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Benthic and Pelagic Coupling of Diatoms (Bacillariaceae) in Response to Hydrodynamic Forces in the Wadden Sea

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Summary

Within the microbenthic community, diatoms play an important role in terms of food source for grazers and suspension feeders. Furthermore, they contribute significantly to the primary production on intertidal flats and in coastal waters world wide. Numerous studies have now documented microalgal biomass, primary production and other aspects of their ecology in many habitats. However, knowledge on the resuspension of diatoms or the effect of hydrodynamic forces at the species level is sparse but a better understanding of processes at the sediment/water interface and of potential consequences for the ecosystem regarding climate change is urgently required. In addition, knowledge of the effect of hydrodynamics in the intertidal is important because this force links and alters various processes from small scale areas at the sediment/water interface to ecosystem as a whole.

The microscopic algae inhabit the sediment and water column and a terminology exists for referring to the habitats occupied by the diatoms, including pennate and centric forms, concerning their life mode: epipsammic (attached to a substratum), epipelic (cells are associated with the sediment, mainly motile) and pelagic diatoms that will occur mainly in the water column. A variety of diatoms are frequently found in both habitats, and often described as tychopelagic: a life mode with pelagic forms that are likely to have settled from the plankton and conversely, benthic diatoms that are readily resuspended. One aim of this thesis was to investigate the diatom community in the water and on the sediment surface and to establish the life mode of selected species in order to gather background information for further studies concerning bentho-pelagic coupling. The increased resolution of the identification and cell counts revealed a discrimination at the species level. Several species, notably of the genera *Diploneis* and *Achnanthes,* were found to react to altered flow conditions by presenting enhanced cell numbers on the sediment under increased flow or reduced flow, respectively. Furthermore, *Diploneis,* previously assumed to be a benthic species, is now shown to adopt a tychopelagic life style.

Settling processes during slack water phases and resuspension caused by wind-induced waves and tidal currents lead to a blurring of the boundaries between the two communities.

The present study investigated for the first time the influence of altered flow conditions and turbulence on diatoms *in situ.* This enabled us to take into consideration the effects of wind direction, wind force and tidal currents on the coupling. For this purpose a three-current-flume construction was deployed modifying the flow velocity. The study was carried out on a Wadden Sea intertidal flat at Sylt island in the North Sea, Germany, on 6 dates between July and September 2003. Analyses of chlorophyll *a* (chl *a*), suspended matter (SPM), cell counts, particulate organic carbon (POC), particulate organic nitrogen (PON) and species analysis on the sediment surface and in the water column served to characterise the relationship between the two communities. Flow characteristics were measured using the Acoustic Doppler Velocimeter (ADV) technique to calculate the physical parameters describing bottom shear stress and turbulence in order to assess the impact of hydrodynamics on diatom species and cell-size groups.

Results showed that wind direction, –velocity and fetch had the greatest influence on the variability of the samples, superimposed as they were on tidal forces.

An increase in flow velocity reduces turbulence, whereas under reduced flow conditions turbulence exerts stochastic resuspension events by lowering the critical bed shear stress. This affects small diatoms (< 20 µm) of the benthic community that are entrained into the water column.

Zusammenfassung

Innerhalb der benthischen Lebensgemeinschaft spielen Diatomeen eine wichtige Rolle hinsichtlich ihrer Verfügbarkeit als Nahrung für Weidegänger und Suspensionsfresser. Des weiteren tragen sie weltweit in erheblichem Maße zur Primärproduktion im Gezeitenbereich der Küstenregionen bei. Zahlreiche Studien dokumentieren bis zum heutigen Tage Mikroalgen-Biomasse, Primärproduktion und weitere ökologische Aspekte in diversen Habitaten. Es besteht jedoch nur ein begrenztes Wissen über das Resuspensionsverhalten von Diatomeen oder den Einfluss von hydrodynamischen Kräften auf Artenzusammensetzung. Ein besseres Verständnis der Prozesse an der Sediment/Wasser Grenzfläche sowie von möglichen Auswirkungen auf das Ökosystem hinsichtlich eines Klimawechsels ist dringend erforderlich. Besonders im Gezeitenbereich sind Kenntnisse über Hydrodynamik erforderlich, da diese Kraft hier diverse Prozesse verbindet und auch verändert, die sowohl im kleinskaligen Bereich der Sediment/Wasser Grenzfläche als auch auf ganzer Ökosystemebene Auswirkung haben.

Die mikroskopisch kleinen Algen leben auf dem Sediment und in der Wassersäule und zeigen dem Habitat entsprechende Lebensweisen: epipsammisch (an ein Substrat angeheftet), epipelisch (mit dem Substrat assoziiert und überwiegend freibeweglich) und pelagische Diatomeen, deren Hauptvorkommen in der Wassersäule liegt.

Eine Anzahl von Arten ist häufig in beiden Lebensräumen zu finden und werden als tychopelagisch bezeichnet; planktische Formen, die sich auf den Boden absinken lassen, und umgekehrt benthische Formen, die leicht in Resuspension gehen.

Ziel dieser Arbeit war unter anderem, die Diatomeengemeinschaft im Wasser und auf dem Sediment zu untersuchen und die Lebensweise festzustellen, um Hintergrundinformationen für weiterführende Studien über benthopelagische Verknüpfungen zu erhalten. Die intensive Bestimmungsarbeit und Zellzählungen ergaben, dass Unterschiede im Resuspensionsverhalten auf Artebene stattfinden. Mehrere Arten, wie z.B. der Gattungen *Diploneis* und *Achnanthes,* reagierten auf Strömungsänderungen mit höheren Abundanzen auf dem Sediment unter beschleunigter Strömung bzw. reduzierter Strömungsgeschwindigkeit. Desweiteren konnte gezeigt werden, dass die bisher als epipelisch geltende *Diploneis* eine tychopelagische Lebensweise führt.

Aussinken während der Hochwasserphasen und Resuspension angetrieben durch windinduzierte Wellen und Gezeitenströmungen führen zu einem Verwischen der Grenzen zwischen den beiden Gemeinschaften.

Die vorliegende Studie untersuchte erstmals *in situ* den Einfluss von veränderten Strömungsbedingungen und Turbulenz auf Diatomeen. Dieses Vorgehen ermöglichte den Einfluss von Windrichtung und Geschwindigkeit sowie den Gezeitenstrom in die Betrachtung von benthopelagischen Beziehungen zu integrieren. Zu diesem Zweck wurde ein Strömungskanal ("three-current-flume") eingesetzt, mit dem die Strömungsgeschwindigkeit manipuliert werden konnte. Die Untersuchung wurde im norddeutschen Teil des Wattenmeeres auf der Insel Sylt an 6 Tagen zwischen Juli und September 2003 durchgeführt. Analysiert wurden Sediment und Wasserproben auf folgende Parameter: Chlorophyll *a* (chl *a*), Schwebstoffkonzentration (SPM), partikulärer Kohlenstoff und partikulärer Stickstoff (POC, PON) sowie Zellzählungen und Artbestimmung der Diatomeengemeinschaften. Die Ergebnisse wurden zum Vergleich der beiden Gemeinschaften (Wasser/Sediment) herangezogen.

Strömungseigenschaften wurden mit Hilfe einer ADV-Sonde (Acoustic Doppler Velocimeter) gemessen und Schubspannungen sowie Turbulenz errechnet. Die Ergebnisse geben Aufschluss über den Einfluss von Hydrodynamik auf Diatomeenarten und Größenklassen.

Es konnte gezeigt werden, dass Windrichtung und Geschwindigkeit sowie "Fetch" den größten Einfluss auf die Variabilität der Resultate hatten. Auch die Auswirkungen der Gezeitenströmungen waren diesen Faktoren untergeordnet.

Ein Anstieg der Strömungsgeschwindigkeit verminderte Turbulenz, wohingegen unter reduzierten Strömungsbedingungen Turbulenz aufgrund kurzfristiger Verringerung der Schubspannung punktuelle Resuspension ausübte. Hiervon betroffen waren kleine Diatomeen (< 20 µm) der benthischen Gemeinschaft, die in die Wassersäule aufgewirbelt werden.

Chapter 1

General Introduction

Intertidal flats

The Intertidal zone, or littoral zone, is the area of shoreline between the high tide and low tide marks. Communities of marine intertidal sediments flat are among the most diverse of aquatic communities. They are highly dynamic systems that are subjected to repeated exposure and inundation as the tide rises and recedes. Particularly during the exposure, this leads to changes in the physical, chemical and biological forces which are often unpredictable due to their inter-related nature and effects of changes of one component on the other are therefore difficult to interpret. The morphology of the sand flat and its location with respect to tidal nodes determines the tidal frequency and range, the change in hydration of the sediment over a tidal cycle and – in so far as the strength of tidal current determines the dynamic energy available for resuspending the sediments – the clarity of the water column and the level of light available to the benthos. Reduction in energy as waves proceed inshore upon inundation results in changes in the sediment grain sizes deposited. Salinity is affected by the strength of evaporation due to solar heating during low tide, as well as by proximity to rivers, which may also bring a high loading of coloured, dissolved substances. During emersion, changes of temperature, hydration, salinity and light availability are often especially strong. Seasonal changes can also be profound with interstitial temperatures above 40 °C during emersion in summer or around zero with ice covering in winter. Owing to exposure to many of these factors, intertidal flats represent a complex ecosystem and comprise a habitat for a large variety of organisms ranging from microfauna/flora and macroflora to fish and wading birds visiting the sand or mudflats at low tide. Therefore, this ecosystem is not only important as a feeding ground but also with regard to commercial aspects. The coasts of the Wadden Sea are important areas for recreation, providing a strong base for tourism, and also for fishery, and should be controlled by responsible coastal management for the protection and sustainability of the ecosystem Wadden Sea. Man made threats such as eutrophication and pollution have a strong impact on coastal regions. The actual climate change and subsequent sea level rise is a subject of great concern for the Wadden Sea and its islands. Considering the fact that marine flora and fauna are closely linked with the environmental changes, the entire coastal ecosystem might be affected.

The Wadden Sea ecosystem can be regarded as comprising several habitats which include, for example, the intertidal zone, the sublitoral zone, with sandy and muddy sediments, seagrass areas, mussel beds and beaches harbouring a great variety of organisms. Each of these biotopes must be studied carefully before its relationship to the others becomes clear and leads to an understanding of the complete ecosystem.

Sylt

Ecological and biological research on Sylt (North Frisian Wadden Sea) has a long tradition dating back 130 years which has resulted in a comprehensive literature database (see for example Gätje & Reise 1998, Asmus & Asmus 1990, Armonies & Reise 2000, Reise 2002). The island is connected to the mainland by a causeway which forms the Sylt-Rømø Basin, a semi enclosed lagoon. Water is exchanged with the North Sea via a 2.8 km wide tidal inlet called Lister Tief. Tides are semi-diurnal with a range of about 2 metres. Salinity ranges between 28 and 32 psu. The influence of freshwater in the basin is negligible (Backhaus et al. 1998). Sandy sediments prevail over muddy sediments and, according to Asmus et al. (1998), 45 % of the gross primary production (309 g C m^{-2} a^{-1}) is produced by microphytobenthos. Figure 1 shows a map of the island of Sylt and an overview of the sampling site.

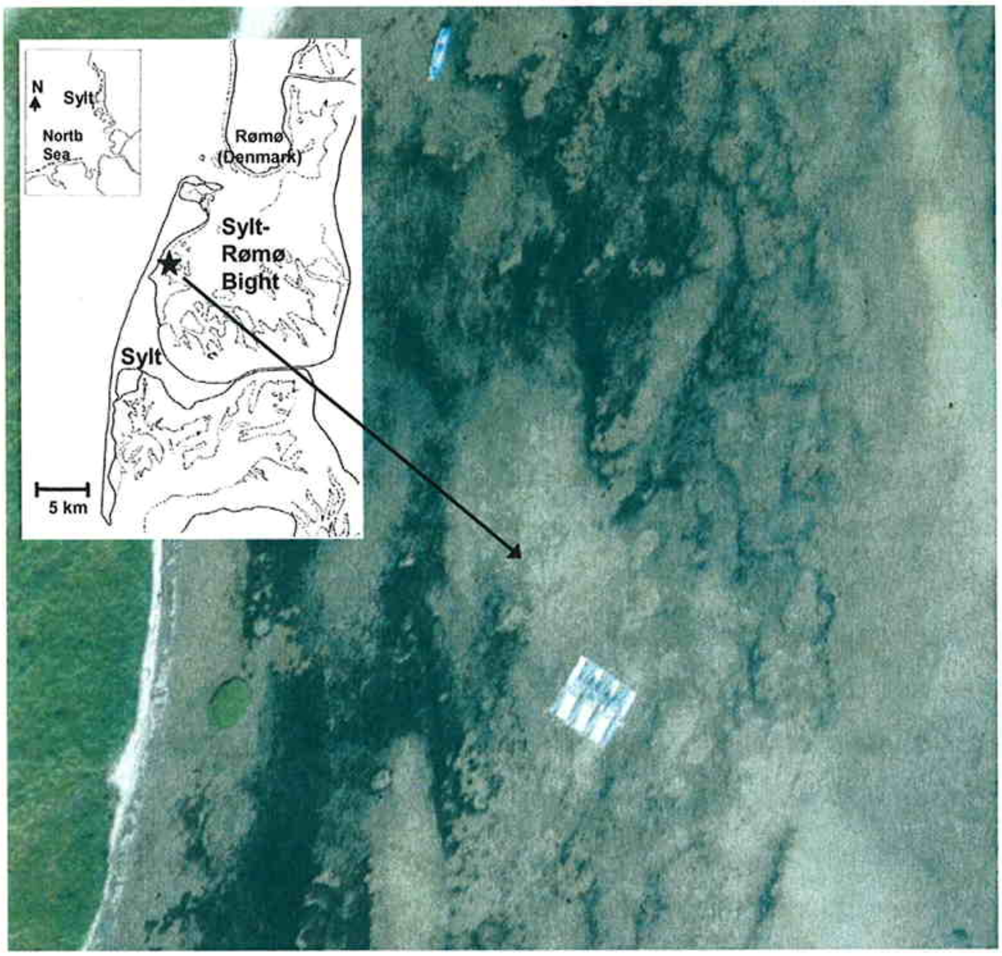

Figure 1. Map of Sylt. Asterisk indicates the sampling site; arrow leading to the site (aerial photo) at the east coast of the island with the three-current-flume device, used to measure the effect of altered current velocities *in situ*.

Diatoms

Diatoms belong to the class of Bacillariophyceae and constitute a major component of the planktonic and microphytobenthic community. The expression microphytobenthos describes microscopic, photosynthetic eukaryotic algae and cyanobacteria that live on seafloor habitats ranging from wave-swept beaches to detritus-laden brackish water lagoons. They inhabit a layer at the sediment-water interface that, depending on grain size, hydrodynamics and light infiltration, might extend from millimetres to a depth of 10 or more centimetres. It is a community that is continually lost due to resuspension and feeding pressure and replenished by sedimentation and growth. The nature of this environment influences both the productivity of the microphytobenthos and the ways in which it is exploited by grazers. The carbon fixed by microphytobenthos supports not only directly grazing macrofauna, meiofauna and microfauna, but also suspension-feeders and deposit-feeders. Thus they play a significant role in trophic interactions and for secondary production (Miller et al., 1996; Sullivan & Moncreiff, 1990). Because of their widespread distribution, their occurrence in the water column and on the sediment bed of intertidal and subtidal zones, diatoms have a key function as primary producers in the open oceans and littoral zones (Colijn & DeJonge 1984, Pinckney & Zingmark 1991, Cahoon 1999).

Although the general ecology of many coastal diatoms is well defined (e.g. Hendey 1964, Denys 1991/92, Zong & Horton 1998), there is still little information about the ecology of various species, particularly their life mode. Due to their size and due to methodological difficulties, the small, benthic species are still largely unquantified and under-represented in research data dealing with sandy intertidal flats. Brockmann (1950) was the first to try to relate species composition to types of sediment and further research indicated that epipelic diatoms can only colonise where the median grain size is sufficiently small (deJonge 1985, Staats et al. 1999) Physiological and ecological studies of benthic diatoms have been mainly restricted to the epipelic fraction. Epipelon and epipsammon are terms that describe organisms living on sediment (unattached) or on sand grains (either attached or unattached), respectively (Round 1981). Epipsammic diatoms living attached to sand grains can be found to use their substratum in different ways. So-called prostrate species like *Cocconeis*, for example, are attached to the flat surfaces with the length of their frustule whereas small *Amphora* or *Navicula* species can be found to inhabit crevices and depressions. Species of the genera *Achnanthes* or *Opephora* live attached to the sand grains by the aid of a strong but flexible stalk of polysaccharides.

Both epipelic and epipsammic forms occur on mixed or sandy sediments, with a decreasing fraction of epipelic forms with intensifying energy (Paterson & Hagerthey 2001). Particle size of sediments is also important for the distribution of diatom taxa. A high diversity of taxa can be found in and on sediments. On tidal flats, a discrimination between sediments with fine grains and high organic content, and sandy substrata where diatom assemblages are dominated by epipsammic species is therefore necessary. Zong and Horton (1998) showed a clear diatom zonation from tidal flat through saltmarsh to upland environments present at all study sites, although environmental conditions varied between the sites. Dominant members of benthic communities are pennate, prostrate forms. But centric forms can also be found associated with the sediment and resuspended into the water column upon inundation, a life mode called tychopelagic (Cahoon 1999). These bentho-pelagic species contribute to the pelagic system in terms of primary production and as a food source for suspension feeders (DeJonge & van Beusekom 1995, DeJong & DeJonge 1995).

The role of diatoms in sediment stability

Diatoms can excrete a considerable part of the photosynthetically fixed carbon as extracellular polymeric substances (EPS) which mainly consist of carbohydrates (Staats 1999). The cells become embedded in a matrix of EPS which is, depending on the coarseness of the sediment, able to bind the sediment, thus forming a biofilm. By forming these biofilms, epipelic diatoms create their own microenvironment that partly protects them from the rapidly changing conditions on intertidal flats but may also provide benefits for the cells by preventing desiccation and by trapping nutrients (Decho 1994). The relative composition and production rates of the low and high molecular weight components of EPS vary over tidal cycles and with light intensity, nutrient availability and the taxonomic composition of the biofilms (Smith & Underwood 1998, 2000; Underwood 1998, DeBrouwer 2005). Formation of a mucilage matrix leads to a decrease of erosion and therefore to sediment stabilisation, which has been subject to many studies (see Paterson 1989; Sutherland et al. 1998; Grant et al. 1985; Amos 1988; Underwood et al. 1993, e.g.). The excretion of EPS is involved in movement of the cell (Edgar & Pickett-Heaps 1984) but also in metabolic overflow production as suggested by Staats (1999). Vertical movement has been reported for a number of organisms forming the microphytobenthic community such as cyanobacteria, euglenoids, chlorophytes and diatoms (Pinckney & Zingmarck 1991, Blanchard et al. 2001). The ability to move towards, and away, from the surface (by means of EPS production) in order to escape environmentally unfavourable conditions is an essential part of survival for organisms in these environments (Smith & Underwood, 2000).

Sedimentation and resuspension

Erosion thresholds and transport rates can be altered by benthic organisms but organism impacts in general decrease with increasing sediment transport rates (Jumars & Nowell 1984). There also occurs a vertical transport or rather cycle, as a result of sedimentation and resuspension, in the overlying water column. Both are functions of physical factors (wave and currents induce erosion) and biotic factors (biologically induced flocculation in the water column may change sedimentation rates, Van Leussen 1986). Wind waves and tidal currents are the primary mechanisms leading to resuspension. Although in various studies the prevailing diatom flora is listed (e.g. Shaffer & Sullivan 1988, DeJonge 1992, DeJong 1995, Lucas 2001) the main focus of the studies to date has been biomass and productivity of cells from sediment and water samples. Early studies by Baillie & Welsh (1980) and Lukatelich & McComb (1986) found that chlorophyll content and number of benthic diatoms in the water column of shallow estuaries were related to tidal currents and wind-induced currents. Gallagher (1975) found that rising tidal waters were responsible for the entrainment of diatoms into the water column.

DeJonge (1994) estimated for the Ems Estuary that on average 13 % of the pennate diatom cells from the sediment are suspended. An increase in current velocity causes a reduction of benthic biomass on the sediment (Safi 2003, Lucas et al. 2001) and leads in turn to a higher optical turbidity within the water column adding to the light-limiting factor for autotrophic organisms.

Fortuitously, of course, organisms in suspension will escape predation by bottom feeders and competition on the bottom (intra or interspecific) for space and light necessary for photosynthesis, however, suspension-feeders may actively filter the cells from the water column. The entrainment into the water column places the cell into a more favourable position for photosynthesis, notwithstanding the danger of being laterally exported or transported into deeper, aphotic layers (see Figure 2).

The continuous, though irregular, supply of cells from the benthos to the water column presents an important food source for grazers in the water column and leads to enhanced grazing by microzooplankton and zooplankton species due to increasing predator-prey encounter rates (Peters et al. 2002). Furthermore, an impact on suspension feeding populations was shown by Muschenheim and Newell (1992), who found that mussels fed preferentially on high concentrations of resuspended benthic diatoms.

Resuspension and sedimentation, and the advective transport of particles such as bacteria, diatoms and detritus across the water-sediment interface, are important factors linking the benthic with the pelagic ecosystem (Rusch et al. 2001, Hüttel & Rusch 2000). The construction of dykes, land reclamation and rising sea level has decreased the overall area of the Wadden Sea, especially the transition zone between land and sea, and increased the tidal current velocity (Lotze et al. 2005). Less mud is deposited near the mainland and a loss of fine-grained sand and particulate organic matter has occurred in the long term (Essink 2005). Since the hydrodynamic regime within the Sylt-Rømø Bight is additionally influenced and changed by the construction of dams, processes of both resuspension and sedimentation may be affected.

An understanding of the balance between sedimentation, growth, resuspension and loss to the system is crucial, as resuspended diatoms present an important food source for herbivorous plankton organisms (deJonge & van den Bergs 1987) or suspension-feeders (Baillie & Welsh 1980) also in winter, when phytoplankton populations are scarce. A severe change, or losses, in community composition will have a cascade effect on the whole ecosystem since diatoms are among the top prey items at the beginning of the food chain.

Experiments with the aim of assessing the effect of shifts in hydrodynamics are of particular relevance to the coastal management of Sylt, as historical incidents demonstrated significant changes since the 1930´s, when the seagrass beds were damaged by the slime mould *Labyrinthula* (Wohlenberg 1935, Den Hartog 1987). Resulting erosion processes had multiple consequences for flora and fauna: The changed sediment morphology led to a loss of spawning grounds and nurseries for various fish species, increase in tidal levels and changes in water masses, for example (Reise 1982, 1998; Riesen & Reise 1982; Reise et al. 1989; Asmus & Asmus 1998, 2000; Jespersen & Rasmussen 1994; Polte 2005) thus changing the entire ecosystem. The construction of causeways between the mainland and islands might have contributed to this development (Asmus & Asmus 2000).

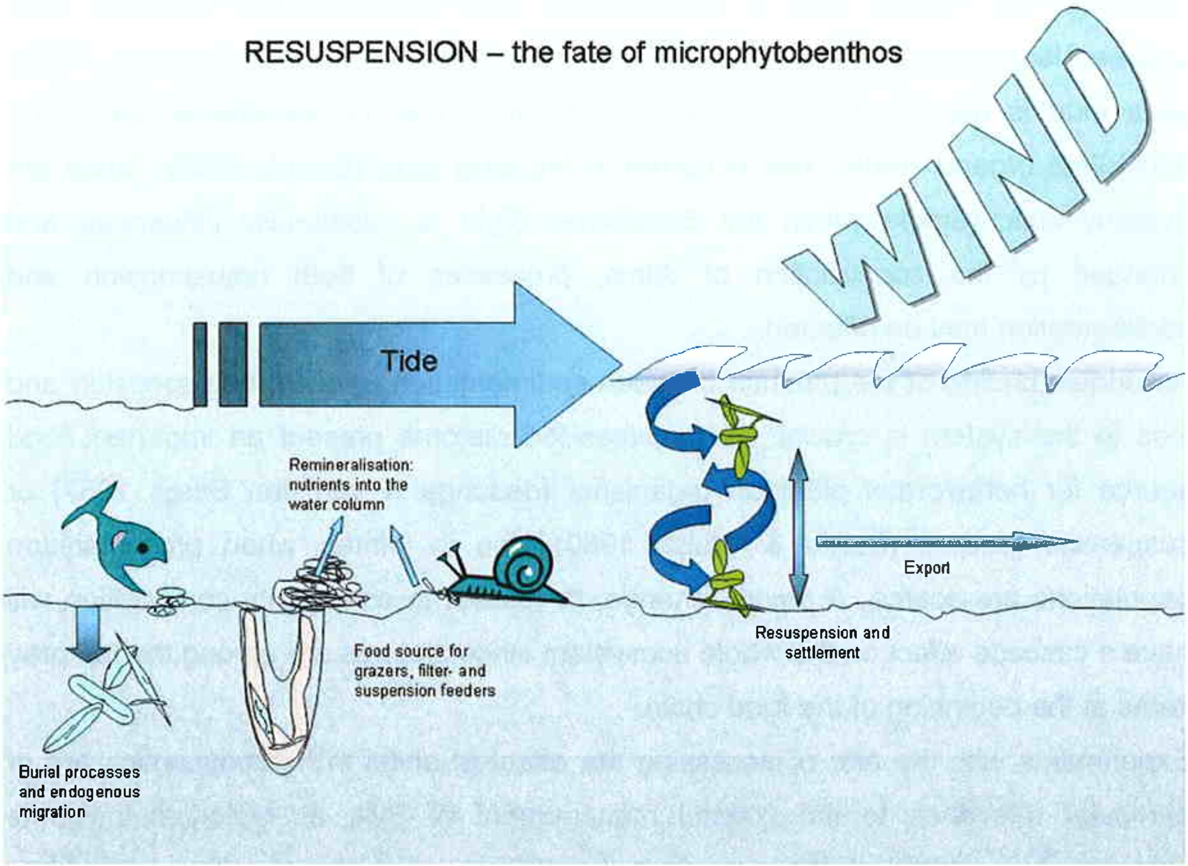

Fig. 2. Schematic diagram showing benthic and pelagic processes, the fate of microphytobenthos, affected by tidal and wind-wave induced hydrodynamic forces. Loss of benthic diatoms due to burial processes, feeding by macro/meiofauna, resuspension and lateral export into the open sea. Contribution to water column primary production by resuspended diatoms and, vice versa, planktonic diatoms enhancing the diversity of the benthic community after sedimentation onto the sediment surface. Export to the open sea or into regions less favourable for the diatom cell in terms of growth or photosynthesis.

Flume experiments – introducing the three-current-flume

Flume systems have become an important tool to support scientists in their research on processes at the water-sediment interface. The publication of the results of a joint experiment between 13 research institutes in Europe using different types of flume devices are in preparation (Jonsson et al. 2005, in prep.). The advantages and drawbacks of the various devices are debatable, but under the premises of well defined requirements every flume can yield useful results. Laboratory set-ups strive to create controlled conditions of laminar flow. In field systems it proves difficult to separate and control the influencing factors, but on the other hand they provide a good overview of field situation and a more realistic picture of processes occurring under natural conditions particularly as regards biological and chemical processes.

Laminar flow patterns as induced in laboratory flume systems do not exist under natural conditions. However, to be sure not to produce hydrodynamic artefacts, the hydrodynamic conditions and resulting requirements for measurements have to be precisely established.

Horizontal flow affects the distribution of organic as well as inorganic material across the intertidal flats. Flumes can be adapted to ecological problems and enable scientists to control the hydrodynamic conditions and thus the processes of the boundary layer (a near-bottom velocity gradient) (Muschenheim et al. 1986).

To date, experiments with different types of *in situ* flumes on Sylt have been carried out to measure various processes. Asmus et al. (1990, 1991, 1992) used a 20 m long double-lane flume *in situ* to quantify benthic-pelagic exchange rates.

The three-current-flume has been deployed for the second time on the intertidal sand flats of Sylt. In 2002, Anja Schanz published her work "Impact of hydrodynamics on development and morphology of intertidal seagrasses in the Wadden Sea", describing the cascading effect flow velocity exerts on the interaction between the mud snail *Hydrobia* and epiphytes on seagrass leaves. Placed onto the tidal flat and adjusted to the bi-directional flow, the durable construction allows in situ sampling over long time periods because it is resistant to harsh weather conditions. Nine lanes can be utilised to give three replicates of three different current regimes. The modified flow across the mid-section is achieved by either widening or narrowing the entrances of the flume, thus creating an increased or reduced flow velocity, respectively. An unaltered flume lane type serves as a reference, mimicking the ambient flow outside the flume. Sampling can be carried out with minimal disturbance to the water or sediment surface by accessing the sampling area from above.

Because of the unique size and construction of the three-current-flume, the present study is the first carried out to thoroughly characterise the hydrodynamic conditions occurring under manipulated flow velocities and their effect on the resuspension behaviour of diatom species. Cell counts of individual species have not previously been attempted in similar studies. Only few studies deal with the resuspension of microphytobenthos at the species level (e.g. (Lucas 2003). However, the present study is not a system study investigating primary productivity or biomass. Rather, it documents the summer community during the year 2003 and indicates the range of variation in abiotic as well as microscopic components that occur as a result of changes in one, important environmental factor, the hydrodynamics.

Thesis outline

The primary objective of this study was the assessment of the influence of hydrodynamic characteristics on the resuspension of benthic and planktonic diatom species, with attention to changes in distribution and abundance of various diatom species in the water column and on the sediment surface. The first step to wards achieving this goal was the description of the benthic and pelagic community under natural hydrodynamic conditions. The three-current-flume was deployed with 3 of the 9 available lanes configured to give unaltered flow for this purpose. The impacts of altered dynamics were then assessed by using the remaining flume lanes to provide increased and reduced flow rates, taking into account tides, wind direction and wind velocity. In all, 180 samples were counted, collected from the sediment water on six sampling days between July and September 2003. Over 230 species were identified.

Chapter 2 introduces the diatom species and genera identified from both sediment and plankton samples. The chapter contains a species list and plates with a selection of diatom photographs taken either with scanning electron microscopy image processing, digital photography of taxa on permanent slides or living algae from plankton samples (colour plate no. 11).

Chapter 3 serves as a framework for chapters 4 & 5 by providing the necessary background information of environmental parameters. For six sampling days (16.07.,30.07.,12.08.,20.08., 26.08. and 17.09. 2003), the following parameters were determined in order to characterise the conditions of the system: chl *a*, suspended particulate matter (SPM), particulate organic carbon and nitrogen (POC and PON), cell counts, tides, wind and current velocity.

Chapter 4 presents a more detailed analysis of the planktonic and benthic diatoms collected from water and sediment samples. Their response to changing hydrodynamic conditions, created by the manipulation of current velocity, was investigated at species level in order to provide information about the ecology of selected species and to assess whether there were clear responses to flow change at species level.

Chapter 5 presents numerically determined characteristics of flow conditions on two selected sampling days, with an analysis of variations in the energy of turbulence and their effects on the resuspension of selected size-class groups of diatoms. The aim here was to discover whether turbulence or flow velocity is the dominating factor influencing the shear stress and thus initialising entailment of diatom cells into the water column.

Study of the benthic and planktonic diatom species of the Wadden Sea coast of Sylt island led to the co-authorship of two publications dealing with the taxonomical description of two new species. *Mediopyxis helysia* is a planktonic species, occurring in samples taken for the purpose of long-term studies of phytoplankton off the coast. The published manuscript is presented in chapter 6. The second, a benthic species was formerly known as *Anaulus simonsenii* but certain morphological details required a revision which finally led to the reclassification into the newly created genus *Paraplagiogramma*. Chapter 7 comprises the manuscript resulting from the co-operation with Professor Lange-Bertalot, Frankfurt, and Professor Witkowski from the University of Stettin, Poland. The discovery and description of two new species following intense studies of the community further illustrates the significance of investigations of the sensitivity of the ecosystem for introduced species.

A final discussion presented in chapter 8 connects the various analytical steps described in this thesis.

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Chapter 2

Diatom species from benthos and plankton off the east coast of Sylt

Abstract

This chapter provides a species list describing the summer diatom (Bacillariaceae) community found on the intertidal sand flat on the east coast of the island of Sylt, near Kampen. The results of the species identification serve as the basis for studies of the impact of hydrodynamics on diatoms at species level presented in later chapters, as well as a reference for future investigations of microphytobenthos. Sediment and water samples were collected on six occasions between July and September 2003. Diatoms were cleaned and prepared for permanent slides as well as for analysis by scanning electron microscopy. 231 species are listed and 11 plates contribute with images of selected species. Cells were identified when possible to species level and classified into epipsammic, epipelic and planktonic species, according to their life mode.

Introduction

Diatoms are unicellular organisms of the class Bacillariophyceae, which often live in colonies. Their size ranges from less than 1 µm to ca. 2 mm, depending on species and stage of growth. The cell is covered with a siliceous wall and an organic layer. By aid of various pigments (e.g. chl *a* and c, beta-carotene, fucoxanthin), and sunlight, the cell converts inorganic carbon into organic complexes by photosynthesis. Most benthic diatoms have bilateral (pennate) symmetry, whereas radial symmetry dominates in planktonic diatoms (Round 1981, Round et al 1990).
Towards the end of the 1970s, about 635 benthic microalgae (comprising diatoms, cyanobacteria and flagellates) were identified from the Wadden Sea (Van den Hoek et al. 1979). Subsequent and numerous descriptions of newly found diatom species indicates a still incomplete picture. Thus, the species list presented in the present chapter does not claim completeness and it should be understood that further studies need to be undertaken on the identification and taxonomy on species in such habitats of high diversity. The plates (1 – 11) picture some of the regularly occurring species encountered in sediment or water samples.

Life mode

Diatom assemblages found on intertidal sediments comprise epipsammic and epipelic species. The expression epipsammon refers to the association of diatoms living attached to sand grains (as described by Round in 1965), whereas the term epipelon includes the life form of diatoms living on or in the sediment. Although for many species the actual life form is still unknown, some species are presumed to live associated with sediments but may well be able to continue their photosynthetic activities while resuspended in the water column during inundation of the tidal flat, thereby using the water column as an alternative habitat. Both centric and pennate diatoms are included in this group, for example *Cylindrotheca closterium*, *Odontella aurita*, *Melosira nummoloides* (Admiraal 1984). Thus, the same algal classes can be found in both the phytoplankton and the microphytobenthos, a life mode referred to as tychopelagic (Bold & Wynne 1985). The benthic species will contribute to the planktonic community due to resuspension especially in shallow water areas. The basis of separation into epipsammic, epipelic, etc. is mainly according to the preferred habitat characteristics and morphology (Drebes 1974, DeJong & DeJonge 1995, DeJonge & van Beusekom 1995). Tidal currents, wind-wave induced turbulences and feeding activities of meio- and macrofauna causes a constant loss of cells from the benthic community that is balanced by growth and sedimentation. Planktonic cells are subjected to sedimentation under still conditions as benthic cells will contribute to the planktonic community by entailment into the water column under rough conditions. Thus, net loss and export or growth and increase under favourable conditions (sufficient nutrient supply, low hydrodynamic impact in terms of turbulences, e.g.) are regulating factors of the community (deJonge 1985, Booth 2000, Bergamasco et al 2003).

On tidal flats, particle size of sediments is also important for the distribution of diatom taxa. A discrimination between sediments with fine grains and high organic content, and sandy substrata where diatom assemblages are dominated by epipsammic species is therefore useful. Zong and Horton (1998) showed a clear diatom zonation from tidal flat through saltmarsh to upland environments present at their study sites, although environmental conditions varied between the sites.

It is apparent from the literature that the same dominant taxa can be found at several locations in Europe. This generalisation holds for England (Hendey 1964) as well as for areas of the Wadden Sea (Sabbe & Vyvermann 1991, Sundbäck 1983,e.g.) and the German coastal regions of the North Sea (Hustedt 1939; Agatz et al. 1999, e.g.). This includes species of the genera *Achnanthes*, *Fragilaria*, *Navicula*, *Opephora*, *Amphora*, *Cocconeis*, *Cymatosira*, *Campylosira* and *Raphoneis*. According to Underwood (1994) seasonality and diversity of diatom assemblages appears to be related to the gradients of environmental stress (Admiraal et al. 1984) and next to this seasonal variability also inter-annual variability is known to occur (DeJonge & Colijn 1994).

Epipsammic diatoms living attached to sand grains can be found to use their substratum in different ways. *Cocconeis* species for example are attached to the flat surfaces with the length of their frustule whereas small *Amphora* or *Navicula* species can be found to inhabit crevices and depressions. *Achnanthes* species live attached to the sand grains by the aid of a stalk of polysaccharides. A sand grain presents not only a habitat for diatoms but also for other microorganisms such as cyanobacteria and other bacteria. For example McIntyre & Moore (1977) reported a study carried out at Etterick Bay (UK) in which up to 2600 diatom cells per mm^2 of sand grain surface were counted on grains from the lower littoral zone. Further modes of attachment can be, for example, to plants (macroalgae, seagrass), a life mode called epiphytic, or epilithic on rocks.

Motility in diatoms

Although movement has been detected in centric diatoms, eg. *Actinocyclus* (Andersen et al., 1986) and *Odontella* (Pickett-Heaps et al. 1986), significant motility is found only among the pennate diatoms bearing a double slit in the valve, termed the raphe. Gliding movements are carried out by the aid of polysaccharide threads passed through this raphe. Adhesion to surfaces such as rocks, plants, sand grains, or other diatoms occurs by the secretion of extra-cellular polymeric substances (EPS) (Harper & Harper 1967; Hoagland et al. 1993). Adhesion prevents motile diatoms from being washed away or, for those species living on the surface of sand or mud, from being subjected to disturbances of the sediment by tides or wind and currents. And although burial due to reworking of the sediment (e.g. by bioturbating macrofauna or wave induced sediment displacement) might create an unfavourable situation, diatoms are able to survive even under light or nutrient limited situations, under anoxic conditions and several species are known to change from autotrophic to heterotrophic (Okamoto 2003, Tolomio 2004)

Highly motile diatom species e.g. *Tropidoneis lepidoptera*, *Hantzschia virgata* and several *Navicula* spp., are found to flourish on unstable wave-exposed sand-flats (Admiraal 1984). Generally, in estuaries, diatoms have to overcome irregular and often violent changes in their environment as there are fluctuations in temperature, salinity and light. Due to hydrodynamic processes during tidal inundation and exposure, the cells may be covered by sediment or disturbed into suspension. In order to safeguard the population against such changes most of the diatoms in this community have the ability to migrate towards or away from the sediment surface. For sandy sediments this doesn't necessarily mean burial beneath light-limiting layers as the size and the shape of sand grains allows light to penetrate deeper into the sediment. Motility is an important factor in restricting the effect of e.g. limiting nutrients and enables the cell to place itself in a more favourable situation for photosynthesis (Palmer & Round 1967; Hopkins 1965, 1966).

The production of EPS (extracellular polymeric substances) and the role of diatoms in sediment stability

Intertidal flats represent a complex ecosystem for many micro organisms such as diatoms, cyanobacteria and other bacteria. The chemical and physical factors controlling this environment require that organisms adapt to survive extreme conditions such as rapid change of salinity range, light, temperature, immersion and emersion. Mud or sandflats are also subjected to wave dynamics, which act to resuspend and transport sediments. Benthic diatoms are among the main primary producers in intertidal zones. At high concentrations, they are visible as brown patches on the sediment surface. Some species show migration behaviour, responding to the light and returning below the sediment surface as the incoming tide encroaches. They migrate deeper into the sediment at the beginning of the dark period. The secretion of extracellular polymeric substances (EPS) acts to stabilise the sediment and allows the cells a degree of motility in the sediment. Thus a matrix is formed, embedding the diatoms (Hoagland et al. 1993). LTSEM (Low Temperature Scanning Electron Microscopy) techniques have shown that established biofilms consist of a continuous fabric of mineral particles embedded in EPS (Underwood and Paterson 1993; Paterson 1995). Extracellular polymeric substances consist of long-chained molecules. EPS are produced and secreted as an integral process in the microbial metabolism. The thereby form tough networks known as microbial mats. They represent an important source of a variety of organic and inorganic compounds (Sutherland et al. 1998). Different organisms produce different mucilage structures, and the adhesive capacity changes even within diatom families due to differences in the chemical structure (solubility) of the produced EPS. Euglenoid flagellates for example do not produce the same copious amount of mucilage as a diatom population and they are more easily washed from the surface of the sediment (Paterson et al. 1989). Biofilms (or microbial mats) are formed by several organisms and can be found in many different habitats including hypersaline coastal lagoons, alkaline lakes and hot springs as well as intertidal mudflats. Depending on the properties of the sediment (grain size, mud content) microbial mats can be dominated either by diatoms or by cyanobacteria: sulphur bacteria which can be colourless and purple and the sulphate-reducing bacteria. The relative composition and production rates of the low and high molecular weight components of EPS vary over tidal cycles and with light intensity, nutrient availability and the taxonomic composition of the biofilm (Smith & Underwood 1998, 2000; Underwood 1994; Staats 1999).

Microbial exopolymers range from tight capsules that closely surround cells to the loose slime matrix associated with aggregates, sediment detritus and other surfaces. 20 to 25% of colloidal carbohydrate present in diatom-rich biofilms is polymeric (EPS) which up to 80% of extracellular carbohydrate consists of nonpolymeric material, mainly simple sugars, leachates, and other photo-assimilates. EPS can be utilized by bacteria, meiofauna and macrofauna as a carbon source (Decho 1990). They are highly adsorptive, readily trap dissolved organic matter and trace metals and therefore play an important role as a transport medium for metals, nutrients and DOM through the lower trophic levels. Secretion of polysaccharides may influence nutrient conditions: an increase in the mud content of the surface results in an increase in the concentration of inorganic nutrients because of EPS remineralisation by bacterial activity (Ruddy et al. 1998). Certain capsular exopolysaccharides may protect microbial cells from digestion (Decho 1990). In his work on microbial exopolymer secretion the author found out that relatively small amounts of EPS can bind relatively large amounts of metals and DOM and can thereby induce aggregation processes.

The ability to move towards and away from the surface (via EPS production) under the environmental conditions mentioned above (burial, deposition events) is essential for cells to survive in intertidal habitats (Smith & Underwood 2000). Formation of a mucilage matrix leads to a decrease in erosion and therefore to sediment stabilisation, which has been the subject of many studies (see Paterson 1989; Sutherland et al. 1998; Grant et al. 1986; Amos 1988; Underwood et al. 1993, for example). Erosion thresholds and transport rates can be altered by benthic organisms but organism impacts in general decrease with increasing sediment transport rates (Jumars and Nowell 1984). There also occurs a vertical transport or rather cycle, as a result of sedimentation and resuspension, in the overlying water column. Both are functions of physical factors (wave and currents inducing erosion) and biotic factors (biologically induced flocculation in the water column may change sedimentation rates) (Van Leussen 1986). Much of the EPS produced by diatoms is left on the surface of sediments when the diatoms migrate down into the sediment before tidal immersion (Underwood & Smith 1998). Exopolymers serve as an effective buffering microenvironment for microbial cells (Decho 1994), one possible function of which is the protection of cells against desiccation when exposed to sunlight on the mudflat. They also present a barrier against other rapid chemical and physical changes and probably serve as a protection against grazing (Staats 1999).

Material and Method

Sampling

For the identification and cell counts of benthic and planktonic diatoms samples were collected on six sampling days between July and September 2003. The sampling site was situated on the east coast of Sylt, within a nature protection area, ca. 1.5 km north of Kampen. The sediments comprised of sand with a grain size median of 0.3 – 0.4 mm. The Sediment samples were taken with a cut-off syringe (1.6 cm diameter), whereby the cylinder was plunged into the sediment, carefully removed after closure of the open end and before expulsion of the first centimetre which was carefully cut off, transferred to a plastic bag and stored at minus 20 °C. All samples were freeze-dried prior to further analysis. Water samples were collected automatically using ISCO STIP automatic sampler, stored in 50 ml brown bottles and preserved with 4 drops of Lugol´s solution.

Preparation

To release the epipsammic diatom fraction from the sandgrains, the samples were transferred to a beaker together with 50 ml of filtered sea water and treated in an ultrasonic bath for two minutes. This time proved sufficient to ensure that cells were detached from the substratum (as tested by repeating the extraction procedure and examining the sample under the microscope). The beaker was gently shaken to bring cells into suspension and then held at an angle for about 20 – 30 seconds to allow the coarse grains and detritus to settle. For cell counts the supernatant was finally transferred to 10 ml settling chambers and allowed to stand for at least 18 hours. The preserved water samples were transferred to 20 or 25 ml settling chambers.

Identification to species level is only possible on cleaned material that shows the fine details of the valves distinguishing different species. For the preparation of permanent slides, samples were acid-cleaned (after Simonsen 1974) to remove the organic contents (e.g. polysaccharides, bacteria and other organisms, cell contents) as well as mucus coatings covering the cell that obscure the fine details of the valve. Both the ultrasonicated sediment slurry and planktonic samples were washed by centrifugation (200 rpm, 5 minutes) to wash out the salt. The supernatant was poured off and the tube refilled with distilled water. This process was repeated three times. $KMnO_4$ (Potassium permanganate) was then added and left over night to oxidise and remove organic matter. The following day HCl (Hydrochloric acid, 37%) was added and the suspension boiled in a water-bath until clear. Chemicals were then washed out with distilled water according to the above described method by six repeated centrifugations. Aliquots were taken for permanent slides on ethanol-cleaned coverslips (18 mm diameter) and also for the preparation of stubs for SEM (Scanning Electron Microscope) (8 mm diameter). After drying, the samples were mounted with Naphrax mounting medium (refractive index 1.73). The coverslips were mounted on stubs and sputtered with a gold-palladium layer for SEM examination.

Identification

Taxa were identified using a Zeiss Axioplan microscope for digital light microscopy and a FEI QUANTA FEG 200 electron scanning microscope. Identification of diatom species was carried out to species level where possible, otherwise to genus level.
The identification of species was based on Cleve (1894), Hendey (1964), Hustedt (1930, 1957, 1959), Krammer & Lange-Bertalot (1986-91), Kützing (1849, 1865), Round et al. (1990), Schmidt (1969), Snoeijs (1993), Snoeijs & Vilbaste (1994), Snoeijs & Potapova (1995), Snoeijs & Kasperoviciene (1996), Snoeijs & Balashova (1998), Van Heurck (1880/81), Witkowski (1994), Witkowski et al. (2000).

To date, it is still common to prepare permanent slides for the identification of cells under the light microscope and for the comparison with established literature which depended on exact drawings of the valve and its structure. SEM technique is used for the identification of very small species and also for the discrimination between easily misidentified species belonging to the same genera which is often determined by details concerning the valve structure. Microscopy techniques allowing to study for example planktonic cells in water samples (or cultures) provide valuable information on the inner, visible structures of the cell such as sometimes species-characteristic situation of the chloroplasts. As in the case of *Catenula adhaerens* and *Delphineis surirella* (Plate 11, figures 1 and 5), the epipsammic life mode by attachment to a sediment grain can be studied *in situ*. Plates 1 – 11, following the species list, show a selection of the common species found on the intertidal flat and in water samples, presenting the three different microscopy techniques. Additionally, the list provides information on the life mode of the species (where known), epipsammic, epipelic, epiphytic epilithic and pelagic. The pictures in plates 1 – 8 were taken using a scanning electron microscope, Plate 9 and 10 show pictures taken using light microscopy and Plate 11 using a water immersion objective for the photographs of living species in a water sample.

Table1. Results of qualitatively analysed samples collected from the sediment and water on six sampling days between July and September 2003. Column at the right indicates the life form: eps. = epipsammic, epp. = epipelic, eph. = epiphytic, epl. = epilithic, pel. = pelagic.

	Species List	**Life-form**
1	*Achnanthes bremeyeri* Lange-Bertalot 1989	eps.
2	*Achnanthes brevipes* Agardh 1824	epp.+epl.
3	*Achnanthes clevei* Grunow in Van Heurck 1880	eps.
4	*Achnanthes lemmermannii* Hustedt 1933	eps.
5	*Achnanthes levanderi* Hustedt 1933	
6	*Achnanthes petersenii* Hustedt 1937	
7	*Achnanthes submarina* Hustedt 1956	eps.+eph.
8	*Actinoptychus senarius* Ehrenberg 1841	eps.+epp.
9	*Amicula specululum* (Witkowski) Witkowski 2000	
10	*Amphora acutiuscula* Kützing 1844	epp.
11	*Amphora arenaria* Donkin 1858	
12	*Amphora beaufortiana* Hustedt 1955	epp.
13	*Amphora cf tenerrima* Aleem & Hustedt 1951	epp.+eph.
14	*Amphora cf wisei* (Salah) Simonsen 1962	epp.
15	*Amphora coffaeformis* (Agardh) Kützing 1844	epp.+eph.
16	*Amphora helenensis* Giffen 1973	epp.
17	*Amphora holsatica* Hustedt 1930	epp.
18	*Amphora hyalina* Kützing 1844	epp.
19	*Amphora inariensis* Krammer 1980	
20	*Amphora marina* W.Smith 1857	
21	*Amphora ostrearia* Brébisson ex Kützing 1849	epp.
22	*Amphora ovalis* (Kützing) Kützing 1844	epp.+epl.
23	*Amphora pediculus* (Kuetzing) Grunow 1875	epp.+epl.
24	*Anaulus balticus* Simonsen 1959	eps.+epp.
25	*Anorthoneis excentrica* (Donkin) Grunow 1868	eps.
26	*Anorthoneis vortex* Sterrenburg 1988	eps.
27	*Astartiella sp.* Witkowski, Lange-Bertalot & Metzeltin 2000	
28	*Asterionellopsis glacialis* (Castracane) Round 1990	
29	*Attheya decora* West 1860	eps.
30	*Aulacodiscus argus* (Ehrenberg) A.Schmidt 1886	
31	*Auliscus sculptus* (W.Smith) Brightwell 1860	eps.
32	*Austariella jamalinensis* (Cleve) Witkowski, Lange-Bertalot & Metzeltin 2000	
33	*Bacteriastrum hyalinum* Lauder 1864	
34	*Bellerochea malleus* (Brigtwell) Van Heurck 1885	
35	*Berkeleya fennica* Juhlin-Dannfelt 1882	epl.+eph.

	Species List	**Life-form**
36	*Berkeleya sp.*Greville 1827	
37	*Biremis ambigua* (Cleve) Mann 1990	epp.
38	*Biremis lucens* (Hustedt) K. Sabbe, Witkowski, & W. Vyverman 1995	eps.
39	*Biremis ridicula* (Giffen) Mann 1990	
40	*Biremis sp.*Mann & Cox 1990	
41	*Brachysira estoniarum* Witkowski, Lange-Bertalot & Metzeltin 2000	
42	*Brockmanniella brockmannii* (Hustedt) Hasle, von Stosch & Syvertsen 1983	epp.
43	*Caloneis crassa* (Gregory) Ross 1986	epp.
44	*Caloneis sp.*Cleve 1891	
45	*Campylosira cymbelliformis* (Schmidt) Grunow 1881	eps.+epp.
46	*Catenula adhaerens* (Mereschkowsky) Mereschkowsky 1902	eps.
47	*Cerataulina pelagica* (Cleve) Hendey 1937	pel.
48	*Cerataulus smithii* Ralfs 1861	
49	*Cerataulus turgidus* (Ehrenberg) Ehrenberg 1843	
50	*Chaetoceros debilis* Cleve 1894	pel.
51	*Chaetoceros spp.*Ehrenberg 1844	pel.
52	*Chamaepinnularia clamans* (Hustedt) Witkowski, Lange-Bertalot & Metzeltin 2000	
53	*Cocconeis clandestina* A.Schmidt 1894	
54	*Cocconeis costata* Janisch 1863	eph.
55	*Cocconeis peltoides* Hustedt 1939	eps.
56	*Cocconeis placentula* Ehrenberg 1838	eph.+epl.
57	*Cocconeis scutellum* Ehrenberg 1833	eph.
58	*Cocconeis speciosa* Gregory 1855	eph.
59	*Cosmioneis eta* (Cleve) Witkowski, Lange-Bertalot & Metzeltin 2000	
60	*Cyclostephanos sp.*Round 1988	
61	*Cyclotella sp.*Kützing 1833	pel.
62	*Cylindrotheca closterium* (Ehrenberg) Reimann & Lewin 1964	epp.+pel.
63	*Cymatosira belgica* Grunow 1881	eps.
64	*Dactyliosolen sp.*Castracane 1886	
65	*Delphineis surirella* (Ehrenberg) Andrews 1981	eps.
66	*Denticula sp.*Kützing 1844	
67	*Dickieia subinflata* (Grunow) Mann 1994	
68	*Dickieia ulvacea* Berkeley ex Kützing 1844	
69	*Dimeregramma minor* (Gregory) Ralfs 1861	eps.+epp.
70	*Diploneis bombus* (Ehrenberg) Ehrenberg 1854	
71	*Diploneis cf notabilis* (Greville) Cleve 1894	
72	*Diploneis coffaeiformis* (A.Schmidt) Cleve 1894	epp.
73	*Diploneis didyma* (Ehrenberg) Ehrenberg 1845	epp.

	Species List	**Life-form**
74	*Diploneis fusca* (Gregory) Cleve 1894	epp.
75	*Diploneis interrupta* (Kützing) Cleve 1894	epp.
76	*Diploneis litoralis* (Donkin) Cleve 1894	epp.
77	*Diploneis smithii* (Brébisson) Cleve 1894	epp.
78	*Ditylum brightwellii* (West) Grunow 1885	pel.
79	*Donkinia sp.*Ralfs 1861	
80	*Donkinia reticulata* Norman 1861	epp.
81	*Ehrenbergia granulosa* (Grunow) Witkowski, Lange-Bertalot, & Metzeltin 2000	
82	*Entomoneis ornata* (Bailey) Reimer 1975	
83	*Entomoneis paludosa* (W.Smith) Reimer 1975	epp.
84	*Entomoneis punctulata* (Grunow) Osada & Kobayasi 1990	epp.
85	*Eucampia zodiacus* Ehrenberg 1839	pel.
86	*Eunotogramma dubium* Hustedt 1939	
87	*Eunotogramma marinum* (W.Smith) Peragallo 1897-1908	eps.
88	*Eunotogramma sp.*Weisse 1854	
89	*Extubocellulus cribriger* Hasle, von Stosch & Syvertsen 1983	
90	*Extubocellulus sp.*Hasle, von Stosch & Syvertsen 1983	
91	*Fallacia clepsidroides* Witkowski 1994	epp.
92	*Fallacia cryptolyra* (Brockmann) Mann 1990	epp.
93	*Fallacia escorialis* (Simonsen) Sabbe & Vyverman 1999	
94	*Fallacia florinae* (Möller) Witkowski 1993	epp.
95	*Fallacia forcipata* (Greville) Stickle & Mann 1990	epp.
96	*Fallacia margino-punctata* Sabbe & Vyverman 1999	eps.
97	*Fallacia pseudony* (Hustedt) Mann 1990	epp.
98	*Fallacia pygmaea* (Kützing) Stickle & Mann 1990	epp.
99	*Fallacia sp.* Stickle & Mann 1990	
100	*Fallacia tenera* (Hustedt) Stickle & Mann 1990	epp.
101	*Fallacia versicolor* (Grunow) Mann 1990	
102	*Fragilaria amicorum* Witkowski & Lange-Bertalot 1993	eps.
103	*Fragilaria eichhornii* Witkowski & Lange-Bertalot 1995	
104	*Fragilaria schulzii* Brockmann 1950	
105	*Fragilaria subsalina* (Grunow) Lange-Bertalot 1991	
106	*Grammatophora marina* (Lyngbye) Kützing 1844	eph.
107	*Guinardia flaccida* (Castracane) Peragallo 1892	pel.
108	*Gyrosigma arcuatum* (Donkin) Sterrenburg 2005	
109	*Gyrosigma balticum* (Ehrenberg) Rabenhorst 1853	epp.
110	*Gyrosigma eximium* (Thwaites) Boyer 1927	epp.
111	*Gyrosigma fasciola* (Ehrenberg) Griffith & Henfrey 1856	pel.+epp.

	Species List	**Life-form**
112	*Gyrosigma prolongatum* (W. Smith) Griffith & Henfrey 1856	
113	*Hantzschia sp.*Grunow 1877	
114	*Haslea ostrearia* (Gaillon) Simonsen 1974	epp.
115	*Helicotheca tamesis* (Shrubsole) Ricard 1987	
116	*Hippodonta sp.*Lange-Bertalot, Metzeltin & Witkowski 1996	
117	*Leptocylindrus danicus* Cleve 1889	pel.
118	*Leptocylindrus minimus* Gran 1915	pel.
119	*Licmophora sp.*Agardh 1827	
120	*Lunella bisecta* Snoeijs 1996	epl.
121	*Lyrella abrupta* (Gregory) Mann 1990	epp.
122	*Lyrella amphoroides* Mann 1997	
123	*Lyrella cf barbara* (Heiden) Mann 1990	epp.
124	*Lyrella lyra* (Ehrenberg) Karayeva 1978	epp.
125	*Mediopyxis helysia* Kühn, Hargraves & Halliger 2006	
126	*Meridion sp.*Agardh 1824	
127	*Metaplagiogramma tenuissimum* (Hustedt) Witkowski & Lange-Bertalot 2006	
128	*Minidiscus trioculatus* (Taylor) Hasle 1973	
129	*Minutocellus polymorphus* (Hargraves & Guillard) Hasle, von Stosch & Syvertsen 1983	
130	*Navicula bipustulata* Mann 1925	epp.
131	*Navicula cruciculoides* Brockmann 1950	epp.
132	*Navicula directa* (W.Smith) Ralfs 1861	epp.
133	*Navicula duerrenbergiana* Hustedt 1934	epl.
134	*Navicula germanopolonica* Witkowski & Lange-Bertalot 1993	eps.
135	*Navicula gregaria* Donkin 1861	epp.+epl.
136	*Navicula lubetii* König 1959	
137	*Navicula meniscus* Schumann 1867	epp.
138	*Navicula microdigitoradiata* Lange-Bertalot 1993	epp.
139	*Navicula palpebralis* Brébisson ex W.Smith 1853	epp.
140	*Navicula paul-schultzii* Witkowski & Lange-Bertalot 1994	epp.
141	*Navicula peregrina* (Ehrenberg) Kützing 1844	
142	*Navicula perminuta* Grunow 1880	eps.
143	*Navicula phyllepta* Kützing 1844	epp.
144	*Navicula platyventris* Meister 1939	
145	*Navicula ramosissima* (Agardh) Cleve 1895	epl.
146	*Navicula salinarum* Grunow 1880	epp.
147	*Navicula veneta* Kützing 1844	
148	*Navicula viminoides* Giffen 1975	eps.
149	*Nitzschia constricta* (Kützing) Ralfs 1861	epp.

	Species List	**Life-form**
150	*Nitzschia delicatissima* Cleve 1897	
151	*Nitzschia distans* Gregory 1857	epp.
152	*Nitzschia dubiiformis* Hustedt 1939	epp.+epl.
153	*Nitzschia frustulum* (Kützing) Grunow 1880	epp.
154	*Nitzschia hybrida* Grunow 1880	
155	*Nitzschia hybridaeformis* Hustedt 1955	
156	*Nitzschia inconspicua* Grunow 1862	epl.
157	*Nitzschia laevis* Hustedt 1939	
158	*Nitzschia longissima* (Brébisson) Grunow 1862	
159	*Nitzschia microcephala* Grunow 1880	epp.+epl.
160	*Nitzschia pararostrata* (Lange-Bertalot) Lange-Bertalot 2000	
161	*Nitzschia parvula* W.Smith 1853	
162	*Nitzschia punctata* (W.Smith) Grunow 1878	
163	*Nitzschia reversa* W.Smith 1853	pel.+epp.
164	*Nitzschia seriata* Cleve 1883	
165	*Nitzschia sigmoidea* (Nitzsch) W.Smith 1853	epp.
166	*Nitzschia valdestriata* Aleem & Hustedt 1951	epp.+epl.
167	*Odontella aurita* (Lyngbye) Agardh 1832	eph.
168	*Odontella regia* (Schultze) Simonsen 1974	
169	*Odontella rhombus* (Ehrenberg) Kützing 1849	
170	*Odontella sinensis* (Greville) Grunow 1884	pel.
171	*Opephora guenter-grassii* (Witkowski & Lange-Bertalot) Sabbe & Wyverman	
172	*Opephora krumbeinii* Witkowski, Witak & Stachura 1998	eps.
173	*Opephora marina* (Gregory) Petit 1888	eps.
174	*Paralia sulcata* (Ehrenberg) Cleve 1873	epp.
175	*Paraplagiogramma* simonsenii (Witkowski & Metzeltin) Klein 2006	
176	*Parlibellus hamulifer* (Grunow) Cox 1988	
177	*Parlibellus plicatus* (Donkin) Cox 1988	epp.
178	*Pauliella taeniata* (Grunow) Round & Basson 1997	pel.
179	*Petrodictyon gemma* (Ehrenberg) Mann 1990	epp.
180	*Petroneis granulata* (Bailey) Mann 1990	epp.
181	*Petroneis humerosa* (Brébisson) Stickle & Mann 1990	epp.
182	*Petroneis latissima* (Gregory) Stickle & Mann 1990	epp.
183	*Petroneis marina* Mann 1990	epp.
184	*Petroneis monilifera* (Cleve) Stickle & Mann 1990	epp.
185	*Pinnularia cruciformis* (Donkin) Cleve 1895	epp.
186	*Pinnularia trevelyana* (Donkin) Rabenhorst 1864	
187	*Plagiogramma staurophorum* (Gregory) Heiberg 1863	eps.

	Species List	**Life-form**
188	*Plagiogrammopsis vanheurckii* (Grunow) Hasle, von Stosch & Syvertsen 1983	
189	*Plagiotropis lepidoptera* (Gregory) Kuntze 1898	epp.
190	*Plagiotropis tayrecta* Paddock 1988	epp.
191	*Planothidium delicatulum* (Kützing) Round & Bukhtiyarova 1996	epp.+eps
192	*Planothidium hauckianum* (Grunow) Round & Bukhtiyarova 1996	
193	*Pleurosigma angulatum* (Quekett) W.Smith 1852	epp.
194	*Pleurosigma balticum* (Ehrenberg) W.Smith 1852	
195	*Pleurosigma obliquum* Grunow 1880	
196	*Pleurosigma strigosum* W.Smith 1852	
197	*Pleurosira laevis f. polymorpha* Compère 1982	eph.+epl.
198	*Protokeelia cholnokyana* (Giffen) Round & Basson 1995	
199	*Psammodiscus nitidus* (Gregory) Round & Mann 1980	eps.
200	*Pseudonitzschia sp.*Peragallo & Peragallo (1897-1908)1900	
201	*Pseudostaurosira perminuta* (Grunow) Sabbe & Vyverman 1995	
202	*Rhaphoneis amphiceros* (Ehrenberg) Ehrenberg 1844	eps.
203	*Rhizosolenia styliformis* Brightwell 1858	
204	*Rhopalodia brebissonii* Krammer 1987	epp.+epl.
205	*Rhopalodia sp.*Müller 1895	
206	*Roperia tesselata* (Roper) Grunow 1883	
207	*Scoliopleura sp.*Grunow 1860	
208	*Scoliotropis latestriata* (Brébisson) Cleve 1894	epp.
209	*Skeletonema costatum* (Greville) Cleve 1873	pel.
210	*Stauroneis plicata* Brockmann 1950	epp.
211	*Staurophora salina* (W.Smith) Mereschkowsky 1903	
212	*Subsilicea fragilarioides* von Stosch & Reimann 1970	
213	*Synedra tabulata* (Ag.) Kützing 1844	
214	*Tabularia cf fasciculata* (Agardh) Williams & Round 1986	eph.
215	*Thalassionema nitzschioides* (Grunow) Mereschkowsky 1902	pel.
216	*Thalassiosira cf partheneia* Schrader 1972	
217	*Thalassiosira cf profunda* (Hendey) Hasle 1973	
218	*Thalassiosira cf proschkinae* Makarova 1979	pel.
219	*Thalassiosira constricta* Gaarder 1938	
220	*Thalassiosira nordenskioeldii* Cleve 1873	
221	*Thalassiosira partheneia* Schrader 1972	
222	*Thalassiosira spp.*Cleve 1873	
223	*Toxonidea insignis* Donkin1858	
224	*Trachyneis aspera* (Ehrenberg) Cleve 1894	epp.
225	*Triceratium alternans* Bailey 1851	

	Species List	**Life-form**
226	*Triceratium reticulum* Ehrenberg 1844	
227	*Tryblionella circumsuta* (Bailey) Ralfs 1861	epp.
228	*Tryblionella coarctata* (Grunow) Mann 1990	epp.
229	*Tryblionella plana* (W.Smith) Pelletan 1889	epp.
230	*Tryblionella punctata* W.Smith 1853	epp.
231	*Tryblionella salinarum* (Grunow) Pantocsek 1901	epp.

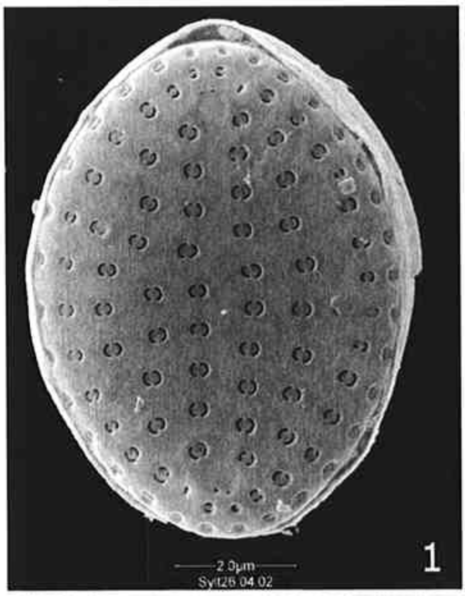
Life-form: eps.=epipsammic, epp.=epipelic, eph.=epiphytic, epl.=epilithic, pel.=pelagic

Plates

Plate 1

1 Delphineis surirella (Ehrenberg) Andrews
2 Amphora helenensis Giffen
3 Diploneis interrupta (Kützing) Cleve 1894
4 Cocconeis speciosa Gregory
5 Entomoneis punctulata (Grunow) Osada & Kobayasi
6 Subsilicea fragilarioides von Stosch & Reimann

Plate 1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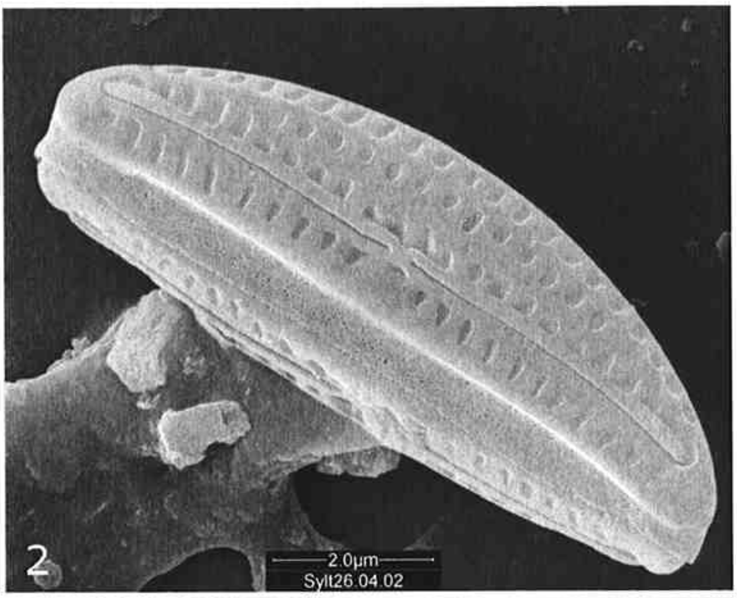
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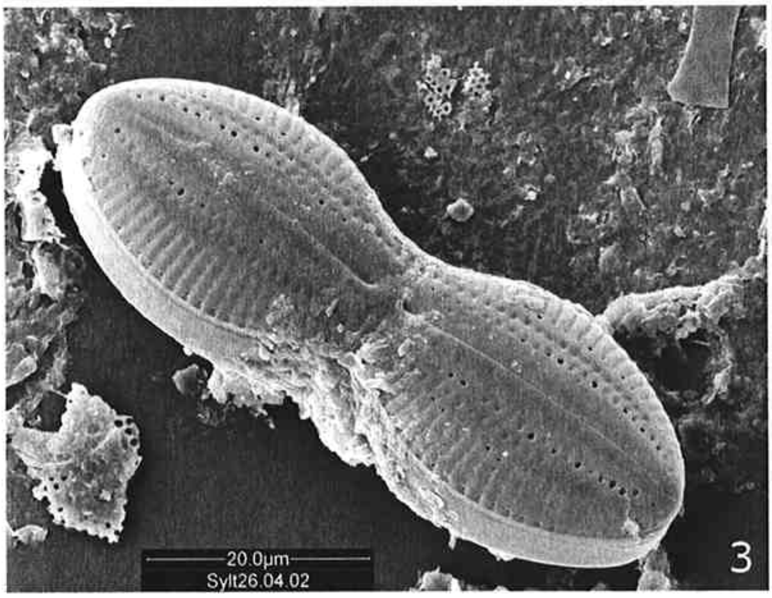
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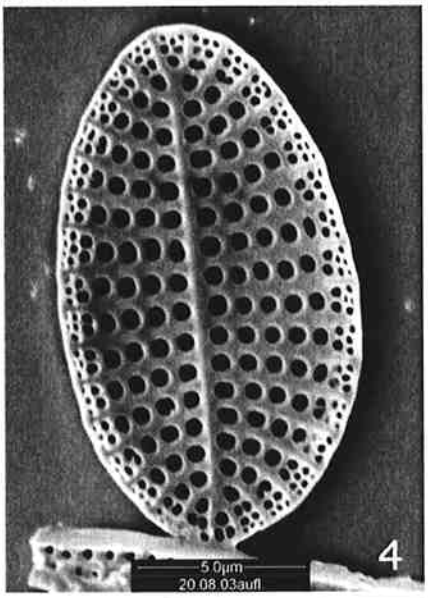
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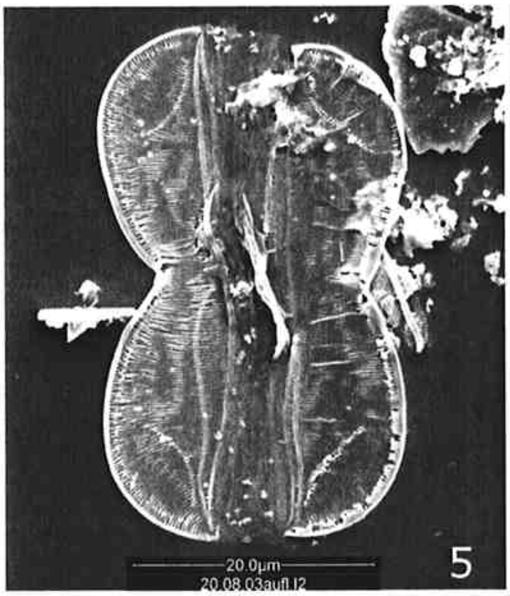
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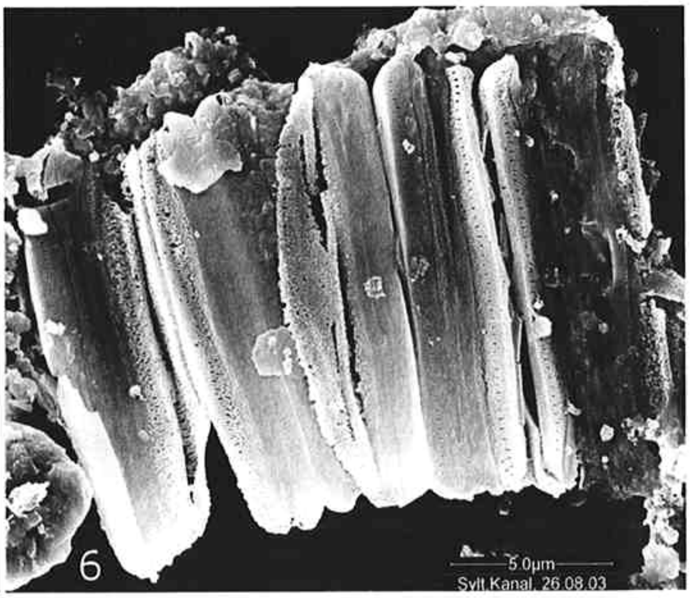
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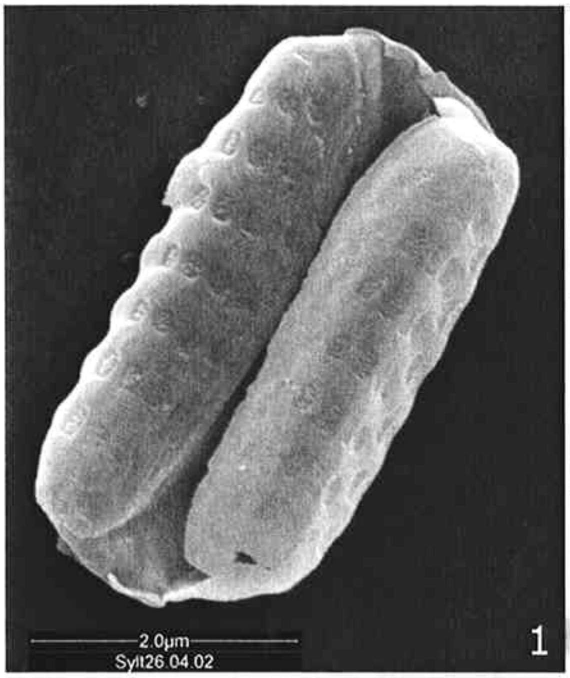
Sylt Kanal, 26.08.03

Plate 2

1 Fragilaria amicorum Witkowski & Lange-Bertalot
2 Opephora guenter-grassii (Witkowski & Lange-Bertalot) Sabbe & Wyverman
3 Protokeelia cholnokyana (Giffen) Round & Basson
4 Protokeelia cholnokyana (Giffen) Round & Basson
5 Haslea ostrearia (Gaillon) Simonsen

Plate 2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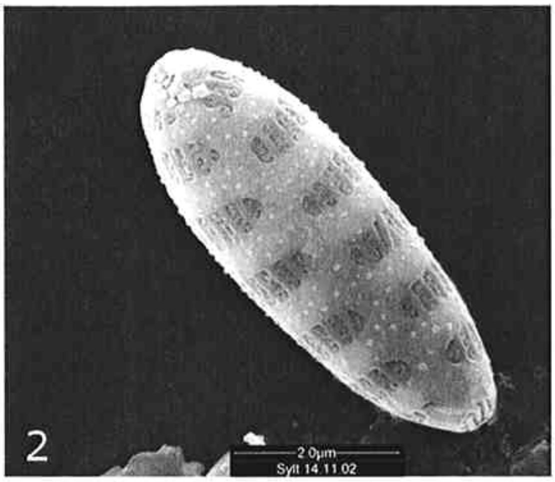
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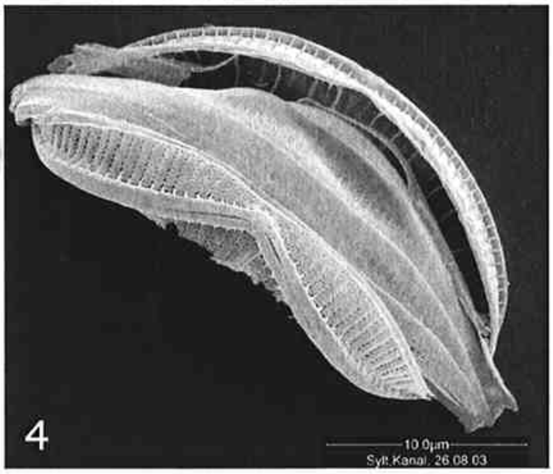
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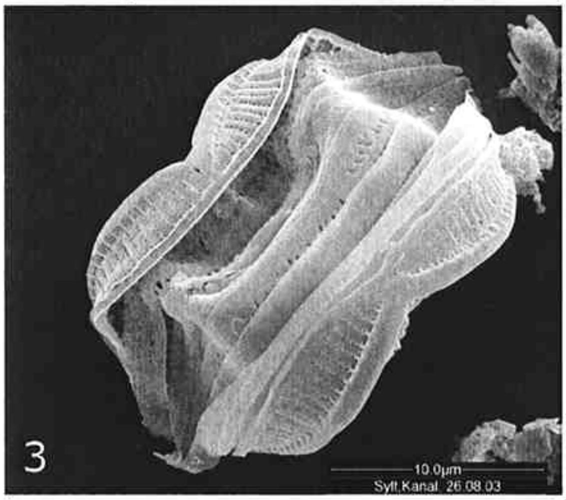
Sylt,Kanal. 26.08.03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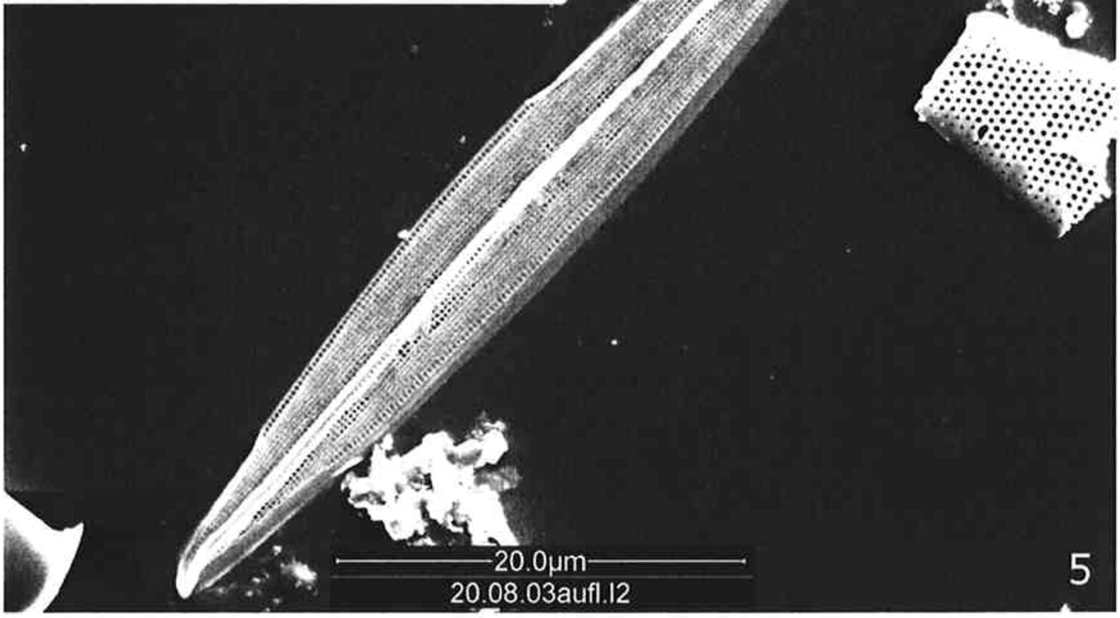
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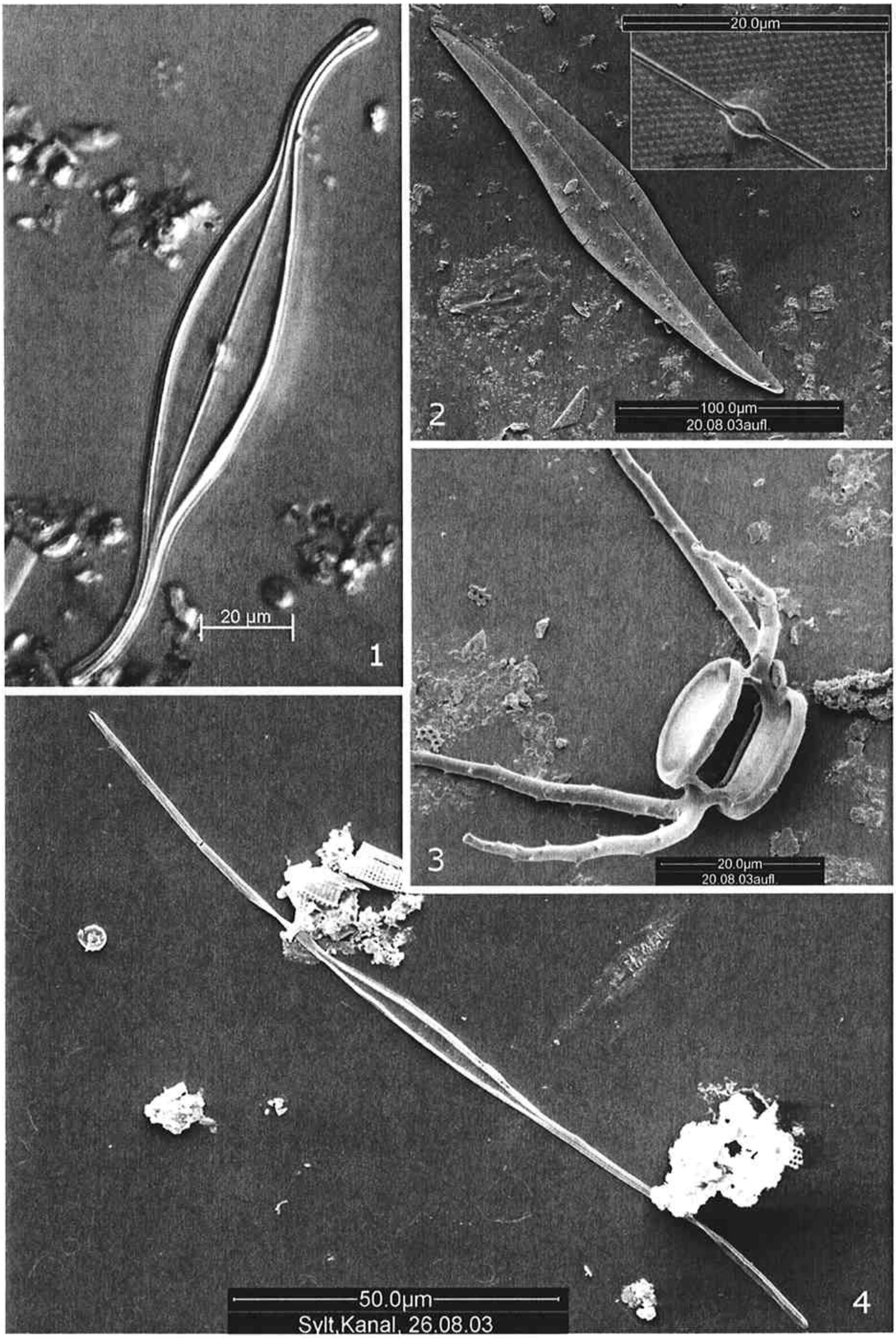
Plate 3

1 Gyrosigma arcuatum (Donkin) Sterrenburg
2 Pleurosigma angulatum (Quekett) W.Smith
3 Chaetoceros sp.
4 Nitzschia reversa W.Smith

Plate 3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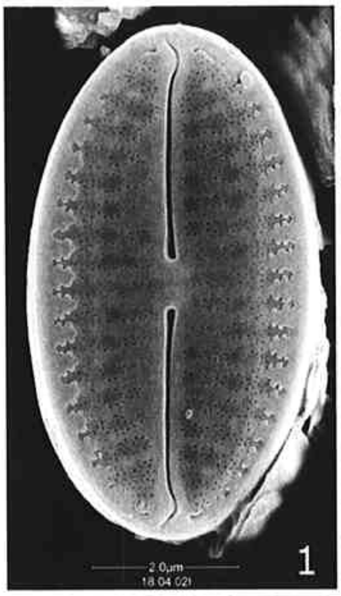
20.08.03aufl.
2
20 µm
1
20.0µm
20.08.03aufl.
3
50.0µm
Sylt,Kanal, 26.08.03
4

Plate 4

1 Fallacia sp.
2 Fragilaria amicorum Witkowski & Lange-Bertalot
3 Eunotogramma sp.
4 Planothidium hauckianum (Grunow) Round & Bukhtiyarova
5 Eunotogramma dubium Hustedt
6 Nitzschia frustulum (Kützing) Grunow
7 Hippodonta sp.
8 Extubocellulus cribriger Hasle, von Stosch & Syvertsen

Plate 4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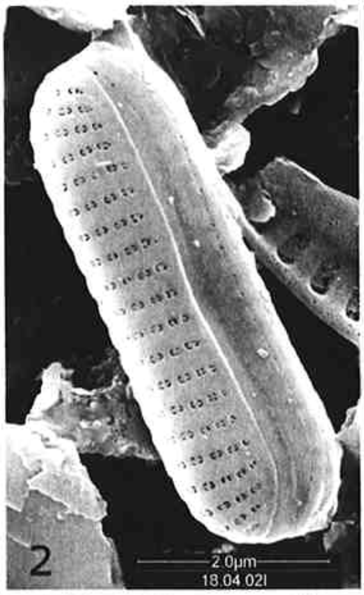
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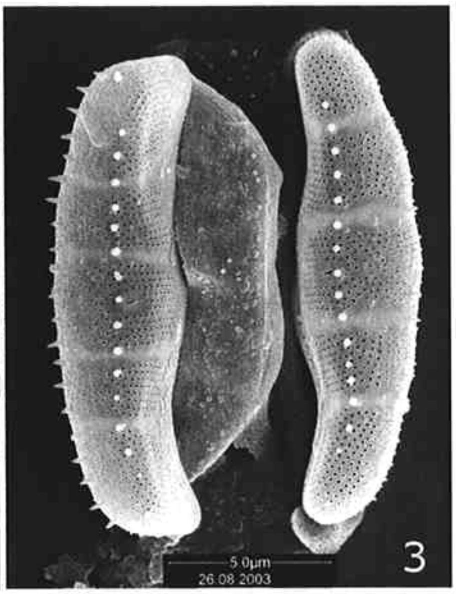
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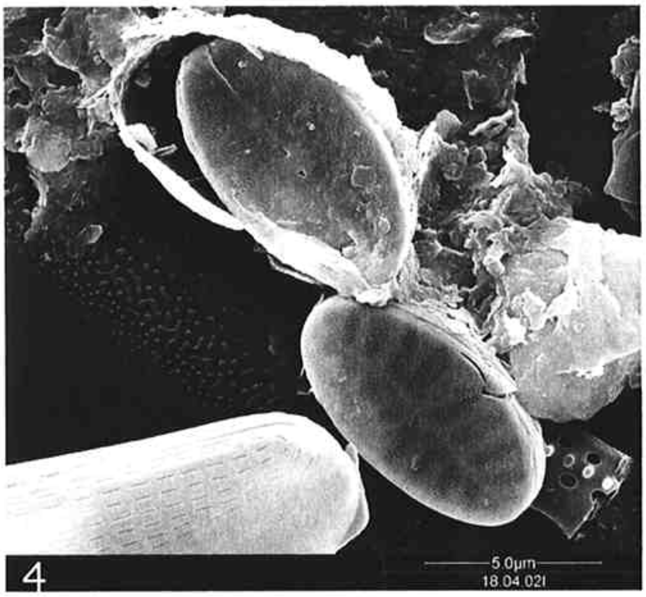
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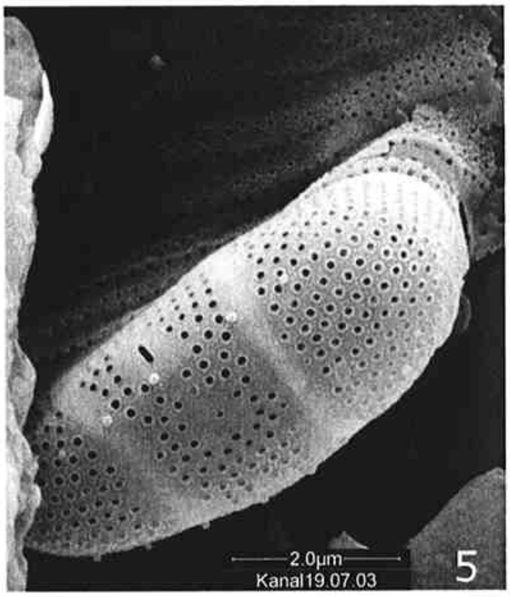
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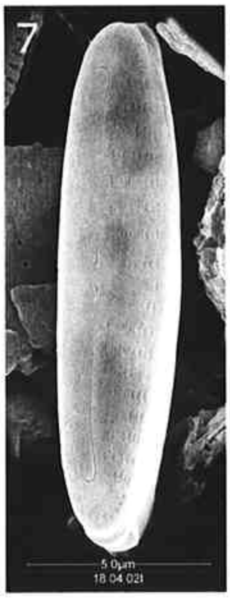
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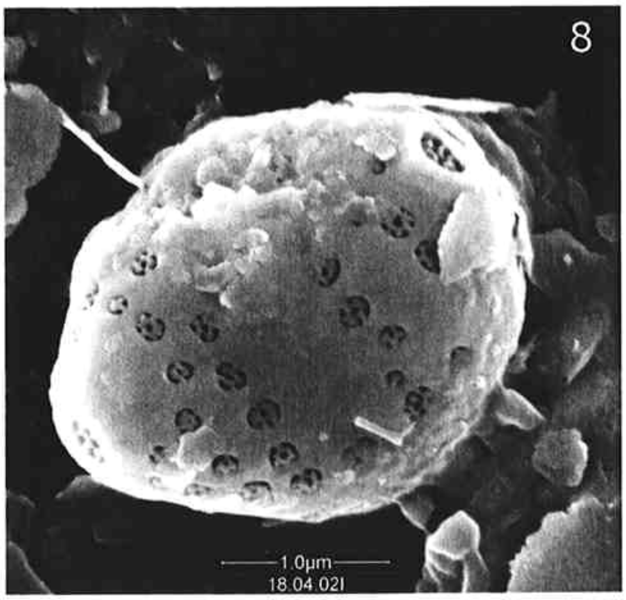
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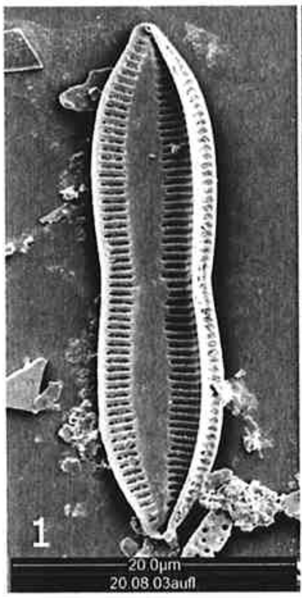
Plate 5

1 Nitzschia constricta (Kützing) Ralfs
2 Dickieia ulvacea Berkeley ex Kützing
3 Dickieia ulvacea Berkeley ex Kützing
4 Thalassiosira cf profunda (Hendey) Hasle
5 Thalassiosira cf proschkinae Makarova
6 Fragilaria subsalina (Grunow) Lange-Bertalot
7 Anorthoneis excentrica (Donkin) Grunow

Plate 5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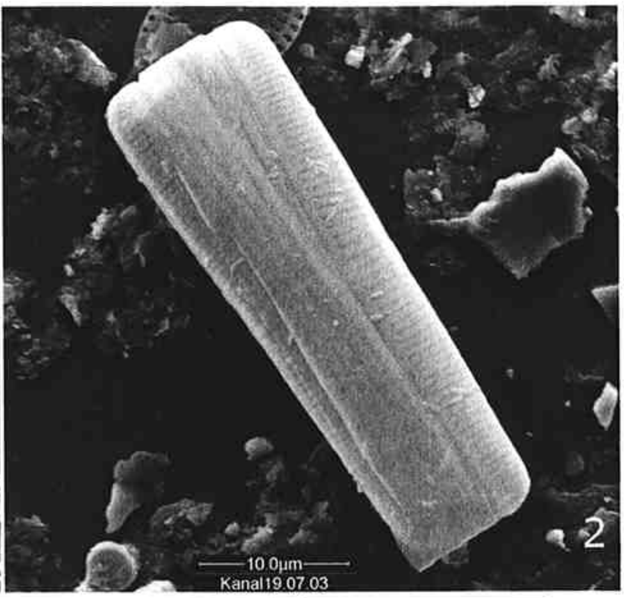
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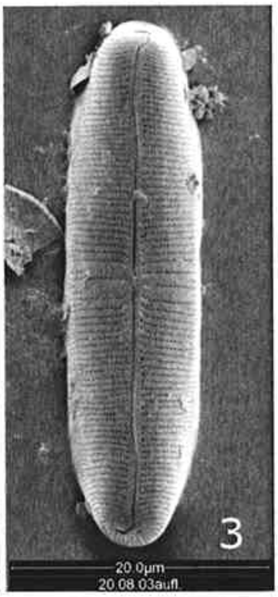
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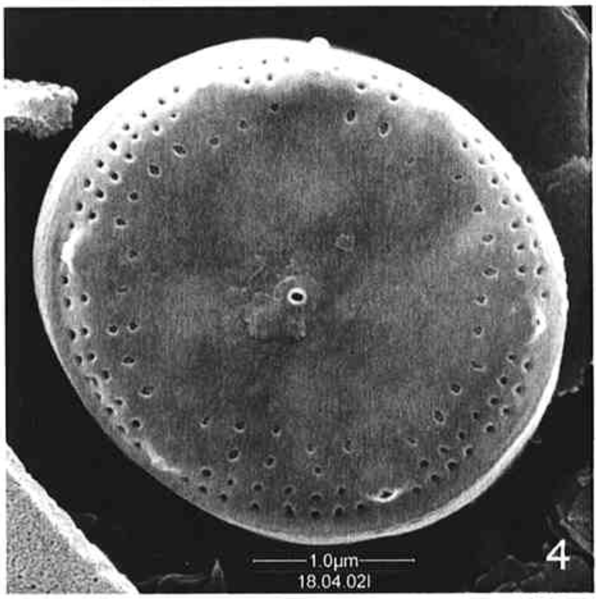
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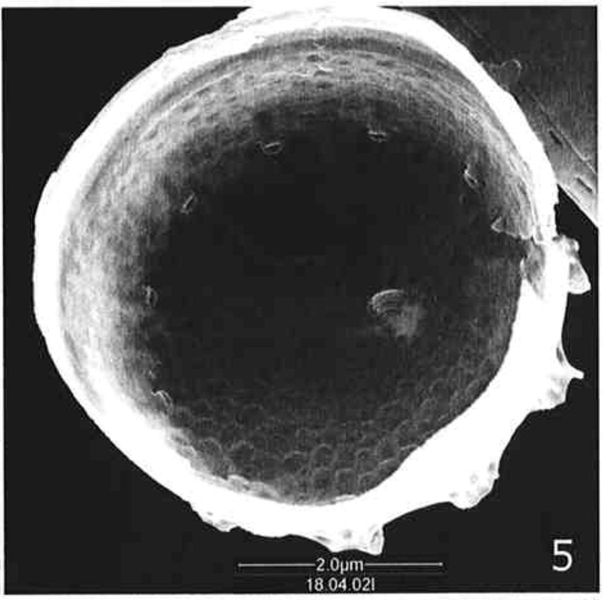
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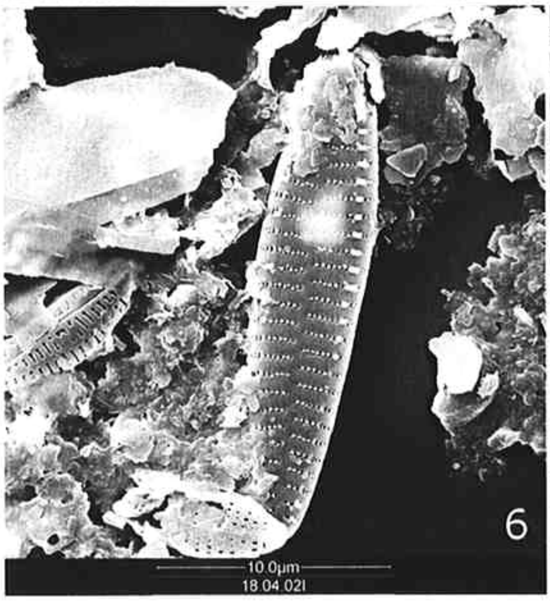
18.04.02l


6
10.0µm
18.04.02l

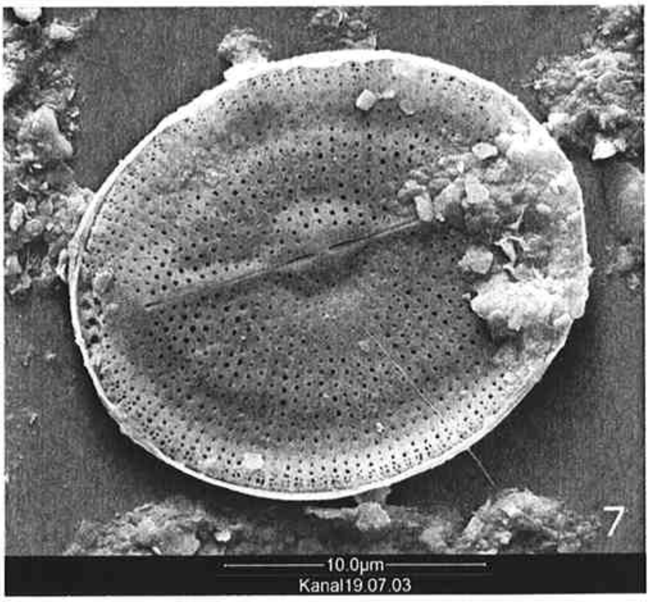
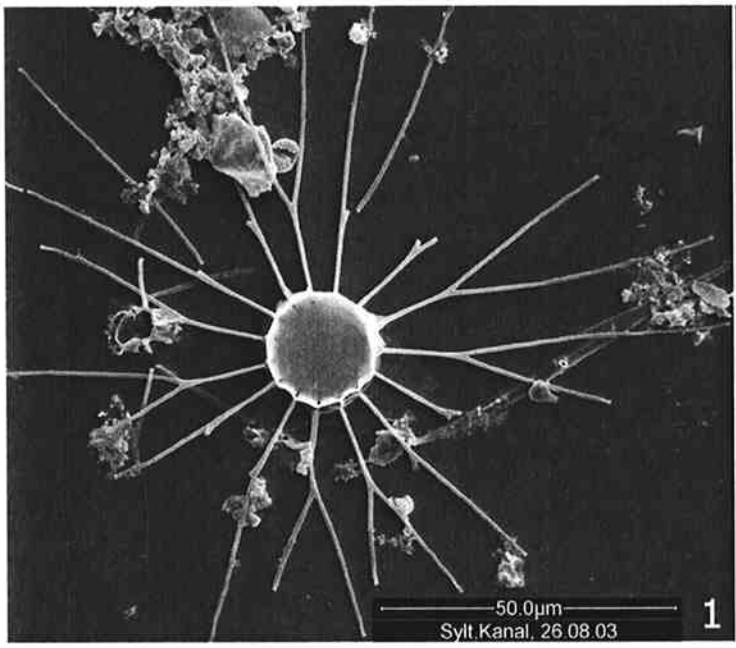
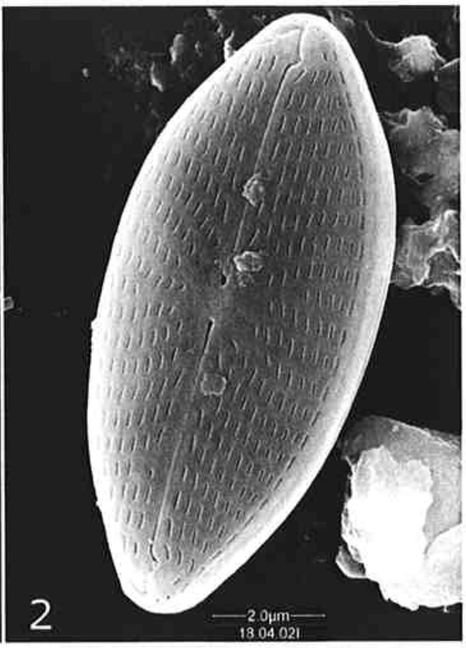

7
10.0µm
Kanal19.07.03

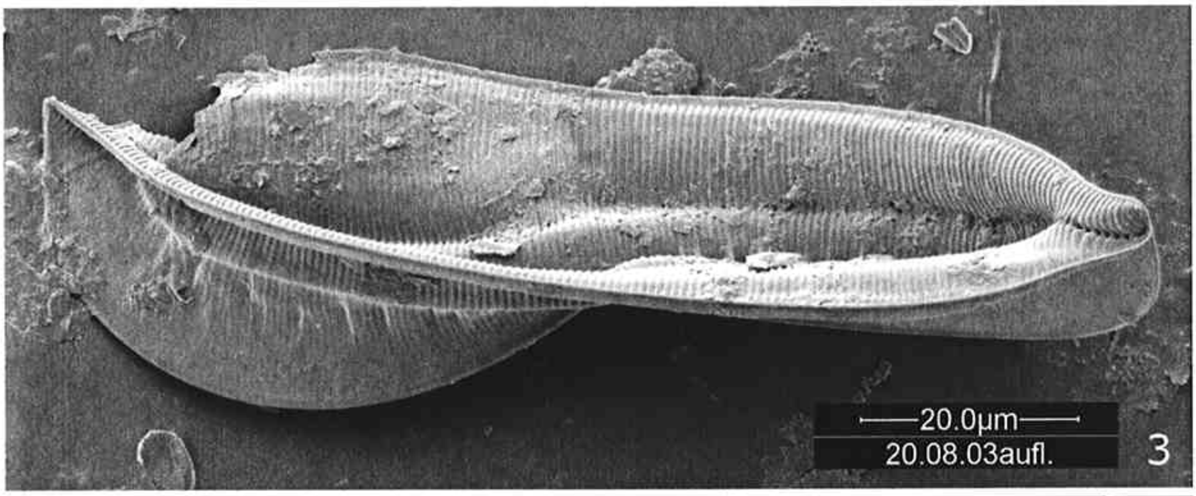
Plate 6

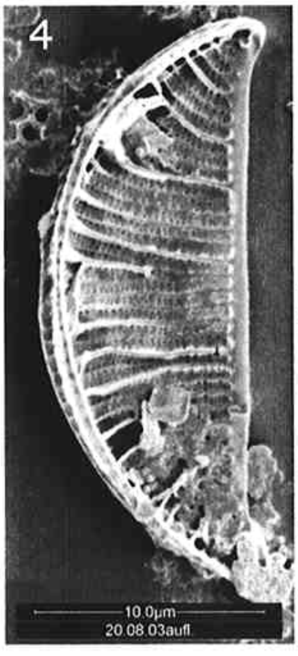
1 Bacteriastrum hyalinum Lauder
2 Navicula salinarum Grunow
3 Entomoneis ornata (Bailey) Reimer
4 Rhopalodia brebissonii Krammer
5 Skeletonema costatum (Greville) Cleve

Plate 6


50.0µm
Sylt,Kanal, 26.08.03
1


2
2.0µm
18.04.02I


20.0µm
20.08.03aufl.
3


4
10.0µm
20.08.03aufl

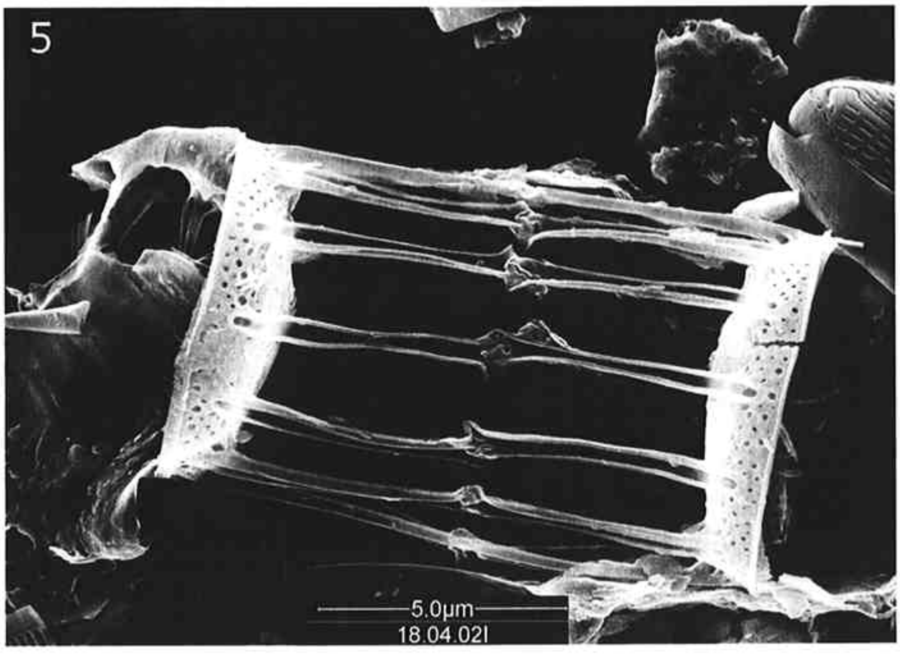
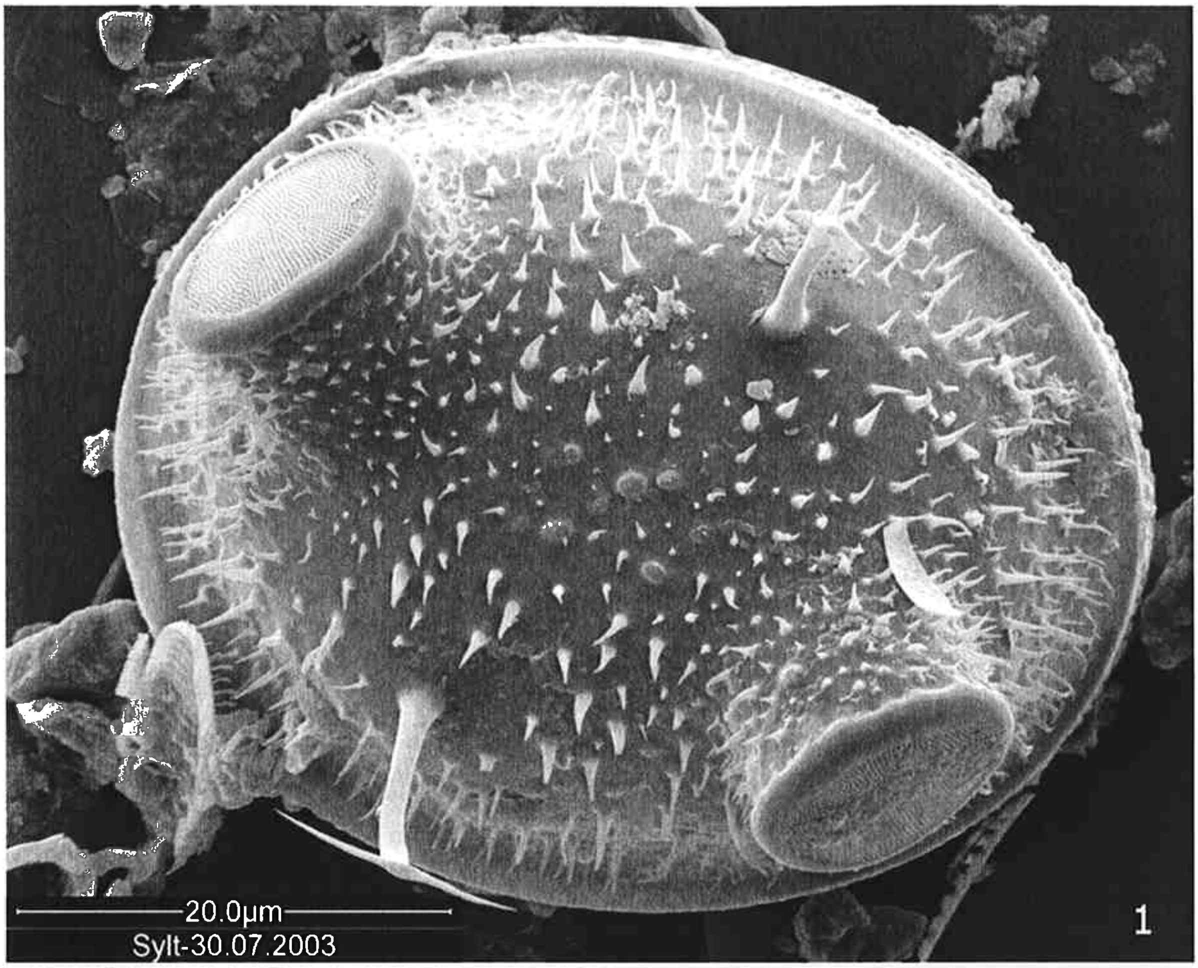

5
5.0µm
18.04.02I

Plate 7

1 Cerataulus turgidus (Ehrenberg) Ehrenberg
2 Cerataulus turgidus (Ehrenberg) Ehrenberg

Plate 7



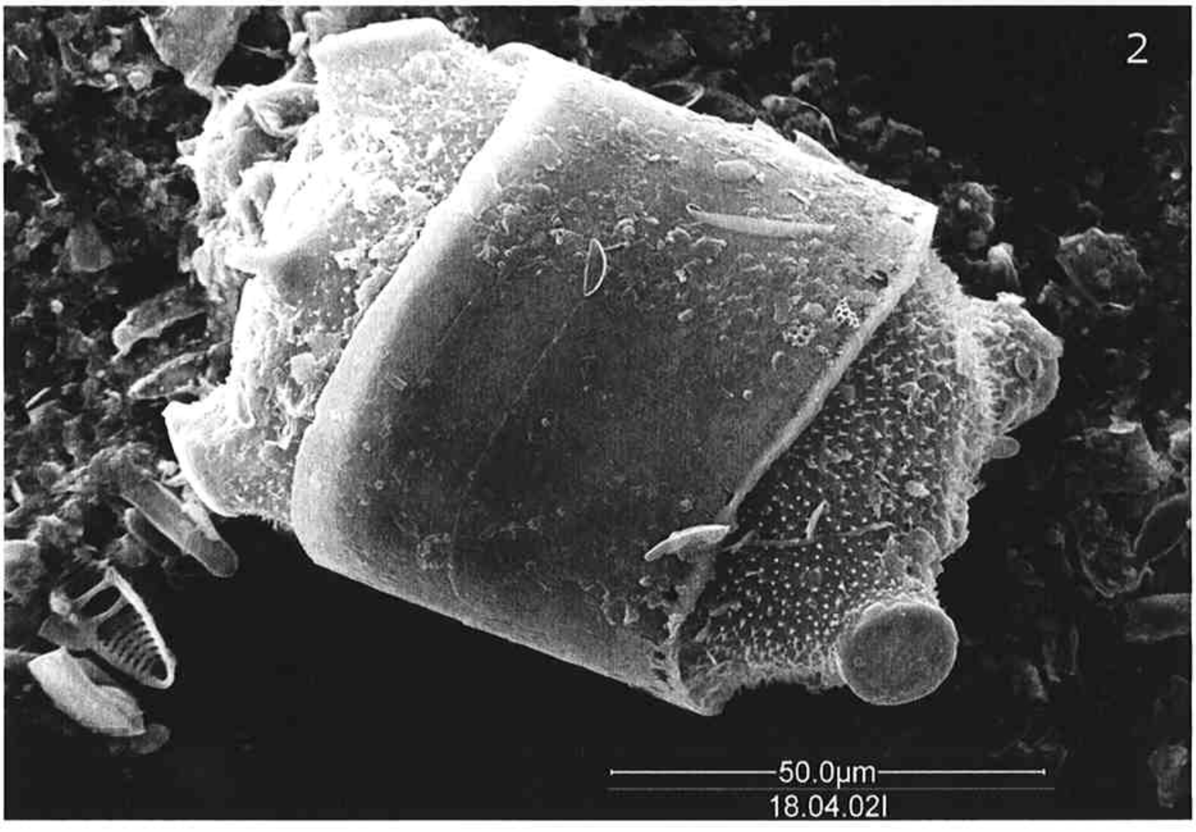
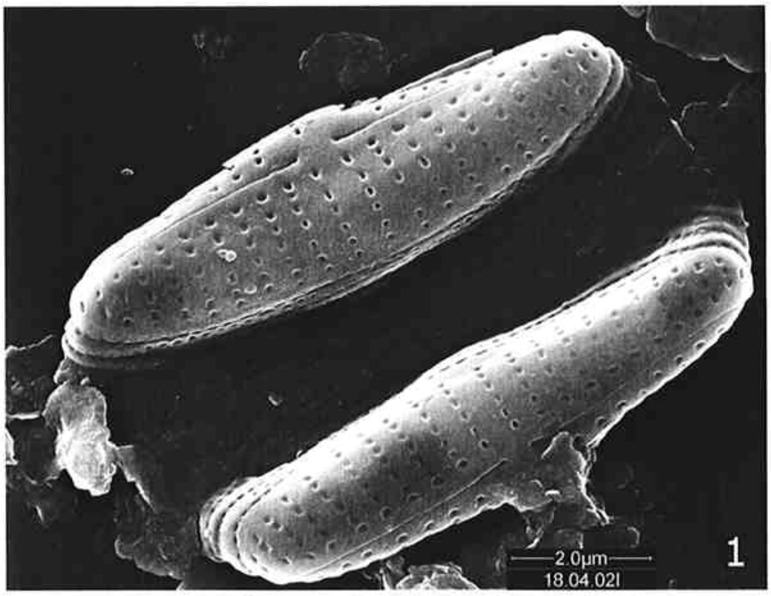


Plate 8

1 Lunella bisecta Snoeijs
2 Amicula specululum (Witkowski) Witkowski
3 Amphora ovalis (Kützing) Kützing
4 Amphora cf wisei (Salah) Simonsen
5 Triceratium alternans Bailey
6 Diatom community on sand, uncleaned
7 Diatom community on sand, uncleaned

Plate 8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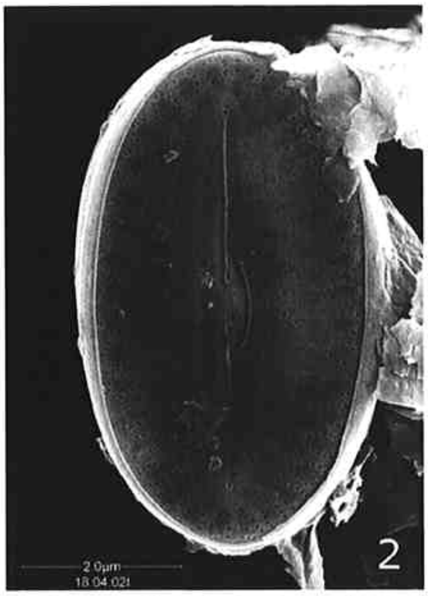
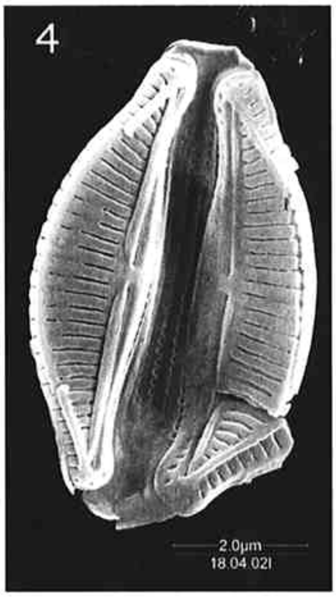
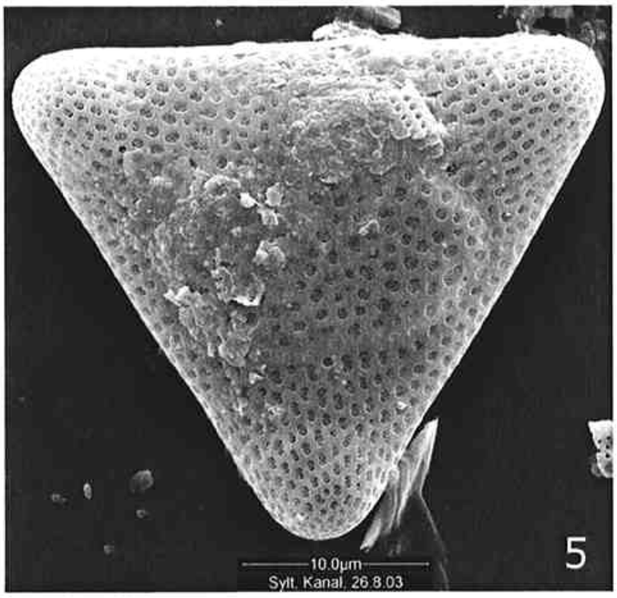
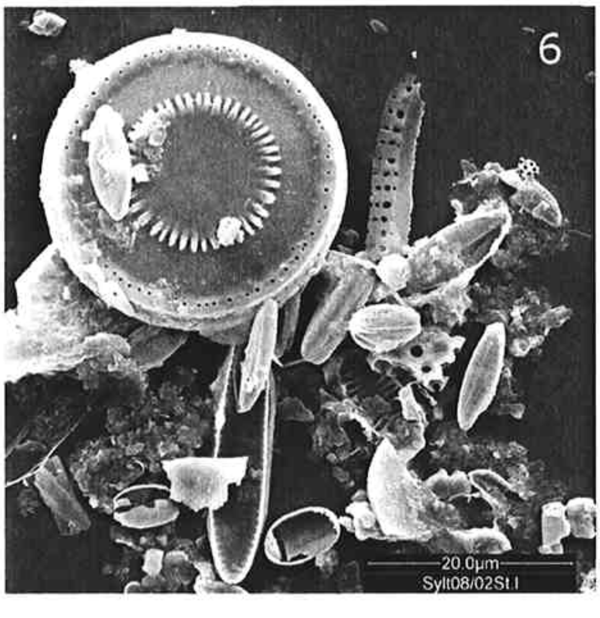
18.04.02I
1


2.0µm
18.04.02I
2


3
10.0µm
20.08.03aufl.


4
2.0µm
18.04.02I


10.0µm
Sylt. Kanal. 26.8.03
5


6
20.0µm
Sylt08/02St.I

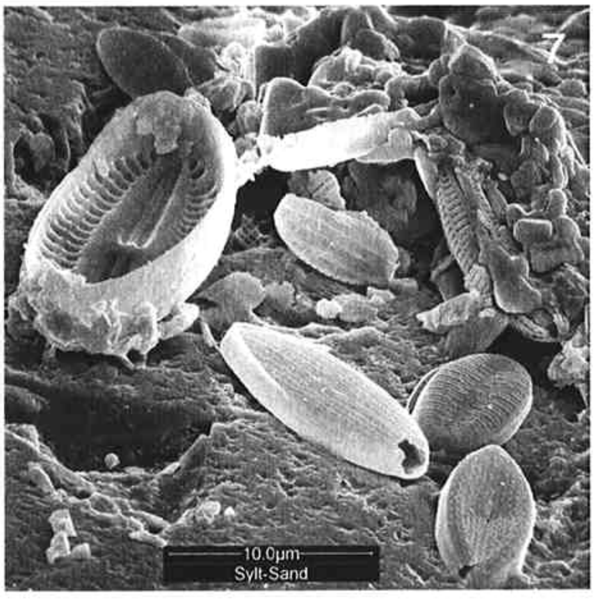
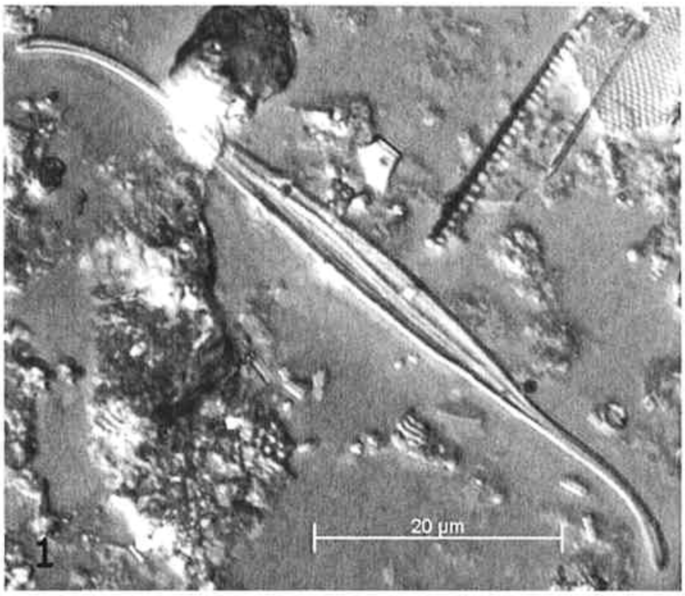
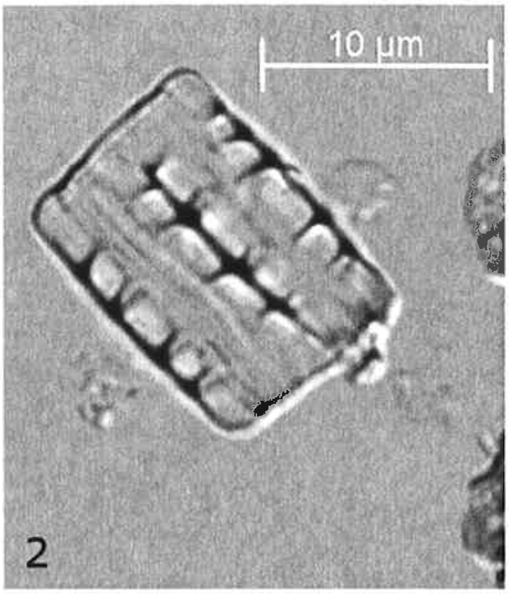

7
10.0µm
Sylt-Sand

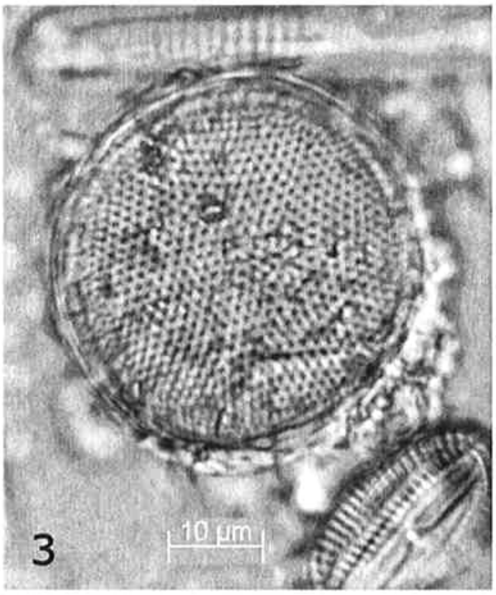
Plate 9

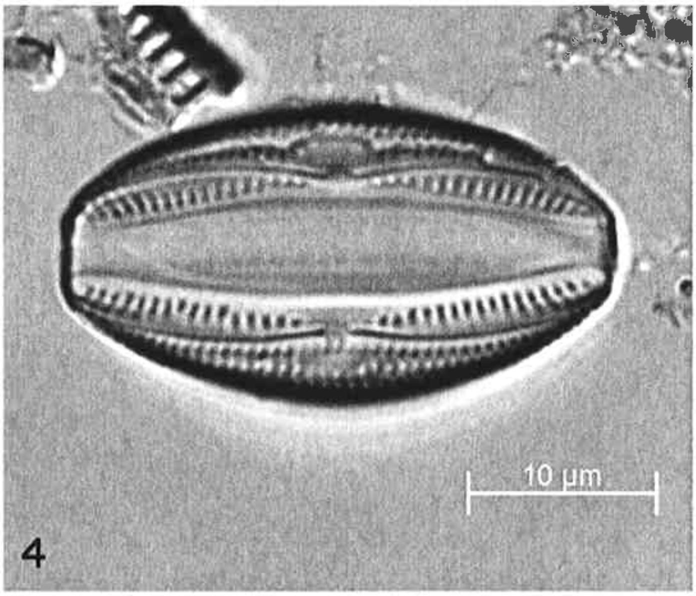
1 Gyrosigma prolongatum (W. Smith) Griffith & Henfrey
2 Eunotogramma dubium Hustedt
3 Thalassiosira sp.
4 Amphora marina W.Smith
5 Nitzschia constricta (Kützing) Ralfs
6 Nitzschia valdestriata Aleem & Hustedt

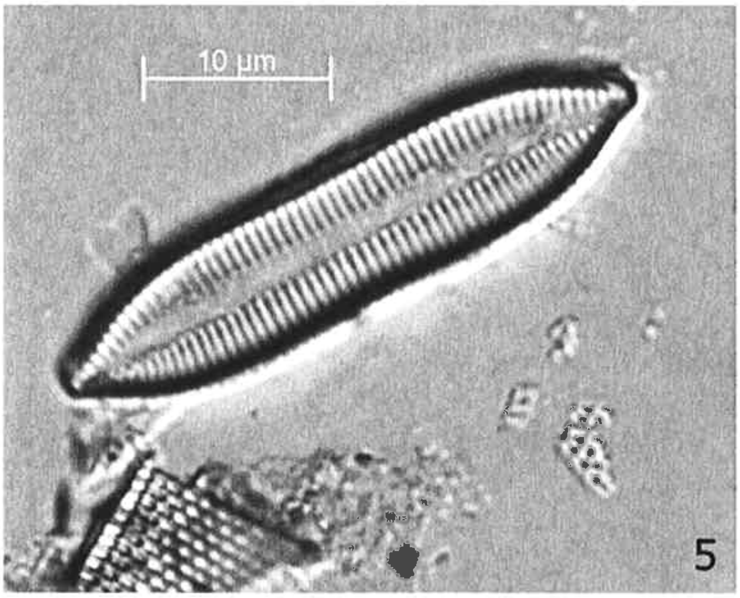
Plate 9











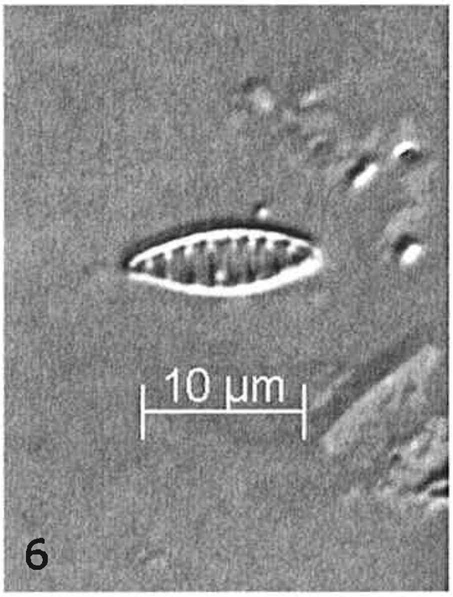
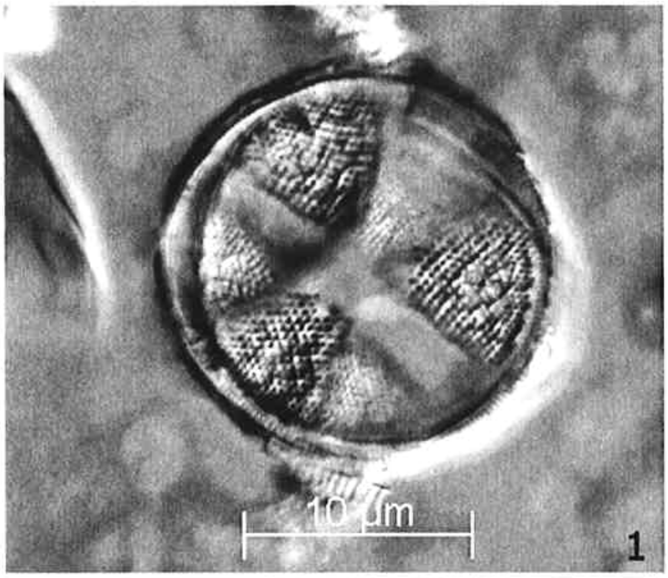
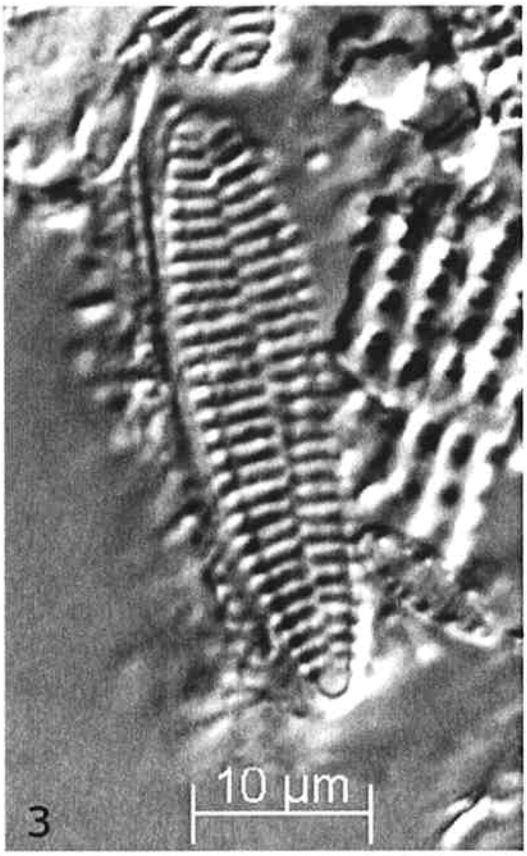


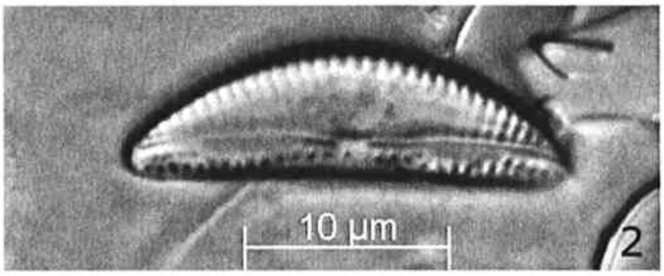
Plate 10

1 Actinoptychus senarius Ehrenberg
2 Amphora ovalis (Kützing) Kützing
3 Fragilaria subsalina (Grunow) Lange-Bertalot
4 Triceratium reticulum Ehrenberg

Plate 10







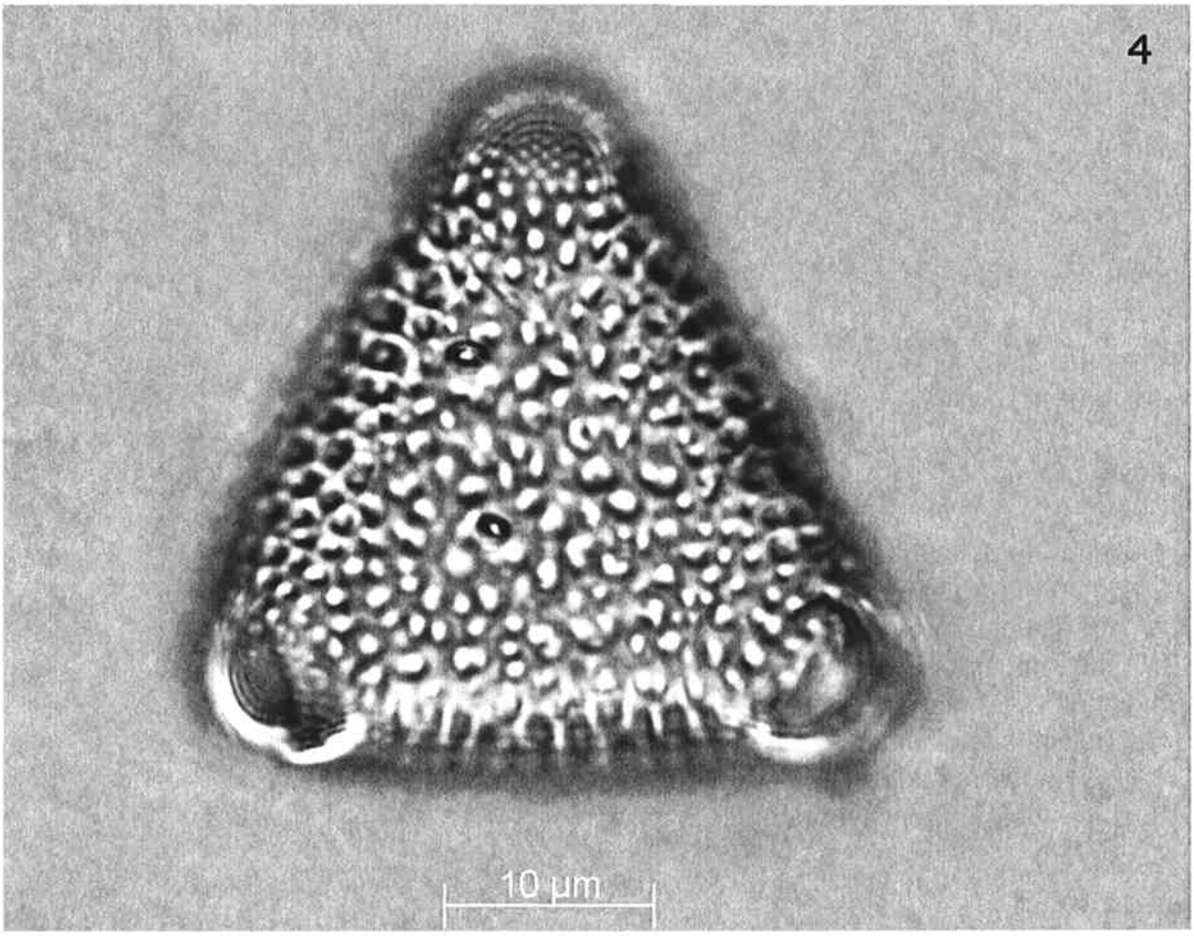
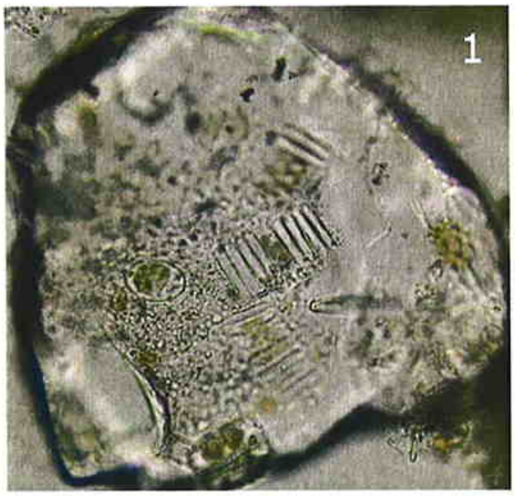
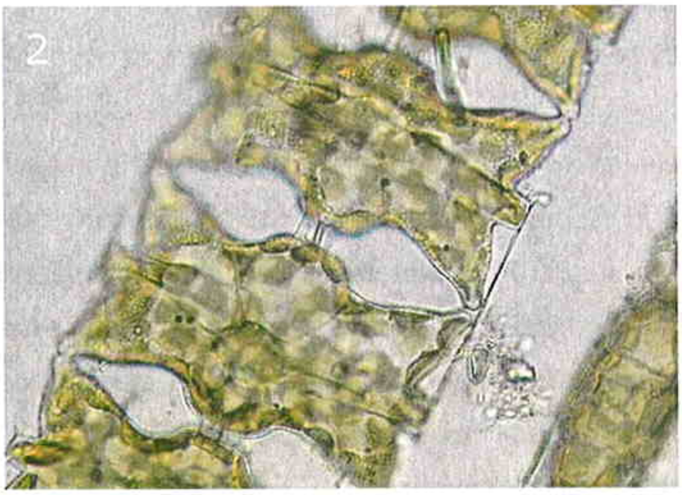


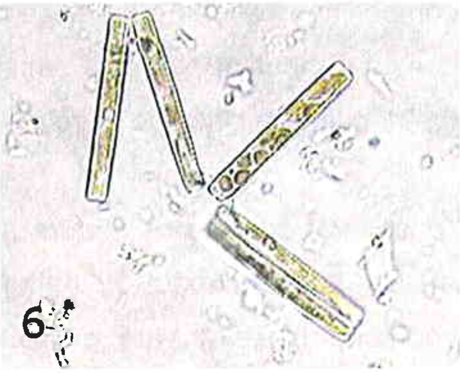
Plate 11

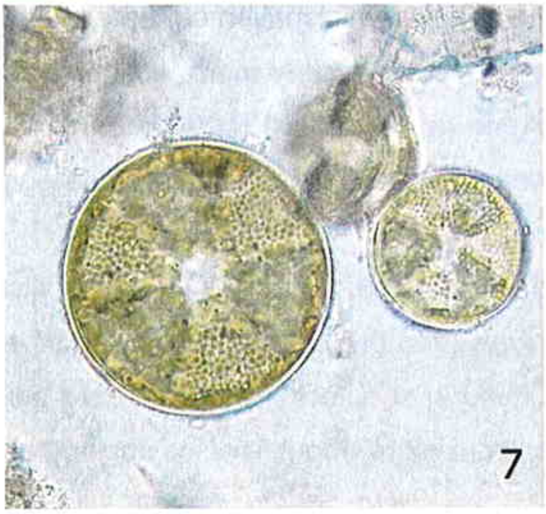
1 Catenula adhaerens (Mereschkowsky) Mereschkowsky
2 Odontella aurita (Lyngbye) Agardh
3 Thalassiosira constricta Gaarder
4 Thalassiosira nordenskioeldii Cleve
5 Delphineis surirella (Ehrenberg) Andrews
6 Thalassionema nitzschioides (Grunow) Mereschkowsky
7 Actinoptychus senarius Ehrenberg
8 Toxonidea insignis Donkin

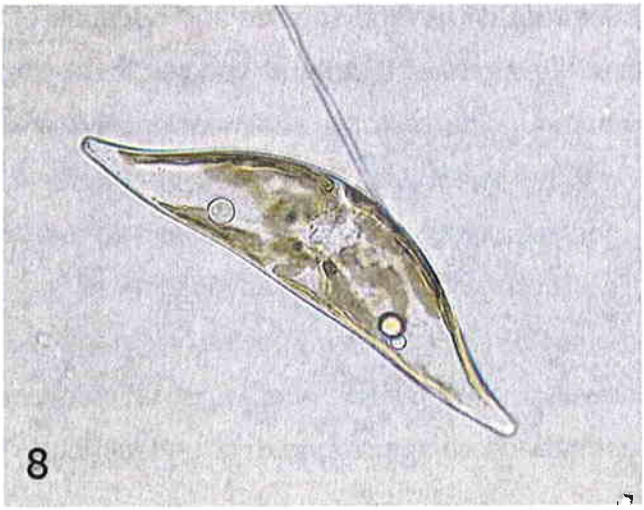
Plate 11











Discussion and Conclusions

Diatom studies on Sylt

In general our taxonomic findings are in accordance with other studies describing the typical community for the Wadden Sea and Sylt in particular (Drebes 1974, Asmus & Bauerfeind 1994, Agatz et al. 1999). The investigations carried out by Asmus (1982) and Asmus & Bauerfeind (1994) concern the community metabolism of primary producers on the intertidal flats of Königshafen bay, at the north-east of Sylt Island, and a microphytobenthic community study, respectively. A difference to the present study can be found, for example, in the abundance of *Achnanthes hauckiana* (syn. *Planothidium hauckianum* Round & Buktiyarova) which, according to Asmus (1982), dominated throughout the year 1980. This species was present during this studies from July to September 2003, although never in dominating abundances. Asmus (1982) stressed the importance of the mudsnail *Hydrobia ulvae* as a grazer of diatom cells, considerably reducing the standing stock of microphytobenthos during periods of low turbulence from April to the end of July 1980. Cell numbers from cell counts for the present study will be presented in chapter 3 and 4, also referring to the possibility of reduced cell abundances on the sediment due to grazing activities by *Hydrobia*. Agatz et al. (1999) found a significant effect of nutrient gradients on species composition caused by a sewage treatment outflow in Königshafen bay. A relatively constant input of nutrients almost eliminated the seasonal variations and favoured the dominance of some species.

Of several species or genera among the 231 taxa identified, the life mode is not exactly known. About 32 pelagic, 45 epipsammic and 107 epipelic species were counted,. however, the expression epipelic does not exclude an attachment to substrata by several species and because of the a lack of information on the ecology and life mode of diatom at species level, there will exist possibly more tychopelagic species using both the sediment and water column as a habitat. Further information on this subject will be provided in chapter 4 which regards the life mode of various species subjected to resuspension and resettling.

The work with diatom identification of samples collected on Sylt has led to the description of one new species, *Mediopyxis helysia*, and one reclassification into the newly created genus *Paraplagiogramma* (described in chapters 6 and 7). There are possibly more species, to date undescribed. To learn more about species ecology as well as about a possible shift in composition due to e.g. climate change, further studies on species level will be essential because diatoms are an important component of the community in terms of primary producers or food source.

This chapter serves as a background for the following chapters 4 and 5, that deal with the resuspension and sedimentation of selected diatom species in different current regimes. The species list is also intended as a basis for future studies on diatoms in the Sylt-Rømø bight, and together with the plates serves as a helpful tool for the time series carried out on Sylt and for the university field courses which take place on the island annually.

Furthermore, a contribution to the current discussion of introduced species (already concerning Sylt with e.g. the oyster C*rassostrea gigas*) could be very valuable easily achieved by a regular monitoring not only of the planktonic but also of the benthic species.

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Chapter 3

The effect of altered hydrodynamic conditions: experiments using an *in situ* three-current-flume

Abstract

Various factors govern the living conditions of biota on an intertidal flat. Sediment grain size and porosity, as well as the prevailing current regime, are among the most significant in influencing the composition of microbenthic communities. These factors are in turn determined by geomorphology, exposure time, hydrodynamic conditions which can be strongly affected by man-made constructions e.g. dams and climate changes thus altering the characteristics of flow and sediment transport processes.

This study is an attempt to determine the influence of an altered current regime on the sediment-water biota , taking as indicators the following parameters measured in the water column and in the sediment: Flow velocity, chlorophyll a (chl *a*), suspended matter (SPM), diatom cell abundance, particulate organic carbon (POC), particulate organic nitrogen (PON) and the particulate organic carbon to nitrogen ratio (C/N). The current velocity was altered using a large, in situ, flume device placed on an intertidal sandflat off the east coast of Sylt and adjusted to the prevailing bi-directional flow. Data from six sampling dates between July and September 2003 were correlated with measured flow velocity of the three flow treatments 'increased', 'mean' and 'reduced', and with wind velocity, also taking into account the wind direction. Results of the field experiments showed a coupling between flow treatment and cell abundances in the water column, with higher cell numbers in the 'increased' and 'mean' flow treatments compared to the 'reduced' flow treatment. Incoming and outgoing tides were found to have a small but statistically insignificant effect. Chl *a* in the sediment displayed higher values in the 'reduced' flow lanes, but cell abundances in sediment samples were higher in the 'increased' flow lanes. Wind velocity and wind direction were found to drive the complex interrelationships between measured variables, together with differing tidal influences and flow velocities.

Introduction

Depending on the nature of a sediment bed, flow will vary in its characteristics and develop turbulences when subjected to rather rough beds. Ripples, tubes, macro algae, faecal mounds and rocks are structures on the sediment surface that alter flow conditions and cause bottom friction. Disturbances in flow result in shear forces in the flow which in turn resuspend the sediment along with the associated microphytobenthos (Beaulieu 2003, Tolhurst et al. 1999). Hydrodynamic forces also determine the distribution of suspended matter in the water column. Suspended matter and chl *a* are usually the measured parameters to characterise flow dynamics or to investigate processes characterising sediment-water exchanges (Edelvang 2004). Smooth turbulent flow or rough turbulent flow across a sediment bed exert different forces affecting the exchange of material and nutrients between the water column and the sediment. Rough turbulent conditions can cause material loss due to resuspension and stress to organisms leading to high costs in terms of energy and adaptation. The composition and structure of epipsammic (attached to sand grains) assemblages varies depending on the frequency and extent of disturbances (Paterson & Hagerthey 2001).

Vertical mixing and sediment resuspension influence important estuarine parameters such as primary and secondary productivity, sediment mass flux and also pollutant dispersal. The wind-induced physical processes are important forcing mechanisms for sediment transport in coastal environments (Booth et al. 2000).
De Jonge & van Beusekom (1995) found that resuspension of mud and chl *a* from the top 0.5 cm of sediments was a linear function of ´effective wind speed´ (wind speed averaged over three high water periods immediately preceding collection of water column samples). Resuspension began at an effective wind speed of 1 m s^{-1} and the highly significant linear regression of effective wind speed against water column chl *a* indicated that a wind speed of 12 ms^{-1} would resuspend 50% of the diatom biomass into the water column, which would eventually reach the main channels of the estuary.

Benthic diatoms present an important food source for zooplankton and benthic suspension feeders as they constantly supply the water column with resuspended cells, available both in summer and in winter, when the productivity of the phytoplankton is low (Lucas 2001, deJonge 1992, Shaffer 1988; Baillie 1980).

Experiments involving flume devices are used to link biological processes to hydrodynamic parameters such as velocity or turbulence. Flumes are useful devices to investigate under controlled conditions factors such as bed shear stress, erodability of sediments, biotic and abiotic processes and the impact of fluid dynamics on, for example, settlement (Stocks K.I. 2002, Snelgrove P.V.R. 1999), food availability and transport processes (Widdows & Brinsley 2002, Widdows et al. 1998), flow conditions (Friedrichs et al. 2000), benthic-pelagic exchange (Lucas 2000, Blanchard 1997), nutrient and oxygen fluxes across mussel banks (Asmus et al. 1990, 1994), and the influence of altered hydrodynamics on seagrass beds (Schanz et al. 2002). The large construction of the three-current-flume employed in the present study enables measurement of physical processes such as resuspension or exchange between the water-sediment interface *in situ* and over any time period desired since the durable construction can be left in the field.

The mechanisms responsible for the resuspension of diatom cells into the water column are manifold and so are the studies related to this subject. However, the majority of studies to date have focussed on quantitative analyses such as productivity and biomass. The aim of this study was to determine flow characteristics on an intertidal sand flat. Knowledge of the dynamical regime is then used to investigate possible effects of altered hydrodynamic conditions on sediment-water exchange processes. The experiments described in this chapter presents basic research results that will serve for further studies of e.g. bentho-pelagic pathways and coupling.

Material and Methods

Study site

The study was conducted on the intertidal sandflat off the east coast of Sylt, North Sea, Germany. The island is situated in the North Frisian Wadden Sea, close to Denmark and connected to the mainland by a causeway. The Sylt-Rømø Bight (54°52' to 55°10' N, 8°20' to 8°40' E) is formed by a further causeway between the Danish island Rømø and the mainland of Denmark. This semi-enclosed lagoon is connected to the North Sea through a 2.5 km broad tidal inlet called Lister Tief (see Figure 1). The bight covers an area of 404 m^2, with an intertidal area of about 135 km^2.

The main fraction of sediments comprises grain sizes of 0.2 – 0.63 mm diameter and the fraction of fine sands (grain size < 0.2 mm) is less than 5 %. The intertidal flats comprise 95 % sandy sediments adjacent to mud flats, seagrass beds and mussel beds. The tidal range in the bight is about 1.8 m with minor deviations due to neap and spring tide or wind. The water residence time in the bight is between 19 and 29 days. The salinity of the water ranges seasonally from 28 to 32 PSU. Mussel beds (*Mytilus edulis*) are present in the intertidal area of the tidal basins (Gätje 1998). Studies by Deussfeld (2003) in the same area have shown that the vertical profile of velocity deviated from known standards e.g., velocities decreasing from water surface to bottom, a characteristic attributed to wind-induced surface currents. The mean water depth at the sampling site is about 80 cm.

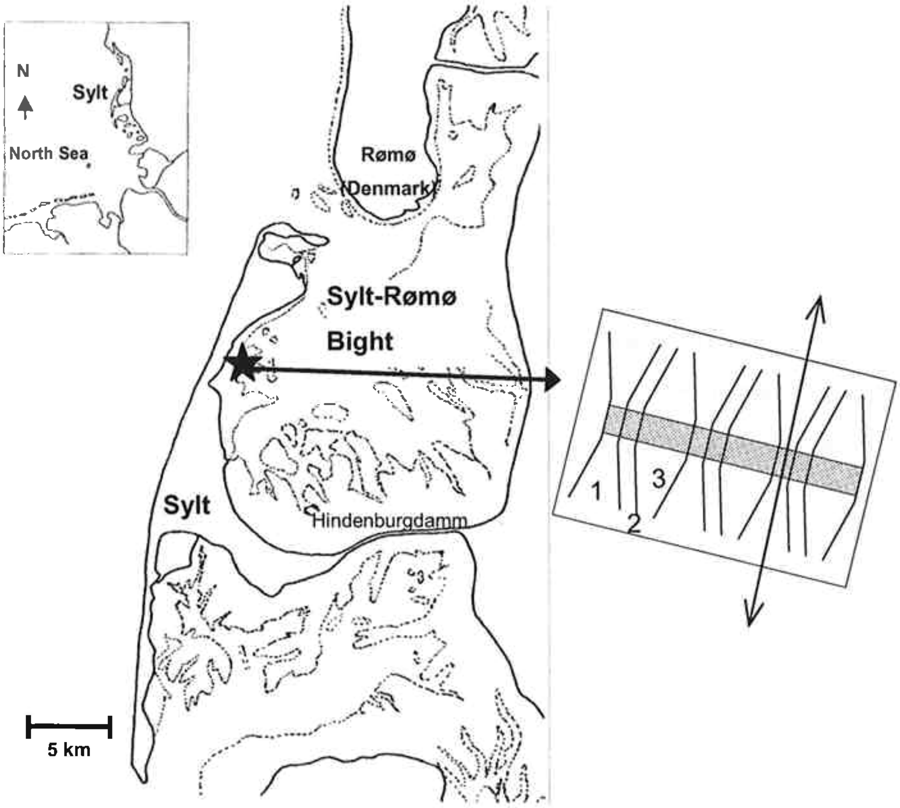

Fig. 1. Study area in the northern Wadden Sea. Inset: general map showing the location of Sylt in the northern Wadden Sea. Asterisk indicates sampling site with arrow leading to a diagram of the three-current-flume aligned to the bi-directional tidal currents (double headed arrow). Numbers 1, 2, 3 indicate the three manipulated flow treatments: 1 increased, 2 mean and 3 reduced.

Three-current-flume

The three-current-flume is designed to allow *in situ* sampling in altered current regimes (Figure 2). It is constructed with steel bars and mantled on the vertical walls with a flexible, durable plastic fabric, forming nine lanes (see diagram in Figure 1). Flexibility of the lane trimming allows wave dynamics to develop as natural a profile as possible without creating wall shear forces. The flume is about 9 m long and 12 m wide, with a height of 90 cm. By narrowing or expanding the width of a given channel the ambient tidal flow can be manipulated into an accelerated or reduced speed. A 'mean' lane serves as control and reflects conditions outside the flume. The sampling area is situated in the centre halfway along the flume, equidistant from the sides, where water and sediment samples were taken in each lane. The flume was aligned to the bi-directional intertidal current (see also Fig.1). The durable construction of the flume allows long term field work as it is resistant to weather conditions. For further technical details see Schanz (2002). Subsequently, the three flow treatments will be referred to as 'increased', 'mean' and 'reduced' flow velocity. All nine lanes were utilised to give three replicates of each current regime.

Fig. 2. Three-current-flume. Close-up view of three flume lanes with different openings thus manipulating current velocity into increased, unaltered or reduced flow across the mid section of the flume. Photo: Anja Schanz

Flow measurements

Flow was measured at three different depths of 10 cm, 20 cm above bottom and close to the water surface using an Acoustic Doppler Velocimeter (ADV, NorTek, Norway) or an induction current meter (Marsh MacBirney 201M). Flow components were measured over one tidal cycle, beginning when the rising tide level approached the minimum required height of about 10 cm. Measurement was terminated when the water level sank below approximately 10 cm. Calculations of velocity represent the 'mean' of three replicates of each current velocity treatment, 'increased', 'mean' and 'reduced'. ADV data sampling frequency amounted to 8 Hertz (SI = 1/s). ADV measurements provided simultaneously data for the three flow component vectors: U (main horizontal, or longitudinal velocity), V (transversel velocity) and W (vertical velocity).

Grain size analysis

For the analysis of grain size, replicate sediment samples taken from each flume lane were freeze-dried and afterwards treated with H_2O_2 to remove organic substances. After rinsing with H_2O the grain size was measured by means of a QUANTACHROME CILAS-Lasergranulometer 1180. Classification was carried out according to the Wentworth scale in size classes of phi-values ($\Phi = -\log_2$ of grain size in mm).

Sampling

Samples were taken on six sampling days between July and September 2003 (see Table 1). One sampling session included the collection of water during in- and outgoing tides using an ISCO-STIP automatic sampler every 15 or 20 minutes. The samples comprised 0.5 litres and were processed immediately after return to the laboratory for analyses of chl *a* and cell counts. The chl *a* content was determined after acetone-extraction using a Uvikon XL Bio-Tech Instruments spectrometer. Calculation of chl *a* content is based on Lorenzen (1967). Between 100 and 200 ml water (depending on seston loading) were filtered through Whatman GF/C filters (0.7 µm pore size) for chl *a* analyses and pre-weighed and pre-combusted GF/C filters (0.7 µm pore size) for SPM and POC/PON analysis. Filters were rinsed with Milli Q water to remove salt, and stored at minus 20 °C until further analysis. POC/PON analysis was conducted using a Flash EA 1112 Thermo Finnigan NC Sediment

Analyser. For taxonomic analysis, 50 ml water were transferred to brown bottles and about 4 drops of Lugol´s solution were added to preserve the sample.

Cell counts and diatom identification

For the assessment of diatom cells, sediment samples were taken with a cut-off syringe (1.6 cm diameter), whereby the cylinder was plunged into the sediment, carefully removed after closure of the open end and before expulsion of the first centimetre which was carefully cut off, transferred to a plastic bag and stored at minus 20 °C. All samples were freeze-dried prior to analysis. Three replicate sediment samples were collected from each flume lane. Prior to microscopic examination, the samples were sonicated for ca. four minutes to detach the epipsammic fraction of the diatom community from the sand grains. After a short period to allow settling of coarse sand grains, the supernatant was decanted into 10 ml settling chambers. For the preserved pelagic phytoplankton samples, settling chambers with a volume of 25 ml were used for cell counts. After settling, the cells were counted using an inverted light microscope (Zeiss Axiovert35) at a magnification of 100- to 400-fold. Only cells containing chloroplasts were counted, on the assumption cells were alive at the point of sampling. Subsamples were treated according to Simonsen (1974) and mounted on cover slips (18 mm diameter) with Naphrax (refraction index n_D = 1.73) for permanent slides. A Zeiss Axioplan light microscope with a digital camera and a FEI QUANTA FEG 200 electron scanning microscope were used to identify diatoms to species level.

Table 1. Sampling day and type of analyses. Current velocities were measured using either an Acoustic Doppler Velocimeter (ADV) or a MarshMcBirney (MMB) induction current meter

Analyses	16.07.	30.07.	12.08.	20.08.	26.08.	17.09.
C:N Water	x	x	x	x	x	x
C:N Sediment	x	x	n.d.	x	x	x
Cc Water	n.d.	n.d.	x	x	x	x
Cc Sediment	n.d.	x	n.d.	x	x	n.d.
Chl *a* Water	x	x	x	x	x	x
Chl *a* Sediment	x	x	n.d.	x	x	x
PON/POC	x	x	x	x	x	x
Current vel. MMB	x	x	x	x	x	n.d.
Current vel. ADP	n.d.	n.d.	x	n.d.	x	n.d.

(n.d. = no data available. Cc = cell counts. PON/POC = particulate organic nitrogen and particulate organic carbon)

Statistical analyses

Spearman Rank correlations were applied to test for significant correlations between cell numbers and wind speed, cell numbers and current velocity and between wind speed and current velocity. Analysis of variances (ANOVA) and Fisher LSD post-hoc tests were applied to determine significant differences between flow treatments and between sampling days. Data were considered significant on a $p < 0.05$ niveau. Tests were carried out using Statistica (StatSoft 6.1).

Results

Wind

Wind data were kindly provided by the List/Sylt weather station (Deutscher Wetterdienst DWD). Figure 3 shows the spectrum of wind data for the six sampling days. The highest wind velocities were found on 26.08.03 with peaks up to 11.5 m s $^{-1}$ from WNW, followed by the 16.07.03 with wind speeds up to 10.1 m s $^{-1}$ from the East and 20.08.03 with 9.9 m s $^{-1}$ from the West. The median values for the 30.07.03 (WSW), 12.08.03 (SW) and 17.09.03 (SW) ranged from 5.0 to 5.8 m s $^{-1}$. The overall range is 1.9 – 11.5 m s $^{-1}$.

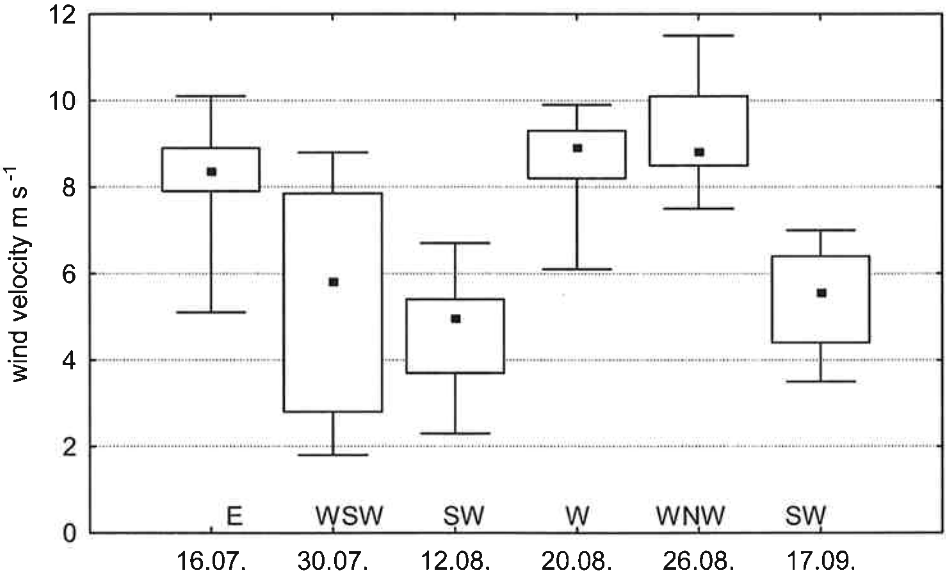

Fig.3. Wind speed [m s $^{-1}$] measured at weather station List/Sylt on six sampling days between 30.07. and 17.09. 2003. Also indicated are the wind directions in capital letters. Central point indicates median value, box: 25% - 75 % quartile, whiskers: min-max .

Flow measurements

An increase in flow velocity can be seen from 4 cm s $^{-1}$ on 16.07.03 to 11.95 cm s $^{-1}$ on 26.08.03. Figure 4a) presents the average values of pooled current velocities from each treatment on the respective sampling day. Due to technical problems no flow data are available for the 17.09.03.

Figure 4b) provides additional information on the flow characteristics of the three manipulated current regimes 'increased', 'mean' and 'reduced': the above mentioned general increase in current velocities is mirrored in each of the three treatments ('increased', 'mean' and 'reduced'). A clear distinction between treatments is seen at each sampling day with higher velocities for the 'increased' lanes of 12.58 cm s $^{-1}$ on 26.08.03 and lowest velocities for the 'reduced' range of 0.98 cm s $^{-1}$ on 12.08.03. High variability in measurements from the 30.07. was probably due to the partially sheltering effect caused by the off shore wind from West.

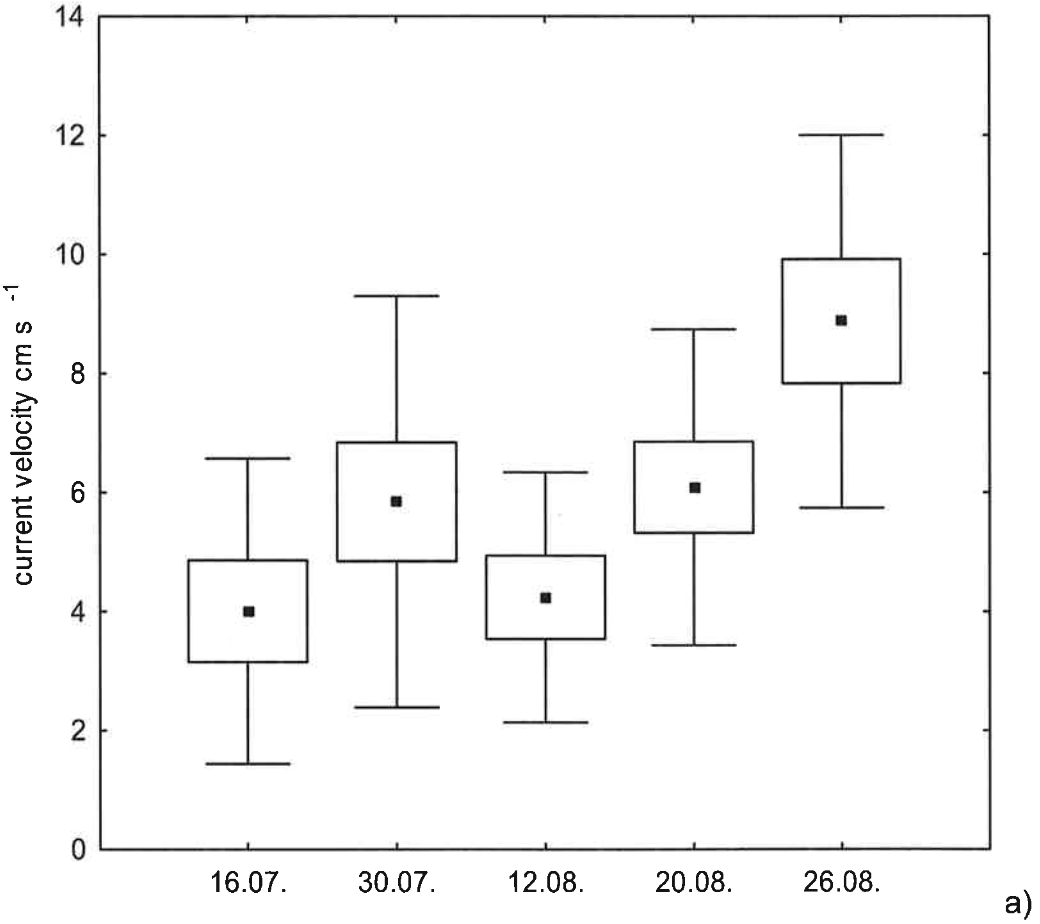

Fig. 4 a), b): a) Mean current velocity in [cm s $^{-1}$] on five sampling days. No current velocity data are available for the 17.09.03. Box: mean ±SE; whiskers: mean ±SD.

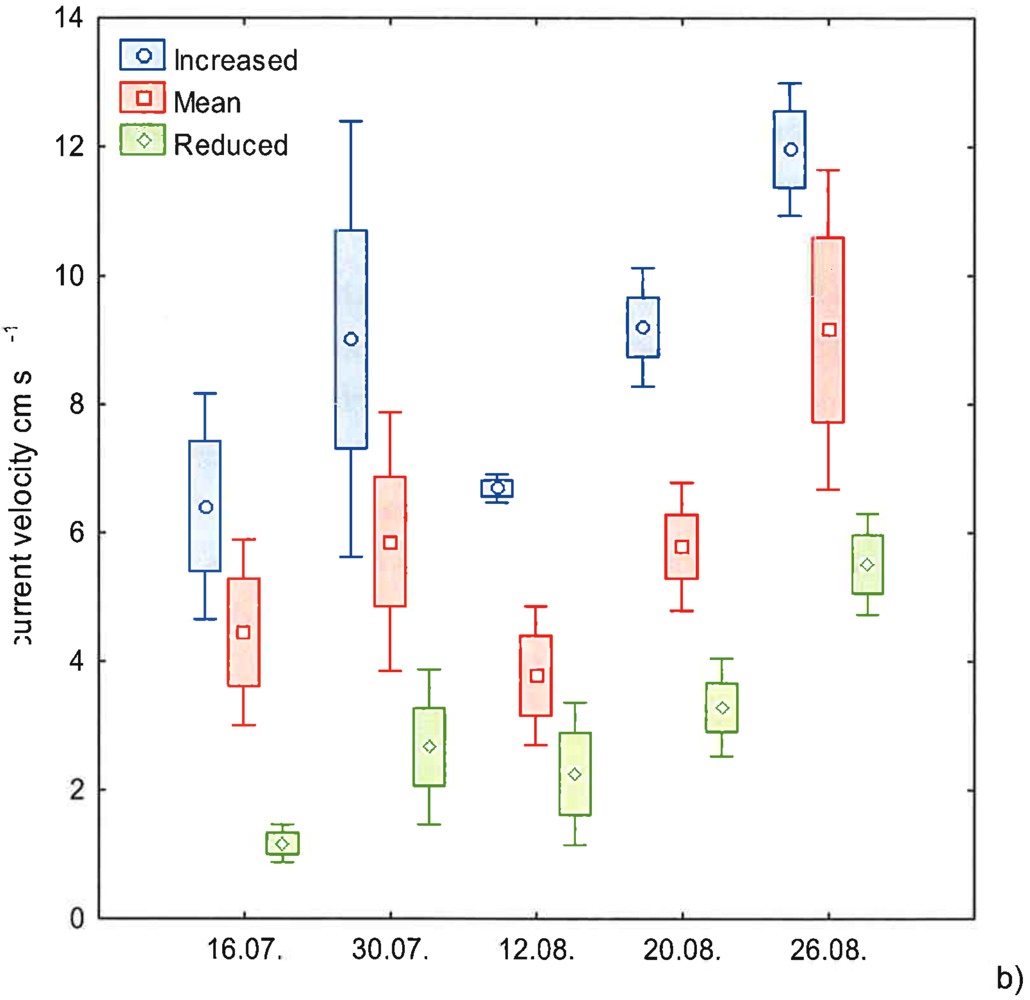

Fig. 4 b): Average values of each flow treatment. Box: mean ±SE; whiskers: mean ±SD.

Grain size

Grain size was approximately 1.5 Φ (sorting coefficient), with a medium diameter of between 0.2 and 0.63 mm. The median (Md) for the upper first centimetre of sediment samples was approximately 0.3 – 0.4 mm, indicating medium to coarse sand according to the Wentworth grade classification. These findings are in accordance with results from Hedtkamp (2005) who measured a mean of 0.35 mm on a sandflat near List, and Deussfeld (2003) who measured a median grain size of surface samples being 0.4 mm close to the sampling site described in this thesis.

Chlorophyll a: sediment and water

Figures 5 a) and b) give an overview of chlorophyll a values from sediment samples on five sampling days (16.07., 30.07., 20.08., 26.08. and 17.09.03) and from water samples (average of whole tidal cycle) on six sampling days (16.07., 30.07., 12.08., 20.08., 26.08., and 17.09.03). Between 16.07.03 and 17.09.03 there appeared to be a constant increase in chl *a* in the sediment with mean values ranging between 11.4 and 18.4 µg chl *a* g $^{-1}$. The detailed Figure 5 b) shows the significantly higher chl *a* values found consistently in the 'reduced' lane on all sampling days ($p = 0.02$). In August and September, the differences between Chl *a* values from the 'increased' and 'reduced' flow treatments were highly significant with $p < 0.01$.

In contrast to the seasonal increase in sediment chl *a*, the opposite tendency was found in water samples with the exceptionally high values of 36.7 µg l $^{-1}$ on 16.07. decreasing to the lowest value of 3.6 µg l $^{-1}$ on 17.09.03. No statistically significant influence of flow treatment on chl a concentrations was observed. However, the influence of incoming or outgoing tide proved to be significant with $p = 0.04$. Also noticeable are the high standard deviations on 16.07. and 30.07.03, with standard deviations of 2.7 and 2.6 being up to 4.5 times higher than the lowest standard deviation value of 0.6 on 26.08.03. Chl *a* concentrations from water in the 'increased' flow treatment on 30.07. showed a very high variability with standard deviations twice those on other sampling days or flow treatments.

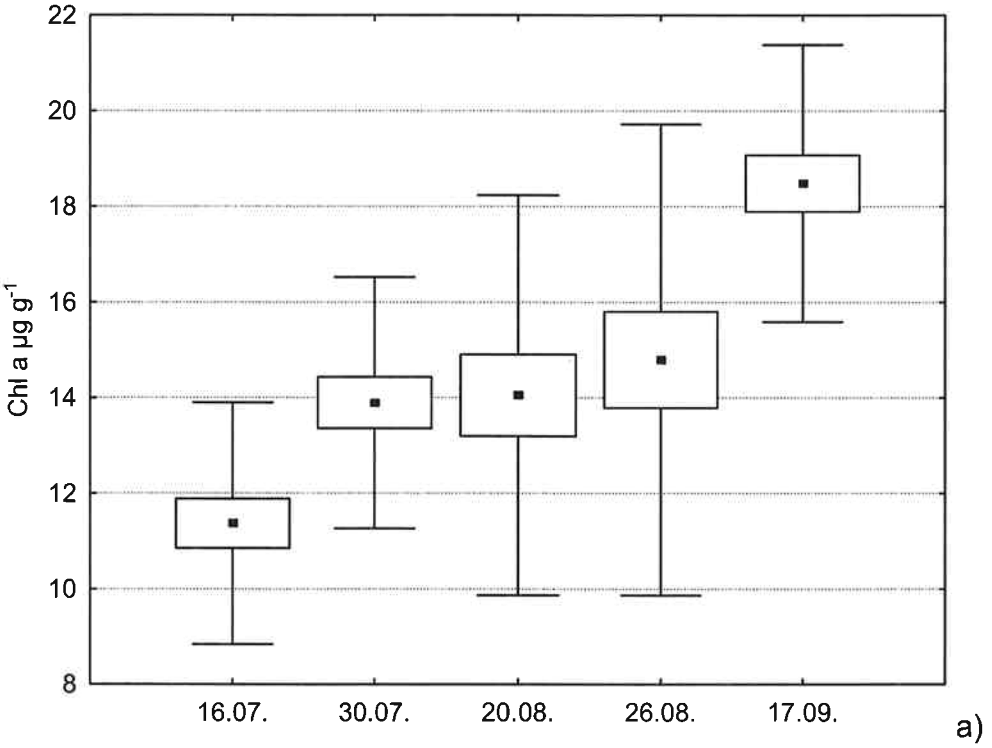

Fig. 5 a), b). Chl *a* µ g^{-1} (in sediment) on five sampling days between July and September. No sediment samples were collected on the 12.08.03. a) Averaged values of all three flow treatments 'increased', 'mean' and 'reduced'. Mean values, box: mean ±SE, whiskers: mean ±SD.

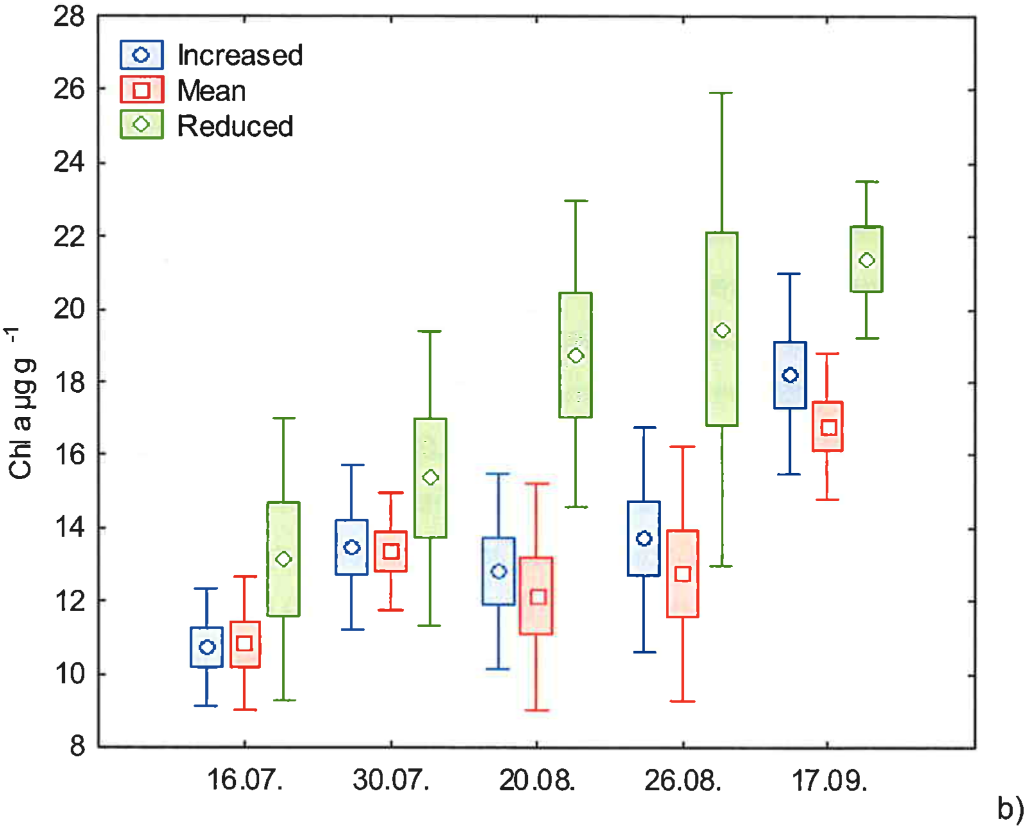

Fig. 5 b) Average values of each flow treatment. Mean values, box: mean ±SE, whiskers: mean ±SD.

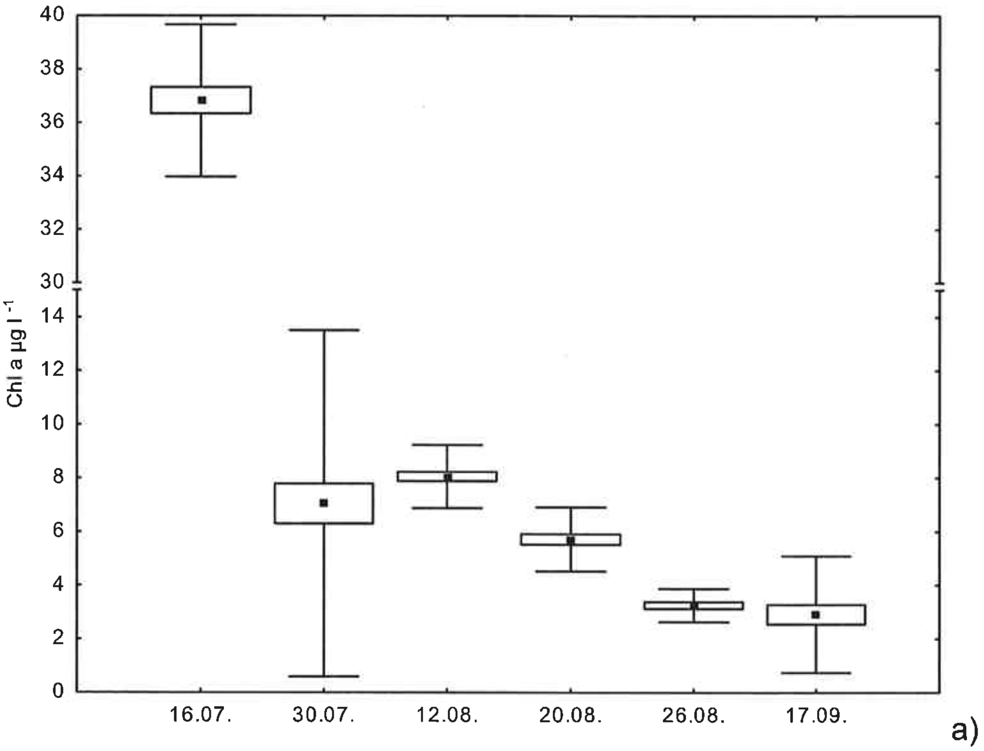

Fig. 6 a), b). Chl *a* µ l^{-1} (in water) on six sampling days between July and September a) Averaged values of all three flow treatments 'increased', 'mean' and 'reduced'. Mean ±SE, whiskers: mean ±SD

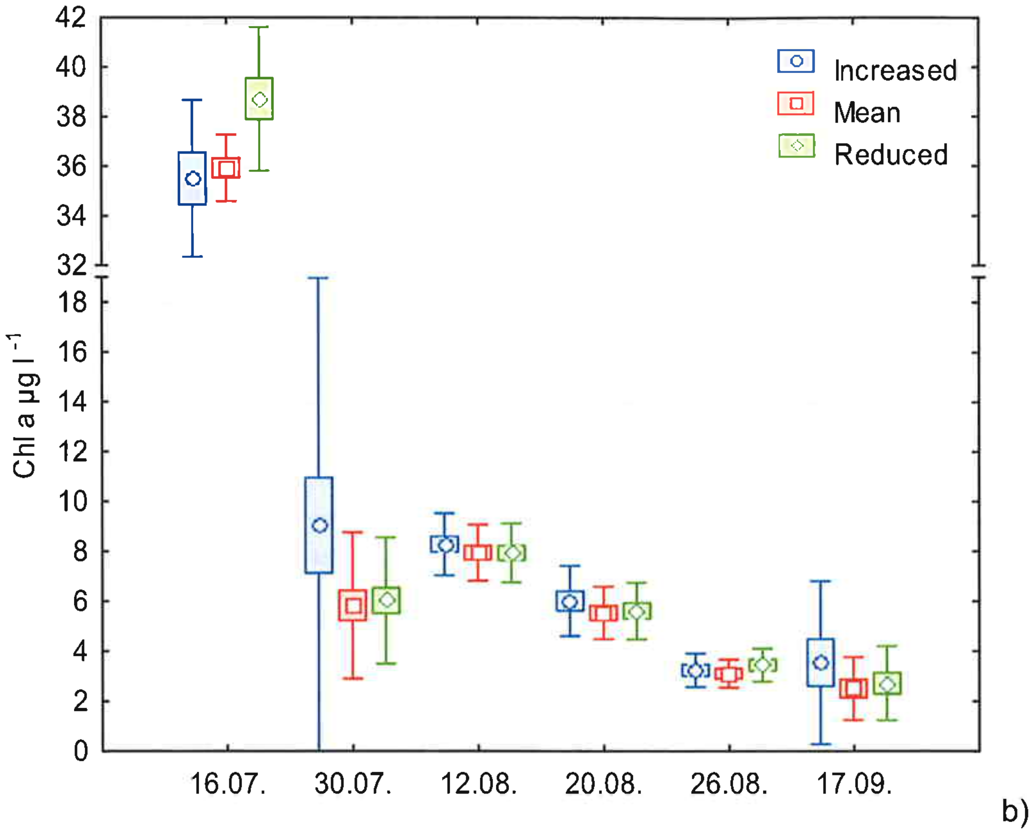

Fig. 6 b). Average values of each flow treatment. Mean values, box: mean ±SE, whiskers: mean ±SD.

Suspended matter (SPM)

Figures 7 a) and b) show mean SPM concentration. SPM was significantly correlated with Chl *a* (Spearman Rank R = 0.73). A test of the differences between incoming and outgoing tide also proved to be significant with p = 0.02 (not shown). SPM concentration was exceptionally high on 16.07.03, with a mean of 172.33 mg l^{-1}, which is more than 8 times the average (21.2 mg l^{-1}) of the remaining 5 sampling days. Like chl *a* values on the 30.07.03, SPM values show conspicuously high standard deviations around the second highest mean value of the season on this date, with a mean of 36.8 mg l^{-1}, and SD = 23.6. Figure 7b) shows SPM concentration for each of the three flow treatments. The highest values for SPM as well as highest standard deviations on 30.07. were found in the ‘increased’ lane. Unlike the case of chl *a* values, no seasonal trend is recognisable, with values for the remaining sampling days of: 18.5 mg l^{-1} on 12.08.03, 19.7 mg l^{-1}on 20.08.03., 12.4 mg l^{-1}on 26.08.03 and 18.6 mg l^{-1} on 17.09.03.

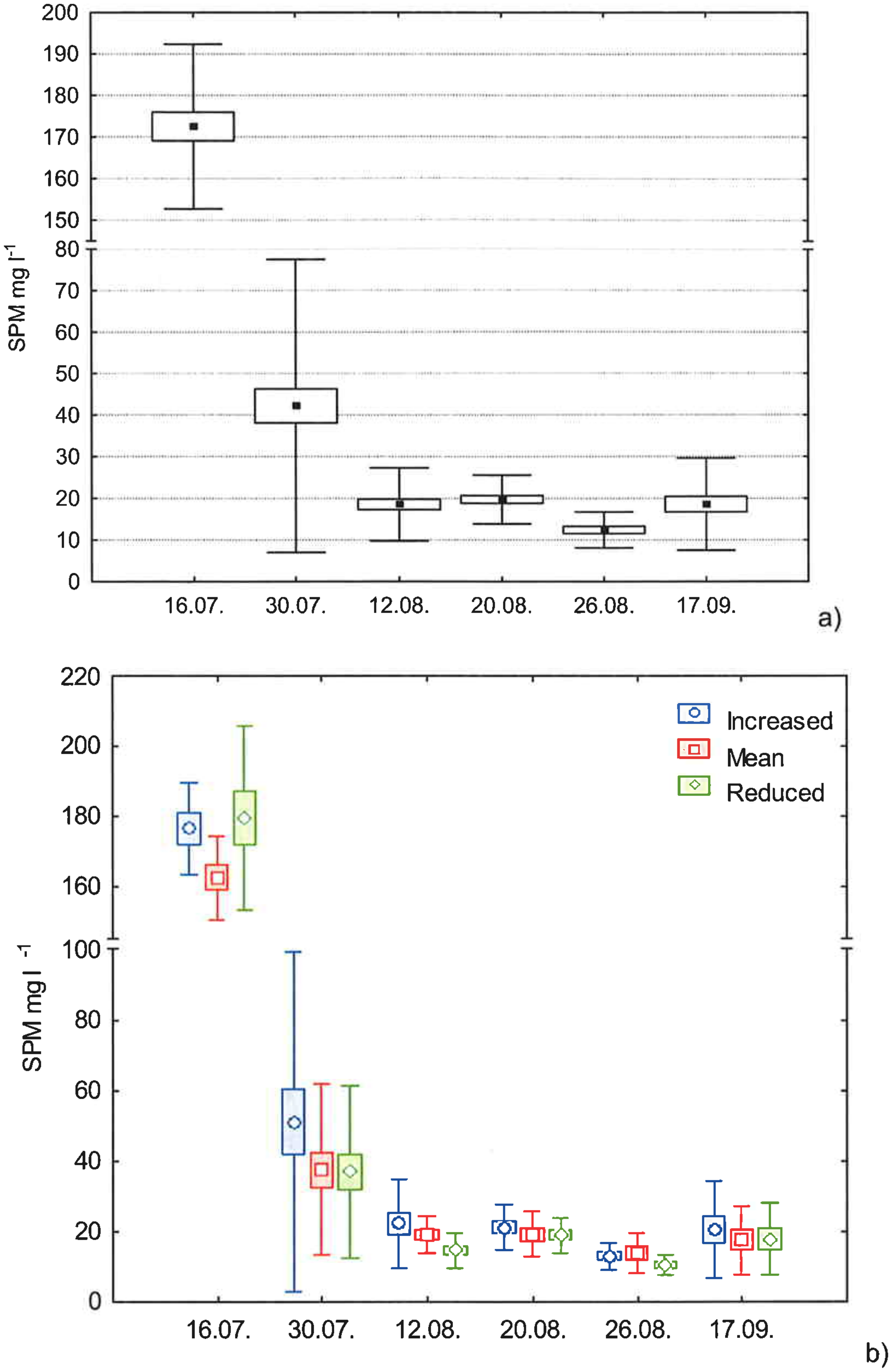

Fig. 7 a), b). Suspended matter (SPM) mg l^{-1} (water) on six sampling days. a) Averaged values of all three flow treatments 'increased', 'mean' and 'reduced'. b) average values of each flow treatment. Mean values, box: mean ±SE, whiskers: mean ±SD.

C:N ratio in water and sediment

Mean C:N ratios in water samples (averaged flow treatments, Figure 8 a), b)) ranged between 3.9 ±1.3 and 8.6 ±0.7 on the six sampling days. The overall mean C:N value was 6.7 ±1.5. Excluding the exceptionally low value of 3.9 on the 12.08.03, the overall mean value was 7.2 ±0.8. Tests for differences between flow treatments showed no significance for both water and sediment samples (Figure 8 b)). The same applies to differences between incoming and outgoing tides for water samples. A high variability between samples in all three flow treatments was found on the 12.08.03 with values ranging between 2.6 and 5.4. This was associated with comparatively high N concentrations in the water during the outgoing tide and could be coupled to the relatively high chl *a* values of 8.3 µg l^{-1}. The mean sediment C:N value was 7.8 ±1.0, but when the 16.07.03 with the lower value of 5.9 was excluded, the mean C:N ratio was 8.3. Standard deviations were generally higher for sediment samples compared to water samples.

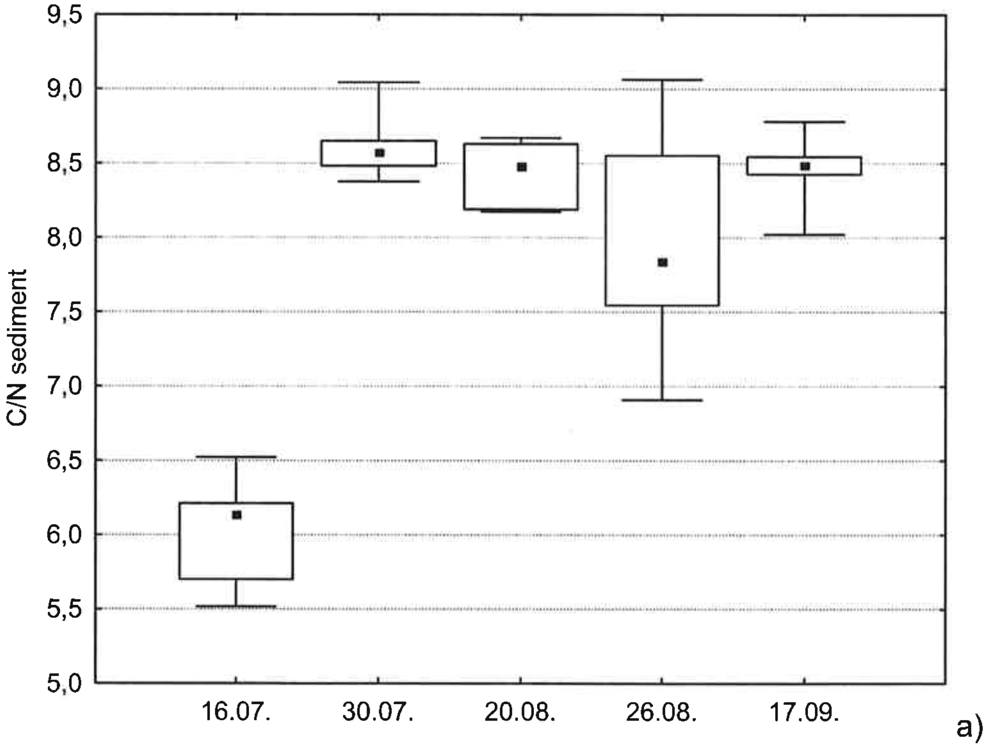

Fig. 8 a), b). Carbon to nitrogen ratio (C:N) in sediment and water. a) C:N in sediment, all flow treatments, on five sampling days. On 12.08. no sediment samples were collected. Point indicates median, box: 25% and 75% percentiles, whiskers: min/max.

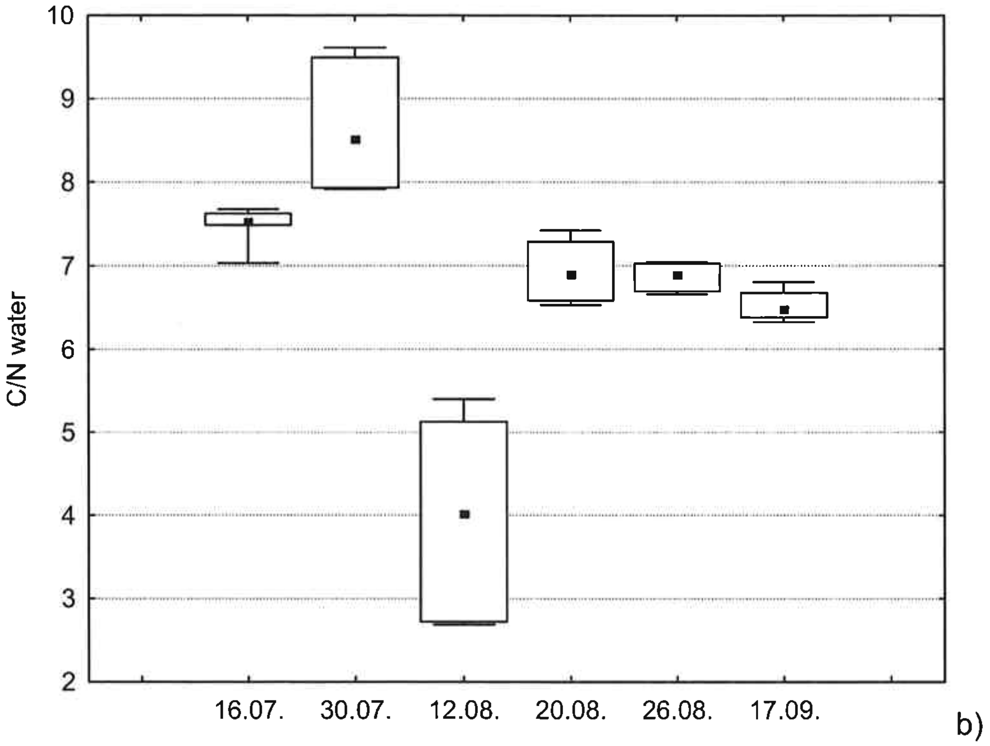

Fig. 8 b). C:N ratio in water samples, all flow treatments, on six sampling days. Point indicates median, box: 25% and 75% percentiles, whiskers: min/max.

Particulate organic carbon and nitrogen (POC, PON) in sediment

The particulate organic carbon content of the sediment was on average 163.47 µmol g^{-1} ± 47.6 % (1961.66 µg g^{-1} ± 47.6 %) and ranged between 62.3 and 488 µmol g^{-1} sediment. This value of 62.3 µmol g^{-1} on the 17.09. is considered as an outlier since the 16.07. presents the day of lowest POC contents in the sediment with an average of 116.4 ± 16.1. A weak trend in increasing values to an average of 181 µmol g^{-1} ± 16.1 on the 17.09. can be seen (see Figure 9, with POC in µg g^{-1} sediment). With p = 0.01, the flow treatment 'reduced' showed a significant effect on POC.

The particular organic nitrogen (PON µmol g^{-1}) content of the sediment had an average of 20.58 ± 41.88 % SD and showed a highly significant correlation with POC at a 99.95 % confidence level, both over the average of all data with $r^2 = 0.93$ and r^2 between 0.97 and 0.99 for the five sampling days between July and September.

No seasonal trend was found in the relationship between carbon and Chl *a* (Figure 10) with an average across all sampling days of 142.92 ± 27.21 %. But both are significantly correlated ($r^2 = 0.55$, $p = 0.05$) and the regression analysis suggests that different carbon sources exist because lower, or non significant correlations on e.g.

16.07. and 30.07. are evident for carbon not linked to chl *a*. For correlations of PON/POC and POC/Chl *a* see Table 2.

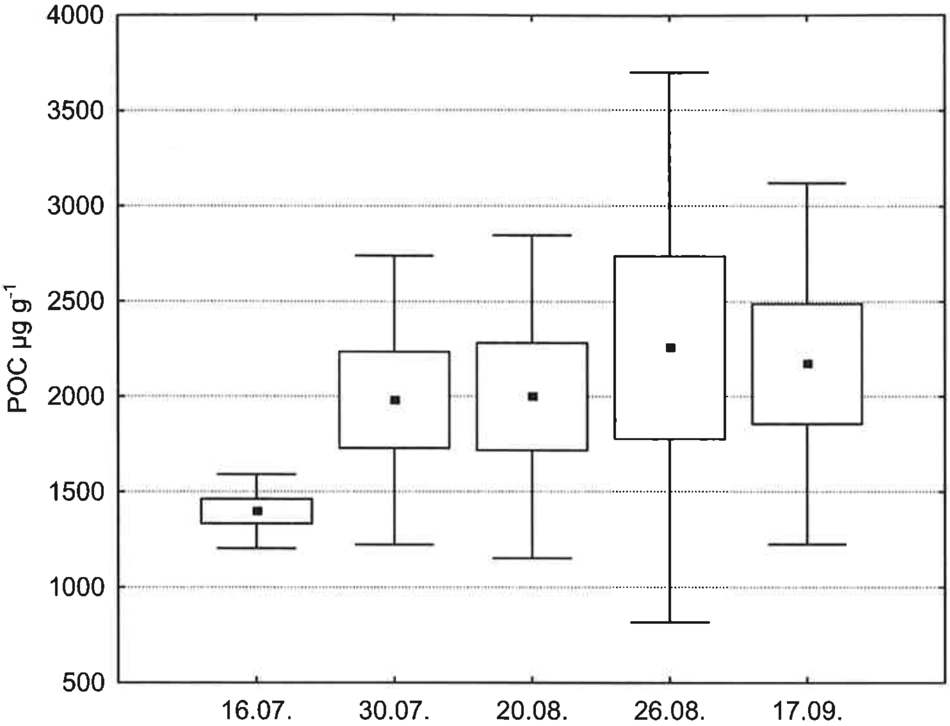

Fig. 9. Particulate organic carbon (POC or µg g^{-1}) in sediment on five sampling days between July and September 2003. Point indicates median, box: 25% and 75% percentiles, whiskers: min/max.

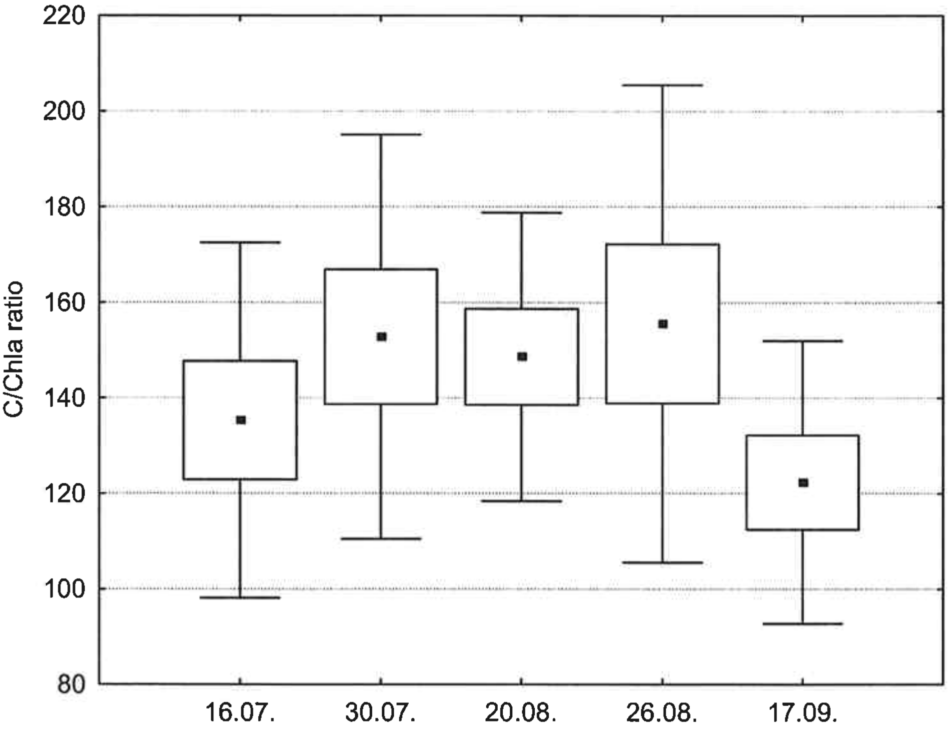

Fig. 10. Carbon to Chl a ratio in sediment on five sampling days between July and September 2003. Point indicates median, box: 25% and 75% percentiles, whiskers: min/max.

Table 2. Sediment particular organic carbon (POC in µmol g^{-1} or µg g^{-1}) and nitrogen (PON µmol g^{-1}) and chl *a* µg g^{-1} averaged across the lanes for all sampling days and for each sampling day, n = 9. Asterisk indicates significant correlation based on student's t-test with the following confidence levels: *** 99.95%; ** 97.5% and * 95%.

CORRELATIONS	PON/POC µmol g^{-1}	POC/Chla µg g^{-1}
All data	y = 8,7527x - 16,66	y = 171,49x - 385,02
	*** R^2 = 0,9363	* R^2 = 0,5599
16.07.	y = 9,6513x - 70,279	y = 27,162x + 1103,7
	*** R^2 = 0,9774	R^2 = 0,1295
30.07.	y = 8,4413x + 2,8534	y = 165,09x - 182,93
	*** R^2 = 0,9973	R^2 = 0,4071
20.08.	y = 8,6945x - 4,8167	y = 186,5x - 489,76
	*** R^2 = 0,9976	** R^2 = 0,7266
26.08.	y = 8,8873x - 17,703	y = 274,07x - 1558,7
	*** R^2 = 0,991	* R^2 = 0,6694
17.09.	y = 8,8873x - 17,703	y = 186,12x - 1033,7
	*** R^2 = 0,991	** R^2 = 0,731

Cell counts: sediment and water

Cell abundances in sediment samples (30.07., 20.08. and 26.08.) showed a distinct sensitivity to the flow treatment (Figure 11 b). The mean was $3.0*10^4$ cells g^{-1} in the reduced flow lanes, this treatment accounting for 29 % of total cell abundance (all lanes). Cell abundances in the 'mean' flow lanes accounted for a further 34 % of total abundance, while the 'increased' lanes contributed the highest proportion (36 %) of total cell abundance. The differences between flow regimes were significant with p = 0.04. Sorted by sampling day, the lowest abundances were found on the 20.08.03 with a total (average of all treatments) of $2.1*10^4$ cells g^{-1}, followed by $3.9*10^4$ cells g^{-1} on the 30.07.03 and $4.4*10^4$ cells g^{-1} on the 26.08.03.

Water samples analysed for diatom cell abundances (12.08., 20.08., 26.08. and 17.09.) revealed lowest cell numbers on the 12.08.03 (3.08 $*10^5$ cells l^{-1}) (Figure 12 a, b). Cell numbers on the remaining sampling days ranged between 8.9 cells l^{-1} and 7.7 cells l^{-1} (on 26.08. and 17.09., respectively). Neither flow treatment nor incoming/outgoing tide proved to be significant factors affecting cell abundance in the water. However, on 20.08. and 17.09.03 the cell numbers were higher during the outgoing tide than during the incoming tide.

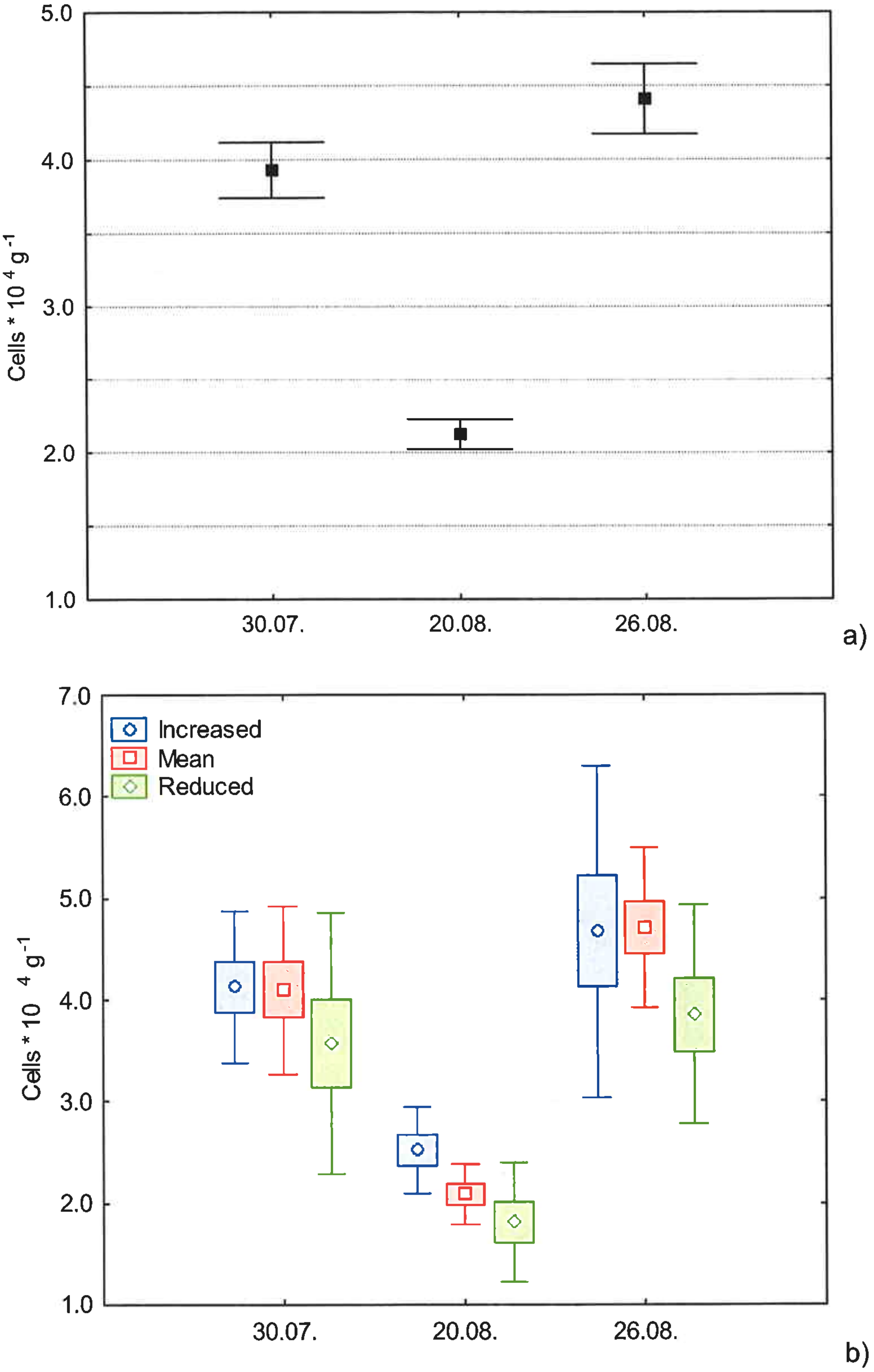

Fig. 11 a), b). Cell abundance [cells * 10 ^{4} g $^{-1}$] in sediment. a) Average cell abundance of all flow treatments, counted for three sampling occasions. b) Average cell abundance of each flow treatment, ‘increased’, ‘mean’ and ‘reduced’. Mean values, box: mean ±SE, whiskers: mean ±SD.

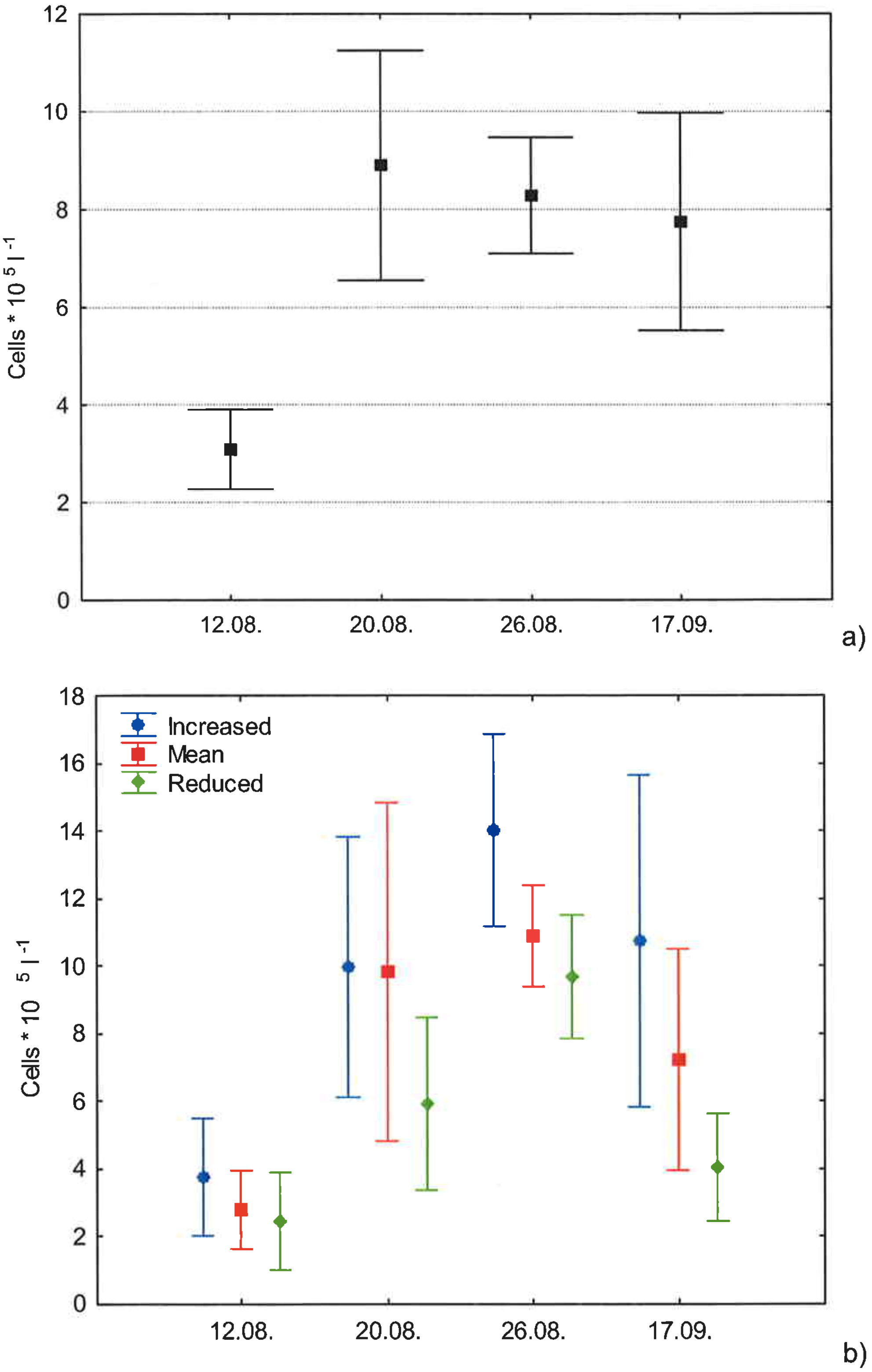

Fig. 12 a), b). Cell abundance [cells * 10 ^{5} l $^{-1}$] in the water column. a) Average cell abundance of all flow treatments, counted for four sampling occasions. b) Average cell abundance of each flow treatments, ‘increased’, ‘mean’ and ‘reduced’. Mean values, whiskers: mean ±SD.

Discussion

Suspended matter (SPM)

Suspended matter (SPM) plays an important role in coastal areas since it leads to a decrease in light availability for photosynthetic activity and organic particulate matter is an important food source in coastal ecosystems. The differences between the values of between 12.4 and 36.7 mg l^{-1} found in the present study and the readings of between 2 and 12 mg l^{-1} taken by Löbl (2005) further off shore are marked. Parameters such as chl *a* and suspended matter are clearly affected by the wind and wind direction. Although the wind velocity values ranged around 8 m s^{-1} during the experiment period and thus did not reach the highest values measured during the whole summer/autumn season, it did gust at peaks up to 10.1 m s^{-1}, directly from the open sea from East on 16.07.03. This implies a fetch (a term for the length of water over which a given wind has blown) that is (1) efficient enough to cause resuspension and (2) transporting resuspended material from the opposite coast across the Sylt-Rømø bight. Both pelagic chl *a* and SPM on this day present by far the highest values measured during the study whereas chl *a* values from sediment samples were the lowest of the five measured (sediment) sampling days. This is either due to seasonal variations in chl *a* content in the sediment, as the 16.07.03 represents the lowest measured chl *a* value with a mean of 11.4 µg g^{-1} compared to 17.09.03 with 18.4 µg g^{-1}, or due to resuspended material from the sediment surface. These findings stress the importance of paying attention to the benthic-pelagic coupling and to which factors drive this system. This is crucial not only for the role of microphytobenthos as a food source for suspension feeders or planktonic organisms (de Jonge & van Beusekom 1992, Muschenheim & Newell 1992, Herman et al. 2000) or their contribution to gross primary production in the water column (Shaffer & Sullivan 1988), but also for quantifying and understanding the benthic contribution to pelagic turn-over rates.

Sandy sediments with high permeability are characterised by enhanced turnover rates (Rusch et al. 2001). The seasonal increase in sediment chl *a* measured here could also be partly explained by an increase in phytodetritus; the summer season displayed extremely high water temperatures (up to 27 °C above the tidal flat) which caused stress and partial dying off of nearby growing seagrass (Schanz et al. 2002).

Particulate organic carbon (POC), organic nitrogen (PON) and chl a

Nutrient release from the sediment in times of low microphytobenthic productivity restores nitrogen to the water column and in turn organic matter import from the water column leads to high remineralisation rates in the benthos (Hedtkamp 2005). The ratio between organic carbon (C) and organic nitrogen compounds (N) provides information about the quality of components in the sediment and in the water column and can be used as an indicator of nutrient limitation. Hillebrand & Sommer (1999) describe an optimum range for C:N being 5 – 10. The authors also suggest that moderate N limitation would be indicated by a C:N ratio exceeding 8.3 which was, in the present study, the case for water samples from the 30.07.03. The lowest value of 5.5 from 16.07.03 indicates high growth rates and no N limitation, while the average sediment C:N ratio of the remaining samples of 7.8 is in accordance with findings by Hedtkamp (2005), who calculated values ranging between 5 and 9 for a similar sampling site on Sylt. With mean C:N ratios of 7.9, 7.8 and 7.9 for the three flow treatments 'increased', 'mean' and 'reduced', respectively, the reduction of the flow was not efficient enough to show a possible effect on the nutrient state in the sediment. An increase of flow velocity is promoting nutrient release from the sediment and thus counteracting a possible nutrient limitation (Asmus et al. 1998).

It can generally be stated that although there are slight fluctuations in sediment C:N ratios between the different flow treatments, the current velocity had little influence on the quality of the biological material in the sediment as reflected by C:N ratio. The high standard deviations of C:N in sediment samples compared to water samples imply a more homogenous distribution of carbon and nitrogen in the water column. The low ratio of 5.9 found on the 16.07.03 is mirrored in low chl *a* values and low current velocity, although not in cell abundances from sediment samples. On the other hand, analysis of the water samples of the same day revealed high C:N ratios and the highest concentration of SPM and chl *a* . This suggests that processes in the water column might be dominated by resuspension and transport due to fetch with a strong exchange between water and benthic compartments. Moreover, high SPM values on the 16.07.03 suggest a transfer of material into the sediment. The fact that on the same day POC/PON as well as POC/chl *a* showed no significant correlation compared to other sampling days, indicates that, possibly due to the prevailing easterly wind, organic matter not associated to chl *a* was transported across the Sylt-Rømø bight, masking the chl *a* signal. Different carbon pools can be comprised of, for example, detritus from grazed microphytobenthos, plant material, and also the production of extracellular polymeric substances (EPS) produced by microphytobenthic organisms will influence the C/Chl *a* ratio.

On the 12.08.03 the mean C:N ratio in the water column of 4 is the lowest of all sampling days and is associated with N values about ten fold higher than were found on other sampling days during the outgoing tide. This low ratio together with comparatively high chl *a* values and low diatom cell abundances in the same samples suggest fresh, living material, e.g. heterotrophic flagellates.

The low nitrogen values between 0.1 and 0.2 µmol l^{-1} from 30.07. – 17.09.03 reflect the summer situation in the Sylt-Rømø Bight. Löbl (2005) measured values below 1 µmol l^{-1} until mid-September.

Although the sediment receives planktonic and resuspended organic debris of microalgal (and macroalgal) origin, the C:N ratio is not significantly lower than the water C:N ratio. This is in accordance with the results of Hedtkamp (2005), indicating a fast turn-over rate of nutrients by the microphytobenthos: A minor exchange of nutrients between sediment and water column takes place as the microphytobenthic community takes advantage of the nutrients remineralised in the sediment. The author also confirmed a high advection capacity of the permeable sediment which ensures a constant supply of nutrients; high temperatures prevailed in the summer of 2003 and, due to higher organic matter loading, remineralisation was higher than uptake by phytobenthos as indicated by the summer maximum of pore water concentrations in the sediment of $Si(OH)_4$, NH_4^+ and PO_4^{3-}.

Chl a

The significant seasonal increase in sediment chl *a* clearly indicates the growth of the microphytobenthic community which comprises not only diatom cells but also photosynthetically active flagellates and cyanobacteria. This is evident in the discrepancy between higher chl *a* values in the 'reduced' flow treatment on the one hand and the consistently lower diatom cell numbers in the same flow treatment on the other. Low suspended matter values point to a favourable light regime for benthic, phototrophic organisms. The fact that current velocity rises parallel to seasonally rising sediment chl *a* values does not indicate causality: these parameters do not necessarily affect each other. Indeed, chl a values remained almost constant across the three current regimes on all but one sample date, suggesting no causal line between these two parameters. Suggesting a seasonal trend, the five data points for current velocity show an increase in flow velocity not withstanding the fact that an assumed, equally low value for the 17.09. as in wind speed would possibly detrend. Therefore, a seasonal trend for the five data points taken between July and August is not assumed. Low concentrations of benthic microalgal biomass generally correspond with periods of strong, frequent wind events such as occur in spring, winter or autumn (Nelson et al. 1999). A high variability of carbon to chl a ratio values can be extracted from the literature, ranging between 10.2 and 153.9 for the sediment (de Jonge 1980), which is also subjected to change seasonally. The mean value of the C/chl *a* ratio in this study is with 142.92 well within the range for benthic calculations of carbon linked to chl a.

Diatom cells in sediment and water

Benthic cell numbers on the 20.08.03 amounted to only half those amount of diatom cells and large dinoflagellates (e.g. species of the genera *Thecadinium* and *Amphidinium*) occurred in copious amounts (pers. obs.) found on other sampling days. This might be a coincidence but the only slight decline of chl *a* values in the 'increased' and 'mean' treatment lanes compared to the drop in cell numbers could be due to high numbers of autotrophic flagellates, with the massive presence of large dinoflagellate cells causing migration of motile diatom cells into deeper sediment layers. Observation of diatom species showed that the community was dominated by epipsammic (attached to substratum) diatoms such as *Amphora* and *Delphineis* and small benthic *Navicula* species associated with the sediment. It is not known whether these dinoflagellates were producing toxic substances but according to Hoppenrath et al. (2004) several representatives of the above named genera are heterotrophic thus playing an important role in the benthic food-web. Furthermore, cell abundances in the 'increased' and 'mean' flow treatment lanes were always, albeit not significantly, higher than those in the 'reduced' flow treatment. The reason for this could be a reduced EPS (extracellular polymeric substances) matrix due to higher flow velocities, which in turn causes an increase in sediment permeability allowing more cells to enter the sediment, either actively or by advectional forces (Hüttel & Rusch 2000, Hedtkamp 2005).

Concerning the water column, two sampling days, 12.08. and 20.08., displayed the highest abundances of flagellates, with about $2.1 \cdot 10^6\ l^{-1}$ cells. Several species feed on diatom cells (e.g. *Gyrodinium undulans, Paulsenella* spp.) which, together with herbivorous zooplankton and a seasonal decrease in nutrients in the water column would explain the decline in chl *a* over the season as well as the decrease in cell abundances analysed in water samples. Löbl (2005) measured the highest net phytoplankton growth rate in August 2003 with biomass doubling almost once per day, but since the grazing impact was in the same range as growth rates, no accumulation of algal biomass occurred. The potential loss of phytoplankton biomass due to the benthic assimilation is assumed to be 7-25 % per day. Furthermore, the activity of benthic filter feeders is very strong in the Sylt-Rømø Bight (Asmus & Asmus 2005) and changes with season and environmental influences including temperature, tidal cycle, and suspended matter concentrations and quality (Widdows et al. 1998).

Higher cell abundances in the water column during the incoming tide compared to the outgoing tide, e.g. at the 26.08.03, were not necessarily due to resuspended diatom cells. Cell counts analysed at species level revealed that the abundance of small benthic species was even lower during the incoming tide, whereas higher numbers of pelagic species had been subjected to tidal import and export, as they occur in vanishingly small numbers only on the sediment surface.

Wind-induced waves enhance local turbidity and turbulences. Bottom stress and resulting resuspension can be generated even by wave-induced bottom orbital velocities that are much smaller than the mean current velocity. This was experimentally confirmed by Anderson (1972), Lesht et al. (1980) and by Carper and Bachmann (1984) who found that concentrations of fine particles in suspension were correlated with the presence of surface waves. For her studies in a sampling area close to the one described in the present study, Deussfeld (2003) calculated that 3-4 % of the wind speed is transmitted into the water column and can cause back-currents of 0.3 – 15 cm s^{-1}.

The noticeable drop in benthos cell numbers on the 20.08.03 could be explained by an antagonistic effect of wind and waves: the wind direction was westerly, therefore the tidal areas in the immediate vicinity of the coast were protected from the offshore wind. This fact plus the reduced turbulence due to antagonistic effects of wave-wind interactions might favour grazers such as Hydrobia to remain undisturbed on the sediment surface, grazing on diatom cells (87 % of *Hydrobia ulvae*´s diet comprises microphytobenthos, Baird et al. 2004, Schanz 2002). Moreover, the wind on the 19.08. was also from West and thus providing a sheltered situation for two days time.

The sheltering effect of the 'reduced' flow treatment seems to be reflected in the significantly higher sediment chl *a* values in the respective lanes. A biofilm can presumably build up, comprising not only diatom cells but also flagellates and cyanobacteria, measurable as chl *a* .

Wind has an important influence not only on the resuspension of matter from the sediment surface but also on the permeability of the sediment. Rusch et al. (2001) found a strong variability in sediments unrelated to seasons and bacteria: Diatoms and detritus in an intertidal sandflat are subject to a highly sufficient transport by advection across the water-sediment interface. Analyses carried out by Hedtkamp (2005) on Sylt confirm that wind speed had the highest influence on sediment permeability. Factors such as fine fraction, chlorophyll a and carbohydrate contents in sediments are subject to change according to permeability.

Measurements of parameters such as SPM and chl *a* differ significantly between samples taken in the intertidal area and offshore (approximately 2 km offshore) as comparison with data from the Sylt time-series studies showed, and this spatial and temporal variability must be taken into account for future calculations of total turn-over rates for the Sylt-Rømø Bight. The same applies to extrapolation of the present benthos data to longer spatial and temporal scales, not only because of the high variability of parameters but also because of the high variability between sites on intertidal flats (e.g. muddy and sandy sites, seagrass areas).

Because resuspension and redistribution of either cells or suspended matter is related to variability in wind, flow velocity and to a certain extent tides, sedimentation will also be dependent on physical factors such as fetch conditions, which are determined by wind direction, and vary seasonally (Edelvang 1997). The influences of spring and neap tide are superposed by factors such as wind direction and wind velocity.

The following chapter 4 is dealing with the implication of wind and wave induced alteration of hydrodynamics on diatom species in regard to resuspension.

Conclusions

The present results suggest that biological processes on intertidal sandflats are subjected to varying environmental factors such as flow velocity, wind velocity and direction. Analysis of sediment samples showed an effect of the three flow treatments, with higher chl *a* and POC values in the 'reduced' flow treatment compared to the 'increased' and 'mean' flow, but higher diatom cell abundances associated with ‘increased’ flow compared to ‘reduced’ flow treatments. With regard to the reduced flow treatment, this finding indicates different carbon sources for example due to sedimentation, varying across the sampling days. Although not statistically significant, there was an influence of incoming or outgoing tide on cell abundances in the water column, indicating resuspension, or either export or import of benthic and pelagic cells, respectively.

The effect of wind direction on hydrodynamic conditions is well known, and less sheltered areas of the coastline will experience stronger wind-wave effects that cause turbulence, resuspension, and enhanced input of allochtonous (both detritus and live) material representing an additional carbon source.

Parameters such as chl *a*, POC and PON in the sediment increase during the season. Because the results of the three sediment sampling days do not indicate a constant seasonal trend in diatom abundance, a cause might be either growth of the mixed microphytobenthic community or a steady accumulation of, for example, detrital material or other carbon sources such as EPS produced by other members than diatoms of the benthic community.

Since the C/N ratio is constant over the season, there seem to be no major changes in the quality of the organic matter and therefore the accumulation in the sediment is founded in the dominance in other members of the benthic community, for example dinoflagellates. Furthermore, the advective pore water flow of the permeable sand led to a constant remineralisation and supply with nutrients.

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Chapter 4

The influence of hydrodynamic forces on diatom species resuspension: a three-current-flume, *in situ* experiment

Abstract

The aim of this study was to characterise the dynamics of benthic and pelagic diatoms (Bacillariaceae) in the intertidal and to assess the influence of three different current regimes on the resuspension characteristics of selected diatom species. This was achieved by employment of a three-current-flume, a device that can be used in situ in order to perform measurements under three different manipulated current velocities: 'increased', 'mean' and 'reduced' flow.

Sediment and water samples collected between July and September 2003 were analysed for diatom taxonomy and cell counts. Water column samples showed erratic compositions of species compared to rather stable occurrences of species from benthos samples. Different wind directions seem to exert different flow characteristics, resulting in controversial patterns concerning a) tides, b) flow velocities, c) cell numbers and d) species distribution (e.g. northerly winds transport higher numbers of pelagic Chaetoceros species into the bight).

The two benthic genera *Amphora* and *Delphineis* show higher abundances in the 'increased' flow and 'reduced' flow, respectively. Preferences for changed sediment conditions are hypothesised.

Resuspension characteristics of seven exemplary genera (*Haslea/Navicula* group, *Gyrosigma/Pleurosigma* group, *Diploneis*, *Amphora*, *Entomoneis* and one group combining small pennate diatoms <15 µm) was analysed by evaluating the proportion of cells found on the sediment as well as in water samples from incoming and outgoing tide.

Introduction

Resuspension of micro algae from the sea bed is influenced by various factors e.g. wind, tidal forces, currents. Bottom friction causes shear forces in the flow which resuspend the sediment and thus the microphytobenthos associated with it. Delgado (1991) calculated that about 25 % of the biomass present in the 0.5 cm top layer of the sediment was permanently resuspended. The resulting vertical mixing process significantly influences primary and secondary productivity, material fluxes at the water-sediment interface and pollutant dispersal. These processes are dominated by wind and waves and tidal influences especially in shallow estuarine areas.

The benthic diatom community comprises different life modes: motile epipelic species that exhibit vertical migration towards and away from the sediment surface by aid of the slit like raphe system, epipsammic species living attached to a substratum, epiphytic on macrophytes and tychopelagic species, that are associated with the sediment but tend to resuspend into the water column and sink back to the bottom at slack tide or low hydrodynamic conditions. Consequently the latter circumstances also cause parts of the planktonic fraction to sink to the bottom. Although epipsammic diatoms are attached to the sand grains, they are still able to move. Harper (1969) measured the movement of *Amphora ovalis v. pediculus* with an average velocity of 1.7 µm s^{-1} and *Navicula oblonga* with 11 µm s^{-1}. Edgar & Pickett-Heaps (1984) report motile diatoms moving at speeds ranging from 1 to 25 µm s^{-1}. Different benthic diatom species are thus more or less subject to resuspension into the water column.

Benthic diatoms contribute significantly to the gross primary productivity of the water column (Shaffer & Sullivan 1988) and tidal resuspension of microphytobenthos is an important mechanism for making benthic microalgae available for filter feeding organisms e.g. bivalves. Compared to planktonic communities, benthic algae show less fluctuations in abundance during the winter season. Thus they are a reliable food source for the filter feeding as well as the suspension feeding community in winter (Baillie & Welsh 1978).

The factors determining algal cell distribution and species composition, both benthic and planktonic, are as numerous as the existing literature. Lauria et al. (1998) suggested that changes in phytoplankton populations in estuarine systems can result from seasonal and inter-annual variations in river flow, but more pronounced variations result from fluctuations in tidal-stirring. Cloern (1991), working in San Francisco Bay, showed that phytoplankton populations are strongly influenced by fluctuations in vertical mixing, with blooms occurring during periods of low mixing during the neap-tide. The spring-neap tidal cycle has been identified as an important factor influencing phytoplankton growth in estuaries and shallow coastal seas (Haas, 1981). Variations in algal biomass have been correlated to this cycle at two stations on the coast of Connemara, Ireland (Roden, 1994), with chlorophyll a maxima occurring during the neap tides. In Southampton waters Kifle and Purdie (1993) found that phytoplankton populations established themselves on the low neap tides and were then apparently flushed from the system during the spring tides. However, it is not only physical disturbance but also pollution and eutrophication that alter community structures (Admiraal & Peletier 1980, Snoeijs 1999, 1994). De Jonge & van Beusekom (1995) found that resuspension of mud and chl *a* from the top 0.5 cm of sediments was a linear function of effective wind speed (wind speed averaged over three high water periods immediately preceding collection of water column samples).

Most studies dealing with microphytobenthos are concerned with the relationship between chl *a* and biomass, the contribution of benthic cells to pelagic production (de Jonge & van Beusekom 1992, Shaffer & Sullivan 1988, Lucas 2003), and the importance of microphytobenthos as food source for benthic and pelagic grazers (Miller et al. 1996, Epstein 1997, Tweddle et al. 2005). Their function as contributors to sediment stabilisation has also been recognised in many studies over the past years (e.g. Paterson 1990, Amos 2004, Madsen 1993). However, few studies endeavour to ascertain the complex interactions of biota in context with hydrodynamic characteristics at the species level (Lucas et al. 2001, deJonge & van den Bergs 1987).

The introduction of flume devices as research tools allowed workers to investigate and link biological and hydrodynamic processes *in situ* or under controlled laboratory conditions. Different flume types, annular, straight or racetrack, depending on the current inducing mechanisms. Most annular types are mobile and can be used in situ, whereas straight ore racetrack flumes can be up to several meters or cover a room filling track of 17.5 m length (NIOO, Netherlands). All types are deployed according to the requirements to investigate parameters such as bed shear stress, erodability of sediments and suspended sediment concentration, biotic and abiotic processes, flow conditions, benthic-pelagic exchange, as well as the impact of fluid dynamics on settlement, food availability, transport processes (e.g. Stocks 2002, Snelgrove et al. 1999, Widdows & Brinsley 2002, Amos 1992 , Friedrichs et al. 2000, Lucas 2000, 2001;

Blanchard et al. 1997, Asmus et al. 1990, 1994, Schanz 2002, Dobereiner & McManus 1987).

To date, not much is known about the behaviour of diatom species under the influence of different hydrodynamic conditions and literature is sparse when it comes to species levels. The aim of this study is to characterise the dynamics of benthic and pelagic diatoms in the intertidal and to assess influences of different current velocities on the resuspension behaviour of selected diatom species. Comparable experiments have not been previously recorded since actual cell counts of individual species have not been attempted so far. There are at least 3 aspects to this: a) controlled experiments are very difficult to perform in coastal waters. The high complexity of interacting and constantly changing factors - physical as well as chemical – require continuous research and long term studies to assess factors/dynamics like, e.g. shifts in species composition, b) in most experiments involving flume devices, usually suspended matter and chl *a* are the measured parameters used to characterise flow dynamics or to investigate processes characterising sediment-water exchanges. Diatoms are merely identified to predicate the general partition into pelagic and benthic species or genera, but c) resolution down to species level is important to gather more information on the ecology of the species.

Material and Methods

Sampling site

The sampling site is situated on the East coast of the island of Sylt, in the Sylt-Rømø Bight, Northern Wadden Sea (Figure 1). Bounded by the islands of Rømø (Denmark) to the North and the Danish/German coastline as well as a causeway to the South (since 1927), the only exchange for the Bight with the North Sea is a 2.5 km broad tidal inlet called Lister Tief. The intertidal flats comprise 95 % sandy sediments with a grain size between 0.2 and 0.63 mm. Fine sediments (grain size < 0.2 mm) account for less than 5 %. The intertidal flats are protected from prevailing westerly winds by the island.
The tidal range in the bight is about 1.8 m with minor deviations due to neap and spring tide or wind. The salinity of the water ranges from 28 to 32 (practical salinity units PSU).

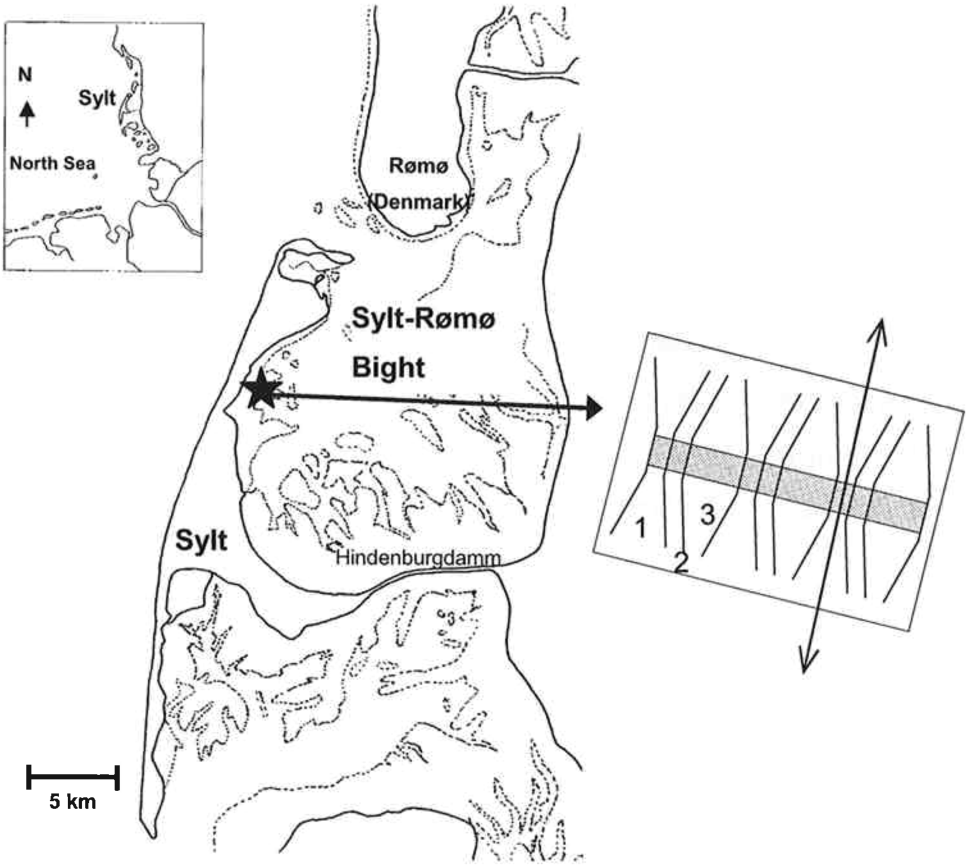


Fig. 1. Study area in the northern Wadden Sea. Inset: general map showing the location of Sylt in the northern Wadden Sea. Asterisk indicates sampling site with arrow leading to a diagram of the three-current-flume aligned to the bi-directional tidal currents (double headed arrow). Numbers 1, 2, 3 indicate the three manipulated flow treatments: 1 increased, 2 mean and 3 reduced.

Three-current-flume

The three-current-flume presents a device to allow *in situ* flow manipulation and sampling. It is constructed with steel bars and mantled on the vertical walls with a flexible, durable plastic fabric thus forming nine different lanes (see diagram in Figure 1). The flume is about 9 m long and 12 m wide, with a height of 90 cm. By narrowing or expanding the width of the respective channel the ambient current velocities can be manipulated into an accelerated, 'increased', or 'reduced' speed. A 'mean' lane serves as control and reflects conditions outside the flume. The sampling area is situated in the centre halfway along the flume, equidistant from the sides, where water and sediment samples were taken in the respective lane. The durable construction of the flume allows long term field work as it is resistant to weather conditions. Subsequently, the three flow treatments characterising an altered current regime will be referred to as 'increased', 'mean' and 'reduced' flow.

Flow measurements

Flow was measured at three different water depths of 10 cm, 20 cm above bottom and close to the water surface using either an Accoustic Doppler Velocimeter (ADV), NorTek, Norway, or an induction current meter (Marsh MacBirney 201M). The devices were employed to measure flow components over one tidal cycle, provided water levels were exceeding the blanking height of about 10 cm. Measurement was terminated, when water level sank below approximately 10 cm. Calculations of velocity represent the 'mean' of three parallels of the respective current velocity treatment, 'increased', 'mean', and 'reduced'. ADV data sampling frequency amounted to 8 Hertz (SI = 1/s).

Grain size analysis

For the analysis of grain size, replicate sediment samples taken from the three flume lanes with three different, manipulated flow velocities were freeze-dried and afterwards treated with H_2O_2 to remove organic substances. After rinsing with H_2O the grain size was measured by 'mean's of a QUANTACHROME CILAS-Lasergranulometer 1180. Classification occurred according to the Wentworth scale in size classes of phi-values (Φ = - $\log_2$ of grain size in mm).

Sampling

Table 1: Sampling day, type of analysis and wind data (daily average in ms^{-1} and direction)

Analyses/ Sampling day	30.07.03	12.08.03	20.08.03	26.08.03	17.09.03
Cell counts water	n.m.	x	x	x	x
Cell counts sediment	x	n.s.	x	x	n.m.
Current velocitiy	x	x	x	x	n.m.
Mean wind velocity. [ms^{-1}] and direction	4.3/ WSW	4.8/SW	8.5/W	10.4/WNW	5.7/SW

(n.m., n.s. = not measured or sampled, respectively)

Samples were analysed for five sampling days between July and September 2003 (see Table 1). One sampling session included the collection of water during in- and outgoing tides using an ISCO-STIP automatic sampler every 15 or 20 minutes. The cylindrical suction head was fixed in the middle of the sampling area of the respective flume lane between 10 - 20 cm above the sediment surface. Sampling started and ended when water level was high enough to cover the suction unit and when too low to enable air-free drawing in of water, respectively. The samples comprised 0.5 litres and were processed instantly after return to the laboratory for analyses of Chl *a* (see chapter 1) and cell counts, the latter samples were stored in brown bottles with four drops of Lugol´s solution added. A total of 24 samples were collected on each flood-ebb cycle.

For the analysis of diatoms from the benthos, three replicate sediment samples were taken from each of the nine flume lanes. Sediment samples were taken with a cut-off syringe (1.6 cm diameter), whereby the cylinder was plunged into the sediment, carefully removed after closure of the open end and before expulsion of the first centimetre which was carefully cut off, transferred to a plastic bag and stored at minus 20 °C. All samples were freeze-dried prior to chl *a* analysis and cell counts. Prior to microscopic investigation the samples were sonicated for ca. four minutes to remove the epipsammic fraction of the diatom community from the sand grains. After a short period to allow the settling of coarse sand grains, the supernatant was decanted into 10 ml settling chambers. For the Lugol preserved phytoplankton samples, settling chambers with a volume of 25 ml were used for cell counts.

Sub samples were treated after Simonsen (1974) and mounted on cover slips (18 mm diameter) with Naphrax (refraction index n_D = 1.73) for permanent slides. A Zeiss Axioplan microscope for digital photography and a FEI QUANTA FEG 200 electron scanning microscope was deployed for taxonomic analyses. To ensure that samples were not contaminated with epiphytic diatoms growing on the flume walls, scratch samples were examined under the microscope. Only filamentous green algae and some single, negligible cells could be discovered.

Cell counts

As particular attention was paid to the epipsammic fraction, sediment samples were diluted in filtered sea water and treated in an ultrasonic bath for two minutes. This time proved sufficient to remove attached cells from the sediment without destroying larger or more delicate frustules. Both fractions, sediment as well as water samples, were transferred into settling chambers and after settling for at least 16 hours, the cells were counted using an inverted light microscope (Zeiss Axiovert 35) at magnification of 400 and 630 fold. Only cells with visible chloroplasts were counted, on the assumption that these cells were alive when sampled. Cells smaller than 15 µm were difficult to identify at species level during cell counts, thus, cells were grouped instead into size and morphological groups (e.g. 'small pennate') or counted at genus or species level when possible. Cell numbers from sediment samples are given in cells per gram sediment, cell numbers from water samples in cells per litre. Species numbers are expressed as relative percentage.

Diatom identification

Permanent slides (Naphrax, refraction index $n_D = 1.73$) from acid cleaned samples were prepared for photo-digital light microscopy of microalgae. Taxonomical analysis was carried out using a Zeiss Axioplan light microscope for digital photography fitted with phase contrast, bright field and polarised illumination. A FEI QUANTA FEG 200 electron scanning microscope was used for identification of small species and resolution of details in diatom cell walls that serve as characteristics for identification.

Statistical analyses

Spearman Rank correlation were applied to test for significant correlations between cell numbers and wind speed, cell numbers and current velocity and between wind speed and current velocity. Analysis of variances (ANOVA) and LSD post-hoc test (Statistica, StatSoft 6.1) was applied to test for differences between flow treatments and sampling days. Data were considered significant on a $p < 0.05$ niveau.

Results

Wind

Wind data were kindly provided by the weather station List/Sylt (Deutscher Wetterdienst DWD).

Figure 2 shows wind data for the six sampling days. Calculations for daily mean values are presented in Table 1. The highest wind velocities can be found for the 26.08.03 with peaks up to 11.5 m s^{-1} from WNW; followed by the 20.08.03 with wind speeds up to 9.9

m s $^{-1}$ from W. The median values for the 30.07.03 (WSW), 12.08.03 (SW) and 17.09.03 (SW) range between 4.95 and 5.8 m s $^{-1}$.

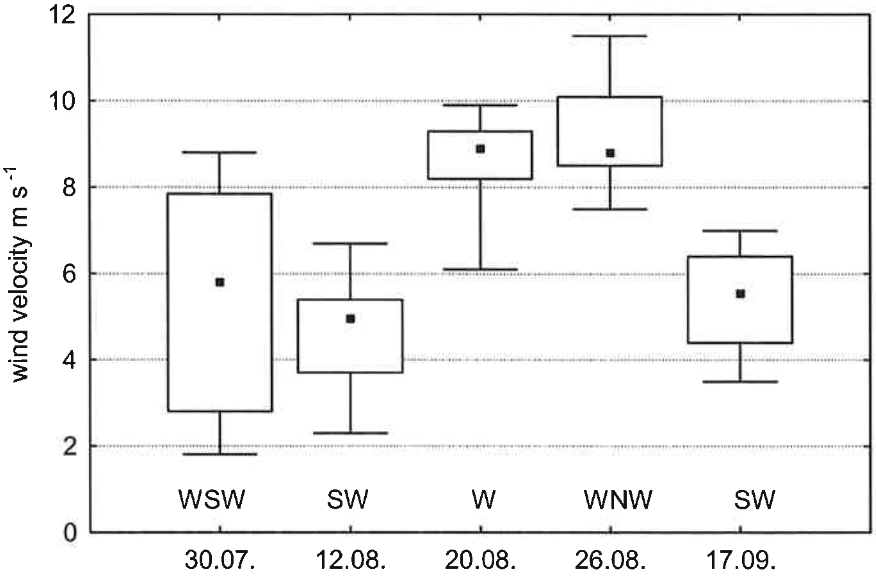


Fig.2 . Wind speed [m s $^{-1}$] measured at weather station List/Sylt on five sampling days between 30.07 and 17.09. 2003. Central point indicates median value, box: 25% - 75 % quartile, whiskers: min-max .

Flow measurements

Figure 3 presents the average data of current velocity on the respective sampling day. Due to technical problems no data are available for the 17.09.03. The highest flow velocities were measured on 26.08.03, with average values of 11.95 cm s $^{-1}$ for 'increased' flow treatment, 9.15 cm s $^{-1}$ for 'mean' flow and 5.51 cm s $^{-1}$ in the 'reduced' flow lane of the flume.

Figure 4 provides additional information on the flow characteristics of the manipulated velocities: a general increase in current velocities can be found between the 30.07.03 and the 26.08.03 and also the clear distribution of each treatment at each sampling day into 'increased' with higher velocities (12.58 cm s $^{-1}$ on 26.08.03) compared to 'reduced' with lowest current velocities (0.98 cm s $^{-1}$ on 12.08.03).

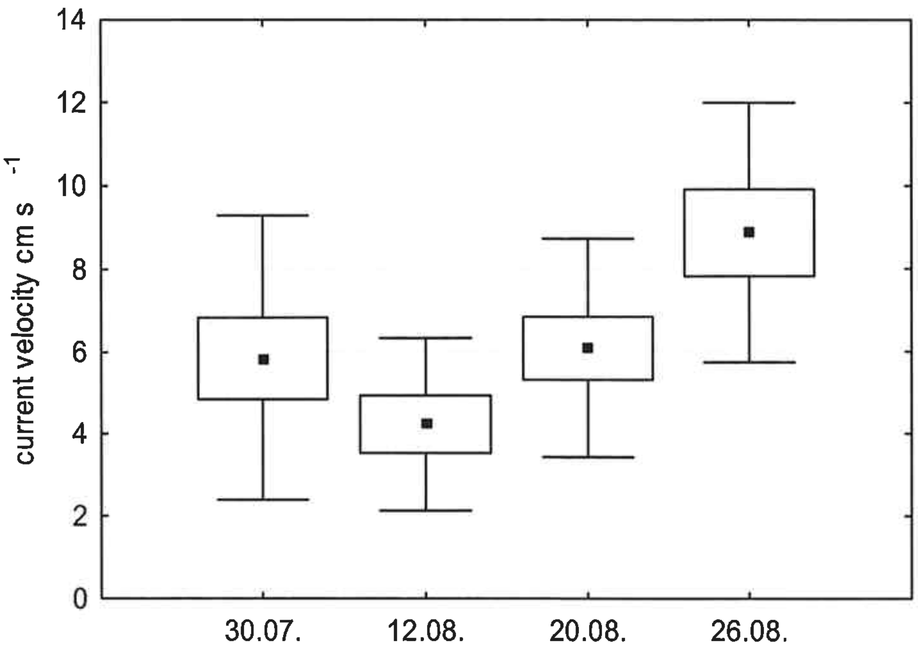


Fig. 3: Current velocity in [cm s $^{-1}$] on four sampling days. No current velocity data are available for the 17.09.03. Box: mean ±SE; whiskers: mean ±SD.

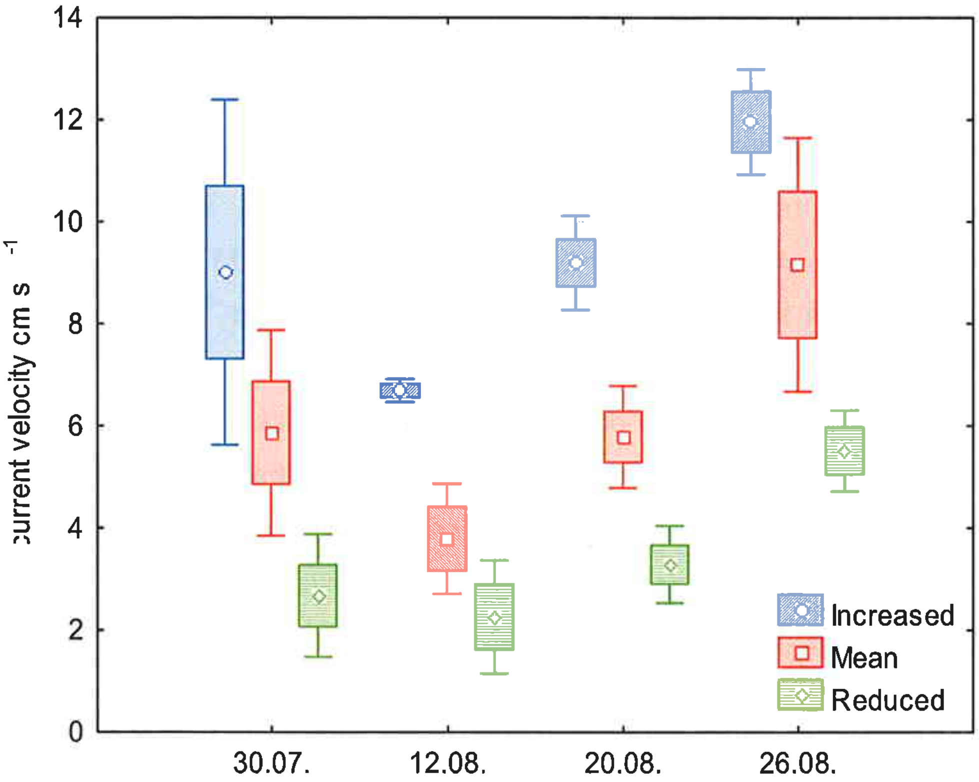


Fig. 4: Current velocity in [cm s $^{-1}$] on four sampling days for the three flow treatments 'increased', 'mean' and 'reduced'. No current velocity data are available for the 17.09.03. Box: mean ±SE; whiskers: mean ±SD.

Diatom analysis

Plate 1 – 3 in the appendix depict scanning electron microscopic and light microscopic photos of the diatoms discussed in this chapter. Taxonomical determination was performed using the keys of Hustedt (1930, 1959), Pankow (1976), Snoeijs (1993, 1994, 1995, 1996, 1998) and Simonsen (1974, 1987). 231 species were taxonomically identified down to species level. A species list can be found in the annex.

The majority of the *centric* species found in the water column are absent or very rare in the benthos samples (e.g. *Chaetoceros*, *Skeletonema*, *Thalassiosira*, *Coscinodiscus*, *Rhizosolenia*) and even in the water samples, the above named genera were rare.

Sediment samples

Grain size is around 1.5 Φ (sorting coefficient), with a medium diameter between 0.2 and 0.63 mm. The median (Md) for the surface first centimetre is approximately 0.3 – 0.4 mm, which means medium to coarse sand, according to the Wentworth grade classification.

The flow treatments showed no effect on the distribution of grain size in the nine lanes of the flume, as analysis from sediment samples taken after the last sampling event in September proved.

Analyses of benthic samples are provided for three sampling dates: 30.07.03, 20.08.03 and 26.08.03. Analysis of variances (ANOVA) showed a significant difference of pooled data (all three sampling days) between 'reduced' flow treatment and 'increased' ($p = 0.005$) as well as for 'reduced' and 'mean' ($p = 0.03$). Sampling days are different with $p = 0.0001$ with exception of 30.07.03 and 26.08.03 ($p = 0.166$).

Figure 5 shows the total abundance of cells per gram sediment and pictures the difference between the three flow treatments: a slight decrease in cell numbers from flow treatment 'increased' towards 'reduced' at all three sampling days ('increased': 3.7×10^5, 2×10^5 and 4.2×10^5 as opposed to 'reduced': 3.2×10^5, 1.6×10^5 and 3.4×10^5 cells g^{-1} sediment). Highest cell numbers were observed on the 26.08.03 with an average over all three treatments of 4×10^5 cells g^{-1} sediment, followed by 30.07.03 with an average of 3.5×10^5 cells g^{-1} sediment. Lowest cell numbers were recorded on 20.08.03 with 1.8×10^5 cells g^{-1} sediment.

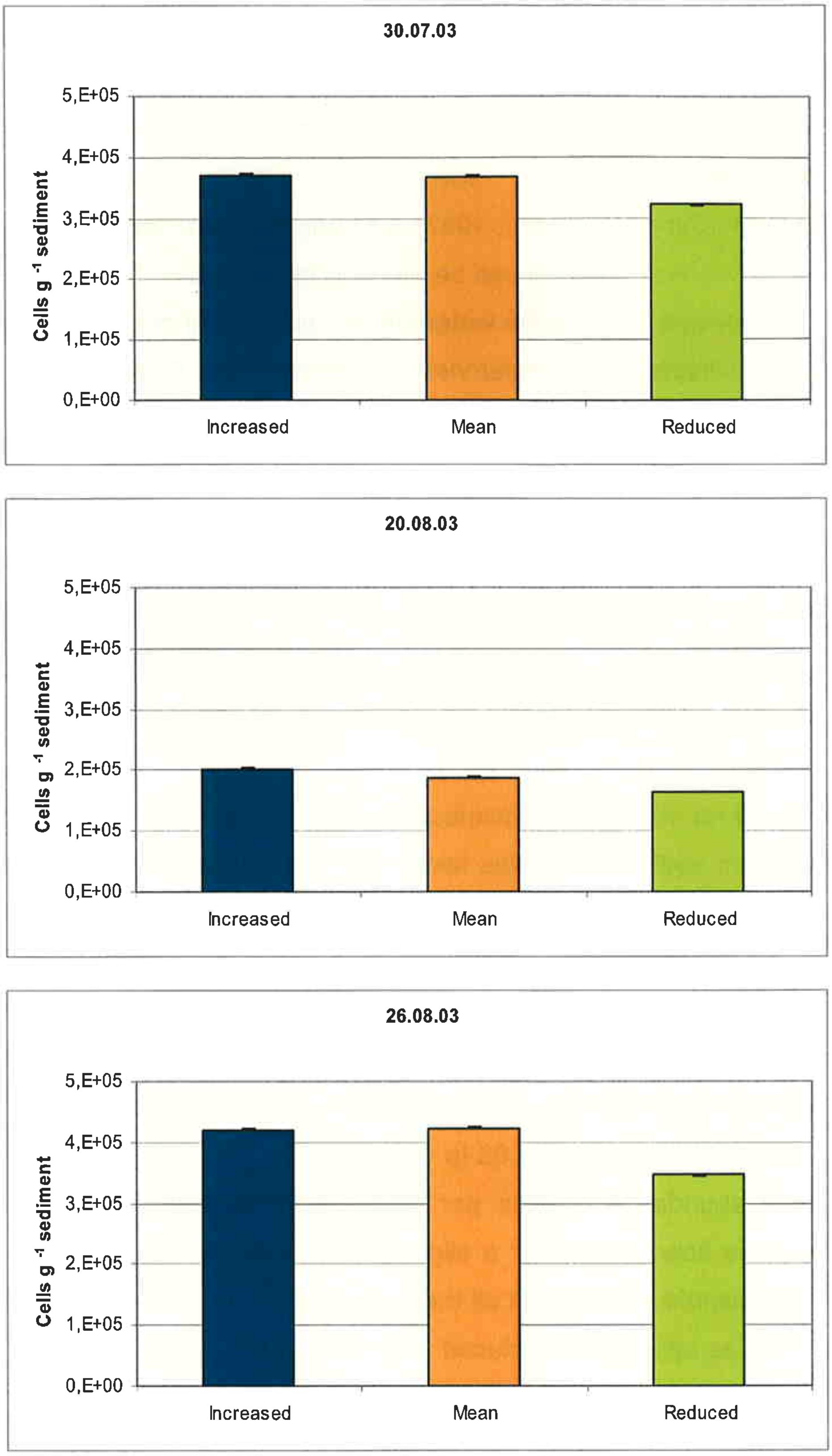
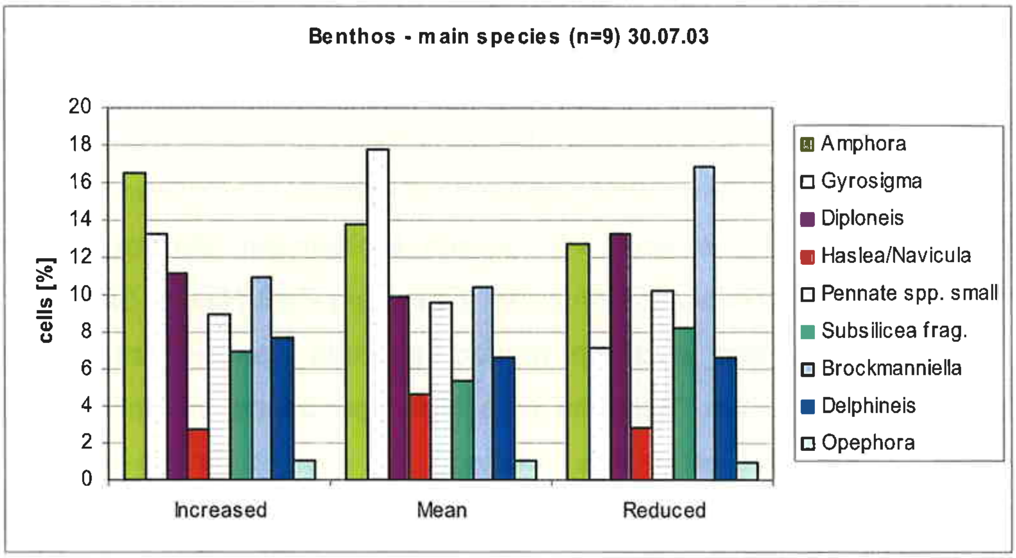
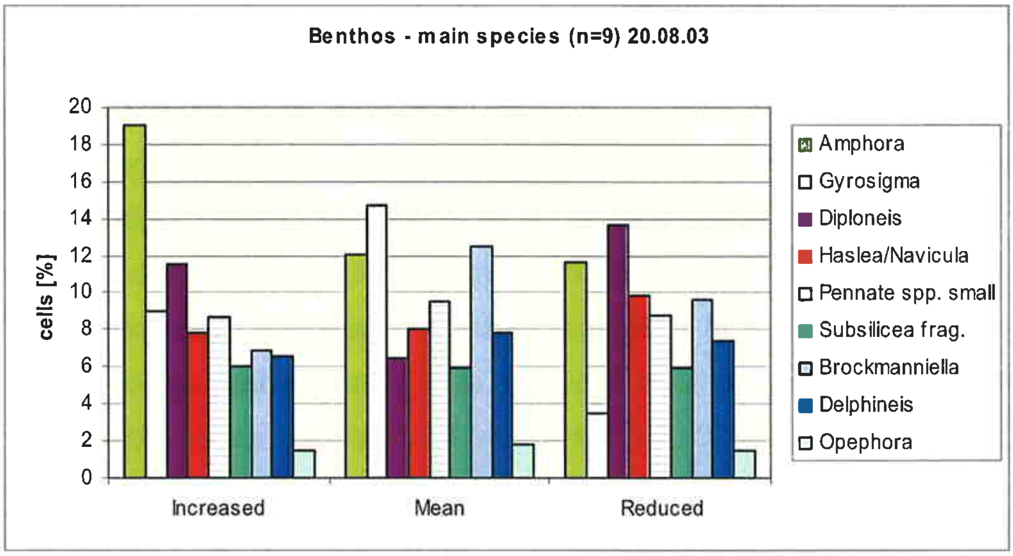


Fig. 5: Cell numbers [g $^{-1}$] sediment in the three flow treatments 'increased', 'mean' and 'reduced'. Mean ±Sd.

About 42 genera were found to occur regularly in all samples and present the basis for the cell counts. Further analysis is restricted to the most common species within these genera. For the 30.07.03, 20.08.03 and 26.08.03 the following selection of genera/ groups for cell counts was made: *Amphora* Ehrenberg ex Kützing, *Gyrosigma* Hassall, *Diploneis* Ehrenberg ex Cleve, *Subsilicea* von Stosch & Reimann, *Brockmanniella* Hasle, von Stosch & Syvertsen, *Delphineis* Andrews, *Opephora* Petit *Haslea* Simonsen together with *Navicula* Bory, and a group named 'pennate species small' with unidentifiable species below 15 µm. Because of a high abundance of *Pleurosigma* Smith species on the 26.08.03, this genus was included in the analysis for this date.

Although 20.08.03 showed the lowest total abundance of all three (sediment) sampling days, relative abundance of most of the genera displayed did not change significantly. Figure 6 shows the relative abundance of the above named genera in respect to the three flow treatments. At all sampling days, *Amphora* shows significantly higher numbers in sediment samples collected in the 'increased' lane with values above 18 % compared to values below 13 % in the 'reduced' lane. A different picture to this result is shown by cells of the genus *Brockmanniella* which were found in higher numbers in the 'reduced' lane (around 16%, 9 % and 13 %) than in the 'increased' lane (around 11 %, 7 % and 10 %). The same pattern applies to *Diploneis* at all sampling days and to species of the group *Haslea/Navicula* on 20.08.03 and 26.08.03 as well as to *Pleurosigma* species on the 26.08.03. Compared to these findings, cells of the genus *Opephora* showed constant values in all three flow treatments on all sampling days (between 1 and 2 %). Also a relatively constant distribution is displayed by the group of small pennate species, apart from the 26.08.03, where a decrease from 'increased' to 'reduced' flow can be detected (around 11 %, 10 % and 7 % in the 'reduced' lane). Cells of the genus *Subsilicea* tend to increase slightly in the 'reduced' treatment (between 8 % and 6 % in the 'reduced' lane compared to around 7 % and 4 % in the 'increased' lane). Conversely *Delphineis* shows slight increases in 'increased' flow on 30.07.03 and 26.08.03, but the opposite, a tendency towards slightly higher numbers in the 'reduced' lane on 20.08.03.





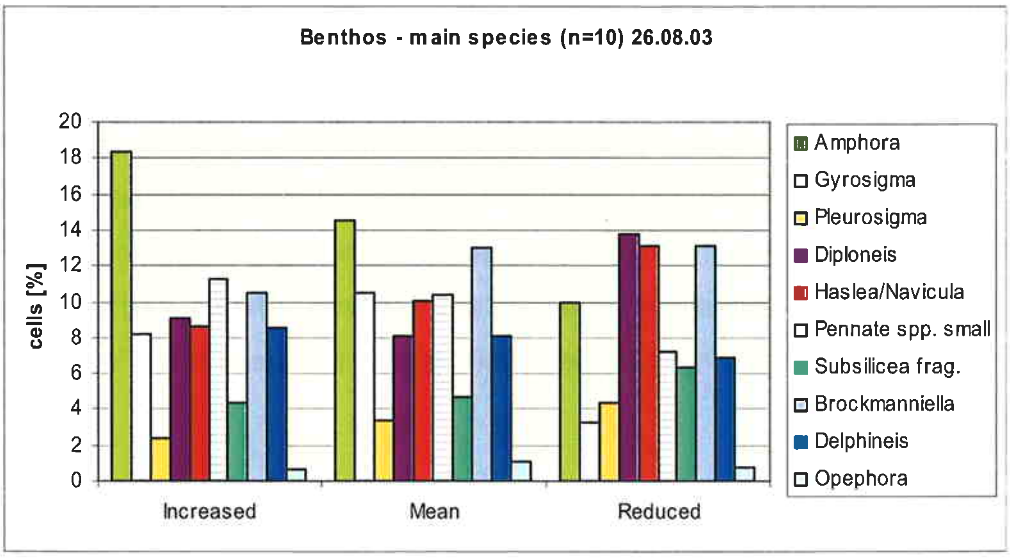


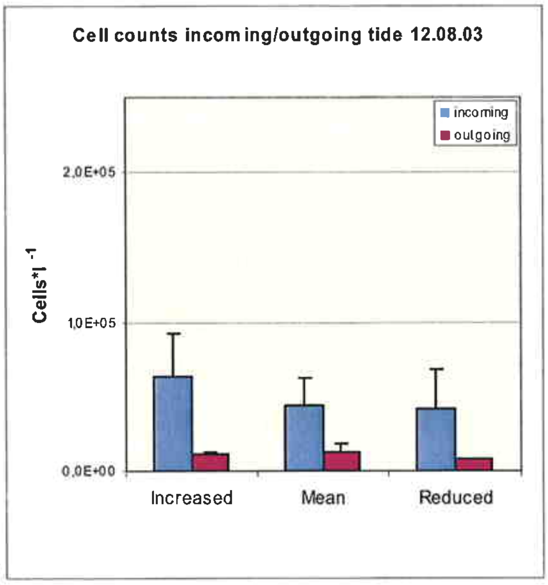
Fig. 6: Relative abundance of species [%] in benthos samples on three sampling days: 30.07.03, 20.08.03 and 26.08.03 in the three flow treatments 'increased', 'mean' and 'reduced'. Pictured are the 9 mainly occurring species with exception to the 26.08.03, where a high abundance of *Pleurosigma* species has been included.

Water samples

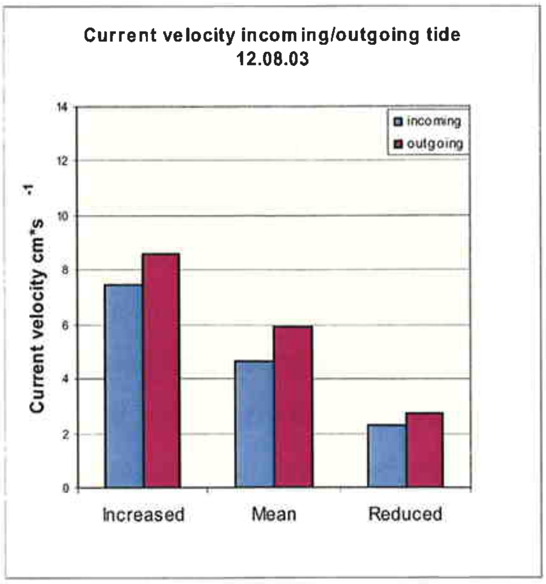
Analysis of diatoms from water samples are provided for four sampling dates: 12.08.03, 20.08.03 and 26.08.03. and 17.09.03. Figures 7a, c, e and g show a fluctuation of cell numbers for incoming and outgoing tide. For all three flow treatments a distinct trend can be found regarding decreasing cell numbers from the 'increased' lane to the 'reduced' lane regardless of the tide (incoming or outgoing). The largest differences between in- and outgoing tide can be found on the 12.08.03 where the cell numbers for the incoming tide exceeds those for the outgoing tide by a factor of 5. On 26.08.03 cell numbers for the incoming tide exceeds those for the outgoing tide by about 1.6 fold higher numbers. The reverse was recorded for the other two sampling days (20.08.03 and 17.09.03), where the outgoing tide counts dominate over the incoming tide by a factor of three or four, respectively.

Corresponding to cell numbers for the incoming and outgoing tide Figure 7b, d and f present the ambient current velocity, also incoming and outgoing tide, for the 12th, 20th and 26th of August 2003. No current velocity data are available for the 17.09.03. Higher flow on the incoming tide was recorded for two days, 20.08.03 and 26.08.03, but does not apply to the 12.08.03, where flow velocity at outgoing tide slightly exceeded flow velocity at incoming tide (1.1 cm s^{-1} in 'increased' lane and 0.47 cm s^{-1} in 'reduced' lane). The 26.08.03 is the only day where increasing current velocity was mirrored in increasing cell numbers. On other occasions a controversial picture can be seen with higher cell numbers at incoming than at outgoing tide opposed to lower current velocities at incoming tide than at outgoing tide on the 12.08.03. The reverse is the case for 20.08.03 (cell numbers low at incoming tide, high at outgoing tide and velocity high at incoming tide and low at outgoing tide).

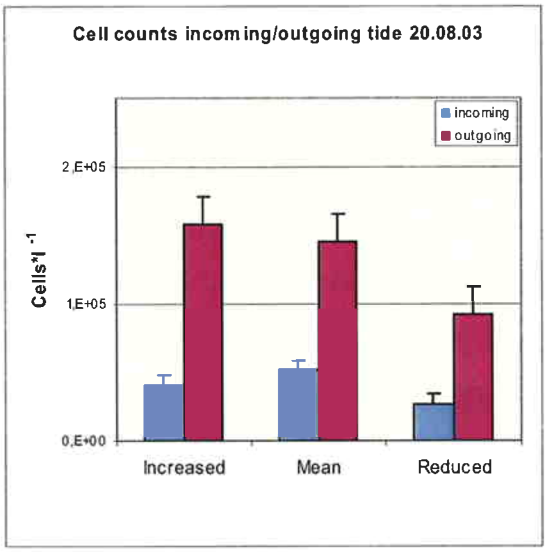
Spearman-Rank correlations were used to test a possible correlation between wind speed, cell numbers and current regime (split up into the three flow treatments). The results are two significant correlations with $p = 0.0096$ for cell numbers and current velocity on the 12.08.03 and $p = 0.004$ for current velocity versus wind speed on 26.08.03.


Cell counts incoming/outgoing tide 12.08.03

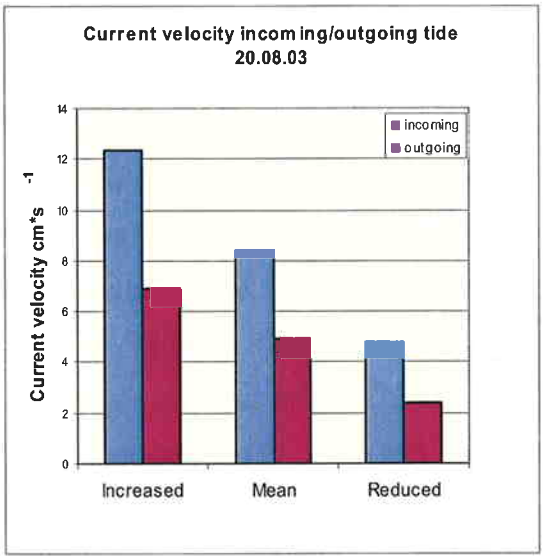
a


Current velocity incoming/outgoing tide 12.08.03

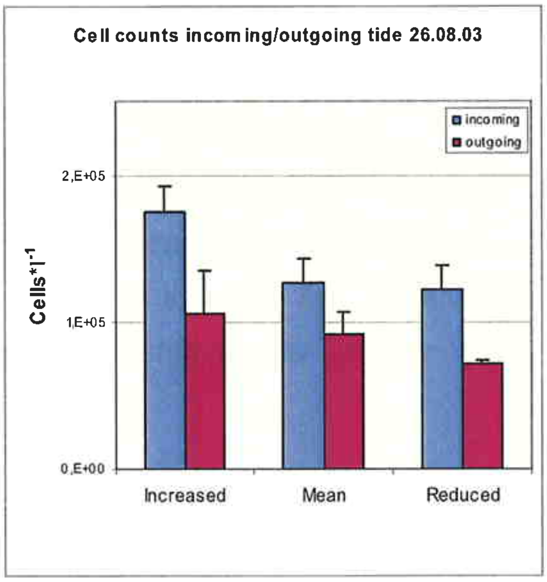
b


Cell counts incoming/outgoing tide 20.08.03

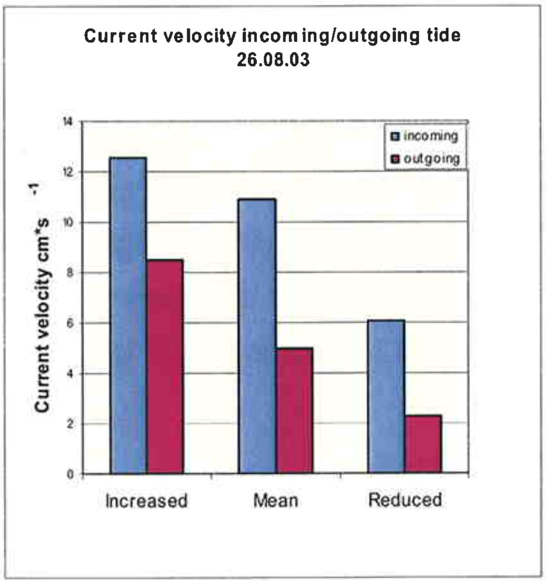
c


Current velocity incoming/outgoing tide 20.08.03

d


Cell counts incoming/outgoing tide 26.08.03

e


Current velocity incoming/outgoing tide 26.08.03

f

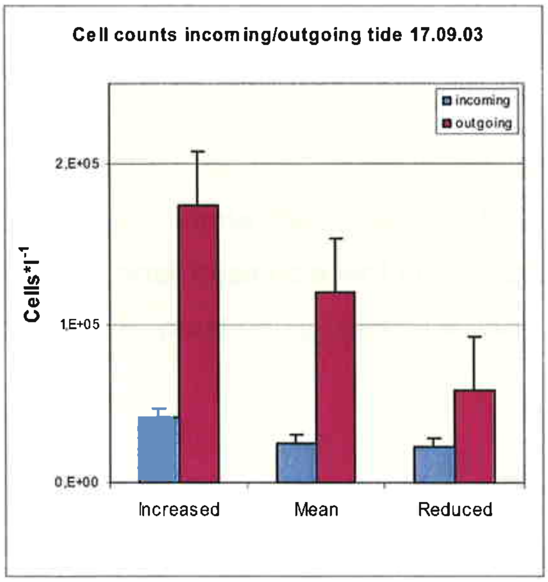


Fig. 7 a – g: Cell abundances [cells l $^{-1}$] in water samples at incoming and outgoing tide (a, c, e, g), and corresponding current velocity [cm s $^{-1}$] (b, d, f) in the three flow treatments 'increased', 'mean' and 'reduced'. No current velocity data are available for 17.09.03. Mw ±Sd.

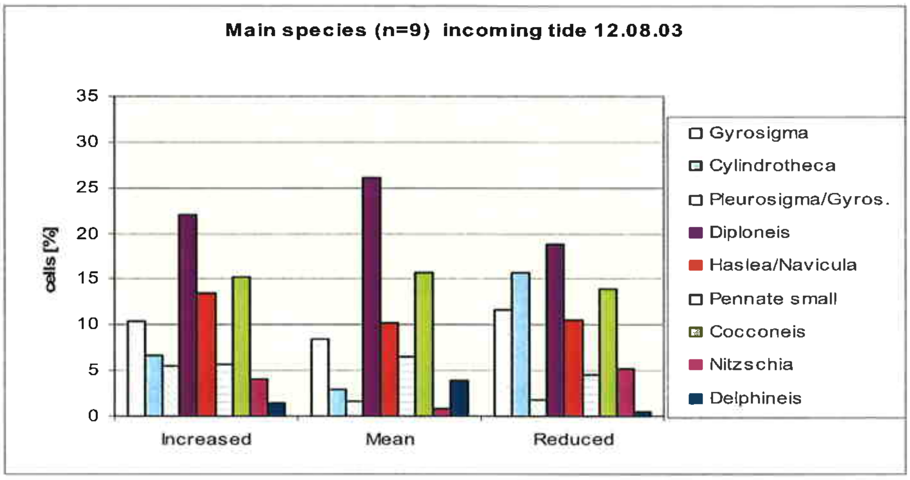
g

Figures 8a - h show the relative abundance of each species (or species group) in the three flow treatments for each sampling day, divided into incoming and outgoing tide, respectively.

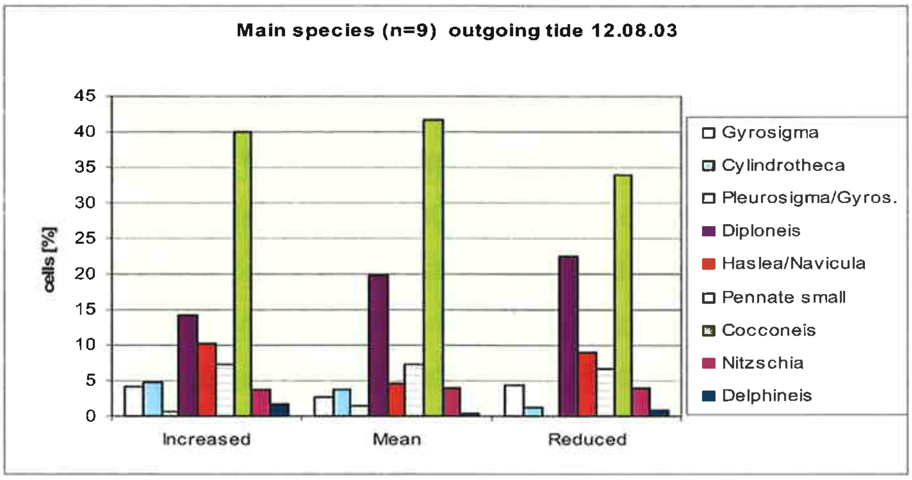
The following genera were included in the analysis of the distribution of species in different current regimes:

Amphora Ehrenberg ex Kützing, *Cocconeis* Ehrenberg, *Gyrosigma* Hassall/*Pleurosigma* Smith, *Diploneis* Ehrenberg ex Cleve, *Haslea* Simonsen/*Navicula* Bory, *Cylindrotheca* Ehrenberg ex Reimann & Lewin, *Entomoneis* Ehrenberg ex Reimer, *Rhopalodia* Smith, *Chaetoceros* Ehrenberg, *Nitzschia* Hassall and again a group of 'pennate species small' with unidentifiable species below 15 µm. On 12.08.03 a high abundance of Cocconeis was counted and accordingly included in the analysis. For each sampling day two or three species can be seen to be dominant. On the 12.08.03 these are represented by *Diploneis* and *Cocconeis*, on 20.08.03 by *Diploneis*, *Haslea/Navicula* and *Cylindrotheca*, on 26.08.03 very distinctly by *Chaetoceros* and *Haslea/Navicula* and on 17.09.03 the pelagic community is dominated by the occurrence of *Cylindrotheca*, small pennate species and again *Haslea/Navicula*.

The distribution of genera in the water column presents a higher variability in species occurrences compared to the benthos. E.g. *Rhopalodia* and *Entomoneis* appeared on all sampling days except on 12.08.03. On the other hand, *Nitzschia* and *Cocconeis* species occurred in higher abundances only on 12.08.03. On 20.08.03, 26.06.03 and 17.09.03 *Cocconeis* was replaced by *Rhopalodia*. On four occasions a distinct difference can be found in the distribution of *Diploneis* with higher numbers for ‘reduced’ velocity compared to ‘increased’ and ‘mean’ flow (12.08.03 outgoing tide, 20.08.03 incoming and outgoing tide, 17.09.03 outgoing tide). Compared to these findings, *Cylindrotheca* was more abundant in the ‘increased’ and ‘mean’ flow treatment than in the ‘reduced’ lane with one exception on the 12.08.03, incoming tide, where it is present with more than 15 % in the ‘reduced’ lane and about 6 % in the ‘increased’ lane. Similar patterns can be detected for *Haslea/Navicula* species, with a tendency to higher numbers in the ‘increased’ flow on most occasions.

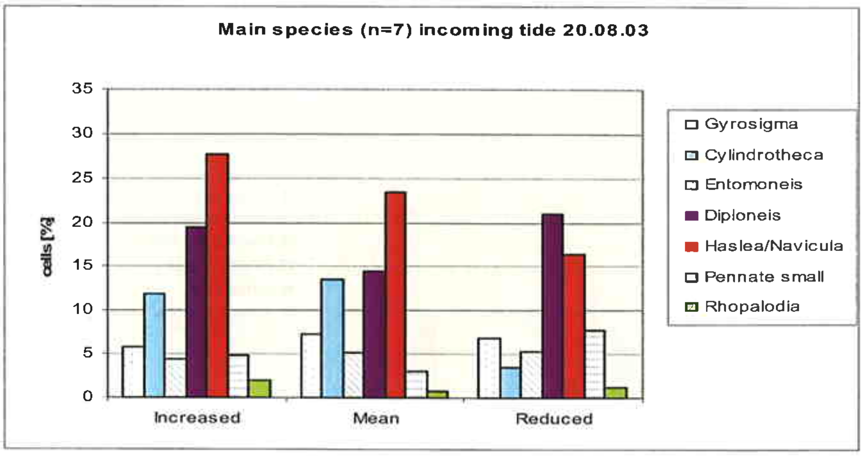


8 a

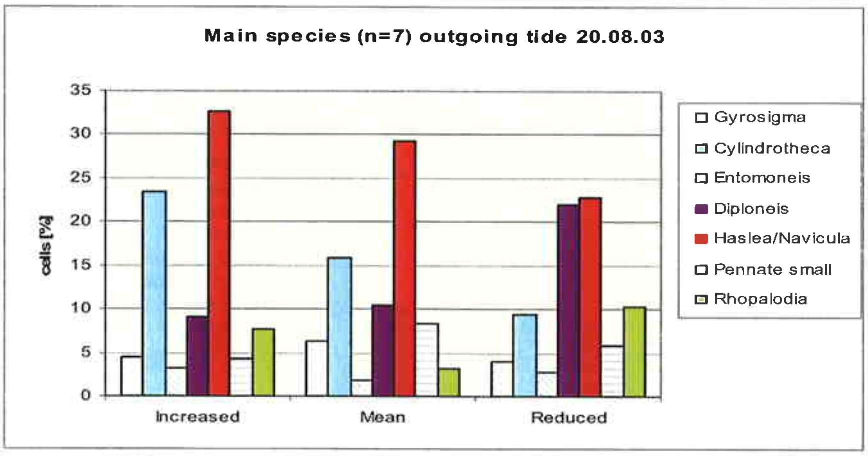


8 b

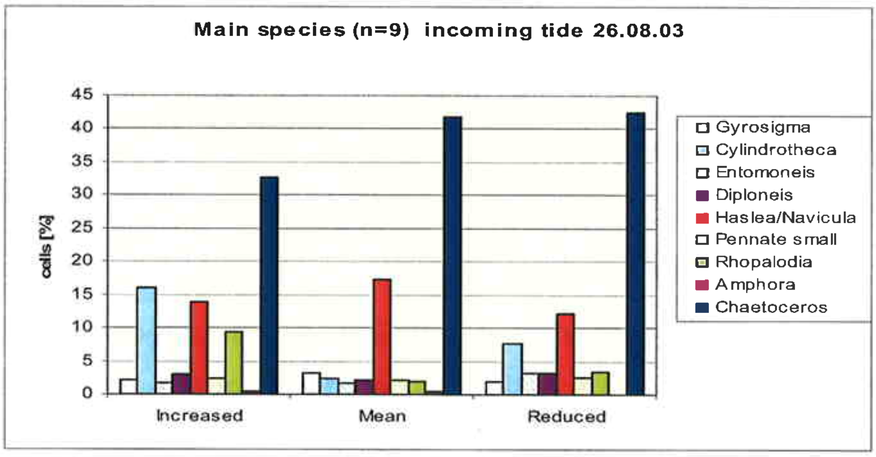
Fig. 8 a - h: Relative abundance of species [%] in water at incoming and outgoing tide and the effect of the three flow treatments ‘increased’, ‘mean’ and ‘reduced’. Pictured are the 9 mainly occurring species with exception to the 20.08.03, with 7 species.


Main species (n=7) incoming tide 20.08.03
cells [%]
35
30
25
20
15
10
5
0
Increased
Mean
Reduced
Gyrosigma
Cylindrotheca
Entomoneis
Diploneis
Haslea/Navicula
Pennate small
Rhopalodia

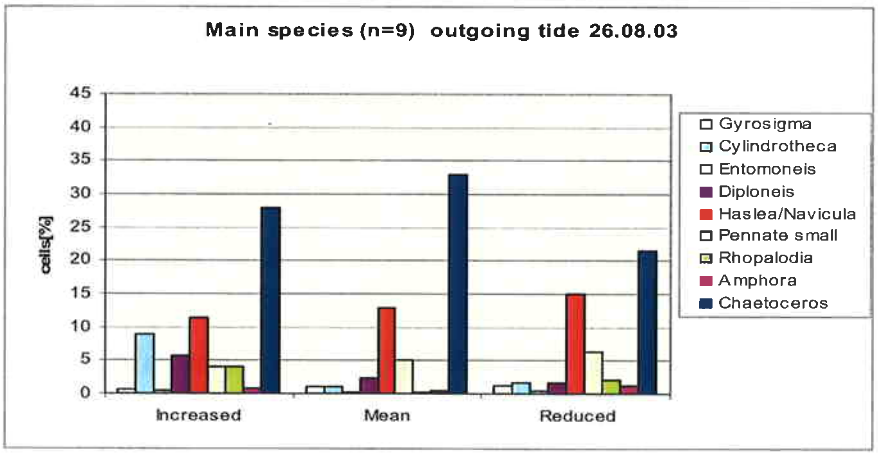
8 c


Main species (n=7) outgoing tide 20.08.03
cells [%]
35
30
25
20
15
10
5
0
Increased
Mean
Reduced
Gyrosigma
Cylindrotheca
Entomoneis
Diploneis
Haslea/Navicula
Pennate small
Rhopalodia

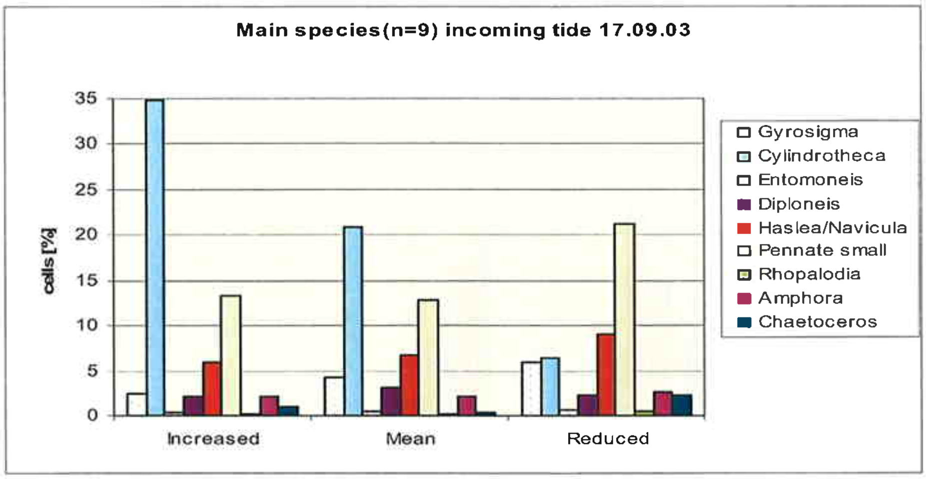
8 d


Main species (n=9) incoming tide 26.08.03
cells [%]
45
40
35
30
25
20
15
10
5
0
Increased
Mean
Reduced
Gyrosigma
Cylindrotheca
Entomoneis
Diploneis
Haslea/Navicula
Pennate small
Rhopalodia
Amphora
Chaetoceros

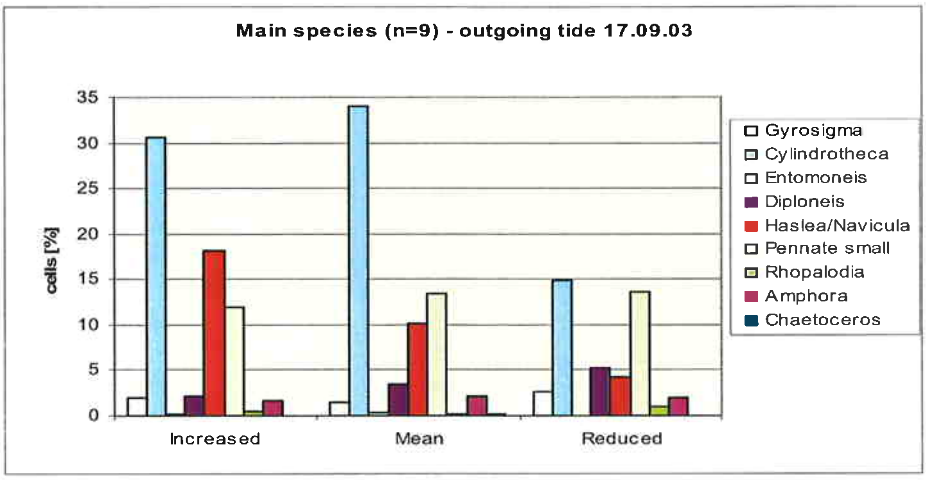
8 e


Main species (n=9) outgoing tide 26.08.03
cells[%]
45
40
35
30
25
20
15
10
5
0
Increased
Mean
Reduced
Gyrosigma
Cylindrotheca
Entomoneis
Diploneis
Haslea/Navicula
Pennate small
Rhopalodia
Amphora
Chaetoceros

8 f



8 g



8 h

Fig. 8 a - h: Relative abundance of species [%] in water at incoming and outgoing tide and the effect of the three flow treatments 'increased', 'mean' and 'reduced'. Pictured are the 9 mainly occurring species with exception to the 20.08.03, with 7 species.

Species sediment/water column

The percentage of six exemplary genera and their occurrence in sediment (bold), in samples from incoming (cross striped), and outgoing tide (lengthwise striped) on the 20.08.03 and 26.08.03 and the effect of the three flow treatments 'increased', 'mean' and 'reduced' is presented in Figures 9a - l. The abundances in percentage are picked out from the respective calculations for the community presented in Figures 6 and 8. Objects of examination were: *Amphora* (epipelic/epilithic), *Gyrosigma/Pleurosigma* (epipelic), *Entomoneis* (epipelic), *Haslea/Navicula* (both planktonic/epipelic), 'small pennates' (presumably predominantly benthic species), and *Diploneis* (epipelic). Because of the similarity of cells of *Gyrosigma* and *Pleurosigma* and the fact that in water samples (settling chambers) the resolution does not allow a reliable differentiation, both genera are here included in one group. The following paragraph explains the charts displaying the above listed genera or group, respectively. Altogether abundances in water samples on 20.08.03 outweigh those from 26.08.03, where they constitute less than half of the benthos abundances. Lower cell abundances in water samples from 26.08.03 is a general appearance, whereas benthos numbers are comparable to the 20.08.03.

Amphora (Figure 9a, b):

On both sampling days, the benthic species of *Amphora* shows a distinct tendency towards higher numbers in the 'increased' lane (about 19 % compared to about 11 % in the 'reduced' flow treatment). Furthermore, the planktonic fraction is below 2 %, on both sampling days and at all flow treatments. There is no recognisable pattern concerning tendencies of distributions between the three flow treatments on incoming or outgoing tide.

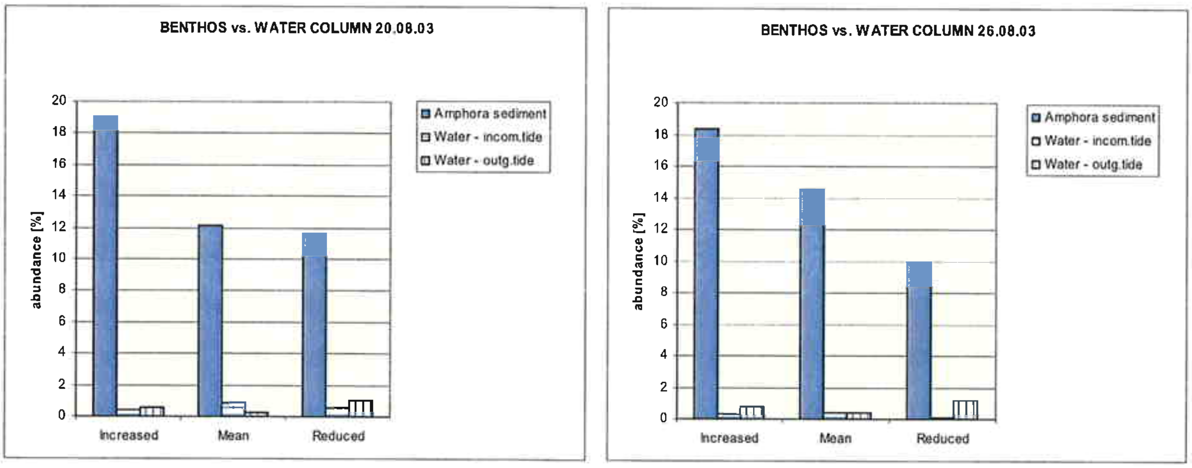


Fig. 9 a, b: *Amphora* abundance on sediment (bold), at incoming tide (cross-striped) and outgoing tide (lengthwise striped).

Gyrosigma/Pleurosigma (Figure 9c, d):

On the 20.08.03. abundances of these epipelic species in water samples lie between 4 and 7 % with slightly higher values for incoming tide. Highest values in 'mean' flow with about 14 % and lowest values with less than 4 % in the 'reduced' flow lane and about 9 % in the 'increased' lane. The 26.08.03 mirrors this picture, only with distinctly lower values for the water fraction with around 2 % for incoming tide and around 1 % for outgoing tide. Concerning the influence of the flow treatment, highest abundances can be found in the 'mean' flow treatment, followed by 'increased' flow and lowest numbers in the 'reduced' current velocity, on both sampling days. Furthermore, on both sampling days numbers in samples from incoming tide slightly increase numbers from outgoing tide.

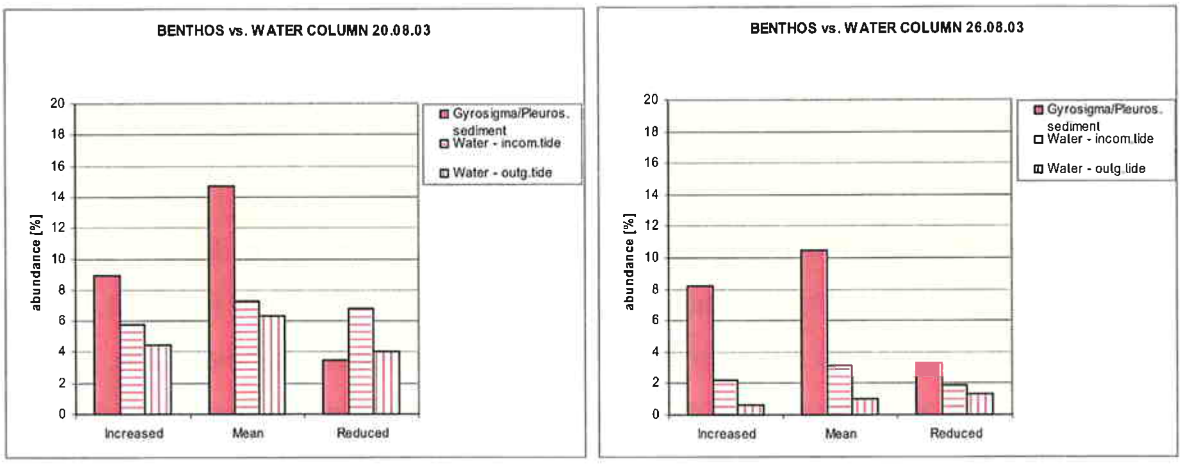


Fig. 9 c, d: *Gyrosigma/Pleurosigma*

Entomoneis (Figure 9e,f):

This genus shows a pronounced majority of cell abundances in the water column, comparing the sediment fraction with less than 1 % abundance and water samples with 4.3 %, 5.1 % and 5.3 % ('increased', 'mean', 'reduced') at incoming tide on 20.08.03 and 1.6 %, 1.7 % and 3.2 % ('increased', 'mean', 'reduced') at incoming tide on 26.08.03. On the same day, values for outgoing tide compared to incoming tide are 4 times lower in the 'increased' flow and 7 times lower in the 'mean' and 'reduced' flow. The differences between tides on the 20.08.03 are similarly pronounced for abundances at outgoing tide being 1.3 times lower at 'increased' flow velocity and 2.7 times and 1.9 lower, respectively, for 'mean' and 'reduced' flow.

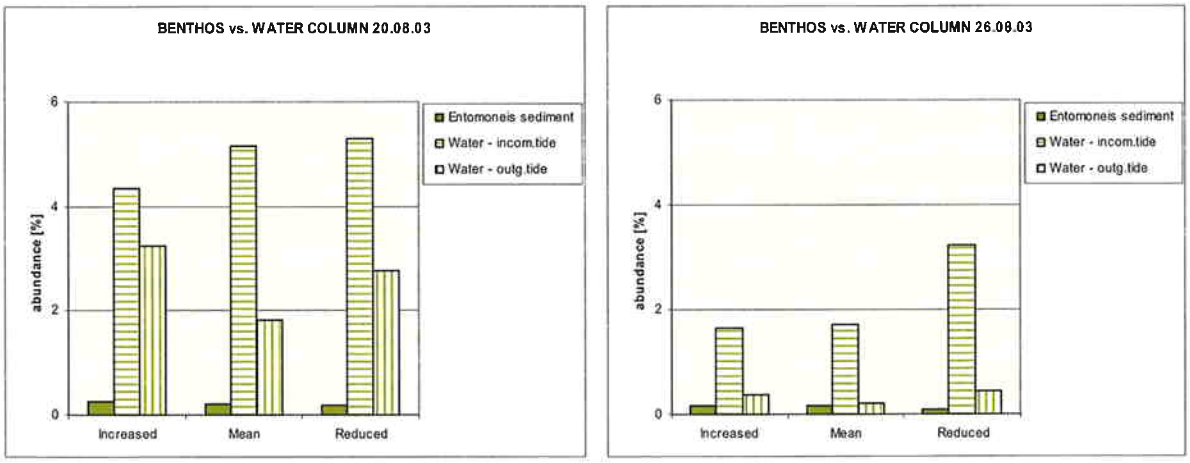


Fig. 9 e, f: *Entomoneis*

Haslea/Navicula (Figure 9g, h):

Compared to the 26.08.03, this epipelic group shows higher abundances in water samples with a pronounced profile on the 20.08.03 (between 16.5 % and 32 %), where a clear tendency for decreasing abundances from 'increased' to 'reduced' flow can be found at both tides, merely about 5 % less at incoming tide. With 9.79 %, the abundances for sediment samples in the 'reduced' flow treatment are higher compared to 'increased' and 'mean' treatment with 7.8 and 8 %, respectively.

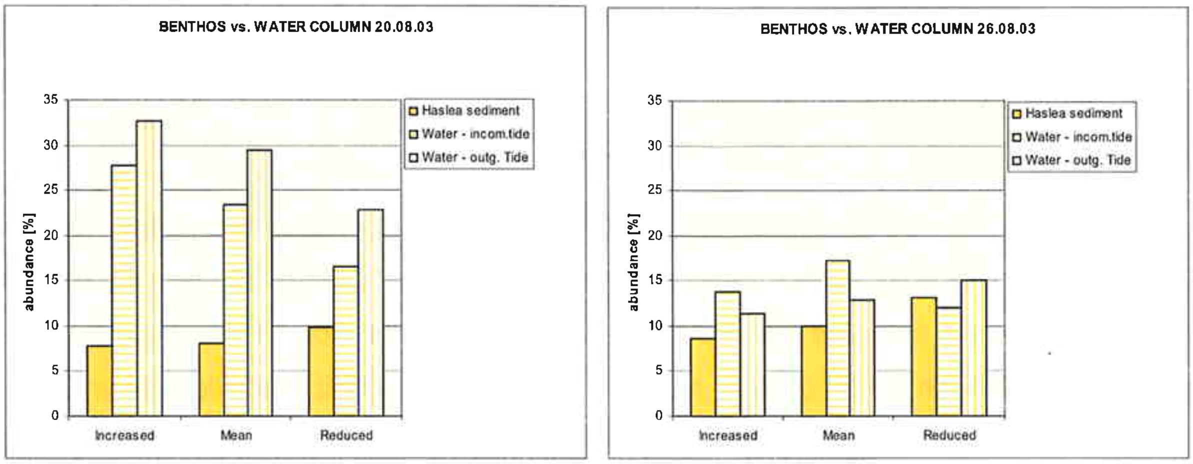


Fig. 9 g, h: *Haslea/Navicula*

On 26.08.03 values for the water fraction are distinctly lower (between 11.3 %, outgoing tide, 'increased' lane and 17.2 %, incoming tide, 'mean' flow treatment). Both, sediment values and abundances for outgoing tide show an increase towards 'reduced' flow treatment (sediment: 8.6, 10 and 13 %, respectively).

Small, pennate species-group (Figure 9i, j):

The group of mainly benthic algae are in the majority in sediment samples on both sampling days. The difference between water and sediment samples is more pronounced on the 26.08.03, where a tendency for the benthos samples in decreasing abundances from 'increased' to 'reduced' can also be found (11, 10 and 7 %, respectively). This pattern is contradicted by increasing numbers from 'increased' flow treatment towards 'reduced' flow at outgoing tide (3.9, 5, and 6.2 %). Incoming tide shows no difference between the flow treatment and values are about half those for outgoing tide. With values around 9 % for all three flow treatments the sediment samples on 20.08.03 do not show any tendency. Water samples feature increasing values between 3.1 and 8.3 % from 'increased' to 'reduced' flow and slightly higher abundances at outgoing tide in the 'mean' and 'reduced' flow treatment.

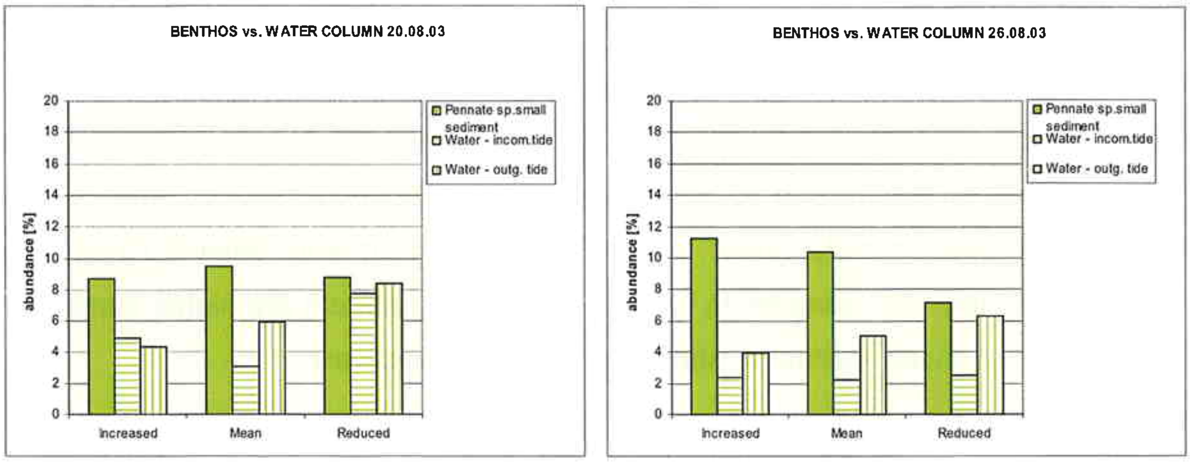


Fig. 9 i, j: *Small pennate species*

Diploneis (Figure 9k, l):

The genus displays different pictures on the two sampling days, the water fraction distinctly exceeding the benthos fraction on both tides on 20.08.03. Highest values for water and sediment samples can be found for the 'reduced' flow. This applies to the sediment samples on 26.08.03 too: both sampling days exhibit a similar picture with abundances around 14 % in the 'reduced' lane followed by 11.4 % (20.08.03) and 9.1 % (26.08.3) in the 'increased' flow and 6 or 8 %, respectively, for the 'mean' flow treatment. A wide difference can be found for water samples between both sampling days, when values from 20.08.03 outweigh abundances from 26.08.03 by more than 3.9 fold. There is no tendency or pattern for incoming tide on either sampling days, apart from a slightly higher value in the 'reduced' lane (21.6 %) compared to 'increased' (19.4 %) and 'mean' flow (14.4 %). Outgoing tide on 26.08.03 reveals a tendency of decreasing abundances towards 'reduced' flow (5.6, 2.4 and 1.7%).

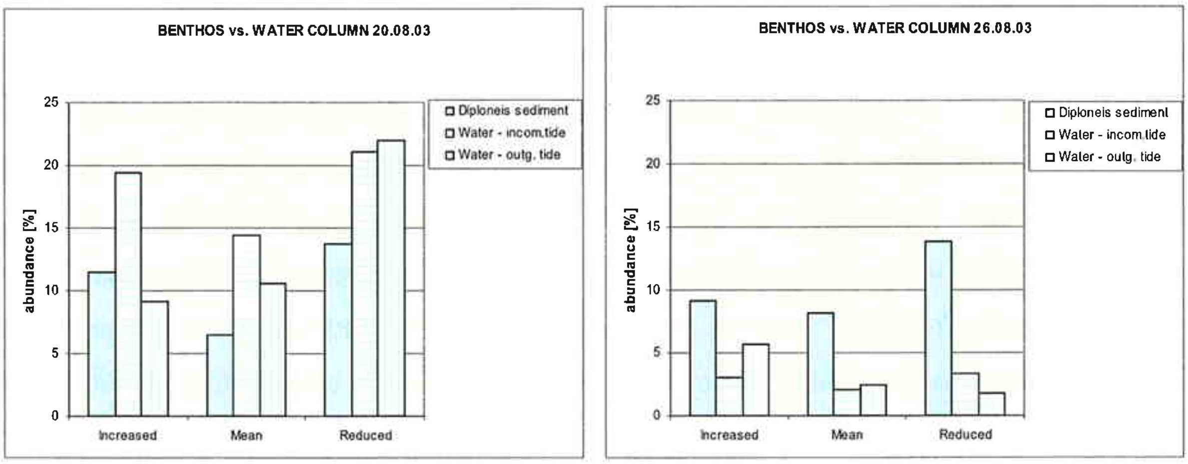


Fig. 9 k, l: *Diploneis*

The general differences in resuspension behaviour can be detected when comparing *Gyrosigma* and *Entomoneis* to *Haslea/Navicula* and the following group of *'small pennate species'*, where the first two species exhibit higher resuspended cell abundances at incoming tide whereas the latter prevail in the outgoing tide. Otherwise this group indicates the affiliation to the benthos with higher abundances in the respective samples. Furthermore, a shift from lower numbers in the 'increased' lane towards higher abundances in the 'reduced' lane can be detected for the water samples. The benthos abundances show a converse pattern, higher abundances in the 'increased' lane compared to lower abundances in the 'reduced' flow lanes.

Discussion

The composition of the benthic diatom community on the Sylt sand flat reflects different life forms. One group includes the epipsammic diatoms, living attached by aid of mucilage secretion to the substratum, in this case sand grains or seagrasses. These diatoms, e.g. *Amphora, Cocconeis, Delphineis*, can occur in chain forming colonies (*Delphineis*) and they are not easy to dislodge from their substratum. Another group includes large, solitary or colonial representatives that are occasionally resuspended into the water column, e.g. *Navicula*, *Paralia*, *Brockmaniella*, but sinking back to the bottom. Although several species from the latter group show this so-called tychopelagic life form, they are possibly capable of attaching themselves to the sand grains (Holland et al. 1974). Grant et al. (1986) showed that diatoms had no significant effect on the sediment stability on intertidal sands in spite of their capacity to bind sediments by excretion of extracellular polymeric substances (EPS). Apart from factors such as grain size, porosity and hydrodynamic conditions prevailing on an intertidal flat, stabilisation of sediments is also determined by the quality of EPS excreted by the microphytobenthos. deBrouwer et al. (2005), Staats et al. (2001) and Alcoverro (2000) confirmed in their studies that consolidation of the sediment depends on the quality of the EPS produced by different diatom species.

Total abundance of cells in the sediment samples

The slight reduction of cell numbers in the 'reduced' flow treatment lane as measured by total abundance of diatom cells from sediment samples may have a number of causes. It is possible that this reduction is due to grazers, e.g. the mud snail *Hydrobia ulvae*, one of the most abundant grazers on tidal flats of the Wadden Sea (Dekker 1989, Asmus & Asmus 1990). Schanz et al. (2002) reports increasing numbers of mud snails in decreasing current velocity during experiments using the same flume device deployed for this thesis. Possibly *Hydrobia* is less endangered to drift off in the reduced flow, thus meeting favourable conditions for grazing. Whether the restricted abundances of certain species in the reduced flow lane is a result of selected feeding by Hydrobia remains a subject of further research.

Cells of the genera *Diploneis, Brockmanniella, Subsilicea* and *Haslea/Navicula* rather showed a general tendency of higher cell numbers in the reduced and/or mean flow treatment lanes where they could suffer less disturbance through e.g. eroded particles such as debris, shells etc.

Tidal influence on cell distribution in suspension

The tidal influence on the distribution of species can be explained in some cases, but must remain speculative in others. Several studies emphasise the different transport processes for incoming and outgoing tide (e.g. Easley et al. 2005, Lucas et al. 2000, Baillie & Welsh 1980). The high abundance of *Cocconeis* on 12.08.03 at outgoing tide (between 35 and 40 % compared to about 15 % at incoming tide) can be explained by the prevailing south-westerly winds, driving the water a long way over the intertidal flats from the south, thus transporting high numbers of cells that might have been washed off from the seagrass areas along the coast.

Significantly higher numbers of *Chaetoceros* species at incoming tide on 26.08.03 (between 33 and 42 % compared to outgoing tide with 22 – 34 % abundance) can also be explained by wind direction: the west-north-westerly wind transports the pelagic *Chaetoceros* straight through the inlet from the open sea into the bight with the incoming tide, thus, the wind direction exerts a synergistic effect on incoming tides.

On this day, we also find a good agreement of higher current velocity in the increased lane resulting in higher cell numbers in the same flow treatment and decreasing towards reduced flow, respectively (see Figure 7e and f). However, this is not true for the 12.08.03 and 20.08.03, where two contrasting patterns can be found: lower current velocity with higher cell numbers at incoming tide compared to higher current velocity and lower cell numbers at outgoing tide on the 12.08.03. The reverse is true for the 20.08.03, with higher current velocities and lower cell numbers at incoming tide compared to lower current velocities and higher cell numbers at outgoing tide.

In all cases a direct effect of the flow treatments can be seen, flow as well as cell numbers are always highest in the increased lane and lowest in the reduced lane (the only exception being higher cell numbers in the 'mean' flow lane at incoming tide on 20.08.03).

It is difficult to explain the patterns with wind direction on all sampling days. One could argue, that on 20.08.03 the straight westerly winds are weakened by the land barrier, and that less cells are transported into the bight through the inlet in the north, thus explaining higher current velocities together with lower cell numbers at incoming tide. At outgoing tide, the cells accumulated on the intertidal flats towards the coast could be transported - due to turbulence induced resuspension – through the flume. Furthermore, next to wind-related transport processes, the differences in values for incoming and outgoing tide at each sampling day could also be related to an increase in standing stock on the intertidal flat during emersion that is resuspended with the next tide.

Unfortunately no current velocity data are available for the 17.09.03 therefore only a comment on the differences between flood and ebb tide can be made. But possibly responsible for high cell numbers at outgoing tide will be wind speed and wind direction which was south-westerly and exerted an effect of fetch (the length of water over which a given wind has blown). Generally the winds grow stronger in late summer/early autumn thus causing a destabilisation of the sediment surface and thus higher resuspension rate of benthic organisms into the water column. Together with the fetch, diatom cells will have been more easily resuspended from a less consolidated sediment surface off the mudflats further south and transported through the flume.

Species - distribution and ecology

In the following section each genus or group is discussed with respect to the findings of benthos samples, water samples, hydrodynamic characteristics and ecological implications.

The pairwise – 12.08.03 and 26.08.03 - comparison of several species and their abundances in (1) sediment samples, (2) water samples incoming tide and (3) water samples outgoing tide indicate the ecology, or life mode, of diatom species (Figure 9a - l). Thus, in most cases the life modus (benthic, planktonic, tychopelagic) is clearly indicated, regardless of the height of abundance at the given sampling day or flood/ebb tide.

The increased flow velocity appears to affect certain species more than others, although higher velocities up to a certain resuspension threshold certainly disfavours many species: *Amphora*, a typical benthic species, shows a higher abundance of cells on the sediment when exposed to increased flow on all sampling occasions, and thus a reaction to the flow treatment whereas abundances in the water samples are negligible. As this pattern occurs regularly, one might hypothesise that the abundance of this species is related to the effect of an altered flow velocity: the sediment in the 'increased' lanes might favour the occurrence of *Amphora* species due to higher oxygen or nutrient levels in the pore water, enriched by the increased flow velocity. Sediment transport and the associated transport of cells due to the higher current velocities in the 'increased' lane can be excluded because in that case other epipsammic species should exhibit similar patterns. In pairwise comparison (12.08.03 and 26.08.03, Figure 9a, b; sediment/incoming-/outgoing tide), *Amphora* occurs with abundances between 10 and 19 % in the benthos and vanishing numbers in the water column (below 1.2 %) and testifies the existence as a benthic genus. By attachment to the substratum resuspension is successfully prevented as figures for water samples show.

In sediment samples, *Gyrosigma* species show highest abundances in the 'mean' flow and lowest in 'reduced' flow on all sampling days. Because the 'mean' flow treatment is the lane where flow is neither increased nor reduced and thus mimics the flow outside the flume, this might be the favourable and in this case natural habitat for the representatives of this genus. Interestingly, it also shows higher abundances in the 'mean' and 'reduced' water samples, apart from one sampling day (12.08.03) where it is slightly higher in the 'increased' lane, both at incoming and outgoing tide. The major part of counted *Gyrosigma* species comprises of the species *G. arcuatum, G. prolongatum* and *G. fasciola*. Because their appearance in the water samples reflects the abundances on the sediment surface (although in lower numbers resuspended than on the sediment) it can be assumed that certain species of the *Gyrosigma* community tend to resuspend into the water column. The only noticeable difference between incoming and outgoing tides occurred on 12.08.03, when abundances are about 10 % for incoming tide and about 5 % or less for outgoing tide. Other representatives of the *Gyrosigma* community possibly migrate into the sediment.

In resuspension studies with benthic diatoms, de Jonge & van den Berg (1987) found that different groups of species become suspended in sequence and that this is caused by cell size and adhesion capacities, as well as by the nature of the particles on which they live. This is also in agreement with the findings by de Brouwer et al. (2005), who confirmed different compositional characteristics of EPS production related to different species. Thus, EPS produced by *Cylindrotheca* induces a minor stabilising effect on the sediment surface compared to e.g. *Nitzschia brevissima* which was more efficient in stabilising the sediment. This result can be explained by the ecological niche the two species occupy: *C. closterium* is a tychopelagic species that occurs both in the water column and on the sediment, thus possibly the EPS produced by *C. closterium* exerts a less stabilising effect than does *N. brevissima*, a typical benthic species. Consequently, species composition influences the quality of EPS produced by diatoms and thus the sediment stability together with grain size. The investigation of species-specific EPS production would therefore provide valuable information on the resuspension behaviour and thus the ecology of diatom species. The occurrence of *Cylindrotheca* in benthos samples in the present study is negligible, only few cells were detected. However, it appears regularly in water samples on all other sampling days, albeit in fluctuating abundances which seems to resemble the *Haslea/Navicula* group. Low abundances in water samples on e.g. 26.08.03 compared to high abundances on 17.09.03 can be explained with respect to two parameters: (1) the above mentioned EPS production and connection with the sediment requires a certain velocity or turbulence threshold to induce resuspension which explains the high fluctuations in abundances and (2) although wind velocity is lower on the 17.09.03 the direction on this day is south-south-westerly causing the high abundances due to fetch induced resuspension.

Many epipelic diatoms are able to pursue a rhythmic migration into deeper sediment layers and back to the surface in response to light (Round & Palmer, 1966). These authors also found that not all littoral populations react to the flood tide with downward migration, but that this rhythm varies from species to species and is also influenced by periods of tidal cover. For example, species of the genus *Pleurosigma* remain on the sand-surface, this might well be the case regarding the cell counts of 26.08., where distinctly more cells of *Pleurosigma* appeared on the sediment surface.

Apart from *Gyrosigma*, *Pleurosigma*, *Navicula* and some representative of the *'small pennate'* fraction, none of the other genera migrate into the sediment. Thus, the occurrence of *Pleurosigma* cells in high abundances on sediment on the 26.08.03 might be due to the fact that this species was sampled after migrating to the sediment surface. Perkins (1960) observed *Pleurosigma* species to stay on the sediment surface although flood already covered the cells to a depth of 46 cm. Alternatively this species might have been resuspended further up the coastline and transported with the water masses pushed by the strong, north-westerly wind prevailing on this day (wind speed up to 11.5 m s^{-1}). This principle is coherent with current velocity, which lies with a mean of 8.8 cm s^{-1} above the three other sampling days (5.9 cm s^{-1} on 20.08.03, 4.2 cm s^{-1} on 12.08.03 and 5.8 cm s^{-1} on 30.07.03). Looking at the pairwise comparison, the group of *Gyrosigma/Pleurosigma* species also exhibits certain patterns: generally higher numbers in benthos abundances compared to presence in water samples, although less pronounced than *Amphora*. This indicates that some parts of the community comprising different species are resuspended while others either remain on the sediment surface or migrate into deeper sediment layers. The same tidal influence can be seen in *Entomoneis* although more pronounced and with sometimes double the abundance at incoming tide compared to outgoing tide. The affiliation to the planktonic community is distinctly the opposite to that of *Amphora*. High numbers in water samples are set against less than 1 % abundance in sediment samples. A very slight tendency towards reduced current velocities can be recognised.

On two sampling days, species of the *Haslea/Navicula* group from sediment samples are found in higher numbers in the reduced lane and lowest numbers in the increased lane. The *Haslea/Navicula* group comprises mainly *Haslea* and very similar looking Navicula cells of about 50 – 80 µm long. Although the samples from 26.08.03 (pairwise comparison) show a less distinct preference for a planktonic life mode compared to 20.08.03, benthic abundances are only marginally higher in the 'reduced' flow. This group shows an effect of flow treatment with slightly higher abundances in the 'reduced' flow velocity for the benthic partition. Water samples at both tides show higher abundances in the 'increased' flow on the 20.08.03 which suggests easy resuspension and preference to stay in the water column whereas lower abundances in benthic samples can be explained by (1) downward migration of the *Navicula* species and (2) lower current velocities in the 'reduced' lane leading to sedimentation.

The group of *small pennate* species shows no noticeable differences on sediment between flow treatments or between the 30.07.03 and 20.08.03. Only on 26.08.03 are there distinctly higher abundances in the 'increased' lane which might be due to the fact that the highest wind velocity (in peaks up to 11.5 ms^{-1}) and direction (NW) caused high current velocities in the 'increased' lane which possibly triggered spasmodic resuspension of the small benthic species not attached to sand grains followed by resettlement in aggregates.

Brockmanniella is a ribbon forming species, the cells are 10-26 µm long and associated with the sediment but resuspended into the water column when a certain resuspension threshold has been passed. The higher abundances in 'mean' and 'reduced' treatment might indicate a sinking of the chains (sometimes more than 25 individuals were observed) due to the reduced current velocity. The same can be applied to *Subsilicea*, also a chain-forming species, with a similar pattern on 30.08.03 and 26.08.03, only on 20.08.03 cells show an equal distribution in the three flow treatments. The chains are associated with the sediment but easily resuspended in turbulent conditions. However, the contribution of cells to the water column samples is low. Possibly the very lightly silicified cells are resuspended higher up into the water column and were not collected.

Opephora shows very constant abundances on all sampling days and in all flow treatment effects on the sediment. This genus is attached to sand grains by aid of a mucus stalk. Because of the fact that the flow velocities are not high enough to resuspend the sediment grains, this species seems to be underneath a suspension threshold high enough to induce entrainment into the water column.

Delphineis is a small species (14 – 40 µm) and, like *Opephora*, a species living attached to the littoral sediment but compared to the latter, *Delphineis* occurs in higher abundances in the 'increased' lane on the 30.07.03 and 26.08.03. Current velocity for the 'increased' lane on the 30.07.03 reflects the wind data, both show a high variability and although the wind direction on this day is WSW, it is pushing the water masses straight through the flume thus transporting more non-attached *Delphineis* cells with the increased flow into the flume lane are subjected to settlement at lower velocities or sink out in aggregates, respectively. However, the same 'preference' as found for *Amphora* might be applicable to *Delphineis* and only the 20.08.03 with higher abundances for 'mean' and 'reduced' flow proves an exception. More samples would be needed to support this theory.

High abundances of *Chaetoceros* cells on 26.08.03 can be explained again by the north-westerly wind, carrying the pelagic species from the open sea into the Sylt-Rømø

Bight. Disturbance and disruption of parts of the benthic community due to local high turbulences can be the reason for the occurrence of high abundances (between 12 and 22 %) of small pennate diatoms (< 15 µm) in September. On all sampling days this group of mainly benthic species shows abundances around 5 % or less and no pattern concerning an effect of the flow treatment. This is in agreement with results by Lucas et al. (2000) who found that the percentage of sedimentary biomass lost during resuspension and export is greater in autumn than in spring because of differences in the dynamic relationship between microphytobenthos and sediments (sediment stability – erodability).

Diploneis in sediment samples generally occurs on all occasions in highest numbers in the reduced lane. This genus has a heavily silicified cell wall and is supposed to be epibenthic. However, it can be found in equally high numbers in the water samples. Contrary to the assumed benthic life mode this genus might be tychopelagic and favours low flow and sediments that could be enriched with e.g. nitrogen components. These derive from faeces from increased numbers of grazers remaining on the sediment surface due to the lower flow velocity. Buoyancy can be achieved by ion exchange or incorporation of lipids.

On two sampling days (12.08.03 and 20.08.03) *Diploneis* is the dominant or co-dominant with two or three other species in water samples, depending on the tide, with abundances between 10 and 26 %. The numbers drop considerably, below 5 %, towards the 26.08.03 and 17.09.03. This is in contrast to the benthos samples, where *Diploneis* occurs in repeatedly constant abundances. The differences in results from water samples cannot be explained by wind-induced resuspension, as the wind directions on the 17.09.03 and 26.08.03 were opposed, blowing from SSW (mean velocity: 5.5 m s^{-1}) and NNW (mean velocity: 8.9 m s^{-1}) thus inducing a synergistic effect that is expected to favour resuspension. One explanation could be a seasonal shift in the diatom community with a decrease in resuspendable *Diploneis* cells or a second explanation might support the theory that *Diploneis* is a tychopelagic species that resists the seasonal increase in wind-current-induced resuspension by stronger association to the substratum and thus avoids the displacement into less favourable regions such as the light-limited sub littoral or the open sea. Finally some patterns for *Diploneis* can be recognised by looking at the distribution in water and sediment samples for the pairwise comparison of 20.08. and 26.08.03: stable abundances in the benthos for both sampling days with a 'preference' for reduced flow (theory stated above) but completely differing pictures for water samples for both tides on both sampling days. Prevailing wind direction and velocity does not explain the higher abundances in the water on 20.08.03 and it could be assumed that a varying capability of attachment to substrata or of buoyancy methods leads to a periodical dislodgement and suspension.

Uncles (2002) reports fortnightly variations (spring-neap), as well as longitudinal tidal currents that can generate transverse circulation patterns (secondary flow) as they respond to geomorphology. Gravitational circulation and wind forces produced mean flow patterns, regardless of wind direction. These findings could well be adapted to our results, where wind direction and wind velocity cannot explain the variability in abundances at ebb and flood tide. Furthermore, lower abundances in water samples in spring could also be related to a period of extended stability at high water, causing less mixing due to less bottom-generated shear stress.

A general statement for the contrasting abundances occurring when comparing incoming to outgoing tide can be made by referring to the ability of the cells to migrate vertically. Round and Palmer (1966) described species-related varying responses to the tidal rhythms. Therefore, a constant, reproducible result can not be expected, only small scale sampling and higher resolution of samples will bring further insight into the influences of tidal cycles on species level.

Conclusions

Factors such as wind force, wind direction, tides, benthic productivity and standing crop are assumed to account for the range of variability between the samples. The effect of wind induced resuspension also seems to superimpose tides, given the fact that cell numbers of 12.08.03 are lower by an order of magnitude compared to 26.08.03 although the first should reflect higher values due to spring tides and the latter lower values due to neap tides.

An erratic composition of species in water samples compared to rather stable occurrences of species from benthos samples in spite of different wind directions and wind speed suggests a highly dynamic exchange between water and sediment with implications for biomass available for plankton and benthos feeders.

The composition is influenced by species introduced from open water through inlet at northerly winds OR by fetch, when easterly winds transport water masses over the intertidal flats off the Danish coast and carry typical benthic species associated with mudflats (pers. obs.).

Due to the high variability of the combined data sets (cell numbers, wind data, current velocity at incoming and outgoing tide) it seems impossible to predict a trend or the characteristics of the system flow-water-sediment-biota. The patterns/factors determining every single process are too complex to schematise. Isolated events, such as the 26.08.03 where different current velocities at both incoming and outgoing tide mirrors cell numbers at incoming and outgoing tide can be explained by wind speed and current velocity etc. However, this can not be applied to other events, where the measured parameters don't present the same causal connexion. This leads to the conclusion that all environmental factors, tidal cycles, neap and spring, wind direction and speed, geomorphology, create a picture of continuously acting elements that can be investigated in snap shots but data are not to be extrapolated arbitrarily.

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Chapter 5

Diatom cell-size: The ups and downs in currents and turbulences

Abstract

In situ experiments with a three-current-flume construction have been carried out on an intertidal flat of the east coast off the island Sylt, North Sea, Germany. This work describes the attempt to integrate *in situ* measurements of turbulence with cell counts of four cell-size groups of diatoms (Bacillariaceae) of 0-10 µm, 10-20 µm, 20-50 µm and >50 µm to gain a better understanding of processes concerning the resuspension behaviour of the cells. Estimates of shear velocity U_*, calculated from TKE (Turbulent Kinetic Energy) and flow covariance U'W' have been used as parameters to predict hydrodynamic conditions on a sandy tidal flat. The determining factor turned out to be wind-turbulence interplay; the wind direction and force cause antagonistic or synergistic effects, thus influencing the current velocity. Erosion effects leading to entrailment of cells into the water column were initiated by small-scale, punctuated high shear velocity. The three manipulated velocities 'increased', 'mean', and 'reduced' inside the flume showed no significant effect, the same applies to tidal influence. High variability within the cell-size groups and high values for bed shear stress and shear velocity U_* within the reduced-flow lane lead to the assumption that turbulence, not current velocity was the determining factor for the resuspension.

Introduction

The main primary producers on intertidal zones are macro- and microalgae. The latter group comprises next to Cyanobacteria, Chlorophyceae and Dinophycaea benthic diatoms, phototrophic, unicellular algae with a silica cell wall or frustule enveloping the cell. The importance of microphytobenthic algae in terms of primary production and sediment stabilisation has been explored for many years (DeJong & De Jonge 1995; DeJong 1995; Underwood 2001). In his review Cahoon (1999) reports figures of benthic microalgal production estimates between 1 g C m^{-2} yr^{-1}, Laholm Bay, Sweden at 19-20 m depth; 115 g C m^{-2} yr^{-1} for the Wadden Sea, Netherlands, up to 840 g C m^{-2} yr^{-1} for St. Croix, Virgin Islands. The strong differences between latitudes and water depth depict the high variability on different scales and the necessity to explore the limiting factors for growth and diversity. The remarkable ability of diatoms to adapt to surrounding conditions makes them a successful inhabitant of different habitats where they are exposed to extreme gradients of light, salinity, temperature and other environmental parameters. Even when exposed to extreme physical conditions such as wave and tidal induced disturbances they can prevail in high abundances.

On mudflats, the diatom community may consist almost exclusively of epipelic species. The expression epipelon refers to species associated with the sediment, generally exhibiting extensive motility. In high abundances, the cells are visible as brown patches on the sediment surface and they respond to changing irradiation or tidal rythms by migrating into deeper sediment at the beginning of the dark period or incoming flood tide (Palmer 1967, Paterson 1989, Tolhurst et al. 2003). The secretion of extracellular polymeric substances (EPS) allows the diatom a degree of motility in the sediment. Thus a matrix is formed, embedding the diatoms and smoothing the sediment surface (Edgar 1984, Hoagland et al. 1993, Underwood & Paterson 1993, Austen et al. 1999). Sediment stabilisation has been subject of many studies during the past years (e.g. (Grant et al. 1986, Paterson et al. 1990, Amos et al. 1992, Sutherland et al. 1998, Paterson & Black 1999, Yallop et al. 2000, Friend et al. 2005). Biofilms – or microbial mats – are formed by several organisms, diatoms, bacteria, cyanobacteria, chlorophyceae, and can be found in many different habitats, in subtidal areas as well as on intertidal flats. Depending on the properties of the sediment (grain size, mud content, porosity) this biofilm is more or less resistant to physical disturbances.

Intertidal muds and sandflats are subject to dynamic processes such as tidal forces, sediment movement and exposure time. The ability to move towards and away from the surface by means of EPS production under such conditions as burial or deposition events is essential for cells to survive in such habitats, subjected to constant change (Smith & Underwood 2000). Erosion thresholds and transport rates can be altered by benthic organisms but organism impact in general decreases with increasing sediment transport rates (Jumars & Nowell 1984). Sandy sediments are characterised not only by the above mentioned epipelic diatoms but also by very small species, exhibiting an epipsammic life style by attaching to the substratum either the whole frustule or by aid of mucus stalks. Thus, diatoms are able to bind and consolidate sediments, although, sandy substrata will be consolidated to a lesser extent than fine sediments, where EPS-excreting, motile species outweigh epipsammic species.

The prevailing hydrodynamic conditions determine the distribution of sediments and finally the diversity of microorganisms in the habitat. High physical stress results in coarse sands, difficult to colonise for epipelic diatoms which in turn would be able to bind and stabilise the sediment via EPS production. In areas with strong hydrodynamic forces, small epipsammic species will prevail. Their small size and ability to attach firmly to the substratum enables them to colonise crevices of the coarse sand grains. Fewer disturbances affect the diversity of microorganisms on the sediment inasmuch as more epipelic species are able to colonise the sediment. For a comprehensive understanding of the interacting factors it is important to have a balanced view of the intertidal system. Physical and biological factors are both inseperably linked (Hagerthey et al. 2002).

Flow is a three-dimensional movement of the water body generated by wind, waves and tides. Currents constitute not only a horizontally distributed motion defined as the flow velocity but also a vertical and a transverse flow component. Small particles may be subject not only to lateral transport processes, but also to vertical resuspension into the water column due, e.g. to tidal currents. Both are functions of physical factors (wave and currents induce erosion) and biotic factors (Van Leussen 1986).

Resuspended microphytobenthos influences the community structure of the phytoplankton and also provides a fresh food source for suspension feeders (i.e. mussels). This fluctuation presents an important influence on microbial food-web dynamics as well as on dynamics on the sediment-water boundary layer.

Turbulent mixing of the water mass is caused by bottom roughness (e.g. ripples, rocks, macroalgae, musselbeds), by tidal currents and wind. DeJonge (1985) states that a large exchange of sand and diatoms occurs between the tidal flats and the channels of an estuary. This dynamic exchange in concert with sediment sorting by currents and waves could lead to changes in species composition of tidal flat diatom assemblages.

To date, only few field investigations using *in situ* measurements attempting to couple water dynamics with the resuspension of benthic diatoms have been carried out, predominantly due to the complexity and inconsistency of the physical system (Amos et al. 1992, Sutherland et al. 1998, Widdows et al. 1998, Shimeta et al. 2002, Biles et al. 2003, Lucas 2003). Laboratory and *in situ* flume studies allow us to study experimentally the influence of various physical factors concerning hydrodynamics on sediment and/or biota; e.g. the importance of biomixing by mussels under controlled high and low current conditions. The advantages and drawbacks of the various devices are debatable, but under consideration of the particular requirements every flume device can yield promising results. Laboratory set-ups strive to create controlled conditions, laminar flow, that doesn't exist under natural conditions. In field systems it proves difficult to seperate and controls the influencing factors, but on the other hand they provide a good overview of the field situation, a more realistic picture of processes occurring under natural conditions. In both cases, to avoid the turnout of hydrodynamic artefacts the flow conditions and resulting requirements of measurements have to be precisely ascertained. Results of such research can contribute to a better understanding of the impact of near-bottom flow conditions on benthic filter feeding communities. Flume experiments have greatly improved the understanding of the implications of altered hydrodynamic conditions for processes in the boundary layer and on biota. Flume systems became an important tool to support research on processes at the water-sediment interface (Grant et al. 1986, Muschenheim et al. 1986, Blanchard et al. 1997, Sutherland et al. 1998, Widdows et al. 1998, Tolhurst et al. 2000, Lucas et al. 2001, Beaulieu 2003, Amos et al. 2004).

(Huettel & Rusch 2000), among others, investigated oxygen flux rates and found decreasing oxygen penetration in the sediment at flow speeds between stagnant water and 0.05 m s^{-1}, resulting in an overall reduction in photosynthesis due to downward migrating diatoms. Shimeta et al., (2002, 2003) employed an annular flume device called Sea Carousel (Amos et al. 1992) to reveal that differences in the resuspension thresholds of ciliate groups were due to differences in taxonomic composition, whereas differences for diatoms were linked to sediment dynamics. This finding implies a possible impact on the microbial food-web ecology in the water column and sediments by linking the communities and creating strong fluctuations across the boundary layer.

In terms of export and import processes on large and on smaller scales in tide-exposed coastal areas it is necessary to have a better understanding of the implications of the factors controlling resuspension and settling processes of both organisms and sediments.

The motivation of this study is to understand to what extent biophysical coupling between turbulence and resuspension affects the microphytobenthos population associated with the sediment. Therefore, a large *in situ*, three-current flume was used which was permanently positioned on the intertidal flat in the study area. The unique construction of the flume device allows to investigate the effect of waves *in situ*, resulting in turbulences, on the sediment surface.

Material and methods

Study site

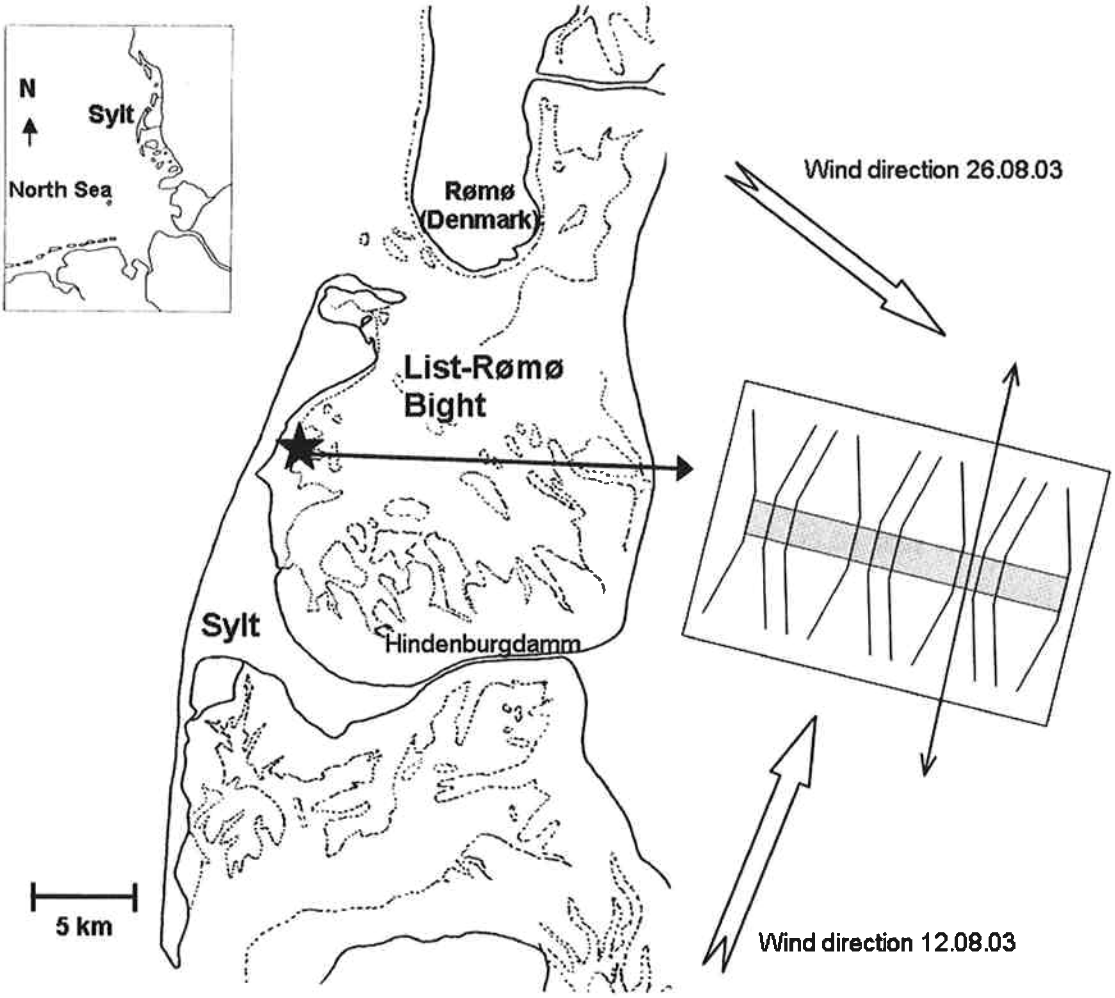


Fig. 1. Study area in the northern Wadden Sea. Inset: general map showing the location of Sylt in the northern Wadden Sea. Asterisk indicates sampling site with arrow leading to a diagramm of the three-current-flume aligned to the bi-directional tidal currents (double headed arrow). White, tailed arrows: wind direction on 12.08.03 and 26.08.03. Stippled line: mean low tide line.

The study area, the Sylt-Rømø Bight, is situated on the east coast of the island of Sylt, in the northern part of the Wadden Sea (Fig. 1). The bight is a semi-enclosed system framed by the islands of Rømø (Denmark) and Sylt, and by a causeway connecting the island with the mainland. The only exchange with the North Sea is a 2.5 km broad tidal inlet called Lister Tief in which the maximum velocity of the tidal currents is about 1.3 m s^{-1}. The intertidal flats comprise 95 % sandy sediments next to mud flats, seagrass beds and mussel beds. The tidal range in the bight is about 1.8 m with minor deviations due to neap and spring tide or wind. Average water height in the sampling area is 0.81 m. The salinity of the water ranges seasonally from 28 to 32 (salinity was measured using the practical salinity scale). Mussel beds (*Mytilus edulis*) are present in the intertidal area of the tidal basins (Gätje & Reise 1998), but subtidal mussel beds are almost absent due to over exploitation.

Studies by (Deussfeld & Pasche 2003) in the same area revealed that the vertical profile of velocity deviated from known standards with e.g., velocities decreasing from water surface to bottom, for which wind induced surface currents can be held responsible.

Flume

The three-current-flume represents a large device for *in situ* research under manipulated current regimes directly on the intertidal flats. The nine lanes of the steel construction, lined with a durable fabric, comprise three parallels of different current velocities further referred to as 'increased', 'mean' and 'reduced' (Fig. 2). The tidal flow is directed through these lanes and current velocity subsequently either increased or reduced by narrowing or widening of the respective lane. For further technical details see (Schanz et al. 2002). The flume was aligned to the bi-directional intertidal current (see also Fig.1). Sampling of water and sediment samples took place in the mid section of the lanes.

Fig. 2. Three-current-flume. Close-up view of three flume lanes with different openings thus manipulating current velocity into increased, unaltered or reduced flow across the mid section of the flume. Measurements: 8 m length, 12 m width, 1 m height. Photo: Anja Schanz

Flow measurements

Flow was measured at three different depths of 10 cm, 20 cm above bottom and close to the water surface using an Acoustic Doppler Velocimeter (ADV), NorTek, Norway. The device was employed to measure flow components over the best part of one tidal cycle (until water fell below the sampling height between 10 – 20 cm above bottom at outgoing tide or the water level had not yet reached the required level, respectively). Calculations of velocity and turbulence represent the mean of three parallels of the respective manipulated current velocity, increased, mean, and reduced. ADV data sampling frequency amounted to 8 Hertz (SI = 1/s).

ADV measurements simultaneously provide data for the three flow components (vectors): U (main horizontal, or longitudinal velocity), V (transveral velocity) and W (vertical velocity). Quantitative terms such as ‘critical erosion threshold’ or ‘turbulent kinetic energy’ (TKE) allow a definition of the forces exerted by the three flow components on the subject of research.

The vector length of the total current velocity can be calculated as vector addition of the three flow components according to the equation:

$$\sqrt{U^2 + V^2 + W^2} = \text{length of vector } [\mathrm{m\ s^{-1}}]$$

Calculations of turbulence

Turbulence was calculated and graphically presented in different ways to extract the important information and to reach valid estimates of shear velocity U_*, which is a value that reflects the steepness of the velocity gradient inside the near-bed boundary layer, but also relates the current velocity to the resulting bed shear stress which can cause erosion or resuspension if it exceeds a typical threshold value.

One method was to calculate turbulence as standard deviation (SD) of the vertical flow component (W), i.e. SD W (see figs. 9 and 12, vertical flow profiles with turbulence presented as bars), in order to obtain a descriptor for the influence of wave action and/or near-bed turbulence related to roughness. The variability of the instantaneous flow fluctuations (U', V'and W') around the mean velocity of each flow component can be used to calculate the Turbulent Kinetic Energy (TKE) or the Reynolds stress.

TKE can be calculated as:

$$\text{TKE}\ [\text{m}^2\ \text{s}^{-2}] = \tfrac{1}{2}\,(\overline{U}'^2 + \overline{V}'^2 + \overline{W}'^2)$$

and Reynolds stress, or turbulent shear stress, the turbulence driven momentum flux along a defined plane the product of instantaneous flow fluctuations, and of the water density ρ (1026 kg m^{-3} at 15°C and salinity = 35):

$$\text{Re stress}\ [\text{N/m}^2] = -\,\rho\,(\overline{U'W'})$$

As the density of the water is relatively constant during an experiment, Reynolds stress values are often simplified to the covariance of two fluctuating components, like e.g. U'W' instead of - ρ U'W'. Calculation of shear velocity from TKE and Re stress are based on the assumption that in the lower part of the boundary layer Re stress approaches a constant value, the so-called constant stress layer. In this layer, shear velocity (U_*) is related to Re stress as:

$$U_*\ [\text{m}\ \text{s}^{-1}] = \sqrt{\frac{\text{Re}\,stress}{\rho}} \qquad \text{and to TKE as:} \qquad U_*\ [\text{m}\ \text{s}^{-1}] = \sqrt{c_1\,\text{TKE}}$$

where c_1 is a proportionality constant with an approximate value of 0.2 (Kim et al. 2000).

As both methods produce rather deviating values within the same type of flow velocity manipulation due to their different mathematical approach which can strongly emphasise the impact of individual contributors to these deviations, it was decided to use the median of both calculations for the analysis of the data (see Fig.6).

Calculations of bed shear stress

Shear stress is the stress component of the fluid force on the bed in flow direction. Bed shear stress can be calculated as:

$$\tau_0 = \rho U_*^2 \text{ [Pa]; where } \rho = \text{density of water } (1026 \text{ kg m}^{-3} \text{ at } 15°\text{C and sal.} = 35)$$

Grain size analysis

For the analysis of grain size replicate sediment samples taken from the three flume lanes with three different, manipulated flow velocities were freeze-dried and afterwards treated with H_2O_2 to remove organic substances. After rinsing with H_2O the grain size was measured by means of a QUANTACHROME CILAS-Lasergranulometer 1180. Classification occurred according to the Wentworth scale in size classes of phi-values ($\Phi = -\log_2$ of grain size in mm).

Sampling

For the identification of size classes of diatom cells and interpretation of turbulence data, two sampling days were analysed: 12.08.03 and 26.08.03 with a representative set of current data collected by means of ADV. Samples from the water column were taken at a depth between 10 and 20 cm above sediment surface and preserved in Lugol's solution. 500 cells were counted in a settling chamber using an inverted micoscope, Zeiss Axiovert 35, and grouped into four size classes representing a range of 0-10 µm, 10-20 µm, 20-50 µm and cells longer than 50 µm.

Statistical analyses

Statistical tests were carried out using STATISTICA 6.0 StatSoft and PRIMER 5 (Clarke & Warwick 2001). In addition to a multidimensional scaling plot (MDS), ANOSIM (Anova of similarity) was applied to test the different influences of factors between groups. MDS (multidimensional scaling) plot of Bray-Curtis similarities visualise valuable information about the superimposed variables velocity (UVW) or turbulence (U_* from TKE and U'W') presented as bubbles. They highlight the value of a further variable measured at the same set of sites.

Results

Grain size

Grain size is around 1.5 Φ (sorting coefficient), with a medium diameter between 0.2 and 0.63 mm. The median (Md) for the surface first centimeter is approximately 0.3 – 0.4 mm, which means medium to coarse sand, according to the Wentworth grade classification.

General flow conditions on 12.08.03 and 26.08.03

The general flow conditions for the three manipulated current velocities are plotted in Fig. 3, with a significant difference between flow within 'increased' and 'reduced' current velocity lanes. ANOSIM mid-range value of R (= 0.594) for the global test of the three flow velocities (fast, medium, slow) established that there is a statistically significant difference between flow velocity in the 'increased' and 'reduced' lane at a < 3 % significance level. The sampling dates are different with a significance of $p < 0.01$.

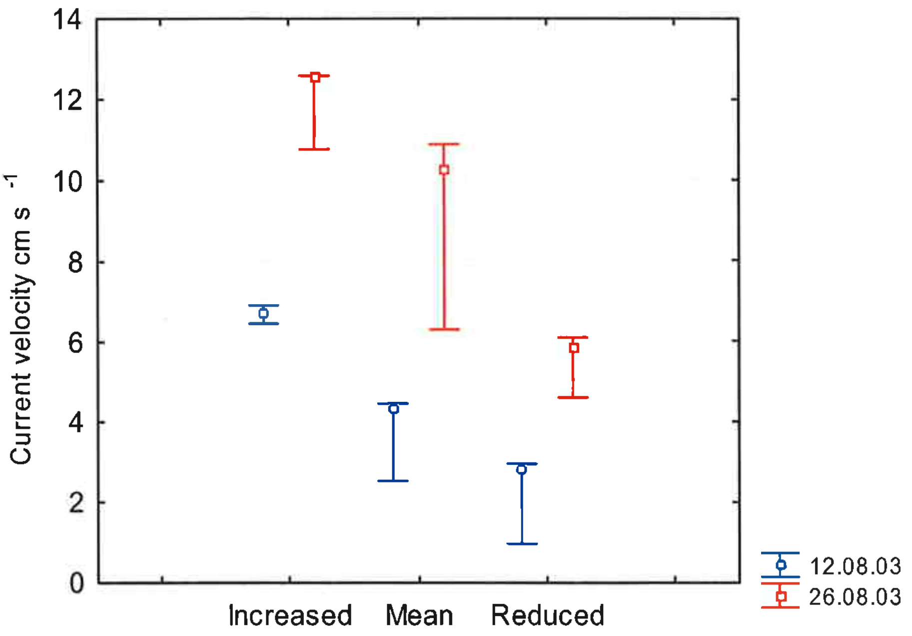


Fig. 3. Current velocities on 12.08.03 and 26.08.03. The symbols indicate the median of the three manipulated flow velocities 'increased', 'mean', and 'reduced'. Whiskers: min.-max.

General wind conditions on 12.08.03 and 26.08.03

Wind data for the sampling days were provided by the weatherstation List/Sylt (Deutscher Wetterdienst DWD). At 12.08.03, winds from WSW, 2.3 – 6.7 m s $^{-1}$ prevail and at 26.08.03 winds from NW, between 7.5 and in peaks 11.5 m s $^{-1}$ (see Fig. 4). The differences between sampling days are significant with $p < 0.001$.

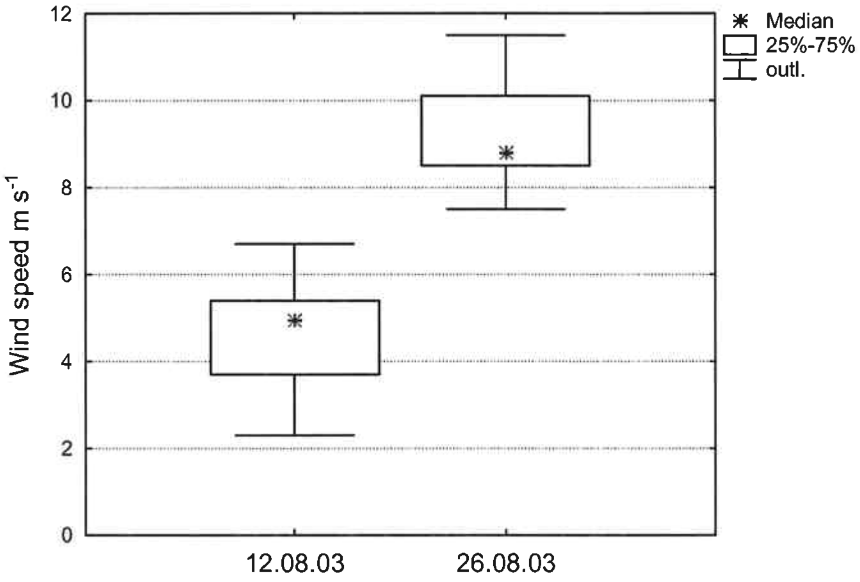


Fig. 4. Wind speed [m s $^{-1}$] on 12.08.03 and 26.08.03.Asterisk indicates median value, box: 25% - 75 % quartile, whiskers: outliers.

Correlation of wind and turbulence on 12.08.03 and 26.08.03

For correlation of wind data for the 12.08.03 and 26.08.03 with turbulence data (standard deviation of flow component W) see Fig. 5. The correlation coefficient r^2 increases from the water surface towards the sampling point 10 cm above the sediment surface (r^2 = 0.23 and 0.56) at incoming tide on the 12.08.03. Outgoing tide shows a higher wind/turbulence correlation above the bottom compared to the water surface (r^2 = 0.41 and 0.19).

A different picture with an almost linear correlation is presented for the 26.08.03, where surface wind/turbulence correlations are higher than the bottom values (r^2 = 0.45 and 0.14 at surface, in- and outgoing tide, compared to the very low correlation values of r^2 = 0.18 and 0.11 in- and outgoing tide at 10 cm above the sea bed).

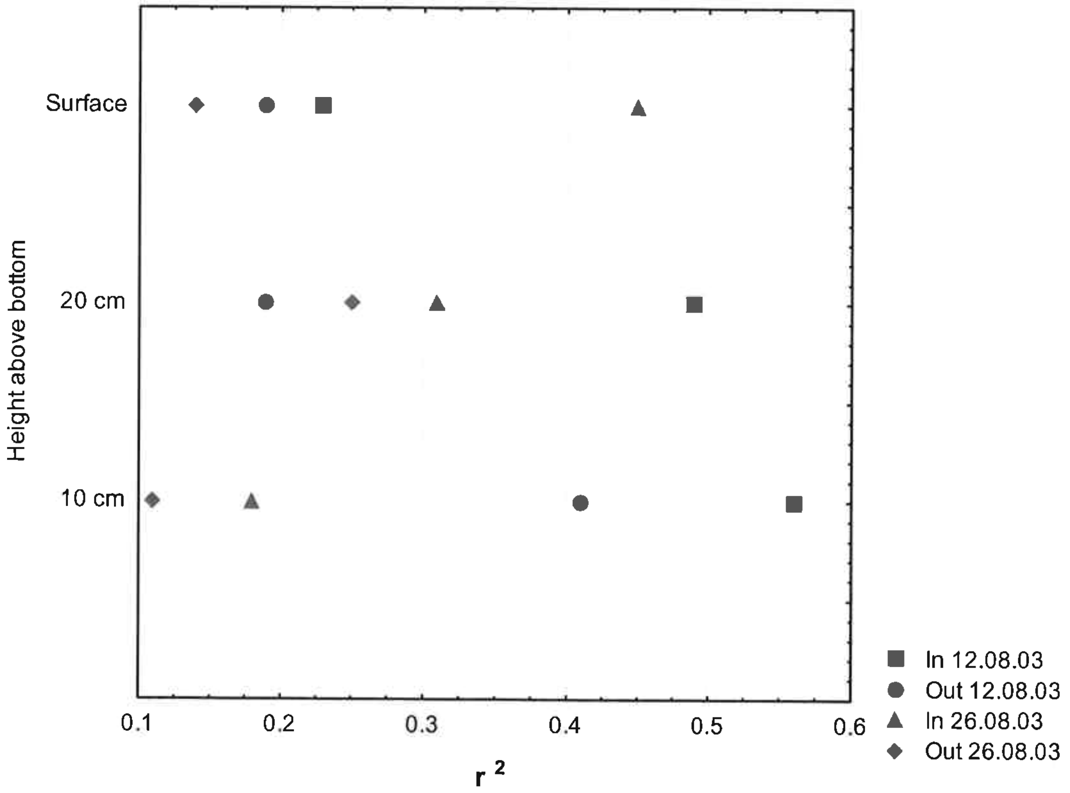


Fig. 5. Correlation (r^2) of wind [m s^{-1}] and turbulence (SD of flow component W) for incoming and outgoing tide at three heights above sediment surface on 12.08.03 and 26.08.03

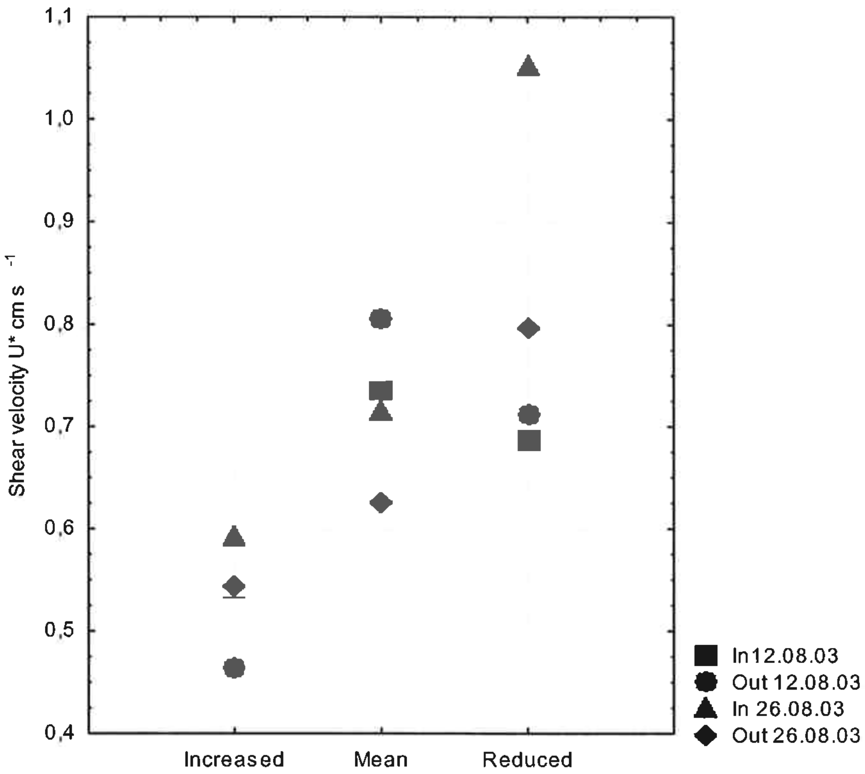


Fig. 6. Median shear velocity values U_*, calculated from turbulence parameters (TKE and Reynolds stress) extracted from the ADV data for incoming and outgoing tide at three flow treatments (increased, mean and reduced) on 12.08.03 and 26.08.03

Distribution of cells into size-class groups

Figure 7 provides a general outline for the distribution of the four size-class groups and their distribution at the two sampling days (12.08.03 and 26.08.03) and the respective flow velocity fast, medium, slow. An increase from smaller to larger sized cells on 12.08.03 is contradicted by a decrease from small to bigger cells on the 26.08.03.

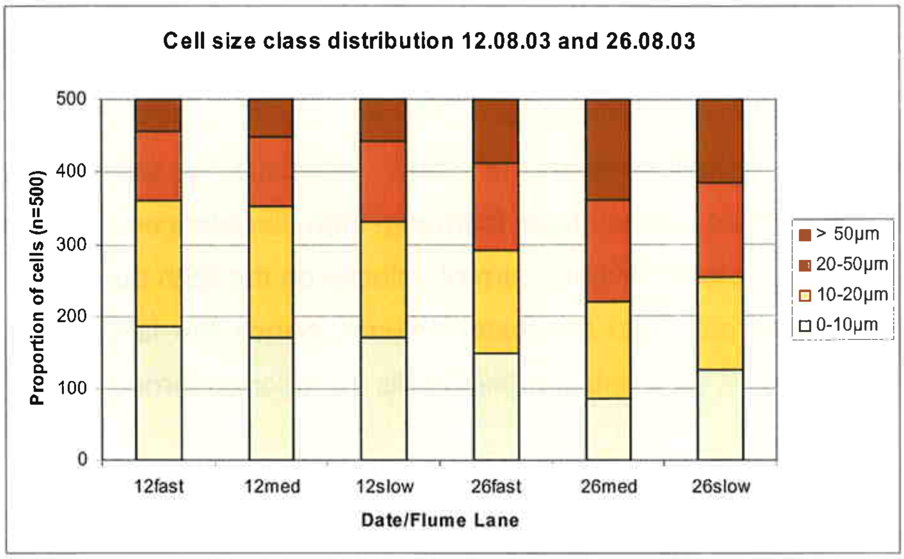


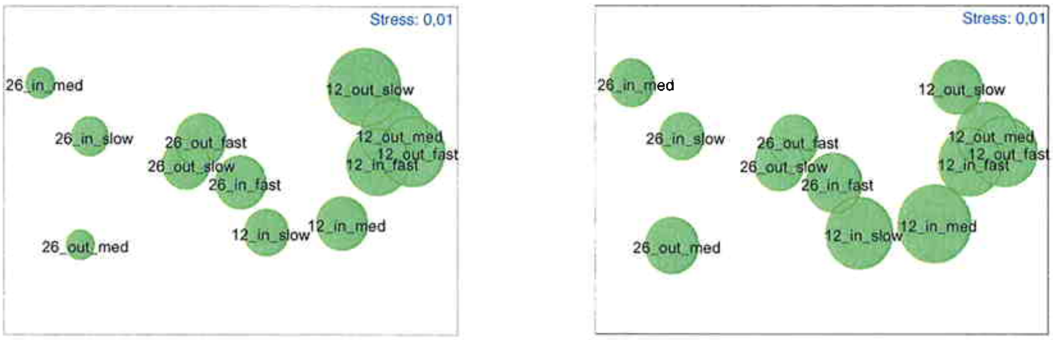
Fig. 7. Distribution of four cell size classes (0-10 µm, 10-20 µm, 20-50 µm and cells above 50 µm). X-axis represents sampling day (12. and 26.08.03) and manipulated flow velocity (increased, mean, reduced).

Figures 8 and 9 show MDS (bubble) plots (based on a Bray-Curtis similarity matrix, data square-root transformed), visualising ecological coherences. Figure 8 represents the abundance of the four different cell-size groups, 0-10 µm, 10-20 µm, 20-50 µm, and cells >50 µm at the respective sampling day, incoming or outgoing tide and the manipulated current velocity (labelled as: 'date_tide_flow velocity'). The circle size increases with abundance in relation to the above named community patterns (date, tide, flow velocity). The plot is similar to the bar chart in figure 7 but is to be correlated with figure 9, presenting the superimposed effect of the velocity vector (UVW at 10-20 cm height) and turbulence (Median of U_* calculated from TKE and U'W' at 10-20 cm height), respectively. The following aspects can be derived from these MDS plots: the separation of data for the relationship between manipulated velocity and turbulence (TKE/U'W') is smallest for the 'increased' flow. This indicates the smallest differences in distribution of cells at incoming as well as at outgoing tide. The same applies to the factor current velocity (UVW). No distinct separation into incoming and outgoing tide can be found that was statistically provable. Giving an R-value of 0.131 (ANOSIM, significance level < 3%) the Null-Hypotheses 'differences between samples considering factor tide' cannot be rejected. By just using the mean values of in- and outgoing tide, information became too diffuse.

While turbulence is high on the 12.08., velocity is low. The reverse applies for the 26.08., where turbulence is low and velocity high. Cell-size distribution responds to either high velocity AND low turbulence, or to low velocity AND high turbulence, not to one in isolation. Higher numbers of small cell-sizes, possibly reflect the composition of the surface assemblage following high turbulences. However, the same does not apply to velocity. Higher current velocity on the 26th does not achieve an entrainment of small cells into the water column; hence the larger part of the dominating larger cell-sizes will contain pelagic cells transported through the flume.

a) Cell-size group 0-10 µm

b) Cell-size group 10-20 µm



c) Cell-size group 20-50 µm

d) Cell-size group >50 µm

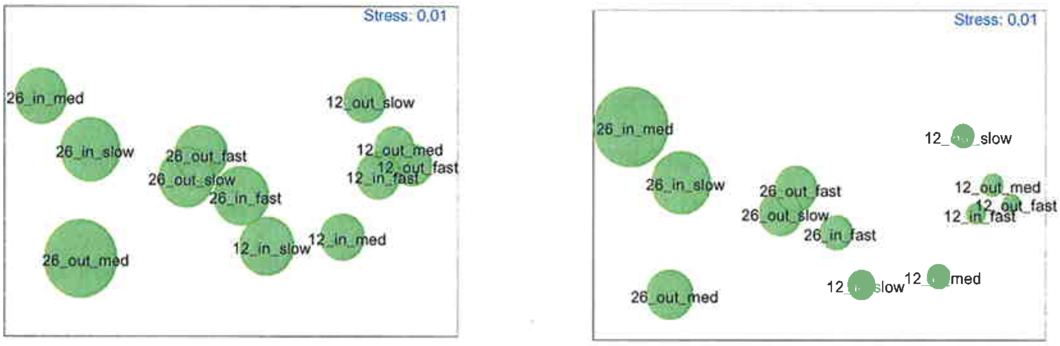
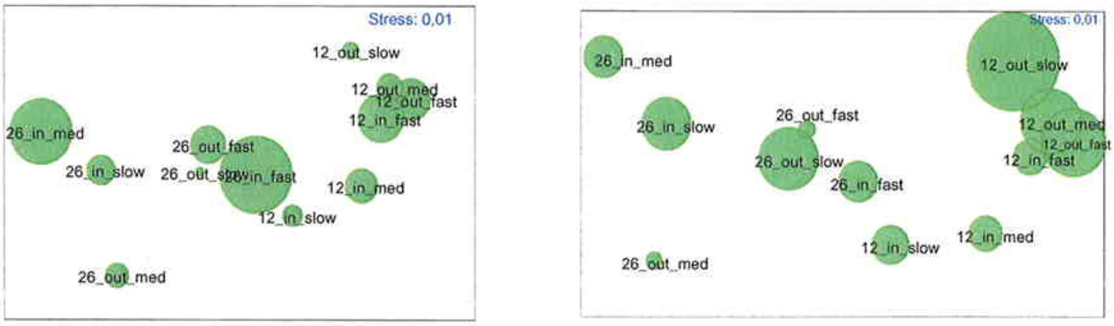


Fig. 8 a) – d). MDS plot displaying individual abundance of size-class group (size of circle) in relation to the overall community pattern within the respective size group at sampling date (12.08.03 and 26.08.03), tide (incoming, outgoing) and modified velocity (increased, mean, and reduced).



a) Cell sizes, UVW 10-20 cm height

b) Cell sizes, Median TKE+U'W' U· 10-20 cm height

Fig. 9 a) – b). MDS of cell-size distribution with superimposed circles indicating increasing size with increasing effect of a) flow velocity vector(UVW) at a height between 10 and 20 cm above sediment surface and b) turbulence (as Median of shear velocity U_* calculated from the flow characteristics Turbulent Kinetic Energy and U'W').

Flow, turbulence and cell-size group data separate for 12.08.03 and 26.08.03

Sampling day 12.08.03

Flow profiles measured in the increased lane show a higher current velocity at all three measure points in the water column with 0.07 m s^{-1} at 10 cm above the sediment surface, 0.08 m s^{-1} at 20 cm height and 0.06 m s^{-1} at the water surface. Compared to that, the reduced lane shows lower values with 0.04 m s^{-1} at 10 cm height, 0.02 m s^{-1} at 20 cm height and a surface current velocity with 0.01 m s^{-1}. The differences between the three flow-treatments were significant ($p = 0.0026$).

Only small differences can be found between values for incoming and outgoing tide; the mean flow velocity inside the reduced-current lane is 0.02 m s^{-1} (± 0.01) for incoming tide compared to a velocity of 0.03 m s^{-1} (± 0.008) for outgoing tidal waters.

Turbulence, expressed as SD of the vertical flow component, shows different pictures for the incoming and the outgoing tide: whereas it increases from bottom to top in the faster flow, the values for turbulence decrease from top to bottom at outgoing tide. In both lanes, increased and reduced, the values increased almost by factor 2 at 10 cm above bottom and show the highest values at this height in the reduced lane (SD 0.033) (see Fig. 10). Furthermore, a zone of less turbulence can be determined at 20 cm height above the bottom.

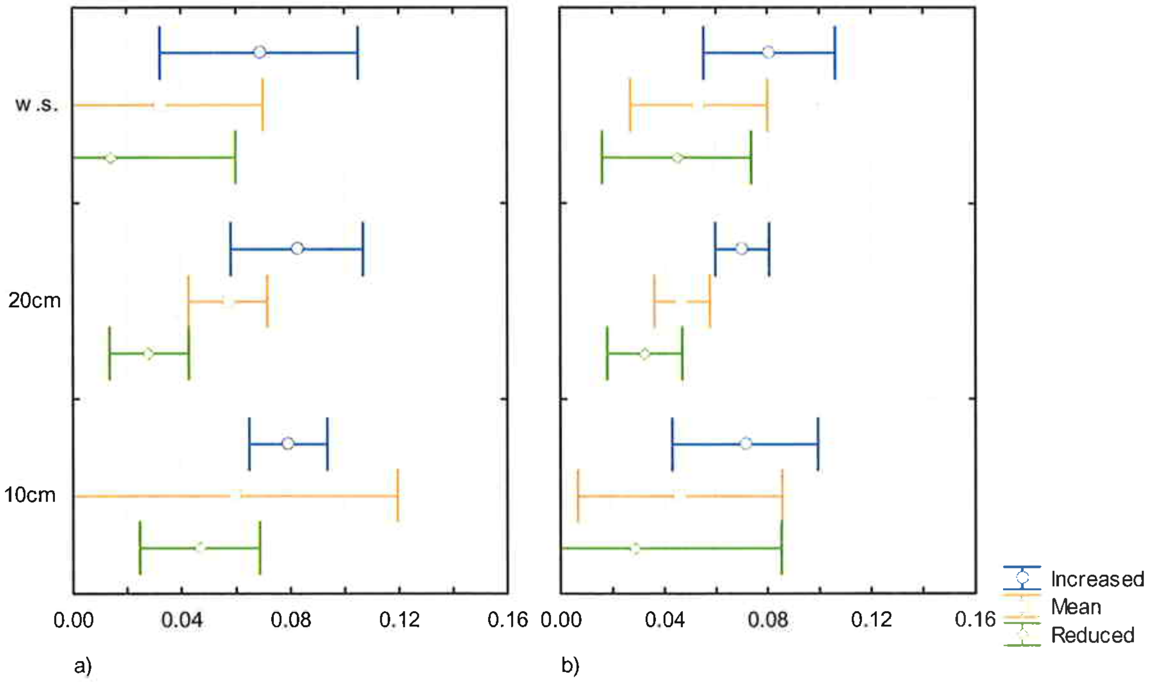


Fig. 10 a) and b). Current velocity vector (U, V, W) [ms^{-1}] of the manipulated flow (increased, mean, and reduced) measured at three points: 10 cm, 20 cm above sediment bed and water surface (w.s.). Bars represent turbulence as SD of vertical flow component W. a) incoming tide, b) outgoing tide 12.08.03

The distribution of cells into the four different cell-size groups showed a significant grouping of the smaller cell sizes 0 – 10 µm and 10 – 20 µm, and separated from these the two groups comprising cells above 20 µm of length (ANOVA, $p < 0.001$; LSD post-hoc test $p < 0.001$, calculation includes all tides and manipulated velocities) (see Fig.11a).

The whisker-plots in Fig. 12a (12.08.03) show a wider distribution of cell-size classes in the increased lane compared to reduced (SD increased = 12.6 and SD reduced = 10.9).

Tests showed that neither of the three manipulated velocities nor the tide had a statistically significant influence on the distribution of cell-size classes.

Among the species counted, a high number of the benthic species *Diploneis bombus* (Ehrenberg) and *Diploneis interrupta* (Kütz.) Cleve were observed, but also cells of *Cylindrotheca closterium* (Ehrenberg) Reiman et Lewin, a species with a bentho-pelagic liyfestyle.

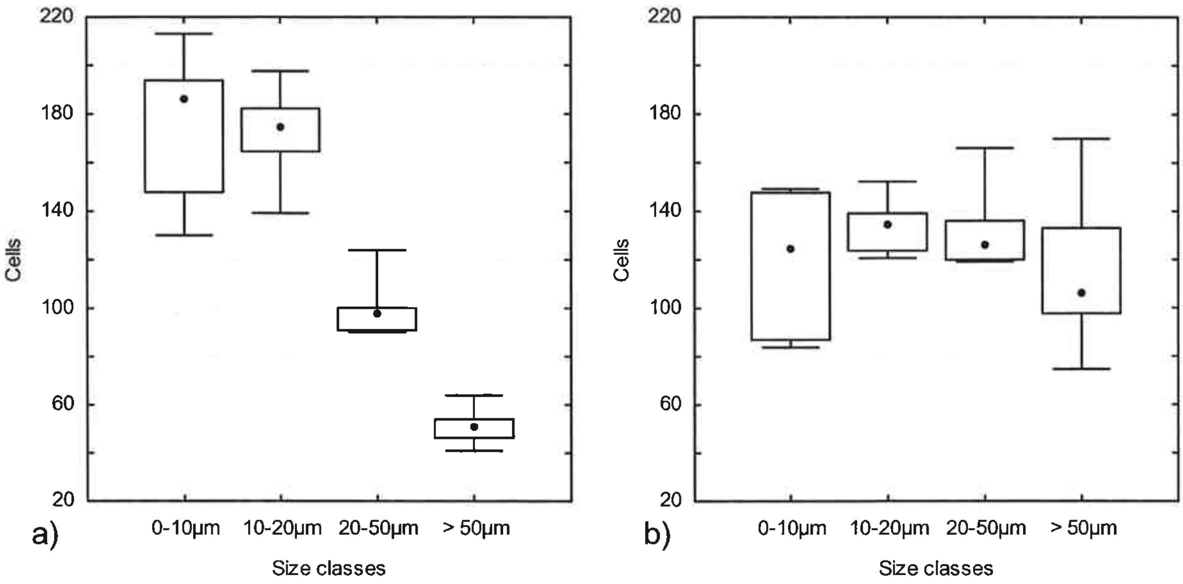


Fig. 11 a), b). Distribution of four cell-size classes (0-10 µm, 10-20 µm, 20-50 µm and cells >50 µm) across all velocity treatments and incoming/outgoing tide on a) 12.08.03 and b) 26.08.03. Median values, whisker: min/max, box: 25%-75% quartile

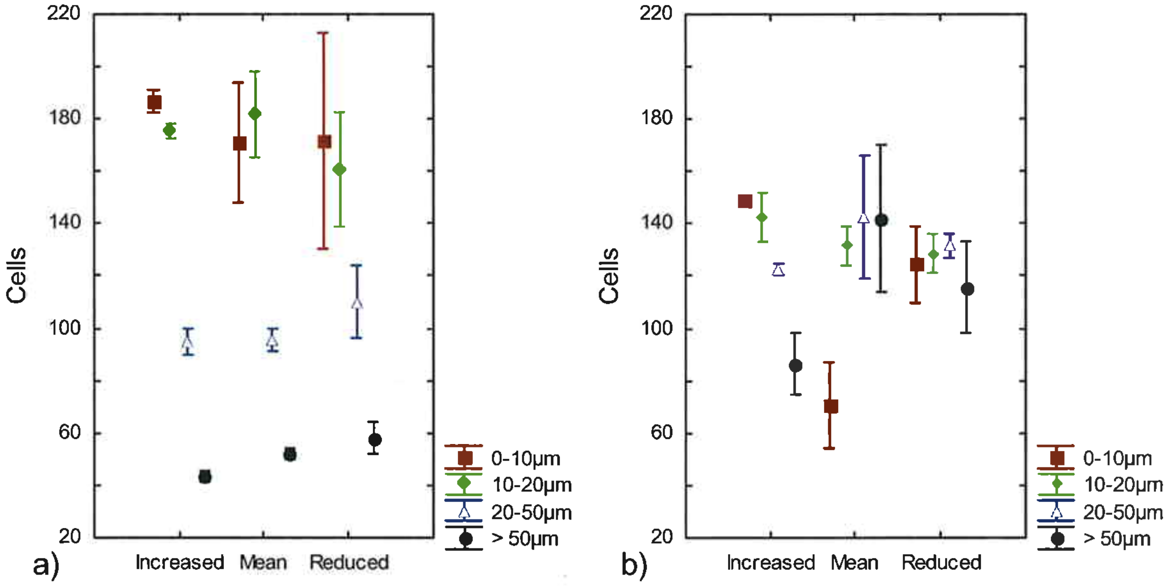


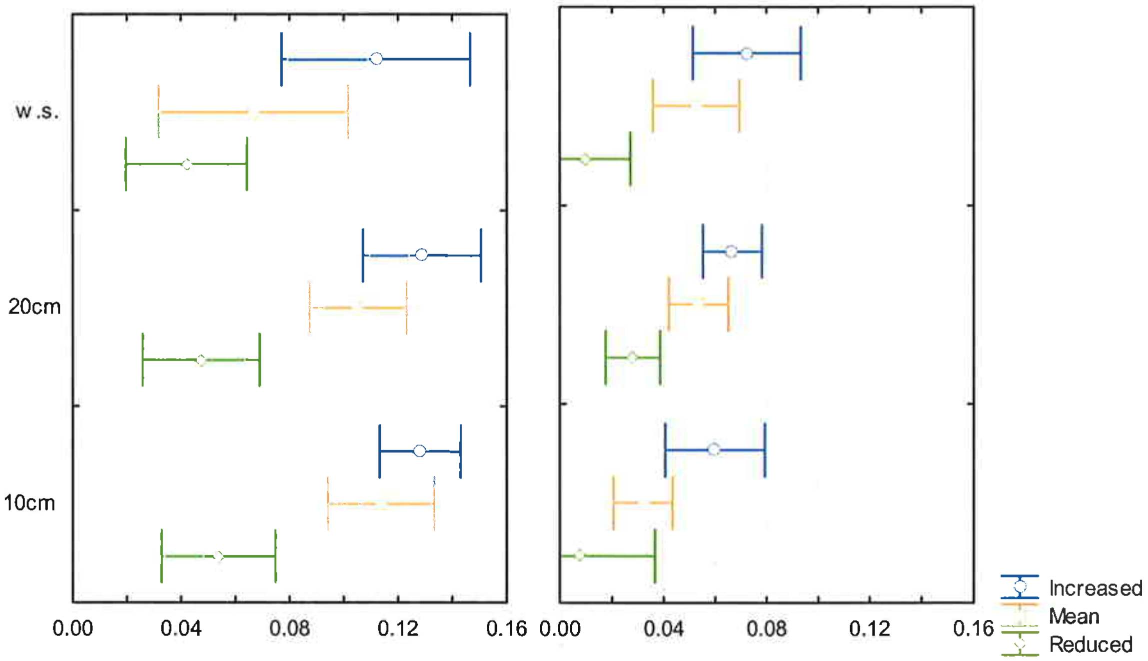
Fig. 12 a), b). Distribution of four cell size classes in three different current regimes (increased, mean, and reduced). a) 12.08.03, b) 26.08.03. Median values, whisker: min/max

Sampling day 26.08.03

Flow velocity measured in the increased lane shows higher values compared to mean and reduced flow profiles with 0.13 m s^{-1} at 10 cm above sediment surface, 0.13 m s^{-1} at 20 cm and 0.11 m s^{-1} at the water surface. In contrast to this, velocity values for the reduced-flow lane are lower with values of 0.05 m s^{-1} for the height of

10 cm above the bottom, 0.04 m s^{-1} at 20 cm height and 0.04 m s^{-1} at the water surface. Significant differences ($p = 0.008$) existed between the flow treatments. Outgoing tide differs from incoming tide in the distribution of velocity values – the differences between lanes are smaller, and also the mean flow velocity is reduced by half (incoming tide, fast flow lane: 0.12 m s^{-1} compared to outgoing tide, fast flow lane: 0.06 m s^{-1}).

The measured values for turbulence show smaller ranges and less variability at outgoing tide compared to incoming tide (mean turbulence at fast flow: 0.023 SD W and 0.017 SD W for incoming and outgoing tide respectively). Values for turbulence are higher at reduced flow velocities at 10 cm above sediment surface compared to fast or medium flow (0.02 and 0.01 SD W at fast/mean flow) (see Fig.13).



a) b)

Fig. 13 a), b). Current velocity vector (U, V, W) [ms^{-1}] of the manipulated flow (increased, mean, and reduced) measured at three points: 10 cm, 20 cm above sediment bed and water surface (w.s.). Bars represent turbulence as SD of vertical flow component W. a) incoming tide, b) outgoing tide 26.08.03

Grouping of cells into the four cell-size classes shows a rather homogeneous distribution with no significant differences. The median of the four groups lies between 21.2 and 26.9. A higher variance inside the group > 50 µm (SD 6.65) can be detected compared to the other groups (see Fig. 11b). Apart from two outliers (group

>50 µm in the fast flow lane and group 0-10 µm in the medium flow lane) the cell-size classes within all three manipulated flow velocities are distributed around a median of 25.8 (increased), 24.3 (mean) and 26.0 (reduced) (see Fig. 12 b).

A high species diversity could be observed, with many pelagic species of e.g. *Chaetoceros* Ehrenberg and *Bacteriastrum* Lauder.

Table 1: Median, min. and max. and standard deviation data for cell-size groups (0-10 µm, 10-20 µm, 20-50 µm, > 50 µm) in % (n = 500) for two sampling days, 12.08.03 and 26.08.03

12.08.03	Median	Minimum	Maximum	Sd
0-10µm	37.30	26.00	42.60	6.23
10-20µm	35.00	27.80	39.60	3.95
20-50µm	19.60	18.00	24.80	2.49
> 50µm	10.20	8.20	12.80	1.56
26.08.03	Median	Minimum	Maximum	Sd
0-10µm	24.90	16.80	29.80	5.98
10-20µm	26.90	24.20	30.40	2.23
20-50µm	25.20	23.80	33.20	3.53
> 50µm	21.20	15.00	34.00	6.65

Table 2: Median, min. and max. and standard deviation data for cell-size group distribution over three velocity treatments (increased, mean, reduced) in % (n = 500) for two sampling days, 12.08.03 and 26.08.03

12.8.03	Median	Minimum	Maximum	Sd
INCREASED	27.20	8.20	38.20	12.60
MEAN	24.80	10.00	39.60	11.87
REDUCED	25.40	10.40	42.60	10.98
26.8.03	Median	Minimum	Maximum	Sd
INCREASED	25.80	15.00	30.40	5.43
MEAN	24.30	16.80	34.00	6.59
REDUCED	26.00	19.60	27.80	2.90

Table 3: Bed shear stress [Pa] for the three velocity treatments (increased, mean, reduced) and incoming/outgoing tide on 12.08.03 and 26.08.03

12.08.03	INCREASED	MEAN	REDUCED
Incoming tide	0.05	0.08	0.06
Outgoing tide	0.02	0.11	0.09
26.08.03			
Incoming tide	0.04	0.05	0.11
Outgoing tide	0.03	0.04	0.06

Discussion

It is difficult to quantify turbulence and its effects in field experiments compared to laboratory flume experiments. In the field, turbulences can be triggered by a variety of factors including e.g. non-uniform structures of bottom roughness such as troughs and crests, rocks, seagrass areas, tufts, or mussel banks carrying the altered flow pattern over a tidal flat. These different influences are manifest in the variability and patchiness of different scales that has to be taken into account when interpreting the data (Hendriks et al. 2006). Flow characteristics in the field are subject to constant changes. Fluctuations in the flow velocity are mainly induced by wind waves, together with tidally forced currents causing long (diurnal) as well as short term oscillation. As turbulences are difficult to control in flume experiments (there is always the problem of turbulences induced by wall shear stress in small flume constructions), therefore, with lab flumes the focus is mostly on a preferably laminar flow, excluding the turbulent flow component if possible.

Shimeta et al. (2002) found a discrepancy between results of the flume (Sea Carousel, annular flume device, see Amos et al. 1992) experiments and samples taken from the boundary layer. The diatom *Navicula transitans* Cleve showed a much higher resuspension threshold in the flume. The scientists assume, that the darkness created by the presence of the Sea Carousel induced downward migration known to be executed by this species, thus elevating the erosion threshold. However, this assumption ignores the possibility of turbulences reducing the erosion threshold and thereby inducing the resuspension into the water column.

Hydrodynamic conditions determine the threshold of entrailment into the water column. Shimeta et al. (2002) found different species to resuspend at different threshold velocities thus providing the water column constantly with cells which might in turn profit from increased light. Christiansen et al. (2002) report the settling velocity for suspended particles with a size of about 210 µm to be 0.039 cm s^{-1}. The settling rates of planktonic species have been subject to investigation by Ruiz et al. (1996) and Smayda (1970). Smayda found sedimentation rates for two centric diatom species, *Thalassiosira pseudonana* (ex *Cyclotella nana* Hustedt) Hasle & Heimdal (4.5-9.5 µm) and *Thalassiosira rotula* Meunier (20-40 µm), to be 0.16 – 0.76 m d^{-1} and 0.39 – 2.1 m d^{-1}, respectively. To date, no studies have been made on settling rates of resuspended benthic diatoms.

On the one hand, resuspension means the displacement into a more favourable zone in terms of photosynthetic potential and escape from bottom feeders. On the other hand resuspension might lead to destruction or damage of the valve and furthermore, cells are now exposed to filter- and suspension feeders.

Resuspension and sediment transport are influenced by bed shear stress, resulting from the velocity of the overlying water column. If exceeding a lower threshold value, the force per unit area initiates the lifting of particles from the sediment surface and entrains them in the flow. Erosion – the removal of sediment from the bed - occurs where bed shear stress is increasing along the bed and passes a critical value. Deposition – addition of sediment on the surface over time – happens with decreasing shear stress along the bed.

Widdows (in prep.) calculated values for critical bed shear stress between 0.1 to 1.1 Pa, for a Sylt sand flat. His data, collected during erosion experiments (annular, lab flumes) on sediments in Königshafen Bay (northern part of Sylt island) are comparable to our values with 0.02 – 0.11 Pa for erosion threshold (table 3). The lower erosion threshold at Königshafen might be attributed to a more readily resuspended fluff layer, the author measured values for critical velocity to be 0.19 m s^{-1} to be sufficient to erode material from the sediment surface. Although similar in sediment structure, the geomorphological differences between the sites might favour the deposition of organic material and thus the development of a fluff layer.

There is also a good agreement with measurements by Deussfeld (2003), who calculated values for bottom shear stress between 0.04 and 0.08 N m^{-2} (1 N m^{-2} = 1 Pa) in a nearby seagrass area (compared to our range of values between 0.02 and 0.11 Pa). Her observations confirmed no visible erosion of sediments during her measurements. It would take a bed shear stress of approximately 0.2 N m^{-2} to erode sediment with the grain size between 0.2 and 0.63 mm (Deussfeld, 2003; Uchiyama 2003). These figures, on the other side, do not take into consideration local peaks of intense turbulences, inducing values for bed shear stress high enough to cause resuspension of particles from the sediment surface. Turbulence varies on temporal and spatial levels in coastal areas depending on many factors, e.g. morphogeologic structures, tides, wind and hydrodynamic forces. For the above mentioned measurement the buffering effect of plants above the sediment surface has of course to be taken into account. The compliance of the values confirms the correct handling of the measuring devices and the opportunity to compare different data sets as well as the reproducibility of data.

Fetch describes the length of water over which a given wind has blown. Along with the wind speed it determines the size of waves produced. This wind-induced wave exposure is an important subject in coastal areas. It defines the transport of material, the shape of a coastline as well as biota along a distance over which the wind blows uninterrupted for a specific direction between two sites along an open-water body (Ekebom et al. 2003). On 12.08.03 the wind direction was SSW, thus pressing against the incoming tidal current and pushing the outgoing tidal water straight through the flume. Higher current velocities on the 26.08.03 can be explained by the wind direction, the north-westerly winds, with peaks up to 11.5 m s $^{-1}$, press the water from the open sea into the bight. The counter-effect with lower current velocities can be seen on the 12.08.03, where the south-southwesterly winds (2.3 – 6.7 m s $^{-1}$) press against the water entering the bight. Compared to the lower bottom shear stress values measured on the 26.08.03 when winds were blowing from NW, transversal wind-induced waves become dissipated from the water surface down to the bottom. This antagonistic effect results in lower turbulence and bed shear stress values: the mean SD W over all velocity treatments and tides being 0.037 on 12.08.03 and 0.019 on 26.08.03. A close look at the flume data representing the three manipulated velocities reveals some conspicuous points: values for bottom shear stress and shear velocity U_* are generally higher in the reduced flow compared to increased flow velocity. The water is slowed down and refracted in the reduced-flow lane of the flume while waves still affect the water body thus inducing higher bottom shear stress and higher shear velocity than measured for the increased flow lane. In fact, the flume lanes modify the current velocity, whereas the wave-induced turbulence remained unaffected. Since the turbulence calculations relate the flow fluctuations to the average velocity, they reach higher values at slow flow, and lower values in the increased flow lane.

Distribution of microphytobenthos (and of course of other organisms) on an intertidal flat is influenced by flow-mediated processes as well as by passive deposition during high tide, provided that there is a slack phase without hydrodynamic forces in terms of velocity or turbulence. High current velocities do not necessarily imply lower turbulences. For the data of 12.08.03 for example, we can detect a higher turbulence at the water surface in the increased lane on the incoming tide. In contrast we find low flow velocity and higher turbulence 10 cm above the sediment surface during the outgoing tide in the reduced lane. An explanation for this variabilty in velocity and turbulence is shear stress caused by wind over the water surface and shear stress caused by tidal forces. Therefore, the impact on the resuspension of microphytobenthos will show a similar variability. The size-class distribution (Fig. 12, 12.08.03) shows a higher variance in the reduced-flow lane compared to the increased-flow lane. This leads to the conclusion, that the cells are subject to resuspension caused by turbulence effects rather than current speed, as the flow velocity is higher in the fast-flow lane.

The boxplots in Fig. 11 (the distribution of cell size classes on 12.08.03 and 26.08.03) illustrate the prevailing wind and wave pattern: on the 12th the two size-classes comprising cells between 0 – 20 µm are present in significantly higher numbers compared to cells 20 - 50 µm long and cells >50 µm length. This is in good agreement with the correlation of wind and turbulence, showing high correlation above the sediment surface on this day. The wind is from the SSW with a long fetch over the intertidal flats across open water, constantly pushing forward the water body with resuspended small, benthic cells. DeJonge & Van Beusekom (1995) found that resuspension from the top 0.5 cm of sediments was a linear function of 'effective wind speed' (wind speed averaged over three high water periods preceding collection of water column samples). Concurrent with the present study the authors found that tidal currents appeared to have a minor effect. A wind speed of 12 m s^{-1} would resuspend 50 % of the diatom biomass into the water column. The wind speed of 11.5 m s^{-1} was probably responsible for the resuspension of a higher diversity of species in our study, assumptions on biomass can´t be made due to differing analyses.

Wave induced resuspension occurs at low water levels and causes high bottom shear stress. The pool of larger cells comprises many pelagic cells, *Cylindrotheca closterium* (Ehrenb.) Reimann & Lewin in this case. Resuspended pelagic cells (e.g. *Gyrosigma* Hassal *spp.*, *Pleurosigma* Smith *spp.*) are less affected by constant flow but only by small punctuated turbulences. A different picture can be derived from the data obtained on 26.08.03 (boxplot Fig. 11b), where the cell-size groups are more uniformly distributed. The higher variance within the group of cells representing the cell size >50 µm is probably due to the prevailing wind coming from north-west. This wind direction ensures more water being carried through the inlet into the bight from the open sea (see diagram in Fig. 1.); the current velocity at incoming tide is nearly 40 % higher in the fast flow lane compared to 12.08.03. The strong wind (5-6 Beaufort, up to 11.5 m s^{-1}) causes a more homogeneous distribution of cell-size groups in the water column, including a transport of larger diatoms into the bay. This is confirmed by the higher surface wind-turbulence correlations on the 26.08.03.

Another physical factor, resuspension through thermic convection, should also be taken into consideration. During the slow flow over the long distances on the intertidal flats, the shallow water can absorb a considerable amount of heat, especially if the sediment surface has already been heated by the sun for a period of hours. Temperature measurements for instance on 12.08.03 provide values of up to 27 °C at a water height of about 10 cm above the sediment surface. Convectional flow might cause small particles to rise from the sediment surface, thus altering the bottom roughness and the boundary layer, where hydrodynamic forces can lead to an upward transport of these particles, either small cells or cells attached to particles.

Migration of motile diatom species is assigned to the prevention of resuspension upon immersion (Delgado et al. 1991, MacIntyre et al. 1996) and also to the escape of grazers (MacIntyre & Cullen 1996). Shimeta et al. (2002) suggest a variation in resuspension dynamics due to the diel migration rythm of various diatom taxa (Round & Palmer 1966). This fact has to be taken into account when research with benthic algae is carried out.

A factor that needs closer examination is the shape of the frustule and the possibility that geometry affects resuspension or settlement or prevents easy entrainment into the watercolumn. Next to size and shape the thickness of the valve might play a role. Cells of the species *Diploneis bombus* Ehrenberg (Fig. 14, juxtaposed to a cell of *Cylindrotheca closterium* (Ehrenberg) Reiman et Lewin to illustrate the differences in valve thickness) exhibit a heavily silicified valve which might discourage resuspension, leading to the conclusion, that this species prefers a benthic life style. Unpublished results (personal observations) from the same flume experiments examined at species level showed unexpected differences between 'light' and 'heavy' valves and their expected resuspension behaviour inasmuch as cells like the above mentioned *Diploneis bombus* do not necessarily sink to the sediment surface at low flow velocity. As expected, the ability and preference of some species to remain and reproduce on the sediment surface as well as in the water column, a behaviour referred to as tychoplanktonic, can be applied to more species than known up to the present. This in turn leads to the necessity to learn more about diatom ecology at the species level. Diatoms are able to regulate the densitiy of intracellular solute composition (e.g. by ion exchange mechanisms, carbohydrate ballasting or by increased silicification) (Moore et al. 1996); thus moving cells into optimal resource supply conditions.

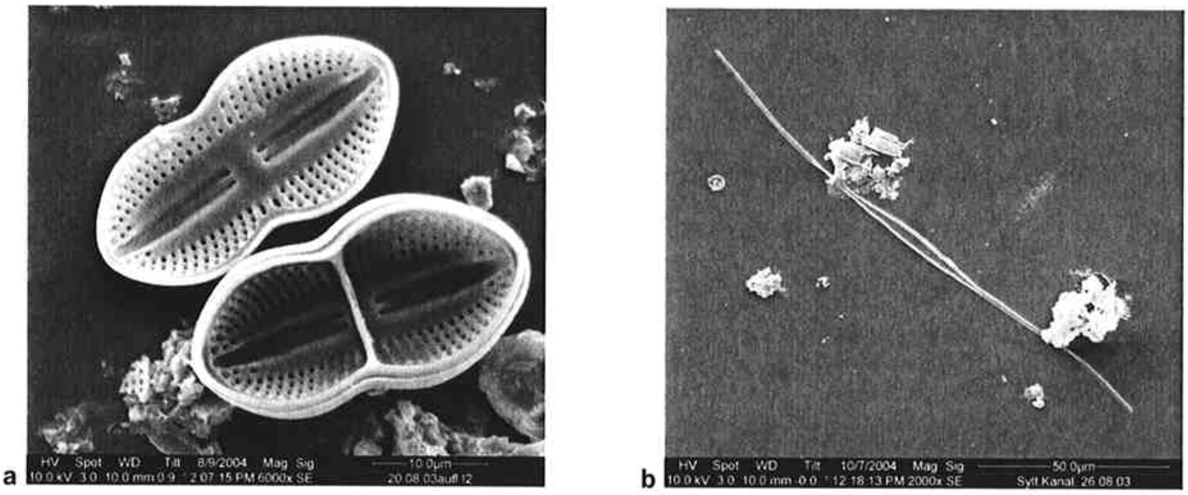


Fig. 14. Scanning electron microscope photos of two diatom cells. a) *Diploneis bombus*, view of insides of valves; b) cell of *Cylindrotheca closterium*, to picture the differences in valve dimensions

Physiological properties can be responsible for resuspension of diatom cells at the species level. Not only morphological differences expressed in the design of the valve but also the ability to produce gas bubbles that might be sufficient along with the kinetic energy of the water to lift the cell from the substratum. A gradient in water pressures due to turbulent movements (even on low levels) changes the size of gas bubbles and thus causes short peaks of local instability (Koehler et al. 2000). This process leads to stationary flow of porewater which finally results in resuspension of the cells even at low values of turbulent kinetic energy in the water column.

It is well known that microphytobenthos can exert a stabilising effect on the erodibility of sediment via EPS excretion and thus causes an increase in the erosion threshold, counteracting organisms such as *Macoma balthica* and many worms with destabilising effects (e.g. Widdows & Brinsley, 2002; Riethmüller et al., 2000; Paterson et al., 2000).

Highly permeable sands allow the advectional flow of water, thus constantly dissolving the fraction of EPS (extracellular polymeric substances) produced by diatoms that otherwise exert a stabilising influence on the sediment (Underwood et al. 1995, Cahoon 1999, Yallop et al. 2000, Staats et al. 2001). The exuded carbohydrates can form a matrix thus trapping fine particles and smoothing the sediment surface. Thus, biological activity can have a significant influence on morphological change and bed composition (see Paarlberg et al. 2005).

During her studies on a Sylt sandflat, Hedtkamp (2005) found a seasonal variability in sediment permeability. The physical forces of waves determined through the wind have a much higher influence than other, biological parameters, (EPS, fine fraction content of sediment, e.g.) suggesting that higher wind speeds will lead to higher permeabilities. She conluded that grain size, permeability and hydrodynamic conditions (wind, waves) at the sampling location are factors diminishing the development of consolidated sediment and thus leading to a lower critical bottom shear stress when compared to consolidated sediments.

The effects of turbulence are not always clearly interpretable because they work on different scales. Hendriks et al. (2006) found that bottom roughness can increase turbulence intensity dramatically in the lower part of the boundary layer but has little effect on turbulence intensity in the water column. This might explain the observed partially high values for turbulence compared to low resuspended cell numbers.

Both components, turbulence and velocity, exert an influence on the distribution of different cell sizes. Further experiments with laboratory flumes will supply information about the resuspension threshold for certain cell sizes and thus lead us to comprehend whether or not the effect of turbulence at some point outweighs the effect of current velocity.

Conclusion

Wind has a pronounced effect on the formation of wave induced turbulences.

Due to the low water levels and and the extensive effective wind-length (fetch) the hydrodynamic characteristics are defined by wind. The results show that the resuspension of different cell-size groups inside the flume is less affected by the current velocity rather than by turbulences.

The hydrodynamic characteristics of the water body covering the Sylt-Rømø Bight are complicated as they include a two-layer flow in periods influenced by wind and tides. Because of this very complex current pattern (layering, waves, and extremely low current) within the sampling area it will be essential to develop a more sensitive sampling and high-resolution measuring technique taking these features into account. The development of a turbulence model comprising a constant data supply would turn out helpful for future interpretations of hydrographical as well as biological data.

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Chapter 6

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A new diatom, *Mediopyxis helysia* gen. nov. and sp. nov. (Mediophyceae) from the North Sea and the Gulf of Maine as determined from morphological and phylogenetic characteristics

by

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With 44 figures and 2 tables

Kühn, S.F., G. Klein, H. Halliger, P.E. Hargraves & L.K. Medlin (2006): A new diatom, *Mediopyxis helysia* gen. nov. and sp. nov. (Mediophyceae) from the North Sea and the Gulf of Maine as determined from morphological and phylogenetic characteristics. – Beiheft zur Nova Hedwigia 130: 307–324.

Abstract: *Mediopyxis helysia* gen. et sp. nov. was isolated from coastal waters of both the North Sea (Germany) and the Gulf of Maine (USA) several years apart. It appears to have only recently been introduced into the North Sea where it has repeatedly been observed in the Wadden Sea off List/Sylt. Its occurrence indicates that *M. helysia* is a cold-temperate species. Morphological characteristics and molecular analyses place *M. helysia* in the Class Mediophyceae and Order Lithodesmiales. It has great plasticity of valve morphology: valves iso- or heteropolar, mostly one but occasionally two labiate processes with varying internal openings, none to several external tubes (without opening into cell interior), varying numbers, distribution, shapes and sizes of external siliceous scales, a wide conspicuous marginal ridge, and occasionally a pseudo-ocellus at one valve apex and occluded processes, the first report of such structures outside the Thalassiosirales.

Introduction

Recent studies of microbial diversity have produced spectacular discoveries of previously unknown microorganisms, many of which have major impacts on oceanic processes. Rich, chemosynthetic microbial communities not only survive but also thrive at deep-sea hydro-

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thermal vents and cold seeps. Abundant Archaea populate oceanic midwaters worldwide. Very large populations of picoplankton are the primary catalysts in carbon fixation and in nitrogen re-cycling. In the last 12 years, four new algal classes have been described from the picoplankton fraction (Moestrup 1991, Andersen et al. 1993, Guillou et al. 1999, Kawachi et al. 2002) and a fifth will soon be published (Valentin & Medlin, unpubl.). It is not surprising that new organisms are found in the bacterial community where less than 1 % can be cultured or in the eukaryotic picoplankton community where the organisms are so small that they have few morphological features that can distinguish them such that one round ball looks the same as another. What is surprising is that new taxa can be found in the nano to micro fractions (2–20 and 20–200 µm, respectively), which are easily observable with light microscopy and often with a wealth of morphological features. In these fractions, the novel aspect that is appearing is the vast extent of cryptic species that abound (Medlin & Kooistra 2004, Sarno et al. 2005). It is less common to report an entirely new genus especially when the report of that genus comes from a long and well established time series site (Wiltshire & Dürselen 2004), where samples are analysed weekly. Here we describe a new diatom genus that was not recorded from Sylt (Wadden Sea, Germany) before Dr. G. Drebes, who monitored the phytoplankton carefully for many years, retired in 1997. Since its first appearance it has most likely been recorded in Sylt time series as *Helicotheca tamesis* (Shrubsole) Ricard because of its stellate protoplast. *Helicotheca* belongs to the Class Mediophyceae (Medlin & Kaczmarska 2004) and the Order Lithodesmiales. This new genus is more closely related to *Bellerochea* based on molecular evidence. Morphologically it shares characters with several of the genera in the order but possesses sufficient unique characters to warrant its description as a new genus.

Materials and Methods

Isolation

One *Mediopyxis helysia* clone was isolated from a plankton sample off the island Helgoland in the German Bight (North Sea) in early June 2003. Apparently, its abundance in the field was very low as it was not present in the plankton samples taken and preserved weekly from that time period (pers. comm. M. Hoppenrath). Two other clones were isolated off List/Sylt in the Wadden Sea (North Sea): one at the end of September 2003 and a second in February 2004. *Mediopyxis helysia* was regularly observed off List/Sylt during the weekly monitoring (MURSYS Monitoring programme) from October 30th 2003 until May 6th 2004 and then only sporadically in July, August, October and December 2004 at water temperatures as low as 1 °C. Several other strains were earlier isolated (by PEH) in 1996 and 1997 from the Damariscotta River Estuary and Boothbay Harbor (Gulf of Maine, USA). These strains are no longer available. Diatom strains from the North Sea were maintained at a 16:8 light:dark light cycle at 15 °C in modified F/2 growth medium. Strains from the Gulf of Maine were maintained at 10 °C in "L1" medium (Guillard & Hargraves 1993).

Light microscopy (LM)

Living material was observed at room temperature with a Leitz Aristoplan microscope using seawater immersion objectives (Leitz). Digital images were obtained using Matrox Imaging Products software.

Scanning electron microscopy (SEM)

Two methods were applied for sample preparation: (i) Material was fixed in formalin (1 %) for at least 24 hours at room temperature, and then filtered onto a 0.2 μm or 2.0 μm Nuclepore PC-membrane filter under gentle vacuum. Afterwards, 30 % ethanol was added for dehydration and left 5–20 min. Subsequently the filter was transferred into acidified (0.05 ml) concentrated HCl, added to 100 ml DMP (2,2-Dimethoxypropan, Merck) for about 30 min, and then kept in DMP until critical point dried (CPD 020, Balzers Union); (ii) Diatoms were kept in concentrated H_2SO_4, for 15 min, then transferred for 20–30 min into saturated $KMnO_4$, subsequently into saturated oxalic acid for 10 min and finally thoroughly rinsed with distilled water. Samples were mounted on stubs and sputter-coated with gold-palladium for 3 min at 45 mA (SCD 050, BAL-TEC). Stubs were studied with a Zeiss DSM 940 A SEM at 15 KV, or F.E.I., Quanta FEG. 200, SEM at varying KV.

Transmission electron microscopy (TEM)

Cells were treated with hydrogen peroxide (30 %) at room temperature for approximately 3 hours prior to examination, rinsed thoroughly with deionised water and air-dried onto copper grids. Samples were viewed and photographed using either a Zeiss 109R or Zeiss EM9STEM.

DNA extraction

Diatoms of two clones (one isolated from Helgoland and one from waters off List/Sylt) were harvested and used directly for DNA extraction. For DNA extraction and purification the protocol and PrestoSpin D kit "Soil" by Molzym (Bremen, Germany) was applied. The clones were analysed individually.

PCR amplification

The SSU rRNA genes of the diatom were amplified using the universal eukaryotic primers 1F (5´- AAC CTG GTT GAT CCT GCC AGT A-3´) and 1528R (5´-GAT CCT TCT GCA GGT TCA CCT AC-3´) as described by Medlin et al. (1988). Each 100 μl PCR reaction contained 10x reaction buffer (100 mM Tris [pH 8.3], 500 mM KCl, 15 mM MgCl2, 0.01 % gelatine), 10 mM dNTP Mix (Sigma), 20 pmol of each primer, 2.5 units of Red Taq Polymerase (Sigma) or Polymerase (Promega) primer and 2 μl template (15 to 30 μg/μl). In cycling protocol, PCR reactions were performed with hot start, using a gradient Mastercycler (Eppendorf, Germany). After the initial denaturation at 95 °C for 2 min, 30 cycles of 95°C for 2 min, annealing at 54 °C for 2 min and elongation 72 °C for 4 min were carried out, followed by a final extension 72 °C for 5 min and cooling to 4 °C. Amplification products were checked for appropriate length and purity by agarose gel electrophoresis. The amplification protocol resulted in high quality PCR products.

Sequencing

PCR products were purified using the Qiagen Quick PCR purification Kit following the instructions of the manufacturer. Sequencing reactions were performed using the Big Dye Terminator Ready Reaction Mix (BigDye v.3.0, Applied Biosystems), following the instructions of the manufacturer. Approximately 15 ng template were added to each reaction mix. The annealing temperature was set to 55°C for all primers used. Sequences were determined with a capillary sequencer (ABI Prism 3100 Genetic Analyzer, Applied Biosystems). To achieve full-length double strand reads of the SSU rDNA, primers 82F (5´-GTGAAACTGCGAATGGCTCAT-3´), 528F (5´-GCGGTAATTCCAGCTCCAA-3´), 1055F (5´-GGTGGTGCATGGCCGTTCTT-3´), 536R (5´-AATTACCGCGGCKGCTGG CA-3´), 1055R (5´-ACGGCCATGCACCACCACCCAT-3´) and 1400R (5´-ACGGGCGGTGTGTACAAA GG-3´) were used in addition to the primer set 1F/1528R. All sequence outputs were checked manually and consensus sequences calculated using different software packages (DNAMAN, BioEdit). The diatom SSU rDNA sequence has the accession number: AJ968728.

Phylogenetic analysis

Previously published rRNA sequences from diatoms (Medlin & Kaczmarska 2004, Medlin et al. 1991, 1993, 1996, Sinninghe-Damsté et al. 2004), some unpublished diatoms sequences from the BMBF Algaterra project, and other chromophytes or oomycetes, dinoflagellates and prymnesiophytes (ARB database March 1997 release) were used to align the 18S rRNA sequences using maximum primary and secondary structural similarity. Bases were aligned with one another according to their pairing across a helix. Our database is maintained in the ARB program (Technical University of Munich, Germany) and contains over 13,000 eukaryotic and prokaryotic sequences. A subset of these sequences was downloaded for further analyses. For the 18S rRNA gene data set, we generated one data set of 23 taxa containing most of the species from the Mediophyceae whose sequences are publicly available.. From these sequences, positional homology was assumed for 1764 positions out of a possible 1800; 764 of these were informative and used in the maximum parsimony (MP) analysis. Details of this data set can be obtained from L.K. Medlin.

The 18S data set was subjected to the model test program to ascertain the appropriate model of evolution for our data set (Posada & Crandall 1998). Using this program, two models were selected as the best representation of the data set. From the hLRTs test, the TrN + I + G model was selected and from this model the following parameters were implemented in the maximum likelihood (ML) and neighbour-joining (NJ) analysis using PAUP* (Swofford 2002): Lset Base = (0.2772 0.1820 0.2421) Nst = 6 Rmat = (1.0000 2.4209 1.0000 1.0000 4.1451) Rates = gamma Shape = 0.6824 Pinvar = 0.3986. The AIC test selected the GTR + I + G model and these parameters were implemented as above: Lset Base = (0.2684 0.1894 0.2497) Nst = 6 Rmat = (0.9281 2.7651 1.4942 1.0140 4.5998) Rates = gamma Shape = 0.6735 Pinvar = 0.3981. Bootstrap analyses were performed with both models.

In addition, the 18S data set was analysed using Bayesian inference (BI) (Huelsenbeck et al. 2001). BI is, like ML, a probabilistic method that uses a given model of evolution and analysis for the best set of trees that are consistent with the model and the data set. The advantages of BI are that it is relatively rapid even when large data sets are used, and generates probabilistic measures of tree strength, which gives posterior probabilities (PP) for the phylogenetic stability. These values are more straightforward to interpret than bootstrap values, because they can be taken as the probability that the topology of a tree is most likely and represents the best-estimated phylogeny. The analysis was done using MrBayes, available at 'http://morphbank.ebc.uu.se/mrbayes/'. We ran the Bayesian search using the GTR model with an undefined gamma distribution, during 500,000 generations, and saving every 100th tree. We discarded the first 1000 trees; the remaining 4000, all with higher PP, were used to construct a consensus tree. On this tree, 'credibility values' for each clade are shown, which represent the percentage of those 4000 trees having the corresponding clades.

MP analyses were implemented with the PAUP* program. Introduced gaps were treated as missing data, and informative characters were treated as multistate and unordered. Unweighted MP trees were obtained using the tree-bisection-reconnection (TBR) branch swapping option and a heuristic search with random additions of the taxa. The most parsimonious tree (MPT) and the data matrix were reanalysed using a re-scaled consistency index within PAUP.

Distance analysis was performed using PAUP*. Dissimilarity values (Fitch & Margoliash 1967) based on pairwise comparisons of sequences were transformed into distances using models determined from the model test program. Branching order stability was estimated by bootstrap analysis as above. Stability of the branching order was estimated using bootstrap analysis (BT) for 1000 replicates for both the distance and the weighted MP trees (Felsenstein 1985). Hillis & Bull (1993) have shown for computer simulated data that bootstrap values greater than 7 % indicate a likelihood that the clade recovered has a 95 % probability of being real; in data sets where there is a large number of characters (i.e. taxa), clades with rates of 5 % are correct.

Results

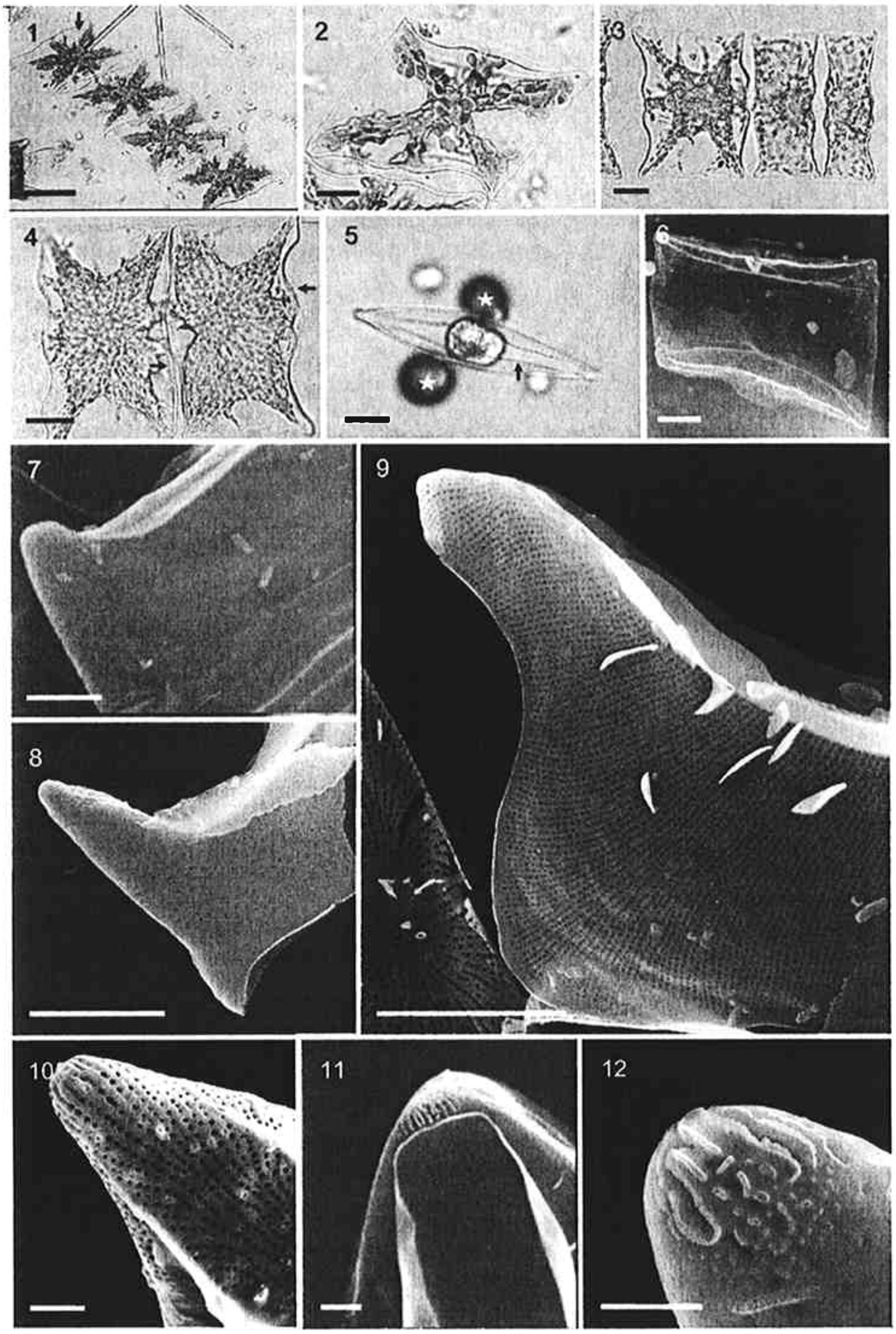
Morphology

Light microscopy. Cells are solitary or in short chains of 2, rarely more than 6 weakly silicified cells (Fig. 1). Chains are separable and individual cells appear like a parallelogram when seen in girdle view. When in chains, cells are connected by overlapping or loose contact of cell ends, which generally have a short, rounded elevation at one corner and a pointed, elongated horn at the other (Fig. 2). Thus the valve is heteropolar. However, both in plankton samples and more often after longer periods of cultivation, these features disappear and cell ends are more or less rounded (Fig. 3) and the valves become isopolar. Gaps occur between cells because of curvature of the valve face. At the valve centre is an inflated circular area with one, sometimes two central labiate processes (LP) per valve (Figs 2, 3). Occasionally, refractive lines are discernible on the junction between valve face and mantle (Fig. 4). The edge of the valve mantle is visible as a thin line (Fig. 1). Valves are bipolar and broadly lanceolate (Fig. 5). Chromatophores are numerous and plate-like. In newly formed cells, the protoplast fully occupies the frustule, whereas in older cells it is partially retracted (Fig. 3). It remains connected to the frustule at specific anchoring sites, such as the valve corners and the internal part of the labiate process on the valve face. When the protoplast radiating from the central nucleus has a stellate appearance, *Mediopyxis* most resembles *Helicotheca*. In girdle view cells are roughly rectangular.

The dimensions of frustules of cells are as follows: in plankton samples the apical axis is 85–125 μm, but most frequently around 100 μm. In culture, the size of the apical axis decreased rapidly within 7 months from 95 to 44 μm. The pervalvar axis at the cell ends is 27–78 μm, on valve face, the sub-lateral depression in relation to the elevated centre is approximately 3 μm; the central depression is approximately 1.5 μm deep; the transapical axis measures 18–22 μm at the cell centre and decreases to 2.0–4.5 μm at apices. No sexual stages or auxospores have been observed.

Electron Microscopy. EM studies revealed a wide variability of frustule structures, even within clonal cultures. Collectively, all clones studied possess several characteristics but not all structures were observed in each clone or are expressed to the same extent (Table 1). In our description we will therefore not distinguish among clones. All cells have a central depression on the valve face and numerous girdle bands (Fig. 6).

Valve. As seen in LM, both cell corners are either rounded, or one corner is more or less elongated (Figs 7–10), but that this difference is associated with different valve structure can only be appreciated with EM. Areolation of the cell corners is generally continuous with that of the valve face but sometimes a pseudo-ocellus with varying patterns is present (Figs 11,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A new diatom, *Mediopyxis helysia* gen. nov. and sp. nov. (Mediophyceae)

Table 1. Comparison of isolates of *Mediopyxis hel*ysia from three locations

	Helgoland	**Sylt**	**Gulf of Maine, USA**
Habitat	marine	marine	coastal marine
Filaments	short (4 to 6 cells) or solitary cells	short (4 to 6 cells) or solitary cells	?up to 8 cells *in vitro*
Valve corners	1 rounded, 1 pointed	1 rounded, 1 pointed	slightly heteropolar
Chloroplasts	numerous small plates		numerous pale yellow plates
External tube of labiate process	1, central, long, laterally flattened	1, central, long, not flattened	1, central, slightly flattened
Occluded processes	none to 7	absent	none to many
Siliceous flaps	numerous; semi-discoid and spine-like	?	absent

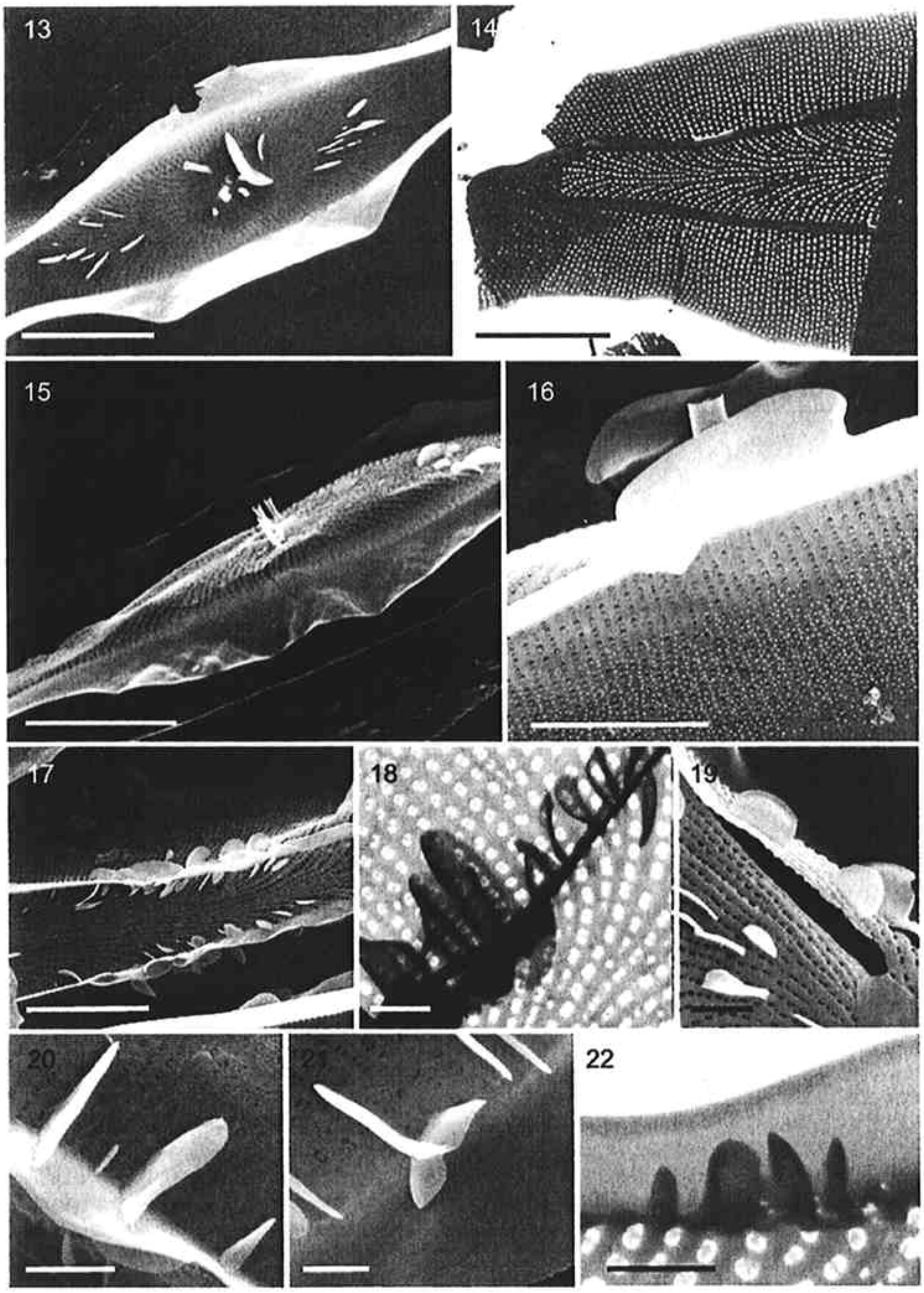
12). Valve structure consists of radially arranged poroid areolae and/or ribs starting from the non-perforated area around the central process (Fig. 13). Areolae on the valve are the same size as those on the valve mantle (Fig. 14), 24 to 32 valve and mantle areolae in 10 μm. Pores are closed by rotae attached at only two points (Figs 16, 18, 22).

Submarginal Ridge. The most prominent structure on the valve face is a wing-like, weakly silicified structure or submarginal ridge that surrounds the entire valve (Figs 11, 13, 15). The wing is unperforated (Figs 21, 22) and its shape can differ among strains. At the valve centre, this wing/ridge can be as high as 5 μm, but towards the valve corner it generally becomes lower. The submarginal wings/ridges are 8–11 μm from each other at valve centre.

Siliceous Structures. Large siliceous flaps occur on the valve (Figs 13, 15). They can be few to many and flattened, semi-circular, discoid (radius ~ 1 to 1.5 μm) or spine-like in shape. They are irregularly scattered on the valve face and the mantle but are predominant in the zone between the submarginal ridge and the mantle and on the ribs (Figs 17–19). Occasionally, the flaps fuse with the submarginal ridge (Fig. 20). Rarely are they tripartite (Fig. 21). They are visible with LM as slightly rounded, solid lines (Fig. 4). Small papillae can also be found scattered on the valve mantle (Fig. 16).

Figs 1–5. LM. Figs 6–12. SEM

Fig. 1. Chain of four cells from plankton sample. The junction between valve and girdle region is visible as a thin line (arrow) (bar: 50 μm). Fig. 2. Cell with one rounded and one pointed valve corner. Fig. 3. One older cell with stellate protoplast and two newly divided cells whose protoplasts fill the entire frustule. Fig. 4. Silica scales visible on valves as solid lines (arrows). Fig. 5. Valve view of cell infected by the parasitoid dinoflagellate *Paulsenella vonstoschii* (asterisks). The submarginal ridge is indicated (arrow). Fig. 6. Girdle view of entire cell. Both cell corners are equally rounded. The submarginal ridge has a rectangular widening at the valve centre where one LP is visible within the rounded central depression (bar: 20 μm). Fig. 7. Detail of one slightly elevated apex (bar: 2 μm). Fig. 8. Elevated apex. The lateral part of valve margin is elongated (bar: 5 μm). Fig. 9. Detail of valve (bar: 10 μm). Fig. 10. Valve view of apex either with no pseudo-ocellus or minimal traces of one (bar: 2 μm). Fig. 11. Pseudo-ocellus at valve end behind submarginal ridge (bar: 2 μm). Fig. 12. Detail of pseudo-ocellus with additional ornamentation (bar: 1 μm).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Processes. In the central depression of each valve, generally one central LP and varying numbers of tubes are present. The exterior part of the process is up to 2 μm long, slightly flattened and generally laterally flared (Figs 23–27). The external tube of the labiate process has either two, or even three wing-like buttresses or is structureless (Figs 24, 25). Occasionally, two LPs were observed (Fig. 27). The internal opening of LP is located at the valve centre (Fig. 29) and is either (i) bilabiate, (ii) bilabiate with one round central opening, (iii) bilabiate with two round, slightly laterally situated openings or (iv) one slit as a normal microlabiate (Figs 31–36). Also, LPs can be found with two internal openings (Figs 31, 32). Within the central depression, zero to 6 tubes are scattered without discernible pattern (Figs 23, 26). These tubes are not solid silica structures (Fig. 28). They apparently do not have an opening into the frustule and as such should be termed occluded processes. In Fig. 28, rotae can be seen at the base of the tube where it meets the valve. This is the first report of such tubes outside the Thalassiosirales.

Girdle. There are many girdle bands, which appear to open at alternate apices (Figs 37–39) and are each 2–3 μm wide. Newly formed copulae appear to be wrinkled (Fig. 40). There is no structural difference between the valvocopulae and the copulae (Figs 41, 42). Pores on the bands are round and number 3 to 7 in 10 μm. They may be in arranged in a line with a tendency to become scattered towards the edge of the copula (Fig. 43).

Phylogenetic analyses

All analyses place *Mediopyxis helysia* as a member of the Class Mediophyceae, Order Lithodesmiales, Family Lithodesmiaceae H. & M. Peragallo 1897–1908 emend. Simonsen 1979 (Kazcmarska et al. 2006) (Fig. 44). It is sister to *Bellerochea malleus* (Brightwell) van Heurck with *Helicotheca tamesis* (Shrubsole) Ricard (syn. *Streptotheca tamesis* Shrubsole), *Lithodesmium undulatum* Ehrenberg and *Ditylum brightwellii* (T. West) Grunow as next relatives. This is a robust relationship being supported by 100 PP and 73 & 90 BT values. In this and in other trees (e.g., Medlin & Kaczmarska 2004), the Lithodesmiaceae (*sensu* Round et al. 1990) is shown to be paraphyletic, In Kaczmarska et al. (2006), the Order Lithodesmiales has been emended to include the Lithodesmiaceae and the Bellerocheaceae, which Round et al. (1990) put into separate orders, but Simonsen (1979) did not. The molecular data fully support the original circumscription of these taxa into one family (Peragallo & Peragallo 1897–1908). As can be seen from our branch length tree, the genetic distance separating the closest relative of each of the genera in the Lithodesmiales is approximately the same, although *Lithodesmium* is most distantly related to *Mediopyxis*.

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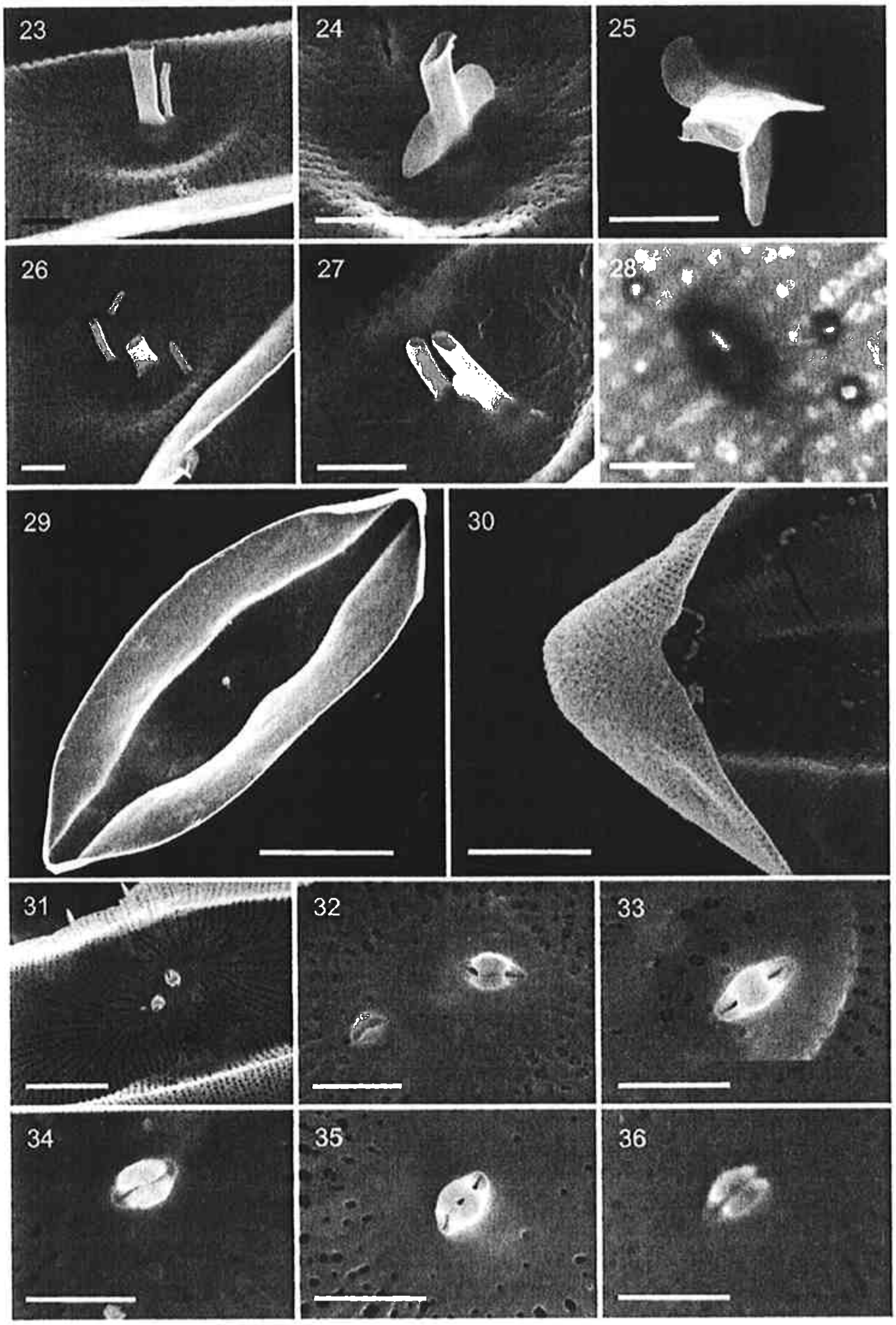
Figs 13, 15–17 and 19–22. SEM. Figs 14 and 18. TEM

Fig. 13. Valve with central rounded depression in which several silicified structures are visible. Areolation radiates from this depression. Siliceous semicircular scales are scattered perpendicularly on the valve face. An unperforated submarginal ridge is present on both sides of the valve at the junction of valve face/valve mantle (bar: 10 μm). Fig. 14. Areolation is continuous from valve face to valve mantle changing from radiate to vertical (bar: 20 μm). Fig. 15. Valve face with submarginal ridge (bar: 10 μm). Fig. 16. Detail of areolae with rotae and papillae on valve mantle. The submarginal ridge with a rectangular widening at the valve centre and the LP are visible (bar: 5 μm). Fig. 17. Siliceous perpendicular scales on valve face appear to fuse with submarginal ridge (bar: 10 μm). Fig. 18. Areolation of valve is continuous across submarginal ridge where scales attach (bar: 1 μm). Fig. 19. Detail of semicircular perpendicular scales with flattened edges on valve face (bar: 2 μm). Fig. 20. Scales apparently fused with submarginal ridge (bar: 2 μm). Fig. 21. Scales with expanded base are loosely touching submarginal ridge. The ridge has no discernible structure (bar: 1 μm). Fig. 22. Continuous transition from valve areolation to unperforated submarginal ridge (bar: 20 μm).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Discussion

There are sufficient morphological and molecular characteristics that distinguish *Mediopyxis helysia* from *Bellerochea malleus* and the other diatom genera in the order to justify the erection of a new genus.

Morphological similarities and differences to other members of the Lithodesmiaceae:

Similarities: All members of this clade/order are chain-forming species with poroid areolae and one special (bilabiate) type of process on each valve. They are planktonic and found in marine temperate to tropical waters, possibly occurring year-round.

Differences: See Table 2 for a comparison of features that distinguish *Mediopyxis* from other members of the Lithodesmiales. *Mediopyxis* differs from *Lithodesmium* and *Ditylum* by the length of the external tube of the labiate process and by the wide spaces between the cells; it differs from *Subsilicea and Neostreptotheca* by the lack of openings between the cells in a chain; it differs from *Helicotheca* by the twisted chain in the latter. It is most difficult to separate from *Bellerochea, which* has very delicately silicified valves really consisting only of radial costae overlying a thicker organic layer. *Mediopyxis* has a much stronger silicified valve. *Bellerochea* also has several split wall regions where the silica valve and the diatotepic layer have become separated. This is not seen in *Mediopyxis*. The marginal ridge is perforated in *Bellerochea* and not in *Mediopyxis*. *Bellerochea* has segmented bands, whereas *Mediopyxis* has open bands. *Bellerochea* species can usually be distinguished by the shape of the open space between cells in a chain. The opening between cells of *B. malleus* is present only at the apices. In *B. horologicalis* Stosch, a tropical species, the opening is closed at the valve centre and at the apices, with the intervening space being described as dumbbell-shaped (Hasle & Syvertsen 1996). In *B. yucatanensis* Stosch, there is no opening between the cells. *Mediopyxis* has its openings most similar to *B. horologicalis* but can be distinguished from that species by the much larger size of *Mediopyxis* and by its distribution. The valve views of *Bellerochea malleus*, *Lithodesmium undulatum*, and *Ditylum brightwellii* are most frequently triangular (though bipolar forms are seen, especially *in vitro*), whereas *Mediopyxis helysia* is consistently bipolar. Similarly, only bipolar forms of *B. horologicalis* and *B. yucatanensis* (Stosch 1977) have been observed, but these species have not been investigated by molecular techniques, so we do not know how the feature of polarity will be placed on our phylogenetic tree within *Bellerochea*.

The siliceous, flattened semi-circular discoid flaps on the valve flange are apparently unknown in other diatoms. They could correspond, however, to the unique structures on *Ditylum* for which Stosch (1986) coined the term *ansula*. However, these structures comprise the mar-

Figs 23–27 and 29–36. SEM. Fig. 28. TEM

Fig. 23. External part of laterally flattened LP in central depression on valve face. Next to LP is one single thin tube (bar: 2 μm). Fig. 24. Single LP with two conspicuous semicircular struts (bar: 2 μm). Fig. 25. LP with three conspicuous semicircular struts (bar: 2 μm). Fig. 26. One central LP and three thinner tubes (bar: 2 μm). Fig. 27. Two LPs, identified by their laterally flattened shape (bar: 2 μm). Fig. 28. TEM: Section through outer part of LP (elongated slit) and three occluded tubes (bar: 1 μm). Note rotae in the tube at 3:00. Fig. 29. Valve interior with opening of one central LP (bar: 20 μm). Fig. 30. Detail of valve apices where both sides of the valve are fused (bar: 5 μm). Fig. 31. Internal openings of two LP surrounded by a large annulus (bar: 5 μm). Fig. 32. Detail of two LP: the one to the left appears to be less clearly shaped and has an intermediate internal opening, the LP to the right is bilabiate (bar: 2 μm). Fig. 33. Bilabiate LP surrounded by an annulus (bar: 2 μm). Fig. 34. The two lateral slits of the bilabiate LP almost meet in the centre (bar: 2 μm). Fig. 35. LP with two lateral slits and one central pore (bar: 2 μm). Fig. 36. Transient slit of LP (bar: 2 μm).

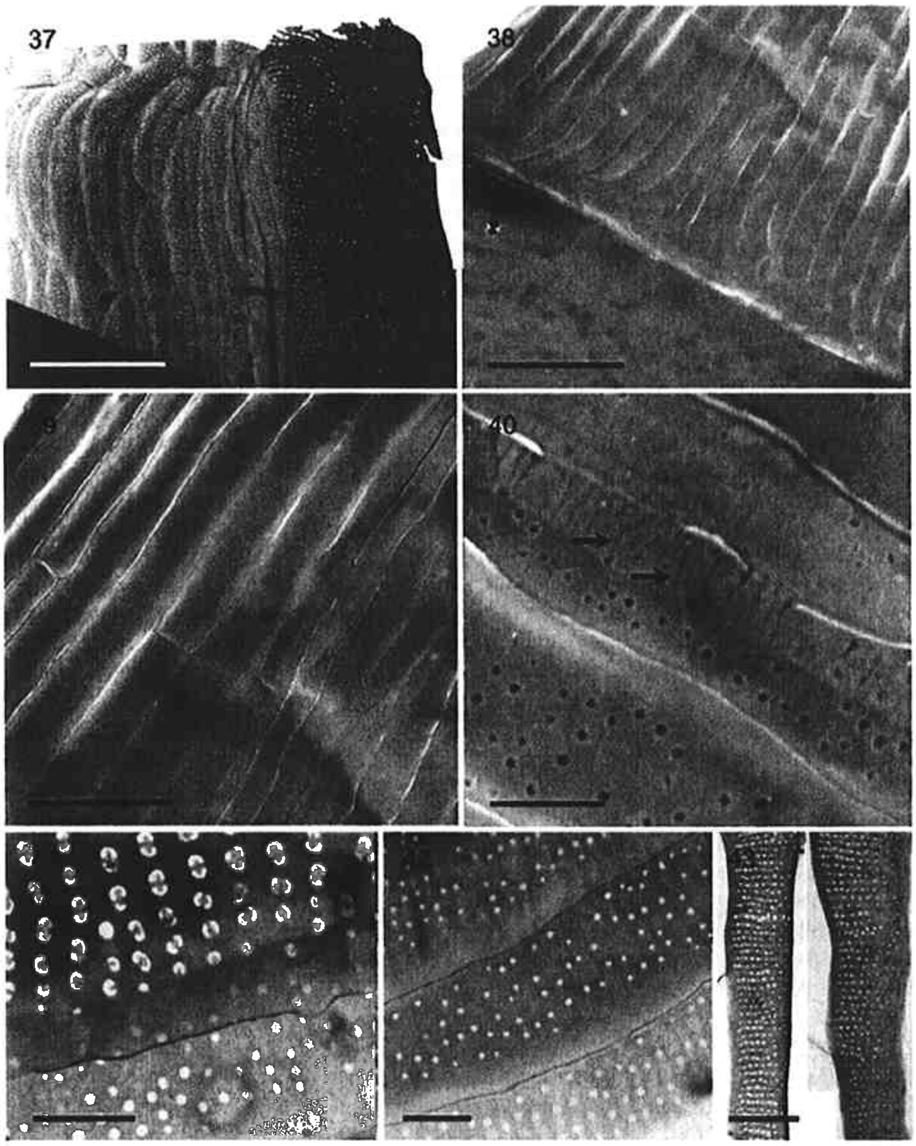

Fig. 37. TEM, Figs 38–43. SEM.
Fig. 37. TEM image of girdle bands (bar: 10 μm). Fig. 38. Girdle region at the apices (bar: 10 μm). Fig. 39. Girdle bands showing random arrangements of pores (bar: 5 μm). Fig. 40. Detail of newly developing copula with folds (arrows) (bar: 1 μm). Fig. 41. Transition from valve margin to valvocopula (bar: 1 μm). Fig. 42. Overlapping copulae (bar: 1 μm). Fig. 43. Linear pattern of pores on copulae, which get more scattered towards the edge of the copula (part which overlaps next copula) (bar: 2 μm).

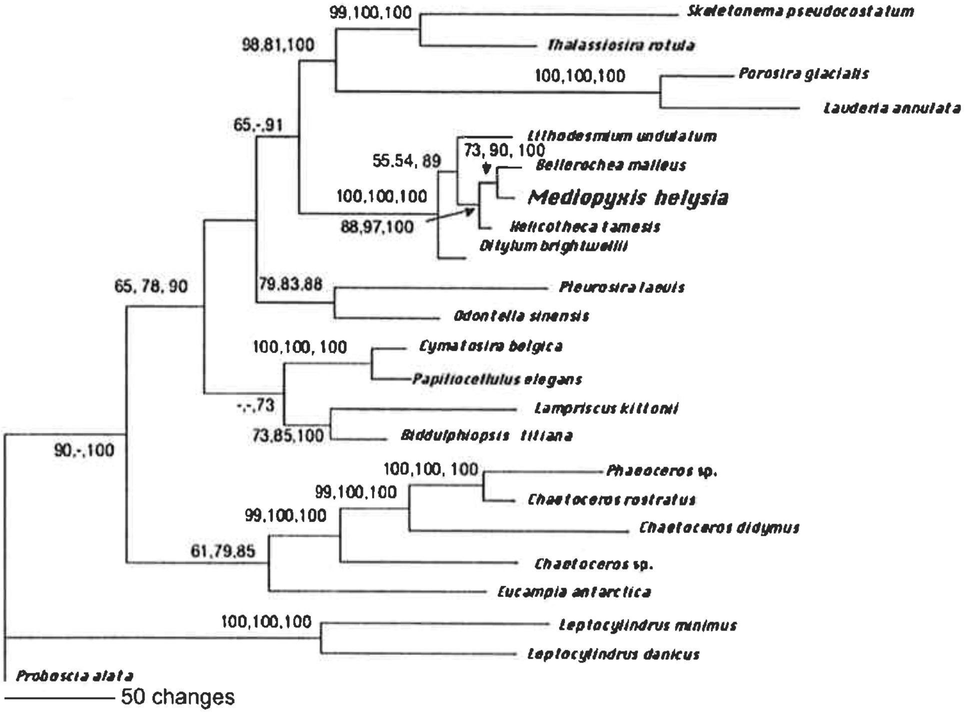

Fig. 44. Phylogram inferred with the Bayesian analysis showing the placement of *Mediopyxis* within the Mediophyceae. Posterior probabilities and bootstrap support > 50% are placed at each node (MP, NJ, BI).

ginal fringe in this genus and do not vary in location. Our structures vary in location. Thus, the only similarity that they share is that they are both additional siliceous ornamentation to the valve. They may also correspond to the flaps found on the valves of certain fragilarioid diatoms (Round et al. 1990, p. 346).

Colonies of *H. tamesis* and *B. yucatanensis* are connected by organic substances and can dissociate under appropriate conditions (Stosch 1977). Cells of *B. malleus* and *B. yucatanensis* colonies are less separable and joined by fusion or interlocking of silica with silica. Our new species forms colonies connected by organic material.

Another confirmation of the taxonomic position of *M. helysia* within the Lithodesmiaceae is its susceptibility to infections by the parasitoid dinoflagellate *Paulsenella vonstoschii* Drebes & Schnepf. This species feeds only on members of the Lithodesmiaceae. It prefers *Helicotheca tamesis*, and only weakly feeds on *B. malleus*, *Lithodesmium undulatum* and *Neostreptotheca subindica* Stosch (Drebes & Schnepf 1988). We observed that *P. vonstoschii* was strongly attracted to *M. helysia* but only few dinospores succeeded to penetrate the girdle region with their feeding tube (peduncle) and suck out the cell contents (Kühn & Medlin 2005). Some cells, especially if infected, attracted many dinospores, whereas others were ignored completely (intraspecific selectivity). Interspecific selectivity clearly favoured *M. helysia* over *B. malleus*. The reasons for this discriminate infection behaviour are not yet clear.

Table 2. Comparison of *Mediopyxis* with other Lithodesmiales

	Mediopyxis	*Bellerochea*	*Neostreptotheca*	*Subsilicea*	*Helicotheca*	*Streptotheca*	*Lithodesmium*	*Lithodesmioides*	*Ditylum*
Marginal ridge	present, non-perforated	present, perforated	not present	present, perforated	not present	not present	present, perforated or non-perforated	present, inconspicuous	present, fringe-like
Chains	yes	yes	yes	yes	yes	yes	yes	no	no
Labiate process	variable	bilabiate	bilabiate in costate basket	none	bilabiate	bilabiate	bilabiate	bilabiate	bilabiate
Occluded processes	yes	no	no	no	no	no	no	no	no
Valves	well-developed areolae	tracery of siliceous costae	well-developed areolae	tracery of siliceous costae	well-developed areolae	well-developed areolae	well-developed areolae	well-developed areolae	well-developed areolae
Bands	open	segmented	segmented	segmented	segmented	open	segmented	segmented	segmented

A new diatom, *Mediopyxis helysia* gen. nov. and sp. nov. (Mediophyceae)

Because of the great plasticity of valve morphology shown in one clone, *M. helysia* would be an ideal species to investigate how environmental conditions can influence frustule morphology. Certain features, such as the tube in the central labiate process, would suggest affinities to the rhyncho process of the fossil genus *Rhynchopyxis*. Medlin & Kaczmarksa (2004) suggested that the group to which *Rhynchopyxis* belongs, represents the ancestral stock for the extant Mediophyceae. Morphogenetic studies could shed light on this hypothesis if the tube is present in the first stages of development of the labiate process and then it disappears when the slit is fully formed. A bilabiate stage could then precede the disappearance of the tube before a true microlabiate is formed.

Mediopyxis appears to have established a stable population in the Wadden Sea where it occurs all year round, even in winter at low temperatures. This indicates that it is a temperate rather than a tropical species. It was first noticed in 2003 and if it occurred before that time it was likely recorded under *Helicotheca tamesis* because of the superficial resemblance to that taxon. Its first report from the Gulf of Maine in 1996 indicates that it is a cold-temperate species, which perhaps has been introduced only recently into the North Sea. In the northwest Atlantic it has been observed only in the coastal waters of the Gulf of Maine. A weekly time series of phytoplankton in Narragansett Bay (about 300 km south of Maine locations; see http://www.gso.uri.edu/phytoplankton/), with slightly warmer sea temperatures, has failed to detect it.

Mediopyxis Medlin & Kühn gen. nov.

Descriptio: Cellulae in catenulas breves leniter silicatas dispositae vel solitariae chloroplastos numerosos lamelliformes atque nucleum centralem continentes. Cellulae in filamenta dispositae tantum ad angulos valvares connexae. Et anguli valvares et processus labiati locos affingentes protoplastorum formantes. Cytoplasma ad hos locos affixum quum e valvis recedens in aspectu stellatum. Lacunae inter cellulas per curvaturam valvarem praesentes. Valva bipolaris. Facies valvaris cavo circulari processu unico longo centraliter posito praedito. Processus centralis labiatus apertura variabili microlabiata usque bilabiata; apertura bilabiata tubo centrali rimas aperturae disjungenti vel nullo praedita. In cavo centrali valvae processus occlusi nulli vel aliquot. Crista marginalis laciniformis laciniis squamiformibus minoribus multis e silica compositis subtenta. Areolae poroideae per rotas clausae. Copulae numerosae poris dispersis praeditae.

Genus description: Cells in short, weakly silicified chains or solitary with many plate-like chloroplasts and a central nucleus. Cells in filaments connected only at valve corners. Valve corners and labiate process are protoplast anchoring points. Cytoplasm appears stellate when retreated from the valve and remaining attached only at these points. Gaps between cells because of valve curvature. Valve bipolar. Circular depression on valve face with one long centrally located labiate process. Central labiate process opening variable from microlabiate to bilabiate with or without a central tube separating the slits of the bilabiate process. Zero to several occluded processes in the central depression of the valve. Marginal ridge flap-like, subtended by several many smaller scale-like flaps of silica. Poroid areolae closed by rotae. Numerous copulae with scattered pores.

Mediopyxis helysia Kühn, Hargraves & Halliger sp. nov.

Descriptio: Species eadem est ut in descriptione generis atque axis cellulae apicalis 85–125 μm; axis pervalvaris 27–78 μm; axis transapicalis in centro cellulae 18–22 μm; axis ad extremitates cellulares 2.0–4.5 μm. Areolae in valva 24–32 per 10 μm; rotae in locos duos affixae.

Species description: As in genus description. Apical cell axis 85–125 µm, pervalvar axis 27–78 µm, transapical axis in cell centre 18–22 µm, at cell ends 2.0–4.5 µm. 24 to 32 areolae on valve in 10 µm, rotae attached at 2 points.

Type locality: clone from plankton off List/Sylt, German Bight, North Sea, October 2003. Holotype slide: Hustedt collection BRM ZU5/92 (leg. G. Klein), Alfred Wegener Institute for Polar and Marine Research, Germany.

Holotypus: Hustedt collection BRMZU5/92, Alfred Wegener Institute for Polar and Marine Research, Germany.

Ethymology: *Mediopyxis* = middle box; the siliceous features of this species link the Lithodesmiaceae with the Thalassiosiraceae and the Rhynchophyaceae;
helysia = combination of the two locations of the type locality: Helgoland and Sylt, with the latter inverted.

Ecology: In the type material, this is a planktonic species of temperate marine waters. Gulf of Maine strains were isolated from mesohaline waters of 5–10 °C. Its distribution is unknown.

Acknowledgements

In 1973, as a high school biology teacher I (LKM) travelled to Hawaii and enrolled in a course called "Plants of the Sea". Frank was the guest lecturer and with the first SEM of a diatom that he showed in class, I fell in love with them. By the end of the course, I decided to return to graduate school to study diatoms. So I thank Frank for a major career change from high school biology to the diatoms and later from taxonomy to molecular systematics for he and I wrote the first molecular grant proposal to study diatom relationships using DNA-DNA hybridisation. Thankfully that quickly gave way to PCR and 18S rRNA analysis paving the way for a love relationship with the taxonomy and molecular biology of the diatoms that has stood the test of time.

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Chapter 7

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Manuscript Draft

Manuscript Number:

Title: Paraplagiogramma and Metaplagiogramma Witkowski, Lange-Bertalot & Klein - new genera in the Family of Plagiogrammaceae

Article Type: Original study

Keywords: marine diatoms (Bacillariophyceae), family Plagiogrammaceae, Paraplagiogramma, Metaplagiogramma

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Abstract: This study focuses on three sediment dwelling diatom species known from marine and estuarine coasts. Paraplagiogramma and Metaplagiogramma are described as new genera split off from Plagiogramma and Anaulus. Electron microscopic studies reveal that the proposed new genera are also clearly distinguished from other established genera (e.g. Eunotogramma, Hustedtiella, Brockmanniella) which appear similar in the light microscope. The differentiation is based on the ultrastructure of valves and valvocopulae, in particular occurrence or absence of septa and pseudosepta, the position of pseudosepta and areolae in the valves, and the different fine structure pattern of the areolae. A formal transfer of Anaulus balticus and A. simonsenii to Paraplagiogramma gen. nov. and of Plagiogramma tenuissimum to Metaplagiogramma gen. nov. are proposed.

INTRODUCTION

In question are three established species: *Anaulus balticus* Simonsen from the Western Baltic Sea (Simonsen 1959), *Anaulus simonsenii* Witkowski, Metzeltin & Lange-Bertalot from the western Baltic Sea (Witkowski *et al.* 2000) and *Plagiogramma tenuissimum* Hustedt from the brackish water of Lago Maracaibo, Venezuela (Hustedt 1952, Simonsen 1987). All have been classified on the generic level according to their characteristics observed in the light microscope (LM) only. None of these species have been studied so far using the electron microscope.

The trigger for our study was the identification of *Anaulus simonsenii* outside of the hitherto known sites. Until now, it was only known from the type locality (Western Baltic Sea) and the Gulf of Oman. Recently, it was found also to be abundant on the North Sea island of Sylt and on the south coast of England. Our further studies using electron microscopy have shown that the generic placing of at least two similar species is obviously not appropriate: *Anaulus balticus* and *Plagiogramma tenuissimum.* Both species appear similar to *Anaulus simonsenii* under LM. These observations encouraged us to investigate the original material to compare the ultrastructure of *Anaulus simonsenii* in scanning electron microscopy (SEM) and transmission electron microscopy (TEM). The results led to the conclusion that neither species coincide with the given definitions of *Anaulus* and *Plagiogramma.*

This paper describes SEM as well as TEM and LM observations performed on the three species in question. The materials originate from the type localities including type slides (see Material and Methods).

MATERIAL AND METHODS

Original material:

- 343/95b in Coll. Hustedt, Alfred Wegener Institute for Polar and Marine Research, Bremerhaven, Germany.
- Di 116, Di 117 in Coll. Simonsen, Alfred Wegener Institute for Polar and Marine Research, Bremerhaven, Germany.
- 564024/5/4 in Coll. Witkowski, Institute of Marine Sciences, University of Szczecin, Poland.

Additional material:

Atlantic Ocean

The North Sea, Southern England: slide ZU 5/ 96 in Coll. Hustedt Alfred Wegener Institute for Polar and Marine Research, Bremerhaven, Germany.

Southern Atlantic, South Africa (Saldanha Bay) – slide no.: 6391, Coll. Witkowski, Institute of Marine Sciences, University of Szczecin, Poland.

Indian Ocean

Gulf of Oman – Coll. Witkowski, Institute of Marine Sciences, University of Szczecin, Poland, slide no.: 10234

Coast of Kenya, Tiwi Beach - Coll. Witkowski, Institute of Marine Sciences, University of Szczecin, Poland, slide no.: 5733

Pacific Ocean

Coast of Oregon, Yaquinia Bay –Philadelphia Academy of Natural Sciences collection slides no.: 62634, 62633, 62632, 62629

Light microscopic studies were carried out with Leitz Diaplan and LEICA DMLB microscopes equipped with x63/1.4 and x100/1.4 PlanAPO oil immersion objectives, respectively. SEM examinations involved a Hitachi S 4500 and a QuantaFEG, Phillips, TEM studies were conducted with a Zeiss EM 109.

RESULTS AND DISCUSSION

Anaulus is a genus belonging to the centric diatoms (e.g. Hustedt 1930, Drebes & Schulz 1981, 1989, Round et al. 1990). In the LM it resembles to a certain extent *Plagiogramma*. The taxa representing both of these genera possess either two (*Anaulus*) or two to four pseudosepta (*Plagiogramma*). *Anaulus* sensu stricto differs from *Plagiogramma* by possession of rimoportulae and ocelli (Round et al. 1990).

Anaulus balticus, *Plagiogramma tenuissimum* and *Anaulus simonsenii* resemble *Anaulus* in girdle view and in valve view, with the two conspicuous (pseudo-)septa crossing the valve. However, SEM observations reveal a completely different structure for *Anaulus* in contrast to *Plagiogramma* (see Round et al. 1990, p. 286,287 and p. 238, 239). No apical processes terminating in ocelli and no rimoportula exist in the three species under discussion here. Concerning other related genera such as *Plagiogrammopsis*, *Brockmanniella*, *Dimeregramma*, *Talaroneis* (syn. *Dimeregrammopsis*), *Hustedtiella*, *Glyphodesmis*, *Eunotogramma*, all are distinguished from the above named species by a much more different pattern of characteristics (cf. genus descriptions in Round et al. 1990 and Kooistra et al. 2004).

The genera of the *Plagiogrammaceae* were formerly regarded to belong to the Pennate diatoms; this was recently confirmed by molecular studies (Kooistra et al. 2004) whilst they were classified under the Centrics by Round et al. (1990).

A. balticus and *A. simonsenii* have two pseudosepta in subpolar position in common, whereas *P. tenuissimum* lacks pseudosepta and possesses septa. This means the conspicuous inwardly directed thickenings are not attached to the valve as in the first two species but to the valvocopula. In both cases perforations are restricted to the distal parts of the valves and mantles, while all proximal parts are unperforated.

Altogether the differentiating characters are so significant that – analogous to comparable cases – introduction of two new genera is more appropriate than a fundamental extension of the diagnosis of *Plagiogramma* as given by Round et al. (1990).

Paraplagiogramma gen. nov.

Typus generis: *Paraplagiogramma simonsenii* (Witkowski, Metzeltin & Lange-Bertalot) Georgia Klein comb. nov.

Basionym: *Anaulus simonsenii* Witkowski, Metzeltin & Lange-Bertalot

Etymology: The name of the genus points to the assumed relationship with *Plagiogramma,* the Greek term 'para' means 'parallel to'.

Diagnosis differens versus *Plagiogramma* Greville 1863

Pseudosepta solum dense prope apices sita utroque nec prope staurum in media parte valvarum. Areolae restrictae in partibus distalibus valvae et limbi inter pseudosepta et apices sed in parte maxima perforationes omnino absunt. Areolae perforationes simplices repraesentant non cribris praeditae nec alteris structuris complicatis nec sitae in depressionibus internis. Ita distinctiones inter campos polares-subpolares porellorum simplicium et areolas normales vacant. Valvocopula ab alteris copulis non differentiata, omnes non perforatae.

Differential diagnosis versus *Plagiogramma* Greville 1863

Pseudosepta occur across the apices only, not on either side of a central stauros. Areolae are restricted to the ends of the valve face and mantle distal to the pseudosepta. The large part between the pseudosepta lacks perforations. Areolae are never large with cribra or other complicated structures and do not open into distinct grooves internally but appear as small, simple perforations. There is no distinction between polar pore fields and normal areolae. The valvocopula and the copulae are barely differentiated, all are unperforated.

Paraplagiogramma balticum (Simonsen) Witkowski & Lange-Bertalot comb. nov.
Basionym: *Anaulus balticus* Simonsen 1959, Kieler Meeresforschung 15, p. 74, figs. 10: 1-3
Original description (translated from Simonsen, emended)
Cells rectangular with rounded apices in girdle view. Two pseudosepta, straight or slightly curved to the outside, protruding deeply into the valve. The two pseudosepta are reinforced at the ends. Valves elongated elliptic with rounded ends, 5.5-14µm long, 2.5-4µm broad. No other structures recognizable in the valves. Distribution: marine, widespread in the Kiel Bight, belts and estuaries but occurring in low abundances (Simonsen 1959, Witkowski 1994, Snoeijs & Balashova 1998, Witkowski et al. 2000). The species was also identified on eastern Pacific coasts – Yaquina Bay, Oregon (Riznyk 1973), recently also identified in San Francisco Bay (Witkowski et al. unpublished observation). Due to the weakly silicified valves the species is easy to overlook.

P. simonsenii (Witkowski, Metzeltin & Lange-Bertalot) Klein comb. nov.
Basionym: *Anaulus simonsenii* Witkowski, Metzeltin & Lange-Bertalot, Iconographia Diatomologica 7, p. 23, figs. 10: 7-12
Original description (emended)

Frustules in girdle view rectangular with acutely rounded apices and two strongly curved pseudosepta which are located close to the apices. Valves narrowly linear-lanceolate with protracted, subcapitate apices, 6-15.5µm long, 1-2µm broad. Fine structure not resolvable in LM.

Distribution: the species is fairly common in the type material, fossil sediments (Littorina) of the Mecklenburg Bay, western Baltic Sea and in the sediments of the Qurum Beach in Oman.

Metaplagiogramma gen.nov.

Typus generis: *Metaplagiogramma tenuissimum* (Hustedt) Witkowski & Lange-Bertalot (vide infra)

Etymology: The name of the genus points to the assumed relationship with *Plagiogramma* and *Paraplagiogramma*, the Greek term 'meta' means 'standing behind'.

Diagnosis differens versus *Paraplagiogramma* gen. nov. (vide supra)

Complexus signorum typicorum quoad maximam partem ut in genere Paraplagiogramma. Vero tamen pseudosepta producta ex valvis prope apices absunt et septa producta ex valvocopulis adsunt.

Differential diagnosis versus *Paraplagiogramma* gen. nov. (see below)

Complex of characters as in *Paraplagiogramma* except for the pseudosepta which are lacking in the valves and are replaced by septa produced by the valvocopulae.

Metaplagiogramma tenusissimum (Hustedt) Witkowski & Lange-Bertalot comb. nov.

Basionym: *Plagiogramma tenuissimum* Hustedt 1952, Ergebnisse der deutschen limnologischen Venezuela-Expedition 1952, Band I, p. 106, figs. 6-8.

Original description (translated from Hustedt and emended)

Cells very delicate, rectangular in girdle band view, chain forming. Frustules narrowly linear with rounded apices, 9-15µm long, ca. 2 µm broad, two strong transapical ribs close to the apices. Valve fine structure very delicate and not resolvable in LM.

Like all species of the genus '*Plagiogramma*' it is ecologically related to the euhalobous taxa and should not be common in the freshwater-dominated basin of the Lago de Maracaibo. It differs from other members of the genus ('*Plagiogramma*') in a very delicate structure as well as small size. The delicate construction of this species resembles the genus *Anaulus* but it is separated by the weak development of the 'pseudosepta' (corrected: read septa) which occur as transapical bars only, whereas these form deeply intruding walls in the species of *Anaulus*. Moreover, the valve faces close to the poles are flatly rounded without protrusions. The most significant characteristic placing this species within the pennates, the apical sternum of the valves, is hardly visible due to the delicate construction.

Acknowledgements

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Explanation to Figures:

Figs 1-13. *Paraplagiogramma balticum* (Simonsen) Witkowski & Lange-Bertalot

Figs 1-3. Reproduction of original drawings of *Anaulus balticus* by R. Simonsen. Figs 4-10. LM. Specimens of *Paraplagiogramma balticum* from the type habitat. Fig. 7. micrograph of the holotype – slide Di 116. Figs 11-13. SEM. Micrographs of specimens from original material. Fig. 11. External valve view of a whole specimen. Note a curvature of a valve surface bent along the transapical axis, relatively deep mantle, the presence of apical pore field and weakly expressed sternum (arrow). Figs 12-13. Valve interior of a specimen. Note the presence of a psudoseptum and areolae fine structure. Fig. 13. Close up of a specimen illustrated in Fig. 12. Note corroded pseudospetum and the sternum (arrow). Scale bar in Fig. 4 = 10 µm for Figs 4-10. Figs 14-27. *Paraplagiogramma simonsenii* (Witkowski, Lange-Bertalot & Metzeltin) Klein Figs 14-17. LM. Specimens of *Paraplagiogramma simonsenii* from the type habitat, the western Baltic Sea. Fig. 16. Specimen from the type slide. Figs 18-21. TEM. Figs 18-19. Specimens illustrated in a girdle view. Figs 20-22. Valve view of different specimens. Note the presence of apical pores fields and of a sternum (arrow in Fig. 20). Figs 23-27. SEM. Figs 23, 25. Fig. 25. Close up of specimen illustrated in Fig. 23. Valve interior. Note the presence of pseudosepta, apical pore fields and a hyaline valve interior. Figs 24, 27. Valve exterior. Specimens showing arched valve face. Note the presence of apical pore fields. Fig. 26. Valve interior. Specimens illustrated in Figs 18-25 and 27 originate from the North Sea coast in Southern England. Scale bar in Fig. 14 = 10 µm for Figs 14-17.

Figs 28-30. *Metaplagiogramma tenuissimum* (Hustedt) Witkowski & Lange-Bertalot Figs 28-30. Reproduction of original drawings of *Plagiogramma tenuissimum* by F. Hustedt. Figs 31-37. LM. Specimens from the type slide. Figs. 38-43. SEM. Figs 38-40. Valve external view. Note the valve face with apical pore fields and weakly developed sternum. Figs 39-40. Close up of specimen illustrated in Fig. 38. Figs 41-43. Valve interior showing the presence of septum (arrow). Figs 38-43. Specimens from the original material. Scale bar in Fig. 31 = 10 µm for Figs 31-37.


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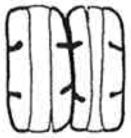
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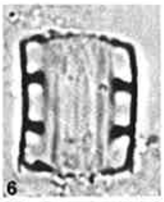
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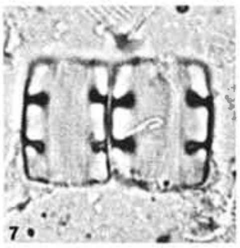
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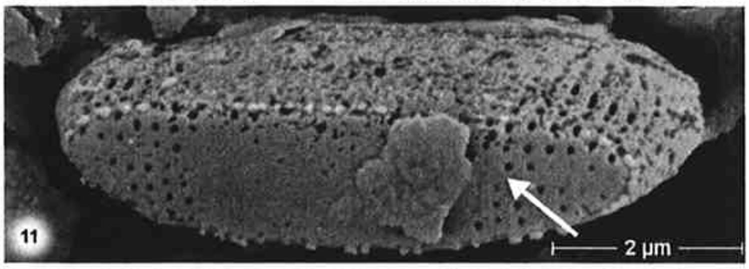
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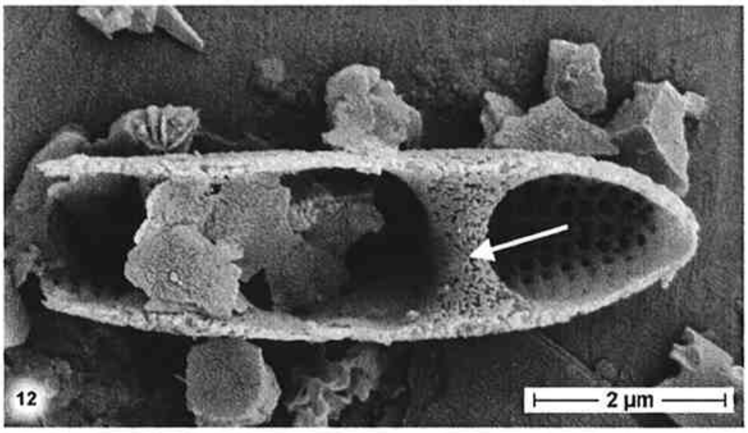
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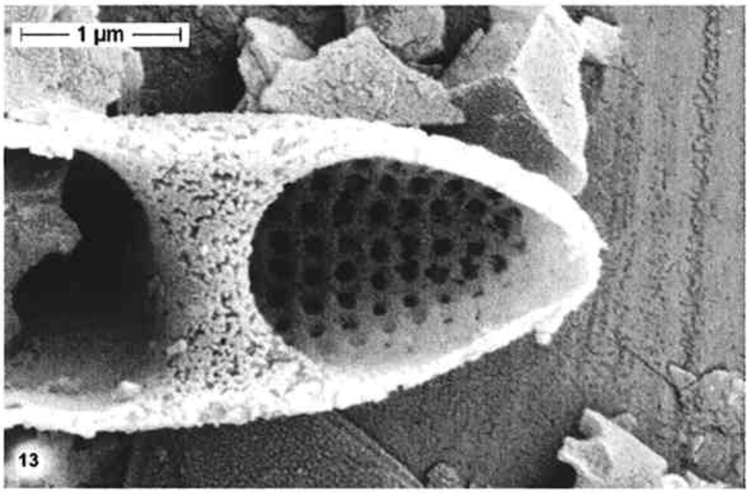
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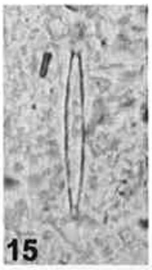
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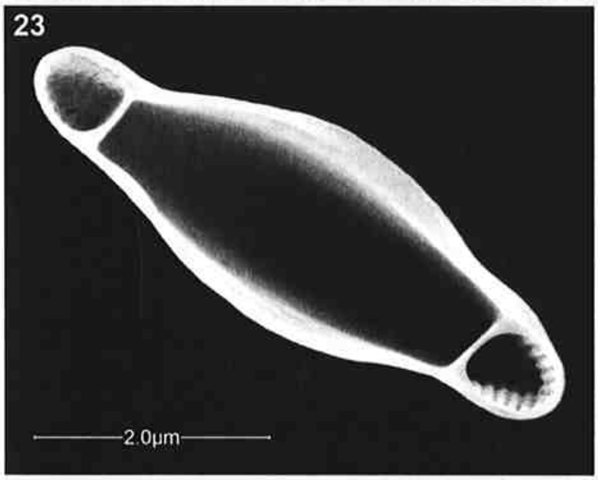
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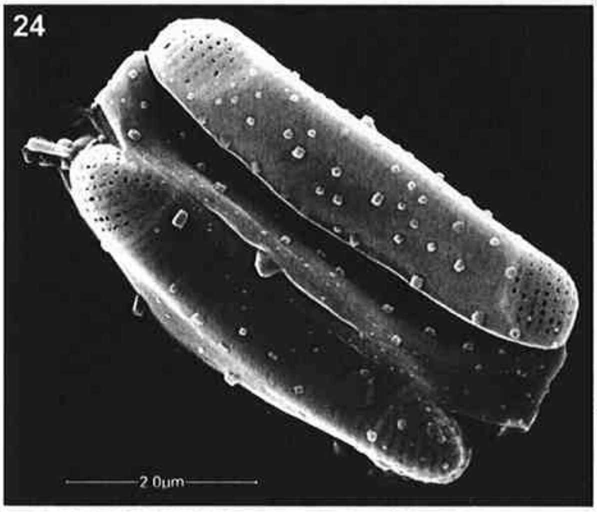
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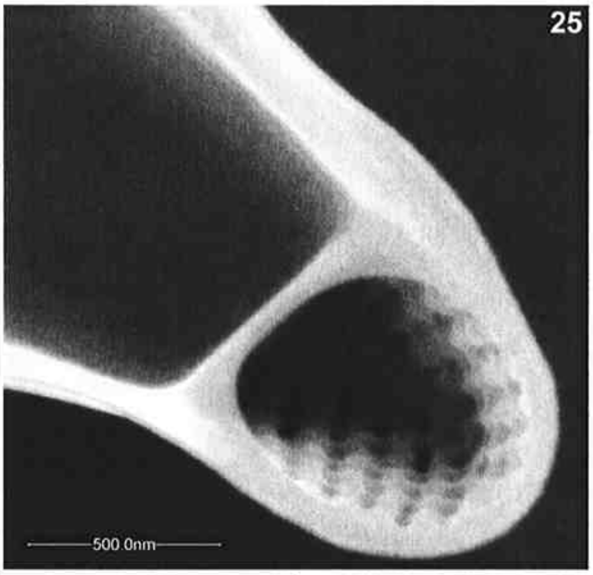
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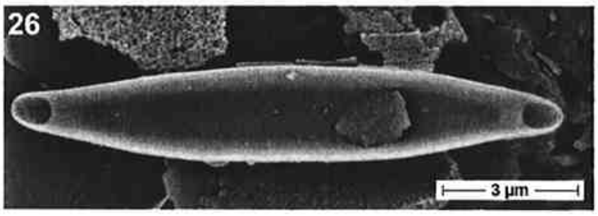
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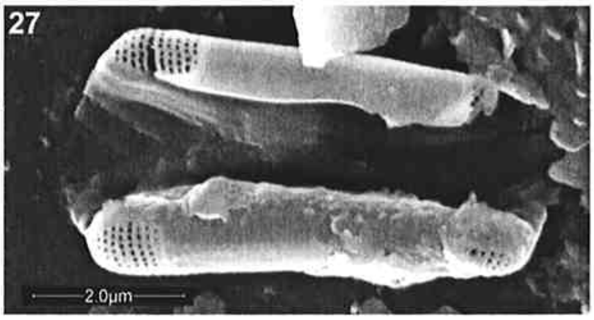
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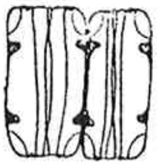

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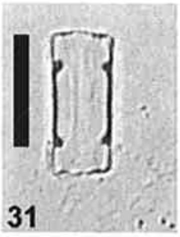

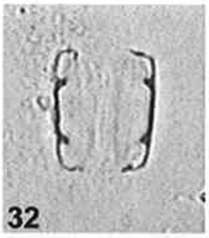

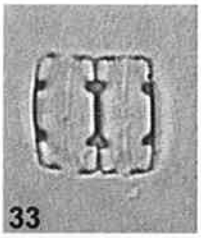

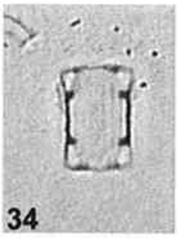

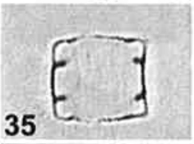

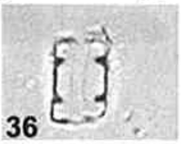

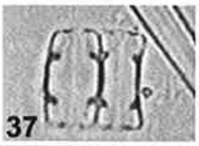

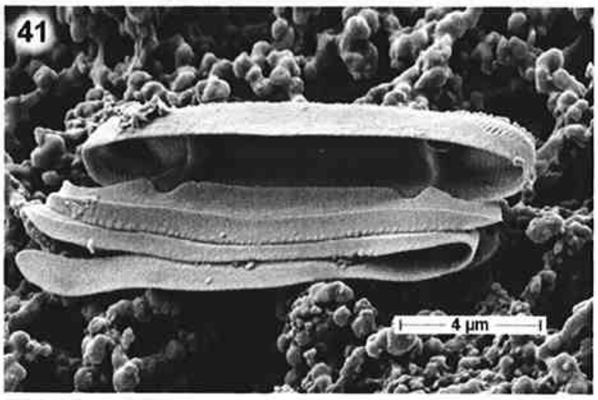

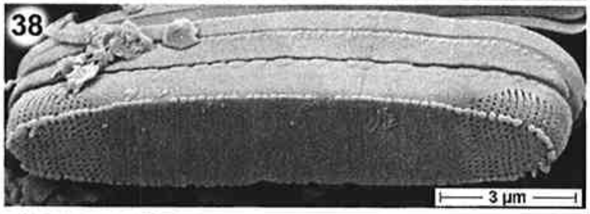

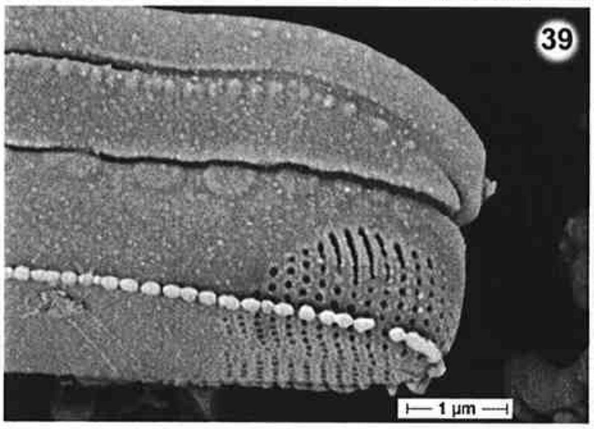

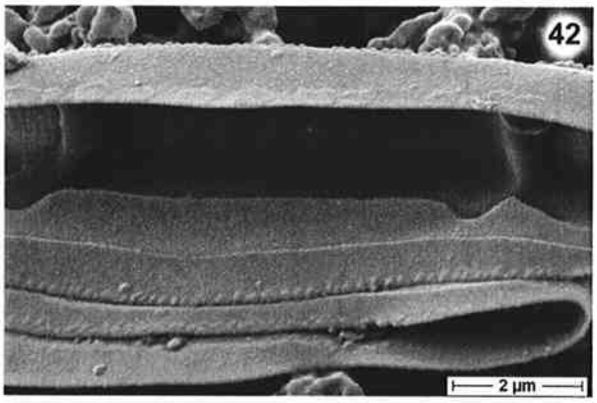

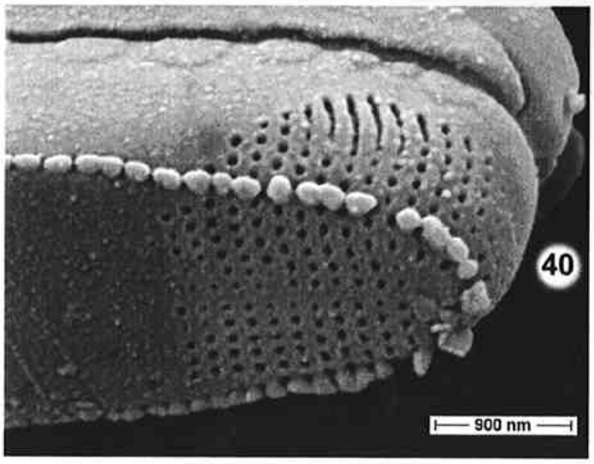

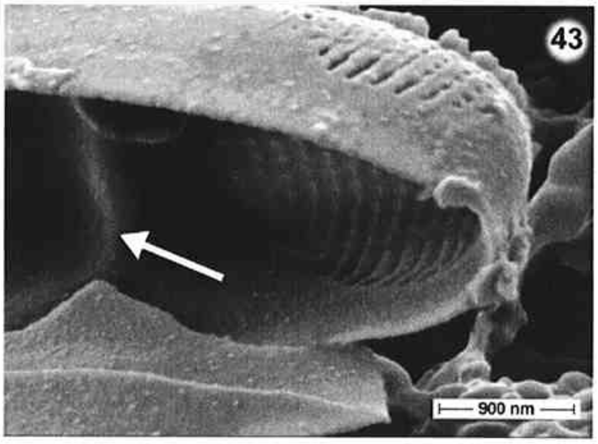

Chapter 8

General discussion

The aim of the present study was to investigate and describe the effects of changed hydrodynamic characteristics on the microphytobenthic community of Sylt.

Analysis of physical and biological elements were combined in order to (1) describe the various factors influenced by hydrodynamics and to characterise the hydrodynamic regime prevailing on an intertidal sand flat taking into consideration tidal and wind forces; (2) to investigate the effect of resuspension of diatom cells at species level and (3) to elucidate the influence of turbulence on particular size classes of diatoms. The investigations were carried out using a three-current-flume to measure *in situ* the effects of altered current velocity. A clear separation into three different current velocities, increased, mean and reduced, was achieved through orientation of the sides of the nine lanes of the flume.

The data collected during *in situ* flume experiments on six sampling occasions between July and September 2003 were analysed to describe the prevailing environmental conditions and provide the basis for future research on the dynamics of Sylt´s intertidal flats.

Diatom communities of the sediment and water column

The configuration of sandy sediments on a given beach results from physical sorting processes determined by the hydrodynamic conditions (tidal currents and waves) and specific loss rates of the benthic microalgae, by processes including resuspension, sorting of grain sizes, export or grazing, are much greater in sandy than in muddy sediments (Herman et al. 2001). Muddy, fine-fractioned sediment can accumulate where low flow velocity allows deposition of particles. Such undisturbed conditions leads to an increase in species able to bind the sediment by EPS production and thus stabilise the sediment surface. Epipelic diatoms only colonise when the median grain size is sufficiently small (Staats et al 1999). However, if a sufficient volume of mud does not build up, the microalgae will be subjected to the above mentioned loss processes and will not be able to stabilise the sediment: the situation stabilises in a state of low mud content and low microalgal biomass. These differences will also be reflected in the species composition of the microalgal assemblage, e.g. the relative dominance of epipelic and epipsammic diatom forms (Herman et al. 2001, Widdows et al. 2000)

The diatom community analysed for the six sampling days between July and September is typical of that found on intertidal sands on the North Sea coasts (e.g. Asmus & Bauerfeind 1994, Colijn & Dijkema 1981, Drebes 1974).

Of the 231 species identified, 45 belonged to the epipsammic fraction, a life mode that is characterised by attachment to the substratum. A further 32 species are pelagic and only rarely found on the sediment surface of the intertidal flat, and 107 species belonged to the epipelic diatom community, living on the sediment surface, more or less associated with the sediment. Several species of this community are closely associated with the benthos but are frequently resuspended into the water column, a life mode referred to as tychopelagic. This life mode has been observed for a variety of centric diatoms that are frequently found in benthic assemblages and are likely to have settled from the plankton, for example *Paralia sulcata* and *Odontella aurita*. For a number of species the life mode is only assumed to be the one or the other. However, findings within this study give a clear picture especially for six ecologically important species. The epipsammic/epipelic *Amphora* species were found to be strictly associated with the sediment, as proven by their rare occurrence in the water column. Interestingly, this species, together with the likewise epipsammic *Delphineis,* showed a reaction to the increased flow treatment, with significantly higher cell numbers on the sediment in the increased flow lanes. It is assumed that the increased flow altered the nutrient conditions or availability for these species in the interstitial porewater of the sediment.

The epipelic species *Entomoneis* exhibited a distinct affiliation for the pelagic, given the 2 to 5 times higher cell abundances in the water samples. Representatives of the group of *Haslea*/*Navicula* species in the water were found to outweigh the numbers on the sediment and seemed to be rapidly resuspended as indicated by the increasing proportion of cells in the water column with increasing current. Contrary to the assumed benthic life mode for *Diploneis*, this heavily silicified species showed varying abundances in the water column and on the sediment surface that could not be explained by currents, modulated by wind velocity and direction, or by flow velocity. It is suggested that *Diploneis* is a tychopelagic species that exerts varying efforts to attach itself to the substratum or alter its buoyancy, leading to a periodical dislodgement and suspension. The question of whether this species has indeed adopted a tychopelagic life mode could be answered by measurements of EPS exudation rate and photosynthesis rate under controlled conditions (see, for example, Staats et al. 1999, DeBrouwer et al. 2005). Our results suggest that such a study would be worth-while before attempting to classify these species correctly regarding their ecology and to understand their chances of success in an environment altered, for example, by climate change.

Tidal influence

Compared to the high variability in planktonic cell numbers over the sampling days, with demonstrated influence of the tides and, furthermore, the erratic dominance of different species contributing to the planktonic community, the benthic community showed greater stability. The influence of tidal forces on ecological conditions was analysed by Jenness & Duineveld (1985) and Wiltshire et al. (1998), who found significant differences in chl *a* and SPM values between the ebb and flood currents, with the ebb flow resuspending less chl *a* from the sediment compared to the flood. Asmus (1992) measured an extraordinarily high export of POC at the end of the tidal cycle. Shimeta et al. (2003) calculated that bottom shear stress (at another sandy site) is greater on flood than on ebb tides and resuspension occurred only with the flood current because of combined wave and flow forcing during flood and opposing forces during ebb. The effect of wind can lead to large changes in residence time of the water body in the bight, according to whether the wind forcing is either delaying or progressing the tidal transport. The variability in our results can be explained by an interaction of wind velocity and direction, tidal forces and the resulting flow velocity. However, there also occurred contrasting patterns that contradicted the interactive effects of these parameters. Therefore, it must be assumed that further hydrodynamic flow patterns, which could not be measured in the flume configuration used here, influenced the dynamics of resuspension and settlement. Uncles (2002) reported longitudinal tidal currents that generate transverse circulation patterns, so called secondary flow, in response to geomorphology. These forces can be induced regardless of wind force and direction and cause resuspension when the threshold for critical shear stress is exceeded. Complex flow patterns were also reported by Deussfeld (2003), who measured flow characteristics in the vicinity of the sampling site described in this study and found a complex layered flow profile to exist for that area. It is possible that the flume walls shielded the lanes from lateral currents, as reflected in the current measurements made within the lanes, but that the water entering and leaving the lanes, thus altering the biological content, was affected by lateral currents up- and downstream of the flume.

Turbulence

When flow measurements are made, current velocity data have to be interpreted carefully. It is common to use mean velocity values to characterise flow over a given time. But flow is a three-dimensional parameter, operating on different spatial and temporal scales. Local turbulence, wind, tide or geomorphologically induced flow patterns, cause small scale resuspension, of either biological compounds alone or additionally of sediments. These complex water-sediment interface interactions must be taken into consideration when processes are discussed. Local effects of turbulence in the present study were revealed by analysis of cell counts of four size-classes of resuspended diatom cells with regard to flow treatment. On average more small cells (< 20 µm) were resuspended, probably the fraction of the community not firmly attached to the sand grains but only loosely associated. However, the high variability among samples from the 'reduced' flow treatment compared to the 'increased' flow leads to the conclusion that (1) accelerated flow leads to resuspension but (2) sporadically increased bottom shear stress can induce a short term disruption not only of higher numbers of larger cells but also of small, sediment-associated cells.

Local effects of resuspension and redistribution/sedimentation at a given location will vary on different time scales and are, together with bottom topography (bottom roughness), also dependent on fetch conditions which are determined by wind direction. These factors – together with current patterns – explain the variability in our results. The current velocities measured at our sampling site, at 0.01 – 0.12 m s^{-1} are low in terms of initiating resuspension; Widdows (pers. com.) suggested that resuspension basically occurs only above flow of 0.2 m s^{-1}. However, Booth et al. (2000) found a wind velocity of 4 m s^{-1} enough to resuspend 45 % of the sediment in Barataria Basin, Louisiana, USA. Van de Koppel et al. (2001) confirmed personal observations: submerging of sediment by rising tides caused biofilms on sand to detach from the sediment. This leads to losses of diatoms from the sediment, even at a current speed insufficient to invoke erosion.

For the present study, we conclude that turbulence, caused by wind-induced waves, tidal forces and advective forces, is the trigger resuspension. Baillie & Welsh (1980) have even found that microflora is resuspended by convection currents caused by the differences in temperature between water and sediment. Due to the high temperatures in summer 2003, this process was probably also active on the tidal flat during the first inundation when the tide came in. Shear velocity was found by Lucas (2003) and van de Koppel et al. (2001) to be the dominant forcing factor for resuspension, and our calculations of bed shear stress are in good agreement with measurements by other authors (e.g. Deussfeld 2003). Shear stress values were sufficient to induce resuspension of microphytobenthos and fluff layers but not high enough to cause a resuspension of the sand grains. The prevailing sediments are too coarse to be the source of shifts in grain size distribution within the different flume lanes. Currents and winds cause transport of coarse sediments into the Sylt-Rømø bight, thus creating the prevailing sandy sediments. Tidal currents alone across the intertidal flats can not transport sand grains of the existing grain size distribution (C. Hass, pers.com).

Effect of flow treatment on benthos

In intertidal sediments, microbenthic algae are regularly mixed by the action of currents and tides (DeJonge 1985). The fraction of biomass which is resuspended or buried is crucial in determining the strength of linkage between the benthic and pelagic components of the ecosystem: the bentho-pelagic coupling. In the present study, the epipelic fraction exceeds the epipsammic by 107:45 species. Considering the capacity of epipelic diatoms to produce higher amounts of EPS which serve to stabilise the sediment and also the possibility of a tychoplanktonic life mode, this suggests a strong bentho-pelagic coupling and a blurring of the boundaries between the two communites. The lower chl *a* values on the sediment found in the 'increased' lanes, with accelerated flow velocity compared to the 'reduced' lane with higher chl *a* values, can be attributed to the higher energy to which the sediments in the increased lane are exposed (although the increased, manipulated flow velocity would not necessarily exert a higher bottom shear stress, Herman et al. 2001). This probably resulted in an export of biomass such that fewer cells were mixed downwards into the sediment (or migrated), with the surface sediments being constantly recolonised by microphytobenthos upon inundation.

Species analysed from benthic samples were found to react differently to the flow treatments with increased cell numbers of the epipsammic/epipelic *Amphora* species in the increased flow lanes and with higher cell numbers of the assumed epipelic *Diploneis* with reduced flow. The latter observation confirms the suggested tychopelagic life mode; even at low flow velocity *Diploneis* is easily resuspended from and resettled onto the sediment surface.

An effect of reduced flow velocity on processes on the sediment was demonstrated. Increased chl *a* and POC values accompanied by lower cell numbers point to the presence of two or more different carbon sources. These could be sedimented suspended matter which increased due to the reduced flow velocity or accumulated microphytobenthic organisms belonging to taxa other than diatoms, for example, cyanobacteria or flagellates which produce EPS. Furthermore, it is suggested that due to the sheltered conditions within the 'reduced' flume lanes conditions were more favourable for the mudsnail *Hydrobia* to graze on diatom cells. *Hydrobia* is known to have a significant impact on the microphytobenthos of intertidal flats and to appear in increasing numbers at reduced current velocities (e.g. Schanz et al. 2002).

Several studies emphasise the influence of nutrients to diatom communities (Admiraal 1980, Sundbäck 1996, Agatz 1999, Underwood & Provot 2000), but as this study clearly shows, the impact of hydrodynamics should also be taken into consideration, especially where coarse, sandy sediments, characterised by enhanced turnover rates, are present (Rusch et al. 2001, Hedtkamp 2005). The uptake of nutrients or the supply of sediment with oxygen is dependent on grain size and permeability (among other factors), which are in turn related to current velocity. The oxygen consumption rate is a function of benthic metabolism and Forster et al. (1996) demonstrated in a flume experiment that the sedimentary oxygen consumption was a function of flow velocity, as higher velocities increased the oxygen levels of the sediment. Particles (bacteria, microalgae, detritus) can be transported several centimetres deep into the sediments by pore water advection. This is of major importance for benthic mineralisation rates as settling of particles is low in sandy areas due to the intense hydrodynamics.

Implications of climate change

Scientific analyses can contribute significantly to provide information about the state of the art or the vulnerability of a system and also on processes pointing to ongoing changes. These data provide the basis for determining political decisions for the protection of the environment. According to the IPCC (Intergovernmental Panel on Climate Change, 2001), the potential changes expected from climate change will be:

(i) Temperature rise
(ii) Sea-level rise
(iii) Precipitation change
(iv) Droughts and floods

The results of the present study suggest that the bentho-pelagic diatom community of Sylt would respond to elements (i) and (ii) in the following ways:

Increasing wind velocities will be the result of strong thermal gradients caused by a rise in temperatures. High energy storm events as well as regularly stronger wind-waves will lead to increased turbulence causing amplified resuspension events. Hedtkamp (2005) showed that the mean average wind speed solely governed the sediment permeability in her study of a Sylt sandflat. Wind-generated waves are well known to be an important forcing factor on physical properties of the sediment (see Grant et al. 1986, de Jonge & van Beusekom 1995, Lucas et al. 2000). The constant reworking of the sediments through wind and tidal regimes results in a large stock of living specimens in the deeper layers of the sediment and consequently prevents major population fluctuations (Amspoker 1977). Sediments will be subjected to higher turn-over rates and higher mineralisation rates due to wave pressure causing, along with higher permeability of the sediment, an increase in advective forces. Thus, organic matter is more readily remineralised and released into the water column. Exposure to wave energy reduces the biomass and productivity of microphytobenthos (Cook et al. 2004). Moreover, the presence of organic matter is necessary as it forms the basis of a biofilm to which organisms can attach and the hydrodynamic forces work against this by preventing microphytobenthos from forming a sediment-stabilising biofilm. This loss of stability, enhanced by the physical sorting of the sediment, would lead to coarser grain size sorting. A change in the sediment properties will take place which in turn will affect the settlement of flora and fauna and create a different habitat for a different diversity of ecosystem inhabitants normally found on high energy, coarse sands. Epipelic species are able to take maximal advantage of irradiance due to their ability to move but are more easily suspended by wind- and tide- induced waves (Van den Hoeck et al. 1979). Fluctuations will therefore be more pronounced in epipelic communities.

An increase in solar radiation/water temperature has implications for organisms both on and in the sediment and for nutrient exchange at the sediment water interface: a rise in the temperature of a water body entering a heated intertidal flat or rapidly warming up of slowly retreating water towards low tide, results in thermal convection. This result in solute exchange rates up to three orders of magnitude higher than those of diffusion (Rocha 1998).

The impacts of sea level rise and floods, element (iv), are closely linked and according to the IPCC report (2001) the global mean sea level is projected to rise by 0.03 to 0.14 m until 2025. A shift towards a mainly epipsammic community due to grain size sorting based on the above-mentioned scenarios can be assumed here.

Furthermore, this shift in species diversity will also be directed towards a subtidal community, as sea level rise will cause shorter inundation periods and loss of intertidal areas. Enhanced suspended matter caused by increased resuspension and particularly soil erosion in the water column leads to a decrease in photosynthetic capacity of benthic as well as pelagic species. This will result in specialisation and reduction in diversity; specialists among benthic diatoms will take advantage of the even more disadvantaged planktonic diatoms which are restricted not only by higher amounts of resuspended matter but also by competition of benthic species in the water column. Thus, less diversity within the benthic and the planktonic community can be expected.

Suspension-feeders exert a grazing pressure on phytoplankton as well as on resuspended phytobenthos (Lassen et al., 2006). The filtering rates of suspension feeders are influenced by hydrodynamics: for example the filter feeding bivalve *Mytilus edulis* is able to filter more than 4 l^{-1} as an adult (Asmus & Asmus 2005). Tidal resuspension of diatoms leads to a vertical distribution of diatoms as a food source. Thus suspension and filter feeders can profit from these transport processes. An increase in current velocity will, at a certain point, lead to a reduction in the feeding rates (see also Lassen et al. 2006 and references herein).

The responses to element (iii), changes in precipitation, would need to be addressed by lab studies under controlled conditions, of individual species. Presumably will a supposed increase in precipitation will have a wash-out effect on EPS in the sediments which would lead, as mentioned above, to a loss of mud particles and to a reduction of sediment stability and further to a shift in sediment grain size and community composition. Furthermore, selection of species which are best able to adapt to a strong salinity gradient caused by an increase in freshwater in the porewater will favour euryhaline species.

The impact of these responses on the ecosystem as a whole would be a shift in the community towards smaller, epipsammic species which are not able to stabilise the sediment due to their lower rate of EPS production. Planktonic as well as benthic species would have to adapt to decreased light availability because of enhanced input of suspended matter and humic acids deriving from resuspension and soil erosion. The latter will furthermore lead to increased damage to the coastal ecosystem. Burial within deeper sediment layers will afford the opportunity to switch to heterotrophy, an ability already found for several species (Tolomio et al. 2002, Zhang et al. 2003). All these factors will lead to intra- and interspecific competition (resuspension of diatoms is accompanied with resuspension of bacteria and protists, e.g. see Shimeta et al, 2002, 2003) and the necessity of adapting to new environmental conditions (see also Widdows & Brinsley 2002).

Climate change and invasive species.

Invasive species of both fauna and flora can change the ecosystem irreversibly. Experiments can help to understand their dispersion mechanisms and also how to prevent further expansion. Sylt, for example, is affected by the introduced oyster *Crassostrea gigas*, which displaces the mussel *Mytilus edulis* and presents a far higher biomass and higher filtering capacity as compared to *Mytilus* (Diederich, pers.com.). The introduced, non-indigenous, common cordgrass *Spartina anglica* creates new structures where organisms find shelter and a new habitat, thus changing the biodiversity on a former two-dimensional area, and constitutes a habitat engineer. These processes are also true for micro organisms such as diatoms. Climatic change may possibly lead to the introduction of different species that will change the community composition and might have negative consequences by dominating or replacing former community structures.

Critical remarks

As the hydrographical variability in tidal areas is very high, hydrographically-induced concentration variations may blur long-term trends in concentrations so that knowledge of hydrographical variations is essential when planning sampling frequency in, for example, nutrient monitoring programs. Consideration has to be given to the heterogeneity of the system: adjacent seagrass areas almost certainly contributed to species changes observed in this study, as the sudden appearance of e.g. *Cocconeis* or *Rhopalodia* in high abundances indicate. As mentioned before, the exceptionally warm water temperatures in summer 2003 led to an augmented stress and an untimely decline of seagrass plants, thus adding epiphytic diatom species to the experimental area.

Different species migrate to and away from the sediment surface over different time scales (Hay et al. 1993). When collecting and analyzing benthic samples, the possible variations in resuspension dynamics due to migrating cells needs to be taken into consideration. A sudden change in the community structure can be related to the presence or absence of species migrating below the sampling depth.

Conclusions

As such this was the first *in situ* study of the diatoms in water and sediment communities and the results showed both the complexity of the system, discrimination at the species level in terms of resuspension and the naïvity of terminology – the boundaries between benthos and plankton being especially blurred in this habitat.

The microbenthic community showed a distinct sensitivity to the altered flow conditions. A reduction in flow velocity caused an increase in chl *a* and POC and a decrease in cell numbers compared to increased current velocity. The low flow velocities are sufficient enough to induce resuspension. A shift in other taxa (euglenoids, flagellates, cyanobacteria, e.g.) within the benthic community can not be excluded.

Our findings support the theory by Riethmüller et al. (2000), who concluded that chl *a* is not a potential general index for sediment surface stability related to diatom cells, as a carbon source clearly accumulates on the sediment surface subjected to reduced flow, however with decreasing diatom cell numbers.

Population composition in the water column was erratic compared to the rather stable benthos community. A clear influence of wind-induced turbulence could be seen in the variety of resuspended species and also of the wind direction which determined the frequency of introduction of species from the open coastal waters (e.g. *Chaetoceros sp.*).

Where variability in species composition could not be explained by wind direction and velocity, the effect of a complex transversal flow pattern (secondary flow) is suggested.

Several species, for example *Diploneis*, were found to react to the altered flow conditions and are suggested to represent a tychopelagic life mode, benefiting by conditions favourable to them on the sediment surface as well as in the water column. The epipsammic/epipelic species *Amphora* appeared to show a preference for increased flow conditions above the sediment, which might create a more favourable environment in terms of higher nutrients in the porewater or better nutrient accessibility. Thus it can be stated that the flow treatments had an effect on community composition at species level although the results are not sufficient to support distinct trends between species numbers and hydrodynamic conditions, and further laboratory flume experiments would be necessary to confirm both the observed preferences for flow characteristics and the effects on sediment constitution.

The varying resuspension behaviour of different species, together with the results of other authors regarding the variability of EPS quality produced by different species, emphasises the importance of diatoms not only as a sediment stabiliser but also as an important food source for benthic and planktonic feeders. Resuspension behaviour has an impact on variability of the quality and quantity of food available, so that chl *a* measurements used for primary productivity measurements in the benthos and in the water column must be regarded carefully.

The greatest influences on the variability of the samples were the wind direction, velocity and fetch. These factors control wind-induced turbulence which in turn lowers the critical bed shear stress, resulting in resuspension. These effects can be stochastic and administer a force which is smoothed out when the average current velocity data is calculated. Furthermore, a reduction in flow velocity caused higher turbulence events compared to increased flow. Generally, turbulence can be initiated not only by wind-waves but also by tidal currents, bottom roughness due to obstacles and geomorphological conditions including ripples.

Outlook

With additional parameters, such as wave height and settling velocity measurements, it would be possible with the aid of a model to gather valuable information about the susceptibility of different benthic organisms to resuspension along with their dynamic behaviour in estuaries and their contribution to the system. Furthermore, a rigorous, long-term study of benthic processes would provide valuable information for further sediment-water coupling studies and could eventually be incorporated into models for network studies (see Baird et al. 2004).

Information on diatom autecology, especially at species level, from estuarine sand flat diatom communities are scarce. Thus, in terms of future work in using diatoms as indicators for environmental change for biomonitoring purposes, this work serves as an important contribution to determining the tolerance of certain benthic diatom species to specific environmental factors, making them potential indicator species for changes in the coastal environment.

Analyses of benthic diatom samples are very time consuming. However, for a better understanding of species ecology and consequently of the whole microphytobenthic community, a longer time-series study such as conducted for the various parameters measured in the Sylt-Rømø Bight would be useful. The Sylt-Rømø Bight is in need of long-term studies because, according to the assumptions of Baird et al. (2004), compared to other bights/bays, the calculated, low, A/DC ratio (ascendancy/development capacity) suggests that the Sylt-Rømø Bight is "not well organised" and therefore possesses no internal stability or resilience to perturbations. This means that the energy pathways could easily be disturbed, perhaps altering the ecosystem permanently, with unforeseeable consequences.

With some alterations, such as the addition of current measurements by fixed sensors deployed outside of the flume to monitor lateral flow, the experimental configuration used here could yield greater depth of knowledge of the study area. The next step toward a fuller understanding of the ecology of this site is a fuller program including more frequent sampling to capture resuspension processes, over a longer period to capture inter-seasonal and inter-annual variability. Such a study would be of great usefulness for fisheries monitoring and for the understanding of climate change impact, but would require considerably more equipment and personel than was available here.

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