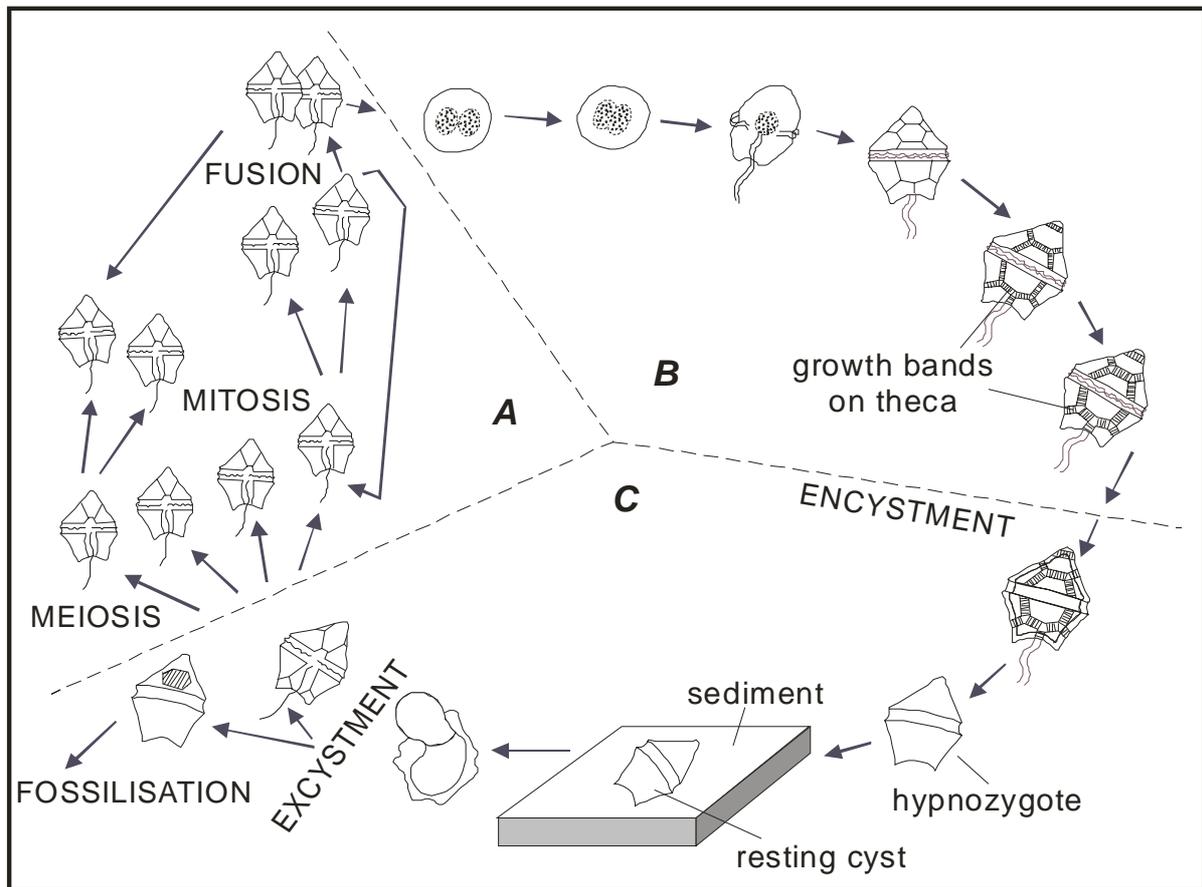


Fig. 1.1. Idealised dinoflagellate life cycle involving sexual reproduction and resting cyst formation. A – cells in this segment are motile and haploid. B – cells in this segment are motile and diploid (nucleus dotted). C – cells in this segment are nonmotile (except for excysted cell shown to the left) and diploid. Hatched area in discarded cyst at bottom left represents the archeopyle. From Fensome et. al (1996) after Vink (2000).

Motile cells living in the water column may reproduce themselves asexually through mitosis. However, for several species a more complicated life cycle has been evidenced, including sexual reproduction (Head, 1996). Dinoflagellates produce different types of gametes. They may be identical to the vegetative cells, or differ from them or / and differ from each other. After conjugation of the gametes the zygotes may form cysts (Pfiester and Anderson, 1987). Encysting cells lose their flagella, become immobile and may sink to the ocean floor where they settle. In natural environments encystment seems to be convergent with conditions optimal for vegetative cell growth (Wall et al., 1970; Kremp and Heiskanen, 1999). Although encystment coincides generally with sexual reproduction it seems that cysts may be important for survival of dinoflagellates in disadvantageous conditions (Sarjeant et al., 1987). Once the cyst is formed, an obligatory dormancy period starts. Its length is highly variable (Pfiester and Anderson, 1987) and only after this period excystment is possible. Cysts form a sort of “seed bank” in aquatic sediments from which the motile stock can be renewed. This is especially important in the case of species developing “red tides”. Recent experiments have shown that cysts of some species can remain alive for at least a decade (Lewis et al., 1999). Cysts in sediments may become fossilised.

### ***1.3. Organic-walled dinoflagellate cyst: state of art***

Fossilised dinoflagellate cyst-assemblages are used to obtain detailed information about past marine environmental conditions and form an important tool to reconstruct the palaeoceanography. Although cysts of dinoflagellate have been used by palaeontologist for many years, some questions remain about the environmental factors which influence dinoflagellate sexuality and encystment. For exploiting the full potential of dinoflagellate cysts in palaeoenvironmental research, detailed information about factors that influence cyst sedimentation and fossilisation is essential. The solution of these problems remained beyond our power for a long time. Results obtained in laboratories are always influenced by artificial conditions and therefore have to be taken into consideration. However, with the development of sediment traps long-time series combining environmental change with material fluxes to the sea floor have become available, filling the gap between laboratory studies and assessment of assemblages in surface sediments.

Dinoflagellate cyst occurrence in sediments from the Atlantic and surrounding areas' sediments has been studied by several authors (e.g. Wall, 1967; Williams, 1971; Williams and Bujak, 1977; Dale, 1988; Matthiessen, 1995; Rochon et al., 1998; Rochon et al., 1999; Devilliers and de Vernal, 2000; Vink et al., 2000; Zonneveld et al., 2001; Dale et al., 2002; Esper and Zonneveld, 2002; Marret and Scourse, 2002). Assemblages have also been investigated for other regions e.g. the Indian Ocean (Marret and de Vernal, 1997; Zonneveld, 1997) or Japanese Islands (Matsuoka, 1999; Matsuoka, 2001). For a recent overview of global cyst occurrence in surface sediments see Marret and Zonneveld (2003). A clear link exists between cyst occurrences in surface sediments and

environmental parameters such as salinity, water stratification, temperature, nutrients input. These relationships are extrapolated to the past by means of transfer functions. However, cyst occurrence in sediments is influenced not only by production in the overlaying surface waters but also by other factors such as relocation of material, transport through the water column or species selective oxygen decay. Especially this last factor seems to have a strong influence on cyst assemblages (Zonneveld et al., 1997). Pure cyst-environment relations can only be assessed without these disturbing factors. The information obtained from sediment traps comes close to this ideal situation. Sediment trap moorings in the open ocean traps enabled investigations of different fluxes (e.g. Ramaswamy et al., 1991; Fischer et al., 1996; Timothy and Pond, 1997; Ratmeyer et al., 1999; Fischer et al., 2000; Abrantes et al., 2002; Romero et al., 2003) including fluxes of foraminifera, diatoms, silicoflagellates or coccolithophores (Takahashi et al., 1989; Knappertsbusch and Brummer, 1995; Treppke et al., 1996; Guptha et al., 1997; Timothy and Pond, 1997; Romero et al., 1999; Conan and Brummer, 2000; Gyldenfeldt et al., 2000; Romero et al., 2002; De Bernardi et al., 2005). However, relatively few trap studies focused on dinoflagellates (Montresor et al., 1998; Harland and Pudsey, 1999; Kremp and Heiskanen, 1999) and our knowledge about dinoflagellate fluxes in tropics and subtropics is very low (Zonneveld and Brummer, 2000; Wendler et al., 2002). Moreover, long time-series of trap observations on organic-walled dinoflagellate are entirely missing. The only information from the tropics we have is derived from the Arabian Sea. There are no data about the Atlantic Ocean.

### ***1.3.1. Variations in cyst morphology***

Usually in paleoecological research variations in cyst associations are used. However, in many species the morphology of the cysts may vary as well. Possible reasons of cysts variations were considered many years ago (May, 1975; Sarjeant et al., 1987) and they are important since morphological characteristics of dinoflagellate cysts are used to differentiate between taxa. In the past, changes in morphology of a biological species have resulted in the creation of several morphospecies (e.g. *Lingulodinium machaerophorum* (Kokinos and Anderson, 1995; Lewis and Hallett, 1997)).

Observations from natural environments indicate that variations in morphology of some dinoflagellates correlate to salinity changes (Wall and Dale, 1973; Nehring, 1994; Dale, 1996; Ellegaard, 2000; Brenner, 2001). However, these correlations can not be considered as a proof of causality. To investigate this problem directly, a number of culturing studies has been carried out (Hallett, 1999; Ellegaard et al., 2002; Lewis et al., 2003). Indeed, a causal relationship exists between morphology and environment and this ecophenotypism might be exploited to increase the precision of paleo-environmental reconstructions (Brenner, 2001; Servais et al., 2004; Brenner, 2005). However, until present only a few species have been experimentally investigated and further experiments on other taxa are needed.

## 1.4. Results

The use of dinoflagellate cysts in reconstructing of palaeoenvironments and changes in the past is determined by the knowledge about the relationship between the specific environmental conditions in the upper water column and particular cyst species appearance as a result of encystment. Sexual reproduction and, in effect, encystment can be influenced by several different environmental factors such as temperature, light, nutrients/food availability or salinity. In order to enhance knowledge about species specific encystment in relation to environment, sediment trap samples from the region off NW Africa (off Cape Blanc) were quantitatively analysed on their organic-walled cyst content. To enlarge our current understanding of factors influencing cyst morphology, experiments on *Tuberculodinium vancampoae* (Rossignol 1962) Wall 1967 (motile affinity: *Pyrophacus steinii* (Schiller 1935) Wall et Dale 1971) were carried out. The results are presented in **Chapters 2 to 4**. **Chapter 5** presents unpublished experiments carried out on *Gonyaulax sp.*

**Chapter 2** (*Organic-walled dinoflagellate cysts production in relation to upwelling intensity and lithogenic influx in the Cape Blanc region (off NW Africa)*) deals with the temporal variation in cyst assemblages from the upwelling area off northwest Africa (off Mauritania) collected by trap CB9. Cyst fluxes have been compared to environmental conditions of the upper water column. The most important environmental factor strongly influencing this area is relatively permanent upwelling. Another element effecting production in this region is the Saharan dust bringing to the surface water eolian aerosol with trace elements such as iron, resulting in enhanced productivity. Marked differences in cyst fluxes are observed which appear to be associated with periods of relatively low/enhanced nutrient availability in the upper water column.

Although region off NW Africa is characterized by strong year to year differences also long-term observations (4 years) on cyst production in this region indicate that dust is the most important element influencing encystment in this region as presented in **Chapter 3** (*Interannual and seasonal variability of the organic-walled dinoflagellate cyst production in the northeast (sub)tropical Atlantic with emphasis on transport and preservation processes*). Off Cape Blanc a transition zone exists between subsurface water masses. Their relative contribution to the upwelled water influences the signature of the primary production at the surface. The quality of upwelled water also influences the organic-walled cyst production. To determine possible relationships between cyst production and environmental parameters redundancy analysis is used. Cysts assemblages are dominated by heterotrophic taxa, however the dominating species differ between years.

An important issue in dinoflagellate research is, how other factors than those influencing cyst production may modify the final cyst assemblages in sediments. The influence of lateral transport was investigated by comparing the cyst assemblages in sediment traps from different depths (730m and 3557m). Comparison of sediment trap assemblages collected during 4 years (including 5

summer/autumn seasons) with underlying sediments indicate that additional factors modify the cyst associations in this region.

Usually in paleoecological researches cyst associations are used, however, not only the assemblages change, also the cyst morphology of several species varies. **Chapter 4** deals with morphological variations of the warm water species *Tuberculodinium vancampoe* (Rossignol 1962) Wall 1967. Cultures of *Pyrophacus steinii* (Schiller 1935) Wall et Dale 1971, producing cyst of *Tuberculodinium vancampoe* were obtained by germinating single resting spores from surface sediment collected in southern Japan. Cultures were exposed to different light intensities, salinities and temperatures. The culture experiments indicate that *T. vancampoe* cysts vary especially when maintained in extreme temperatures. Also salinity has influence on cyst morphology. During this study also other taxa were cultured to establish morphological variation in other species. Although cyst production stopped during the experiment, the yielded useful information is presented in **Chapter 5**. Cultured *Gonyaulax sp.* grown in a width temperature and light window. Growth of the cultures was monitored daily by chlorophyll-*a* measurements indicating that dinoflagellates may have trouble adapting to very low irradiances.

## ***1.5. Material and methods***

### ***1.5.1. Environmental study (trap material)***

The sediment trap material studied was derived off Cape Blanc (NW Africa). The trap samples were collected using large aperture time-series sediment traps of type SMT 234 Aquatec Meerestechnik, Kiel, deployed from 15.03.1989 and 03.05.1991 (traps CB2, CB3 upper, CB3 lower and CB4) and between 11.06.1998 and 07.11.1999 (CB9). The details of the sampling and splitting procedure are given in Chapter 2 and 3 and in Wefer and Fischer (1993) and Fischer et al. (1996). The combination of particle sedimentation with measurements of the physical environment, biological processes in the upper ocean could be assessed (Deuser, 1986). The long-term studies also provide useful information about cyst production in the open ocean. Measurement of current speeds around the moorings indicate that traps were not disturbed by high current velocities (Fischer et al., 1996; Helmke, 2003) and a fast and almost undisturbed downward transport was observed (Ratmeyer et al., 1999) so that it may be assumed that observed cyst fluxes mirror cyst production in the surface waters.

### ***1.5.2. Experimental study***

#### ***1.5.2.1. Set up of dinoflagellate cultures***

To experiment with species environment relations dinoflagellate cultures were set up. The cultures were obtained from single cysts (Wall et al., 1967). The fresh surface sediment to set up the

cultures was collected from Spieka (south-eastern North Sea) in February 2002 and from Omura Bay, southern Japan in September 2003. Surface sediment was kept cold (4°C) and dark until processing. Individual cysts were isolated with a micropipette under inverted light microscope (Zeiss Axiovert 25°C). Cultures were maintained in incubators at 15°C and 24°C depending on the species. For culturing K medium without Si was used (Keller et al., 1987). For experiments, material was prepared in Erlenmayer flasks (250ml) with 100ml of medium. Cultures were not axenic. Details are given in Chapter 4 and 5.

### **1.5.2.2. Equipment**

In experiments a temperature gradient box (TGB) and light gradient box (LGB) were used. The TGB (Karwath et al., 2000; Meier et al., 2004) (Fig.1.2) allows the simultaneous culturing of phytoplankton strains throughout a temperature gradient. It is made of aluminium block with four rows of 30 holes. In each hole a tube containing up to 40 ml can be located. To provide a suitable temperature the block can be cooled at one end and heated at the other. Light is supplied from below by cool white fluorescent lamps (an irradiance of 60-90 $\mu\text{mol m}^{-2} \text{s}^{-1}$ ). During experiments tubes were filled with 30ml of medium and inoculated with 1 ml of dense culture. In order to ensure comparable cell densities in all tubes, stock cultures were homogenized by shaking prior to inoculation.

For the light experiments a light gradient box (LGB; Karwath, 1999) was used. Two cool white fluorescent lamps are covered lengthways with different strips of semi-transparent film. To stabilize equal temperature in the gradient box fans are located. The gradient boxes are located in a dark-room.

Growth of the cultures was monitored every day by chlorophyll-a measurements. They were carried out with a laboratory fluorometer (TD-700, Turner Designs); cultures were shortly mixed with a vortex stirrer before placing tubes in the fluorometer. Evaporated water in the test tubes was replenished twice a week to stabilize salinity. Experiments on *Gonyaulax* sp. were terminated after the cultures reached the stationary phase.

At the termination of experiments, each culture material was fixed with formaldehyde (1/20 of culture volume). After 24 hours, the cultures were washed with distilled water, sieved with a 20 $\mu\text{m}$  sieve and shortly ultrasonicated to remove small particles. The sieved residue was centrifuged and transferred into a 1.5 ml Eppendorf reaction vessel. Prior to microscopic analyses, the homogenized residue was placed on a glass slide, embedded in glycerine jelly and sealed using paraffin wax.

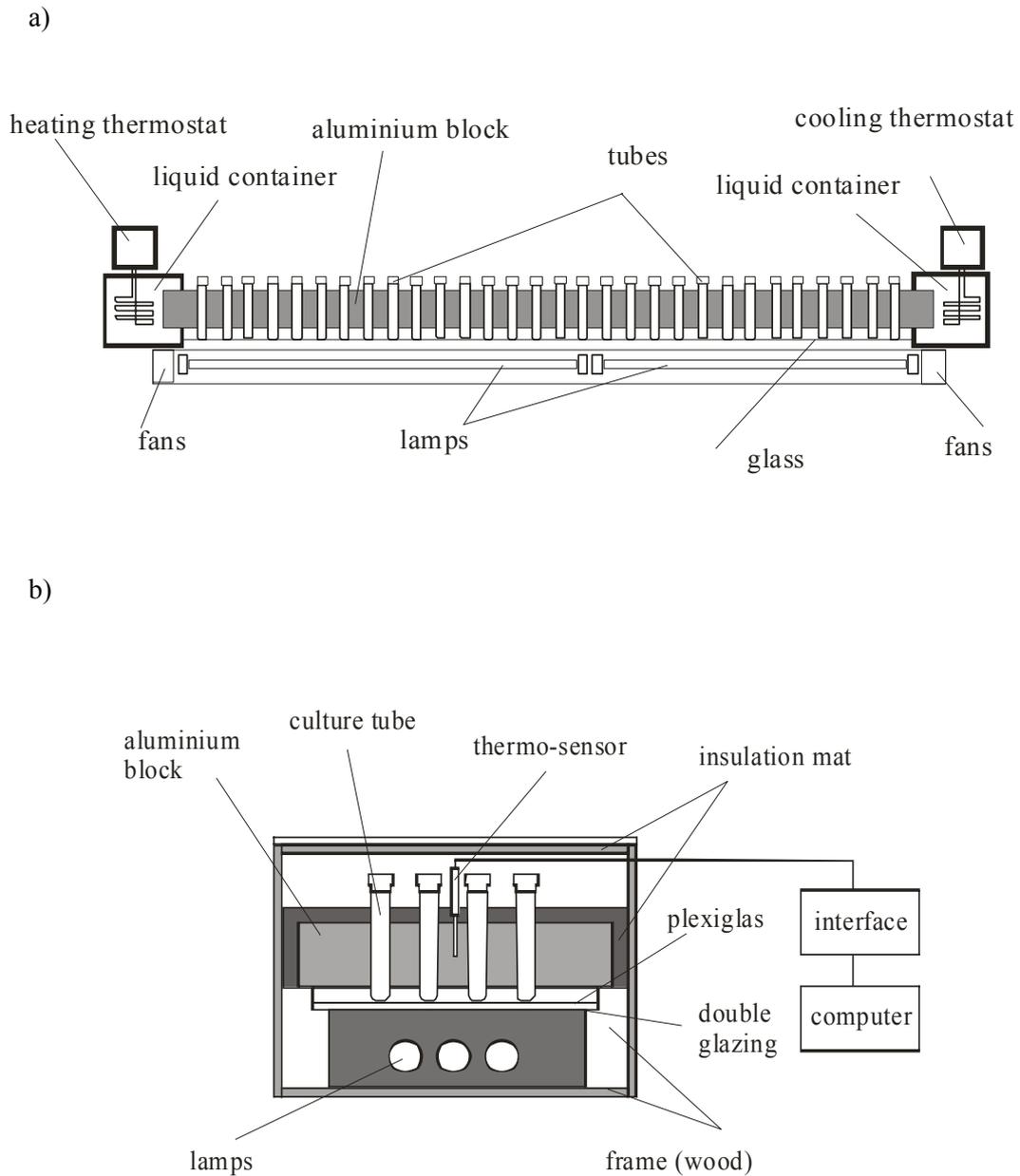


Fig.1.2. Schematic drawing of the temperature gradient box. (TGB); (Karwath et al., 2000)

(a) Sectional drawing, longitudinal axis without frame and insulation.

(b) Sectional drawing, lateral axis.

### 1.5.2.3. Growth phases

Growth of the culture within a constant volume of unchanged medium is usually described by a sigmoid growth curve (Sorokin, 1973). Growth of most batch-cultures can be divided into several phases:

- lag phase – the growth rate is usually increasing, but net growth may also be absent during a portion of the phase or there may even be a decline in cell volume per unit of cell suspension.
- exponential phase – the mass of cells doubles over each of successive time intervals: the growth rate is constant during the entire exponential phase
- declining phase – the doubling time for the cell mass is increasing
- stationary phase – a stable concentration of cell mass per unit volume of cell suspension is maintained.

#### **1.5.2.4. *Tuberculodinium vancampoeae* measurements**

Cyst size measurements were made at a 1000 x magnification under Zeiss Axioskop 50 light microscope. To assess variations in cyst morphology, central body length and width as well as tubercle length and width were measured. To determine tubercle length and width the tubercles with the most extreme length and width were measured for each cyst. Photos were taken by digital camera under a 400 x magnification.

#### **REFERENCES**

- Abrantes, F., Meggers, H., Nave, S., Bollman, J., Palma, S., Sprengel, C., Hendriks, J., Spies, A., Salgueiro, E., Moita, T., Neuer, S., 2002. Assessment of geochemical and micropaleontological sedimentary parameters as proxies of surface water properties in the Canary Islands region. *Deep Sea Research II* 49 (17), 3599-3629.
- Baker, A.C., Starger, C.J., McClanahan, T.R., Glynn, P.W., 2004. Shifting to new algal symbionts may safeguard devastated reef from extinction. *Nature* 430, 741-741.
- Brenner, W.W., 2001. Organic-walled microfossils from the central Baltic Sea, indicators of environmental change and base for ecostratigraphic correlation. *Baltica* 14, 40-51.
- Brenner, W.W., 2001. Distribution of organic-walled microfossils within single lamina from the Gotland Basin, and their environmental evidence. *Baltica* 14, 34-39.
- Brenner, W.W., 2005. Holocene environmental history of the Gotland Basin (Baltic Sea) - a micropalaeontological model. *Palaeogeography, Palaeoclimatology, Palaeoecology* 220, 227-241.
- Burkholder, J.M., Noga, E.J., Hobbs, C.H., Glasgow, H.B.J., Smith, S.A., 1992. New 'phantom' dinoflagellate is the causative agent of major estuarine fish kills. *Nature* 358, 407-410.
- Cachon, L., Cachon, M., 1987. Parasitic dinoflagellates. In: Taylor, F.J.R.s (Eds.), *The biology of dinoflagellates*. Blackwell, Oxford, pp. 571-610.
- Conan, S.M.-H., Brummer, G.J.A., 2000. Fluxes of planktic foraminifera in response to monsoonal upwelling on the Somalia Basin margin. *Deep Sea Research Part II: Topical Studies in Oceanography* 47 (9-11), 2207-2227.

- Dale, B. 1988. Low salinity dinoflagellate cyst assemblages from recent sediments of the Baltic region. Abstract. Brisbane, p. 33
- Dale, B., 1996. Dinoflagellate cyst ecology: modeling and geological applications. In: Jansonius, J., Mcgregor, D.C.s (Eds.), *Palynology: Principles and Applications*. AASP Foundation, Salt Lake City, pp. 1249-1275.
- Dale, B., Yentsch, C.M., 1978. Red tide and paralytic shellfish poisoning. *Oceanus* 21, 41-49.
- Dale, B., Dale, A.L., Jansen, J.H.F., 2002. Dinoflagellate cysts as environmental indicators in surface sediments from the Congo deep-sea fan and adjacent regions. *Palaeogeography, Palaeoclimatology, Palaeoecology* 185, 309-338.
- De Bernardi, B., Ziveri, P., Erba, E., Thunell, R.C., 2005. Coccolithophore export production during the 1997–1998 El Nino event in Santa Barbara Basin (California). *Marine Micropaleontology* 55, 107-125.
- Deuser, W.G., 1986. Seasonal and interannual variation in the deep-water particle fluxes in the Sargasso Sea and their relation to surface hydrography. *Deep Sea Research* 33, 225-246.
- Devilliers, R., de Vernal, A., 2000. Distribution of dinoflagellate cysts in surface sediments of the northern North Atlantic in relation to nutrient content and productivity in surface waters. *Marine Geology* 166, 103-124.
- Ellegaard, M., 2000. Variations in dinoflagellate cyst morphology under conditions of changing salinity during the last 2000 years in the Limfjord, Denmark. *Review of Palaeobotany and Palynology* 109 (1), 65-81.
- Ellegaard, M., Lewis, J., Harding, I., 2002. Cyst-theca relationship, life cycle, and effects on temperature and salinity on the cyst morphology of *Gonyaulax baltica* sp.no. (Dinophyceae) from the Baltic Sea area. *Journal of Phycology* 38, 775-789.
- Esper, O., Zonneveld, K.A.F., 2002. Distribution of organic-walled dinoflagellate cysts in surface sediments of the Southern Ocean (eastern Atlantic sector) between the Subtropical Front and the Weddell Gyre. *Marine Micropaleontology* 46, 177-208.
- Falkowski, P.G., Katz, M.E., Knoll, A.H., Quigg, A., Raven, J.A., Schofield, O., Taylor, F.J.R., 2004. The Evolution of Modern Eukaryotic Phytoplankton. *Nature* 305, 354-360.
- Fischer, G., Ratmeyer, V., Wefer, G., 2000. Organic carbon fluxes in the Atlantic and the Southern Ocean: relationship to primary production compiled from satellite radiometer data. *Deep-Sea Research II* 47 (9-11), 1961-1997.
- Fischer, G., Donner, B., Ratmeyer, V., Davenport, R., Wefer, G., 1996. Distinct year-to-year particle flux variations off Cape Blanc during 1998-1991: relation to  $d^{18}O$ -deduced sea-surface temperatures and trade winds. *Journal of Marine Research* 54, 73-98.
- Gibson, C.H., Thomas, W.H., 1995. Effects of turbulence intermittency on growth inhibition of a red tide dinoflagellate, *Gonyaulax polyedra* Stein. *Journal of Geophysical Research* 100 (C12), 24,841-824,846.

- Goodman, D.K., 1980. Dinoflagellate cysts in ancient and modern sediments. In: Taylor, F.J.R.s (Eds.), The biology of dinoflagellates. Blackwell, Oxford, pp. 649-722.
- Guptha, M.V.S., Curry, W.B., Ittekkot, V., Muralinath, A.S., 1997. Seasonal variation in the flux of planktic foraminifera: sediment trap results from the Bay of Bengal, northern Indian Ocean. *Journal of Foraminiferal Research* 27 (1), 5-19.
- Gyldenfeldt, A.-B.v., Carstens, J., Meincke, J., 2000. Estimation of the catchment area of a sediment trap by means of current meters and foraminiferal tests. *Deep Sea Research II* 47, 1701-1717.
- Hagen, E., 2001. Northwest African upwelling scenario. *Oceanologica Acta* 24, 113-128.
- Hallegraeff, G.M., 1993. A review of harmful algal blooms and their apparent global increase. *Phycologia* 32 (2), 79-99.
- Hallett, R.I., 1999. Consequences of Environmental Change on the Growth and Morphology of *Lingulodinium polyedrum* (Dinophyceae) in Culture. London, University of Westminster, pp.109. Ph.D. thesis.
- Harland, R., Pudsey, C.J., 1999. Dinoflagellate cysts from sediment traps deployed in the Bellingshausen, Weddell and Scotia seas, Antarctica. *Marine Micropaleontology* 37 (2), 77-99.
- Harwood, J., 1998. What kills the monk seals? *Nature* 393, 17-18.
- Head, M.J., 1996. Modern dinoflagellate cysts and their biological affinities. In: Jansonius, J.,McGregor, D.C.s (Eds.), *Palynology: Principles and Applications*. American Association of Palynologists Stratigraphic Foundation, Dallas, TX, pp. 1197-1248.
- Helmke, P., 2003. Remote sensing of the Northwest African upwelling and its production dynamics. FB5 Geosciences, Bremen, University of Bremen, pp.165. PhD dissertation thesis.
- Hernández, M., Robinson, I., Aguilar, A., González, L.M., López-Jurado, L.F., Reyero, M.I., Cacho, E., Franco, J., López-Rodas, V., Costas, E., 1998. Did algal toxins cause monk seal mortality? *Nature* 393, 28-29.
- Herring, P.J., 1998. Dolphins glow with the flow. *Nature* 393, 731-732.
- Karwath, B., 1999. Ecological studies on living and fossil calcareous dinoflagellates of the equatorial and tropical Atlantic Ocean. Department of Geology, Bremen, Bremen University, pp.175. Ph.D. thesis.
- Karwath, B., Janofske, D., Tietjen, F., Willems, H., 2000. Temperature effects on growth and cell size in the marine calcareous dinoflagellate *Thoracosphaera heimii*. *Marine Micropaleontology* 39 (1-4), 43-51.
- Keller, D.M., Selvin, R.C., Claus, W., Guillard, R.R.L., 1987. Media for the culture of oceanic ultraphytoplankton. *Journal of Phycology* 23, 633-368.
- Knappertsbusch, M., Brummer, G.J.A., 1995. A sediment trap investigations of sinking coccolithophorids in the North Atlantic. *Deep Sea Research I* 42 (7), 1083-1109.

- Kokinos, J.P., Anderson, D.M., 1995. Morphological development of resting cysts in cultures of the marine dinoflagellate *Linulodinium polyedrum* (= *L. machaerophorum*). *Palynology* 19, 143-166.
- Kremp, A., Heiskanen, A.-S., 1999. Sexuality and cyst formation of the spring-bloom dinoflagellate *Scrippsiella hangoei* in the coastal northern Baltic Sea. *Marine Biology* 134, 771-777.
- Levandowsky, M., Kaneta, P.J., 1987. Behaviour in dinoflagellates. In: Taylor, F.J.R.s (Eds.), *The biology of dinoflagellates*. Blackwell, Oxford, pp. 360-397.
- Lewis, J., Hallett, R., 1997. *Lingulodinium polyedrum* (*Gonyaulax polyedra*) a blooming dinoflagellate. *Oceanography and Marine Biology: an Annual Review* 35, 96-161.
- Lewis, J., Harris, A., Jones, K., Edmonds, R., 1999. Long-term survival of marine planktonic diatoms and dinoflagellates in stored sediment samples. *Journal of Plankton Research* 21 (2), 343-354.
- Lewis, J., Ellegaard, M., Hallett, R.I., Harding, I., Rochon, A. 2003. Environmental control of cyst morphology in gonyaulacoid dinoflagellates. Nagasaki, Japan, p. additional abstract
- Marret, F., de Vernal, A., 1997. Dinoflagellate cyst distribution in surface sediments of the southern Indian Ocean. *Marine Micropaleontology* 29, 367-392.
- Marret, F., Scourse, J., 2002. Control of modern dinoflagellate cyst distribution in the Irish and Celtic seas by seasonal stratification dynamics. *Marine Micropaleontology* 895, 1-16.
- Marret, F., Zonneveld, K.A.F., 2003. Atlas of modern organic-walled dinoflagellate cyst distribution. *Review of Palaeobotany and Palynology* 125 (1-2), 1-200.
- Matsuoka, K., 1999. Eutrophisation recorded in dinoflagellate cyst assemblages - a case of Yokohama Port, Tokyo Bay, Japan. *Sci. Total Environ.* 231, 17-35.
- Matsuoka, K., 2001. Further evidence for a marine dinoflagellate cyst as an indicator of eutrophication in Yokohama Port, Tokyo Bay, Japan. Comments on a discussion by B. Dale. *Sci. Total Environ.* 264, 221-233.
- Matthiessen, J., 1995. Distribution patterns of dinoflagellate cysts and other organic-walled microfossils in recent Norwegian-Greenland Sea sediments. *Marine Micropaleontology* 24, 307-334.
- May, F.E., 1975. Functional morphology, paleoecology and systematics of *Dinogymnium* tests. *Palynology* 1, 103-121.
- Meier, K.J.S., Höll, C., Willems, H., 2004. Effect of temperature on culture growth and cyst production in the calcareous dinoflagellates *Calciadinellum albatrosianum*, *Leonella granifera* and *Pernambugia tuberosa*. *Micropaleontology* 50 (supplement no.1), 93-106.
- Montesor, M., Zingone, A., Sarno, D., 1998. Dinoflagellate cyst production at a coastal Mediterranean site. *Journal of Plankton Research* 20 (12), 2291-2312.
- Nehring, S., 1994. Spatial distribution of dinoflagellate resting cysts in recent sediments of Kiel Bight, Germany (Baltic Sea). *Ophelia* 39, 137-158.

- Okaichi, T., 2003. Red Tides. Terra Scientific Publishing Company; Kluwer Academic Publishers, Tokyo; Dordrecht, London, Boston, pp. 439
- Pfiester, L.A., Anderson, D.M., 1987. Dinoflagellate reproduction. In: Taylor, F.J.R.s (Eds.), The biology of dinoflagellates. Blackwell, Oxford, pp. 611-648.
- Prézelin, B., 1987. Photosynthetic physiology. In: Taylor, F.J.R.s (Eds.), The biology of dinoflagellates. Blackwell, Oxford, pp. 174-223.
- Ramaswamy, V., Nair, R.R., Manganini, S., Haake, B., Ittekkot, V., 1991. Lithogenic fluxes to the deep Arabian Sea measured by sediment traps. Deep Sea Research 38, 169-184.
- Ratmeyer, V., Fischer, G., Wefer, G., 1999. Lithogenic particle fluxes and grain size distributions in the deep ocean off northwest Africa: Implications for seasonal changes of aeolian dust input and downward transport. Deep Sea Research Part I: Oceanographic Research Papers 46 (8), 1289-1337.
- Rochon, A., de Vernal, A., Sejrup, H.-P., Hafliðason, H., 1998. Palynological evidence of climatic and oceanographic changes in the North Sea during the last deglaciation. Quaternary Research 49, 197-207.
- Rochon, A., de Vernal, A., Turon, J.-L., Matthiessen, J., Head, M., 1999. Distribution of Recent Dinoflagellate cysts in surface sediments from the North Atlantic Ocean and adjacent seas in relation to sea-surface parameters. AASP Contr. Ser. 35, 1-150.
- Romero, O.E., Lange, C.B., Wefer, G., 2002. Interannual variability (1988-1991) of siliceous phytoplankton fluxes off northwest Africa. Journal of Plankton Research 24 (10), 1035-1046.
- Romero, O.E., Lange, C.B., Fischer, G., Treppke, U.F., Wefer, G., 1999. Viability in export production documented by downwards fluxes and species composition of marine planktic diatoms: observations from tropical and equatorial Atlantic. In: Fisher, G., Wefer, G.s (Eds.), Use of proxies in Palaeoceanography: examples from the south Atlantic. Springer-Verlag, Berlin Heidelberg, pp. 356-392.
- Romero, O.E., Dupont, L., Wyputta, U., Jahns, S., Wefer, G., 2003. Temporal variability of fluxes of eolian-transported freshwater diatoms, phytoliths, and pollen grains off Cape Blanc as reflection of land-atmosphere-ocean interactions in northwest Africa. Journal of Geophysical Research 108 (C5), 22-21 - 22-12.
- Rowan, R., Knowlton, N., Baker, A., Jara, J., 1997. Landscape ecology of algal symbionts creates variation in episodes of coral bleaching. Nature 388, 265-269.
- Sarjeant, W.A.S., Lacalli, T., Gaines, G., 1987. The cysts and skeletal elements of dinoflagellates: speculations on the ecological causes for their morphology and development. Micropaleontology 33 (1), 1-36.
- Sarthou, G., Baker, A.R., Blain, S., Achterberg, E.P., Boye, M., Bowie, A.R., Croot, P., Laan, P., Baar, H.J.W.d., Jickells, T.D., Worsfold, P.J., 2003. Atmospheric iron deposition and sea-

- surface dissolved iron concentrations in the eastern Atlantic Ocean. *Deep Sea Research Part I* 50 (10-11), 1339-1352.
- Schnepf, E., Elbrachter, M., 1992. Nutritional strategies in dinoflagellates: A review with emphasis on cell biological aspects. *European Journal of Protistology* 28, 3-24.
- Servais, T., Stricanne, L., Montenari, M., Pross, J., 2004. Population dynamics of galeate acritarchs at the Cambrian-Otdrovcian transition in the Algerian Sahara. *Paleontology* 47, 395-414.
- Sorokin, C., 1973. Dry weight, packed cell volume and optical density. In: Stein, J.R.s (Eds.), *Handbook of phycological methods: culture methods and growth measurements*. University Press, Cambridge, pp. 321-343.
- Takahashi, K., Honjo, S., Tabata, S., 1989. Siliceous phytoplankton flux: interannual variability and response to hydrographic changes in the northeastern Pacific. In: Peterson, D.H.s (Eds.), *Aspects of Climate Variability in the Pacific and Western Americas*. Amer. Geophys. Union, pp.151-160.
- Taylor, F.J.R., 1987. General group characteristic; special features of interest; short history of dinoflagellate study. In: Taylor, F.J.R.s (Eds.), *The biology of dinoflagellates*. Blackwell, Oxford, pp. 1-23.
- Taylor, F.J.R., 1987. Dinoflagellate morphology. In: Taylor, F.J.R.s (Eds.), *The biology of dinoflagellates*. Blackwell Scientific Publications, Oxford, pp. 24-91.
- Thomas, W.H., Vernet, M., Gibson, C.H., 1994. Mechanisms of *Gonyaulax polyedra* (Dinophyceae) Inhibition by Small-Scale Turbulence: Photosynthesis, Pigmentation, Cell Division, and Cell Sizes. *Journal of Phycology*
- Timothy, D.A., Pond, S., 1997. Describing additional fluxes to deep sediment traps and water-column decay in a coastal environment. *Journal of Marine Research* 55, 383-406.
- Treppke, U.F., Lange, C.B., Donner, B., Fischer, G., Ruhland, G., Wefer, G., 1996. Diatom and silicoflagellate fluxes at the Walvis Ridge: an environment influenced by coastal upwelling in the Benguela system. *Journal of Marine Research* 54, 991-1016.
- Vink, A., Zonneveld, K.A.F., Willems, H., 2000. Organic-walled dinoflagellate cysts in western equatorial Atlantic surface sediments: distributions and their relation to environment. *Review of Palaeobotany and Palynology* 112 (4), 247-286.
- Wall, D., 1967. Fossil microplankton in deep-sea cores from the Caribbean Sea. *Palaeontology* 10 95-123.
- Wall, D., Dale, B., 1973. Paleosalinity relationships of dinoflagellates in the Late Quaternary of the Black Sea - a summary. *Geoscience and Man* 7, 95-102.
- Wall, D., Guillard, R.R.L., Dale, B., 1967. Marine dinoflagellate cultures from resting spores. *Phycologia* 6 (2-3), 83-86.
- Wall, D., Guillard, R.R.L., Dale, B., Swift, E., 1970. Calcitic resting cysts in *Peridinium trochoideum* (Stein) Lemmermann, an autotrophic marine dinoflagellate. *Phycologia* 9 (2), 151-156.

- Wefer, G., Fischer, G., 1993. Seasonal patterns of vertical particle flux in equatorial and coastal upwelling area of the eastern Atlantic. *Deep Sea Research I* 40 1613-1645.
- Wendler, I., Zonneveld, K.A.F., Willems, H., 2002. Production of calcareous dinoflagellate cysts in response to monsoon forcing off Somalia: a sediment trap study. *Marine Micropaleontology* 46 (1-2), 1-11.
- Williams, G.L. 1971. The occurrence of dinoflagellates in marine sediments. Cambridge, p. 231-243
- Williams, G.L., Bujak, J.P., 1977. Distribution patterns of some North Atlantic dinoflagellate cysts. *Marine Micropaleontology* 2, 223-233.
- Zonneveld, K.A.F., 1997. Dinoflagellate cyst distribution in surface sediments from the Arabian Sea (northwestern Indian Ocean) in relation to temperature and salinity gradients in the upper water column. *Deep-Sea Research II* 44 (6-7), 1411-1443.
- Zonneveld, K.A.F., Brummer, G.J.A., 2000. (Palaeo-)ecological significance, transport and preservation of organic-walled dinoflagellate cysts in the Somali Basin, NW Arabian Sea. *Deep-Sea Research II* 47 (9-11), 2229-2256.
- Zonneveld, K.A.F., Versteegh, G.J.M., Lange, G.J.d., 1997. Preservation of organic-walled dinoflagellate cysts in different oxygen regimes: a 10,000 year natural experiment. *Marine Micropaleontology* 29 (3-4), 393-405.
- Zonneveld, K.A.F., Hoek, R.P., Brinkhuis, H., Willems, H., 2001. Geographical distributions of organic-walled dinoflagellate cysts in surficial sediments of the Benguela upwelling region and their relationship to upper ocean conditions. *Progress in Oceanography* 48 (1), 25-72.

**ORGANIC-WALLED DINOFLAGELLATE CYST PRODUCTION IN RELATION  
TO UPWELLING INTENSITY AND LITHOGENIC INFLUX IN THE CAPE  
BLANC REGION (OFF NW AFRICA)**

**Ewa Susek<sup>1</sup>, Karin A. F. Zonneveld<sup>1</sup>, Gerhard Fischer<sup>1</sup>, Gerard J. M. Versteegh<sup>2, 3</sup> and Helmut Willems<sup>1</sup>**

<sup>1</sup>Fachbereich 5-Geowissenschaften, University of Bremen, Postfach 330440, D-27412 Bremen, Germany

<sup>2</sup>Hanse-Wissenschaftskolleg, Lehmkuhlenbusch 4, 27753 Delmenhorst, Germany

<sup>3</sup>Organic Geochemistry Unit, Faculty of Earth Sciences, Utrecht University, Budapestlaan 4, 3584 CD, Utrecht, the Netherlands.

*Phycological Research* 2005; **53**: 97-112

## Organic-walled dinoflagellate cyst production in relation to upwelling intensity and lithogenic influx in the Cape Blanc region (off north-west Africa)

Ewa Susek<sup>1</sup>, Karin A. F. Zonneveld<sup>1</sup>, Gerhard Fischer<sup>1</sup>, Gerard J. M. Versteegh<sup>2,3</sup> and Helmut Willems<sup>1</sup>

<sup>1</sup>Fachbereich 5-Geowissenschaften, University of Bremen, Postfach 330440, D-27412 Bremen, Germany

<sup>2</sup>Hanse-Wissenschaftskolleg, Lehmkuhlenbusch 4, 27753 Delmenhorst, Germany

<sup>3</sup>Organic Geochemistry Unit, Faculty of Earth Sciences, Utrecht University, Budapestlaan 4, 3584 CD, Utrecht, the Netherlands.

### ABSTRACT

Fossil dinoflagellate cyst assemblages are increasingly used in paleoclimatic research to establish palaeoenvironmental reconstructions. To obtain reliable reconstructions, it is essential to know which physical factors influence the cyst production. Most information about the relationship between variations in physical parameters and cyst production is known from middle and higher latitudes. Information from the (sub)tropics is rare. To increase this information, the temporal variation in cyst assemblages from the upwelling area off north-west Africa (off Mauritania) has been compared to environmental conditions of the upper water column. Samples were collected by the sediment trap CB9, off north-west Africa (Cape Blanc, 21°15'2''N, 20°42'2''W) between 11 June 1998 and 7 November 1999 at 27.5-day intervals. Off Cape Blanc, upwelling occurs throughout the year with variable intensity. This region is also characterized by frequently occurring Saharan dust storms. Seasonal variations in dust input, upwelling intensity and sea surface temperature are reflected by the production of organic-walled dinoflagellate cyst assemblages. Several cyst taxa are produced throughout the sampling interval, with the highest fluxes at times of strongest upwelling relaxation and/or dust input (*Echinidinium aculeatum* Zonneveld, *Echinidinium delicatum* Zonneveld, *Echinidinium granulatum* Zonneveld, *Echinidinium* spp., *Impagidinium aculeatum* (Wall) Lentin et Williams, *Impagidinium sphaericum* (Wall) Lentin et Williams, *Protoperidinium americanum* (Gran et Braarud) Balech, *Protoperidinium stellatum* (Wall in Wall et Dale) Rochon *et al.*, *Protoperidinium* spp., *Selenopemphix nephroides* (Benedek) Benedek et Sarjeant and *Selenopemphix quanta* (Bradford) Matsuoka). Species such as, for example, *Bitectatodinium spongium* (Zonneveld) Zonneveld et Jurkschat and *Impagidinium patulum* (Wall) Stover et Evitt do not show any production pattern related to a particular season of the year or to specific environmental conditions in the upper water column. The production of cysts of *Protoperidinium monospinum* (Paulsen) Zonneveld et Dale is restricted to intervals with increased nutrient concentrations in upper waters when sea surface temperatures at the sampling site is below approximately 24°C.

**Key words:** dust, north-west Africa, organic-walled dinoflagellate cysts, sediment trap, upwelling.

## INTRODUCTION

Several dinoflagellate species produce cysts as a part of their life cycle. They are used as (paleo)environmental proxies because of their ability to fossilize. Although the modern geographic distribution of cysts in relation to surrounding environment is quite well known (e.g. Marret and Zonneveld, 2003) there are still some unsolved questions about which and to what extent environmental factors influence or trigger dinoflagellate sexuality, encystment and the rate of cyst formation (Kremp and Heiskanen, 1999; Olli and Anderson, 2002). Comparison of the modern distribution patterns of cyst species with environmental conditions of overlaying water masses gives no direct answer to these questions because surface sediments contain assemblages that are deposited over many years and the ecologic ‘signal’ can be altered by secondary processes, such as aerobic decay and selective transport (Zonneveld et al., 1997). By studying sediment trap material, a direct correlation of the cyst production with environmental conditions of surrounding water masses can be made (Montresor et al., 1998; Harland and Pudsey, 1999; Zonneveld and Brummer, 2000; Wendler et al., 2002). Here we aim to enhance the insight in the relationships between variations in turbulence, nutrient availability and temperature and the timing and rate of cyst production of individual species by studying trap samples of the high productivity area off north-west Africa, Mauritania. This area is characterized by permanent upwelling in seasonally varying intensity. Frequently occurring dust storms bring terrestrial elements into the region. We show that cyst production of individual taxa is strongly related to these environmental changes.

## OCEANOGRAPHIC SETTING

The upwelling area off north-west Africa belongs to the system of Eastern Boundary Currents (for overview of these current systems see Barton et al., 1998). The surface water circulation of the region between 20°N and 25°N is predominantly determined by the southward flowing Canary Current that bends from the continental margin to the south-west at about 21°N (Fig. 2.1; Barton 1998). Similar to other eastern ocean boundaries in the trade wind belt, a dominant feature of the region is the presence of coastal upwelling of cool and nutrient-rich subsurface water, which results in high bioproductivity on the shelf. The primary upwelling band is 20–30 km wide (Mittelstaedt, 1991). Further offshore a second upwelling band can occur along the shelf break (Mittelstaedt et al., 1975). A dominant steering role of upwelling length and intensity are the trade winds that blow equatorward. Between 20°N and 24°N upwelling occurs throughout the year, with maximum intensity during spring and autumn (Fig. 2.2; Speth et al., 1978; Speth and Detlefsen, 1982; Mittelstaedt, 1983; 1991). Subsurface waters consist of South Atlantic Central Water (SACW) and North Atlantic Central Water (NACW; Mittelstaedt, 1983, 1991; Klein and Tomczak, 1994). The SACW is transported poleward off Cape

Blanc at depths between 200 and 400 m (Mittelstaed, 1983; Hagen, 2001), whereas NACW follows equatorward the Canary Current at depths of 100–600 m (Sarnthein et al., 1982).

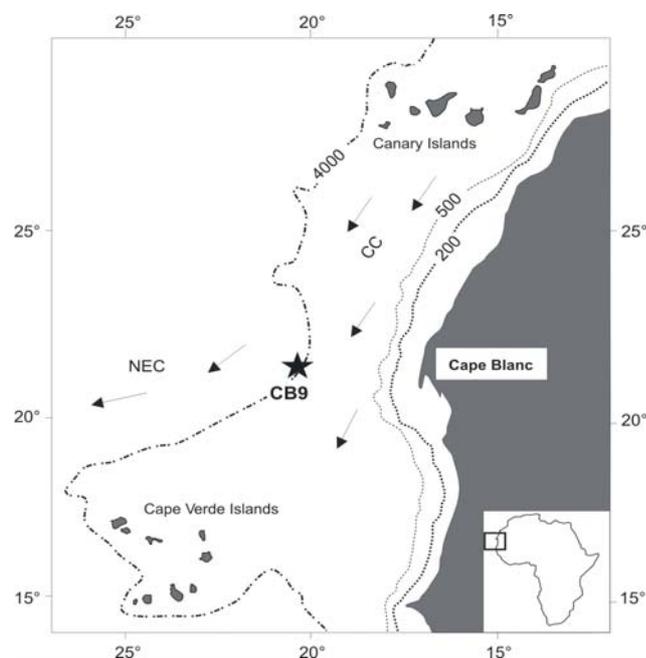


Fig.2.1 Location of the mooring site off Cape Blanc. CC, Canary Current, NEC, North Equatorial Current.

The most intensive mixing of their waters takes place at 22–23°N. The SACW is characterized by high nutrient concentrations compared to the NACW (Minas et al., 1982). According to Hagen (2001) enhanced productivity off Cape Blanc occurs when SACW feeds the onshore transport of upwelled water. This occurs especially during winter and spring (Mittelstaedt, 1991). Characteristic for this region are giant filaments of relatively cold, chlorophyll-rich water that persist throughout the year. They spread offshore over 450 km from the coast (Van Camp et al., 1991). The frequency of occurrences of these filaments during the year is coupled to the general pattern of upwelling in this region (Kostianoy and Zatsopin, 1996).

As a result of the coastal upwelling, the sea surface temperatures (SST) at the shelf are lower than in the open ocean. The upwelling intensity can, therefore, be documented by sea surface temperature anomaly (SSTA) (Speth et al., 1978), the difference between the coastal zone SST and the open Atlantic SST.

The region off north-west Africa is also characterized by frequent Saharan dust storms. Saharan dust aerosols influence the nutrient dynamics of ocean and have a significant effect on oceanic productivity (Middleton and Goudie, 2001). Dust particles from dry regions are easily mobilized and transported westwards within the north-east trade wind system over long distances (Moulin et al., 1997). Deposition of this dust enriches the surface water trace with elements such as iron, resulting in enhanced productivity (e.g. Sarthou and Jeandel, 2001; Pittman, 2002).

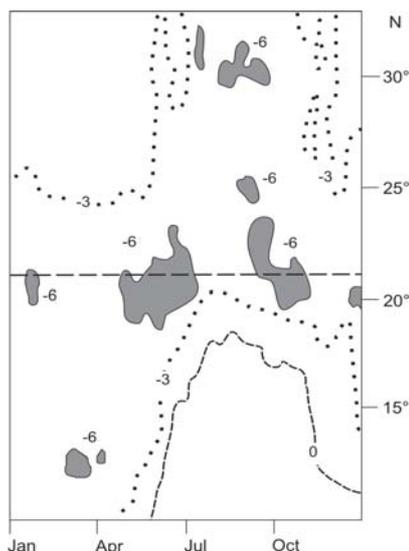


Fig.2.2. Mean sea surface temperature anomaly (SSTA) based on data from 1969 to 1971 (Speth et al., 1978). Strongest anomalies in gray. Position of CB9 is indicated by a line at 21°N.

## MATERIALS AND METHODS

Samples were collected with trap CB9 (21°15'2''N, 20°42'2''W) from the north-west Africa upwelling area, off Cape Blanc, Mauritania, between 11 June 1998 and 7 November 1999 (514 days). During that time 20 samples were collected every 27.5 days (with exception of the first sample, 7.5 days, and the last, 11.5 days). The Kiel model mooring (0.5 m<sup>2</sup> collecting surface) was located at a depth of 3580 m (bottom depth 4121 m). The sampling cups were stained with HgCl<sub>2</sub>. Samples were stored in darkness at 4°C until further treatment. Information about SST was obtained from <http://ingrid.ideo.columbia.edu/> (Fig.2.3). SSTA for the sampling period was calculated by comparison of SST in the coastal area (21°50'N, 17°50'W) with that of the open ocean (21°50'N, 40°50'W). It is assumed that sinking velocity of marine particles is such that it takes 2 weeks to reach the sampling depth (Fisher et al., 1996; Siggelkow et al., 2002).

Therefore, SSTA was calculated with a 2-week phase lag. Within the sampling period, four events of intensified upwelling (separated by upwelling relaxation periods) could be identified: (i) June 1998; (ii) January/February 1999; (iii) May 1999; and (iv) September/October 1999 (gray blocks in Figs 2.3–2.5). For the sampling interval, high concentrations of lithogenic input were collected by CB9 from August to September 1998 and from January to April 1999 (Figs 2.4, 2.5). Because of minor fluvial input in the Cape Blanc region (Tomczak, 1977; Sarnthein et al., 1982) this material can be regarded to be of eolian origin (Saharan dust).

For the present study, 1/125th splits of the original samples were investigated. They were rinsed with distilled water through a 20 µm stainless steel sieve to remove HgCl<sub>2</sub>. Material preparation was carried out according to the method described by Vink et al. (2000): the sediment was treated with

cold 10% HCl in order to remove carbonates, neutralized with 10% KOH and washed over a 20- $\mu\text{m}$  nickel precision sieve (Stork Veco, mesh: 570). Subsequently, the material was treated with cold 38% HF and agitated for 2 h in order to remove silicates. After having stood in HF for an additional 2 days, samples were carefully neutralized with 40% KOH under continuous mixing and without allowing the solution to become alkaline at any time, to avoid damage on individual cyst species. The sieved residue was centrifuged and transferred into a 1.5-mL Eppendorf reaction vessel that had a 0.5 mL scale. The volume was reduced to 0.1 mL and 50 or 100  $\mu\text{L}$  of the homogenized residue was placed on a glass slide, embedded in glycerin jelly and sealed using paraffin wax. All prepared material was analyzed. Identification of organic-walled dinoflagellate cyst species was accomplished using light microscope, at magnification 400x.

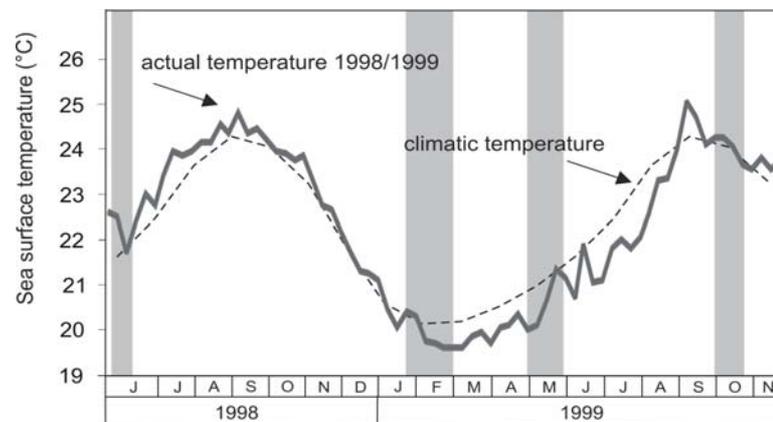


Fig.2.3. Sea surface temperature (SST). Grey bars indicate periods with intense upwelling. Actual and climatic temperatures are based on <http://ingrid.ldeo.columbia.edu/>. Actual temperature: SST derived from ship, buoy and bias-corrected satellite data at a 1 degree square block at the study site. Climatic temperature: mean SST within a 2 degrees square block at the study site for the period between 1971 and 2000.

Cyst fluxes are calculated by dividing the number of collected cysts per  $\text{m}^2$  in the investigated time intervals by the number of collecting days. Mean relative abundance of cyst species (mean percentage) are calculated by dividing the number of cyst of the individual species by the total number of cysts counted in all trap samples. Relative abundances (%) of cyst species in individual samples are calculated by dividing the number of cysts of certain species with number of all cysts in that sample. Relative abundance of cyst species in the summer/autumn season of 1998 is calculated for samples 1–6 and for summer/autumn season of 1999 for samples 15–20. The taxonomy for the dinoflagellate cysts is used. The cysts-theca relations are given in Table 2.1 and follow Marret and Zonneveld (2003). The group of *Protoperidinium* spp. includes round brown cysts without spines.

Because trap CB9 was not disturbed by high current velocities (Helmke, 2003), a fast and almost undisturbed downward transport was observed (Ratmeyer et al., 1999). As a result, we assume that observed cyst flux reflects cyst production.

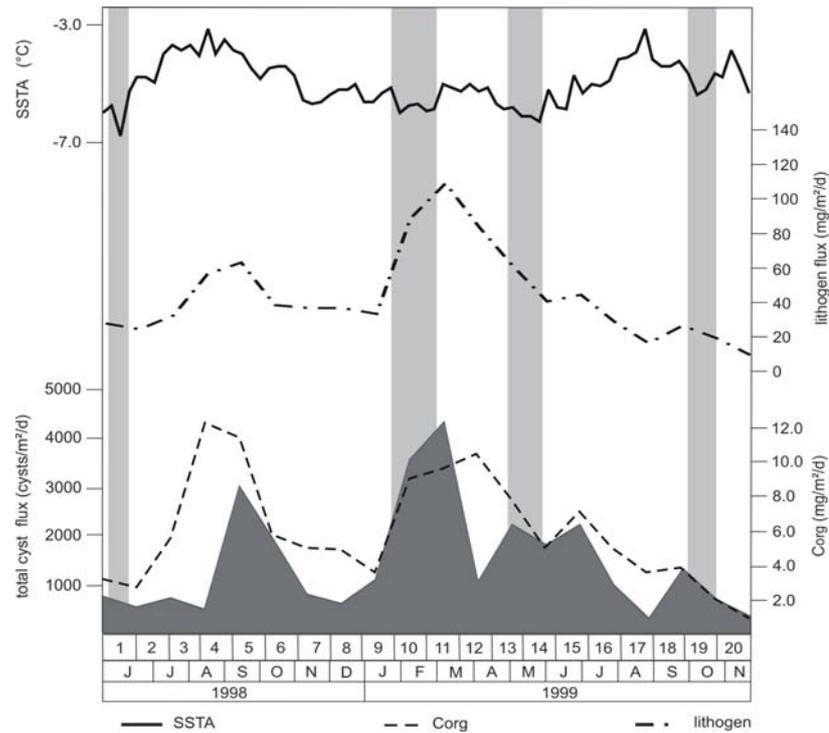


Fig. 2.4. Compilation of sea surface temperature anomaly (SSTA), organic carbon content of sediment trap samples, total organic dinoflagellate cyst flux (dark gray) and lithogen flux. Low values of SSTA (calculated as difference between coastal and open ocean SST) reflect strong upwelling (gray bars).

## RESULTS

A total of 22 different cyst types were recorded in the present study. Detailed information about cyst fluxes is given in Table 2.2. The fluxes of the most abundant cyst species are illustrated in Figure 2.5. Highest total cyst flux can be observed at times of elevated nutrient availability in surface waters as a result of lithogenic input and/or upwelling filaments passing the sampling site. This pattern is comparable to that of organic carbon fluxes (Fig. 2.4). The cyst assemblages are strongly dominated by heterotrophic species (Fig. 2.6). Mean annual abundance of cysts from autotrophic species constitute only 1.5% (maximal mean abundance of 6%).

Several cyst taxa are produced throughout the sampling interval, with the highest fluxes at times of strongest upwelling relaxation and/or dust input: *Echinidinium granulatum* Zonneveld, *Echinidinium* spp., cyst of *Protoperidinium stellatum* (Wall in Wall et Dale) Rochon et al., and cysts of *Protoperidinium* spp. Temporal production pattern of *Echinidinium aculeatum* Zonneveld, *Echinidinium delicatum* Zonneveld, *Impagidinium aculeatum* (Wall) Lentin et Williams, *Selenopemphix nephroides* (Benedek) Benedek et Sarjeant and *Selenopemphix quanta* (Bradford) Matsuoka can be positively related to elevated lithogenic input. These species are observed after upwelling periods of (ii) January/February 1999 (iii) May 1999 and (iv) September/October 1999, but not after the upwelling period of June 1998. *Impagidinium sphaericum* (Wall) Lentin et Williams and

cyst of *Protopteridinium americanum* (Gran et Braarud) Balech are produced at times of elevated upper water nutrient availability, but only at times when SST is relatively low. The temporal production pattern of the other species can not be related to a particular season or to specific environmental conditions in the upper water column (e.g. *Bitectatodinium spongium* (Zonneveld) Zonneveld et Jurkschat, *Protopteridinium monospinum* (Paulsen) Zonneveld et Dale and *Impagidinium patulum* (Wall) Stover et Evitt). No species with enhanced cyst production at conditions of low nutrient concentration in the upper water masses is observed.

Table 2.1. List of observed dinoflagellate cyst taxa

Species	Motile affinity
<i>Bitectatodinium spongium</i> (Zonneveld) Zonneveld et Jurkschat	unknown
<i>Echinidinium aculeatum</i> Zonneveld	unknown
<i>Echinidinium delicatum</i> Zonneveld	unknown
<i>Echinidinium granulatum</i> Zonneveld	unknown
<i>Echinidinium</i> spp.	
<i>Impagidinium aculeatum</i> (Wall) Lentin et Williams	<i>Gonyaulax</i> sp.
<i>Impagidinium patulum</i> (Wall) Stover et Evitt	<i>Gonyaulax</i> sp.
<i>Impagidinium sphaericum</i> (Wall) Lentin et Williams	<i>Gonyaulax</i> sp.
<i>Impagidinium</i> spp.	
<i>Impagidinium striatum</i> (Wall) Stover et Evitt	<i>Gonyaulax</i> sp.
<i>Lingulodinium machaerophorum</i> (Deflandre et Cookson) Wall	<i>Lingulodinium polyedrum</i> (von Stein) Dodge
Cyst of <i>Polykrikos schwartzii</i> Bütschli	<i>Polykrikos schwartzii</i> Bütschli
Cyst of <i>Protopteridinium americanum</i> (Gran et Braarud) Balech	<i>Protopteridinium americanum</i> (Gran et Braarud) Balech
Cyst of <i>Protopteridinium monospinum</i> (Paulsen) Zonneveld et Dale	<i>Protopteridinium monospinum</i> (Paulsen) Zonneveld et Dale
Cyst of <i>Protopteridinium</i> spp.	
<i>Selenopemphix nephroides</i> (Benedek) Benedek et Sarjeant	<i>Protopteridinium subinermis</i> (Paulsen) Loeblich III
<i>Selenopemphix quanta</i> (Bradford) Matsuoka	<i>Protopteridinium conicum</i> (Gran) Balech
<i>Spiniferites membranaceus</i> (Rossignol) Sarjeant	<i>Gonyaulax</i> sp.
<i>Spiniferites delicatus</i> Reid	<i>Gonyaulax</i> sp.
<i>Spiniferites hypercanthus</i> (Deflandre et Cookson) Cookson et Eisenack	<i>Gonyaulax</i> sp.
Cyst of <i>Protopteridinium stellatum</i> (Wall in Wall et Dale) Rochon <i>et al</i>	<i>Protopteridinium stellatum</i> (Wall in Wall et Dale) Rochon
<i>Trinovantedinium applanatum</i> (Bradford) Bujak et Davies	<i>Protopteridinium pentagonum</i> (Gran) Balech

After Marret and Zonneveld 2003, modified.

The most abundant taxa are *Protopteridinium* spp. (40.9–100%; mean relative abundance, 56%) and *P. monospinum*. During comparable seasons of 1998 and 1999 different cyst associations are observed. The 1998 summer/autumn season is dominated by *Protopteridinium* spp. Cysts, whereas in 1999 the co-dominance of *Protopteridinium* spp. and *P. monospinum* is observed (Fig. 2.7).

## DISCUSSION

The phenomenon of upwelling throughout the year in the region off Cape Blanc results in coastal subsurface waters characterized by relatively low temperatures and high nutrient

concentrations. Variations in upwelling intensity are indicated by SSTA. Comparison of SSTA and lithogenic input at the trap position with total cyst fluxes shows that cyst fluxes are high during periods of elevated nutrient levels in the upper water column. The relation between cyst flux and upwelling is consistent with other regions (Zonneveld and Brummer, 2000; Wendler et al., 2002). The encystment of the majority of cyst species is thought to be related to sexual reproduction (Pfiester and Anderson, 1987). In contrast to our results, a number of laboratory experiments suggest nutrition depletion as the main trigger for sexuality and cyst production (Anderson et al., 1984; Anderson and Lindquist, 1985; Blanco, 1995). This relationship can often not be found in natural environments.

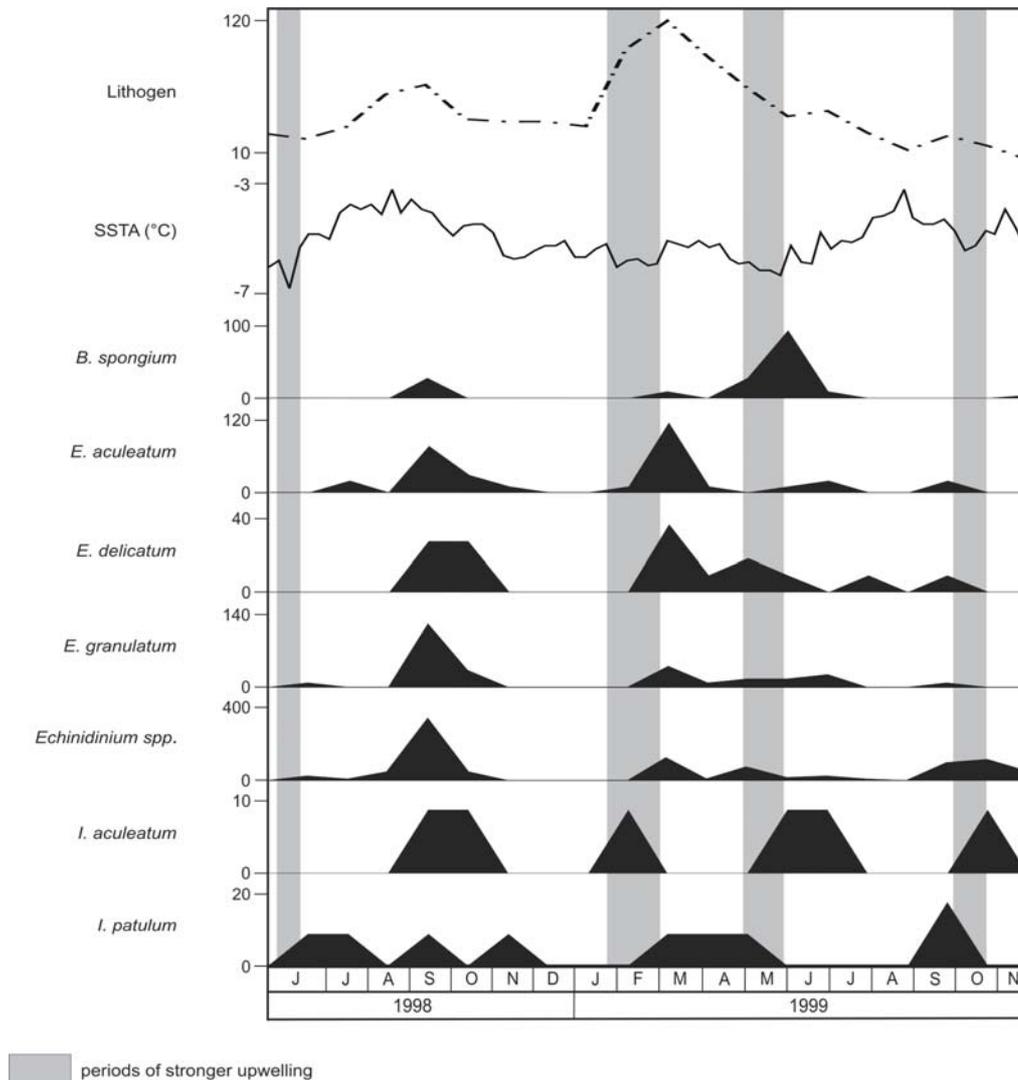


Fig.2.5. Cyst fluxes of selected species (cysts/m<sup>2</sup>/day). Lithogen flux in mg/m<sup>2</sup>/day

(Kremp and Heiskanen, 1999; Godhe et al., 2001). Field and trap studies generally document highest cyst abundances related to high nutrient concentrations at times of maximal vegetative growth. This

indicates that cyst production seems to be convergent with conditions optimal for vegetative cell growth (Wall et al., 1970; Anderson et al., 1983; Kremp and Heiskanen, 1999). A possible explanation for this paradox is that at maximal vegetative growth, nutrient depletion can occur within individual cells or their microhabitat and, as such, trigger enhanced sexuality. Other factors that might influence encystment are temperature, day length, irradiance and an endogenous encystment rhythm.

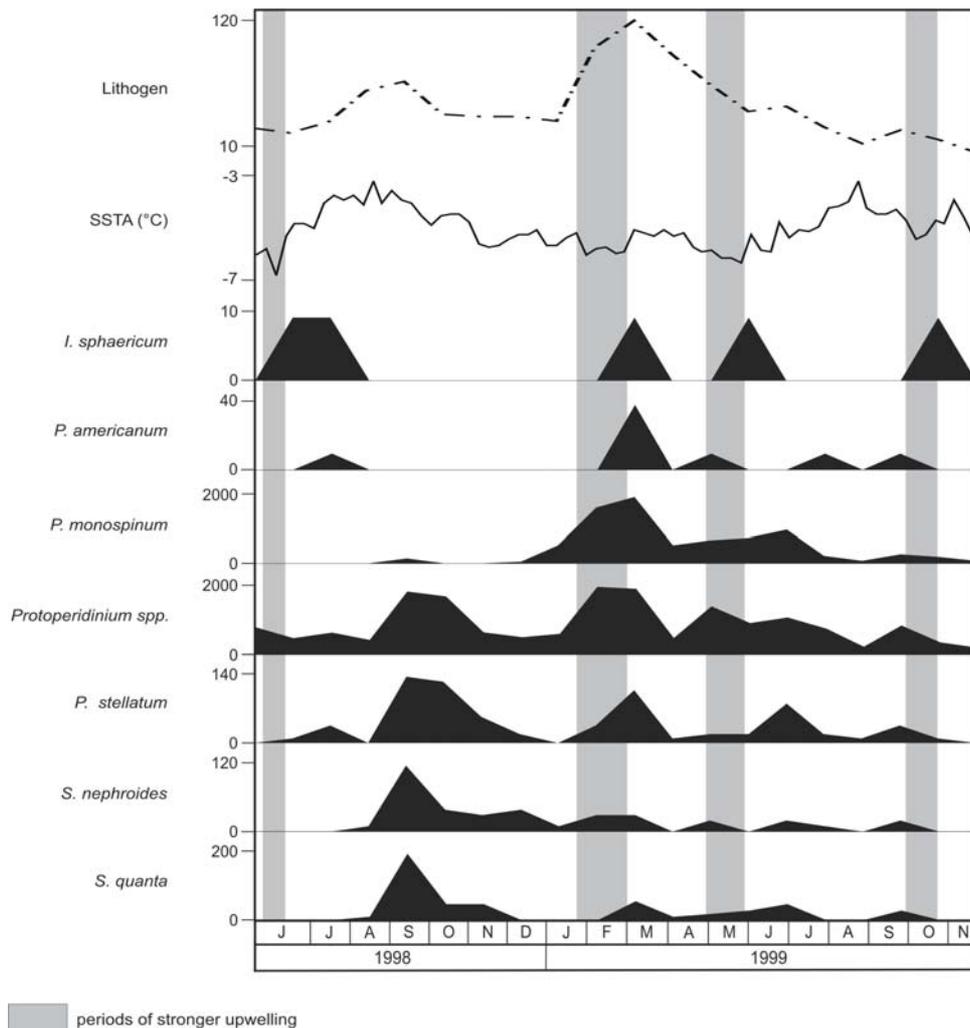


Fig.2.5. *Continued.*

Several dinoflagellates are able to produce cysts in a limited temperature window only (Anderson et al., 1984, 1985; Sgroso et al., 2001). Temperature itself, however, is not a triggering factor. In general, encystment of dinoflagellates in the field is not related to stress, but is rather favored by optimal conditions for vegetative growth. Godhe et al. (2001) showed for a Swedish fjord that the most important factors affecting cyst formation were surface water temperature and the intensity of solar radiation.

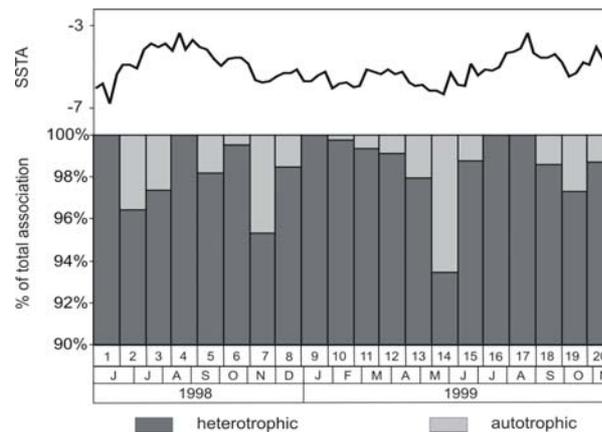


Fig.2.6. Relative abundances of the autotrophic and heterotrophic organic-walled dinoflagellate cysts.

The vegetative reproduction rate of dinoflagellates depends on a variety of factors such as nutrient, light and/or food availability and water movements. Field measurements and laboratory studies indicate high, species specific, sensitivity of dinoflagellates to turbulence (Thomas and Gibson, 1992; Gibson and Thomas, 1995; Gibson, 2000). Generally, the dinoflagellate production is negatively influenced by turbulence (Gibson, 2000). Phototrophic species are bound to the upper water layers; that is, the photic zone that is influenced by wind and waves causing turbulence. A reason for the low autotrophic cyst flux observed in the trap off Cape Blanc might be the presence of upwelling persisting throughout the year, preventing phototrophic dinoflagellates from establishing a standing stock large enough to produce a sufficient amount of cysts. Earlier observations (Gillbricht, 1977; Mitchell-Innes and Walker, 1991; Pitcher et al., 1991) showed that in upwelling areas at times of active upward water motion the phytoplankton community is dominated by small diatoms. Over the gradual change towards less intense water movement there is a phytoplankton succession from smaller to larger diatom species and, eventually, to dinoflagellates. In the studied area, the mixed layer is often deeper than the euphotic zone as a result of the generally strong winds. Maximum productivity is observed during periods of wind relaxation and weaker vertical mixing when the mixed layer depth is reduced (Dugdale and Wilkerson, 1985). In newly upwelled waters of the active upwelling cells, bioproduction is generally low (although nutrient concentrations are extremely high) because the extreme mixing of the upper water layer prevents phytoplankton from remaining in the photic zone and so inhibits the rapid build-up of a phytoplankton standing stock. In the Benguela, as well as in the Somali, upwelling areas dinoflagellates are absent from these active upwelling cells, but appear later in the phytoplankton succession succession (Shannon and Pillar, 1986; Mitchell-Innes and Walker, 1991; Pitcher et al., 1991; Veldhuis et al., 1997). Dinoflagellates become dominant in the more stratified, matured waters in which nutrient concentrations have declined, but are still enhanced compared to non-upwelled waters. High amounts of dinoflagellates can also be observed in the water column during periods of upwelling relaxation, or in upwelling filaments transported offshore. In the Benguela Region

dinoflagellates only dominate the phytoplankton association during quiescent conditions when a well-developed thermocline is present (Shannon and Pillar, 1986; Mitchell-Innes and Walker, 1991; Pitcher et al., 1991). In other regions, dinoflagellates become abundant in phytoplankton assemblages when the upper water layers get stratified (e.g. Taylor, 1987; Thomas and Gibson, 1992; Lewis and Hallet, 1997). Our study site is not located in the actual upwelling area, but at a site where giant filaments pass. Within these filaments, nutrition content is still high compared to surrounding waters, but vertical water movement is not as strong as in upwelling bands. According to Gabric et al. (1993), nutrients are not exhausted on the shelf and within the giant filaments, enabling in situ growth of phytoplankton, including dinoflagellates, in offshore waters. The most abundant (probably) phototrophic taxon observed is *B. spongium* (Zonneveld and Jurkschat, 1999). This species is characteristic for areas with well-mixed surface waters and prefers SST above 23.9°C (Zonneveld and Jurkschat, 1999; Marret and Zonneveld, 2003). In CB9 its occurrence was not restricted to periods with intensified upwelling. Cysts were found also at times of weak upwelling but with elevated chlorophyll concentrations (September 1998) related to enhanced Saharan dust input (Thomas et al., 2001; Gregg, 2002). In the present study, highest fluxes were observed at time of upwelling relaxation in May/June 1999 when SST was between 20.1°C and 22.0°C. This suggests that *B. spongium* can be produced in colder environments than previously suggested. Our results also suggest that although *B. spongium* tolerates mixing of upper water masses it is not restricted to upwelling and/or well-mixed surface water, but can be related to eutrophic environmental conditions.

In the present study, no species with increased cyst fluxes have been observed at times of relatively low nutrient concentrations. *Impagidinium* species are often considered to be characteristic for oligotrophic regions such as the open ocean. This can not be concluded from the present study where *I. sphaericum* is found at times of strong upwelling relaxation, *I. aculeatum* cysts at times of more intense upwelling and/or dust input and *I. patulum* throughout the studied interval.

In September–October 1998, the cyst flux of several taxa is exceptionally high (Fig. 2.5), which is consistent with an increase in general primary bioproduction (Gregg, 2002). During this interval, surface ocean temperature was relatively high and no anomalous situation in wind stress or wind direction could be observed, indicating that upwelling was not markedly intense. A possible mechanism causing the exceptionally high flux of several taxa in September–October 1998 could be the advection of material. Siggelkow et al. (2002) suggested that material collected by the CB array at a depth approximately 3500 m below sea level might be influenced by lateral cyst transport from the more onshore area. Zonneveld and Brummer (2000) noted extremely high cyst fluxes in sediment trap material from the Arabian Sea related to advection of resuspended sediment (Koning et al., 1997; Van Weering et al., 1997; Conan and Brummer, 2000). However, they found transported cysts only in the sediment trap closer onshore (on the mid continental slope; Conan et al., 2002), and not further offshore, at a site position similar to our CB9 trap. No evidence for enhanced advection of material presently exists for the studied trap. Consequently, we assume that lateral transport did not cause the

observed increase in cyst flux.

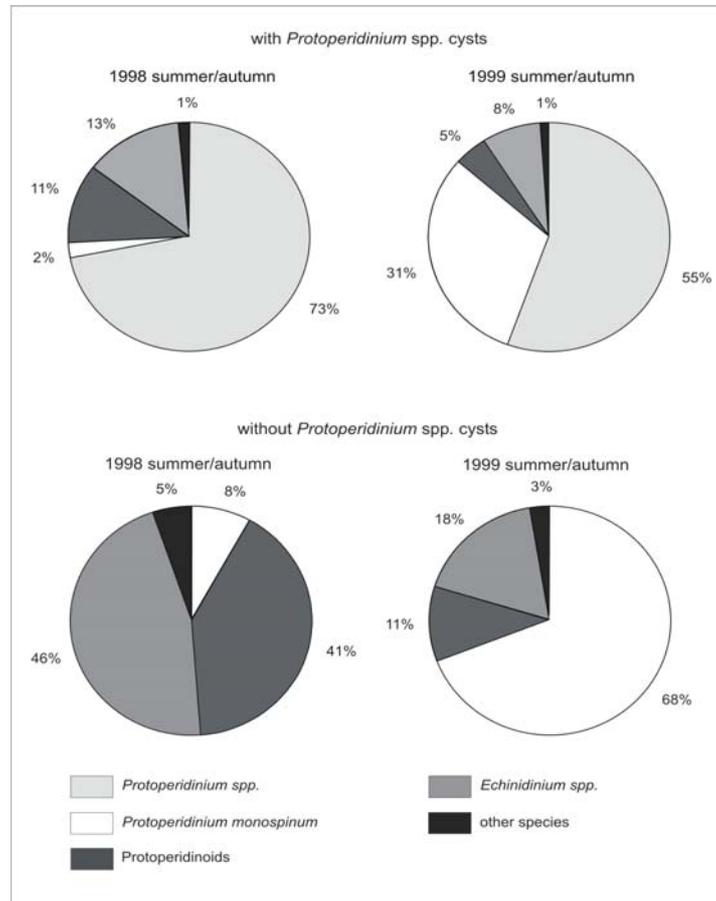


Fig.2.7. Relative cyst abundances of selected species and groups of species in 1998 and 1999. *Echinidinium* spp.: *Echinidinium aculeatum*, *Echinidinium delicatum*, *Echinidinium granulatum*. Protoperidinioids: cyst of *Protoperidinium americanum*, cyst of *Protoperidinium stellatum*, *Selenopemphix nephroides*, *Selenopemphix quanta*, *Trinovantedinium applanatum*. Other species: *Bitectatodinium spongium*, *Impagidinium aculeatum*, *Impagidinium patulum*, *Impagidinium sphaericum*, *Impagidinium strialatum*, *Spiniferites delicatus*, *Spiniferites hypercanthus*, *Spiniferites membranaceus*, *Lingulodinium machaerophorum*, cyst of *Polykrikos schwartzii*.

According to Gregg (2002), this phenomenon can be subscribed to enhanced Saharan dust input. Indeed, elevated lithogenic material concentrations are found in the trap samples in August/September 1998 (Fig. 2.4). Dust from the Sahara plays an important role in bringing nutrients to ocean (Kremling, 1985; Kremling and Streu, 1993; Sarthou et al., 2003). In this region, high atmospheric deposition occurs and might be one of the dominant sources of iron to the upper part of the water column (Sarthou et al., 2003). Iron plays an important role in world oceans as a limiting factor for primary production (Coale et al., 1996; Boyd et al., 2000; Boyd and Law, 2001; Smetacek, 2001; Pittman, 2002). In the present study, not all species show an increase in flux during this period of enhanced lithogenic input (e.g. cyst of *P. americanum* and *P. monospinum*). Other factors, such as the relatively high SST and a stratified water column, might be limiting the production of these species.

A second increase in lithogenic input was observed in February/March 1999. It coincides with strong upwelling. Here we observed the highest total cyst flux for the studied interval. During this time the quality of the waters upwelled in the region might have influenced the dinoflagellate cyst production. SACW contains more nutrients and is less salty than NACW. Strong admixture of SACW in upwelled water masses is especially present during winter and spring. Consequently, the high cyst fluxes might have been induced by a double nutrient ‘loading’ in this interval. For some species, the fluxes (e.g. *E. granulatum*, *P. stellatum* and *Selenopemphix nephroides*) were lower than during first dust input. A deep mixed layer might also be limiting the cyst production during the second dust period.

Cyst assemblages in the trap are dominated by cysts of *Protoberidinium* spp. All biological species included within this morphospecies are thought to be heterotrophic. The most important factor influencing the seasonal dynamics of individual *Protoberidinium* species is thought to be food availability (Kjæret et al., 2000). Several *Protoberidinium* species appear to be diatom grazers. According to Romero et al. (2002), the seasonal and annual diatom fluxes and species assemblages vary considerably in the studied region. This might be a reason for the rather unclear *Protoberidinium* flux pattern. The *Protoberidinium* spp. flux pattern does not provide any detailed ecologic information because the individual biological species most probably differ in their ecologic requirements.

Similar to *Protoberidinium* spp., increased fluxes of *E. granulatum*, *Echinidinium* spp. and cysts of *P. stellatum* coincide with periods of elevated nutrient content in the upper water column related to both upwelling and dust input events. Newly formed *E. granulatum* cysts were observed by Zonneveld and Brummer (2000) from sediment trap material collected at times of active upwelling. The present study suggests that the cyst production of this species is not restricted to the presence of upwelling filaments, but might be characteristic for eutrophic/mesotrophic conditions. Several studies suggest that cysts of *P. stellatum* are characteristically formed in upwelling areas or at times of active upwelling (Zonneveld and Brummer, 2000; Marret and Zonneveld, 2003). Our results show that the presence of upwelling is not a requirement for *P. stellatum* to produce cysts.

*Echinidinium aculeatum*, *E. delicatum*, *I. aculeatum*, *S. nephroides* and *S. quanta* show no elevated flux rates in June 1998 at times of maximal upwelling. Their enhanced fluxes during enhanced lithogenic input suggest, however, that their production is stimulated by increased nutrient input. The presence of upwelling filaments does not seem to be a requirement for these species. This confirms earlier observations that *S. nephroides*, *S. quanta*, *E. delicatum* and *E. aculeatum* are characteristic for regions with mesotrophic to eutrophic surface waters (see overview in Marret and Zonneveld, 2003)

The production of species of *I. sphaericum* and *P. americanum* is restricted to times of maximal upwelling. For *P. americanum*, this confirms earlier studies demonstrating that this species characterizes the north-west African and Benguela upwelling regions (Dale and Fjellså, 1994; Zonneveld et al., 2001). *Impagidinium* species were traditionally characterized as being characteristic

for oligotrophic, open oceanic conditions. The global distribution of *I. sphaericum* is, however, not restricted to these areas. In contrast, high abundances can be found in extremely eutrophic areas (Marret and Zonneveld, 2003). In spite of the low recovery rate, our results seem to suggest that this species might even occur, although in low amounts, within upwelling filaments. Clearly, the ecology of this species requires further investigation.

A characteristic temporal distribution is documented for cysts of *P. monospinum*. This species is practically absent in 1998 and dominates the association in 1999. The year 1999 was characterized by lower SST at the sampling site than the summer/autumn of 1998 (23.6°C and 21.8°C on average in 1998 and 1999, respectively). Conditions began to change by January 1999. Exceptionally strong south-westward winds and reduced SST (1.11°C cooler in February 1999 than in the analogous period of 1998) indicate anomalously strong upwelling in 1999 for the region (Gregg, 2002). The relatively high temperatures in 1998 could, therefore, have been a limiting factor for the production of *P. monospinum* cysts. To date, there is hardly any information available on the ecology of *P. monospinum*. The cysts of this species have been described by Zonneveld and Dale (1994) from the Oslo Fjord, Norway, which is characterized by relatively low surface water temperatures. In our data, cysts were only found during intervals with SST between 19.6°C and 25.3°C, whereby cysts with cell content were restricted to intervals with SST between 19.6°C and 23.5°C. Consequently, it can be suggested that *P. monospinum* might require eutrophic environments and/or SST lower than approximately 24°C.

Although in the present paper we have focused on the relationship between cyst productivity and a limited amount of physical parameters in the upper water column, it is obvious that other parameters not included in the present study, for example dissolved gases, light intensity (Pfiester and Anderson, 1987) might have influenced cyst production.

## CONCLUSIONS

During the studied time interval seasonal variations in sea surface temperature, upwelling intensity and Saharan dust input are reflected in the production of organic walled dinoflagellate cyst assemblages. Off north-west Africa Saharan dust bringing nutrients (e.g. iron) to the upper water column seems to be the most important factor influencing production of organic-walled dinoflagellates. Cysts of *Protoperidinium* spp. dominate cyst assemblages throughout the year. *E. granulatum*, *Echinidinium* spp., cysts of *P. stellatum* and cysts of *Protoperidinium* spp. show highest production in intervals of strongest upwelling relaxation and high lithogenic input. *E. aculeatum*, *E. delicatum*, *S. nephroides* and *S. quanta* show enhanced production when lithogenic input is elevated, but their flux pattern does not always coincide with periods of strong upwelling relaxation. *I. sphaericum* and cyst of *P. americanum* are produced at times of elevated upper water nutrient availability and relatively low SST. The production of cysts of *P. monospinum* is restricted to

intervals with enhanced nutrient concentrations in upper waters when SST at the sampling site is below approximately 24°C. Cysts of *Impagidinium* are predominantly found during periods with elevated nutrient content. None of the species showed elevated cyst production when nutrient concentration in the upper water masses was low.

## ACKNOWLEDGMENTS

This research is funded by the Deutsche Forschungsgemeinschaft as a part of European Graduate College 'Proxies in Earth History' EUROPROX, Bremen University. The present paper benefited greatly from the constructive reviews by André Rochon and an anonymous reviewer.

## REFERENCES

- Anderson, D. M. and Lindquist, N. L. 1985. Time-course measurements of phosphorus depletion and cyst formation in the dinoflagellate *Gonyaulax tamarensis* Lebour. *J. Exp. Mar. Biol. Ecol.* **86**: 1–13.
- Anderson, D. M., Chisholm, S. W. and Watras, C. J. 1983. Importance of life cycle events in the population dynamics of *Gonyaulax tamarensis*. *Mar. Biol.* **76**: 179–89.
- Anderson, D. M., Kulis, D. M. and Binder, B. J. 1984. Sexuality and cysts formation in the dinoflagellate *Gonyaulax tamarensis*: cyst yield in batch cultures. *J. Phycol.* **20**: 418–25.
- Anderson, D. M., Coats, D. W. and Tyler, M. A. 1985. Encystment of the dinoflagellate *Gyrodinium uncatenatum*: temperature and nutrient effects. *J. Phycol.* **21**: 200–6.
- Barton, E. D. 1998. Eastern boundary of the north Atlantic: northwest Africa and Iberia. In Robinson, A. R. and Brink, K. H. (Eds) *The Sea*. John Wiley & Sons, New York, pp. 633–57.
- Barton, E. D., Aristegui, J., Tett, P. *et al.* 1998. The transition zone of the Canary Current upwelling region. *Prog. Oceanogr.* **41**: 455–504.
- Blanco, J. 1995. Cyst production in four species of neritic dinoflagellates. *J. Plankton Res.* **17**: 165–82.
- Boyd, P. W. and Law, C. S. 2001. The Southern Ocean Iron Release Experiment (SOIREE) – introduction and summary. *Deep-Sea Res. II.* **48**: 2425–38.
- Boyd, P. W., Watson, A. J., Law, C. S. *et al.* 2000. A mesoscale phytoplankton bloom in the polar Southern Ocean stimulated by iron fertilization. *Nature* **407**: 695–702.
- Coale, K. H., Johnson, K. S., Fitzwater, S. E. *et al.* 1996. A massive phytoplankton bloom induced by an ecosystem scale iron fertilization experiment in the equatorial Pacific Ocean. *Nature* **383**: 495–501.
- Conan, S. M.-H. and Brummer, G. J. A. 2000. Fluxes of planktic foraminifera in response to monsoonal upwelling on the Somalia Basin margin. *Deep-Sea Res. II.* **47**: 2207–27.

- Conan, S. M.-H., Ivanova, E. M. and Brummer, G.-J. A. 2002. Quantifying carbonate dissolution and calibration of foraminiferal dissolution indices in the Somali Basin. *Mar. Geol.* **182**: 325–49.
- Dale, B. and Fjellså, A. 1994. Dinoflagellate cysts as paleoproductivity indicators: state of the art, potential and limits. In Zahn, R., Pedersen, T. F., Kaminski and M. A., Labeyrie, L. (Eds) *Carbon Cycling in the Global Ocean: Constrains on the Ocean's Role in the Global Change*. Springer-Verlag, Berlin Heidelberg, pp. 521–37.
- Dugdale, R. C. and Wilkerson, F. P. 1985. Primary production in the Cap Blanc region. In Bas, C., argalef, R., Rubies, P. (Eds) *International Symposium on the Most Important Upwelling Areas Off Western Africa (Cape Blanco and Benguela)*, Barcelona, 1983. Instituto de Investigaciones Pesqueras, Barcelona, Spain, pp. 233–43.
- Fisher, G., Donner, B., Ratmeyer, V., Davenport, R. and Wefer, G. 1996. Distinct year-to-year particle flux variations off Cape Blanc during 1998–1991: relation to  $\delta^{18}\text{O}$ -deduced sea-surface temperatures and trade winds. *J. Mar. Res.* **54**: 73–98.
- Gabric, A. J., Garcia, L., Van Camp, L., Nykjaer, L., Eifler, W. and Schrimpf, W. 1993. Offshore export of shelf production in the Cape Blanc (Mauritania) giant filament as derived from Coastal Zone Color Scanner imagery. *J. Geophys. Res.* **98**: 4697–712.
- Gibson, C. H. 2000. Laboratory and ocean studies of phytoplankton response to fossil turbulence. *Dynam. Atmos. Oceans* **31**: 295–306.
- Gibson, C. H. and Thomas, W. H. 1995. Effects of turbulence intermittency on growth inhibition of a red tide dinoflagellate, *Gonyaulax polyedra* Stein. *J. Geophys. Res.* **100**: 841–6.
- Gillbricht, M. 1977. Phytoplankton distribution in the upwelling area off NW Africa. *Helgol. Wiss. Meeresuntersuch.* **29**: 417–38.
- Godhe, A., Norén, F., Kuylenstierna, M., Ekberg, C. and Karlson, B. 2001. Relationship between planktonic dinoflagellate abundance, cysts recovered in sediment traps and environmental factors in the Gullmar Fjord, Sweden. *J. Plankton Res.* **23**: 923–38.
- Gregg, W. W. 2002. Tracking the SeaWiFS record with a coupled physical/biogeochemical/radiative model of the global oceans. *Deep-Sea Res. II.* **49**: 81–105.
- Hagen, E. 2001. Northwest African upwelling scenario. *Acta Oecol.* **24**: 113–28.
- Harland, R. and Pudsey, C. J. 1999. Dinoflagellate cysts from sediment traps deployed in the Bellingshausen, Weddell and Scotia seas, Antarctica. *Mar. Micropaleontol.* **37**: 77–99.
- Helmke, P. 2003. Remote sensing of the northwest African upwelling and its production dynamics. PhD Dissertation, University of Bremen, Bremen.
- Kjærøet, A. H., Naustvoll, L.-J. and Paasche, E. 2000. Ecology of the heterotrophic dinoflagellate genus *Protoperidinium* in the inner Oslofjord (Norway). *Sarsia* **85**: 453–60.
- Klein, B. and Tomczak, M. 1994. Identification of diapycnal mixing through optimum multiparameter analysis. 2. Evidence for unidirectional diapycnal mixing in the front between

- North and South Atlantic Central Water. *J. Geophys. Res.* **99**: 275–80.
- Koning, E., Brummer, G.-J., Van Raaphorst, W., Van Bennekom, J., Helder, W. and Van Iperen, J. 1997. Settling, dissolution and burial of biogenic silica in the sediments off Somalia (northwestern Indian Ocean). *Deep-Sea Res. II.* **44**: 1341–60.
- Kostianoy, A. G. and Zatsepin, A. G. 1996. The West African coastal upwelling filaments and cross-frontal water exchange conditioned by them. *J. Mar. Sys.* **7**: 349–459.
- Kremling, K. 1985. The distribution of cadmium, copper, nickel, manganese, and aluminium in surface waters of the open Atlantic and European shelf area. *Deep-Sea Res. I.* **32**: 531–55.
- Kremling, K. and Streu, P. 1993. Saharan dust influenced trace element fluxes in deep North Atlantic subtropical waters. *Deep-Sea Res. I.* **40**: 1155–68.
- Kremp, A. and Heiskanen, A.-S. 1999. Sexuality and cyst formation of the spring-bloom dinoflagellate *Scrippsiella hangoei* in the coastal northern Baltic Sea. *Mar. Biol.* **134**: 771–7.
- Lewis, J. and Hallett, R. 1997. *Lingulodinium polyedrum* (*Gonyaulax polyedra*) a blooming dinoflagellate. *Oceanogr. Mar. Biol. Ann. Rev.* **35**: 96–161.
- Marret, F. and Zonneveld, K. A. F. 2003. Atlas of modern organic-walled dinoflagellate cyst distribution. *Rev. Paleobot. Palynol.* **125**: 1–200.
- Middleton, N. J. and Goudie, A. S. 2001. Saharan dust: sources and trajectories. *Trans. Inst Br. Geogr.* **26**: 165–81.
- Minas, H. J., Codispoti, L. A. and Dugdale, R. C. 1982. Nutrients and primary production in the upwelling region off Northwest Africa. *Rapp. P.-V. Réun. Cons. Int. Explor. Mer* **180**: 148–83.
- Mitchell-Innes, B. A. and Walker, D. R. 1991. Short-term variability during an anchor station study in the southern Benguela upwelling system: Phytoplankton production and biomass in relation to specie changes. *Prog. Oceanogr.* **28**: 65–89.
- Mittelstaedt, E. 1983. The upwelling area off northwest Africa – a description of phenomena related to coastal upwelling. *Prog. Oceanogr.* **12**: 307–31.
- Mittelstaedt, E. 1991. The ocean boundary along the northwest African coast: circulation and oceanographic properties at the sea surface. *Prog. Oceanogr.* **26**: 307–55.
- Mittelstaedt, E., Pillsbury, D. and Smith, R. L. 1975. Flow patterns in the northwest African upwelling area. *Dtsch. Hydrogr. Z.* **28**: 145–67.
- Montresor, M., Zingone, A. and Sarno, D. 1998. Dinoflagellate cyst production at a coastal Mediterranean site. *J. Plankton Res.* **20**: 2291–312.
- Moulin, C., Lambert, C. E., Dulac, F. and Dayan, U. 1997. Control of atmospheric export of dust from North Africa by the North Atlantic Oscillation. *Nature* **387**: 691–4.
- Olli, K. and Anderson, D. M. 2002. High encystment success of the dinoflagellate *Scrippsiella* cf. *lachrymosa* in culture experiments. *J. Phycol.* **38**: 145–56.
- Pfiester, L. A. and Anderson, D. M. 1987. Dinoflagellate reproduction. In Taylor, F. J. R. (Ed.) *The*

- Biology of Dinoflagellates*. Blackwell, Oxford, pp. 611–48.
- Pitcher, G. C., Walker, D. R., Mitchell-Innes, B. A. and Moloney, C. L. 1991. Short-term variability during an anchor station study in the southern Benguela upwelling system: phytoplankton dynamics. *Prog. Oceanogr.* **28**: 39–64.
- Pittman, T. 2002. A correlation analysis of satellite chlorophyll to iron dust flux in the world's oceans. *HURJ* **1**: 18–21.
- Ratmeyer, V., Fischer, G. and Wefer, G. 1999. Lithogenic particle fluxes and grain size distributions in the deep ocean off northwest Africa: implications for seasonal changes of aeolian dust input and downward transport. *Deep-Sea Res. I.* **46**: 1289–337.
- Rochon, A., de Vernal, A., Turon, J.-L., Matthiessen, J., Head, M. 1999. Distribution of recent dinoflagellate cysts in surface sediments from the North Atlantic Ocean and adjacent seas in relation to sea-surface parameters. *AASP Contr. Ser.* **35**: 1–150.
- Romero, O. E., Lange, C. B. and Wefer, G. 2002. Interannual variability (1988–1991) of siliceous phytoplankton fluxes off northwest Africa. *J. Plankton Res.* **24**: 1035–46.
- Sarnthein, M., Thiede, J., Pflaumann, U. *et al.* 1982. Atmospheric and oceanic circulation patterns off northwest Africa during the past 25 million years. In von Rad, U., Hinz, K., Sarnthein, M. and Seibold, E. (Eds) *Geology of the Northwest African Continental Margin*. Springer-Verlag, Berlin, Heidelberg, pp. 545–604.
- Sarthou, G. and Jeandel, C. 2001. Seasonal variations of iron concentrations in the Ligurian Sea and iron budget in the Western Mediterranean Sea. *Mar. Chem.* **74**: 115–29.
- Sarthou, G., Baker, A. R., Blain, S. *et al.* 2003. Atmospheric iron deposition and sea-surface dissolved iron concentrations in the eastern Atlantic Ocean. *Deep-Sea Res. I.* **50**: 1339–52.
- Sgrosso, S., Esposito, F. and Montresor, M. 2001. Temperature and daylength regulate encystment in calcareous cyst-forming dinoflagellates. *Mar. Ecol. Prog. Ser.* **211**: 77–87.
- Shannon, L. V. and Pillar, S. C. 1986. The Benguela ecosystem, part III. Plankton. *Oceanogr. Mar. Biol. Ann. Rev.* **24**: 65–170.
- Siggelkow, D., Vink, A. and Willems, H. 2002. Calcareous dinoflagellate cyst production, vertical transport and preservation off Cape Blanc during 1990: a sediment trap study [abstract]. *JNR* **24**: 160.
- Smetacek, V. 2001. EisenEx: international team conducts iron experiment in Southern Ocean. *USJGOFs Newsletter* **11**: 11–14.
- Speth, P. and Detlefsen, H. 1982. Meteorological influences on upwelling off northwest Africa. *Rapp. P.-V. Réun. Cons. Int. Explor. Mer* **180**: 29–34.
- Speth, P., Detlefsen, H. and Sierst, H.-W. 1978. Meteorological influence on upwelling off northwest Africa. *Dtsch. Hydrogr. Z.* **31**: 95–104.
- Taylor, F. J. R. 1987. Ecology of dinoflagellates: general and marine ecosystems. In Taylor, F. J. R. (Ed.) *The Biology of Dinoflagellates*. Blackwell, Oxford, pp. 399–502.

- Thomas, A. C., Carr, M.-E. and Strub, P. T. 2001. Chlorophyll variability in eastern boundary currents. *Geophys. Res. Lett.* **28**: 3421–4.
- Thomas, W. H. and Gibson, C. H. 1992. Effect of quantified small-scale turbulences on the dinoflagellate, *Gymnodinium sanguineum (splendens)*: contrast with *Gonyaulax (Lingulodinium) polyedra*, and the fishery implication. *Deep-Sea Res.* **39**: 1429–37.
- Tomczak, M. 1977. Continuous measurement of near-surface temperature and salinity in the NW African upwelling region between Canary Islands and Cap Vert during the winter of 1971–72. *Deep-Sea Res. I.* **24**: 1103–19.
- Van Camp, L., Nykjaer, L., Mittelstaedt, E. and Schlittenhardt, P. 1991. Upwelling and boundary circulation off Northwest Africa as decipied by infrared and visible satellite observations. *Prog. Oceanogr.* **26**: 357–402.
- Van Weering, T. C. E., Helder, W. and Schalk, P. 1997. The Netherlands Indian Ocean expedition 1992–1993, first results and an introduction. *Deep-Sea Res. II.* **44**: 1177–93.
- Veldhuis, M. J. W., Kraay, G. W., Van Bleijswijk, J. D. L. and Baars, M. A. 1997. Seasonal and spatial variability in phytoplankton biomass, productivity and growth in the northwestern Indian Ocean: the southwest and northeast monsoon, 1992–1993. *Deep-Sea Res. I.* **44**: 425–49.
- Vink, A., Zonneveld, K. A. F. and Willems, H. 2000. Organic-walled dinoflagellate cysts in western equatorial Atlantic surface sediments: distributions and their relation to environment. *Rev. Paleobot. Palynol.* **112**: 247–86.
- Wall, D., Guillard, R. R. L., Dale, B. and Swift, E. 1970. Calcitic resting cysts in *Peridinium trochoideum* (Stein) Lemmermann, an autotrophic marine dinoflagellate. *Phycologia* **9**: 151–6.
- Wendler, I., Zonneveld, K. A. F. and Willems, H. 2002. Production of calcareous dinoflagellate cysts in response to monsoon forcing off Somalia: a sediment trap study. *Mar. Micropaleontol.* **46**: 1–11.
- Zonneveld, K. A. F. and Dale, B. 1994. The cyst-motile stage relationships of *Protoperidinium monospinum* (Paulsen) Zonneveld et Dale comb. nov. & *Gonyaulax verior* (Dinophyta, Dinophyceae) from Oslo Fjord (Norway). *Phycologia* **33**: 359–68.
- Zonneveld, K. A. F. and Jurkschat, T. 1999. *Bitectatodinium spongium* (Zonneveld, 1997) Zonneveld et Jurkschat, comb. nov. from modern sediments and sediment trap samples of the Arabian Sea (northwestern Indian Ocean): taxonomy and ecological affinity. *Rev. Paleobot. Palynol.* **106**: 153–69.
- Zonneveld, K. A. F. and Brummer, G. J. A. 2000. (Palaeo-) ecological significance, transport and preservation of organic-walled dinoflagellate cysts in the Somali Basin, NW Arabian Sea. *Deep-Sea Res. II.* **47**: 2229–56.
- Zonneveld, K. A. F., Versteegh, G. J. M. and Lange, G. J. d. 1997. Preservation of organic-walled dinoflagellate cysts in different oxygen regimes: a 10,000 year natural experiment. *Mar.*

*Micropaleontol.* **29**: 393–405.

Zonneveld, K. A. F., Hoek, R. P., Brinkhuis, H. and Willems, H. 2001. Geographical distributions of organic-walled dinoflagellate cysts in surficial sediments of the Benguela upwelling region and their relationship to upper ocean conditions. *Prog. Oceanogr.* **48**: 25–72.

Table 2.2.

Fluxes of individual species or groups of species recovered at CB9 mooring.

CB 9	starting date	closing date	cyst of <i>Protoperidinium</i> spp.	cyst of <i>Protoperidinium americanum</i>	cyst of <i>Protoperidinium monospinum</i>	cyst of <i>Protoperidinium stellatum</i>	<i>Selenopemphix nephroides</i>	<i>Selenopemphix quanta</i>	<i>Trinovantedinium applanatum</i>
1	11.06.98	18.06.98	733	0	0	0	0	0	0
2	18.06.98	16.07.98	445	0	0	9	0	0	0
3	16.07.98	12.08.98	591	9	0	36	0	0	9
4	12.08.98	09.09.98	400	0	0	0	9	9	0
5	09.09.98	06.10.98	1682	0	155	136	109	191	45
6	06.10.98	03.11.98	1555	0	0	127	36	45	0
7	03.11.98	30.11.98	600	0	0	55	27	45	0
8	30.11.98	28.12.98	473	0	55	18	36	0	0
9	28.12.98	24.01.99	564	0	527	0	9	0	0
10	24.01.99	21.02.99	1809	0	1627	36	27	0	0
11	21.02.99	20.03.99	1755	36	1945	109	27	55	0
12	20.03.99	17.04.99	455	0	527	9	0	9	0
13	17.04.99	14.05.99	1291	9	664	18	18	18	9
14	14.05.99	11.06.99	845	0	745	18	0	27	0
15	11.06.99	08.07.99	991	0	982	82	18	45	0
16	08.07.99	05.08.99	700	9	218	18	9	0	0
17	05.08.99	01.09.99	218	0	64	9	0	0	0
18	01.09.99	29.09.99	782	9	273	36	18	27	0
19	29.09.99	26.10.99	336	0	182	9	0	0	0
20	26.10.99	07.11.99	191	0	83	0	0	0	0

Table 2.2. (continued)

CB 9	<i>Echinidinium aculeatum</i>	<i>Echinidinium delicatum</i>	<i>Echinidinium granulatum</i>	<i>Echinidinium</i> spp.	<i>Bitectatodinium spongium</i>	<i>Impagidinium aculeatum</i>	<i>Impagidinium patulum</i>	<i>Impagidinium sphaericum</i>	<i>Impagidinium striatum</i>	<i>Impagidinium</i> spp.	<i>Spiniferites delicatus</i>
1	0	0	0	0	0	0	0	0	0	0	0
2	0	0	9	27	0	0	9	9	0	0	0
3	18	0	0	9	0	0	9	9	0	0	0
4	0	0	0	55	0	0	0	0	0	0	0
5	73	27	136	373	27	9	9	0	0	9	0
6	27	27	36	55	0	9	0	0	0	0	0
7	9	0	0	0	0	0	9	0	9	0	9
8	0	0	0	0	0	0	0	0	0	0	0
9	0	0	0	0	0	0	0	0	0	0	0
10	9	0	0	0	0	9	0	0	0	0	0
11	109	36	45	136	9	0	9	9	0	0	0
12	9	9	9	9	0	0	9	0	0	0	0
13	0	18	18	82	27	0	9	0	0	0	0
14	9	9	18	18	91	9	0	9	9	0	0
15	18	0	27	27	9	9	0	0	0	9	0
16	0	9	0	9	0	0	0	0	0	0	0
17	0	0	0	0	0	0	0	0	0	0	0
18	18	9	9	109	0	0	18	0	0	0	0
19	0	0	0	127	0	9	0	9	0	0	0
20	0	0	0	57	4	0	0	0	0	0	0

Table 2.2. (continued)

CB 9	<i>Spiniferites hypercanthus</i>	<i>Spiniferites membranaceus</i>	<i>Lingulodinium machaerophorum</i>	cyst of <i>Polykrikos schwartzii</i>	total	cysts with cell content	trap surface (m <sup>2</sup> )	days
1	0	0	0	0	733	0	0.5	7.5
2	0	0	0	0	509	0	0.5	27.5
3	0	0	0	0	691	64	0.5	27.5
4	0	0	0	0	473	36	0.5	27.5
5	0	0	0	0	2982	0	0.5	27.5
6	0	0	0	0	1918	9	0.5	27.5
7	9	0	0	0	773	0	0.5	27.5
8	0	9	0	0	591	0	0.5	27.5
9	0	0	0	0	1100	36	0.5	27.5
10	0	0	0	0	3518	27	0.5	27.5
11	0	0	0	9	4291	0	0.5	27.5
12	0	0	0	0	1045	9	0.5	27.5
13	0	0	9	0	2191	36	0.5	27.5
14	0	0	0	0	1809	0	0.5	27.5
15	0	0	0	0	2218	18	0.5	27.5
16	0	0	0	0	973	27	0.5	27.5
17	0	0	0	0	291	0	0.5	27.5
18	0	0	0	0	1309	0	0.5	27.5
19	0	0	0	0	673	0	0.5	27.5
20	0	0	0	0	335	4	0.5	11.5

**INTERANNUAL AND SEASONAL VARIABILITY OF THE ORGANIC-WALLED  
DINOFLAGELLATE CYST PRODUCTION IN THE NORTHEAST  
(SUB)TROPICAL ATLANTIC WITH EMPHASIS ON TRANSPORT AND  
PRESERVATION PROCESSES.**

**Ewa Susek and Karin A.F. Zonneveld**

Fachbereich 5-Geowissenschaften, University of Bremen, Postfach 330440, D- 28334 Bremen, Germany

*Submitted to Deep-Sea Research*

## **Interannual and seasonal variability of the organic-walled dinoflagellate cyst production in the northeast (sub)tropical Atlantic with emphasis on transport and preservation processes.**

**Ewa Susek and Karin A. F. Zonneveld**

Fachbereich 5-Geowissenschaften, University of Bremen, Postfach 330440, D- 28334 Bremen, Germany

### **ABSTRACT**

Living dinoflagellate cysts in marine sediments form a seed bank from which their motile planktic stock can be renewed. Excessive growth of dinoflagellates in the upper water column can have major environmental and economic consequences especially when toxin producing species are involved. Fossilised cyst-associations are used to obtain detailed information about past marine environmental conditions and form therefore a sufficient tool to reconstruct the palaeoceanography. To estimate this risk, and for adequate use of dinoflagellate cysts in palaeoenvironmental research, it is essential to have detailed information about factors that influence cyst formation, sedimentation and fossilisation. Within this study, we enhance this information by presenting results of a sediment trap study from the upwelling region off NW Africa that is characterised by strong seasonal and interannual variability. Cyst production of organic-walled dinoflagellate cysts has been related to environmental conditions in the upper water column over a period of 4 years (including 5 summer/autumn seasons), notably to variations in sea surface temperature, upwelled water salinity, upwelling intensity and Sahara dust input. We show that enhanced cyst production coincides with high nutrient availability in the upper water column. The most important environmental parameters affecting cyst production in the region appear to be the amount of dust input and the quality of upwelled water reflected by the water salinity. No clear relationship between surface temperatures, upwelling intensity and cyst production is found. Cysts assemblages are dominated by heterotrophic taxa: *Brigantedinium* spp. and *Protoperidinium monospinum*. Autotrophic taxa constitute max 4% of the assemblages. Production of cysts of *P. americanum* and *P. monospinum* is positively related to the Saharan dust input. Increased production of *Lingulodinium machaerophorum* is observed in periods with relatively high South Atlantic Central Water content of the upwelled water. Fluxes of *Brigantedinium* spp. show similar variability as the total diatom flux. Species selective aerobic decay strongly influences surface sediment cysts association resulting in an enhanced concentration of autotrophic taxa in surface sediments compared to that of heterotrophic taxa.

**Key words:** organic-walled dinoflagellate cyst, sediment trap, interannual differences, dust, NACW/SACW, NW Africa.

## INTRODUCTION

Dinoflagellates constitute together with diatoms and coccolithophorids the majority of the marine eukaryotic phytoplankton and are, therefore, important as primary producers. About 200 marine species are known to produce resting stages (so called resting cysts) as part of their sexual reproduction cycle (Pfiester and Anderson, 1987). During encystment the dinoflagellates lose their flagella and become immobile. As a result they sink through the water column towards the sea bottom where they sediment and may become fossilized. Cysts may form a sort of seed bank in aquatic sediments from which the motile stock can be renewed. Recent experiments have shown that cysts of some species can remain vital for at least almost a decade (Lewis et al., 1999). Especially cysts form by toxin producing species form a risk to develop, so called, toxic blooms. Such blooms can have major economic consequences for the fish industry as well as forming a severe risk for public health. To optimise the estimates about these risks, it is essential to have detailed information about the environmental factors that influence cyst production of individual species as well as their sedimentation behaviour. Such information is also required within the palaeoceanographic and palaeoclimatic research fields where the ecological information of fossilised cyst can be used to establish detailed reconstructions of past oceanographic and environmental conditions.

Until now the majority of the required information is derived by comparing the modern distribution patterns of cyst species within surface sediments with environmental conditions of overlaying water masses (e.g. Marret and Zonneveld, 2003). However, this method has its restrictions since surface sediments contain assemblages that are deposited over many years and the ecological “signal” can be disturbed by secondary processes such as species selective aerobic decay and transport (Zonneveld et al., 1997). By studying sediment trap material, a direct correlation of the cyst production with environmental conditions of surrounding water masses can be obtained (Montresor et al., 1998; Harland and Pudsey, 1999; Zonneveld and Brummer, 2000; Wendler et al., 2002). Information about transport processes through the water column and the fossilization potential of individual species can be obtained by comparing several traps at different water depths at one site with each other and with the underlying surface sediments. However, until now sediment trap studies of dinoflagellate cysts are restricted to short time intervals only. In regions with strong year to year variability such as for instance upwelling areas information is required from a time span of at least several years, to address this variability (Fischer et al., 1996; Ratmeyer et al., 1999; Romero et al., 2002; Romero et al., 2003). In this study we are the first to present information about the dinoflagellate cyst production over a 4-year period from the NW African upwelling area, one of the most important upwelling areas in the world. We aim to enhance the presently available knowledge on the ecological affinity, transport and preservation of tropical organic walled dinoflagellate cysts by comparing the cyst content of four sediment traps with upper ocean conditions (Fig. 3.1). By studying

the cyst content from traps at different water depths in one year, information is retrieved about processes of decay and transport within the water column. Information about secondary transport and preservation in the sediments is obtained by comparing the cyst associations recovered from the traps with those of the underlying sediments.

### OCEANOGRAPHIC SETTING

The intensity and duration of coastal upwelling off NW Africa is directly coupled to the northeast trade wind blowing alongshore NW Africa toward the southwest (Mittelstaedt, 1983). During upwelling, subsurface, nutrient rich waters replace the surface water masses on the continental shelf resulting in regionally restricted enhanced primary productivity in the upper water column. Since

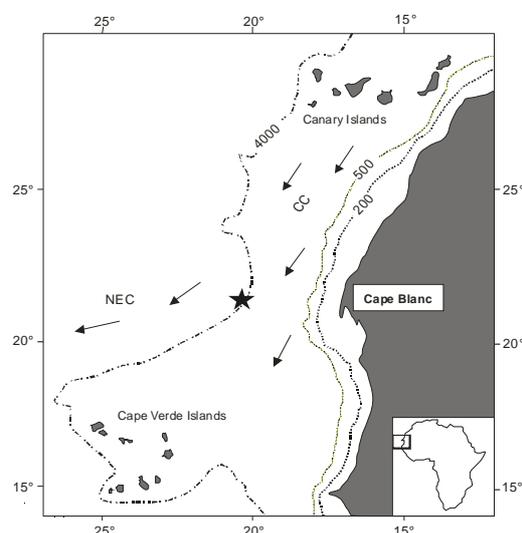


Fig. 3.1. Location of the traps and the surface sediment sample GeoB 3402-9 off Cape Blanc. CC = Canary Current, NEC = North Equatorial Current.

upwelled waters are relatively cold, a lowering of sea surface temperature (SST) is observed. The upwelling intensity can therefore be documented by sea surface temperature anomaly (SSTA) the difference between the coastal zone SST and the open Atlantic SST (Speth et al., 1978). Between 20 and 24°N upwelling occurs throughout the year with maximum intensity during spring and autumn (Speth et al., 1978; Speth and Detlefsen, 1982; Mittelstaedt, 1991). Variability in upwelling intensity is modified by short-term intensification and relaxation of the wind stress on a scale of days to weeks (Barton, 1998; Nykjaer and Van Camp, 1994). Apart from short term and seasonal variability, upwelling intensity can change remarkably at an interannual scale (Bory et al., 2001; Fischer et al., 1996; Nykjaer and Van Camp, 1994; Ratmeyer et al., 1999; Romero, et al., 2002; Thomas et al., 2001).

Table 3.1. Location, deployment depths, sampling duration and intervals (Fischer et al.1996)

Trap name	Trap type (opening)	Position	Water depth (m)	Trap depths (m)	Sampling duration	Samples x days
CB2	Mark V (1.17m <sup>2</sup> )	21°08.7' N 20°41.2' W	4092	3502	15.03.89 - 24.03.90	22 x 17
CB3	Kiel SMT 230 (0.5m <sup>2</sup> )	21°08.3' N 20°40.3' W	4094	730 3557	08.04.90 - 30.04.91 29.04.90 - 08.04.91	18 x 21.5 16 x 21.5
CB4	Kiel SMT 230 (0.5m <sup>2</sup> )	21°08.7' N 20°41.2' W	4108	3562	03.05.91 - 19.11.91	20 x 10
CB9	Kiel SMT 234	21°15.2' N 20°42.2' W	4121	3580	11.06.98 - 07.11.99	1 x 7.5; 18 x 27.5; 1 x 11.5

At periods of extreme, strong upwelling intensity, a cold upwelling belt can become separated from the coast by a zone of well-mixed water (Barton et al., 1977; Hagen, 2001). Although the major upwelling zone is found on the shelf-slope waters such a band of “primary upwelling” can be observed about 20–30km offshore (Mittelstaedt, 1991). A “secondary upwelling” band can develop along the shelf break. On the contrary to the above described features this type of upwelling induces not a strong biological response (Mittelstaedt et al., 1975; Minas et al., 1982). The generally strong winds in the Cape Blanc region induce strong turbulences in the photic zone. Maximal primary production in upwelling area is observed during periods of wind relaxation since the phytoplankton is not able to build up a considerable standing stock at times of strong mixing (Dugdale and Wilkerson, 1985).

Characteristic for this region are “giant filaments” of relatively cold, chlorophyll- and nutrient-rich water that persist throughout the year. They spread offshore over 450 km from the coast (VanCamp et al., 1991). The occurrence of these filaments during the year is coupled to the general pattern of upwelling in this region. Between 20°30’-22°N the highest concentration of “giant filaments” is observed (Kostianoy and Zatsepin, 1996).

The surface circulation in this area is dominated by the cold Canary Current flowing equatorward. About 21°N it bends from the continental margin southwestward to the open ocean to supply the North Equatorial Current (Barton, 1998). The water column between 150-600m depth forms a frontal zone between less saline, nutrient rich and slightly cooler the South Atlantic Central Water (SACW) and saltier, relative nutrient depleted the North Atlantic Central Water (NACW) (Hughes and Barton, 1974; Barton 1998; Klein and Tomczak, 1998; Vangriesheim et al., 2003). The SACW is transported northward by a counter current at depths between 150-400m, whereas the NACW follows the Canary Current at depth between 100-600m. Although the SACW can be traced as far north as 25°-26°N, the strongest mixing of the SACW and the NACW occurs between 22°-23°N

(Tomczak and Hughes, 1980; Sarnthein et al., 1982). Enhanced productivity off Cape Blanc occurs when the SACW feeds the upwelled water masses what takes place especially during winter and spring (Mittelstaedt, 1991; Hagen, 2001). Below 2000m the water masses are formed by the North Atlantic Deep Water (NADW). Below 4000m occasionally Antarctic Bottom Water (AABW) can be traced (Sarnthein et al., 1982). Apart from upwelling, nutrients can be brought into the oceanic system by frequently occurring dust storms from the Sahara. These storms transport dust westward within the trade wind or Hartmann wind system over long distances (Moulin et al., 1997; Ratmeyer et al., 1999). Saharan dust aerosols influence the nutrient dynamics of ocean and have a significant effect on the oceanic productivity (Middleton and Goudie, 2001). Aeolian dust contains appreciable quantities of iron (Zhu et al., 1997; Goudie and Middleton, 2001) which can enhance plankton productivity by reducing nitrogen limitation stress as a result of stimulation of N<sub>2</sub>-fixation (Gruber and Sarmiento, 1997).

## **MATERIAL AND METHODS**

### ***Sampling and preparation of material***

The trap samples were collected with cone-shaped multisampled sediment traps between 15.03.1989 and 03.05.1991 (traps CB2, CB3 lower and CB4) and between 11.06.1998 and 07.11.1999 (CB9). The moorings CB2-4 and 9 were located 235 nautical miles off Cape Blanc at 3550 m depth (Fig. 2.1). An additional trap located at 730 m depth (CB3 upper) was collected between 08.04.90 - 30.04.91. The sampled material was stained with HgCl<sub>2</sub>. The details of the sampling and splitting procedure are given in Wefer and Fischer (1993) and Fischer et al. (1996). For this study 1/64 (CB2), 1/40 (CB3upper and lower) and 1/64+1/80 (CB4) and 1/125th (CB9) of the original samples were investigated. They were rinsed with distillate water to remove HgCl<sub>2</sub> and than prepared according to method described by Susek et al. (2005). The surface sediment sample GeoB 4302-9 was collected at 21°13'4''N and 20°42'0''W during MS Meteor cruise (M38/1). 50% of material was counted. Identification of organic-walled dinoflagellate cyst species was accomplished using light microscope at magnification 400xs. Data of CB9 are from Susek, et al. (2005).

Off Cape Blanc upwelled waters ascend from depths of about 200m (Mittelstaedt, 1983). The upper water layer (50-100m) can be, temporarily, influenced by tropical warm water from the south. Therefore, to establish upwelled water masses data from the depth 157.5m (temperature) and from 160.51m (salinity) are used. Monthly data at the mooring position are extracted from UMD Carton goa beta7: beta7 (<http://iridl.ldeo.columbia.edu/SOURCES/UMD/.Carton/.goa/.beta7/>).

As an indicator for upwelling intensity the sea surface anomaly (SSTA) is calculated by comparison of coastal (21°50'N 17°50'W) and open ocean (21°50'N 40°50'W) SST. SST data from

ship buoy and bias-corrected satellite sources at a one-degree square block around the study site are obtained from [http:// Ingrid.ldeo.columbia.edu/SOURCES/IGOSS](http://Ingrid.ldeo.columbia.edu/SOURCES/IGOSS).

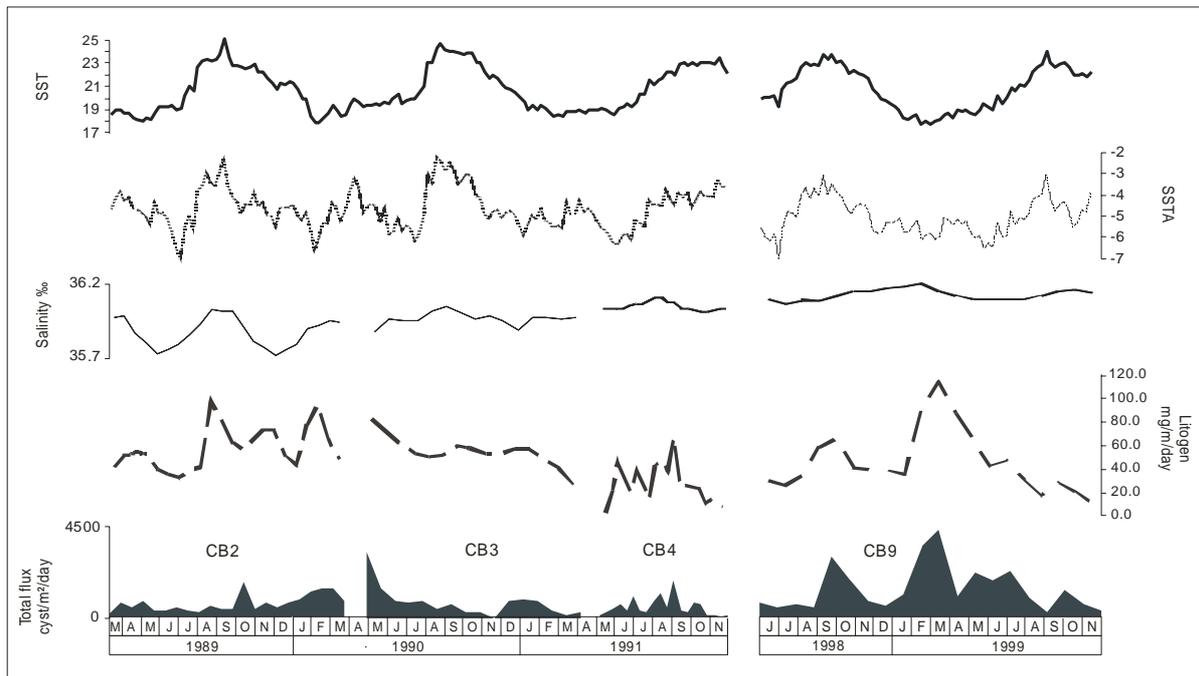


Fig.3.2. Compilation of total organic dinoflagellate cyst flux (black), salinity, lithogen flux, SST and SSTA.

Cyst fluxes are calculated by dividing the number of collected cysts in the trap per  $m^2$  by the number of collecting days. Mean relative abundance of cyst species in the sediment trap (mean %) are calculated by dividing the total number of cyst of an individual species in all samples by the total number of cyst counted in all trap samples. Mean relative abundances of cyst species in surface sediments are calculated by dividing the number of cyst of the individual species by the total number of cyst counted in the sediment sample.

The studied moorings did not have a sample covering of complete years. However, all moorings collected material in the summer and autumn seasons (June – November). For adequate acquisition of the interannual variability, we have focussed our comparison to these seasons. Material collected in summer-autumn correspond to samples 6-14 (CB2; 1989), samples 4-10 (CB3 lower; 1990), samples 5-19 (CB4; 1991), samples 1 to 6 (CB9; 1998) and 15 to 20 (CB9; 1999).

The nomenclature of dinoflagellate cysts is used. The cysts-theca relations are given in Table 3.2. and follow Marret and Zonneveld (2003). The group of *Brigantedinium* spp. includes round brown cysts without spines.

Since traps were not disturbed by high current velocities (Helmke, 2003) a fast and almost undisturbed downward transport was observed (Ratmeyer et al., 1999) we assume that observed cyst

fluxes reflect cyst production. Lithogen data concerning CB2-4 are obtained from Ratmeyer, et al. (1999).

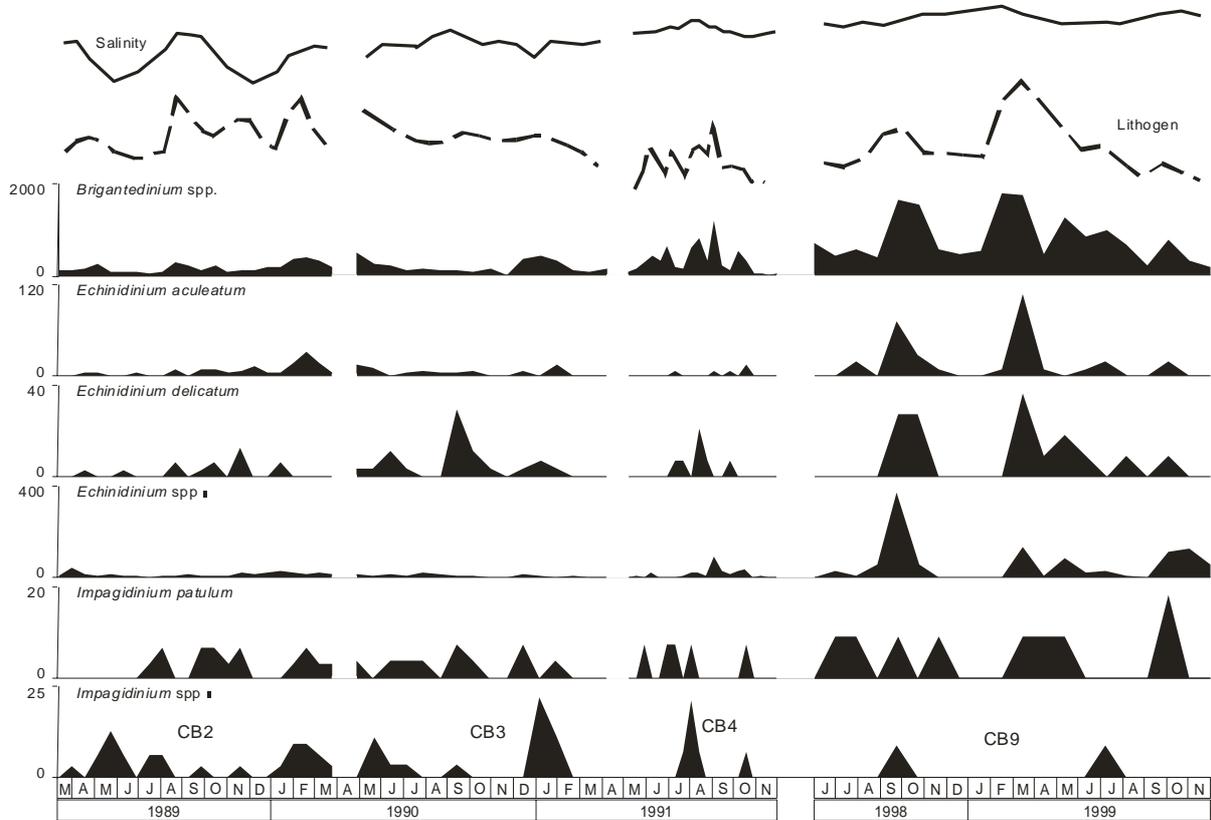


Fig.3.3a. Cyst fluxes of selected species (cysts/m<sup>2</sup>/day). Lithogen flux in mg/m<sup>2</sup>/day.

### Statistical methods

To determine the relationship between the environmental conditions in the upper water column and cysts production, a visual comparison of cysts fluxes with environmental/physical parameters such as salinity (as indicator of upwelled water masses), lithogen, sea surface temperature and SSTA can be made. However, ecological parameters influence the cyst production simultaneously, as a complex. The use of statistical methods can be helpful to elucidate these relationships. Here we use the method of redundancy analysis (RDA) to establish a direct correlation between cysts production and environmental variables using the programme CANOCO for Windows (CANONical Community Ordination: version 4.0, author C.J.F. Ter Braak, 1998, Wageningen, The Netherlands). RDA is based on the assumption that species show a linear response to changing environmental gradients (Hill and Gauch, 1980; Jongman et al., 1987). Previous to our RDA analysis our dataset has been tested on its linearity by a detrended correspondence analysis (DCA).

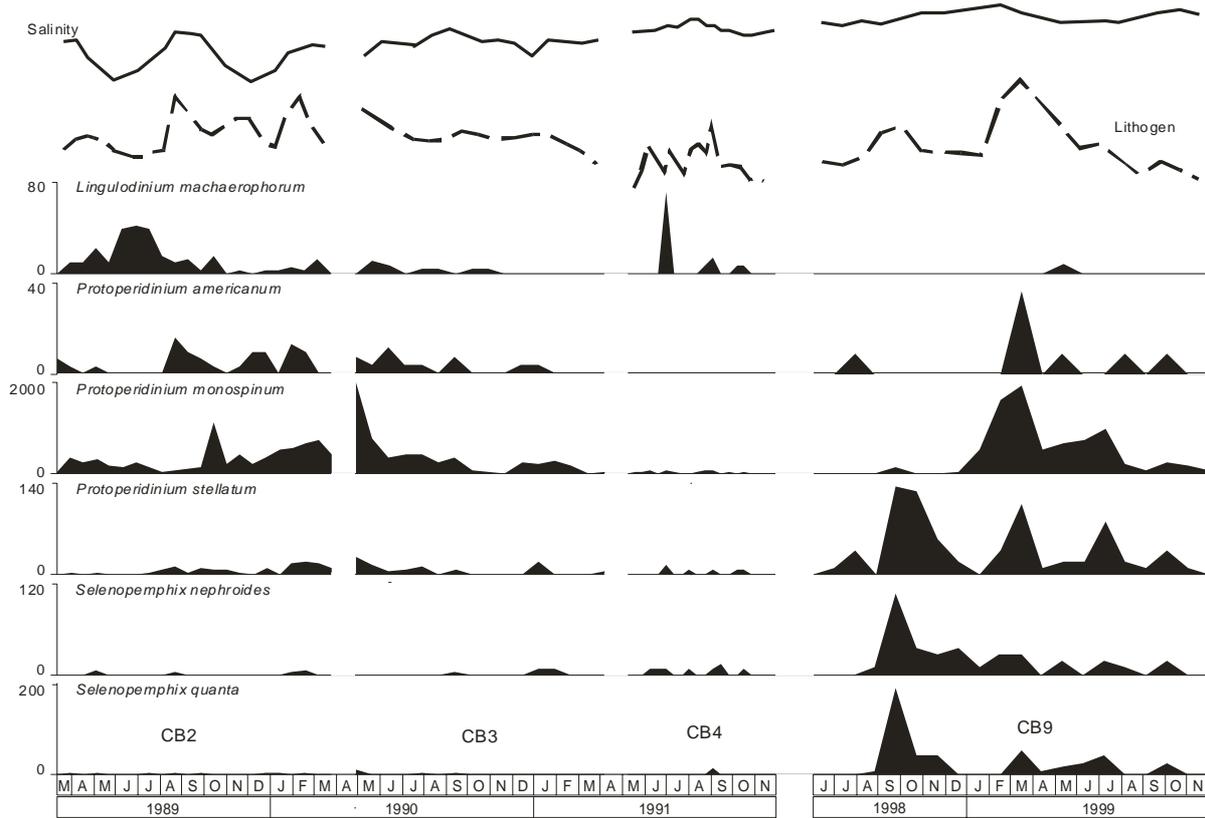


Fig.3.3b. Cyst fluxes of selected species (cysts/m<sup>2</sup>/day). Lithogen flux in mg/m<sup>2</sup>/day.

Results of a RDA analysis are depicted in a two dimensional space. Results of both species and environmental variables are depicted by arrows. Directions of the arrows point in the direction of increased species accumulation rate or variable value, respectively. The length of an arrow of an environmental variable is a function of that variable's importance in determining the species variation (see Fig. 3.4). Species that plot close to the centre of the diagram (i.e. having short lines) are most likely not significantly affected by the environmental gradients. The correlation coefficient between a species and the environmental gradient corresponds to the cosine of the angle between the species line and that of the gradient: a positive score represents increasing abundance of a species along the gradient and a negative score the opposite. The known environmental variables available for the analysis are: (a) SST, (b) SSTA, (c) salinity at depth 160.51m (17.5°W 21.5°N), (d) lithogen. It is assumed that sinking velocity of marine particles is such that it takes meanly two weeks to reach the sampling depth (Fisher et al., 1996; Siggelkow et al., 2002) salinity, temperature at depth 157.5m (17.5°W 21.5°N), SST and SSTA were therefore compared to productivity with a two week phase lag.

## RESULTS

A total of 30 different organic-walled dinoflagellate cyst morphotypes are recorded (Table 3.3.). Within the studied surface sediment 18 taxa have been recorded. Total cyst flux is illustrated in Fig. 3.2. The fluxes of the selected cyst species in CB 2-4 and CB9 are illustrated in Fig. 3.3a and 3.3b.

### *Redundancy analysis (RDA)*

The results of the RDA analysis are illustrated in Fig.3.4. Of the studied environmental variables only lithogen (or Sahara dust input) and salinity appear to be significantly related to the variability in cyst production of individual species explaining 40% and 10%, respectively, of the variability in the dataset. The following relationships can be indicated:

Cyst production of *Protoperidinium monospinum* and *P. americanum* can be positively correlated to lithogen. *Lingulodinium machaerophorum* production is negatively correlated with salinity. The production of *Brigantedinium* spp., *Echinidinium aculeatum*, *P. stellatum*, *Selenopemphix nephroides* and *Selenopemphix quanta* is positively correlated to both lithogen and salinity. The abundances of other species do not show clear correlation with the environmental parameters studied.

### *Interannual variations*

Although the associations of all traps at 3550 m depth are dominated by heterotrophic taxa (Fig.3.5) the species composition varies annually. The assemblages collected by CB2 (1989) and CB3 (1990) are dominated by *Protoperidinium monospinum* (respectively 59% and 59%) whereas those of CB4 (1991) and CB9 (1998/1999) are dominated by *Brigantedinium* spp. (78% and 45%, respectively) (Fig.3.6).

Our study covers five summer/autumn seasons. Cyst assemblages of these seasons in 1989 (CB2) and 1990 (CB3) are dominated by *Protoperidinium monospinum* (respectively 56% and 60%) with *Brigantedinium* spp. forming the second most important species. In 1991 (CB4), 1998 (CB9) and 1999 (CB9) assemblages of these seasons are dominated by *Brigantedinium* spp. (respectively 78%, 73% and 55%). In the summer/autumn season of 1999 *Protoperidinium monospinum* forms 31% of the assemblages whereas in 1991 and 1998 it forms only a small part of the association (Fig.3.7).

Comparison of the average daily flux of dinoflagellate cyst in comparable seasons shows minor differences between 1989, 1990 and 1991 (respectively: 469.0, 470.4 and 480.7 cyst/d/m<sup>2</sup>). In 1998 the flux is strongly increased compared to previous years (1217.7 cyst/d/m<sup>2</sup>) whereas the flux in 1999 is of intermediate high (Fig.3.8). The average daily flux of autotrophic species is highest in 1989 (CB2 – 29.0 cyst/d/m<sup>2</sup>) and the lowest in 1999 (CB9 – 11.2 cyst/d/m<sup>2</sup>).

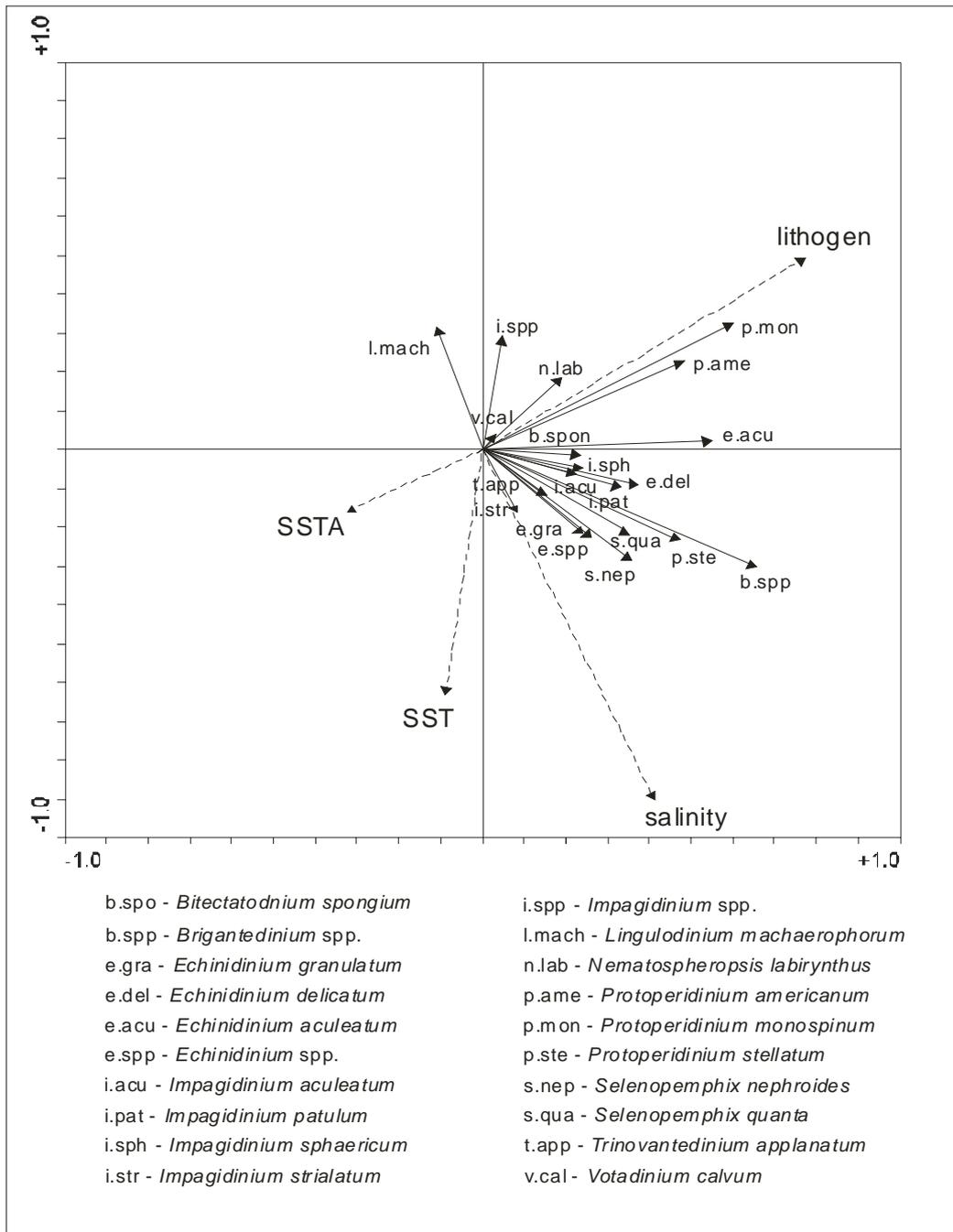


Fig.3.4. Redundancy analyses (RDA) diagram showing the relative distributions of organic walled dinoflagellate cyst occurrence in relation to the known environmental variables. Values along the first and the second axes represent standard deviation.

Several species are observed throughout the years (i.e. in every mooring): *Brigantedinium spp.*, *Echinidinium aculeatum*, *Echinidinium delicatum*, *Echinidinium granulatum*, *Echinidinium spp.*, *Impagidinium aculeatum*, *Impagidinium patulum*, *Impagidinium spp.*, *Protoperidinium monospinum*,

*Protoperidinium stellatum*, *Selenopemphix nephroides* and *Selenopemphix quanta*. Occurrence of other taxa varies among individual traps.

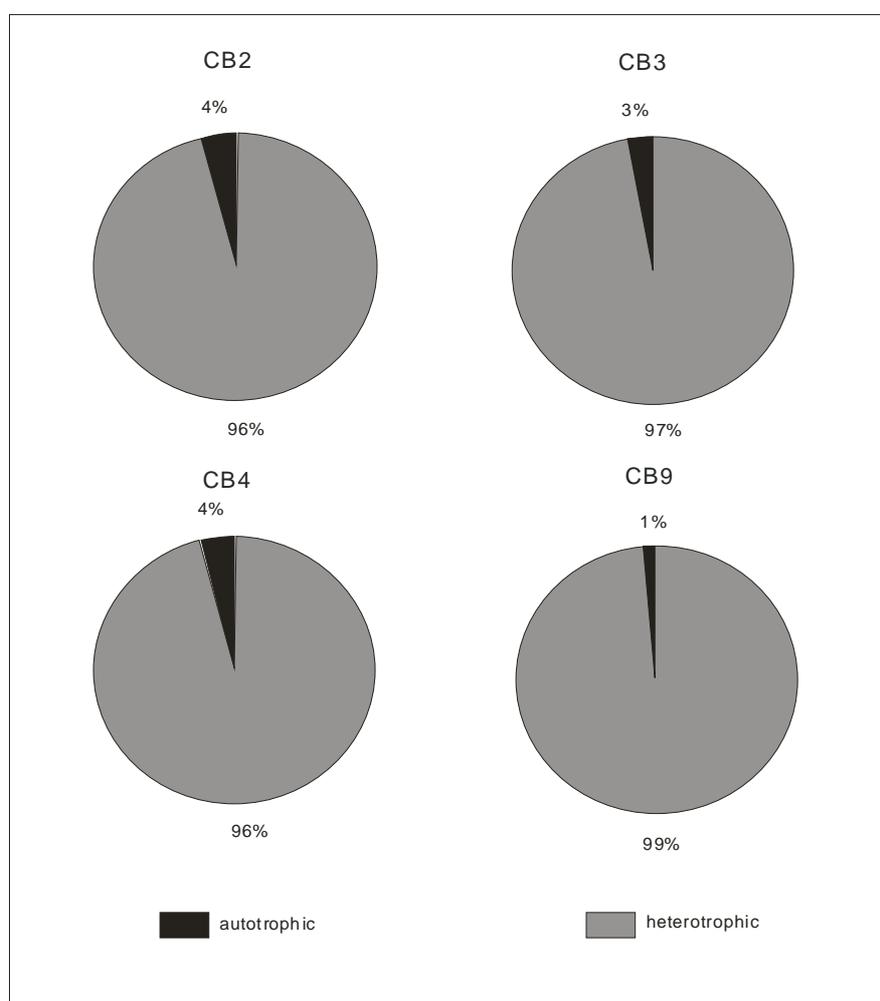


Fig.3.5. Relative abundances of the autotrophic and heterotrophic organic-walled dinoflagellate cysts in traps.

#### ***Comparison of upper and lower CB3 trap***

The flux rates in upper and lower trap are on the average at level 774 and 663 cyst/d/m<sup>2</sup>, respectively. In both traps cyst assemblages are dominated by heterotrophic taxa (with autotrophic species constituting 2 and 3% respectively). Comparison of associations indicates some differences: upper trap assemblages are dominated by *Brigantedinium* spp. (73%), whereas material collected by the lower trap is dominated by *Protoperidinium monospinum* (59%; Fig. 3.9).

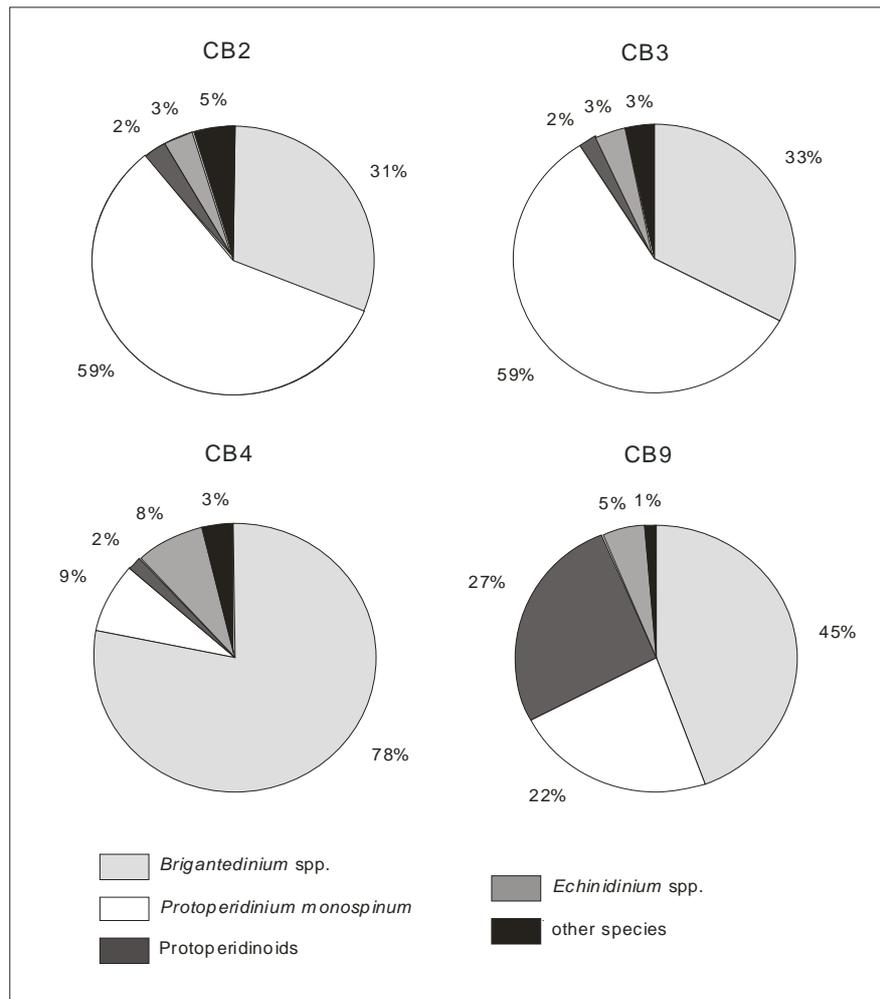


Fig.3.6. Relative cyst abundances of selected species and groups of species in CB2-4 and CB9. *Echinidinium* spp.: *E. aculeatum*, *E. delicatum*, *E. granulatum*, *Echinidinium* spp.

Protoperidinioids: cyst of *Protoperidinium americanum*, cyst of *P. stellatum*, *Selenopemphix nephroides*, *S. quanta*, *Trinovantedinium applanatum*, *Votadinium calvum*, *Votadinium spinosum*.

Other species: *Bitectatodinium spongium*, *Impagidinium aculeatum*, *I. patulum*, *I. sphaericum*, *I. striatum*, *Impagidinium* spp., *Lingulodinium machaerophorum*, *Nematospheropsis labyrinthus*, *Operculodinium centrocarpum*, *Operculodinium israelianum*, cyst of *Polykrikos schwartzii*, *Polysphaeridium zoharyi*, *Spiniferites delicatus*, *S. hypercanthus*, *S. membranaceus*, *S. pachydermus*, *Spiniferites* spp.

The temporal distribution pattern of total dinoflagellate cyst assemblages collected by the upper and lower CB3 mooring are comparable and do not show strong discrepancies. Comparison of *Brigantedinium* spp. and *Protoperidinium monospinum* fluxes in upper and lower CB3 mooring indicate no or 1 cup (21.5 day) time lag between upper and lower trap (Fig. 3.10). The fluxes of other taxa are lower and do not show clear time relationship between upper and lower traps.

### ***Surface sediment***

In consistence with the trap samples, the cyst association of the surface sample is dominated by heterotrophic taxa (Fig. 3.11). However while autotrophic species in the traps constitute on the average only 2.5% (1-4%) of association, their contribution in the surface sediment sample collected at the trap site compose 29%. The most abundant autotrophic species is *Impagidinium aculeatum* constituting 12.3% of total surface sediment assemblage and 42.2% of autotrophic part of association. The second most abundant taxon is *Impagidinium* spp. (6.8% and 23%, respectively). The heterotrophic part of assemblage is co-dominated by *Brigantedinium* spp. and *Protoberidinium monospinum*. All taxa observed in surface sediment material are found in the trap material as well. The species *Echinidinium granulatum*, *Impagidinium striatum*, *Nematospheropsis labyrinthus*, *Operculodinium centrocarpum*, *Polyspheridium zoharyi*, *Protoberidinium americanum*, *Selenopemphix quanta*, *Spiniferites delicatus*, *Spiniferites hypercanthus*, *Trinovantedinium applanatum*, *Votadinium calvum* and *Votadinium spinosum* found in the traps are, however, not observed in underlying sediments. Sediment material contains 439.1 cyst/gram (autotrophic: 127.8 cyst/gram).

### **DISCUSSION**

The coastal upwelling regions are known to be characterised by high productivity related to fertilization of the upper water column due to upward movement nutrient rich water to the surface. The region off Cape Blanc is characterised by relatively permanent upwelling with seasonal and interannual variability in strength (Bory et al., 2001; Fischer et al., 1996; Nykjaer and Van Camp, 1994; Ratmeyer et al., 1999; Romero et al., 2002; Thomas et al., 2001). Our study site is not located in the actual upwelling area, but at a site where “giant filaments” pass. Within these filaments nutrient concentrations are is still high compared to surrounding waters but vertical water movement is, although still severe, not as strong as in the active upwelling bands. Within the filaments nutrients are not exhausted and enable in situ growth of phytoplankton, including dinoflagellates (Gabric et al., 1993). For the region of active upwelling off Cape Blanc, maximum biological productivity during periods of wind relaxation and weaker vertical mixing is observed (Dugdale and Wilkerson, 1985). We do not observe a relationship between dinoflagellate cyst production and wind stress or relaxation. As discussed before, the trap position is located further offshore outside the region of active upwelling and local conditions are not directly influenced by wind intensity.

Field observations indicate that enhanced dinoflagellate cyst production can be related to increased nutrient availability (Godhe et al., 2001; Kremp and Heiskanen, 1999; Marino et al., 1984; Montresor et al., 1998; Susek et al., 2005; Wendler et al., 2002; Zonneveld and Brummer, 2000). For the Arabian Sea Zonneveld and Brummer (2000) and Wendler et al. (2002) have shown that cyst

production is enhanced in periods of intense upwelling. In our study, however, upwelling intensity appears to be no significant factor influencing the cyst association. This can be explained by the fact that upwelling in the studied area is almost permanent forming a rather continuous nutrient supply. In the Arabian Sea upwelling is strongly seasonally constrained which results in marked differences in nutrient availability in different seasons.

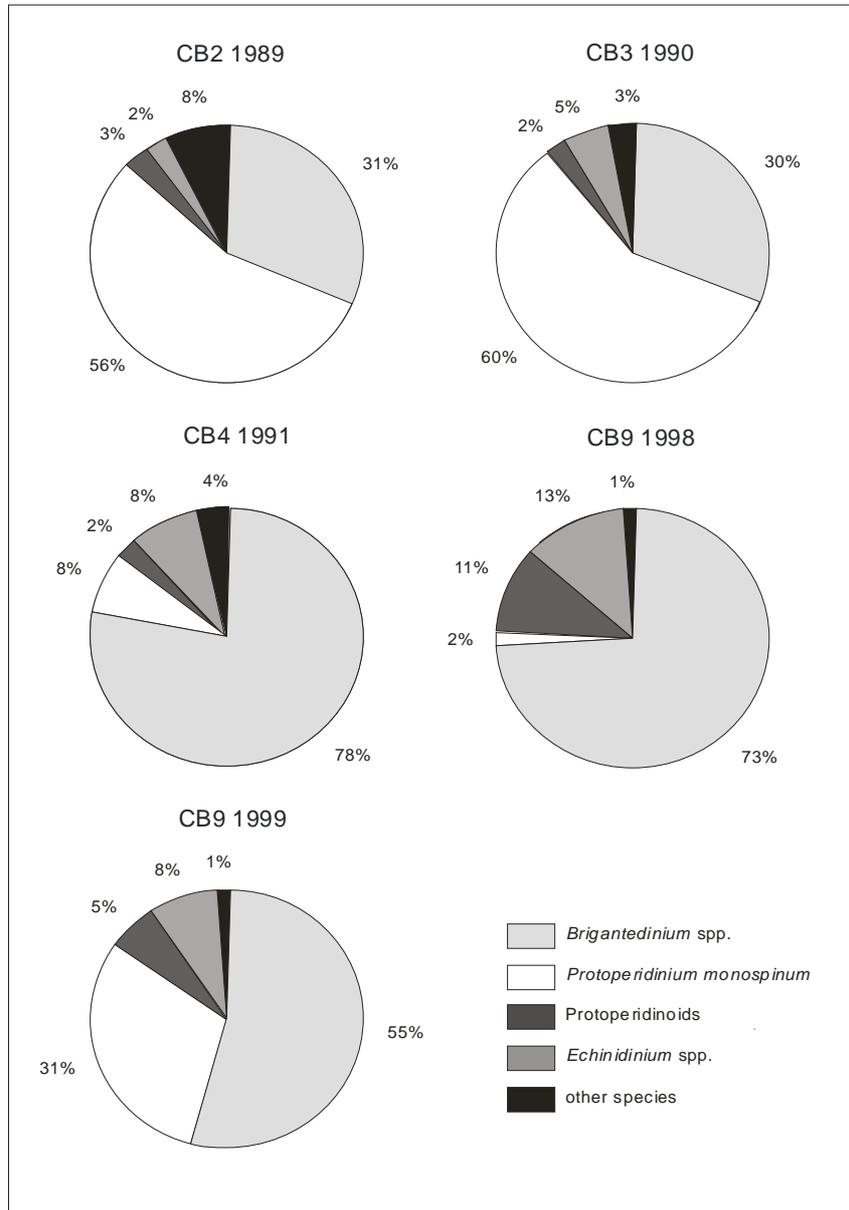


Fig.3.7. Relative cyst abundances of selected species and groups of species in summer/autumn seasons  
*Echinidinium* spp.: *E. aculeatum*, *E. delicatum*, *E. granulatum*, *Echinidinium* spp.  
 Protope ridinoids: cyst of *Protope ridinium americanum*, cyst of *P. stellatum*, *Selenopemphix nephroides*, *S. quanta*, *Trinovantedinium applanatum*, *Votadinium calvum*, *Votadinium spinosum*.  
 Other species: *Bitectatodinium spongium*, *Impagidinium aculeatum*, *I. patulum*, *I. sphaericum*, *Impagidinium* spp., *Lingulodinium machaerophorum*, *Operculodinium israelianum*, cyst of *Polykrikos schwartzii*, *Polysphaeridium zoharyi*, *S. hypercanthus*, *S. pachydermus*, *Spiniferites* spp.

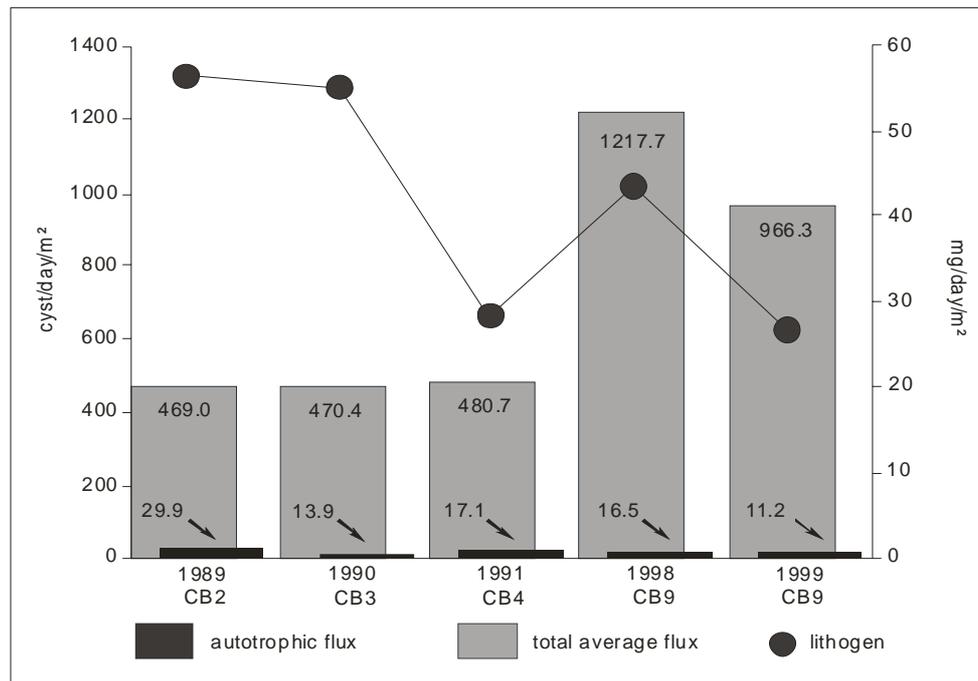


Fig.3.8. Average flux in summer/autumn seasons compared with average lithogen flux.

Laboratory experiments indicated nutrient depletion, especially nitrogen and/or phosphorus limitation as primary trigger for sexuality and encystment of dinoflagellates (Anderson and Lindquist, 1985; Anderson et al., 1984; Anderson et al., 1985; Blanco, 1995; Pfister and Anderson, 1987). The discussion about the possible causes of this discrepancy is, however, beyond the scope of this paper and we would like to refer to Susek et al. (2005), Zonneveld et al. (2005) and references therein for more detailed information about this subject.

The results of the redundancy analysis indicate that the most important parameter influencing cyst production over a longer time span is lithogen concentration related to dust input. This is not surprising since in this region Saharan dust deposition plays an important role bringing trace elements to ocean (Kremling, 1985; Kremling and Streu, 1993; Sarthou et al., 2003). For the high nutrient/low productivity areas in the Southern Ocean it has been shown that trace elements such as iron form the factor limiting biogenic production (Boyd and Law, 2001; Boyd et al., 2000; Coale et al., 1996; Gregg, 2002; Moulin et al., 2001; Pittman, 2002; Smetacek, 2001). In the studied region a similar situation occurs with nutrients being refilled continuously through upwelling and with mineral dust deposition forming the main source of iron supply to the upper water column (Sarthou et al., 2003).

Dust input seems to be one of the most important parameters influencing cyst production. Comparison of total dinoflagellate cyst flux with lithogen (Fig.3.2) shows distinct convergence. However, no clear relationship between average total cyst-flux in summer/autumn and average dust

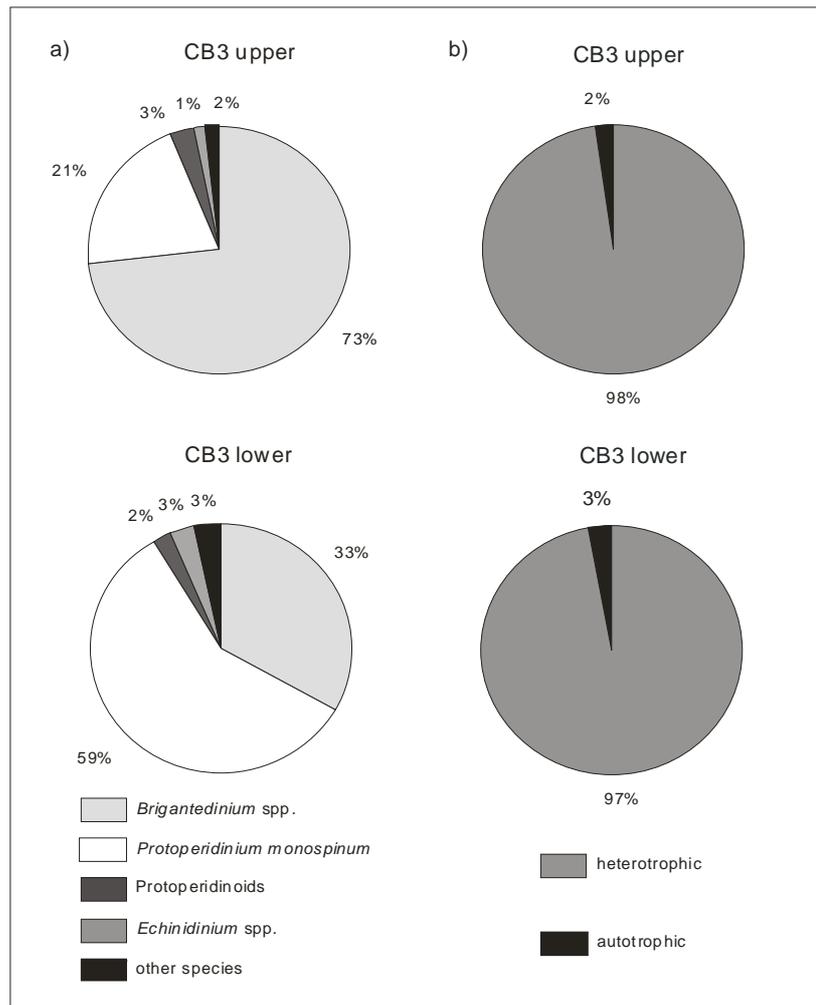


Fig.3.9. Relative cyst abundances in CB3 upper and CB3 lower: a) abundances of the autotrophic and heterotrophic cyst, b) abundances of selected species and groups of species.

*Echinidinium* spp.: *E. aculeatum*, *E. delicatum*, *E. granulatum*, *Echinidinium* spp.

Protoperidinoids: cyst of *Protoperidinium americanum*, cyst of *P. stellatum*, *Selenopemphix nephroides*, *S. quanta*, *Trinovantedinium applanatum*, *Votadinium calvum*, *Votadinium spinosum*.

Other species: *Bitectatodinium spongium*, *Impagidinium aculeatum*, *I. patulum*, *I. sphaericum*, *I. striatum*, *Impagidinium* spp., *Lingulodinium machaerophorum*, *Operculodinium centrocarpum*, *Operculodinium israelianum*, cyst of *Polykrikos schwartzii*, *Polysphaeridium zoharyi*, *Spiniferites* spp.

input can be observed (Fig.3.8). The average total cyst-flux in summer/autumn remained relatively stable in 1989, 1990 and 1991 independent of fluctuations in lithogen level. In 1998, however, the total cyst-flux was the highest of the studied period whereas lithogen input was of intermediate level. A possible explanation for this finding might be that the combination of lithogen influx with stratification of the upper water column influenced the total cyst production in this season. During August/September 1998 SST was relatively high indicating that upwelling was less intense. A more

stable upper water column (relatively less mixing) with a still high level of nutrient and trace element input could have favoured total-cyst production in this season of this year.

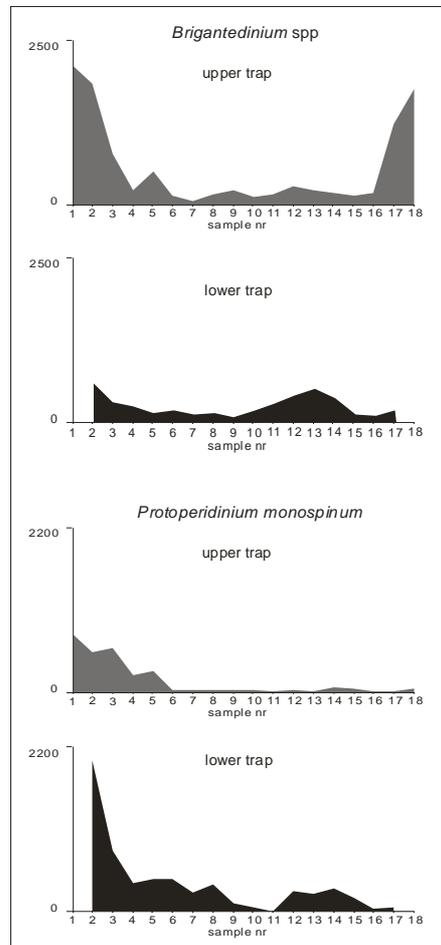


Fig.3.10. Fluxes of *Brigantedinium* spp. and *Protoperidinium monospinum* in the upper and lower CB3 trap

Observations by Wolf and Kaiser (1978) indicate that production on the NW African shelf is related also to quality of upwelled water. Off Cape Blanc there is a transition zone between the NACW and the SACW. The latter water mass is less salty but more enriched in nutrients. As a consequence, biological production is markedly accelerated during periods with increased admixture of the SACW in the onshore transported intermediate waters that form the source of the upwelling waters. Hagen (2001) and Klein and Tomczak (1994) characterise T-S water properties of both water masses and it appears that in our study region salinity reflects the composition of the mixture of NADW and SACW and as such can be used to trace the upwelled water quality (Fig.3.12). Since the absolute variability in salinity over our 4 years study interval are much lower as can be expected to be of direct influence on the cyst production (see for instance Marret and Zonneveld, 2003 and references therein) we conclude that the documented significant relationship between cyst production and salinity reflect the upwelled water quality.

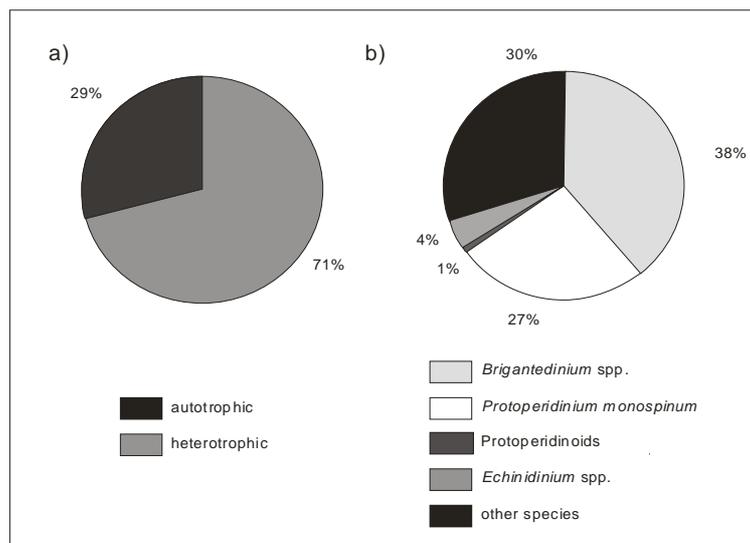


Fig.3.11. Relative cyst abundances of selected species and groups of species in the sediment sample GeoB 4302-9: a) abundances of the autotrophic and heterotrophic cyst, b) abundances of selected species and groups of species.

*Echinidinium* spp.: *E. aculeatum*, *E. delicatum*, *Echinidinium* spp.

Protoperidinoids: cyst of *P. stellatum*, *Selenopemphix nephroides*.

Other species: *Bitectatodinium spongium*, *Impagidinium aculeatum*, *I. patulum*, *I. sphaericum*, *Impagidinium* spp., *Lingulodinium machaerophorum*, *Operculodinium israelianum*, cyst of *Polykrikos schwartzii*, *S. membranaceus*, *S. pachydermus*, *Spiniferites* spp.

All studied samples are dominated by heterotrophic taxa. We observe extreme low relative abundance of autotrophic species. Phototrophic species are compelled to stay in the upper water layers, i.e. the photic zone that is influenced by wind and where strong turbulences persist. A reason for the low autotrophic cyst abundance observed in the trap off Cape Blanc might be the presence of upwelling persisting throughout the year with a mixed layer that is often deeper than the euphotic zone (Dugdale and Wilkerson, 1985). This might make it difficult for phototrophic dinoflagellates to remain present in the photic zone long enough to establish a standing stock that can produce a high amount of cysts. Highest average daily flux is noted for 1989 what might be related to the observed relatively weak winds enabling appearing of stratified surface water conditions (Fischer et al., 1996; Ratmeyer et al., 1999).

Cyst production of *P. americanum* and *P. monospinum* are positively correlated to lithogen input. *P. americanum* is thought to be typical for upwelling regions (Dale and Fjellså, 1994). In our study *P. americanum* is however, absent in 1991 (CB4) that is characterised by relatively strong upwelling. The fact that 1991 was characterised by strong upwelling may be confirmed by relatively strong winds, low SST and stronger contribution of neritic diatoms in sediment collected by CB4 mooring (Fischer et al., 1996; Ratmeyer et al., 1999; Romero et al., 2002). Dale and Fjellså (1994) suggest relatively high percentages of this species in surface sediments off Mauritania (6-16%) in roughly the area

approximating the region where our trap was moored. However, they do not give information on the precise position of the samples. We therefore cannot verify if high amounts of cyst abundances were found by these authors at sites where active upwelling in the upper water column prevails or in surrounding area's. Nevertheless in the Benguela region and similarly in the Arabian Sea, the distribution of this species could not be related to centres of active upwelling (Zonneveld et al., 2001). Based on the observed correlation of enhanced productivity of this species at times of high dust input we suggest that this taxon is related to high nutrient content in the upper water column rather than to active upwelling.

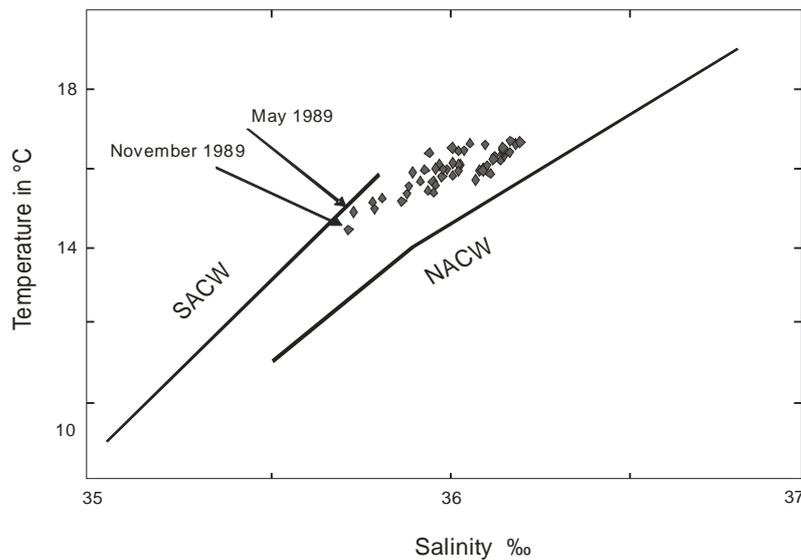


Fig.3.12. Temperature-salinity diagram of intermediate water masses off Cape Blanc (after Klein and Tomczak, 1994; modified). The lines show the water mass definitions for NACW and SACW. Grey rhombs indicate upwelled water masses calculated for moorings' periods.

A production pattern similar to *P. americanum* is observed for *P. monospinum*. Until now this species is not documented from upwelling areas. However, the morphology of this species is such that it might often be missed as individual species and its counts being included in species groups like *Echinidinium* spp. or *Islandinium* spp. The cyst-theca relationship of *P. monospinum* is described from the Oslo Fjord (Zonneveld and Dale, 1994) where it was collected at a site in the harbour where rather eutrophic conditions prevailed (Zonneveld, personal communication). Taking this into account, together with the here observed positive correlation between lithogen content and cyst production we assume that *P. monospinum* cyst production is related to high trophic level in the upper water column.

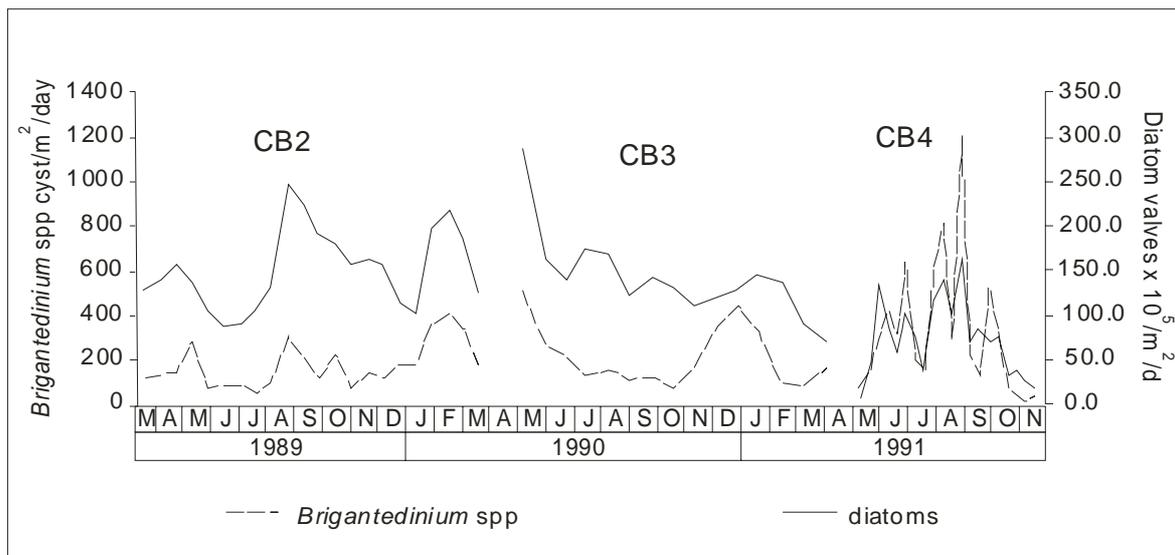


Fig.3.13. *Brigantedinium* spp. and total diatom fluxes (Romero et al., 2002) in CB 2-4.

The results of our RDA analysis show a negative correlation between salinity and cyst production of *Lingulodinium machaerophorum*. *L. machaerophorum* is known as a euryhaline species that can be found in regions with extreme high and low salinity content (Lewis and Hellett, 1997; Marret and Zonneveld, 2003 and references therein). Consequently, salinity itself forms not a factor that could have directly influenced cyst production. As discussed above, salinity forms an indication for the source waters of the upwelling waters at the studied site. When salinity in the upper waters is relatively low, this is an indication that upwelled waters consist for the major part of SACW rather than NADW. Compared to NADW, SACW is slightly warmer and contains more nutrients resulting in enhanced productivity in upper waters when SACW supports the upwelled water masses (Hagen, 2001). Our results suggest therefore, that the conditions of the upwelling source waters can be of major importance for the production of individual dinoflagellate species. Highest fluxes of *L. machaerophorum* can be observed in 1989 (CB2). Apart from SACW forming the major source of the upwelled waters, this year is characterised by relatively low wind speeds resulting in less severe turbulence of the upper water column. Our results are therefore in agreement with previous studies that document high production of *Lingulodinium machaerophorum* cysts in regions characterized by high nutrient input and relatively stratified surface water conditions such as during upwelling relaxation periods (Eppley and Harrison, 1975; Lewis and Hallett, 1997; Lewis et al., 1985; Marasovic, 1989; Marasovic et al., 1991).

High daily fluxes of *Brigantedinium* spp., *Echinidinium aculeatum*, *P. stellatum*, *Selenopemphix nephroides* and *S. quanta* are observed at intervals of enhanced lithogen input. This suggests that enhanced production can be found at times of highest nutrient concentrations in the upper waters related to dust input. This is in consistence with environmental information based on geographical distribution

studies that characteristically document *Echinidinium aculeatum*, *P. stellatum*, *Selenopemphix nephroides* and *S. quanta* in regions with mesotrophic to eutrophic conditions in the upper waters (Marret and Zonneveld, 2003).

*Brigantedinium* spp. generally dominates the assemblage. All motile species included within this morphotype are thought to be heterotrophic. Several species are diatom grazers and food availability and composition is thought to be the most important factor influencing the seasonal dynamics of individual *Protoperidinium* species (Kjæret et al., 2000). In the studied region the seasonal and annual diatom fluxes vary considerably. Despite these fluctuations the composition of the diatom assemblages shows only little variability (Romero et al., 2002). The flux patterns of *Brigantedinium* spp. and total diatoms accumulation (CB2-4) are very similar and no lag phase can be observed (Fig.3.13). This is in contrast to observations of Gillbricht (1977), Mitchell-Innes and Walker (1991) and Pitcher et al. (1991) who observe a clear phytoplankton succession in upwelling areas starting with small diatoms towards bigger diatoms and finally, to dinoflagellates. A possible explanation of this “lost” succession might be the relatively long sampling time of our samples, covering 10 to 21.5 days.

#### ***Transport within the water column***

By comparing material collected by traps at one site at different water depths information about sinking velocities and possible transport of particle in the water column can be obtained.

We observe that the flux patterns of individual species are similar in the upper and lower trap of CB3 with a phase lag of maximal 1 cup lag (21.5 days) indicating high sinking velocities. This is consistent with earlier findings on calcareous dinoflagellate cysts for which a maximal phase lag of 1 cup is recorded as well for site CB3 (Siggelkow et al., 2002). Also in the seasonal upwelling region of the western Arabian Sea sinking velocities of organic-walled dinoflagellate cysts were such that no phase lag between cyst fluxes of individual species could be observed in traps that were separated by 2000 m of water column. Previous studies in the region studied here, suggest that the settling speed of the organic matter fraction of marine particles, varies considerably between the different organic matter types and for different years in the order of 59 – 280 m d<sup>-1</sup> (Fischer et al., 1996; Helmke, 2004). Comparison of the upper and lower traps of CB3 showed a phase lag of 48 days for alkenones, whereas for CB4 a lag phase of 10 days is assumed (Müller and Fischer, 2001). For CB 9 Helmke (2004) observed that chlorophyll-a peaks at the surface correspond with total sedimentation peaks in the trap showing an average lag of 47.6 days varying between 21 and 61 days. As results of their size (30-60µm) dinoflagellate cyst were thought to behave as silt particles in the water column (Anderson and Lively, 1985; Dale, 1983; Dale, 1996). Although sinking rates of individual cysts have been observed to vary between about 0.011 and 0.013 cm/s (Anderson and Lively, 1985) recent studies suggest that in natural environments they sink much faster incorporated in faecal pellets or flocculated material (Mudie, 1996; Zonneveld and Brummer, 2000). Such an effect can also be observed for coccoliths and

coccospheres, that sink much faster when incorporated in faecal pellets and marine snow relative to what can be expected on their size (Winter and Siesser, 1994).

Both traps are dominated by heterotrophic taxa and although the species composition is similar, the relative abundances of the species varies. Whereas the upper trap association is dominated by *Brigantedinium* spp., the most abundant cyst in the lower trap is *Protoperidinium monospinum*. A possible explanation of this discrepancy could be the effect of lateral particle advection within the nepheloid layer (Freudenthal et al., 2001). Siggelkow et al. (2002) suggested that material collected by the lower CB 3 trap might be influenced by lateral cyst transport from the more onshore areas. Romero et al. (2002) documented for the lower traps CB2-4 benthic diatoms, typical for near-shore regions. However, both authors find no univocal evidence that lateral particle transport within the nepheloid layer has taken place and current velocities over the ocean floor during the sampling interval are so low (mean  $2.9\text{cm s}^{-1}$ ; May – November 1991) that no disturbance as a result of current transport could be documented (Helmke, 2004). We also have no evidence that *Brigantedinium* spp. or *P. monospinum* are produced in higher amounts in the near shore regions of NW Africa. We therefore cannot conclude nor exclude the possibility of lateral particle transport within the nepheloid layer influencing our data.

Another factor that might have influenced the cyst association is that the upper and lower traps are located in different water masses. The upper trap was located within the Antarctic Intermediate-Mediterranean Water-mass (AAIW – MW; Zenk et al., 1991) with current speeds ranging from 1 to almost  $20\text{cm s}^{-1}$  from different directions. The lower traps were located in the North Atlantic Deep Water-mass (NADW) with significantly lower velocities and southward flow direction (Fischer et al., 1996). With the presently available limited amount of information about the cyst distribution of individual cysts in the current region no conclusion can be drawn about to what account this fact has influenced our results. Both water masses are characterized by different oxygen concentrations with NADW being most enriched in oxygen. As discussed below individual dinoflagellate cyst species show different sensitivity towards aerobic decay. Species selective degradation within the water column with *Brigantedinium* spp. being more sensitive for aerobic decay than *P. monospinum*, might be an explanation for our observation but more research is needed to test this hypothesis.

### ***Preservation – Comparison of trap associations with the underlying sediment***

The final cysts burial in sediments is depended on several factors such as production, transport through the water column, species selective decay and relocation of sediment. We observe a marked difference between the cyst associations of the traps, with a maximum of 4% phototrophic dinoflagellates, and the surface sediments at the sample location that contain 29% phototrophs. This difference is much larger than the interannual variability we document in this study. Taking into account the high accumulation rates in upwelling areas off NW Africa (Kuhlmann, 2004) and relatively

stable environmental and climatic conditions during the last century in the region, we assume that the here documented interannual variability might be representative for a much longer period. As such it cannot be the cause of the difference in cyst association of the traps and surface sediments.

A likely explanation for this observation might be species selective preservation. (Zonneveld et al., 1997; Zonneveld et al., 2001) have shown that cysts formed by phototrophic dinoflagellate species such as *Impagidinium*, are much more resistant to aerobic decay than cyst of heterotrophic species. Bottom sediments at the trap site are bathed in oxygen rich NADW (Sarnthein et al., 1982). Similar findings are recorded for the Arabian Sea where surface sediments were enriched in species resistant against aerobic decay compared to sensitive cyst species relative to the trap samples. We therefore conclude that species selective aerobic degradation in bottom sediments and at the sediment/water interface forms an important factor that can affect cyst association in oceanic sediments.

## CONCLUSIONS

In the studied area cysts production and association strongly varies seasonally and interannually. The most important environmental parameters affecting cyst production in the region appear to be the amount of dust input and the quality of upwelled water reflected by the sea surface salinity. No clear relationship between surface temperatures, upwelling intensity/wind strength or relaxation and cyst production is found. This might be due to the fact that the trap position is outside the region of active upwelling with local conditions not directly influenced by wind intensity. Furthermore, upwelling in the region is almost permanent forming a rather continuous nutrient supply. Trace elements are, however, provided into the system through dust input.

Cyst assemblages in the region are dominated by the heterotrophic dinoflagellate cysts *Brigantedinium* spp. and cysts of *Protoperidinium monospinum*. Phototrophs constitute 1-4% of the individual traps. Production of cysts of *P. americanum* and *P. monospinum* is positively related to the Saharan dust input. Their cyst production is related to eutrophic/mesotrophic conditions in the upper water column. Increased production of *Lingulodinium machaerophorum* is observed in periods of relatively high South Atlantic Central Water content of the upwelled water.

Fluxes of *Brigantedinium* spp. show similar variability as the total diatom flux.

Species selective aerobic decay strongly influences surface sediment cysts association resulting in an enhanced concentration of autotrophic taxa in surface sediments compared to that of heterotrophic taxa.

## Acknowledgments

This research is funded by the Deutsche Forschungsgemeinschaft as a part of European Graduate College "Proxies in Earth History" EUROPROX, Bremen University.

## REFERENCES

- Anderson, D.M., Lindquist, N.L., 1985. Time-course measurements of phosphorus depletion and cyst formation in the dinoflagellate *Gonyaulax tamarensis* Lebour. *Journal of Experimental Marine Biology and Ecology* 86, 1-13.
- Anderson, D.M., Lively, J.J., 1985. Sinking characteristics of dinoflagellate cyst. *Limnology and Oceanography* 30 (5), 1000-1009.
- Anderson, D.M., Kulis, D.M., Binder, B.J., 1984. Sexuality and cysts formation in the dinoflagellate *Gonyaulax tamarensis*: cyst yield in batch cultures. *Journal of Phycology* 20, 418-425.
- Anderson, D.M., Coats, D.W., Tyler, M.A., 1985. Encystment of the dinoflagellate *Gyrodinium uncatenatum*: temperature and nutrient effects. *Journal of Phycology* 21, 200-2006.
- Barton, E.D., 1998. Eastern boundary of the north Atlantic: northwest Africa and Iberia. In: Robinson, A.R., Brink, K.H.s (Eds.), *The Sea*. John Wiley & Sons, New York, pp. 633-657.
- Barton, E.D., Huyer, A., Smith, R.L., 1977. Temporal variability observed in the hydrographic regime near Cabo Corveiro in the northwest African upwelling period, February to April 1974. *Deep-Sea Research* 24, 7-23.
- Blanco, J., 1995. Cyst production in four species of neritic dinoflagellates. *Journal of Plankton Research* 17 (1), 165-182.
- Bory, A., Jeandel, C., Leblond, N., Vangriesheim, A., Khripounoff, A., Beaufort, L., Rabouille, C., Nicolas, E., Tachikawa, K., Etcheber, H., Buat-Menard, P., 2001. Downward particle fluxes within different productivity regimes off the Mauritanian upwelling zone (EUMELI program). *Deep Sea Research Part I: Oceanographic Research Papers* 48 (10), 2251-2282.
- Boyd, P.W., Law, C.S., 2001. The Southern Ocean Iron RElease Experiment (SOIREE)--introduction and summary. *Deep Sea Research Part II: Topical Studies in Oceanography* 48 (11-12), 2425-2438.
- Boyd, P.W., Watson, A.J., Law, C.S., Abraham, E.R., Trull, T., Murdoch, R., Bakker, D.C.E., Bowie, A.R., Buesseler, K.O., Chang, H., Charette, M., Croot, P., Downing, K., Frew, R., Gall, M., Hadfield, M., Hall, J., Harvey, M., Jameson, G., LaRoche, J., Liddicoat, M., Ling, R., Maldonado, M.T., McKay, R.M., Nodder, S., Pickmere, S., Pridmore, R., Rintoul, S., Safi, K., Sutton, P., Strzepek, R., Tanneberger, K., Turner, S., Waite, A., Zeldis, J., 2000. A mesoscale phytoplankton bloom in the polar Southern Ocean stimulated by iron fertilization. *Nature* 407, 695-702.
- Coale, K.H., Johnson, K.S., Fitzwater, S.E., Gordon, R.M., Tanner, S., Chavez, F.P., Ferioli, L., Sakamoto, C., Rogers, P., Millero, F., Steinberg, P., Nightingale, P., Cooper, D., Cochlan, W.P., Landry, M.R., Constantinou, J., Rollwagen, G., Trasvina, A., Kudela, R., 1996. A

- massive phytoplankton bloom induced by an ecosystem scale iron fertilization experiment in the equatorial Pacific Ocean. *Nature* 383, 495-501.
- Dale, B., 1983. Dinoflagellate resting cysts: benthic plankton. In: Fryxell, G.A.s (Eds.), *Survival strategies of the algae*. Cambridge Univ. Press, Cambridge, pp. 69-136.
- Dale, B., 1996. Dinoflagellate cyst ecology: modeling and geological applications. In: Jansonius, J., Mcgregor, D.C., (Eds.), *Palynology: Principles and Applications*. AASP Foundation, Salt Lake City, pp. 1249-1275.
- Dale, B., Fjellså, A., 1994. Dinoflagellate cysts as paleoproductivity indicators: state of the art, potential and limits. In: Zahn, R., Pedersen, T.F., Kaminski, M.A., Labeyrie, L. (Eds.), *Carbon Cycling in the Global Ocean: Constrains on the Ocean's Role in the Global Change*. Springer-Verlag, Berlin Heidelberg, pp. 521-537.
- Dugdale, R.C., Wilkerson, F.P., 1985. Primary production in the Cap Blanc region. In: Bas, C., Margalef, R., Rubies, P. (Eds.), *International Symposium on the Most Important Upwelling Areas off Western Africa (Cape Blanco and Benguela)*, Barcelona 1983. Instituto de Investigaciones Pesqueras, pp. 233-243.
- Eppley, R.W., Harrison, W.G., 1975. Physiological ecology of *Gonyaulax polyedra* a red water dinoflagellate of southern California. In: LoCicero, V.R. (Ed.), *Proceedings of the first international conference on toxic dinoflagellate blooms*, Wakefield MA. Massachusetts Science and Technology Foundation, pp. 11-22.
- Fischer, G., Donner, B., Ratmeyer, V., Davenport, R., Wefer, G., 1996. Distinct year-to-year particle flux variations off Cape Blanc during 1998-1991: relation to  $d^{18}O$ -deduced sea-surface temperatures and trade winds. *Journal of Marine Research* 54, 73-98.
- Freudenthal, T., Neuer, S., Meggers, H., Davenport, R., Wefer, G., 2001. Influence of lateral particle advection and organic matter degradation on sediment accumulation and stable nitrogen isotope ratios along a productivity gradient in the Canary Islands region. *Marine Geology* 177 (1-2), 93-109.
- Gabric, A.J., Garcia, L., Van Camp, L., Nykjaer, L., Eifler, W., Schrimpf, W., 1993. Offshore export of shelf production in the Cape Blanc (Mauritania) giant filament as derived from Coastal Zone Color Scanner Imagery. *Journal of Geophysical Research* 98 (C3), 4697-4712.
- Gillbricht, M., 1977. Phytoplankton distribution in the upwelling area off NW Africa. *Helgolaender wissenschaftliche Meeresuntersuchungen* 29, 417-438.
- Godhe, A., Norén, F., Kuylenstierna, M., Ekberg, C., Karlson, B., 2001. Relationship between planktonic dinoflagellate abundance, cysts recovered in sediment traps and environmental factors in the Gullmar Fjord, Sweden. *Journal of Plankton Research* 23 (9), 923-938.
- Goudie, A.S., Middleton, N.J., 2001. Saharan dust storms: nature and consequences. *Earth-Science Reviews* 56 (1-4), 179-204.

- Gregg, W.W., 2002. Tracking the SeaWiFS record with a coupled physical / biogeochemical / radiative model of the global oceans. *Deep-Sea Research II* 49 (1-3), 81-105.
- Gruber, N., Sarmiento, J.L., 1997. Global patterns of marine nitrogen fixation and denitrification. *Global Biogeochemical Cycles* 11, 235-266.
- Hagen, E., 2001. Northwest African upwelling scenario. *Oceanologica Acta* 24, 113-128.
- Helmke, P., 2004. Remote sensing of the Northwest African upwelling and its production dynamics. Ph.D. Thesis. Bremen University, Bremen, Germany, [http://elib.suub.uni-bremen.de/publications/dissertations/E-Diss884\\_diss.pdf](http://elib.suub.uni-bremen.de/publications/dissertations/E-Diss884_diss.pdf).
- Hill, M.O., Gauch, H.G.J., 1980. Detrended correspondence analysis: an improved ordination technique. *Vegetatio* 42, 47-58.
- Hughes, P., Barton, E.D., 1974. Stratification and water mass structure in the upwelling area off northwest Africa in April/May 1969. *Deep-Sea Research* 35, 611-628.
- Jongman, R.H.G., Ter Braak, C.J.F., van Tongeren, O.F.R., 1987. Data analysis in community and landscape ecology. *Ecology. Cent. Agric. Publ. Doc. (Pudoc)*, Wageningen, the Netherlands, pp.229.
- Kjæret, A.H., Naustvoll, L.-J., Paasche, E., 2000. Ecology of the heterotrophic dinoflagellate genus *Protoperidinium* in the inner Oslofjord (Norway). *Sarsia* 85, 453-460.
- Klein, B., Tomczak, M., 1994. Identification of diapycnal mixing through optimum multiparameter analysis. 2. Evidence for unidirectional diapycnal mixing in the front between North and South Atlantic Central Water. *Journal of Geophysical Research* 99 (C12), 25275-225280.
- Kostianoy, A.G., Zatsepin, A.G., 1996. The West African coastal upwelling filaments and cross-frontal water exchange conditioned by them. *Journal of Marine Systems* 7 (2-4), 349-459.
- Kremling, K., 1985. The distribution of cadmium, copper, nickel, manganese, and aluminium in surface waters of the open Atlantic and European shelf area. *Deep-Sea Research I* 32 (5), 531-555.
- Kremling, K., Streu, P., 1993. Saharan dust influenced trace element fluxes in deep North Atlantic subtropical waters. *Deep-Sea Research I* 40 (6), 1155-1168.
- Kremp, A., Heiskanen, A.-S., 1999. Sexuality and cyst formation of the spring-bloom dinoflagellate *Scrippsiella hangoei* in the coastal northern Baltic Sea. *Marine Biology* 134, 771-777.
- Kuhlmann, H., 2004. Reconstruction of paleoceanography off NW Africa for the last 40,000 years: influence of local and regional factors on sediment accumulation. *Marine Geology* 207 (1-4), 209-234.
- Lewis, J., Hallett, R., 1997. *Lingulodinium polyedrum* (*Gonyaulax polyedra*) a blooming dinoflagellate. *Oceanography and Marine Biology: an Annual Review* 35, 96-161.
- Lewis, J., Tett, P., Dodge, J.D., 1985. The cyst-theca cycle of *Gonyaulax polyedra* (*Lingulodinium machaerophorum*) in Creran, a Scottish west coast sea-loch. In: Anderson, D.M., White, A.W., Baden, D.G. (Eds.), *Toxic Dinoflagellates*. Elsevier Science Publishing Co., Amsterdam, pp. 85-90.

- Marasovic, I., 1989. Encystment and Excystment of *Gonyaulax polyedra* During a Red Tide. *Estuarine, Coastal and Shelf Science* 28, 35-41.
- Marasovic, I., Gacic, M., Kovacevic, V., Krstulovic, N., Kuspilic, G., Pucher-Petkovic, T., Odzak, N., Solic, M., 1991. Development of a red tide in the Kastela Bay (Adriatic Sea). *Marine Chemistry* 32, 375-385.
- Marino, D., Modigh, M., Zingone, A., 1984. Marine Phytoplankton and Productivity. *Lecture Notes on Coastal and Estuarine Studies. Journal* 8 (Issue), 89-100.
- Marret, F., Zonneveld, K.A.F., 2003. Atlas of modern organic-walled dinoflagellate cyst distribution. *Review of Palaeobotany and Palynology* 125 (1-2), 1-200.
- Middleton, N.J., Goudie, A.S., 2001. Saharan dust: sources and trajectories. *Transactions of the Institute of British Geographers* 26, 165-181.
- Minas, H.J., Codispoti, L.A., Dugdale, R.C., 1982. Nutrients and primary production in the upwelling region off Northwest Africa. *Rapp. P.-v. Réun. Cons. int. Explor. Mer* 180, 148-183.
- Mitchell-Innes, B.A., Walker, D.R., 1991. Short-term variability during an anchor station study in the southern Benguela upwelling system: Phytoplankton production and biomass in relation to specie changes. *Progress in Oceanography* 28 (1-2), 65-89.
- Mittelstaedt, E., 1983. The upwelling area off northwest Africa - a description of phenomena related to coastal upwelling. *Progress in Oceanography* 12, 307-331.
- Mittelstaedt, E., 1991. The ocean boundary along the northwest African coast: circulation and oceanographic properties at the sea surface. *Progress in Oceanography* 26, 307-355.
- Mittelstaedt, E., Pillsbury, D., Smith, R.L., 1975. Flow Patterns in the Northwest African Upwelling Area. *Deutsche Hydrographische Zeitschriften* 28 (3), 145-167.
- Montresor, M., Zingone, A., Sarno, D., 1998. Dinoflagellate cyst production at a coastal Mediterranean site. *Journal of Plankton Research* 20 (12), 2291-2312.
- Moulin, C., Lambert, C.E., Dulac, F., Dayan, U., 1997. Control of atmospheric export of dust from North Africa by the North Atlantic Oscillation. *Nature* 387, 691-694.
- Moulin, C., Gordon, H.R., Chomko, R.M., Banzon, V.F., Evans, R.H., 2001. Atmospheric correction of ocean color imagery through thick layers of Saharan dust. *Geophysical Research Letters* 28 (1), 5-8.
- Mudie, P.J., 1996. Faecal pellets. Pellets of dinoflagellate - eating zooplankton. In: Jansonius, J.,Mcgregor, D.C. (Eds.), *Palynology: Principles and Applications*. AASP Foundation, Salt Lake City, pp.1087-1089.
- Müller, P.J., Fischer, G., 2001. A 4-year sediment trap record of alkenones from the filamentous upwelling region off Cape Blanc, NW Africa and a comparison with distributions in underlying sediments. *Deep-Sea Research I* 48 (8), 1877-1903.

- Nykjaer, L., Van Camp, L., 1994. Seasonal and interannual variability of coastal upwelling along northwest Africa and Portugal from 1981 to 1991. *Journal of Geophysical Research* 99 (C7), 14197-114207.
- Pfiester, L.A., Anderson, D.M., 1987. Dinoflagellate reproduction. In: Taylor, F.J.R. (Ed.), *The biology of dinoflagellates*. Blackwell, Oxford, pp. 611-648.
- Pitcher, G.C., Walker, D.R., Mitchell-Innes, B.A., Moloney, C.L., 1991. Short-term variability during an anchor station study in the southern Benguela upwelling system: Phytoplankton dynamics. *Progress in Oceanography* 28 (1-2), 39-64.
- Pittman, T., 2002. A Correlation Analysis of Satellite Chlorophyll to Iron Dust Flux in the World's Oceans. *Hopkins Undergraduate Research Journal* 1, 18-21.
- Ratmeyer, V., Fischer, G., Wefer, G., 1999. Lithogenic particle fluxes and grain size distributions in the deep ocean off northwest Africa: Implications for seasonal changes of aeolian dust input and downward transport. *Deep Sea Research Part I: Oceanographic Research Papers* 46 (8), 1289-1337.
- Romero, O.E., Lange, C.B., Wefer, G., 2002. Interannual variability (1988-1991) of siliceous phytoplankton fluxes off northwest Africa. *Journal of Plankton Research* 24 (10), 1035-1046.
- Romero, O.E., Dupont, L., Wyputta, U., Jahns, S., Wefer, G., 2003. Temporal variability of fluxes of eolian-transported freshwater diatoms, phytoliths, and pollen grains off Cape Blanc as reflection of land-atmosphere-ocean interactions in northwest Africa. *Journal of Geophysical Research* 108 (C5), 3153.
- Sarnthein, M., Thiede, J., Pflaumann, U., Erlenkeuser, H., Fütterer, D., Koopmann, B., Lange, H., Seibold, E., 1982. Atmospheric and Oceanic Circulation Patterns off Northwest Africa During the Past 25 Million Years. In: von Rad, U., Hinz, K., Sarnthein, M., Seibold, E. (Eds.), *Geology of the northwest African continental margin*. Springer-Verlag, Berlin, Heidelberg, pp. 545-604.
- Sarthou, G., Baker, A.R., Blain, S., Achterberg, E.P., Boye, M., Bowie, A.R., Croot, P., Laan, P., Baar, H.J.W.d., Jickells, T.D., Worsfold, P.J., 2003. Atmospheric iron deposition and sea-surface dissolved iron concentrations in the eastern Atlantic Ocean. *Deep Sea Research Part I* 50 (10-11), 1339-1352.
- Siggelkow, D., Vink, A., Willems, H., 2002. Calcareous dinoflagellate cyst production, vertical transport and preservation off Cape Blanc during 1990: a sediment trap study [abstract]. *Journal of Nannoplankton Research* 24 (2), 160.
- Smetacek, V., 2001. EisenEx: International Team Conducts Iron Experiment In Southern Ocean. *USJGOFS Newsletter* 11 (1), 11-14.
- Speth, P., Detlefsen, H., 1982. Meteorological influences on upwelling off Northwest Africa. *Rapports et Procès-Verbeaux des Reunions, conseil International pour l'Exploration de la Mer* 180, 29-34.

- Speth, P., Detlefsen, H., Sierst, H.-W., 1978. Meteorological Influence on Upwelling off Northwest Africa. *Deutsche Hydrographische Zeitschriften* 31 (3), 95-104
- Susek, E., Zonneveld, K.A.F., Fischer, G., Versteegh, G.J.M., Willems, H., 2005. Organic-walled dinoflagellate cyst production in relation to upwelling intensity and lithogenic input in the Cape Blanc region (off NW Africa). *Phycological Research* 53 (2), doi: 10.1111/j.1440-183.2005.00377.x
- Ter Braak, C.J.F., CANOCO, a FORTRAN program for canonical community ordination by partial detrended canonical correspondance analysis, principal components analysis and redundancy analysis (version 2.1). Agric. Math. Group, Wageningen, the Netherlands.
- Thomas, A.C., Carr, M.-E., Strub, P.T., 2001. Chlorophyll variability in eastern boundary currents. *Geophysical Research Letters* 28 (18), 3421-3424.
- Tomczak, J., Matthias, Hughes, P., 1980. Three dimensional variability of water masses and currents in the Canary upwelling region. "Meteor" *Forschungsergebnisse A*, 1-24.
- VanCamp, L., Nykjaer, L., Mittelstaedt, E., Schlittenhardt, P., 1991. Upwelling and boundary circulation off Northwest Africa as depicted by infrared and visible satellite observations. *Progress in Oceanography* 26, 357-402.
- Vangriesheim, A., Bournot-Marec, C., Fontan, A.-C., 2003. Flow variability near the Cape Verde frontal zone (subtropical Atlantic Ocean). *Oceanologica Acta* 26 (2), 149-159.
- Wefer, G., Fischer, G., 1993. Seasonal patterns of vertical particle flux in equatorial and coastal upwelling area of the eastern Atlantic. *Deep Sea Research I* 40, 1613-1645.
- Wendler, I., Zonneveld, K.A.F., Willems, H., 2002. Production of calcareous dinoflagellate cysts in response to monsoon forcing off Somalia: a sediment trap study. *Marine Micropaleontology* 46 (1-2), 1-11.
- Winter, A., Siesser, W.G., 1994. *Coccolithophores*. Cambridge University Press, pp.242.
- Wolf, G., Kaiser, W., 1978. Über den Jahreszyklus der T-S - Eigenschaften quasipermanenter Wasserarten und Variationen produktionsbiologischer Parameter auf den Schelf vor Cap Blanc. *Geodätische und geophysikalische Veröffentlichungen* 4 (24), 1-81.
- Zenk, W., Klein, B., Schröder, M., 1991. Cape Verde Frontal Zone. *Deep Sea Research* 38, 505-530.
- Zhu, X.R., Prospero, J.M., Millero, F.J., 1997. Daily variability of soluble Fe(II) and soluble total Fe in North African dust in the trade winds at Barbados. *Journal of Geophysical Research* 102 (D17), 21297-21305.
- Zonneveld, K.A.F., Dale, B., 1994. The cyst-motile stage relationships of *Protoperidinium monospinum* (Paulsen) Zonneveld et Dale comb. nov. and *Gonyaulax verior* (Dinophyta, Dinophyceae) from Oslo Fjord (Norway). *Phycologia* 33 (5), 359-368.
- Zonneveld, K.A.F., Brummer, G.J.A., 2000. (Palaeo-)ecological significance, transport and preservation of organic-walled dinoflagellate cysts in the Somali Basin, NW Arabian Sea. *Deep-Sea Research II* 47 (9-11), 2229-2256.

- Zonneveld, K.A.F., Versteegh, G.J.M., Lange, G.J.d., 1997. Preservation of organic-walled dinoflagellate cysts in different oxygen regimes: a 10,000 year natural experiment. *Marine Micropaleontology* 29 (3-4), 393-405.
- Zonneveld, K.A.F., Hoek, R.P., Brinkhuis, H., Willems, H., 2001. Geographical distributions of organic-walled dinoflagellate cysts in surficial sediments of the Benguela upwelling region and their relationship to upper ocean conditions. *Progress in Oceanography* 48 (1), 25-72.
- Zonneveld, K.A.F., Meier, K.J.S., Esper, O., Siggelkow, D., Wendler, I., Willems, H., 2005. The (palaeo-) environmental significance of modern calcareous dinoflagellate cysts: a review. *Paläontologische Zeitschrift* 79 (1) (in press).

Table 3.2. List of observed dinoflagellate cyst taxa. (after Marret and Zonneveld, 2003)

Species	Motile affinity
<i>Bitectatodinium spongium</i> (Zonneveld) Zonneveld et Jurkschat	unknown
<i>Brigantedinium</i> spp.	
<i>Echinidinium aculeatum</i> Zonneveld	unknown
<i>Echinidinium delicatum</i> Zonneveld	unknown
<i>Echinidinium granulatum</i> Zonneveld	unknown
<i>Echinidinium</i> spp.	
<i>Impagidinium aculeatum</i> (Wall) Lentin et Williams	<i>Gonyaulax</i> sp.
<i>Impagidinium patulum</i> (Wall) Stover et Evitt	<i>Gonyaulax</i> sp.
<i>Impagidinium sphaericum</i> (Wall) Lentin et Williams	<i>Gonyaulax</i> sp.
<i>Impagidinium</i> spp.	
<i>Impagidinium striatum</i> (Wall) Stover et Evitt	<i>Gonyaulax</i> sp.
<i>Lingulodinium machaerophorum</i> (Deflandre et Cookson) Wall	<i>Lingulodinium polyedrum</i> (von Stein) Dodge
<i>Nematospheropsis labyrinthus</i> (Ostenfeld) Reid	<i>Gonyaulax spinifera</i> (Claparède et Lachmann) Diesing
<i>Operculodinium centocarpum</i> Wall et Dale 1966	<i>Protoceratium reticulatum</i> (Claparède et Lachmann) Bütschli
<i>Operculodinium israelianum</i> (Rossignol) Wall	? <i>Protoceratium</i> sp. (Claparède et Lachmann) Bütschli
cyst of <i>Polykrikos schwartzii</i> Bütschli	<i>Polykrikos schwartzii</i> Bütschli
<i>Polysphaeridium zoharyi</i> (Rossignol) Bujak et al.	<i>Pyrodinium bahamense</i> Plate <i>Protopteridinium americanum</i> (Gran et Braarud) Balech
cyst of <i>Protopteridinium americanum</i> (Gran et Braarud) Balech	<i>Protopteridinium monospinum</i> (Paulsen)
cyst of <i>Protopteridinium monospinum</i> (Paulsen) Zonneveld et Dale	Zonneveld et Dale <i>Protopteridinium subinermis</i> (Paulsen) Loeblich III
<i>Selenopemphix nephroides</i> (Benedek) Benedek et Sarjeant	
<i>Selenopemphix quanta</i> (Bradford) Matsuoka	<i>Protopteridinium conicum</i> (Gran) Balech
<i>Spiniferites membranaceus</i> (Rossignol) Sarjeant	<i>Gonyaulax</i> sp.
<i>Spiniferites delicatus</i> Reid	<i>Gonyaulax</i> sp.
<i>Spiniferites hypercanthus</i> (Deflandre et Cookson) Cookson et Eisenack	<i>Gonyaulax</i> sp.
<i>Spiniferites pachydermus</i> (Rossignol) Reid	? <i>Gonyaulax</i> spp.
<i>Spiniferites</i> spp.	
cyst of <i>Protopteridinium stellatum</i> (Wall in Wall et Dale) Rochon et al.	<i>Protopteridinium stellatum</i> (Wall in Wall et Dale) Rochon et al.
<i>Trinovantedinium applanatum</i> (Bradford) Bujak et Davies	<i>Protopteridinium pentagonum</i> (Gran) Balech
<i>Votadinium calvum</i> Reid	<i>Protopteridinium oblongum</i> (Aurillius) Parke & Dodge
<i>Votadinium spinosum</i> Reid	<i>Protopteridinium claudicans</i> (Paulsen) Balech

Table 3.3. Fluxes of individual species or groups of species recovered at sites CB 2-4, CB3 upper and cysts counted in sample GeoB 4320-9

1 = *Bitectatodinium spongium*, 2 = *Brigantedinium* spp., 3 = *Echinidinium aculeatum*, 4 = *Echinidinium delicatum*,  
5 = *Echinidinium granulatum*, 6 = *Echinidinium* spp., 7 = *Impagidinium aculeatum*, 8 = *Impagidinium patulum*,  
9 = *Impagidinium sphaericum*, 10 = *Impagidinium* spp., 11 = *Impagidinium striatum*, 12 = *Lingulodinium machaerophorum*,  
13 = *Nematospheropsis labyrinthus*, 14 = *Operculodinium centocarpum*, 15 = *Operculodinium israelianum*, 16 = cyst of  
*Polykrikos schwartzii*, 17 = *Polysphaeridium zoharyi*, 18 = cyst of *Protoperidinium americanum*, 19 = cyst of *Protoperidinium*  
*stellatum*, 20 = cyst of *Protoperidinium monospinum*, 21 = *Selenopemphix nephroides*, 22 = *Selenopemphix quanta*,  
23 = *Spiniferites delicatus*, 24 = *Spiniferites hypercanthus*, 25 = *Spiniferites mambranaceus*, 26 = *Spiniferites pachydermus*,  
27 = *Spiniferites* spp., 28 = *Trinovantedinium applanatum*, 29 = *Votadinium calvum*, 30 = *Votadinium spinosum*, total = total  
cyst.

Table 3.3. Fluxes of individual species or groups of species recovered at sites CB 2-4, CB3 upper and cysts counted in sample GeoB 4320-9

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	total		
CB2																																	
1	0	122	0	0	0	3	0	0	0	0	0	0	0	0	0	0	6	0	48	0	0	0	0	0	0	0	0	0	0	0	0	0	180
2	0	132	0	0	0	42	3	0	0	3	0	10	0	0	0	16	0	3	3	376	0	3	0	0	0	0	0	0	0	0	0	0	592
3	0	148	3	3	0	10	0	0	3	0	0	10	0	0	0	6	0	0	0	248	0	0	0	0	0	0	0	0	0	0	0	0	431
4	0	280	3	0	3	6	3	0	0	6	0	23	0	0	0	6	0	3	3	341	6	6	0	0	0	0	0	0	0	0	0	0	692
5	0	84	0	0	0	13	0	0	0	13	0	10	0	0	0	0	0	0	0	190	0	0	0	0	0	0	3	0	0	0	0	312	
6	3	93	0	3	0	3	0	0	0	6	0	39	0	0	0	3	0	0	0	151	0	0	0	0	0	0	0	0	0	0	0	0	302
7	0	93	3	0	0	3	0	0	0	0	0	42	0	0	0	0	0	0	0	277	0	0	0	0	0	0	0	0	0	0	0	0	418
8	0	61	0	0	0	0	0	3	0	6	0	39	0	0	0	0	0	0	3	161	0	6	0	0	0	0	0	0	0	0	0	0	280
9	0	103	0	0	0	6	6	6	6	6	0	16	0	0	0	3	0	0	6	42	0	0	0	0	0	0	0	0	0	0	0	0	203
10	0	302	10	6	3	6	0	0	3	0	0	10	0	0	0	13	0	16	13	84	3	3	0	0	0	0	0	0	0	0	0	0	473
11	0	212	0	0	0	10	0	0	0	0	0	13	0	0	3	13	0	10	3	113	0	0	0	0	0	0	0	0	0	0	0	0	376
12	0	122	10	3	0	3	3	6	3	3	0	3	0	0	0	13	0	6	10	171	0	6	0	0	0	0	0	0	0	0	0	0	364
13	0	235	10	6	3	3	0	6	0	0	0	16	0	0	0	19	3	3	6	1142	0	0	0	0	0	0	0	0	0	0	0	0	1454
14	0	90	3	0	0	3	3	3	0	0	0	0	0	0	0	3	0	0	6	235	0	0	0	0	0	0	0	0	0	3	0	351	
15	0	138	6	13	0	16	0	6	0	3	0	3	0	0	0	0	3	3	3	428	0	0	0	0	0	0	0	0	0	3	0	627	
16	0	129	13	0	0	13	0	0	0	0	0	0	0	0	0	6	0	10	0	241	0	0	0	0	0	0	0	0	0	0	0	0	415
17	0	183	3	0	0	23	0	0	0	0	0	3	0	0	0	6	0	10	10	380	0	3	0	0	0	0	0	0	0	0	0	0	621
18	0	187	3	6	0	29	0	0	0	3	0	3	0	0	0	6	0	0	0	534	0	3	0	0	0	0	0	0	0	0	0	0	775
19	0	360	16	0	0	23	0	3	0	10	0	6	0	0	0	16	0	13	16	589	3	0	0	0	0	0	0	0	3	0	0	1059	
20	13	412	32	0	0	13	0	6	3	10	0	3	3	0	0	3	0	10	19	679	6	6	0	0	0	0	0	0	0	0	0	0	1220
21	0	351	16	0	0	16	6	3	0	6	0	13	0	0	0	6	0	0	16	740	0	0	0	0	0	0	0	0	6	0	0	1181	
22	0	183	3	0	3	13	0	3	0	3	0	0	0	0	0	0	0	0	10	441	0	0	0	0	0	0	0	0	6	0	0	666	

Table 3. (continued)

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	total	
CB3																																
2	15	517	15	4	4	11	7	4	0	0	0	0	0	0	0	0	0	7	26	2032	0	11	0	0	0	0	0	0	4	0	0	2668
3	7	279	11	4	11	4	0	0	4	11	0	11	0	0	1	0	0	4	15	815	0	0	0	0	0	0	0	0	0	0	0	1183
4	0	216	0	11	0	15	4	4	0	4	0	7	0	0	2	0	0	11	4	368	0	0	0	0	0	0	0	0	0	0	0	647
5	0	130	4	4	0	4	7	4	0	4	0	0	0	0	0	0	0	4	7	432	0	0	0	0	0	0	0	0	4	0	603	
6	4	164	7	0	0	22	7	4	4	0	0	4	0	0	0	0	0	4	11	428	0	4	0	0	0	0	0	0	0	0	0	662
7	4	112	4	0	0	11	0	0	0	0	0	4	0	0	0	0	0	0	0	246	0	0	0	0	0	0	0	0	0	0	0	380
8	0	127	4	30	7	7	4	7	0	4	0	0	0	0	0	0	0	7	7	361	4	4	0	0	0	0	0	0	0	0	0	573
9	0	71	7	11	11	4	0	4	0	0	0	4	0	0	0	0	0	0	0	100	0	0	0	0	0	0	0	0	0	0	0	212
10	0	160	0	4	0	0	0	0	4	0	0	4	0	0	0	0	0	0	0	45	0	0	0	0	0	0	0	0	0	0	0	216
11	no sample																															
12	4	353	7	4	4	15	4	7	4	0	0	0	0	0	0	0	0	4	0	272	0	0	0	0	0	0	0	0	0	0	0	681
13	7	450	0	7	0	7	7	0	0	22	0	0	0	0	0	0	0	4	19	234	7	0	0	0	0	0	0	0	0	0	0	767
14	4	331	15	4	0	0	4	4	11	11	0	0	0	0	0	0	0	0	0	305	7	0	0	0	0	0	4	0	0	0	700	
15	7	104	0	0	0	4	4	0	7	0	0	0	0	0	0	0	0	0	0	182	0	0	0	0	0	0	0	0	0	0	309	
16	0	97	0	0	0	0	0	0	4	0	0	0	0	0	0	0	0	0	0	30	0	0	0	0	0	0	0	0	0	0	130	
17	0	160	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	4	45	0	0	0	0	0	0	0	0	0	0	208	

Table 3. (continued)

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	total
CB4																															
1	0	78	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	14	0	0	0	0	0	0	0	0	0	0	92
2	0	156	0	0	0	7	0	0	0	0	0	0	0	0	0	0	0	0	0	50	0	0	0	0	0	0	0	0	0	0	213
3	0	299	0	0	0	0	0	7	0	0	0	0	0	0	0	0	0	0	0	50	0	0	0	0	0	0	0	0	0	0	356
4	0	427	0	0	7	21	0	0	0	0	0	0	0	0	0	0	0	0	0	64	7	0	0	0	0	0	0	0	0	0	533
5	0	320	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	7	7	0	0	0	0	0	0	0	0	0	320
6	0	647	0	0	7	0	21	7	0	0	0	71	0	0	0	0	0	0	14	92	7	0	0	0	0	0	0	0	7	0	875
7	0	199	7	7	7	0	0	7	0	0	0	0	0	0	0	7	0	0	0	57	0	0	0	0	0	0	0	0	0	0	292
8	0	164	0	7	7	7	0	0	0	7	0	0	0	0	0	0	0	0	0	14	0	0	0	0	0	0	0	0	0	0	206
9	0	612	0	0	0	21	0	7	0	21	0	0	0	0	0	7	0	7	7	7	7	0	0	0	0	0	0	0	0	0	690
10	0	818	0	21	50	21	7	0	0	7	0	0	0	0	14	0	0	0	0	50	0	0	0	0	0	0	0	0	0	0	988
11	0	320	0	7	14	7	0	0	0	0	0	7	0	0	0	0	0	0	0	78	0	0	0	0	0	0	0	0	7	0	441
12	0	1202	7	0	64	92	0	0	0	0	0	14	0	0	0	7	0	0	7	78	7	14	0	0	0	0	0	0	14	0	1508
13	0	220	0	0	0	28	0	0	0	0	0	0	0	0	0	0	0	0	0	14	14	0	0	0	0	0	0	0	0	0	277
14	0	135	7	7	21	14	0	0	0	0	0	0	0	0	0	0	0	0	0	50	0	0	0	0	0	0	0	0	14	0	249
15	0	533	0	0	21	28	0	0	0	0	0	7	0	0	0	0	0	0	7	14	0	0	0	0	0	0	0	0	0	0	612
16	0	348	14	0	57	36	7	7	0	7	0	7	0	0	0	0	0	0	7	57	7	0	0	0	0	0	7	14	0	0	576
17	0	71	0	0	7	0	0	0	0	0	0	0	0	0	0	0	0	0	0	21	0	0	0	0	0	0	0	0	0	0	100
18	0	50	0	0	0	7	0	0	0	0	0	0	0	0	0	0	0	0	0	7	0	0	0	0	0	0	0	0	0	0	64
19	0	14	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	14
20	0	50	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	7	0	0	0	0	0	0	0	0	0	0	57

Table 3. (continued)

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	total	
CB3upper																																
1	4	2110	4	45	0	15	4	4	0	11	0	0	0	0	4	0	4	7	778	0	4	0	0	0	0	0	0	0	0	0	4	2995
2	0	1846	4	22	4	15	4	7	0	7	0	0	0	0	8	4	0	11	536	4	7	0	0	0	0	0	0	0	7	0	2486	
3	0	781	0	0	0	4	0	4	0	0	0	0	0	0	4	4	0	0	595	4	0	0	0	0	0	0	0	0	0	0	1395	
4	0	212	4	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	223	0	0	0	0	0	0	0	0	0	0	0	439	
5	0	506	0	0	4	26	0	4	4	7	0	0	0	0	0	0	0	0	290	0	0	0	0	0	0	0	0	0	0	0	841	
6	0	145	0	0	0	0	0	0	0	4	0	0	0	0	0	0	0	0	30	0	0	0	0	0	0	0	0	0	0	0	179	
7	0	56	0	0	0	0	0	0	0	4	0	0	0	0	0	0	0	0	22	4	0	0	0	0	0	0	0	0	0	0	86	
8	0	156	0	0	4	0	4	0	0	4	0	0	0	0	0	0	0	0	22	0	0	0	0	0	0	0	0	0	0	0	190	
9	0	223	0	0	0	0	4	0	0	7	0	0	0	0	0	0	0	0	4	22	0	4	0	0	0	0	0	0	4	0	268	
10	4	119	0	4	0	0	7	0	0	0	0	0	0	0	0	0	0	0	26	4	0	0	0	0	0	0	0	0	0	0	164	
11	0	160	7	0	0	0	7	0	0	0	11	0	0	0	0	0	0	0	11	0	0	0	0	0	0	0	0	0	0	0	197	
12	4	290	4	4	0	0	7	4	0	0	26	0	0	0	0	0	0	0	60	19	4	0	0	0	0	0	0	4	0	424		
13	0	223	0	0	0	0	4	7	0	0	0	0	0	0	0	0	0	0	134	15	0	0	0	0	0	0	0	0	0	0	383	
14	0	179	0	0	0	0	0	0	0	0	7	0	0	0	0	0	0	0	45	67	0	0	0	0	0	0	0	0	0	0	298	
15	7	141	0	0	0	15	22	7	0	0	0	0	0	0	7	0	0	0	15	45	0	15	0	0	0	0	0	0	0	0	275	
16	0	186	0	0	0	7	0	0	0	0	0	0	0	0	0	0	0	0	15	7	0	0	0	0	0	0	0	0	0	0	216	
17	0	1235	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	7	0	0	0	0	0	0	0	0	0	0	1235		
18	0	1771	0	0	0	0	7	0	0	0	0	0	0	0	0	0	0	0	19	52	0	4	0	0	0	0	0	0	0	0	1853	
GeoB 4302-9																																
1	84	3	2	0	4	27	7	2	15	0	7	0	0	1	1	0	0	1	60	1	0	0	0	1	1	1	0	0	0	220		



**EFFECT OF TEMPERATURE, LIGHT AND SALINITY ON CYST PRODUCTION  
AND MORPHOLOGY OF *TUBERCULODINIUM VANCAMPOAE* (ROSSIGNOL  
1962) WALL 1967 (*PYROPHACUS STEINII* (SCHILLER 1935) WALL ET DALE  
1971).**

**Ewa Susek and Karin A. F. Zonneveld**

Fachbereich 5-Geowissenschaften, University of Bremen, Postfach 330440, D-28334 Bremen, Germany

*in preparation*

**Effect of temperature, light and salinity on cyst production and morphology of *Tuberculodinium vancampoe* (Rossignol 1962) Wall 1967 (*Pyrophacus steinii* (Schiller 1935) Wall et Dale 1971).**

**Ewa Susek and Karin A. F. Zonneveld**

Fachbereich 5-Geowissenschaften, University of Bremen, Postfach 330440, D-28334 Bremen, Germany

**ABSTRACT**

Cyst forming dinoflagellate cysts are useful to reconstruct past environments. For accurate application it is essential to know how environmental parameters such as salinity, temperature and light influence the dinoflagellate cyst production and morphology. Here we studied the effect of variation in these parameters on the cyst production and morphology of *Tuberculodinium vancampoe* (= *Pyrophacus steinii*). Encystment of *T. vancampoe* has been observed in all executed culture-experiments although only a few cysts are being formed at the edges of the temperature range studied (16.5°C and 34.8°C). Highest cyst production has been found to occur at 27°C. In light and salinity experiments highest cyst production has been documented for temperate to strong illumination and a salinity concentration of 34.5psu, respectively. Our results are in agreement with field data where *T. vancampoe* is observed in surface sediments of regions characterised by mean sea surface temperatures between 12.7°C and 29.5°C and sea surface temperatures between 16.9 and 36.6 psu. Temperature and salinity control the morphology of the cysts. Extreme temperatures result in a reduction of the tubercule size.

Our results indicate that *T. vancampoe* is not heterothallic species as was previously suggested.

**Key words:** *Tuberculodinium vancampoe*, dinoflagellate, cyst, morphological variation, temperature, salinity, light.

**INTRODUCTION**

Dinoflagellate cysts are a useful proxy for reconstructing past environmental conditions (e.g. Lewis et al., 1990; Harland, 1994; Versteegh, 1994; Rochon et al., 1998). Since cyst morphology is species specific, the amount and distribution of cysts in fossil sediments is determined by the ecology of the cyst forming dinoflagellate. Many studies have shown that fossil cyst associations in detail reflect past environmental conditions such as temperature, salinity, nutrient input or industrial pollution (Wall and Dale, 1974; Dale, 1996; Sætre et al., 1997; Thorsen and Dale, 1997; Thorsen and

Dale, 1998; Dale et al., 1999; Matsuoka, 1999; Ellegaard, 2000). During such palaeoenvironmental studies it has often been observed that there is morphological variation within a cyst population of a single species. Their possible causes form a point of discussion for decades since cyst taxonomy is based on cyst morphology (e.g. May, 1975; Sarjeant et al., 1987). Observations of morphological variation within a species in natural environments made several authors suggest that they might be related to environmental changes (Wall and Dale, 1973; Nehring, 1994; Dale, 1996; Ellegaard, 2000; Brenner, 2001). Indeed, recent studies have shown that changing environmental conditions can have such a severe effect on cyst morphology that different morphotypes are being interpreted to be different species in older literature (e.g. *Lingulodinium machaerophorum* (Deflandre et Cookson 1955) Wall 1967; Kokinos and Anderson, 1995; Lewis and Hallett, 1997). Recently a number of studies have been carried out to investigate the effect of individual environmental parameters on cyst morphology (Hallett, 1999; Ellegaard et al., 2002; Lewis et al., 2003). It appears that morphological variations can be used to reconstruct past environment and the observed ecophenotypism might increase the precision of palaeo- reconstructions (Servais et al., 2004; Brenner, 2005). However, until now only the species *Lingulodinium machaerophorum*, *Gonyaulax baltica* Ellegaard, Lewis et Harding 2002 and *Gonyaulax spinifera* (Claparède et Lachmann 1859) Diesing 1866 have been studied in detail. To enable ecophenotypism to be used in palaeoenvironmental research it is important to enlarge the present information for other species.

Dinoflagellate sexuality and, as result, cyst production is influenced by nutrient availability, temperature, irradiance, turbulence and by endogenic encystment rhythms. (e.g. Ishikawa and Taniguchi, 1996; Montresor et al., 1998; Sgrosso et al., 2001; Olli and Anderson, 2002; Meier et al., 2004). It has been shown that several dinoflagellates are able to produce cysts in a narrow temperature window. Temperature itself however, is not a triggering factor.

Recent studies on the encystment of several dinoflagellate species show an inverse relationship between day length at temperatures between 20°C and 25°C. This inverse relationship was not the result of a relationship with total daily irradiance and an increased cyst production was prevented by light breaks during the dark phase of the photocyclus (Sgrosso et al. 2001). In general reproduction of phototrophic organisms is strongly influenced by factors as the intensity and angle of radiation, the amount of surface reflection and the transparency of the water column (Dawson, 1966; Kirk, 1983; Tett, 1990; Balzer and Hardeland, 1991; Godhe et al., 2001). Salinity in itself is not a factor known to influence the amount of cyst produced but studies on *Lingulodinium machaerophorum* indicate that it can have a strong effect on the cyst morphology (Hallett, 1999).

First occurrences of *Tuberculodinium vancampoae* (Rossignol 1962) Wall 1967 are known from the Lower Miocene (Wall and Dale, 1971). The species is a resting stage of the phototrophic dinoflagellate *Pyrophacus steinii* (Schiller 1935) Wall et Dale 1971 (Wall and Dale, 1971; Faust, 1998; Pholpunthin et al., 1999). *Tuberculodinium* possess characteristic bulbous processes cause that it can easily be distinguished from other cysts (Wall and Dale, 1971; Harland, 1983; Matsuoka, 1985).

Marret and Zonneveld (2003) document its present day geographical distribution in surface sediments and observe that *T. vancampoae* is found subtropical to tropical coastal areas which are characterised by extreme salinities.

Here we present results of experiments where *Tuberculodinium vancampoae* is cultured under different temperature, light and salinity conditions to test if and how the production and morphology of *T. vancampoae* is influenced by the above mentioned environmental variables.

Table 4.1. Alphabetical list of cited species and genera with authors.

---

<i>Alexandrium catenella</i> (Whedon et Kofoid) Balech, 1985
<i>Ceratium cornutum</i> (Ehrenberg) Claparède et Lachmann
<i>Gonyaulax baltica</i> Ellegaard, Lewis et Harding 2002
<i>Gonyaulax spinifera</i> (Claparède et Lachmann 1859) Diesing 1866
<i>Gymnodinium catenatum</i> Graham 1943
<i>Lingulodinium</i> Wall 1967
<i>Lingulodinium machaerophorum</i> (Deflandre et Cookson 1955) Wall 1967
<i>Protoceratium</i> Bergh 1881
<i>Pyrophacus steinii</i> (Schiller 1935) Wall et Dale 1971
<i>Spiniferites</i> Mantell 1850
<i>Thoracosphaera heimii</i> (Lohmann 1920) Kamptner 1944
<i>Tuberculodinium vancampoae</i> (Rossignol 1962) Wall 1967

---

## MATERIAL AND METHODS

Cysts were isolated from surface sediment sample collected in September 2003 from the Omura Bay (Nagasaki Prefecture, Kyushu, Japan). The sediment samples were stored at 4°C and in dark until further treatment. Subsamples were rinsed with artificial sea water (salinity 34.5 psu; HW Meersalz Professional, Wiegandt GmbH, Krefeld, Germany) and sieved through a 20µm nickel precision sieve (Stork Veco, mesh: 570). Subsequently the sieved residue was cleaned by ultrasonication and rinsed through the sieve again. Individual cysts were isolated with a micropipette under inverted light microscope (Zeiss Axiovert 25C). After rinsing the individual cysts in drops of clean medium (K medium –Si; Keller et al., 1987) they were transferred into 24-chambers microwells (Corning Inc., Corning, NY, USA; Costar 3524) containing ~ 1.0mL of the culture medium (K medium –Si). The medium was made of seawater collected off NW Africa with the RV Meteor during cruise 58-2 with a salinity of 36.6 psu. Since the highest number of *T. vancampoae* cysts is recorded from regions with sea surface salinity (SSS) of ~34.5psu (Marret and Zonneveld, 2003) seawater was diluted with demineralised water to obtain 34.5psu before medium was prepared.

Microwells were incubated at 24°C and a 12:12 hours light and dark cycle. Light in incubator was provided by cool white fluorescent tubes.

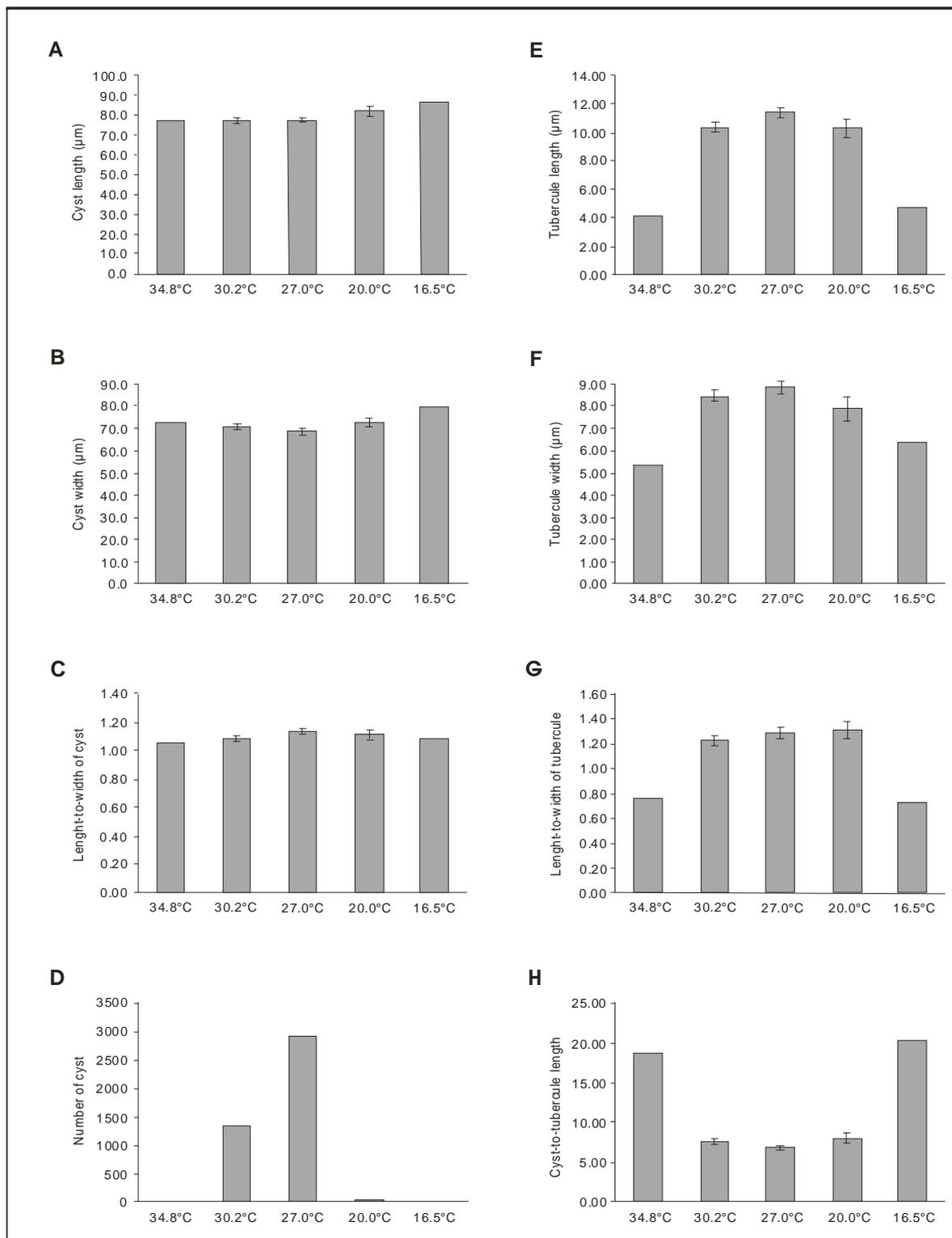


Fig. 4.1. Results of temperature experiment. A - average central body length, B - average central body width, C – length-to-width central body ratio, D – number of cyst produced in experiment, E - average tubercule length, F - average tubercule width, G - length-to-width tubercule ratio, H - central body –to-tubercule ratio.

The microwells were regularly examined for germinating cysts once a week. Since survival of small number of dinoflagellate motile cells in medium is influenced greatly by the volume of medium (Wall et al., 1967), the cells were transferred to a 6-chambers microwell (Corning Inc., Corning, NY, USA; Costar 3516) containing 50mL medium when an individual microwell contained approximately 15 motile cells. To avoid morphological variations related to genetic differences between strains obtained from different cysts we have used one strain for our experiments (GeoB1010). When well growing strain GeoB 1010 was dense, cells were transferred to 250mL Erlenmeyer flask containing 100mL of medium to establish material for further experiments. Material used in experiment was non-axenic.

To examine cysts produced at different light and temperature regimes a Light Gradient Box (LGB) and a Temperature Gradient Box (TGB) were used. The details of the equipment construction and parameters are given in Karwath (1999) and Karwath et al. (2000). The culture tubes contained 30mL of K medium –Si (35psu) inoculated with 1mL of dense culture. The LGB cultures were exposed to light intensities of 25, 40, 70, 120 and 250 $\mu\text{Em}^{-2}\text{s}^{-1}$  in a 12:12 day and night cycle. K medium –Si (35psu) was used. Temperature in LGB varied between 23.6°C and 25.7°C (average 24.7°C).

In TGB cultures were maintained in 16.5°C, 20°C, 27°C, 30.2°C and 34.8°C and with a 12:12 hours light and dark cycle. The culture tubes were lighted from below by cool white fluorescent tubes (Osram L18W/11-869). Temperature in both gradient boxes was controlled by sensors positioned in boxes and connected with a computer via interface. Evaporated water from each tube was refilled twice a week with demineralised autoclaved water to stabilize salinity.

Additionally motile cells from strain GeoB 1010 were transferred to microwells containing 5mL of K medium –Si at salinity levels 20, 30, 35, 40 and 45 psu. Salinity levels lower than 36.5psu were achieved by dilution with demineralised water and levels above by addition of artificial sea salt (HW Meersalz Professional, Wiegandt GmbH, Krefeld, Germany). Subsequently the nutrients and vitamins were added to the seawater.

At the termination of experiments, each culture material was fixed with formaldehyde (1/20 of culture volume). After 24 hours cultures were washed with distillate water through 20 $\mu\text{m}$  sieve and shortly ultrasonicated. The sieved residue was centrifuged and transferred into a 1.5mL Eppendorf reaction vessel. The homogenized residue was placed on a glass slide, embedded in glycerine jelly and sealed using paraffin wax.

Cyst size measurements were made at a 1000 fold magnification under Zeiss Axioskop 50 light microscope. Number of measurements is given in Table 1. Central body length and width as well as tubercule length and width were measured. To determine tubercule length and width tubercules characterised by most extreme length and width (longest-shortest, thinner- wider, respectively) were measured.

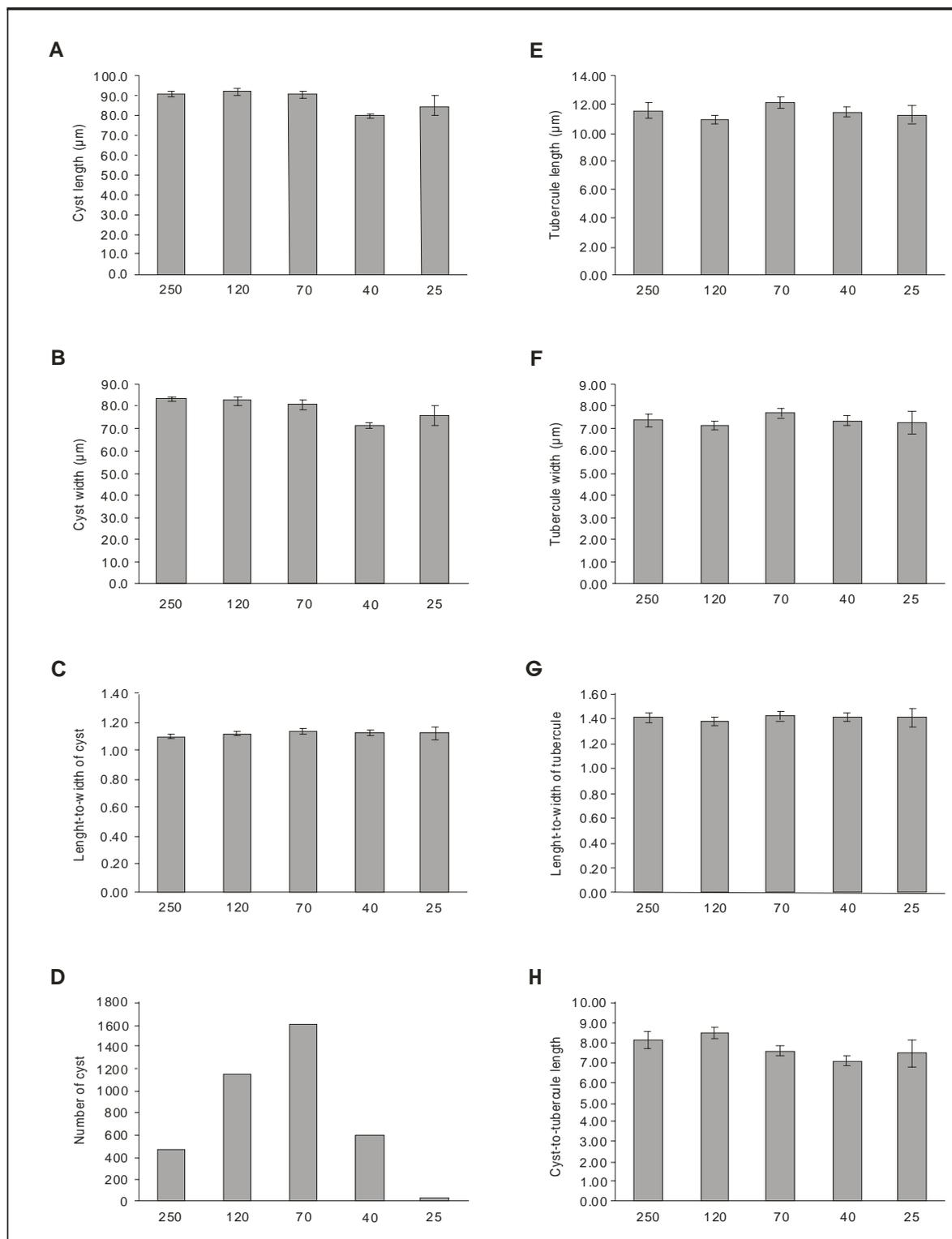


Fig. 4.2. Results of light experiment. A - average central body length, B - average central body width, C - length-to-width central body ratio, D - number of cyst produced in experiment, E - average tubercule length, F - average tubercule width, G - length-to-width tubercule ratio, H - central body -to-tubercule ratio. Light intensities in  $\mu\text{Em}^{-2}\text{s}^{-1}$ .

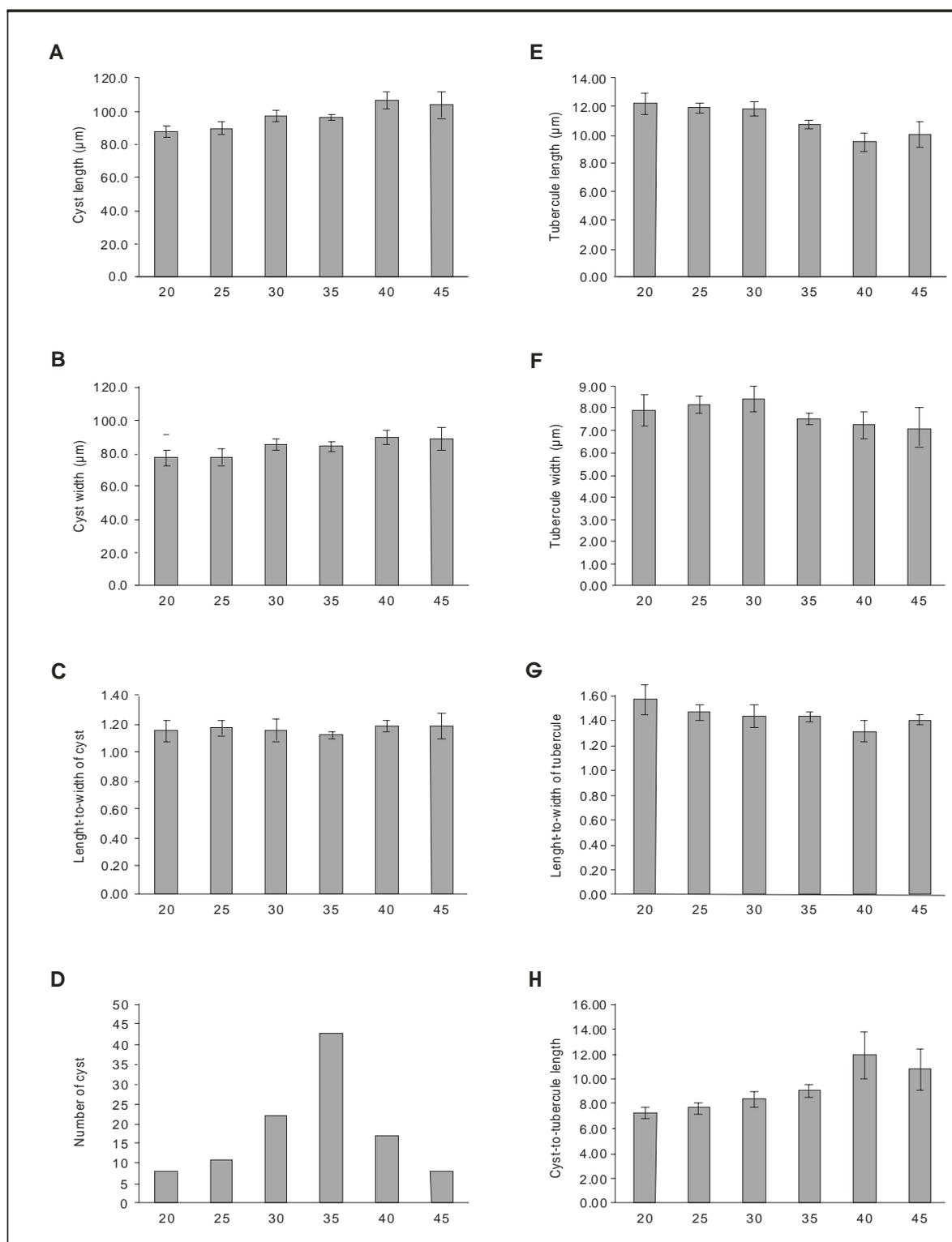


Fig. 4.3. Results of salinity experiment. A - average central body length, B - average central body width, C – length-to-width central body ratio, D – number of cyst produced in experiment, E - average tubercule length, F - average tubercule width, G - length-to-width tubercule ratio, H - central body –to-tubercule ratio. Salinity (20-45) in psu.

## RESULTS

Within 22 strains of *Pyrophacus steinii* (GeoB1010-1017, 1019-1021 and 1023) three of them produced cysts in non-crossed strains (GeoB 1010, 1014 and 1017).

### *Temperature experiment*

In cultures maintained in TGB growth and cyst production occurred under all tested temperatures (Fig. 4.1). The maximal number of cyst was produced at 27°C (2905 cysts). At 30.2°C cyst production was also relatively high (1322 cysts) whereas at 34.8°C, 20°C and 16.5°C cyst production was much reduced.

The ratio of central body length/width as well as the tubercule length/width ratio varies between tested temperatures and were maximal in 27°C. Minimal central body length/width is observed at 34.8°C. At 16.5°C and 34.8°C cyst possessing flat tubercules dominate the assemblage. At 27°C they occur only in low relative amounts. A T-test indicates that the relationship between tubercule length and temperature significant at the 95% confidence interval. This is also the case if only the shortest or longest spines are taken into consideration. Relation between length of central body and tubercules shows that relatively longest tubercules are found in 27°C.

### *Light experiment*

In LGB growth and cyst production was observed under all tested light conditions (Fig. 4.2). The maximal cyst production is found at light intensity of 70  $\mu\text{Em}^{-2}\text{s}^{-1}$  (1601cysts). At 25 $\mu\text{Em}^{-2}\text{s}^{-1}$  cyst production was the lowest (18 cysts). Central body length remained similar in higher light intensities (250, 120 and 70  $\mu\text{Em}^{-2}\text{s}^{-1}$ ) and was only slightly decreased at 40 and 25 $\mu\text{Em}^{-2}\text{s}^{-1}$ . A similar relationship is observed for central body width resulting in a constant length/width ratio of the central body. No differences in tubercule morphology are observed. Relatively shorter tubercules are observed at high light intensities.

### *Salinity experiment*

Maximal cyst production is observed at 35psu (Fig. 4.3). At the salinities 20 and 45 psu, cyst production is very low. The ratio between central body and length of tubercules increases with increasing salinity between 20 and 40psu and is slightly lower at 45psu indicating relatively longer tubercules in low salinities. According to t-test comparison of neighbouring samples indicates not significant differences between 20 and 40psu; however samples that are not neighbouring (20 and 30, 30 and 40, 25 and 35 and also 35 and 40psu) show a significant trend.

Central body length as well as width increases between 20 and 40 psu with increasing salinity. Tubercule length decreases between 20 and 40 psu with increasing salinity.

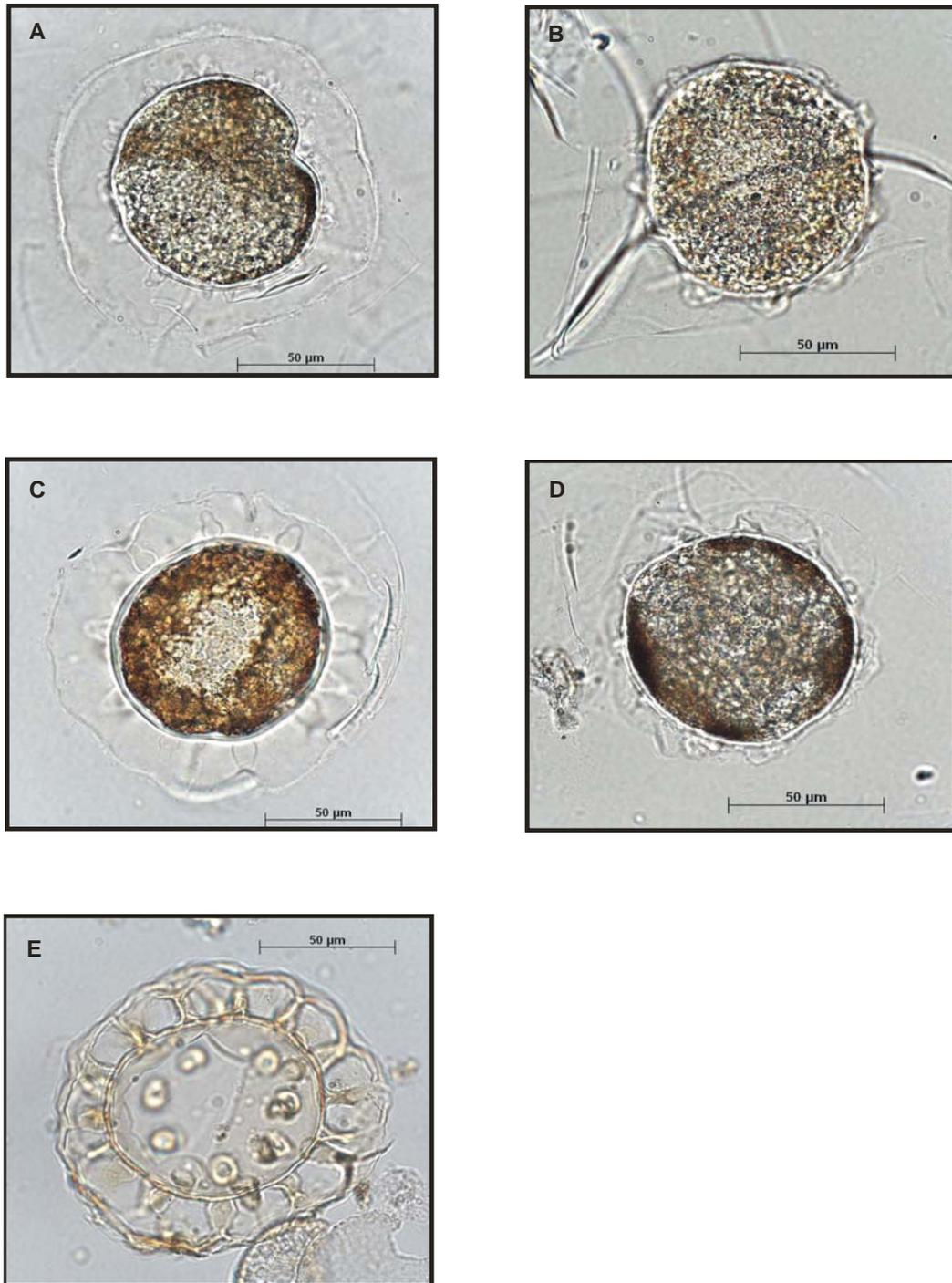


Fig.4.4. Light micrographs of *Tuberculodinium vancampoae* illustrating the morphological variations of cysts under different temperature conditions. A - 20°C, B - 16.5°C, C - 27°C, D - 34.8°C and E - cyst from sapropel 3, Crete, core T87/2/20G, 168-169.

## DISCUSSION

Among our 22 strains we have found three of them that produce cysts in non-crossed cultures. This indicates that homothally can occur in this species. Our results do not agree with results by (Pholpunthin et al., 1999) which suggested that in marine dinoflagellates, *Pyrophacus steinii* is the only species known to have heterothallism in its sexual process. Most marine species are homothallic. Heterothally is recorded only in *Alexandrium catenella* (Whedon et Kofoid) Balech, 1985 and *Gymnodinium catenatum* Graham 1943. In freshwater dinoflagellates, *Ceratium cornutum* (Ehrenberg) Claparede et Lachmann is the only species recorded as heterothallic (Pholpunthin et al., 1999 and references therein).

### *Temperature experiment*

Temperature is known to be a parameter influencing encystment (Anderson et al., 1984; Anderson et al., 1985; Nuzzo and Montresor, 1999; Godhe et al., 2001; Sgrosso et al., 2001). Depending on dinoflagellate taxa cyst production can occur in wide or narrow temperature window and/or in high or low temperature value (Nuzzo and Montresor, 1999; Sgrosso et al., 2001). In natural environment cyst of *T. vancamptoe* are known from surface sediments of regions where sea surface temperature (SST) vary between 7.1°C and 29.5°C. However, with some exceptions it has not been found in areas with summer sea surface temperature below 14.5°C and winter SST below 12.7°C (Marret and Zonneveld, 2003). The motile producing *T. vancamptoe* cysts, *Pyrophacus steinii* is known from warm temperate to tropical waters (Faust, 1998 and references therein). She records maximal cyst occurrence from the region of East Asia (Japan) and northern coast of Gulf of Guinea. In our experiments cyst production is observed in the complete temperature window studied (16.5°C – 34.8°C), with maximal production at 27°C in consistence with the above discussed field data.

Although we have no direct data from TGB regarding 24-25°C we have observed also relatively high cyst production during the same time in LGB where temperature remained on average 24.7°C (apart from extreme elucidations). Of course in laboratory conditions cultures might be exposed to stressful conditions resulting in encystment window failing to meet with environmental results. This problem might be especially important in the case of deep dwelling species (Meier et al., 2004) but it rather not influence of results obtained on *T. vancamptoe* in so far as this taxon is mainly reported from coastal environment (Marret and Zonneveld, 2003 and references therein). As the strain GeoB 1010 is isolated from Japanese coast it is also possible that observed results might be related to ecophenotyp characteristic for this region (Meier et al., 2004). The majority cysts noted from the field is found in the region of Japan (Marret and Zonneveld, 2003) and it might be the cause observed similarity between our experimental and field data.

Reduction in process length has been thought to can result from different environmental factors. However, usually salinity is thought to be a factor influencing processes size. The effect of temperature on process length has not been documented previously but is significant for *T. vancampoae* (Fig. 4.1). Size and shape of tubercles vary with maximal length values within cysts produced in 27°C. At extreme temperatures we observed that cyst possessing “flat” tubercles form a large, dominating the assemblage. However, occurrences of these cysts are not restricted to these extreme temperatures. Our data show that temperature might cause morphological deformities of *T. vancampoae* cysts so extreme that in palaeoenvironmental studies these morphotypes would not be considered to be formed by *P. steinii* (Fig. 4.4).

#### *Light experiment*

Light is thought to be another important factor influencing dinoflagellate life cycle affecting encystment and germination (Binder and Anderson, 1986; Balzer and Hardeland, 1991; Nuzzo and Montresor, 1999; Godhe et al., 2001; Sgrosso et al., 2001). However, there is only little information about potential influence of light intensity on cyst production and morphology. Algae are able to acclimate to differentiated light conditions (Kirk and Tilney-Basset, 1978; Karwath, 1999). (Karwath, 1999) observed for *Thoracosphaera heimii* (Lohmann 1920) Kamptner 1944 growth between 10 and 800 $\mu\text{Em}^{-2}\text{s}^{-1}$  and noted that between 20 and 40 $\mu\text{Em}^{-2}\text{s}^{-1}$  there is a zone where, for this dinoflagellate, adaptation to such low irradiances gets problematic. Similarly in our results at 25 and 40  $\mu\text{Em}^{-2}\text{s}^{-1}$  cyst production was very low. We observe maximal cysts production at light intensity 70  $\mu\text{Em}^{-2}\text{s}^{-1}$ . Higher light intensity caused a significant reduction of cyst production. It might therefore be suggest that at about 70 $\mu\text{Em}^{-2}\text{s}^{-1}$  illumination that is optimal for encystment of this species since. In natural environment it is observed that encystment coincides with favourable conditions for a species (Wall et al., 1970; Anderson et al., 1983; Kremp and Heiskanen, 1999). Our results might therefore imply that the optimal growing conditions of *P. steinii* might be about 70 $\mu\text{Em}^{-2}\text{s}^{-1}$ . Karwath (1999) noted that the final yield of 2 strains of *T. heimii* was maximal at 40  $\mu\text{Em}^{-2}\text{s}^{-1}$  and 130  $\mu\text{Em}^{-2}\text{s}^{-1}$ . Our results suggest a similar pattern for *T. vancampoae* with high production at 70 and 130 $\mu\text{Em}^{-2}\text{s}^{-1}$ .

We observed no significant changes in cyst morphology during this experiment. It seems that light intensity have rather small influence on cysts morphology.

#### *Salinity experiment*

Observations from the Limfjord, Denmark (Ellegaard, 2000), Baltic Sea (Dale, 1988; Nehring, 1994; Brenner, 2001) and from the Black Sea (Wall and Dale, 1973) have shown that variations in cyst morphology of species belonging to genera *Lingulodinium* Wall 1967, *Protoceratium* Bergh 1881 and *Spiniferites* Mantell 1850 can be strongly influenced by salinity changes. Also experimental work has confirmed these observations. Hallett (1999) has showed that *Lingulodinium polyedrum* (Stein)

Dodge 1989 develops relatively higher numbers of cysts possessing reduced processes lengths at low salinity. Similar results are documented in an experiment by Ellegaard et al. (2002) where *Gonyaulax baltica* produced cysts with shorter processes at lower salinities. Although we obtained only a low number of cysts in our salinity experiment our results suggest that also for *Tuberculodinium vancampoe* there is a relation between salinity and cysts morphology although not as pronounced as in our temperature experiments. We observed that the cyst length/tubercule length ratio differs slightly between neighbouring samples with a distinct trend towards larger values at high salinities. Unfortunately the low number of cysts being produced during the salinity experiment makes firm conclusions premature.

The reason why only a low number of cysts have been produced in our salinity experiment might be stressful conditions. Within our experiments much higher cyst production rate is observed when experimental tubes contained more medium (Wall et al., 1967). The negative influence of unknown factors effecting the cysts production in cultures has been previously observed during several experiments (Hallett, 1999; Ellegaard et al., 2002; Meier et al., 2004). In several cases the laboratory results differed from natural conditions indicating that other than the investigated factors influence cyst production. For instance, although Hallett (1999) and Ellegaard et al. (2002) have observed a similar forcing of salinity on cyst morphology in laboratory and natural environments, cyst were produced in a more narrow salinity range than in surface sediments.

For *T. vancampoe* salinity has no clear effect on cyst central body. However, in low salinities (20, 25 and 30psu) cysts were slightly longer. Observations on other dinoflagellate cysts (*L. polyedrum* (Hallett, 1999), *Gonyaulax baltica* (Ellegaard et al., 2002)) also indicate that cyst diameter remains rather independent of salinity changes. Although relation between increasing salinity and cyst-to-tubercule length remains insignificant for small salinity changes (5psu), it seems to be worth to indicate. Comparison of data from salinity 20, 30 and 40psu shows that this relationship might be significant.

In natural environments *T. vancampoe* has been found in brackish as well as in full marine conditions with sea surface salinity (SSS) ranking between 16.9 and 36.6 psu. Maximal number of cyst is known from regions where salinity varies within the year between c. 33 and 34.5 psu (average at 34.3psu; (Marret and Zonneveld, 2003)). Our results indicate that high salinity is not a factor that limits cyst production and that encystment can occur over 36.6psu.

As mentioned above laboratory experiments have their restrictions as cysts are being grown under unnatural conditions. The result of this study are, however, in remarkable agreement with field observations indicating that culture experiments can enhance our knowledge about factors influencing dinoflagellate cyst production. We document here for the first time the effect of environmental factors of the cyst morphology of a tropical species. Similarly to *Lingulodinium machaerophorum*, *Spiniferites baltica*, *Spiniferites* spp. and *Protoceratium reticulatum*, changes in *Tuberculodinium*

*vancampoae* morphology can be strongly influenced by changing environmental gradients. Although until now the effect of environmental factors is documented for a restricted amount of species, the present results suggest that environmentally induced morphological variation within the species might be a commonly occurring phenomenon. This implies that this effect might have been underestimated in dinoflagellate taxonomy and that different cyst species or even genera might belong to a single biological species. On the contrary, recent studies on ribosomal DNA internal transcribed spacers ITS1 and ITS2 suggest the presence of “cryptic” species within previously considered single (morpho) species. Information about if environmental stress might cause beside a phenotypic effect a genotypic effect is one of the questions that might be investigated in future culture experiments.

## CONCLUSIONS

Our results indicate that *T. vancampoae* can be homothallic and is not exclusively heterothallic species as has previously been suggested for this species.

Our experiments indicate that similarly to other organic-walled dinoflagellate cyst *Tuberculodinium vancampoae* encystment rate and morphology can be influenced by changing environmental conditions. In contrast to previous studies, changing temperatures and not salinity had the most pronounced effect on the cyst morphology. *T. vancampoae* cysts produced in extreme temperatures show strongly shortened tubercles. The longest tubercles are found at 27°C where also maximal cysts production is observed. The relationship between cyst production rates and temperature found in this study corresponds to field observations.

Cyst production is observed in the complete salinity range studied 20 – 45psu. Maximal cyst production has been found at 35psu. Between 20 and 40psu increasing central body-to-tubercle ratio indicates relatively shorter tubercles in relation to cyst central body.

Light intensity appears to have a neglecting influence on cyst morphology although low intensities coincide with slightly smaller tubercle length and width. Maximal encystment is noted at  $70\mu\text{E m}^{-2}\text{s}^{-1}$ .

## ACKNOWLEDGMENT

This research is funded by the Deutsche Forschungsgemeinschaft as a part of European Graduate College “Proxies in Earth History” EUROPROX, Bremen University. Thanks for Gerard Versteegh and Krystyna Kowalczyk for their help in statistic. We thank Monika Kirsch for helping in preparation phase. These experiments would not have been possible without her and Nicole Zatloukal help. Photo of fossilized *T. vancampoae* was taken from Gerard Versteegh’s slide (core T87/2/20G, Crete, 138-169 org (1); Versteegh, 1993).

Table 4.2. Number of measurements.

	Cyst length	Cyst width	Tubercule length	Tubercule width	Cyst length-to-width	Tuberc length-to-width	Cyst-to-tubercule length
temperature							
(°C)							
34.8	1	1	2	2	1	1	1
30.2	60	60	120	120	60	60	60
27	60	60	120	120	60	60	60
20	20	20	40	40	20	20	20
16.5	4	4	8	8	4	4	4
light ( $\mu\text{E}^{-2}\text{s}^{-1}$ )							
250	60	60	120	120	60	60	60
120	60	60	120	120	60	60	60
70	60	60	120	120	60	60	60
40	60	60	120	120	60	60	60
25	10	10	20	20	10	10	10
salinity							
(psu)							
45	8	8	16	16	8	8	8
40	16	16	32	32	16	16	16
34.5	42	37	86	86	37	43	42
30	21	22	44	44	21	22	21
25	11	11	22	22	11	11	11
20	8	8	16	16	8	8	8

## REFERENCES

- Anderson, D.M., Chisholm, S.W., Watras, C.J., 1983. Importance of life cycle events in the population dynamics of *Gonyaulax tamarensis*. *Marine Biology* 76, 179-189.
- Anderson, D.M., Kulis, D.M., Binder, B.J., 1984. Sexuality and cysts formation in the dinoflagellate *Gonyaulax tamarensis*: cyst yield in batch cultures. *Journal of Phycology* 20, 418-425.
- Anderson, D.M., Coats, D.W., Tyler, M.A., 1985. Encystment of the dinoflagellate *Gyrodinium uncatenatum*: temperature and nutrient effects. *Journal of Phycology* 21, 200-206.
- Balzer, I., Hardeland, R., 1991. Photoperiodism and effect of indoleamines in a unicellular alga, *Gonyaulax polyedra*. *Science* 253, 795-797.
- Binder, B.J., Anderson, D.M., 1986. Green light-mediated photomorphogenesis in a dinoflagellate resting cysts. *Nature* 322, 659-661.
- Brenner, W.W., 2001. Organic-walled microfossils from the central Baltic Sea, indicators of environmental change and base for ecostratigraphic correlation. *Baltica* 14, 40-51.

- Brenner, W.W., 2005. Holocene environmental history of the Gotland Basin (Baltic Sea) - a micropalaeontological model. *Palaeogeography, Palaeoclimatology, Palaeoecology* 220, 227-241.
- Dale, B. 1988. Low salinity dinoflagellate cyst assemblages from recent sediments of the Baltic region. Abstract. Brisbane, p. 33
- Dale, B., 1996. Dinoflagellate cyst ecology: modelling and geological applications. In: Jansonius, J.,Mcgregor, D.C.s (Eds.), *Palynology: Principles and Applications*. AASP Foundation, Salt Lake City, pp. 1249-1275.
- Dale, B., Thosen, T.A., Fjellså, A., 1999. Dinoflagellate Cysts as Indicators of Cultural Eutrophication in the Oslofjord, Norway. *Estuarine, Coastal and Shelf Science* 48, 371-382.
- Dawson, E.Y., 1966. *Marine botany - an introduction*. Holt, Rinehart, Winston, Inc. New York, 371 pp.
- Ellegaard, M., 2000. Variations in dinoflagellate cyst morphology under conditions of changing salinity during the last 2000 years in the Limfjord, Denmark. *Review of Palaeobotany and Palynology* 109 (1), 65-81.
- Ellegaard, M., Lewis, J., Harding, I., 2002. Cyst-theca relationship, life cycle, and effects on temperature and salinity on the cyst morphology of *Gonyaulax baltica* sp.no. (Dinophyceae) from the Baltic Sea area. *Journal of Phycology* 38, 775-789.
- Faust, M.A., 1998. Morphology and life cycle events in *Pyrophacus steinii* (Schiller) Wall et Dale (Dinophyceae). *Journal of Phycology* 34, 173-179.
- Godhe, A., Norén, F., Kuylenstierna, M., Ekberg, C., Karlson, B., 2001. Relationship between planktonic dinoflagellate abundance, cysts recovered in sediment traps and environmental factors in the Gullmar Fjord, Sweden. *Journal of Plankton Research* 23 (9), 923-938.
- Hallett, R.I., 1999. Consequences of Environmental Change on the Growth and Morphology of *Lingulodinium polyedrum* (Dinophyceae) in Culture. London, University of Westminster, pp.109. Ph.D. thesis.
- Harland, R., 1983. Dinoflagellate cysts in bottom sediments from the North Atlantic Ocean and adjacent seas. *Paleontology* 26 (2), 321-387.
- Harland, R., 1994. Dinoflagellate cysts from the glacial/postglacial transition in the northeast Atlantic Ocean. *Paleontology* 37, 263-283.
- Karwath, B., 1999. Ecological studies on living and fossil calcareous dinoflagellates of the equatorial and tropical Atlantic Ocean. Department of Geology, Bremen, Bremen University, pp.175. Ph.D. thesis.
- Karwath, B., Janofske, D., Tietjen, F., Willems, H., 2000. Temperature effects on growth and cell size in the marine calcareous dinoflagellate *Thoracosphaera heimii*. *Marine Micropaleontology* 39 (1-4), 43-51.

- Keller, D.M., Selvin, R.C., Claus, W., Guillard, R.R.L., 1987. Media for the culture of oceanic ultraphytoplankton. *Journal of Phycology* 23, 633-368.
- Kirk, J.T.O., 1983. Light and photosynthesis in aquatic ecosystems. Cambridge University Press. Cambridge, 401 pp.
- Kirk, J.T.O., Tilney-Basset, R.A.E., 1978. The plastids. Elsevier. Amsterdam, 960 pp.
- Kokinos, J.P., Anderson, D.M., 1995. Morphological development of resting cysts in cultures of the marine dinoflagellate *Linulodinium polyedrum* (= *L. machaerophorum*). *Palynology* 19, 143-166.
- Kremp, A., Heiskanen, A.-S., 1999. Sexuality and cyst formation of the spring-bloom dinoflagellate *Scrippsiella hangoei* in the coastal northern Baltic Sea. *Marine Biology* 134, 771-777.
- Lewis, J., Hallett, R., 1997. *Lingulodinium polyedrum* (*Gonyaulax polyedra*) a blooming dinoflagellate. *Oceanography and Marine Biology: an Annual Review* 35, 96-161.
- Lewis, J., Dodge, J.D., Powell, A.J., 1990. Quaternary dinoflagellate cysts from the upwelling system offshore Peru, hole 686B, ODP Leg 112. *Journal (Issue)*, 323-327.
- Lewis, J., Ellegaard, M., Hallett, R.I., Harding, I., Rochon, A. 2003. Environmental control of cyst morphology in gonyaulacoid dinoflagellates. Nagasaki, Japan, additional abstract.
- Marret, F., Zonneveld, K.A.F., 2003. Atlas of modern organic-walled dinoflagellate cyst distribution. *Review of Palaeobotany and Palynology* 125 (1-2), 1-200.
- Matsuoka, K., 1985. Cyst and thecate forms of *Pyrophacus steinii* (Schiller) Wall et Dale, 1971. *Trans. Proc. Palaent. Soc. Japan* 140 240-262.
- Matsuoka, K., 1999. Eutrophisation recorded in dinoflagellate cyst assemblages - a case of Yokohama Port, Tokyo Bay, Japan. *Sci. Total Environ.* 231 17-35.
- May, F.E., 1975. Functional morphology, paleoecology and systematics of *Dinogymnium* tests. *Palynology* 1, 103-121.
- Meier, K.J.S., Höll, C., Willems, H., 2004. Effect of temperature on culture growth and cyst production in the calcareous dinoflagellates *Calciodinellum albatrosianum*, *Leonella granifera* and *Pernambugia tuberosa*. *Micropaleontology* 50 (supplement no.1), 93-106.
- Nehring, S., 1994. Spatial distribution of dinoflagellate resting cysts in recent sediments of Kiel Bight, Germany (Baltic Sea). *Ophelia* 39, 137-158.
- Nuzzo, L., Montresor, M., 1999. Different excystment patterns in two calcareous cyst-producing species of the dinoflagellate genus *Scrippsiella*. *Journal of Plankton Research* 21 (10), 2009-2018.
- Pholpunthin, P., Fukuyo, Y., Matsuoka, K., Nimura, Y., 1999. Life History of a Marine Dinoflagellate *Pyrophacus steinii* (Schiller) Wall et Dale. *Botanica Marina* 42, 189-197.
- Rochon, A., de Vernal, A., Sejrup, H.-P., Hafliðason, H., 1998. Palynological evidence of climatic and oceanographic changes in the North Sea during the last deglaciation. *Quaternary Research* 49, 197-207.

- Sætre, M.M., Dale, B., Abdullah, M.I., Sætre, G.-P., 1997. Dinoflagellate cysts as potential indicators of industrial pollution in a Norwegian fjord. *Marine Environmental Research* 44 (2), 167-189.
- Sarjeant, W.A.S., Lacalli, T., Gaines, G., 1987. The cysts and skeletal elements of dinoflagellates: speculations on the ecological causes for their morphology and development. *Micropaleontology* 33 (1), 1-36.
- Servais, T., Stricanne, L., Montenari, M., Pross, J., 2004. Population dynamics of galeate acritarchs at the Cambrian-Ordovician transition in the Algerian Sahara. *Paleontology* 47, 395-414.
- Sgroso, S., Esposito, F., Montresor, M., 2001. Temperature and daylength regulate encystment in calcareous cyst-forming dinoflagellates. *Marine Ecology Progress Series* 211, 77-87.
- Taylor, F.J.R., 1987. Ecology of dinoflagellates: general and marine ecosystems. In: Taylor, F.J.R.s (Eds.), *The biology of dinoflagellates*. Blackwell, Oxford, pp. 399-502.
- Tett, P., 1990. The photic zone. In: Campbell, A.K., Whitfield, M., Maddock, L.s (Eds.), *Light and Life in the Sea*. Cambridge University Press, Cambridge, pp. 59-87.
- Thorsen, T., Dale, B., 1998. Climatcally influenced distribution of *Gymnodinium catenatum* during the past 2000 years in coastal sediments of southern Norway. *Palaeogeography, Palaeoclimatology, Palaeoecology* 143, 159-177.
- Thorsen, T.A., Dale, B., 1997. Dinoflagellate cysts as indicators of pollution and past climate in a Norwegian fjord. *The Holocene* 7, 334-446.
- Versteegh, G., 1993. New Pliocene and Pleistocene calcareous dinoflagellate cysts from southern Italy and Crete. *Review of Palaeobotany and Palynology* 78 353-380.
- Versteegh, G., 1994. Recognition of cyclic and non-cyclic environmental changes in the Mediterranean Pliocene; a palynological approach. *Marine Micropaleontology* 23, 147-171.
- Wall, D., Dale, B., 1971. A reconsideration of living and fossil *Phyrophacus* Stein, 1883 (Dinophyceae). *Journal of Phycology* 7 221-235.
- Wall, D., Dale, B., 1973. Paleosalinity relationships of dinoflagellates in the Late Quaternary of the Black Sea - a summary. *Geoscience and Man* 7, 95-102.
- Wall, D., Dale, B., 1974. Dinoflagellates in the late Quarternary deep-water sediments of Black Sea. In: Degens, E.T., Ross, D.A.s (Eds.), *The Black Sea - geology, chemistry and biology*. American Association of Petroleum Geologists, Memoir, 20, pp. 364-380.
- Wall, D., Guillard, R.R.L., Dale, B., 1967. Marine dinoflagellate cultures from resting spores. *Phycologia* 6 (2-3), 83-86.
- Wall, D., Guillard, R.R.L., Dale, B., Swift, E., 1970. Calcitic resting cysts in *Peridinium trochoideum* (Stein) Lemmermann, an autotrophic marine dinoflagellate. *Phycologia* 9 (2), 151-156.

**TEMPERATURE, LIGHT AND NUTRIENT EFFECT ON GROWTH OF  
*GONYAULAX SP.***

**Ewa Susek and Karin A.F. Zonneveld**

Fachbereich 5-Geowissenschaften, University of Bremen, Postfach 330440, D- 28334 Bremen, Germany

## Temperature, light and nutrient effect on growth of *Gonyaulax sp.*

Ewa Susek and Karin Zonneveld

### Abstract

To enlarge our knowledge about encystment and morphological variation of organic-walled dinoflagellates in relation to environmental factors, an experiment was carried out. Cultures of organic-walled dinoflagellates were established by germinating single resting cysts isolated from surface sediment samples collected from the southern North Sea coast, Spieka (Germany). Only 2 of the 9 cultures obtained produced cysts: GeoB 1005 (*Pentahparsodinium dalei* Indelicato and Loeblich III) and GeoB1007 (*Gonyaulax sp.*). Strain GeoB1007 was used in further experiments. The homothalic culture was exposed to different temperature, light and nutrient conditions. The culture was able to grow between 7.5°C and 27.8°C with maximal growth at 18°C and between 10 and 250 $\mu\text{Em}^{-2}\text{s}^{-1}$  with maximal growth between 120 and 250 $\mu\text{Em}^{-2}\text{s}^{-1}$ . Growth of the cultures was controlled every day by chlorophyll *a* measurements. Experiments were ended when the cultures started the declining phase. Cyst production halted during the experiments probably caused by the species specific endogenous rhythm.

### Introduction

Resting cysts of dinoflagellates are formed by about 200 marine dinoflagellates. Paleontological research uses organic-walled dinoflagellate cysts to reconstruct ecological conditions in the past (e.g. Lewis et al., 1990; Harland 1994; Versteegh, 1994; Rochon et al., 1998). Cysts of some of dinoflagellates contain extremely resistant, geologically preservable organic polymer – dinosporin (Fensome et al., 1993; Kokinos et al., 1998) and therefore they can be well preserved in sediments. During palaeoecological studies there were state morphological variations of several cysts' species. Several variations were observed in species of genera *Spiniferites* in the Baltic Sea, the Black Sea and the Limfjord, Denmark (Wall and Dale, 1973; Nehring, 1994; Dale, 1996; Ellegaard, 2000) and they have been coupled with salinity changes. However, this correlation can not be regarded as the cause. Possible reasons of cysts variations were considered many years ago (May, 1975; Sarjeant et al., 1987). Laboratory experiments on *Lingulodinium machaerophorum* (Deflandre et Cookson 1955) Wall 1967 (Hallett, 1999) and *Gonyaulax baltica* Ellegaard, Lewis et Harding 2002 (Ellegaard et al., 2002; Lewis et al., 2003) indicate that changes in salinity effect in processes of reduced length. For *Gonyaulax*

*baltica* have observed also reduction of central body length in increasing temperatures (Ellegaard et al., 2002).

*Spiniferites* is a cyst-base genera with over 100 recognized species and subspecies. It is known from the Cretaceous to the present. For cyst of *Spiniferites*, the motile stage is referred to *Gonyaulax* (Lewis et al., 1999 and references therein). Better understanding of observed ecophenotypism might increase precision of paleoreconstructions (Servais et al., 2004; Brenner, 2005).

To increase information about growth, encystment and morphological cyst variation in relation to different environmental conditions (temperature, nutrient availability and light intensity), experiments have been carried out. By establishing cultures from individually isolated cyst, we were able to test cyst production and variations in the morphology of cysts produced under different conditions.

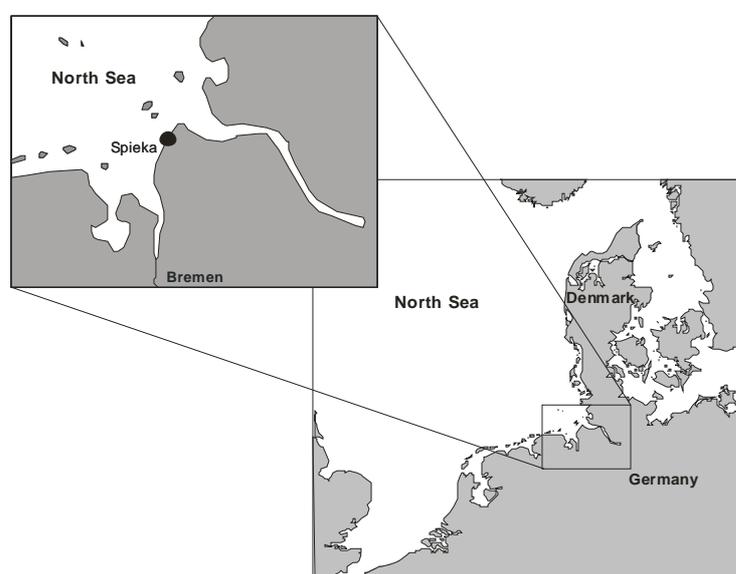


Fig. 5.1. Map showing sediment sample locality.

## Material and methods

The dinoflagellate cultures were obtained by germinating a single resting cyst (Wall et al., 1967). The fresh surface sediment to set up the cultures was collected from the coast at Spieka (south-eastern North Sea, Fig.5.1) in February 2002. The material was kept cold (4°C) and dark. Subsamples were rinsed with artificial sea water (20psu; HW Meersalz Professional, Wiegandt GmbH, Krefeld, Germany) and sieved through a 20µm nickel precision sieve (Stork Veco, mesh: 570). Subsequently the sieved residue was cleaned by ultrasonication and rinsed through the sieve again. Individual cysts were isolated with a micropipette under inverted light microscope (Zeiss Axiovert 25C). After rinsing every individual cyst in drops of clean medium (K medium –Si; Keller, et al., 1987) they were transferred into 24-chambers microwells (Corning Inc., Corning, NY, USA; Costar 3524) containing

~ 1.0mL of the culture medium (K medium –Si). The culture medium was made of artificial sea water (20psu). Cultures were incubated at 15°C, with a 12:12 dark-to-light photoperiod. Survival of dinoflagellate motile cells in medium is influenced greatly by the volume of medium (Wall et al., 1967). Therefore, when an individual microwell contained over 10 motile cells, the cells were transferred to a 6-chambers microwell (Corning Inc., Corning, NY, USA; Costar 3516) containing 50mL medium to secure better growth conditions. Species identification was accomplished using inverted light microscope and SEM. For further experiments strain GeoB1007 (*Gonyaulax* sp.) was chosen. Using homothalic strain enabled us to avoid morphological variations related to genetic differences between strains. Material used in experiments was non-axenic. Cyst production started spontaneously. To obtain material for experiment, cells were transferred to 250mL Erlenmeyer flask containing 100mL of medium.

To examine cysts produced at different light and temperature regimes, a Light Gradient Box (LGB) and a Temperature Gradient Box (TGB) were used. The details of construction are given in Karwath et al. (2000) and Meier et al. (2004). The culture tubes contained 30mL of K medium –Si (20psu) inoculated with 1mL of dense culture. In the Temperature Gradient Box (TGB) culture material was exposed to temperature gradient of 5°C to 34°C and a 12:12 hours light and dark cycle.

The LGB cultures were exposed to light intensities of 10, 13, 25, 40, 70, 120, 150 and 250 $\mu\text{Em}^{-2}\text{s}^{-1}$  in a 12:12 day and night cycle. K medium –Si (20psu) and encystment medium (K medium –Si (20psu) with nitrogen capacity reduced to 10%) were used. Temperature in LGB was on average 22°C.

Temperature in both gradient boxes was controlled by sensors positioned in boxes and connected with a computer via interface. To avoid salinity variation, evaporated water from each tube was refilled twice a week with demineralised autoclaved water. Growth of the cultures was controlled every day by chlorophyll *a* measurements. They were carried out with a laboratory fluorometer (TD-700, Turner Designs); cultures were shortly mixed with a vortex stirrer before placing tubes in the fluorometer. Experiments were ended when the cultures started the declining phase.

## Results

Only 2 of the 9 cultures obtained produced cysts: GeoB 1005 (*Pentapharsodinium dalei* Indelicato and Loeblich III) and GeoB1007 (*Gonyaulax* sp.). Strain GeoB1007 was used for further experiments.

During the experiment in the TGB, *Spiniferites* sp. was able to grow between 7.5°C and 27.8°C with maximal growth rates at 18°C (Fig.5.2). In the LGB growth occurred between 40 and 250  $\mu\text{Em}^{-2}\text{s}^{-1}$  and was highest between 120 and 250 $\mu\text{Em}^{-2}\text{s}^{-1}$  in normal medium (Fig.5.3). In the encystment medium growth was similar but the declining phase started earlier (Fig.5.4). Photos of *Gonyaulax* sp. obtained under standard conditions (15°C, a 12:12 dark-to-light photoperiod) are presented in Fig.5.5.

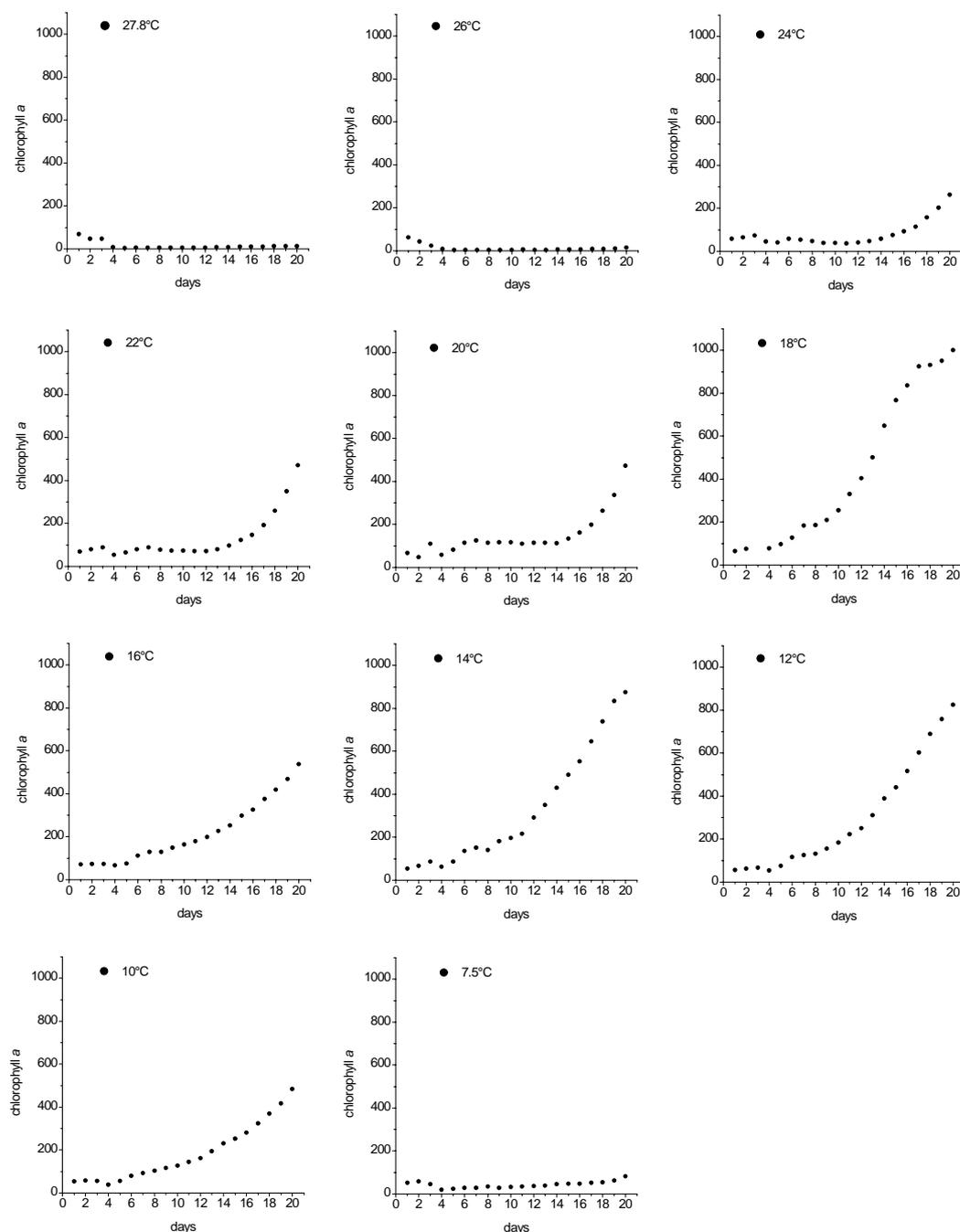


Fig.5.2. Chlorophyll measurements during temperature experiment on *Gonyaulax* sp.; K medium.

Cyst production halted during the experiments. This was probably caused by the species specific endogenous rhythm. To restore encystment of *Spiniferites*, the culture was maintained in K medium with different level of nitrogen: 100%, 10%, 5% and 0%. Only very rarely induced the formation of the cysts during next two months and thereafter encystment was not observed.

Cysts formation in strain GeoB 1005: *Pentahparsodinium dalei* Indelicato and Loeblich III occurred spontaneously and encystment was unstable.

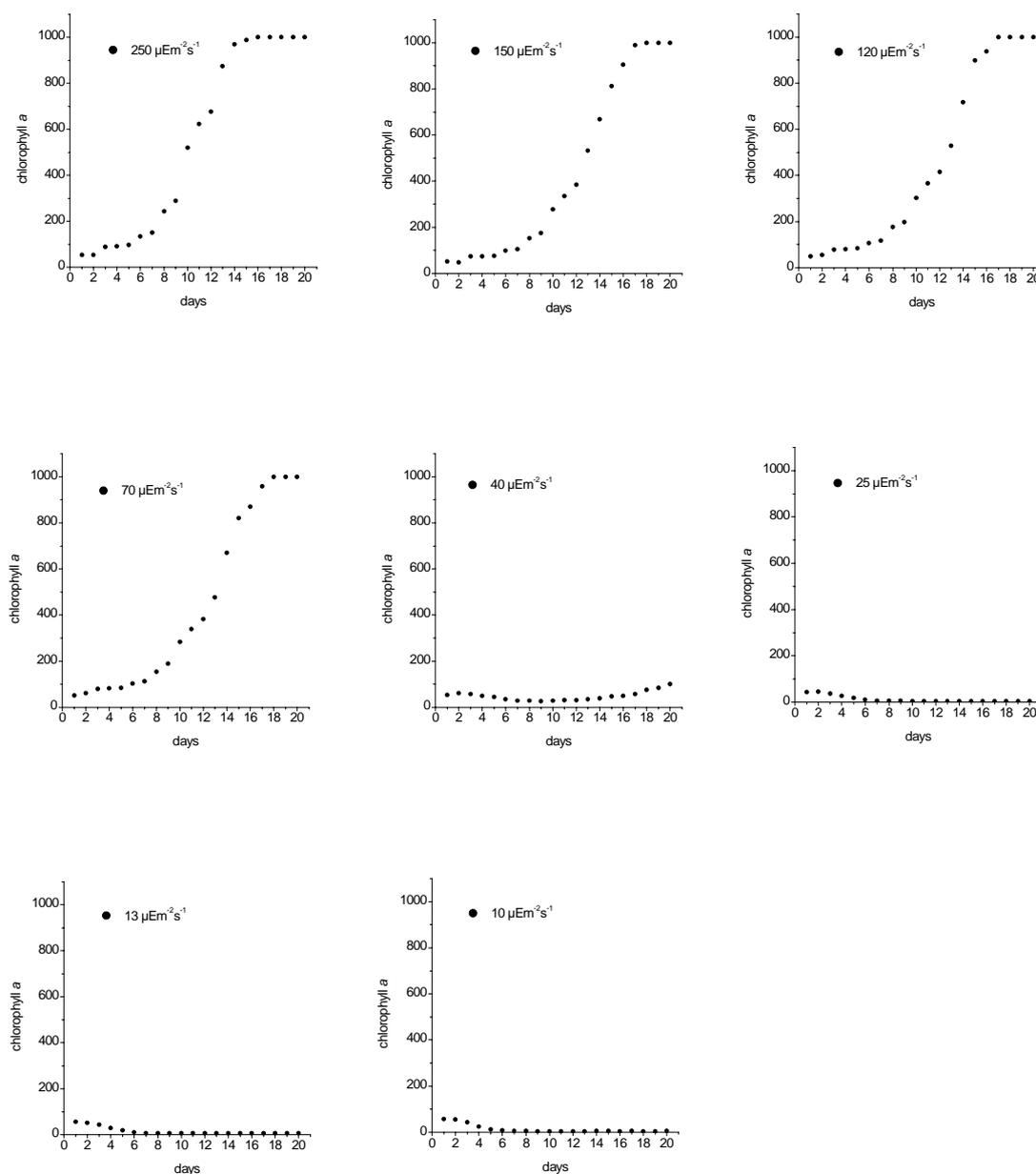


Fig. 5.3. Chlorophyll measurements during light experiment on *Gonyaulax* sp.; K medium.

## Discussion

The *Spiniferites* experiment in the TGB indicates that this taxon is able to adapt to low as well as to high temperatures. In the region where the cyst were collected, temperatures vary from 4.7°C in February and March to 16.3 in August (IGOSS nmc Reyn\_SmithOlv2 climatology c7100 Sea Surface Temperature 7.5E 56.5N; sea surface temperature (SST)). Although this strain was able to grow at temperature 27°C, optimal growth was observed at 18°C which represents the summer temperature in the region of origin. During the light experiment cultures grew very weakly below 40  $\mu\text{Em}^{-2}\text{s}^{-1}$ . Also for

*Thoracosphaera heimii* (Lohmann 1920) Kamptner 1944 adaptation to such low irradiances gets problematic somewhere between 20 and 40  $\mu\text{Em}^{-2}\text{s}^{-1}$  (Karwath, 1999). Other authors indicate that below about 50-100  $\mu\text{Em}^{-2}\text{s}^{-1}$  growth of dinoflagellates stops and many cell functions can not be maintained, although the physiological changes associated with low light responses vary among species (Prézélin, 1987 and references therein). Present observations suggest also that in nutrient depleted environments the point of adaptation to low irradiance might be elevated (Fig. 5.4), probably since it is more difficult to produce organic substances in the case of double stress.

Although laboratory experiments indicate that nutrient depletion is the main trigger for sexuality and encystment (Anderson et al., 1984; Anderson and Lindquist, 1985; Blanco, 1995), data obtained from natural environment indicate that encystment coincides rather with optimal growth conditions (Wall et al., 1970; Anderson, et al., 1983; Kremp and Heiskanen, 1999). The present results indicate that in laboratory conditions sexual reproduction resulting in encystment may be spontaneous. This situation was observed also for other species e.g. *Protoceratium reticulatum* (Claparède et Lachmann) Bütschli (Ellegaard et al., 2002) or *Polykrikos kofoidii* Chatton (Morey-Gaines and Ruse, 1980). In cultures of *Pentahparsodinium dalei* encystment also occurred spontaneously, however cyst were observed only in old cultures. Although generally cyst production is considered to result from sexual reproduction (Pfiester and Anderson, 1987), encystment may be a strategy for overcoming problems such as surviving of disadvantageous conditions (Sarjeant et al., 1987).

During the light experiment cyst production of *Spiniferites* stopped probably as a result of the species specific endogenous rhythm. Ellegaard et al. (2002) noted this problem in cultures of *Protoceratium reticulatum*, *Spiniferites membranaceus* (Rossignol) Sarjeant 1970 and *Spiniferites elongatus* Reid 1974. For old cultures noted that encystment may cease (in the cultures over c. 2 years old; Lewis, personal communication) but our culture was relatively young (c. 6 months). Since several laboratory experiments suggested nutrient manipulations and especially nitrogen starvation as a key to obtain cyst production (e.g. Pfiester and Anderson, 1987), strain GeoB 1007 was transferred to encystment media containing 10%, 5% and 0% of normal nutrient content. However, this did not re-induce cyst production. Since temperature as well as day-to-light rhythm were also reported to influence encystment (Anderson et al., 1984; Anderson et al., 1985; Nuzzo and Montresor, 1999; Godhe et al., 2001; Sgrosso et al., 2001), the culture was also exposed to lower and subsequently to higher temperatures (10°C and 18°C, respectively). Because encystment still did not occur, the photoperiod was changed (day:night - 14:10 hours). Also this manipulation had not effect on cyst production and further work on cyst formation of this culture remained impossible.

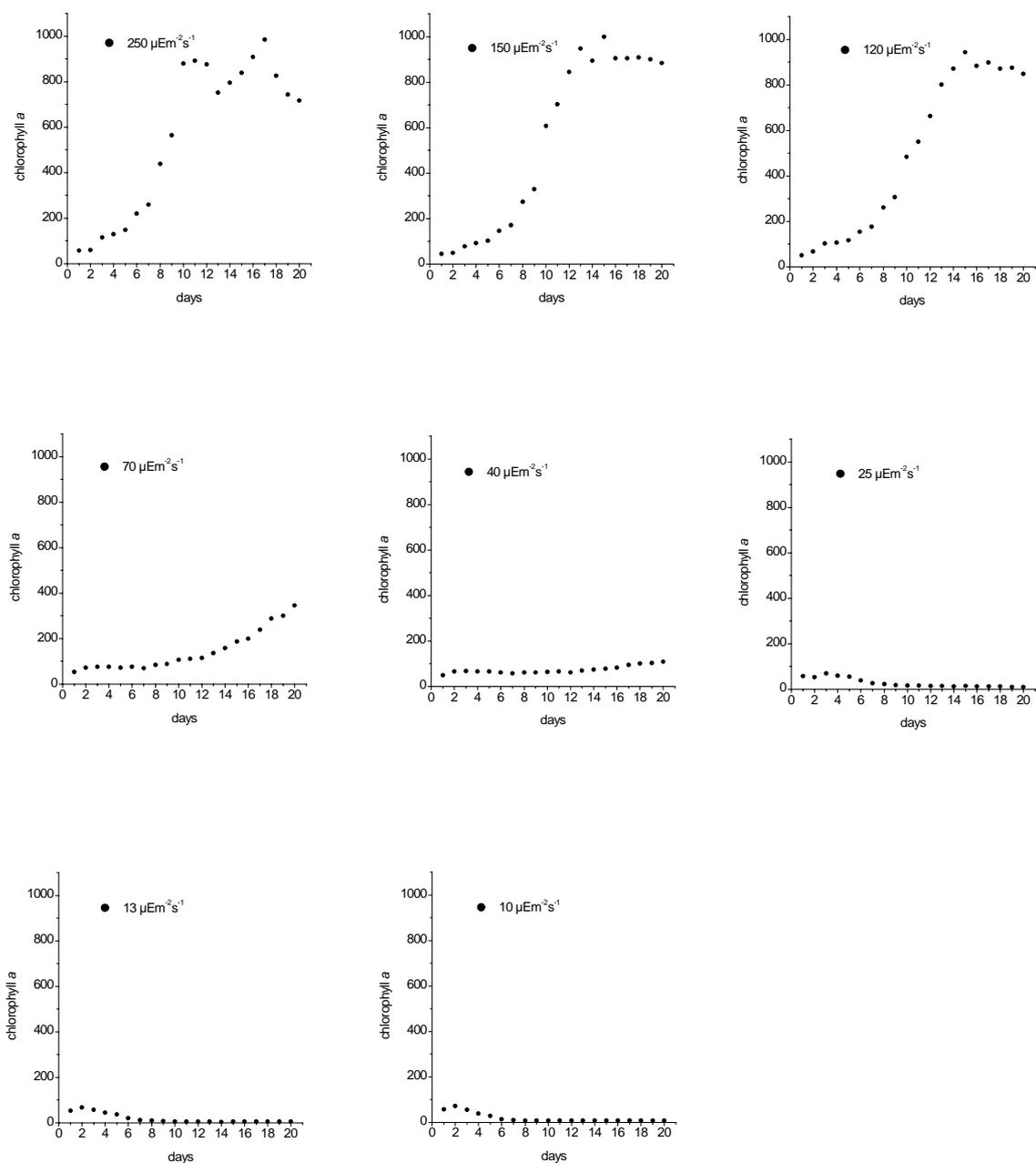


Fig. 5.4. Chlorophyll measurements during light experiment on *Gonyaulax* sp.; K encystment medium.

### Acknowledgment

This research is funded by the Deutsche Forschungsgemeinschaft as a part of European Graduate College “Proxies in Earth History” EUROPROX, Bremen University. We would like to thank Monika Kirsch. This research was possible owing to her help.

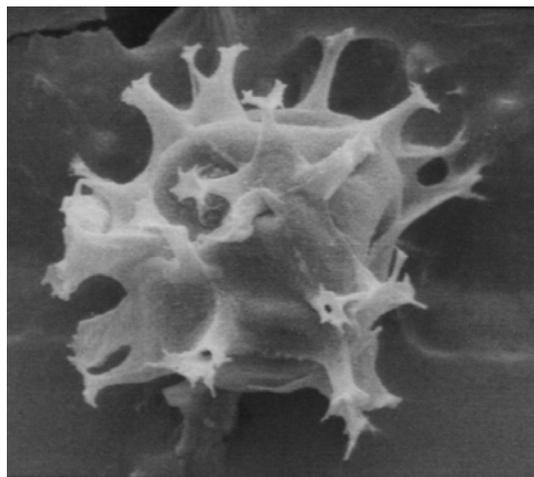


Fig.5.5. Cyst of *Gonyaulax* sp. from the culture (SEM)

## LITERATURE

- Anderson, D.M., Chisholm, S.W., Watras, C.J., 1983. Importance of life cycle events in the population dynamics of *Gonyaulax tamarensis*. *Marine Biology* 76, 179-189.
- Anderson, D.M., Coats, D.W., Tyler, M.A., 1985. Encystment of the dinoflagellate *Gyrodinium uncatenatum*: temperature and nutrient effects. *Journal of Phycology* 21 200-206.
- Anderson, D.M., Kulis, D.M., Binder, B.J., 1984. Sexuality and cysts formation in the dinoflagellate *Gonyaulax tamarensis*: cyst yield in batch cultures. *Journal of Phycology* 20, 418-425.
- Anderson, D.M., Lindquist, N.L., 1985. Time-course measurements of phosphorus depletion and cyst formation in the dinoflagellate *Gonyaulax tamarensis* Lebour. *Journal of Experimental Marine Biology and Ecology* 86 1-13.
- Blanco, J., 1995. Cyst production in four species of neritic dinoflagellates. *Journal of Plankton Research* 17 (1), 165-182.
- Brenner, W.W., 2005. Holocene environmental history of the Gotland Basin (Baltic Sea) - a micropalaeontological model. *Palaeogeography, Palaeoclimatology, Palaeoecology* 220, 227-241.
- Dale, B., 1996. Dinoflagellate cyst ecology: modelling and geological applications. In: Jansonius, J.,Mcgregor, D.C.s (Eds.), *Palynology: Principles and Applications*. AASP Foundation, Salt Lake City, pp. 1249-1275.
- Ellegaard, M., 2000. Variations in dinoflagellate cyst morphology under conditions of changing salinity during the last 2000 years in the Limfjord, Denmark. *Review of Palaeobotany and Palynology* 109 (1), 65-81.

- Ellegaard, M., Lewis, J., Harding, I., 2002. Cyst-theca relationship, life cycle, and effects on temperature and salinity on the cyst morphology of *Gonyaulax baltica* sp.no. (Dinophyceae) from the Baltic Sea area. *Journal of Phycology* 38, 775-789.
- Fensome, R.A., Taylor, F.J.R., Norris, G., Sarejant, W.A.S., Wharton, D.I., Williams, G.L., 1993. A calssification of living and fossil dinoflagellates. *Micropaleontology* (special publication) 7 351pp.
- Godhe, A., Norén, F., Kuylenstierna, M., Ekberg, C., Karlson, B., 2001. Relationship between planktonic dinoflagellate abundance, cysts recovered in sediment traps and environmental factors in the Gullmar Fjord, Sweden. *Journal of Plankton Research* 23 (9), 923-938.
- Hallett, R.I., 1999. Consequences of Environmental Change on the Growth and Morphology of *Lingulodinium polyedrum* (Dinophyceae) in Culture. London, University of Westminster, pp.109. Ph.D. thesis.
- Harland, R., 1994. Dinoflagellate cysts from the glacial/postglacial transition in the northeast Atlantic Ocean. *Paleontology* 37, 263-283.
- Karwath, B., 1999. Ecological studies on living and fossil calcareous dinoflagellates of the equatorial and tropical Atlantic Ocean. Department of Geology, Bremen, Bremen University, pp.175. Ph.D. thesis.
- Karwath, B., Janofske, D., Tietjen, F., Willems, H., 2000. Temperature effects on growth and cell size in the marine calcareous dinoflagellate *Thoracosphaera heimii*. *Marine Micropaleontology* 39 (1-4), 43-51.
- Kokinos, J.P., Anderson, D.M., 1995. Morphological development of resting cysts in cultures of the marine dinoflagellate *Linulodinium polyedrum* (= *L. machaerophorum*). *Palynology* 19, 143-166.
- Kremp, A., Heiskanen, A.-S., 1999. Sexuality and cyst formation of the spring-bloom dinoflagellate *Scrippsiella hangoei* in the coastal northern Baltic Sea. *Marine Biology* 134, 771-777.
- Lewis, J., Dodge, J.D., Powell, A.J., 1990. Quaternary dinoflagellate cysts from the upwelling system offshore Peru, hole 686B, ODP Leg 112. *Journal (Issue)*, 323-327.
- Lewis, J., Ellegaard, M., Hallett, R.I., Harding, I., Rochon, A. 2003. Environmental control of cyst morphology in gonyaulacoid dinoflagellates. Nagasaki, Japan, additional abstract.
- May, F.E., 1975. Functional morphology, paleoecology and systematics of *Dinogymnium* tests. *Palynology* 1, 103-121.
- Meier, K.J.S., Höll, C., Willems, H., 2004. Effect of temperature on culture growth and cyst production in the calcareous dinoflagellates *Calciodinellum albatrosianum*, *Leonella granifera* and *Pernambugia tuberosa*. *Micropaleontology* 50 (supplement no.1), 93-106.
- Morey-Gaines, G., Ruse, R.H., 1980. Encystment and reproduction of the predatory dinoflagellate, *Polykrikos kofoidi* Chatton (Gymnodiniales). *Phycologia* 19 (3), 230-236.

- Nehring, S., 1994. Spatial distribution of dinoflagellate resting cysts in recent sediments of Kiel Bight, Germany (Baltic Sea). *Ophelia* 39, 137-158.
- Nuzzo, L., Montresor, M., 1999. Different excystment patterns in two calcareous cyst-producing species of the dinoflagellate genus *Scrippsiella*. *Journal of Plankton Research* 21 (10), 2009-2018.
- Pfiester, L.A., Anderson, D.M., 1987. Dinoflagellate reproduction. In: Taylor, F.J.R.s (Eds.), *The biology of dinoflagellates*. Blackwell, Oxford, pp. 611-648.
- Prézelin, B., 1987. Photosynthetic physiology. In: Taylor, F.J.R.s (Eds.), *The biology of dinoflagellates*. Blackwell, Oxford, pp. 174-223.
- Rochon, A., de Vernal, A., Sejrup, H.-P., Haflidason, H., 1998. Palynological evidence of climatic and oceanographic changes in the North Sea during the last deglaciation. *Quaternary Research* 49, 197-207.
- Sarjeant, W.A.S., Lacalli, T., Gaines, G., 1987. The cysts and skeletal elements of dinoflagellates: speculations on the ecological causes for their morphology and development. *Micropaleontology* 33 (1), 1-36.
- Sarjeant, W.A.S., Lacalli, T., Gaines, G., 1987. The cysts and skeletal elements of dinoflagellates: speculations on the ecological causes for their morphology and development. *Micropaleontology* 33 (1), 1-36.
- Servais, T., Stricane, L., Montenari, M., Pross, J., 2004. Population dynamics of galeate acritarchs at the Cambrian-Ordovician transition in the Algerian Sahara. *Paleontology* 47, 395-414.
- Sgrosso, S., Esposito, F., Montresor, M., 2001. Temperature and daylength regulate encystment in calcareous cyst-forming dinoflagellates. *Marine Ecology Progress Series* 211 77-87
- Versteegh, G., 1994. Recognition of cyclic and non-cyclic environmental changes in the Mediterranean Pliocene; a palynological approach. *Marine Micropaleontology* 23, 147-171.
- Wall, D., Dale, B., 1973. Paleosalinity relationships of dinoflagellates in the Late Quaternary of the Black Sea - a summary. *Geoscience and Man* 7, 95-102.
- Wall, D., Guillard, R.R.L., Dale, B., 1967. Marine dinoflagellate cultures from resting spores. *Phycologia* 6 (2-3), 83-86.
- Wall, D., Guillard, R.R.L., Dale, B., Swift, E., 1970. Calcitic resting cysts in *Peridinium trochoideum* (Stein) Lemmermann, an autotrophic marine dinoflagellate. *Phycologia* 9 (2), 151-156.



## Conclusions and further perspectives

In the eastern part of north (sub)tropical Atlantic Ocean, conditions in the upper part of water column appear to be suitable for the production of organic-walled dinoflagellate cysts. Conditions off Cape Blanc are characterised by mesotrophy/eutrophy due to the year-round upwelling. However, over 4 years of detailed observations indicate upwelling intensification or relaxation have no clear influence on encystment. Nutrients can be brought into the region also by frequently occurring dust storms from the Sahara (Moulin, et al., 1997). The Saharan dust aerosols have a significant effect on the oceanic productivity due to the appreciable quantities of iron and other trace elements that they introduce (Zhu, et al., 1997; Goudie and Middleton, 2001; Middleton and Goudie, 2001; Pittman, 2002; Sarthou, et al., 2003). Encystment of *Protoperidinium americanum* appears to be closely related to elevated dust input. This contrasts with the view that the species is characteristic for upwelling regions (Dale and Fjellså, 1994). *P. americanum* can thus be applied more widely, to reconstruct mesotrophic to eutrophic conditions, rather than upwelling only. Also high fluxes of *Protoperidinium monospinum* cysts are positively correlated to the dust input. Our study documents this taxon from an upwelling area for the first time. Most probably cysts of this species have been assigned to *Echinidinium* or *Islandinium* previously. High daily fluxes of several other species such as of *Brigantedinium* spp., *Echinidinium aculeatum*, *Protoperidinium stellatum*, *Selenopemphix nephroides* and *Selenopemphix quanta* are observed at intervals of enhanced lithogen input. The temporal changes in the fluxes of *Lingulodinium machaerophorum* suggest that the composition of the upwelling source waters can be of major importance for the production of individual dinoflagellate species in studied region. Encystment of *L. machaerophorum* coincides also with relatively stratified surface water conditions. All above mentioned relations show positive correlation between high nutrient content and encystment as observed also in other environmental studies (Marino, et al., 1984; Montresor, et al., 1998; Kremp and Heiskanen, 1999; Zonneveld and Brummer, 2000). Cyst production of the heterotrophic *Brigantedinium* spp. increases with increasing fluxes of the food source of their motiles which are diatoms.

In contrast to the field studies mentioned above, a number of laboratory experiments suggest nutrition depletion as the main trigger for sexuality and cyst production (Anderson, et al., 1984; Anderson and Lindquist, 1985). Although *Impagidinium* species are often considered to be characteristic for oligotrophic regions such as the open ocean during this study no correlation between their fluxes and periods of depreciate nutrient content in the upper water column was observed. Our results suggest therefore, that encystment is convergent with conditions of optimal vegetative cell growth.

Observed variations in organic-walled dinoflagellate cyst fluxes and trap assemblages composition provide a particularly illustrative example of how organic-walled dinoflagellate cysts can be applied to reconstruct rapid local and regional changes in surface water conditions with respect to

nutrient contents. However, for a complete understanding the environmental picture that is usually obtained through the study of surface sediments and sediment cores, secondary processes effecting cyst assemblages in sediments have to be assessed. Analyses of material from sediment traps and underlying surface sediments reveals a clear discrepancy between the cyst assemblages produced in the upper water column and the cyst assemblages in the surface sediments. The relative increase of phototrophic taxa in the sediments compared to the traps, demonstrates that species selective oxygen degradation in bottom sediments and at the sediment/water interface forms an important factor affecting cyst association in oceanic sediments. For the application of organic-walled dinoflagellate in environmental reconstructions this fact has to be taken into account.

Laboratory experiments on *Tuberculodinium vancampoae* show morphological variations related to changes in temperature and salinity. Although a reduction in process length at low and high temperature levels is immediately obvious under light microscope, the differences between cyst body-to-tubercle length and changing salinity are recognised only after thorough statistical analysis of the measurements. Therefore, application of variations in tubercle length appears to be more useful.

Although new information has been obtained on factors triggering encystment of organic-walled dinoflagellate in the present study, this research was confined to a relatively small and specific region and the future applications will obviously require evidence also from other regions covering a broader range of environments from different oceans and different regimes. The unexplained halted cyst production during experiments on *Gonyaulax* sp. indicates that still some questions about parameters influencing cyst production remains unsolved. Another open question is if other organic-walled dinoflagellate than presently known (*Lingulodinium machaerophorum*, *Spiniferites baltica*, *Tuberculodinium vancampoae*) also show variations in cyst morphology in relation to environmental change. To answer this problem further laboratory experiments are needed.

As discussed in this thesis a number of laboratory experiments suggest that environmental stress e.g. nutrition depletion to be the main trigger for sexuality and encystment whereas present results, similarly to other findings, indicate that cyst production is convergent with conditions optimal for vegetative cell growth. A possible explanation for this paradox is that at maximal vegetative growth, nutrient depletion can occur within individual cells or their microhabitat and, as such, trigger enhanced sexuality. It is also plausible that in such a heterogeneous group as dinoflagellates, the factors that influence sexuality resulting in cyst production differ between the species. This problem appears also important because cysts may form a sort of seed bank in aquatic sediments from which the motile stock can be renewed – it is especially important in the case of blooming species. However, this idea also needs further environmental observations and laboratory work.

Further investigations are also needed to better understand secondary processes influencing cyst assemblages in sediments. Some experiments on species selective oxygen decay have just started (Zonneveld, pers. commun., 2005). In addition, chemical analysis of the cyst wall of *Tuberculodinium*

*vancampoae* obtained from cultures will be done by Gerard Versteegh. Cysts are already isolated and awaiting removal of cell contents and further analysis.

#### Literature

- Anderson, D.M., Lindquist, N.L., 1985. Time-course measurements of phosphorus depletion and cyst formation in the dinoflagellate *Gonyaulax tamarensis* Lebour. *Journal of Experimental Marine Biology and Ecology* 86, 1-13.
- Anderson, D.M., Kulis, D.M., Binder, B.J., 1984. Sexuality and cysts formation in the dinoflagellate *Gonyaulax tamarensis*: cyst yield in batch cultures. *Journal of Phycology* 20, 418-425.
- Dale, B., Fjellså, A., 1994. Dinoflagellate cysts as paleoproductivity indicators: state of the art, potential and limits. In: Zahn, R., Pedersen, T.F., Kaminski, M.A., Labeyrie, L.s (Eds.), *Carbon Cycling in the Global Ocean: Constrains on the Ocean's Role in the Global Change*. Springer-Verlag, Berlin Heidelberg, pp. 521-537.
- Kremp, A., Heiskanen, A.-S., 1999. Sexuality and cyst formation of the spring-bloom dinoflagellate *Scrippsiella hangoei* in the coastal northern Baltic Sea. *Marine Biology* 134, 771-777.
- Marino, D., Modigh, M., Zingone, A., 1984. *Marine Phytoplankton and Productivity. Lecture Notes on Coastal and Estuarine Studies*. Springer-Verlag, Berlin, pp. 89-100
- Montresor, M., Zingone, A., Sarno, D., 1998. Dinoflagellate cyst production at a coastal Mediterranean site. *Journal of Plankton Research* 20 (12), 2291-2312.
- Zonneveld, K.A.F., Brummer, G.J.A., 2000. (Palaeo-)ecological significance, transport and preservation of organic-walled dinoflagellate cysts in the Somali Basin, NW Arabian Sea. *Deep-Sea Research II* 47 (9-11), 2229-2256.



---

## Acknowledgments

This work was carried out at the Geosciences Department of Bremen University, and was supported by the Deutsche Forschungsgemeinschaft within the European Graduate College „Proxies in Earth History“.

I express my entire gratitude to Professor Dr. Helmut Willems for giving me the chance to produce this doctoral thesis and for his general support. Many sincere thanks are due to Dr. Karin Zonneveld for always being there when I needed her advice. She invested in me a lot of time through discussions, correction of manuscripts, good advice and ideas. Karin, thanks a lot for standing my English... for your indulgence – even when I hit up my cultures. I am especially grateful to Dr. Gerard Versteegh for great support during my first months at work and his openness to discussions during my entire stay. Almost every discussion fructified with new ideas and a lot of talks ended for me in much better humour.

All members of the Division of Historical Geology and Palaeontology are thanked for the very good working atmosphere – it was a real pleasure to meet them every day during the past 3 years, and I will miss them a lot.

My gratitude also goes to Ulrike (Uli) Holzwarth, Matthias Bork and Frank Bockelmann, who helped me in the beginning with laboratory work. Discussions with Uli were very helpful. I am very grateful to Oliver Esper and Matthias Bork for their immediate help with computer problems - sometimes I was really up-to-date with viruses so they have had some work to do.

For over 3 years I shared office with Katarzyna Bison – it is long time and she was always good companion and friend. We had scientific talks, but also a lot of warm, friendly and clever chats related to life. For good atmosphere and a lot of support I have to also gratitude Dorit Siggelkow. Erna Friedel and Maria Petrogiannis are also warmly thanked. They were always very helpful and competent. Monika Kirsch was a perfect teacher of dinos' culturing – her knowledge and experience helped me a lot. Nicole Zatloukal was very good companion during both “Meteor” cruises: M58/2 off NW Africa and M 63/1” in SW Indian Ocean. During the cruise off NW Africa I met Meral Kölbrich – she helped us a lot and our talks were always fruitful and a pleasure – thank you. I also thank all other people who helped us during cruises.

I sincerely gratitude my father, Stanisław Susek, for his general support, his believe in me and love – dziękuję Ci, Tato, za wszystko. I have to, and want to, express my great gratitude to my best fiend Krystyna Kowalczyk. She helped me during my stay here every time I needed her. Thanks also for the almost monthly lifts to Szczecin for over 3 years.

My gratitude goes also to all the old friends from home, which in spite of the distance, were always close.

**Dziękuję Wam wszystkim – Thanks to all of you**