Impact of pore water advection on transport and remineralization of planktonic diatoms in permeable shelf sediments

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TABLE OF CONTENTS

Chapter 1

General Introduction

INTRODUCTION

This thesis is concerned with the investigation of diatom degradation in permeable shelf sediments. Shelf areas are characterized by a high primary production, which is mostly supported by diatoms. Diatom growth is dependent on silicate availability, and the decline of the diatom spring bloom is usually initiated by silicate depletion. Thus, the remineralization of biogenic silica is an important process for maintaining high primary production rates in shelf environments.

Continental Shelf Areas

Continental shelves are submerged continental margins which slope very gently seawards from the littoral zone, generally to depths of about 100 to 250 m at the shelf break (Brown et al. 1989). Shelf areas constitute an important link between the continents and the open ocean, and cover approximately 7.5% of the total ocean area (Wollast 2003). Despite this small percentage, shelf environments show a high biological productivity, which amounts to 30% of the total oceanic primary production (Jørgensen 1996). This high biological productivity is caused by a variety of factors, including the input of nutrients from rivers, upwelling of nutrient-rich deep waters, the close coupling of benthic and pelagic systems (Wollast 1991) and the aeolian input of trace elements, as iron and selenium, from the close-by continent. Due to the shallow nature of shelf areas, up to 50% of the primary production can settle through the water column (Jørgensen et al. 1990). Thus, shelf sediments are important sites of organic matter degradation.

The majority of shelf sediments along the mid- to high latitudes originate from the weathering and erosion of the continents (terrigenous sediments), and the most important solid products are rock fragments, quartz grains and clay minerals (Brown et al. 1989). Rivers are significantly involved in the transport of these terrigenous sediments to the ocean margins, but volcanic eruption, wind and ice transport may be locally important. Large areas (approximately 70%) of the shelves today are covered by coarse relict sediments (Emery 1968). These relict sediments were deposited in terrestrial environment when large areas of the continental shelves were exposed during the sea-level minima associated with glaciations. Rivers and ice-sheets originally deposited a large extent of relict sediments; therefore, they often contain a mixture of gravels, sands and muds. Relict sediments were deposited in equilibrium

with their environment in the past, but the environment changed and the time until now was not adequate to achieve a new equilibrium by burial or erosion.

The shallow coastal zone is an extremely dynamic environment, where wave-induced, tidal and storm currents cause frequent sediment erosion, redeposition and lateral transport. Together with the presence of large areas with coarse relict sands, these processes result in the predominance of sandy, permeable sea beds in shelf environments. Another consequence of boundary layer turbulence is that organic particulate material also goes through many cycles of deposition and resuspension on the shelf before it is finally completely mineralized, buried or exported to the open ocean. Thus, only the most refractory organic matter is likely to be exported (Bacon et al. 1994). Liu et al. (2002) have estimated that only small amounts of the organic matter, which represents 12% of the coastal primary production, are exported from the shelf

The North Sea

The North Sea, a shelf sea covering approximately 580000 km^2 with a averaged depth of approximately 70 m, is hydrologically coupled to the north-eastern Atlantic Ocean. The hydrography of the North Sea is strongly influenced by the input of saline waters from the Atlantic Ocean at the northern boundary and by the British Channel in the south-west. The coastal areas in the south-east are heavily influenced by riverine input of freshwater and associated nutrients. The annual primary production in the North Sea is high, especially in the southern coastal areas with values of 370 g C m^2 yr^1 for the Southern Bight (Wollast 1991). This high primary productivity makes the North Sea to one of the most fish-rich areas in the world ocean.

The German Bight is a shallow region of the south-eastern North Sea with depths mainly between 20 and 40 m. The complex hydrographic structure and nutrient gradients in the coastal waters of the German Bight are heavily influenced by inputs from the rivers Elbe and Weser (Hesse et al. 1995). Salinity varies between 27 and 34. The predominant sediment types in the German Bight are sand, mud or a mixture of both. The ample intertidal areas, the Wadden Sea, which cover approximately 13% of the German Bight, are characterized by a high primary production of benthic diatoms. In the south-eastern corner of the German Bight, the Frisian barrier islands separate the Wadden Sea from the remaining German Bight, e.g. Spiekeroog Island. The mean tidal range offshore of Spiekeroog is approximately 2.5 m and peak tidal current

velocities at 1 m above the sea-bed are in the range of 30 to 60 cm s^{-1} (Antia 1993). Tides, waves and storm currents play a key role in sediment transport processes of this high-energy environment.

Diatoms

Shelf areas are largely influenced by climate, as annual surface temperature fluctuations are more extreme as in oceanic areas. Therefore, the water surface temperature in shelf areas heats up faster in spring compared to the open ocean, resulting in a thermal stratification in the near-surface water. In northern temperate latitudes, as the North Sea, the beginning of the phytoplankton spring bloom depends on the stabilization of this water stratification. The high biological productivity of shelf environments is partly explained by the early beginning of the growing phase.

The typical seasonal succession in the North Sea starts with a diatom-dominated phytoplankton community in spring. Spring diatom blooms are often the events of highest annual new production and carbon sedimentation in the coastal ocean (Goering et al. 1973), thus, providing the bulk of the annual food supply to the benthos (Conley & Johnstone 1995). Diatoms contribute to the total primary productivity up to 35% in oligotrophic oceans and 75% in coastal areas and the Antarctic (Tréguer et al. 1995). Egge & Jacobsen (1997) proposed that the success of diatoms is based on their high growth rate at non-limiting nutrient concentrations.

Diatoms (Bacillariophyceae) need silicon to build up their frustules (biogenic silica or opal, 96.5% SiO_2), that enclose their cell with two shells. Therefore, they take up silicate ($Si(OH)_4$) from the surrounding seawater at a ratio of 1:1 to nitrogen (Lewin 1965, Brzezinski 1985). Usually silicate depletion in the seawater concludes the spring bloom, as the remineralization of biogenic silica by inorganic dissolution (Schrader & Schuette 1981) is much slower than the decomposition of organic bonded nitrogen and phosphorus. In the case of nitrate and phosphate availability, a bloom of flagellates follows the spring bloom in summer. In autumn, increasing storm activities can recycle remineralized silicate from the sediment back to the surface water, inducing a second diatom bloom.

The majority of coastal bloom diatoms are small, spiny, chain-forming and have thin frustules, in contrast to oceanic diatoms that have many large, smooth-walled representatives (Smetacek 1985). Apart from diatoms, only a few other phytoplankton species, as *Phaeocystis*, form colonies by aggregating their cells into chains through

various means of attachment (Smayda 1970). With exception of the *Skeletonema* chain type, where single cells are linked by intercellular silica rods, chain-formation favours an increased sinking rate (Smayda 1970). This suggests that chain-formation cannot be invoked as a mechanism to reduce sinking speed, but rather serves as anti-predation device. During winter and spring, the water column can be completely mixed carrying the diatoms down to the sediment. Thus, colony formation and spines of coastal diatoms also may be important to avoid benthic filtration, as permeable sediments may advectively filter approximately 100 L m^{-2} d^{-1} (Precht & Huettel in press). The colony size is not constant, as cell numbers per chain decrease with increasing age (Smayda 1970). Thus the sinking rate is reduced with increasing age, except for *S. costatum*, where the sinking rate increases. The causes of colony breakage are unknown, and aggregation or disintegration of chains during sedimentation differs between species (Smetacek 1985).

Planktonic diatoms do not have any structures facilitating locomotion, but possess a variety of mechanisms to retard sinking, e.g. small cell size, cell shape or ionic regulation (Round et al. 1990). The advantage of being small comprises that the surface to volume ratio is enlarged, which reduces the sinking rate of living cells (Lalli & Parsons 1993) and enhances the nutrient uptake efficiency (Sournia 1982). Upon nutrient depletion, sinking rates can increase drastically (Smetacek 1985), and aggregation after intense blooms further can accelerate the sinking rates (Passow 1991). Several authors (e.g. Peinert et al. 1982, Brussaard et al. 1995) have shown that sedimentation is the major loss factor inducing the decline of diatom blooms, as the impact of zooplankton grazing on the spring bloom is relatively low (Wollast 1991). The sinking dynamics of coastal bloom diatoms are an integral part of their life history and represent the transition from a reproductive pelagic stage to a benthic resting stage, which enables them to survive over long periods in cold, dark environments (Smetacek 1985).

Benthic diatoms include motile and non-motile species, e.g. epipelic species (growing on mud) usually are motile, while epipsammic species are attached to sand grains. The secretion of extracellular polymeric substances (EPS) that consist of carbohydrate polymers is a major characteristic of motile epipelic diatoms (Little 2000). These algae exude EPS in order to move, and their migration within the sediment is subject to an internal rhythm, which is re-enforced by light and tide. At the beginning of the dark period or high tide, they migrate to deeper sediment layers. One consequence of

EPS production is the stabilization of sediments, leading to decreased erosion and permeability of the sediment. Benthic diatoms are important primary producers in many estuarine, intertidal and shallow-water environments.

The silica cycle

Silicate is an essential nutrient for many phyto- and zooplanktonic microorganisms, e.g. diatoms, silicoflagellates and radiolarians, whose growth is dependent on the availability of dissolved silica (Köhler & Völsgen 1998). The major contribution of dissolved silica to the world ocean comes from rivers (6.1 ± 2.0 teramoles silicon yr^{-1}, approx. 80%). These net inputs are nearly balanced by the net outputs of biogenic silica (7.1 ± 1.8 teramoles silicon yr^{-1}) to the marine sediments (Tréguer et al. 1995). The gross production of biogenic silica in surface waters was estimated to be 240 ± 40 teramoles silicon yr^{-1}. Diatoms contribute to this approximately 90% (Calvert 1966), thus, controlling chiefly the silica cycle in the ocean.

Remineralization and recirculation of biogenic silica is ecologically very important, because the hydrosphere contains only a relatively low amount of silicate due to the low solubility of silicon compounds (Köhler & Völsgen 1998). The frustule of a living diatom is covered by an organic coating that protects the silica frustule against dissolution in the silicate-undersaturated seawater (Lewin 1961). After cell death, the organic matrix is degraded by bacteria, promoting the dissolution of the silica frustule (Bidle & Azam 1999). Subsequently, the dissolution rate is mainly controlled by the state of saturation of the surrounding water (Kamatani & Riley 1979), as the dissolution rate is linear near equilibrium, but rises exponentially with increasing undersaturation (van Cappellen & Qiu 1997). Other factors affecting the dissolution rate are temperature, pH, the exposed surface area of the frustule and the content of metals, especially aluminum, incorporated into the silica frustules (Lewin 1961, Hurd 1972). Bacterial metabolites, like organic acids, can also influence silica remineralization. Assmy (1999) observed an accelerated dissolution of biogenic silica after the addition of 10 mM citrate. Meio- and macrofauna grazing can have both, adverse and beneficial effects on the preservation of the frustules. The incorporation in faecal pellets may move the frustules into a less active solution, but the crushing and breakdown of diatom cells during digestion increases the specific surface area and removes the protective organic coating (Hurd 1972).

Sediment types and sediment-water exchange processes

Mud particles generally accumulate where currents are low, e.g. in bays, estuaries and in sheltered regions (Little 2000). Muddy sediments include all particles less than 63 μm and typically consist of clay with a variable silt content (Brown et al. 1989). Clay particles in muds have electrochemically charged sites that attract ions and allow hydrogen bonding. Therefore, the particles bind together, and muds have cohesive properties, which stabilize the sediment (Little 2000). This allows organisms to create and maintain burrows in the sediment that would be impossible in sand. Another consequence of this stabilization is that mudflats, once deposited, can only be eroded by higher velocities than needed to erode sand. Solute transport in fine-grained, cohesive sediments is mostly driven by diffusion (Huettel et al. 1998) except where sediments are mixed or irrigated by bottom dwelling organisms (Huettel et al. 1996).

Fierce wave action and strong currents generally produce coarse-grained, sandy sediments. The particles are non-cohesive, so unless they are held together by the actions of organisms, the sediment is unstable (Little 2000). Most fauna is infauna, with a high diversity of organisms, but a low biomass. Burrowing is the most widespread adaptation. The classification of sands according to size, based on the Wentworth scale, is very fine (63 to 125 μm), fine (125 to 250 μm), medium (250 to 500 μm), coarse (500 to 1000 μm) and very coarse sand (1000 to 2000 μm) (Brown et al. 1989).

Non-cohesive sandy sediments with a permeability exceeding 10^{-12} m^2 allow pore water flows that effectively transport dissolved and particulate matter through their interstices (Huettel et al. 1998). The permeability is the capability of sediment to permit flow through it. The driving forces for these advective pore water flows are pressure gradients, which are generated when unidirectional or oscillating bottom currents interact with sediment topography, e.g. sediment ripples and biogenic structures (Huettel & Webster 2001). Water is forced into the sediment up- and downstream of the surface structures where the pressure is increased and pore water emerges where the pressure is lowest near the highest point of protruding structures (Huettel & Gust 1992).

Sediment ripples are produced from the interaction of waves or unidirectional currents on a sediment surface, and are ubiquitous on non-cohesive coastal sea beds (Ziebis et al. 1996b), but may also occur on muddy sediments.

The intensity of the advective water flows depends on the sediment permeability (Huettel & Gust 1992), flow velocity (Forster et al. 1996), and topography height (Huettel et al. 1996). The permeability of sediments is determined by a variety of factors, including sand grain size, its sorting and state of consolidation (Hsü 1989), bioturbation (Ziebis et al. 1996a), bacterial and algal exopolymers (Dade et al. 1990, Yallop et al. 1994) and the density and viscosity of the pore fluid (Klute & Dirksen 1986).

Laboratory flume experiments have shown that advective pore water flow enhance the nutrient efflux (Huettel et al. 1998), as well as the oxygen penetration (Ziebis et al. 1996b) and consumption (Forster et al. 1996) in permeable sediments. Thus, advective exchange facilitates a close coupling between the production process in the water column and the mineralization process in the sediment.

Besides diffusion and advection, bioturbation and bioirrigation are important transport processes for solutes in permeable sediment (Huettel 1990). Bioturbation and bioirrigation can increase the oxygenated sediment volume (Forster 1996) and thereby increase nitrification in the sediment (Huettel 1990). Asmus (1986) demonstrated that macrofaunal activity enhances the flux of nitrogen from intertidal sediments, as well as the release of silicate.

Sediments do not only serve as a source, but can also act as sink for regenerated nutrients (Hall et al. 1996). Nutrients may be incorporated into benthic bacterial (Kirchman 1994) or diatom biomass (Marinelli et al. 1998), and phosphate and silicate can be adsorbed onto particles (Tuominen et al. 1999). Therefore, intensive mineralization of organic material can take place in sediments without corresponding nutrient effluxes across the sediment-water interface (Hall et al. 1996).

Organic matter degradation

The greatest portion (>95%) of the organic carbon produced by primary production or imported from the ocean into shelf areas is remineralized in the water column and sediments (de Haas et al. 2002). Thus, most shelf sediments do not accumulate organic matter. Only locally, where conditions favour accumulation, considerable amounts of organic carbon are buried, e.g. in upwelling regions.

The degradation of deposited fresh organic matter in fine-grained sediments occurs to a large extent at the sediment surface, unless mixing through lateral sediment flows (Jenness & Duineveld 1985) or bioturbation (Boudreau 1994) carries the material in

deeper sediment layers. Compared to coarse-grained sediments, the organic matter content of fine-grained sediments is relatively high. This strong relationship between organic matter content and sand grain size is generally accepted to result from the lower accumulation of small organic particles in turbulent shelf areas and the lower specific surface area of coarse grained sediments, having a lower adsorption capability for organic matter (Mayer 1993). The low organic matter content of permeable sediments has led to the view that the biogeochemical activity in these sands also is low (Shum & Sundby 1996). Nevertheless, Grant et al. (1991) have shown, that the oxygen consumption of a coarse-grained shelf sediment was only two to three times lower than the consumption in a nearby fine-grained sediment despite a 20 times higher carbon content. Moreover, several authors have demonstrated in flume studies and *in-situ*, that permeable sediments can advectively filter organic particles, like phytoplankton cells, from the water column (Pilditch et al. 1998, Huettel & Rusch 2000, Rusch & Huettel 2000). Thus, the decomposition of organic matter can be shifted from the sediment surface to deeper sediment layers, preventing resuspension and removal of the material by waves and strong bottom currents, common in the shallow shelf area (Huettel & Rusch 2000). Huettel & Rusch (2000) found that in coarse grained sediments a larger number of algae was degraded than in fine grained sediment when exposed to the same algal concentration in the water column, and concluded, that the penetration of algae into the sands accelerated the degradation process. The effective pore water exchange in sandy sediments seems to enhance the decomposition of the trapped organic material. Consequently, the contribution of sandy sediments to the degradation of organic matter in the continental shelf may be larger than inferred from the low organic content (Shum & Sundby 1996) and advective filtration of planktonic algae and suspended organic particles could be of general importance for the cycling of matter.

Experimental setup and general methods

All experiments conduced for this thesis, were carried out in acrylic cylindrical chambers (31 cm height, 19 cm inner diameter) (Fig. 1), which were covered by black foil preventing any light penetration to the incubated water and sediments. A horizontal disk (17 cm diameter), rotating approximately 10 cm above the sediment surface at 20 rpm stirred the water inside each chamber.

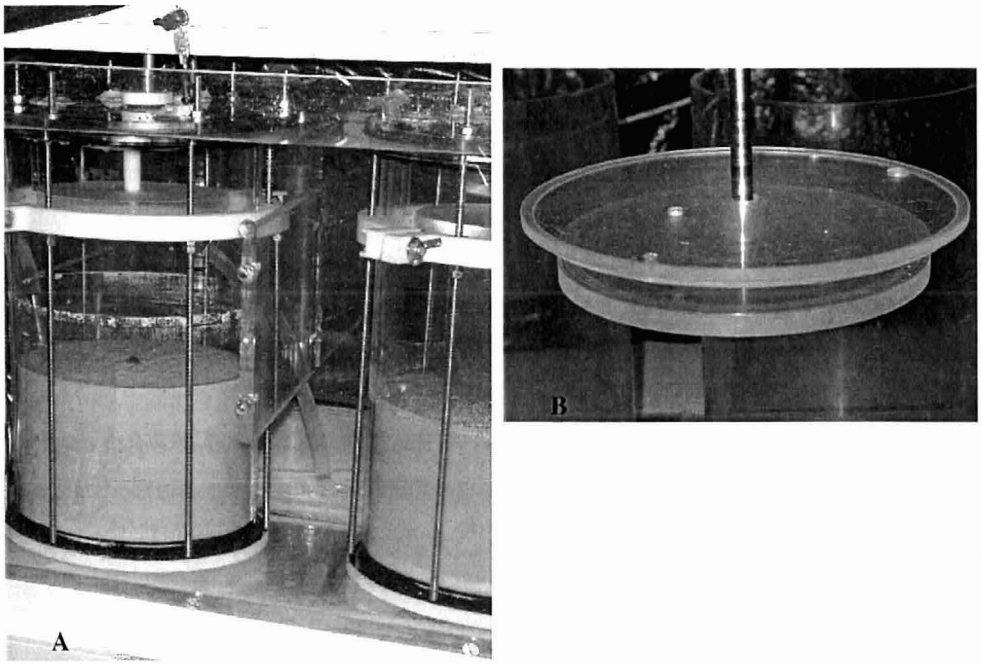

Fig 1. (A) Stirred chamber filled with sediment. (B) Detail picture of the chamber lid with the attached disk.

The rotating water produces a radial pressure gradient with lowest pressures in the center and highest at the outer rim of the chamber. The magnitude of this pressure gradient (approx. 1.5 Pa cm^{-1}) is comparable to that developing in the natural environment at sediment ripples of 2 cm height exposed to relatively slow boundary layer flow of 10 cm s^{-1} at 10 cm above the sediment-water interface (Huettel & Rusch 2000) (Fig. 2). This pressure gradient generates advective pore water flows in permeable sediments. The water is forced into the sediments at the outer rim of the chamber, and flows along curved paths towards the center, where it is released from the sediment.

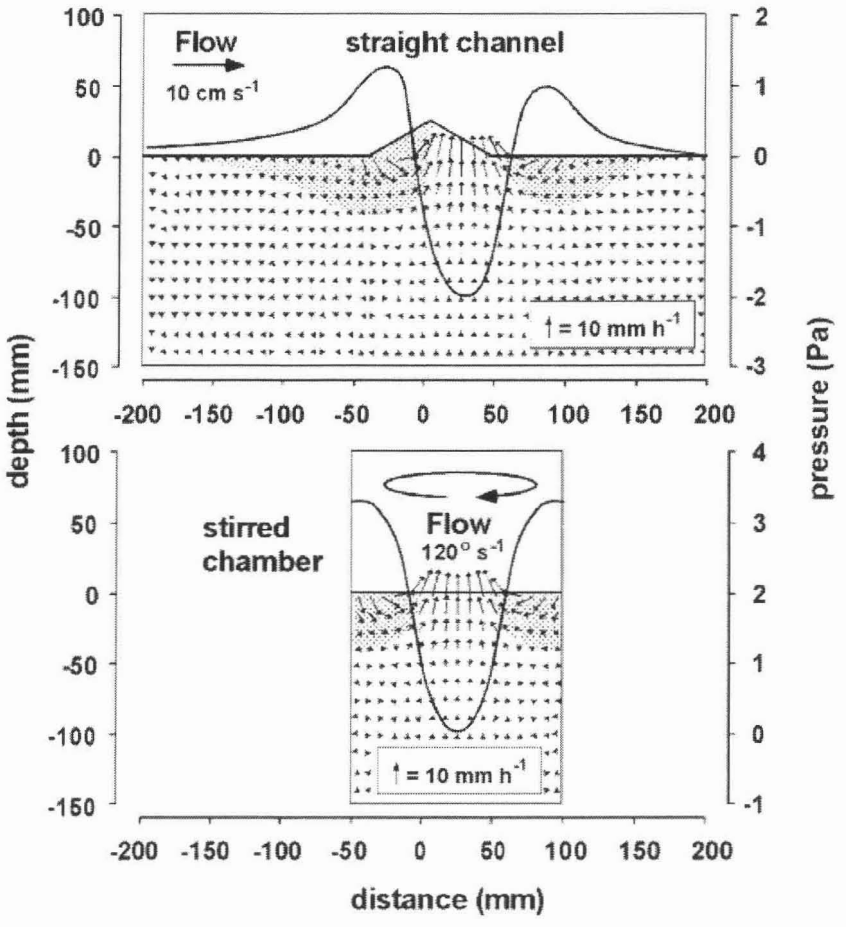

Fig. 2. Schematic of the advective pore water flow field under sediment topography exposed to unidirectional flow in a straight open channel and in sediment exposed to a rotating water column in a stirred chamber. Solid curved line: pressure distribution at the sediment-water interface; shaded areas: water intrusion zones; arrows: direction and magnitude of advective pore water flows. Figure taken from Huettel & Rusch (2000), with permission.

For the *in-situ* and on-board experiments, the chambers were deployed and recovered by divers. A motor device drove the discs in the stirred chambers. The motor was attached on a framework that also served for the transportation of the chambers (Fig. 3).

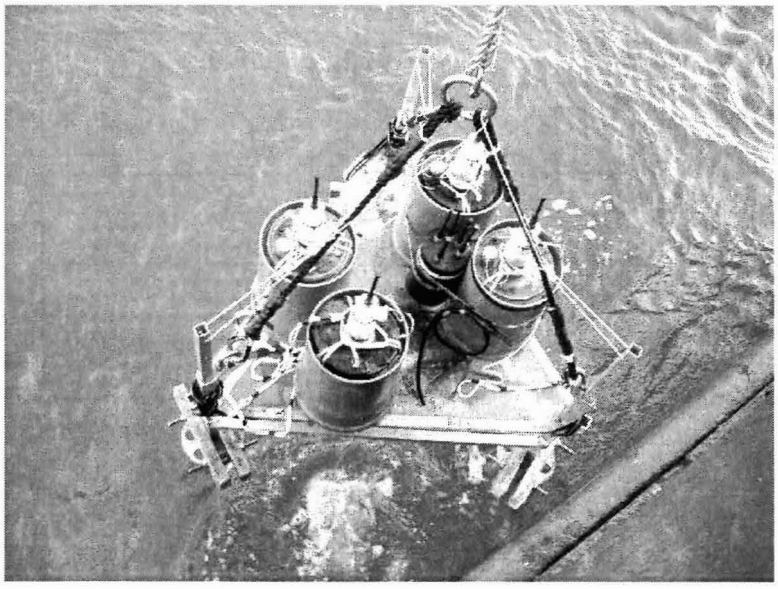

Fig. 3. Framework with the motor device and 4 brackets for the transportation of the experimental chambers. For the incubations, the motor was connected by wires to the single chambers in order to operate the rotating disk.

Altogether, we used three different diatom species for the chamber incubations: *Skeletonema costatum* and *Thalassiosira rotula* (Thalassiosiraceae, Centrales) for the laboratory chamber experiments (Chapter 2); and *Ditylum brightwellii* (Biddulphiales, Centrales) for the *in-situ* experiments (Chapter 3 and 4) (Fig. 4). All diatoms are planktonic, common species in the North Sea and have been reported to form blooms in spring (Raabe et al. 1997). In *S. costatum* (diameter 5 to 10 µm) and *T. rotula* (diameter 8 to 55 µm), single cells are linked by intercellular silica rods (*S. costatum*) or gelatinous threads (*T. rotula*) forming chains (Smayda 1970). These can reach a length of 800 µm in *S. costatum* (Karp-Boss & Jumars 1998). *T. rotula* chains are typically shorter. *D. brightwellii* cells have a diameter between 25 and 100 µm and live solitary or form short chains.

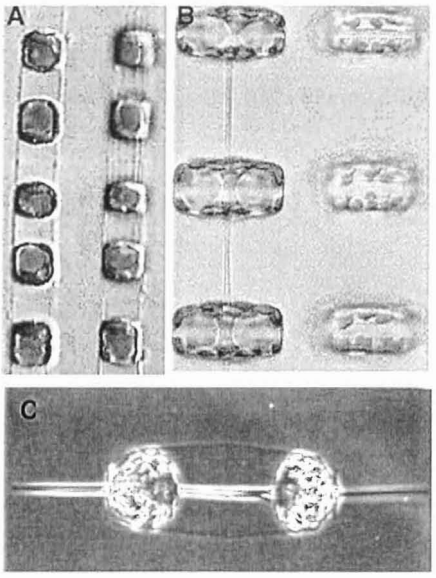

Fig. 4. (A) *Skeletonema costatum* chain at different focus. (B) *Thalassiosira rotula* chain at different focus. (C) *Ditylum brightwellii* cell, picture taken from Round et al. (1990), with permission. Mats Kuylenstierna provided pictures (A) and (B) (http: //www.marbot.gu.se/sss/ssshome.htm, with permission).

The *in-situ* experiments presented in this thesis were part of a project initiated by Ursula Witte at the Max Planck Institute for Marine Microbiology. This project was focused on the degradation and uptake of particulate organic matter by benthic organisms in subtidal sandy North Sea sediments of different permeabilities. In order to follow the pathway of organic carbon in the sediments, the diatom carbon was enriched with the stable carbon isotope ^{13}C. The labeled diatom carbon differs significantly from the natural carbon isotopic signature of phytoplankton, and several studies have proven successfully use of ^{13}C-labeled organic matter in tracking the pathways of carbon within the sediment, pore water and benthic organisms (Blair et al. 1996, Levin et al. 1997, Levin et al. 1999, Middelburg et al. 2000, Moodley et al. 2000).

As a part of this study, my work was focused on the transport of the added algal carbon ($PO^{13}C$, cell counts) into the different sediments (Chapter 3), and on the decomposition of the organic material into inorganic nutrients (Chapter 4) and DOC (Chapter 3). Within this project, the total remineralization of the algal carbon to $^{13}CO_2$

(Witte et al. unpublished data) and the incorporation of algal carbon into bacterial phospholipid-derived fatty acids (Buehring et al. unpublished data), macrofauna (Kamp 2002) and meiofauna (Witte unpublished data) were investigated (Fig. 5).

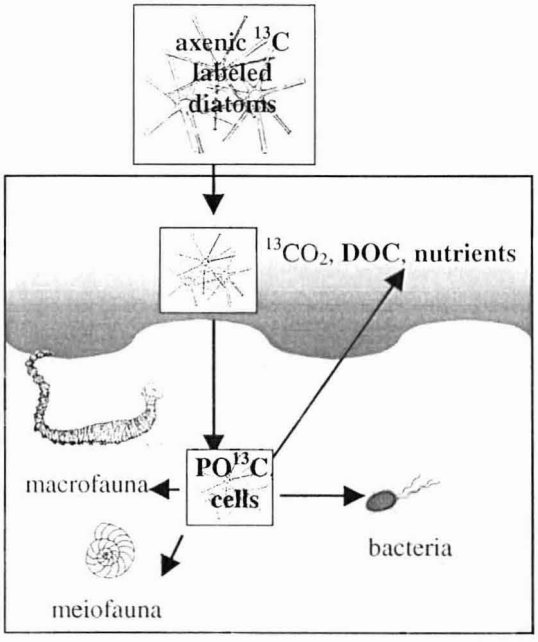

Fig. 5. Schematic of the *in-situ* chamber experiments on subtidal North Sea sediments. Blue front: investigated in this thesis.

For the determination of the carbon isotope ratios, samples were combusted in a CE Instruments™ CHN-Analyzer and the evolved CO_2 was passed online via a ThermoFinnigan™ interface to a ThermoFinnigan™ isotope-ratio mass spectrometer (IRMS) in a continuous flow of helium. An IRMS measures the isotopic ratios between the heavy and light isotopes (e.g. $^{13}C/^{12}C$) and results are always calibrated against an international standard.

OBJECTIVES OF THIS THESIS

The aim of this thesis was to reveal the importance of permeable shelf sediments for the degradation of planktonic diatoms with focus on the associated nutrient regeneration.

In the first study (Chapter 2) the details of the transport and spatial degradation of chain-forming planktonic diatoms in sandy sediments of different permeabilities were investigated in the laboratory. The working hypotheses were that coarser sediments filter more diatoms from the water column, and that the dissolution of the trapped diatom frustules would be more effective in coarser sands due to the strong advective solute exchange. Advective solute exchange rates that increase with increasing permeability prevent the build up of dissolved silica concentrations in the pore water, thereby maintaining lowest pore water silicate saturation and ensuing highest opal dissolution rates of the trapped diatoms.

In order to test the results of the laboratory experiments *in-situ*, chamber experiments on subtidal sandy North Sea sediments were carried out during three cruises. These experiments had three main goals. The first was to investigate the interfacial transport rates of ^{13}C labeled diatoms into three sandy sediments with different permeabilities. Second, to assess if the incorporation of planktonic diatoms occurs in this high-energy environment (Chapter 3). The third was focused on the remineralization and nutrient release from the added diatoms in the different sands (Chapter 4). These data were used to interpret the seasonal nutrient and phytoplankton dynamics in the water column and the response to these variations in the nutrient pore water concentrations of these three different permeable sediments. The working hypotheses of the *in-situ* study were first, that advective pore water flows provide a fast pathway of suspended diatoms into deeper layers of sandy sediments, thus, preventing the resuspension from the sediment surface by strong bottom currents and waves. Second, that high flushing rates in sands accelerate the remineralization of the trapped diatoms, resulting in a fast release and cycling of nutrients back to the primary production in the water column. The results may be helpful for a better understanding of the significance of permeable sediments for the recycling of carbon and nutrients in shelf environments.

PUBLICATIONS OUTLINE

This thesis includes four articles. Two of them have been submitted to international journals and two will be submitted soon. One of the articles investigated the details of the transport and degradation of chain-forming planktonic diatoms in permeable sediments under laboratory conditions (Chapter 2). Two of the articles investigate the importance of permeable shelf sediments for the degradation of planktonic diatoms and the associated nutrient regeneration *in-situ* (Chapter 3 and 4). The other article gives an overview of sediment-water exchange processes and their impact on biogeochemical processes (Chapter 5).

1) Ehrenhauß S. and Huettel M.

Advective transport and decomposition of chain-forming planktonic diatoms in permeable sediments

This study was initiated by M. Huettel and S. Ehrenhauß who also carried out the experiments. S. Ehrenhauß evaluated the data and wrote the manuscript with editorial help and input by M. Huettel. This article has been submitted to Journal of Sea Research.

2) Ehrenhauß S., Witte U., Buehring S.I. and Huettel M.

Effect of advective pore water transport on distribution and degradation of diatoms in permeable North Sea sediments

M. Huettel and U. Witte initiated this study. Experiments were carried out by S. I. Buehring, S. Ehrenhauß and A. Kamp. S. Ehrenhauß evaluated the data and wrote the manuscript with editorial help and input by M. Huettel and U. Witte. This article has been submitted to Marine Ecology Progress Series.

3) Ehrenhauß S., Witte U., Kamp A., Janssen F. and Huettel M.

Decomposition of diatoms and nutrient dynamics in permeable North Sea sediments

M. Huettel and U. Witte initiated this study. Experiments were carried out by S.I. Buehring, S. Ehrenhauß, A. Kamp and F. Janssen. S. Ehrenhauß evaluated the data and wrote the manuscript with editorial help and input by M. Huettel, U. Witte and F. Janssen. This article has been submitted to Continental Shelf Research.

4) Huettel M., Røy H., Precht E. and Ehrenhauß S.

Hydrodynamical impact on biogeochemical processes in aquatic sediments

M. Huettel wrote the manuscript and included some results of H. Røy, E. Precht and S. Ehrenhauß. This article has been accepted for publication in Hydrobiologia.

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Chapter 2

Advective transport and decomposition of chain-forming planktonic diatoms in permeable sediments

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ABSTRACT

In laboratory chamber experiments we demonstrate that permeable sediments (>7 × 10^{-12} m^2) exposed to boundary flows filter chain-forming coastal bloom diatoms (*Skeletonema costatum* and *Thalassiosira rotula*) from the water column, causing rapid transfer of fresh organic particulate matter into sediment layers as deep as 5 cm within 72 h. The penetration depth of the diatoms depends on the permeability of the bed and the length of the chains. The fast advective transfer of phytoplankton cells into sandy sediments may be an important process facilitating organic matter uptake and preventing resuspension of deposited organic material in high-energy coastal environments. High advective flushing rates in medium- and coarse-grained sandy sediments enhanced the remineralization of the trapped diatoms (2300 to 3200 μmol C m^{-2} d^{-1}), stimulated benthic oxygen consumption (2300 to 3000 μmol O_2 m^{-2} d^{-1}), as well as nitrification (up to 20 μmol NO_3^- m^{-2} d^{-1}), relative to sediment where diffusion dominated the solute exchange. Advective solute exchange rates that increase with increasing permeability prevent the build up of dissolved silica concentrations in the pore water, thereby maintaining lowest pore water silicate saturation and ensuing highest opal dissolution rates (95 to 101 μmol $Si(OH)_4$ m^{-2} d^{-1}) of the trapped diatoms. Our results suggest that advective filtration of planktonic diatoms into permeable sediments can boost mineralization and cycling of organic matter in high energetic shelf areas.

KEY WORDS

Permeable sediments – advection – diatoms – silicon cycle – sediment-water exchanges – benthic filtration

INTRODUCTION

This contribution addresses the decomposition of planktonic diatoms in permeable shelf sands with emphasis on the associated biogenic silicate dissolution.

The main organic matter input to shallow shelf sediments is the deposition of the local phytoplankton community (Jørgensen 1996). Typically, nutrient-rich coastal zones, are inhabited by siliceous phytoplankton, in most cases these are diatoms (Schrader & Schuette 1981). In temperate latitudes, as the North Sea, diatom blooms develop in spring (Reid et al. 1990). The majority of coastal bloom diatoms are small, spiny, chain-forming and have thin frustules, in contrast to oceanic diatoms that have many large, smooth-walled representatives (Smetacek 1985). Reduction of grazing pressure (Smayda 1970) may be the main reason for colony formation and spines of coastal diatoms, however, these characteristics may also reduce benthic filtration, as permeable sediments, which cover large areas of the shallow continental shelves (Emery 1968), may advectively filter approximately 100 L m^{-2} d^{-1} (Precht & Huettel 2003).

Diatoms need silicon to build up their frustules (96.5% SiO_2) and take up silicate ($Si(OH)_4$) from the surrounding seawater at a ratio of 1:1 to nitrogen (Lewin 1965, Brzezinski 1985). Usually silicate depletion in the seawater concludes the spring bloom, as the remineralization of biogenic silica by inorganic dissolution (Schrader & Schuette 1981) is much slower than the decomposition of organic bonded nitrogen and phosphorus. Upon nutrient depletion diatom sinking rates can increase drastically (Smetacek 1985), and due to the shallow depths and low impact of zooplankton grazing on the spring bloom (Wollast 1991), up to 50% of the built up phytoplankton biomass reaches the sea bed (Jørgensen et al. 1990).

In areas dominated by fine-grained sediments, the degradation of organic matter takes place to a large extent at the sediment surface, unless mixing through lateral sediment flows (Jenness & Duineveld 1985) or bioturbation (Boudreau 1994) carries the deposited material in deeper layers. Likewise, solute transport in such fine-grained, cohesive sediments is mostly driven by diffusion except where sediment is mixed or irrigated by bottom dwelling organisms (Huettel et al. 1996).

In contrast, sediments with a permeability exceeding 10^{-12} m^2 allow pore water flows that effectively transport dissolved and particulate matter through the interstitial space (Huettel et al. 1998). This pressure-driven advective pore water flow is generated when bottom currents interact with sediment topography (Huettel et al. 1996), like

biogenic structures and sediment ripples, which are ubiquitous on coastal sea beds (Ziebis et al. 1996). The intensity of the interfacial water flows depends on sediment permeability (Huettel & Gust 1992a), flow velocity (Forster et al. 1996), and topography height (Huettel et al. 1996).

Flume experiments have shown that advective pore water flows enhance the nutrient efflux (Huettel et al. 1998), as well as the oxygen penetration (Ziebis et al. 1996) and consumption (Forster et al. 1996) in permeable sediments. Advective transport of phytoplankton into permeable beds has been demonstrated in flume studies and *in-situ* (Pilditch et al. 1998, Huettel & Rusch 2000). Through this process, the mineralization of the organic matter can be shifted from the sediment surface to deeper sediment layers, preventing resuspension and removal of the material by waves and strong bottom currents, common in the shallow shelf area (Huettel & Rusch 2000).

Permeable sediments usually contain a relatively small amount of organic material (Shum & Sundby 1996). The strong relationship between organic matter content and sand grain size is generally accepted to result from the lower accumulation of small organic particles in turbulent shelf areas and the lower specific surface area of coarse grained sediments, having a lower adsorption capability for organic matter (Mayer 1993). However, Jenness & Duineveld (1985) demonstrated that considerable amounts of phytoplankton can be incorporated into sandy sediments without simultaneous mud deposition, and Huettel & Rusch (2000) demonstrated with *in-situ* experiments in intertidal sand flats that permeable sediments can efficiently filter organic particles from the water column. Consequently, the contribution of sandy sediments to the degradation of organic matter in the continental shelf may have been underestimated and advective filtration of planktonic algae and suspended organic particles could be of general importance for the cycling of matter.

Remineralization and recirculation of biogenic silica is ecologically very important, because the hydrosphere contains only a relatively low amount of silicate due to the low solubility of silicon compounds (Köhler & Völsgen 1998). The frustule of a living diatom is enclosed by an organic coating that protects the silica frustule against dissolution in the silicate-undersaturated seawater (Lewin 1961). After cell death, the organic matrix is degraded by bacteria, promoting the dissolution of the silica frustule (Bidle & Azam 1999). Subsequently, the dissolution of the diatom frustule is mainly a function of temperature, pH, silicate saturation of the surrounding water and the exposed surface area of the frustule (Lewin 1961, Hurd 1972). The dissolution rate of

biogenic silica is linear near equilibrium, but rises exponentially with increasing undersaturation (van Cappellen & Qiu 1997).

In-situ chamber experiments with ^{13}C-labeled diatoms on permeable sediments in the southern German Bight revealed increasing advective transport of diatoms into natural sediments with increasing permeability (Ehrenhauß et al. 2003a). Furthermore Ehrenhauß et al. (2003a) reported that planktonic diatom frustules, e.g. *Coscinodiscus* spp, were present in these sands indicating that phytoplankton can be incorporated into the sediment in this highly dynamic area.

This laboratory work was initiated to investigate the details of the transport and degradation of two typical chain-forming bloom diatoms in permeable sediments. The two major goals of this study were: first, to assess the efficiency of sandy sediments of different permeabilities in trapping living planktonic diatoms. The second goal was to determine how the different advective pore water exchange rates in these sediments affect the mineralization of the diatoms in the sands. Our working hypotheses were that coarser sands filter more diatoms from the water column, and that the strong advective solute exchange in these sediments enhances the dissolution of biogenic silicate relative to the dissolution in less permeable, fine-grained sediments. In order to test these hypotheses, we conducted laboratory chamber experiments with sandy sediments of different permeabilities.

MATERIALS AND METHODS

Experiments

Two laboratory chamber experiments were conducted: The first chamber experiment focused on the interfacial transport of living diatoms into six sediments with different permeabilities, and the second experiment addressed the degradation of dead diatom cells in the permeable sands (Table 1).

In the *first chamber experiment*, the penetration of the planktonic diatom *Skeletonema costatum* (Bacillariophyceae, Thalassiosiraceae, Fig. 1) into sieved sands of various grain sizes was assessed.

Table 1. Sediment characteristics and pore water solute exchange of the sediments used for both chamber experiments. For the porosity, pore size and sediment POC, averages (± s.d.) are given. The volumes of water exchange were calculated from the Fluorescein concentration decrease within the first 10 h. Average penetration depth of the tracer was calculated from the concentration changes after 10 h and the porosity data. n.a.: not analyzed.

1.experiment Sand type	Sand grain size (μm)	Permeability k ($\times 10^{-12}$ m^2)	Porosity (vol. %)	Pore size diameter (μm)	Water exchange (L m^{-2} d^{-1})	Fluorescein penetration depth after 10 h (cm)	Sediment POC (% dry mass)
Very coarse	2000-1000	432.5	34 (± 2.0)	188 (± 92)	18	2.2	n.a.
Coarse	1000-500	200.5	35 (± 1.5)	97 (± 33)	20	2.4	n.a.
Medium	500-250	24.3	35 (± 0.4)	53 (± 20)	12	1.4	n.a.
Fine	250-125	22.6	36 (± 0.8)	30 (± 11)	8	1.0	n.a.
Very fine	125-63	7.6	33 (± 1.5)	54 (± 32)	0	0.0	n.a.
Impermeable	300-90 + 20% caolinite	3.8	32 (± 3.3)	-	-1	-0.1	n.a.
2. experiment Sand type							
Coarse	1000-500	242.4	n.a.	n.a.	n.a.	n.a.	0.027 (± 0.004)
Medium	500-250	45.0	n.a.	n.a.	n.a.	n.a.	0.023 (± 0.001)
Very fine	125-63	7.4	n.a.	n.a.	n.a.	n.a.	0.029 (± 0.005)

We used pre-cleaned quartz sands originating from the Weser River estuary, which were sieved prior to the experiment (Table 1). Each sand was treated with 1.25 M HCl for one hour to remove possible traces of organic matter, then washed thoroughly with MilliQ-water and dried at 90°C. 3 L of each sediment were inserted into cylindrical chambers (30 cm height, 19 cm inner diameter), which then were carefully filled with 1.5 L 0.2 µm filtered North Sea seawater and 1.5 L of a 10 day exponentially grown *S. costatum* culture. The diatom *S. costatum* was isolated near Sylt in February 1997 and grown at 15°C in F/2-media (Guillard & Ryther 1962) with a salinity of 31 and a pH of 7.8. The final salinity in the chambers was 31 and the pH at the beginning of the experiment was 8.0. Between the lid of the chambers and the water surfaces an airspace of 4 cm was left to permit gas exchange. To inhibit photosynthesis and replication of the diatoms all chambers were covered by black foil preventing light penetration to the incubated water and sediments. A horizontal disk (17 cm diameter), rotating approx. 7 cm above the sediment surface with 20 rpm stirred the water inside each chamber. The rotating water produces a radial pressure field with lowest pressure at the center of the sediment surface and highest pressure at the outer rim (Huettel & Gust 1992b). The magnitude of the pressure gradient (ca. 1.5 Pa cm^{-1}) is comparable to that developing in the natural environment at small sediment topography (protrusion of 2.5 cm height, 9 cm base width) exposed to relatively slow boundary layer flow (10 cm s^{-1} at 8 cm above the sediment-water interface) (Huettel & Gust 1992a, Huettel & Rusch 2000). The pressure gradient in the chamber generates advective pore water flows in incubated permeable sediments. 6 unstirred chambers with the same sediments served as controls.

The experiment ran for 3 days. During this time, water samples for diatom numbers were taken at regular time intervals. At the end of the experiment, sediment cores for the assessment of diatom penetration, porosity and permeability were taken. For assessment of diatom penetration, one core was taken at the outer rim of each chamber with a cut off 60 ml syringe, expecting the highest penetration of algae in this zone according to the pressure regime. The sediments then were sliced in intervals of 2×0.5 cm and 5×1.0 cm (very coarse and coarse sand), 5×0.2 cm, 2×0.5 cm and 3×1.0 cm (medium and fine sand) and 6×0.1 cm, 2×0.2 cm and 2×1.0 cm (very fine and impermeable sand).

In order to quantify the advective fluid exchange between the sediment and water column in the stirred chambers, we conducted a tracer experiment with Fluorescein dye. Fluorescein dissolves in the water but does not adsorb to the quartz grains. The sodium Fluorescein solution was added to the water column above the same six sediments to produce final concentrations of 1.25 µM. The experiment ran for 3 days under the same conditions as the first experiment. During this time, water samples for Fluorescein concentration measurements were taken in regular time intervals.

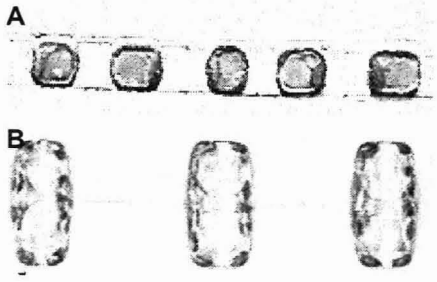

Figure 1. (A) *Skeletonema costatum* chain. (B) *Thalassiosira rotula* chain. Both pictures were provided by Mats Kuylenstierna (http://www.marbot.gu.se/sss/ssshome.htm)

In the *second chamber experiment,* we investigated the remineralization of the planktonic diatom *Thalassiosira rotula* (Bacillariophyceae, Thalassiosiraceae, Fig. 1) in sediments of different permeabilities.

Prior to the experiment, the quartz sand was sieved (Table 1), cleaned and pre-incubated for 6 weeks in the dark with 0.8 µm filtered North Sea water of a salinity of 32 to allow bacterial colonization of the sand grains. A mixture of carbohydrates and amino acids as used for the cultivation of pelagic North Sea bacteria (Eilers et al. 2000) was added to the seawater in order to enhance the growth of the bacteria.

Prior to filling 3 L of the various sediments into the chambers, samples for bacterial abundance and particulate organic carbon were taken. The bacterial counts revealed 3.32 ± 0.09, 2.51 ± 0.21 and $1.74 \pm 0.16 \times 10^6$ cells per ml wet sediment for the very fine, medium and coarse sand respectively. 3 unstirred chambers with the same set of sieved sediments served as controls. All 6 chambers were filled with the same 0.8 µm filtered North Sea water and closed with a gas-tight lid such that no air was left in the chambers.

The diatom *T. rotula* was cultivated as described for *S. costatum* and harvested by centrifugation (404 **g**, 4 min). The concentrated material was rinsed with an isotonic sodium chloride solution to remove any remaining nutrients and centrifuged again. Samples for dry mass, particulate organic carbon and nitrogen (POC/PON), dissolved organic carbon (DOC) and nutrients were taken, and the algal material was stored frozen until use. This treatment killed the cells. Before the addition of the algae to the chambers, the sediments were incubated for one week to study the oxygen consumption and nutrient fluxes without organic enrichment.

Then, 60 ml of the prepared diatom material was added to each chamber, which corresponded to 48023 ± 1175 µmol C m^{-2} (32% as DOC) and 6003 ± 147 µmol N m^{-2}. Assuming an average N:Si:P mole ratio of 16:16:1 of marine diatoms (Brzezinski 1985), the added silicon was equivalent to the added amount of nitrogen, and the added amount of phosphorus corresponded to 375 µmol P m^{-2}. The experiment ran in the dark for 7 d at 15°C and a salinity of 32. During this time water samples for diatom and bacteria numbers, nutrients, pH, dissolved inorganic carbon (DIC) and DOC were taken at regular time intervals. The sampled water volume was replaced by 0.2 µm filtered seawater. Before sampling, the water columns of the unstirred control chambers were carefully mixed by turning the disk three times for one rotation alternately in both directions. Additionally, the oxygen consumption in the water columns of the chambers was measured with oxygen micro-optodes and Winkler titration. At the end of the experiment, one core from each chamber was taken for the permeability measurement, and the rest of the sediments were sliced in intervals of 2 × 0.5 cm, 5 × 1.0 cm and 1 × 5.0 cm and every depth interval was carefully mixed. From this homogenized sediment, samples for diatom and bacterial numbers pore water nutrient and DIC concentrations were taken.

Analytical techniques

Water samples for diatom numbers were preserved with hexamethylenetetramine buffered formaldehyde (end concentration 2%) and Lugol solution (end concentration 1%), and kept refrigerated in dark glass bottles until analysis. To separate the algae from the sand grains, 1 ml sediment was resuspended two times in 5 ml 0.2 µm filtered seawater, containing formaldehyde and Lugol in the same final concentration as for the water samples. The supernatant was collected after 30 s of deposition time

and filtered on black membrane filters (0.2 µm pores). All diatom cells of 20 randomly chosen counting grids of three parallel filters per sample were counted under a Zeiss™ Axiophot epifluorescence microscope (excitation wave length 510-560 nm, magnification 1300 ×).

To test the extraction efficiencies, a known concentration of the *S. costatum* (first experiment) or *T. rotula* culture (second experiment) respectively, was mixed into the various sediments and incubated for 3 (first experiment) or 7 days (second experiment) in the dark. Diatom cells were extracted with 0.2 µm filtered seawater as described above. Extraction efficiencies for *S. costatum* frustules were 99 ± 11% (2000-1000 µm sand), 93 ± 12% (1000-500 µm sand), 89 ± 11% (500-250 µm sand), 89 ± 13% (250-125 µm sand), 99 ± 12% (125-63 µm sand) and 85 ± 15% (impermeable sand). Extraction efficiencies for *T. rotula* frustules were 85 ± 10% (63-125 µm sand), 92 ± 14% (250-500 µm sand) or 94 ± 9% for the 500-1000 µm sand respectively. The high extraction efficiencies do not indicate degradation of algal material. This is caused by the slow dissolution of biogenic silica, leading to a longer residence time of frustules within the sediment compared to organic carbon and nitrogen.

For the dry mass determination of the *T. rotula* culture, 1 ml sample was filtered on pre-combusted (500°C, 6 h), pre-weighed GF-F filters, rinsed with distilled water to remove the sodium chloride, dried for 24 h at 60°C and weighed again.

Samples for the POC/PON content of the culture were filtered on pre-combusted GF-F filters, pre-treated with HCl to remove the bicarbonate and dried at 60°C. Samples for sediment POC were dried at 60°C, pulverized, pre-treated with HCl, dried again, and subsamples were exactly weighed into tin cups. The particulate carbon and nitrogen contents were measured using a Fisons™ NA1500 elemental analyzer.

For the bacteria counts, water samples were preserved with formaldehyde (end concentration 4%) and kept at 4°C. Sediment samples were preserved by adding 2 ml sediment to 8 ml of sodium chloride solution (32 g L^{-1}) containing formaldehyde (end concentration 4%) and stored at 4°C. Bacterial cells were dislodged from the sand grains by ultrasonic treatment (Epstein & Rossel 1995) for 100 s (fine and medium sediment) or 300 s (coarse sediment) respectively. Bacteria were concentrated on black membrane filters (0.2 µm pores) and stained with DAPI for 10 min. 10 randomly chosen counting grids of two parallel filters per sample were counted under

a Zeiss™ Axiophot epifluorescence microscope (excitation wave length 365 nm, magnification 1300 ×).

The permeability k of the different sediments was determined with the constant head method (Klute & Dirksen 1986). Sediment porosities were calculated from weight loss of wet sediment slices after drying at 60°C for 1 week.

The average pore size of the different sediments was assessed by taking a digital stereolense picture of one sand layer, projecting the picture with a beamer, and measuring interstices between the sand grains with a ruler.

Samples for nutrients were filtered (0.2 µm) and preserved with mercury chloride at an end concentration of 0.01% and kept refrigerated until analysis. Pore water for nutrient analysis was obtained by centrifugation (2772 **g**, 10 min) of 20 cm^3 of each sediment slice using centrifuge vials with 2 compartments separated by cellulose-acetate filters (0.2 µm), and treated as described for the water samples. Silicate (810 nm), phosphate (880 nm), ammonia (630 nm), nitrate and nitrite (540 nm) in the seawater were determined spectrophotometrically with a 5-channel Skalar™ Continuous-Flow-Analyzer. The chemistry of the reactions was that described in Grasshoff et al. (1999).

Water samples for DOC were filtered through pre-combusted GF-F filters into likewise pre-combusted glass vials and stored frozen until analysis. The DOC concentrations were measured by high-temperature catalytic oxidation using a Shimadzu™ TOC-5050A analyzer. Three parallels were measured per sample.

For DIC analysis, 1.5 ml aliquots were filtered (0.45 µm pores) into gas-tight glass vials containing 100 µL mercury chloride and kept at 4°C. For the sediment centrifugation (2772 **g**, 10 min), pre-combusted GF-F filters were used, and the retained pore water was preserved as described for the water samples. The DIC concentration was measured using a flow-injection system. For details see Hall & Aller (1992). Three parallels were measured per sample.

The principle of the oxygen measurement with micro-optodes was described by Klimant et al. (1995) and details about phase angle based measurements and temperature sensitivity can be found in Holst et al. (1997). Because the optodes were permanently installed in the chambers, the calibration of the sensors was only preformed at the beginning and end of the experiment. For confirmation of the optode measurements, water samples for the determination of oxygen after the *Winkler*

method (Grasshoff et al. 1999) were taken during the experiment. This is necessary, because the intensity of the optode signal can decrease over time.

The Fluorescein concentrations in the water of the tracer experiment were determined with a Hitachi™ Fluorescence Spectrophotometer f-2000 (Excitation: 490 nm; Emmission: 515 nm).

RESULTS

Trapping of planktonic diatoms by sediments of different permeabilities

In the first experiment, *S. costatum* cell numbers in the water columns of all chambers decreased exponentially within the first 24 hours and almost no cells could be found in the water after the first day.

The rate of decrease of *S. costatum* cells in the water column was much larger in the stirred chambers with both coarse sands, compared to the unstirred controls (Table 2). For the chambers with medium, fine and very fine sand no difference between the stirred and unstirred chambers could be observed. For impermeable sediment, the loss of diatom cells from the water column was most pronounced in the unstirred control.

Table 2. First chamber experiment: Decrease of *Skeletonema costatum* cells, measured in the water column. The decrease of algal cells is given for the first three hours of the experiment.

Sand type	Stirred (+/-)	Algal concentration decrease ($\times 10^4$ cells ml^{-1} h^{-1})
Very coarse	-	1.0
	+	3.3
Coarse	-	1.4
	+	4.0
Medium	-	0.8
	+	0.9
Fine	-	1.0
	+	1.3
Very fine	-	1.2
	+	1.2
Impermeable	-	4.0
	+	1.2

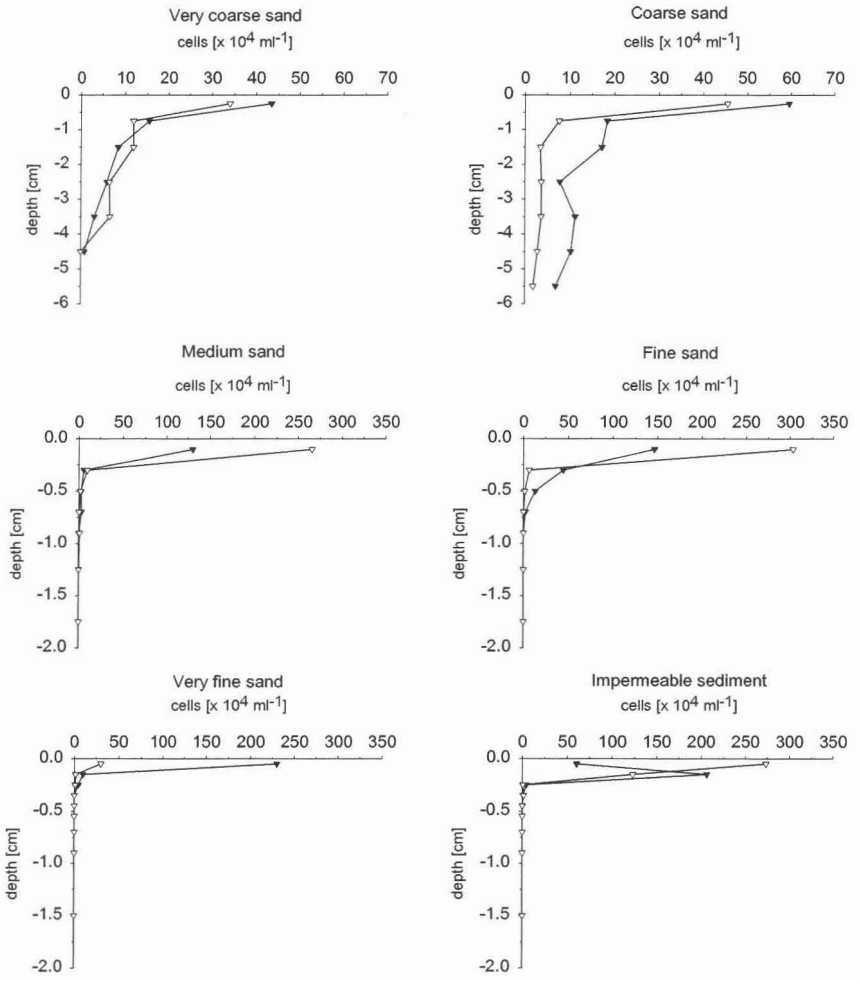

Figure 2. First chamber experiment: Distribution of *Skeletonema costatum* in the sediment of the unstirred (empty triangles) and stirred (filled triangles) chambers after an incubation time of 3 d. No cells were found in the water column. Please note different scales.

Algal penetration depth (Fig. 2) into the different sediments increased with sand grain size and sediment permeability, with exception of the chamber with very coarse sand. Here the algae were transported down to 4.5 cm and no difference could be found between the stirred and unstirred chambers. In the stirred and unstirred chambers with coarse sand algae penetrated down to 5.5 cm (total sampling depth), however, more algae reached the layers below 1.5 cm depth in the stirred chamber. In the medium

and fine sand, the penetration depth of the diatoms was much smaller than in coarse sand: 0.7 cm for the stirred and 0.5 cm for the unstirred chambers. In very fine sand and impermeable sediment the diatoms accumulated in a fluffy-layer on the sediment surface and no algae could be found below 0.3 cm.

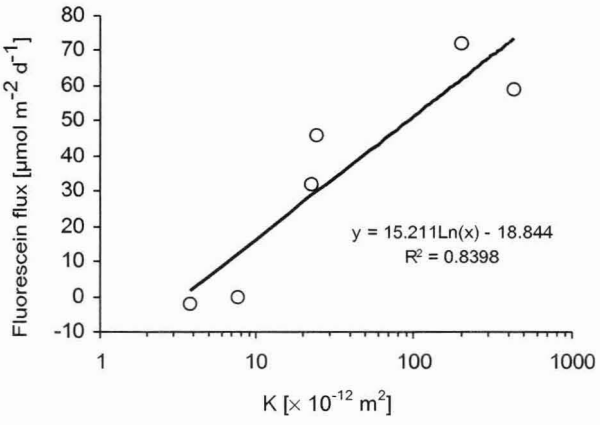

Figure 3. First chamber experiment: Fluorescein flux into the sediments incubated in the stirred chambers vs. permeability.

Solute exchange between sediment and water column, measured as decrease of fluorescein concentrations in the water, showed a positive correlation with the permeabilities of the different sediments, with exception of very coarse sand that did not follow the trend of the curve (Table 1, Fig. 3). Highest pore water exchange (20 L m^{-2} d^{-1}) and penetration depth of the tracer (2.4 cm after 10 h) was recorded in coarse sand. For impermeable and fine sand no advective exchange could be observed.

The transport of the diatom *T. rotula* into the different sands of the second experiment also increased with permeability (Fig. 4), and penetration depths were always higher in the stirred chambers. In the latter, maximal penetration depth was 3.5 cm (coarse sand), 1.5 cm (medium sand) and 0.8 cm (very fine sand) respectively. The transport of the diatoms into the sediment of the unstirred chambers was much smaller: 1.5 cm for coarse sand, 0.8 cm for medium sand and 0.3 for very fine sand.

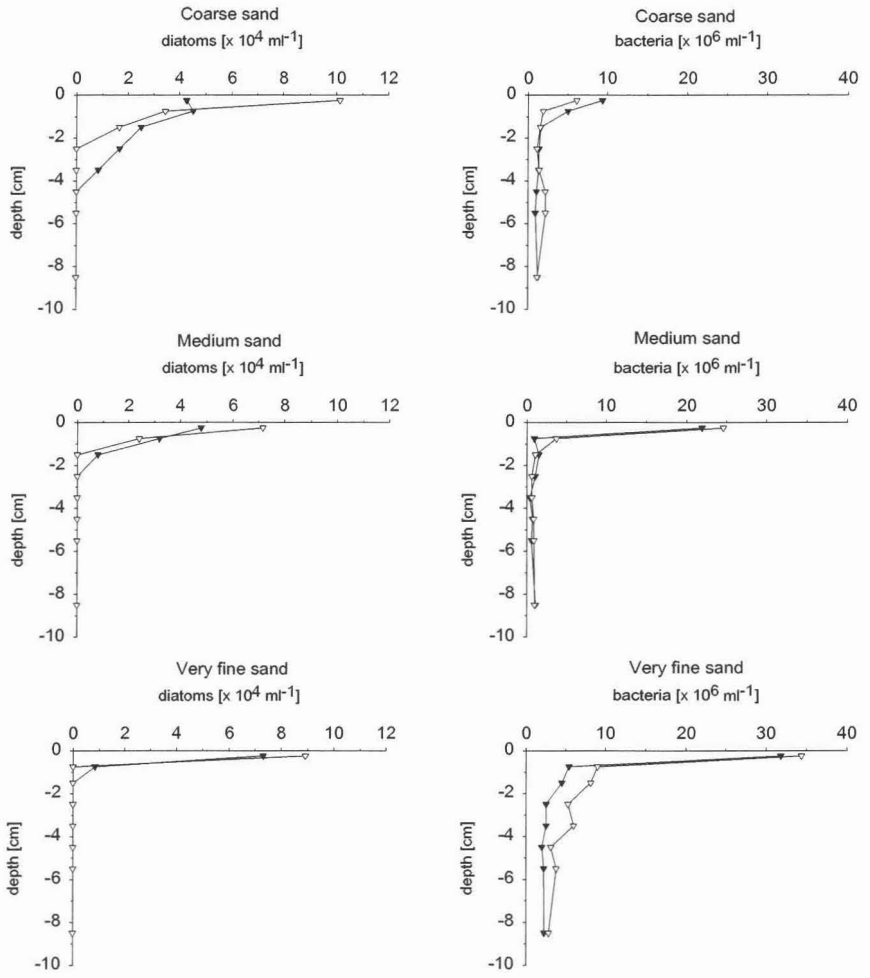

Figure 4. Second chamber experiment: Distribution of *Thalassiosira rotula* (left side) and bacteria (right side) in the sediment of the unstirred (empty triangles) and stirred (filled triangles) chambers after an incubation time of 7 d. No diatom cells were found in the water column.

Bacterial activity and algal decomposition

Total remineralization of the added algal carbon to DIC and the release to the overlying water was always higher in the stirred chambers compared to the unstirred controls with fluxes below 1400 μmol m^{-2} d^{-1} (Table 3) (<2% d^{-1} of the added carbon, Table 4). Comparing the different sediment types, the same amount of DIC was released to the water of the stirred chambers with coarse and medium sands (3669 μmol m^{-2} d^{-1}, 8% d^{-1} of the added carbon), and 6420 μmol m^{-2} d^{-1} (14% d^{-1}) for very fine sand, respectively.

DOC in the water was consumed during all incubations, especially in the stirred chambers (Table 3).

Oxygen consumption before algae addition was approximately –3500 μmol m^{-2} d^{-1} in the stirred chambers and –1500 μmol m^{-2} d^{-1} in the unstirred chambers (Table 3). After the addition of the diatoms, oxygen concentrations decreased in all chambers and the decrease was more pronounced in the stirred chambers, with exception of very fine sand. Highest oxygen consumption after the addition of algae occurred in the stirred chambers with medium sand.

Total bacterial numbers integrated over depth in the sediments decreased with permeability (Fig. 4), and no difference could be found between the stirred and unstirred chambers, with exception of very fine sand. Here, bacterial numbers were higher in all sediment depths of the unstirred chamber. In all incubations, bacteria were most abundant in the upper sediment centimeter with values of approximately 10 $\times$ 10^6 ml^{-1} (coarse sand), 25 $\times$ 10^6 ml^{-1} (medium sand) and 35 $\times$ 10^6 ml^{-1} (very fine sand). Bacterial numbers in the water column of all chambers increased within the first 50 h of the experiment, and then started to decline (Fig. 5). Again the highest bacterial numbers (about 50 $\times$ 10^6 ml^{-1} after 50 h) were counted in the chamber with very fine sand. Bacterial numbers in the water of the other two sediment types were relatively similar, with maximum numbers of approximately 40$\times$ 10^6 ml^{-1} after 50 h.

Table 3. Second chamber experiment: Flux of nutrients, oxygen consumption, DIC and DOC fluxes, and pH changes in the water column after the addition of diatoms. Nutrient fluxes in the chambers were corrected for the concentration changes recorded in the water columns of the control chambers without algae addition, and were calculated from the slope of a linear regression curve (unstirred chambers: $0.1<R^2>0.2$; stirred chambers (silicate and phosphate): $0.5<R^2>0.9$; stirred chambers (ammonia and nitrate + nitrite): $0.1<R^2>0.3$). Oxygen fluxes are based on the concentration changes within the first 24 hours (linear regression: $0.7<R^2>0.9$). Oxygen consumption in the chamber water without sediment and algal addition was determined by a separate bottle incubation and amounted to 41.4 (± 35.0) µmol m^{-2} d^{-1}. For DIC and DOC concentrations, averages (± s.d.) are given. Positive fluxes are directed from the sediment into the water column. The pH at the beginning of the experiment was approximately 7.7.

Sand type	stirred (+/-)	$Si(OH)_4$ (µmol m^{-2} d^{-1})	PO_4^{3-} (µmol m^{-2} d^{-1})	NH_4^+ (µmol m^{-2} d^{-1})	$NO_3^- + NO_2^-$ (µmol m^{-2} d^{-1})	Oxygen Without (µmol m^{-2} d^{-1})	Oxygen With diatoms (µmol m^{-2} d^{-1})	DIC (µmol m^{-2} d^{-1})	DOC (µmol m^{-2} d^{-1})	pH (pH units d^{-1})
Coarse	-	20	7	237	0	-1266	-6724	459 (± 318)	-206 (± 45)	-0.03
	+	115	-74	82	20	-3516	-9714	3669 (± 794)	-2729 (± 146)	-0.03
Medium	-	6	9	202	91	-1782	-8688	1376 (± 265)	-1412 (± 43)	-0.03
	+	107	-23	100	89	-3332	-10988	3669 (± 701)	-2310 (± 480)	-0.03
Very fine	-	19	1	157	57	-1386	-7724	917 (± 371)	-1158 (± 219)	-0.02
	+	25	-10	193	-33	-3670	-7371	6420 (± 1736)	-3878 (± 8)	-0.03

Table 4. Second chamber experiment: Calculated daily conversion rates of the added organic material into inorganic nutrients and carbon, and release to the overlying water. Rates were obtained from the differences between the nutrient and carbon fluxes before and after the addition of diatoms (Table 3), and calculated as percentage of the maximum concentrations and fluxes assuming complete conversion of the added algae into inorganic nutrients. Positive fluxes are directed from the sediment into the water column.

Sand type	stirred (+/-)	$Si(OH)_4$ (% d^{-1})	PO_4^{3-} (% d^{-1})	NH_4^+ (% d^{-1})	$NO_3^- + NO_2^-$ (% d^{-1})	DIC (% d^{-1}) (± s.d.)	DOC (% d^{-1}) (± s.d.)
Coarse	-	0.10	0.61	3.07	0.00	0.96 (± 0.66)	-0.43 (± 0.09)
	+	0.56	-6.43	1.06	0.08	7.64 (± 1.65)	-5.68 (± 0.30)
Medium	-	0.03	0.78	2.61	0.34	2.87 (± 0.55)	-2.94 (± 0.09)
	+	0.52	-2.00	1.29	0.33	7.64 (± 1.46)	-4.81 (± 1.00)
Very fine	-	0.09	0.09	2.03	0.21	1.91 (± 0.77)	-2.41 (± 0.46)
	+	0.12	-0.87	2.50	-0.12	13.37 (± 3.62)	-8.08 (± 0.02)

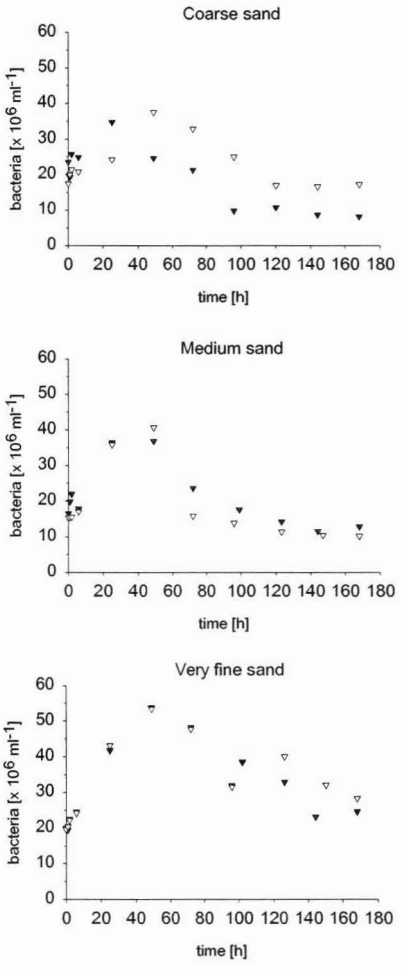

Figure 5. Second chamber experiment: Bacterial abundances in the water column of the unstirred (empty triangles) and stirred (filled triangles) chambers.

Changes in nutrient fluxes after a simulated diatom bloom

In the second experiment, silicate release due to the added diatom frustules was always higher in the stirred chambers compared to the control cores (Table 3). With increasing sediment permeability, more particulate biogenic silica was dissolved in the stirred chambers, which corresponded to 0.56, 0.52 and 0.12% d^{-1} of the added opal for coarse, medium and very fine sands respectively (Table 4). Increase of silicate in the unstirred chambers was low and the conversion rate of the added opal into dissolved silicate was less than 0.10% d^{-1} of the initial opal addition.

Release of phosphate to the overlying water column could only be observed in the unstirred chambers (Table 3), however fluxes were very low and amounted to less than 1% d^{-1} of the added organic phosphorus (Table 4). In all stirred chambers, the sediment took up phosphate and the flux increased with increasing sediment permeability, corresponding to –0.87 to –6.43% d^{-1} of the added phosphorus.

Ammonia releases from the sediments in the stirred chambers with medium and coarse sands were about 100 µmol m^{-2} d^{-1} smaller than those measured in the unstirred controls (Table 3). The opposite was found for very fine sand, where ammonia release in the stirred chamber was about 50 µmol m^{-2} d^{-1} higher than in the controls. The amount of the particulate organic nitrogen decomposed to ammonia corresponded to about 1% d^{-1} (stirred chambers) and 3% d^{-1} (control) for medium and coarse sand, and 2.5% d^{-1} (stirred chambers) and 2% d^{-1} (control) for very fine sand (Table 4).

Highest increases of the nitrate + nitrite concentrations occurred in the stirred and unstirred chambers with medium sand (about 90 µmol m^{-2} d^{-1}, Table 3), which corresponds to 0.3% d^{-1} of the added PON (Table 4). No flux could be observed in the unstirred chamber with coarse sand. The stirred chamber with very fine sand acted as sink for nitrate + nitrite. During the experiment, pH values in the water of all chambers (Table 3) changed only slightly (approx. 0.03 d^{-1}).

Influence of the food pulse on the pore water nutrient profiles

The pore water profiles of the coarse sand showed lower and homogeneous concentrations of silicate, ammonia and DIC in the stirred chamber compared to the control, but with exception of ammonia, concentrations were higher in the water column of the stirred chambers (Fig. 6). Phosphate concentrations always remained below 2 µM in the sediments of the stirred and unstirred chambers (data not shown). Nitrate + nitrite concentrations in the deeper sediment layers of the stirred chamber (2-9 cm) were 2-fold higher than in the controls.

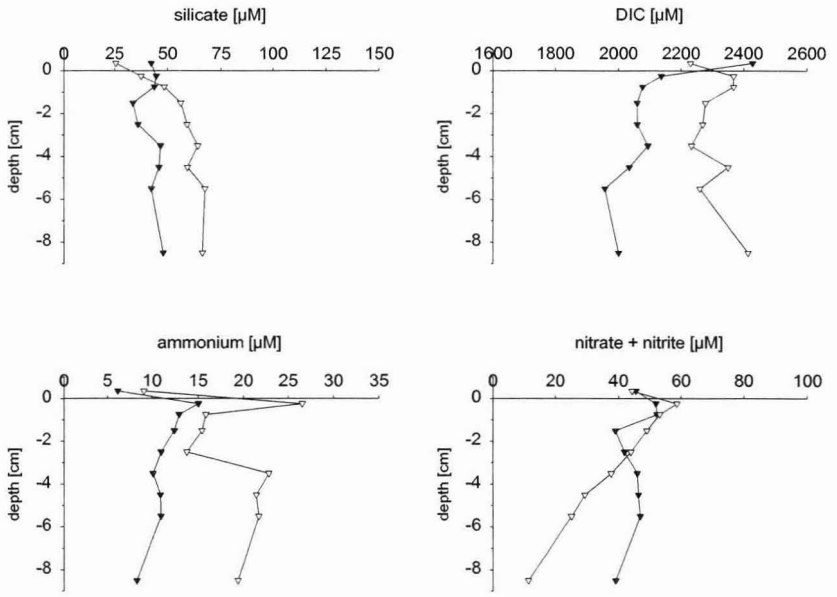

Figure 6. Second chamber experiment: Nutrient and DIC pore water concentrations in the unstirred (empty triangles) and stirred (filled triangles) chambers with coarse sand.

The pore water concentrations of the stirred and unstirred chamber with medium sand did not show a significant difference, with exception of silicate (Fig. 7). Also here the silicate pore water concentrations were reduced in the stirred chamber, whereas the concentrations in the water were higher.

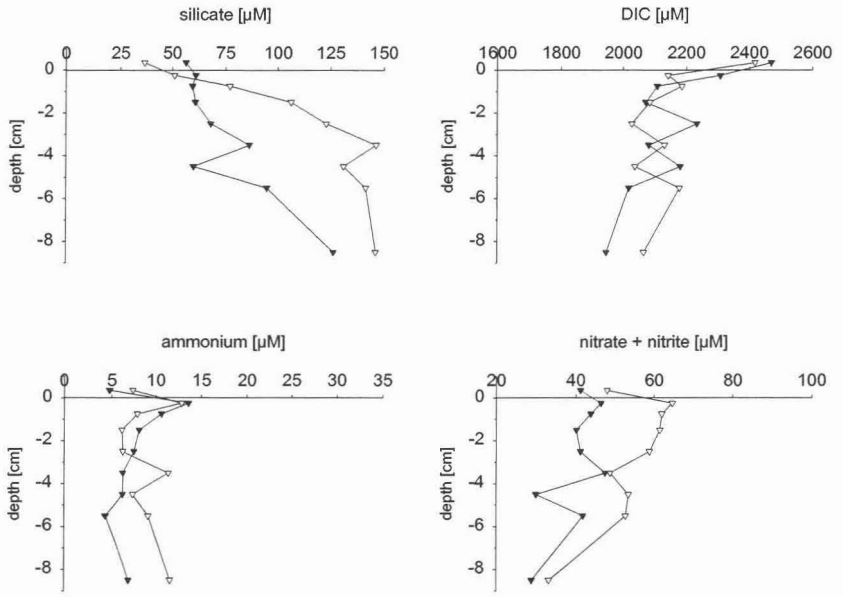

Figure 7. Second chamber experiment: Nutrient and DIC pore water concentrations in the unstirred (empty triangles) and stirred (filled triangles) chambers with medium sand.

The difference between the silicate profiles in the stirred and unstirred chamber with very fine sand was not as pronounced as in the medium and coarse sands, but still visible (Fig. 8). For phosphate (data not shown) and ammonia, no difference could be observed between the stirred and unstirred chamber. Nitrate + nitrite pore water concentrations were higher in the unstirred chamber, whereas DIC concentrations were lower compared to the stirred chamber.

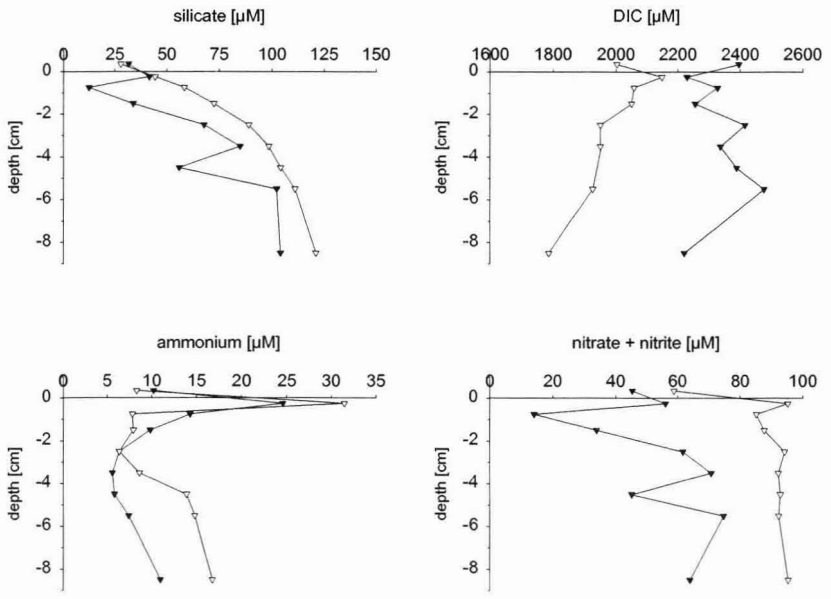

Figure 8. Second chamber experiment: Nutrient and DIC pore water concentrations in the unstirred (empty triangles) and stirred (filled triangles) chambers with very fine sand.

DISCUSSION

Impact of sediment permeability and sand grain size on the deposition of diatoms

Our experiments demonstrate that interfacial water flows in sandy sediments can transport living planktonic diatoms rapidly to sediment layers as deep as 5 cm depending on the permeability of the bed (Fig. 9). The chamber incubations reveal fast decomposition of the algal material in the sandy sediments, with highest remineralization rates in the sediment with the strongest advective flushing, the coarse sand. In both diatom species we used in the experiments, single cells are linked by intercellular silica rods (*S. costatum*) or gelatinous threads (*T. rotula*) forming chains (Smayda 1970) (Fig. 1), that can reach a length of 800 µm in *S. costatum* (Karp-Boss & Jumars 1998). *T. rotula* chains are typically shorter. With exception of the *Skeletonema* chain type, chain-formation favours an increased sinking rate (Smayda 1970). This suggests that chain-formation cannot be invoked as a mechanism to reduce sinking speed, but rather serves as anti-predation device (Smayda 1970). The

colony size is not constant, as cell numbers per chain decrease with increasing age (Smayda 1970). Thus the sinking rate is reduced with increasing age, except for *S. costatum*, where the sinking rate increases. The causes of colony breakage are unknown, and aggregation or disintegration of chains during sedimentation differs between species (Smetacek 1985). Chain disintegration has been reported for *S. costatum* in container experiments (Nöthig 1984), but long chains have been collected in sediment traps below the surface layer (Smetacek et al. 1978), indicating that chain disintegration is preceded by rapid sinking. *T. rotula* chains have been reported as extreme fragile (Smayda 1970), which would favour disintegration of cells during sedimentation.

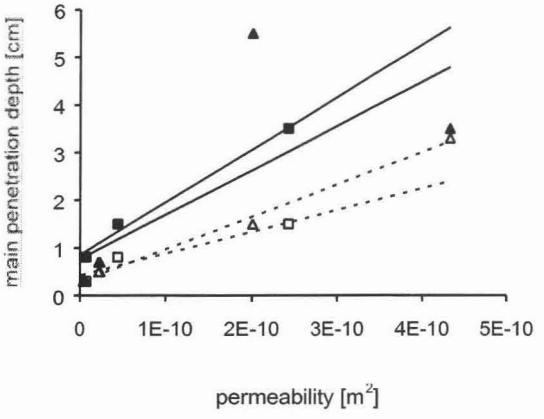

Figure 9. Main penetration depth of *Skeletonema costatum* (triangles) and *Thalassiosira rotula* (squares) in the unstirred (empty symbols) and stirred chambers (filled symbols) depending on the sediment permeability.

Because the average pore sizes in the experimental sediments (Table 1) were 97 ± 33 µm, 53 ± 20 µm and 54 ± 32 µm in diameter for the coarse, medium and very fine sand single cells can be transported much easier into the sediment. Thus, the breakup of the diatom chains determines to a large extent how many cells are carried into the sediment especially in the stirred chambers. It is likely that here mechanical stress accelerated the break down of the chains. Also, the diatoms for the second experiment (*T. rotula*) were stored frozen, which separated the chains into shorter fragments of 2 to 4 cells (microscopic observation). In the chambers with very fine sand or

impermeable sediment respectively, algal aggregates accumulated on the sediment surface in the center of the chamber, due to the flow regime. No such accumulations could be observed in the coarse sediments or the control cores.

In the first experiment, the faster decrease of *S. costatum* cell abundance in the water of the stirred chambers with coarse sand relative to the controls (Table 2) demonstrated the greater filtration capacity of these very permeable sands due to advective transport of algae into sediment (Fig. 2). The faster decrease of cell abundance in the unstirred chamber with the sand-caolinite mix may have been caused by an effect of the caolinite, that formed aggregates with the diatom cells and thereby increased the sinking rate (Hamm 2002), while stirring reduced that effect and kept them longer in suspension. The cell size of our *S. costatum* culture varied between 5 to 10 µm. A single cell is small enough to be transported through the pores of 188 ± 92 µm in the very coarse sand (Table 1). The large size of the pores made it possible, that the diatoms could penetrate gravitationally into the unstirred very coarse sand, which explains the similar distribution in both chambers. Highest transport of diatoms into the sediment occurred in the stirred chamber with coarse sand, which had also the highest sediment-water exchange rates (Table 1). This was caused by the better sorting of the coarse sand and the more spherical grains, leading to interstices of 97 ± 33 µm. A vertical distribution of trapped algae in the sediment with a subsurface maximum, as observed in the stirred chamber with coarse sand at 3.5 cm, can develop in permeable sediments due to the vertical velocity gradient of the advective pore water flows (Huettel & Rusch 2000). As the velocity of the advective flow decreases with depth (Huettel et al. 1996), the penetration of the diatoms into the sediment is limited. The algae accumulate in a layer where the pore water moves too slowly to overcome the friction between cells and sand grains (Huettel & Rusch 2000). Due to the smaller pore size of the medium and fine sands (between 30 and 53 µm) and lower advective pore water exchange (Table 1, Fig. 3), the transport of the diatoms was restricted to the upper 0.7 cm. No diatoms penetrated deeper as 0.3 cm into the sediments that did not show any advective pore water exchange: the very fine sand and impermeable sediment. The negative water exchange rate of the impermeable sediment is an experimental artifact and may have been caused by the caolinite that disturbed the fluorometric measurement. These results indicate, that the

penetration of *S. costatum* into sediments does not occur at and below a permeability of 7×10^{-12} m^2 and a sand grain size of 125-63 µm.

With a diameter between 8 to 55 µm *T. rotula* cells (second experiment) were small enough to be transported through the interstices of coarse (97 ± 33 µm) and medium sand (53 ± 20 µm) (Table 1 and Fig. 4), and also here the advective algae transport was limited to sands with a permeability of more than 7×10^{-12} m^2. The maximal penetration depth of *T. rotula* (3.5 cm) into coarse sand was lower compared to *S. costatum* (5.5 cm), because of the different size of the diatom cells. Besides the cell size, the penetration depth is determined by the shape, density and surface characteristics of the algae (Huettel & Rusch 2000). Flume experiments (Huettel & Rusch 2000) demonstrated the advective transport of *Dunaliella* cells (average diameter of 8 µm) into sediments with a permeability exceeding 1.4×10^{-12} m^2. *Dunaliella* cells are very motile, have a spherical shape, their cell surface is smooth and the cells are relatively soft and can be deformed. Therefore the transport of *Dunaliella* cells through the sand pores should be easier compared to diatom frustules that have spines, sharp edges and hard, inflexible cell walls.

In the case of coastal bloom diatoms, whose cells are often united in chains, the chain length furthermore determines the diatom penetration depth. Laboratory experiments in coarse sand with *T. rotula* chains of different cell numbers revealed that the penetration depth of chains exceeding 8 cells reached only 4 cm compared to shorter chains that penetrated down to 8 cm (example see Fig. 10). Investigations in permeable North Sea sediments confirm our laboratory data, as the maximum penetration depth of non-motile diatoms into fine, medium or coarse sand decreased with increasing chain length (Ehrenhauß et al. 2003a). These results support our hypothesis that colony formation of coastal diatoms may also be an adaptation to reduce benthic filtration. However, the penetration depth of diatom chains consist of 5 to 6 cells increased with increasing sediment permeability, and were 3 cm, 4 cm and 7 cm for a fine (3×10^{-12} m^2), medium (26×10^{-12} m^2) and coarse sand (77×10^{-12} m^2), respectively (Ehrenhauß et al. 2003a). This was caused by the larger interstices between the sand grains in coarser sediments and reveals that these sands are not only very effective traps for single phytoplankton cells, but also for longer diatom chains.

Our results indicate the high filtration capability of permeable sediments in trapping suspended planktonic diatoms. Boon et al. (1998) demonstrated that a substantial part,

up to 40%, of the primary production was buried and subsequently degraded in non-depositional areas of the southern and central North Sea. Permeable sediments actively filter plankton from the water column and thus cause relatively rapid deposition and incorporation of fresh organic particulate matter into sandy sea beds in environments where strong bottom currents theoretically would prevent the sedimentation of low-density organic material. This effect can fuel high-energy zone sediments and boost mineralization and cycling of matter in these regions.

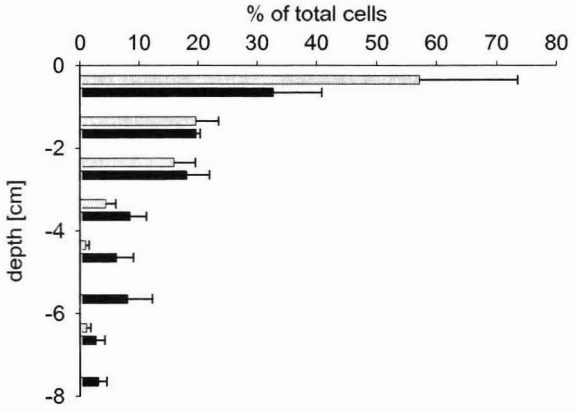

Figure 10. Distribution of *Thalassiosira rotula* chains consisted of 4 (black bars) and 10 cells (grey bars) in coarse sand (n=3).

Algal decomposition

In the second chamber experiment, advective pore water flows enhanced the oxygen consumption in all incubations before algal addition by a factor of 2 to 3, while diffusive oxygen fluxes in all control chambers were relatively similar (variation within factor 1.4) (Table 3). Algal addition induced an increase in oxygen consumption in all incubations and highest consumption rates were recorded in the stirred chambers with medium and coarse sand (Table 3). Oxygen uptake was enhanced two (very fine sand) to three (medium and coarse sand) times and five to six fold in the controls. This relative stronger enhancement in the control cores was mainly due to their low consumption prior to the algal addition. Due to the lack of advective pore water flow, the active surface area that could be reached by oxygenated water was much smaller in the stagnant cores relative to the stirred cores. Enoksson (1993) reported that the sedimentation of a diatom bloom, which deposited

ten times the amount of carbon as we added to each chamber, onto a coastal sediment from the Kattegat consisting of muddy sand increased the oxygen consumption of that sediment only about 1.6-fold. This discrepancy may be explained by the quality of the deposited material, as lysis of algal cells, which results in the release of cell contents, can be substantial at the end of a bloom (Brussaard et al. 1995). Thus, in contrast to the diatoms we added to our chambers, the material that reaches the sediment surface *in-situ* can be already partly degraded. In the stirred chambers, the food pulse caused a stronger stimulation of oxygen consumption with increasing sediment permeability than in the stagnant controls. Higher oxygen utilisation after algal addition in a coarse sand compared to a fine sand was also demonstrated in flume experiments by Forster et al. (1996). Compared to *in-situ* oxygen fluxes of 12000 μmol m^{-2} d^{-1} reported for sandy, organic-poor sediments with median grain sizes between 100 and 200 μm from the North Sea (van Raaphorst et al. 1990), our measured fluxes are low, maybe a result of less organic input and the absence of macrofauna. In our experiment CO_2 release was always smaller than oxygen consumption (Table 3). The respiratory quotient RQ (ratio of CO_2 to O_2 fluxes) was 0.9, 0.3 and 0.4 for the stirred chambers with very fine, medium and coarse sand. This is low compared to other studies in coastal areas where RQ usually was higher than 1 (Hopkinson et al. (2001) and references within), indicating that anaerobic mineralization processes, e.g. sulphate reduction, are important. Due to the short incubation time, high sediment permeability and low organic matter input, the community of anaerobic bacteria was likely less well developed in our sediments in comparison to natural sediments. Strictly anaerobic processes like sulphate reduction, which is the second important carbon oxidation process in coastal areas after oxic respiration (Canfield 1993, Jørgensen 1996), thus probably were a less important mineralization process in our study. Oxygen was also consumed by the oxidation of ammonia (nitrification) as revealed by the nitrate release from the sediments (except in stirred very fine sand and stagnant coarse sand) (Table 3). Additionally, the added algal carbon was immobilised in bacterial biomass, as bacterial numbers in the water increased immediately after the food pulse (Fig. 5). The influence of the organic enrichment on bacterial growth was most pronounced in the very fine sand with higher numbers down to approximately 3 cm depth (Fig. 4). In the medium and coarse sand enhanced bacterial growth was restricted to the upper sediment cm. The higher bacterial numbers in the very fine sand can be explained by the larger specific surface area of fine sand compared to the

coarser sands (Dale 1974). Higher bacterial abundance in the very fine sand may be responsible for the higher DIC and DIN release rates compared to the medium and coarse sand (Tables 3-4). Bacterial numbers were slightly lower in the stirred chamber compared to the control (Fig. 4), but carbon mineralization in the stirred chamber was considerable higher with 13% d^{-1} of the added algal carbon compared to 2% d^{-1} in the control (Table 4). This indicates that advective pore water flows stimulated the complete remineralization of the added diatom carbon to CO_2 and its release to the overlying water. For the incubations with medium and coarse sand, which had bacterial abundance in the same order of magnitude (Figs. 4-5), the carbon mineralization rates were also low in the controls (1 to 3% d^{-1}), but considerable higher in the stirred chambers (8% d^{-1}). As the POC content were comparably low for all investigated sands (Table 1), the CO_2 release can be mostly attributed to the mineralization of the added algal material. Carbon turnover rates have been measured in different coastal sediments, and results ranged between 2500-80000 µM C m^{-2} d^{-1} for permeable sediments of the south-eastern US continental shelf (Jahnke et al. 2000), and approx. 27000 µM C m^{-2} d^{-1} for an intertidal sandflat North Sea sediment (Rusch et al. 2000). DIC fluxes measured in our laboratory study lied in the lower range of these *in-situ* results, maybe due to less organic input and the absence of macrofauna.

Average benthic DOC fluxes reported for coastal sediments were 910 µM m^{-2} d^{-1} (Burdige et al. 1999), but in our study DOC was rather consumed than released. The high loss of DOC in the chambers (Table 3) indicates that the CO_2 release at the beginning was mainly caused by the bacterial degradation of the added diatom DOC. The freezing of the algal material led to a release of 32% of the total diatom carbon as DOC due to the disruption of the cell walls, maybe leading to an overestimation of the carbon mineralization rates. However, sediment movement in shallow coastal areas may also cause cell damage due to mechanical stress leading to release of DOC from damaged cells. Henrichs & Doyle (1986) and Hansen & Blackburn (1992) reported carbon remineralization rates of diatoms, which were also previously frozen, that were lower (3.5 to 5.0% d^{-1} for the first days) than the rates we observed. Studies of the mineralization of fresh diatoms in sandy sediments (stagnant conditions) revealed daily carbon conversion rates of 2 to 4% (Andersen & Kristensen 1992, Andersen 1996). In our study, carbon remineralization to CO_2 were significant higher in all stirred chambers (8 to 13% d^{-1}), but lower for the unstirred chambers (1 to 3% d^{-1}).

These results support the hypothesis, that advective solute transport can efficiently enhance the carbon remineralization in permeable sediments.

Regeneration of nutrients

The second chambers experiment showed a clear relationship between the remineralization of biogenic silica and sediment permeability: more opal was dissolved with increasing permeability (Table 3). The pH decrease was in the same order of magnitude in all chambers (Table 3), therefore the pH effect on the dissolution of the silica frustules, i.e. decreasing dissolution with decreasing pH, should be comparable in all chambers. As in all control chambers silicate release caused by diatom addition was very low and similar for all tested sediments, the higher opal dissolution in the stirred chambers with coarser sediments can be attributed to the advective pore water exchange. Because we used the same sediments as in the first experiment, fluid exchange rates were in the same order of magnitude, and the exchange rates calculated from the Fluorescein flux data of the first experiment can be used for comparison. Advective exchange was recorded for all sediments coarser than the 63-125 μm sand and fluid exchange increased with permeability (Table 1, Fig. 3). Due to the vertical velocity gradient in the advective pore water flows, particulate matter that is transported into the bed cannot be easily removed again from the sediment by upwelling pore water because relatively high pore flow velocities are needed to dislocate material that accumulated in a specific depth layer (Huettel & Rusch 2000). In contrast to particulate matter, the volume of fluid that is transported into the bed is equal to that released from the bed because mass balance has to be maintained. The dissolution rate of particulate silica in the marine environment is mainly dependent on the state of saturation of the surrounding seawater (Kamatani & Riley 1979). High flushing rates that increase with increasing permeability prevent the build up of dissolved silica concentrations in the pore water, thereby maintaining lowest pore water silicate saturation and ensuing highest opal dissolution rates. The depth range of advective pore water exchange increases with increasing sediment permeability (Huettel et al. 1996) (Table 1), which is also reflected in the silicate pore water profiles of the 3 different sands (Figs. 6-8). Advective solute transport led to reduced silicate concentrations down to 8 cm in coarse and medium sand, and 4.6-fold (coarse sand) and 4.3-fold (medium sand) higher fluxes of silicate to the overlying water compared to very fine sand.

In-situ chamber experiments with diatoms on permeable sediments in the southern German Bight (Ehrenhauß et al. 2003b) revealed comparable daily conversion rates of 0.64%. These dissolution rates also require a faster bacterial degradation of the protective organic coating that covers the diatom frustules in the highly permeable sands.

DIN fluxes from the sediment in the second experiment were dominated by ammonia (Table 3), but nitrate + nitrite fluxes were positive for almost all incubations, indicating that nitrification takes place after the food pulse. This assumption is also supported by the fact that nitrate + nitrite pore water concentrations exceeded ammonia for all incubations (Figs. 6-8). Ammonia release from the sediment of the stirred chambers decreased with increasing permeability (Table 3). Ammonia release was more pronounced in the unstirred chambers, with exception of the very fine sand. Higher nitrification rates and uptake of ammonia by bacteria in the stirred chambers can be an explanation for this observation. Ziebis et al. (1996) demonstrated in flume experiments an increasing advective oxygen transport into permeable sediments with increasing permeability. The higher oxygen consumption in the stirred chambers with coarse and medium sand compared to the controls (Table 3) is also a consequence of the higher advective transport of oxygen into the sediment. Higher nitrate and lower ammonia concentration in the deeper layers of the stirred chamber with coarse sand compared to the control (Fig. 6) reveal that nitrification was stimulated at depth by the advective oxygen supply. Similar results were obtained in flume experiments by Huettel et al. (1998), which showed that advective pore water flows can enhance nitrification in permeable sediments.

Phosphate was consumed in all stirred chambers and the consumption rate increased with permeability. Studies in sandy, organic poor North Sea sediments have shown that the sediment-water fluxes of ammonia and phosphate were reduced with increasing bacterial production (van Duyl et al. 1993). Another explanation for the loss of phosphate in the more oxygenated stirred sediments is the adsorption of phosphate onto iron-rich particles under oxic conditions which causes that in oxic sediments often more phosphate is bound than in anoxic sediments (Gunnars & Blomqvist 1997). Pore water phosphate concentrations in all sediments were below 3 µM, with the lowest concentrations in the coarse sand (data not shown).

The uptake of phosphate (about 5% d^{-1} of the added organic phosphorus) by permeable sediments was also observed in *in-situ* chamber experiments with diatoms

in the southern German Bight (Ehrenhauß et al. 2003b). In these *in-situ* experiments, ammonia regeneration rates were higher (5 to 10% d^{-1} of the added PON) than the rates observed in this study (1 to 3% d^{-1} of the added PON), indicating the importance of macrofauna in nitrogen mineralization, as demonstrated by several studies (Henriksen et al. 1983, Asmus 1986, Hansen & Kristensen 1998). Daily conversion rates of diatoms added to muddy Baltic Sea sediments (Conley & Johnstone 1995) amounted to 0.52, 0.35 and 0.02% for silicate, ammonia and nitrate respectively. Compared to our data, slightly more opal was remineralized in our coarse sand incubation (0.56% d^{-1}), ammonia regeneration was higher for all incubations (between 1 to 3% d^{-1}) and as well was nitrate (0.0 to 0.3% d-1), except in the stirred very fine sand. Higher regeneration of ammonia in sandy sediments (1.0 to 1.3% d^{-1}) compared to muddy sediments (0.1 to 0.4% d^{-1}) after algal addition was also reported by Hansen & Kristensen (1998).

Our laboratory experiments demonstrate that sediments with a permeability exceeding 7×10^{-12} m^2 can efficiently trap small planktonic diatoms (diameter: 5 to 55 µm). Studies on permeable North Sea sediments (Ehrenhauß et al. 2003a) furthermore revealed that even more permeable sands ($k>26 \times 10^{-12}$ m^2) are effective traps for longer diatom chains (up to 6 cells $chain^{-1}$). High advective flushing rates in sandy sediments further enhance the remineralization of the trapped organic carbon and stimulate the benthic oxygen consumption, as well as nitrification. Additionally the dissolution rate of the deposited opal is accelerated with increasing sediment permeability, as silicate does not accumulate in the pore water.

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Chapter 3

Effect of advective pore water transport on distribution and degradation of diatoms in permeable North Sea sediments

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ABSTRACT

This contribution addresses the incorporation and degradation of diatoms in coastal fine, medium and coarse North Sea sands. During three cruises in 2001 to a highly dynamic, non-depositional area in the southern German Bight, the transport of ^{13}C-labeled diatoms into these different permeable sand beds was assessed by *in-situ* and on-board chamber experiments. Enhanced advective transport of diatom frustules and ^{13}C-enriched diatom carbon into sandy sediments with increasing permeability was demonstrated. Highest transport rates were observed in the coarse sand where 21% of the added algae were found below 0.5 cm after only 20 h incubation time.

Broken frustules of *Thalassiosira* sp., which dominated the diatom spring bloom 2001, were found in the sedimentary diatom distribution in the medium and coarse sand in autumn. This indicates that advective transport and to some limited extent also bioturbation deposits phytoplankton into sandy sediments, where strong bottom currents theoretically would prevent the sedimentation of this low-density organic material. The trapped cells are rapidly degraded, as observed in our chamber experiments, where 28% of the added diatom carbon was released as DOC per day after the third incubation day.

Permeable sediments represent expansive coastal filter systems, where high advective flushing rates boost remineralisation of trapped algal cells. These processes promote a fast recycling of organic matter and thus may be important for maintaining high primary production rates in shelf environments.

KEY WORDS

German Bight – permeable sediments – advective transport – planktonic and benthic diatoms – ^{13}C-labelling – remineralization

INTRODUCTION

The German Bight is a shallow region of the south-eastern North Sea with depths mainly between 20 and 40 m. This region is characterized by a high primary productivity and large standing stock of algae except during the winter months (Boon et al. 1998). Offshore of Spiekeroog Island, near-bottom current velocities range from 30 to 60 cm s^{-1} (Antia 1993). In this high-energy environment, tides, waves and storm-generated bottom currents cause frequent sediment erosion, redeposition and lateral transport resulting in coarse-grained, highly permeable sediments (Antia 1995). Consequently, organic particulate material also goes through many cycles of deposition and resuspension before it is finally completely mineralized or buried (Bacon et al. 1994). For the southern North Sea, it has been postulated that only small amounts of the primary production are incorporated into the sediments, because this material has to be transported to less turbulent zones where it can settle (Creutzberg & Postma 1979). However, Jenness & Duineveld (1985) demonstrated the deposition of considerable amounts of phytoplankton into sandy North Sea sediments without simultaneous mud deposition. In contrast to muddy, cohesive sediments, in which molecular diffusion is the major transport process for solutes through the sediment, advective transport processes gain significance in sediments with permeabilities exceeding 10^{-12} m^2 (Huettel et al. 1998). The driving forces for these interstitial pore water flows are pressure gradients, which are generated when unidirectional or oscillating bottom currents interact with sediment topography, e.g. sediment ripples and biogenic structures (Huettel & Webster 2001, Precht & Huettel in press). Advective pore water flows provide an effective transport mechanism for dissolved and particulate matter through the interstitial space (Huettel et al. 1998). Flume experiments have shown that such pore water flows enhance the nutrient release (Huettel et al. 1998), as well as oxygen penetration depth (Ziebis et al. 1996) and consumption (Forster et al. 1996) in permeable sediments. Advective transport of phytoplankton into permeable beds has been demonstrated in flume studies and *in situ* (Pilditch et al. 1998, Huettel & Rusch 2000). Thus, the degradation of organic matter can be shifted from the sediment surface to deeper sediment layers, preventing resuspension of the material by waves and strong bottom currents (Huettel & Rusch 2000).

Nevertheless, the organic carbon content of sandy sediments is generally low (Shum & Sundby 1996), and this has led to the view that the biogeochemical activity in these

beds also is low. However, studies on the oxygen consumption in shelf environments revealed that the oxygen uptake in a coarse sediment was only two to three times lower than the uptake in a nearby fine-grained sediment despite a 20 times higher carbon content (Grant et al. 1991). Consequently, the contribution of sandy sediments to organic matter degradation in the shallow shelf may be larger than inferred from the low organic content (Shum & Sundby 1996).

Spring diatom blooms are often the events of highest yearly new production and carbon sedimentation in the coastal ocean (Goering et al. 1973). Planktonic diatoms do not have any structures facilitating locomotion, but a variety of mechanisms retard sinking, e.g. small cell size to increase the surface to volume ratio, cell shape or ionic regulation (Round et al. 1990). Planktonic diatoms have considerable physiological control over buoyancy (Smayda 1970). As some of these controls are energy dependent, sinking rates can increase drastically upon nutrient depletion (Smetacek 1985). Aggregation after intense blooms further can accelerate the sinking rates (Passow 1991). Several authors (e.g. Peinert et al. 1982, Brussaard et al. 1995) have shown that sedimentation, and not grazing, is the major loss factor of diatom spring blooms. The sinking dynamics of coastal bloom diatoms are an integral part of their life history and represent the transition from a reproductive pelagic stage to a benthic resting stage, which enables them to survive over long periods in cold, dark environments (Smetacek 1985).

In contrast to planktonic diatoms, benthic diatoms include motile and non-motile species. Epipelic species (growing on mud), for example, usually are motile, while epipsammic species (growing on sand) are non-motile. Benthic diatoms are important primary producers in many estuarine, intertidal and shallow-water environments.

The purpose of this study was to assess the vertical distribution of diatoms in coastal sediments with different permeabilities, and the potential role of advective transport processes on this distribution. Therefore, we collected sediment cores on three nearshore subtidal sandy sediments, that revealed the distribution and abundance of planktonic and benthic diatoms in the different sands. For the investigation of the entrainment depth and the time scale of the interfacial transport of planktonic diatoms into the different sands, we conducted three on-board and two *in-situ* chamber experiments. The diatoms were labeled with ^{13}C, which facilitates to follow the pathway of the algal carbon within the sediment (Levin et al. 1997). In order to assess

whether interfacial water flows enhance the degradation of the added diatoms, samples for dissolved organic carbon (DOC) were analyzed.

MATERIALS AND METHODS

Study area

Sediment collection and experiments were carried out on nearshore subtidal sands during 3 cruises of R.V. Heincke (HE 145, HE 148 and HE 154) to an area seawards of Spiekeroog Island (south-eastern German Bight) (Fig. 1). This environment is strongly influenced by tides, waves and storm currents (Antia 1995). The mean tidal range at the study site is 2.5 m. Salinity varied between 31-32.

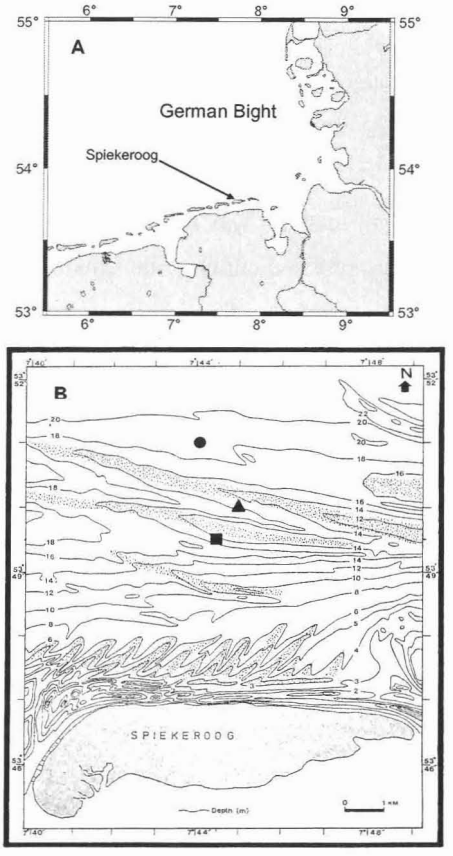

Fig. 1. (A) Position of Spiekeroog Island in the German Bight (south-eastern North Sea). (B) Bathymetry of the Spiekeroog shoreface as given by Antia (1993), and locations of the 3 stations. A circle indicates the station with the fine sand, a triangle the medium and a square the coarse sand.

For the measurements, *in-situ* and on-board experiments, three well-studied sites (Antia 1993, Antia 1995, Janssen & Witte in prep.) with different sediment characteristics were chosen (Table 1), all located within a radius of 2500 m (Fig. 1).

Sediment collection

For the characterization and distribution of planktonic and benthic diatom species, 3 (fine and medium sand) or 1 (coarse sand) sediment cores were taken with a multicorer on the September cruise (HE 154). These cores were sliced in intervals of 2×0.5 cm and 9×1 cm and analyzed in the same manner as described below for the chamber cores.

Cultivation of ^{13}C-enriched phytoplankton

For the experiments, an axenic clone of *Ditylum brightwellii* (Bacillariophyceae, Biddulphiales) (Fig. 2) was cultured in sterile artificial seawater with a salinity of 33 (Grasshoff et al. 1999) enriched with f/2 medium (Guillard & Ryther 1962) at 25°C. This medium contained 25% ^{13}C-enriched bicarbonate (99% $NaH^{13}CO_3$, Cambridge Isotope Laboratories). The algal material was harvested by centrifugation (404 **g**, 4 min), rinsed 3 times with an isotone sodium chloride solution and centrifuged again. From this concentrated material, samples for dry mass, particulate organic carbon (POC), DOC, diatom numbers, label efficiency and bacterial phospholipid-derived fatty acids (PLFA), were taken, and then the algae were stored frozen until use. This treatment killed the cells. The axenic state of the culture was verified by microscopic observation of DAPI stained cells and by measuring the PLFA. Neither bacteria nor bacterial PLFA could be found in the material (Buehring et al. unpublished data). The produced algal carbon consisted of 15% $\delta^{13}C$ (HE 145), 9% $\delta^{13}C$ (HE 148) and 10% $\delta^{13}C$ (HE 154) and the carbon content of the added algae per chamber corresponded to 0.31 g C m^{-2} (HE 145), 0.36 g C m^{-2} (HE 148) and 0.50 g C m^{-2} (HE 154).

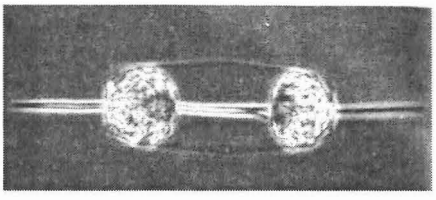

Fig. 2. *D. brightwellii* picture, taken from Round et al. (1990).

Table 1. Positions, sediment and water characteristics of the study sites at the south-east corner of the German Bight (Spiekeroog Island). The permeability, the porosity, the median grain size and the POC concentrations of the sediments are taken from Janssen & Witte (in prep.). Additionally to the experimental sediment cores retrieved by divers, sediment cores were taken with a multicorer for the assessment of background diatom numbers and $PO^{13}C$ in the different sediments (fine and medium sand: n = 3; coarse sand: n = 1). n.a.: not analyzed

Cruise	Date	Position	Sand type	k (10^{-12} m^2) (± s.d.)	Porosity (vol. %) (± s.d.)	Median grain size (µm) (± s.d.)	Water depth (m)	Water temperature (°C)	Bottom water POC (mg L^{-1}) (± s.d.)	Sediment POC (% dry mass) (± s.d.)	Chamber experiment with diatoms
HE 145	08. – 18.04. 2001	53°51´N, 7°44´E	Fine	3.02 (± 1.66)	44.9 (± 1.6)	164 (± 1)	19	9	0.96 (± 0.02)	n.a.	On-board (12 h, 30 h, 132 h; n=2)
HE 148	07. – 15.06. 2001	53°51´N, 7°44´E	Fine	3.02 (± 1.66)	44.9 (± 1.6)	164 (± 1)	19	13	1.22 (± 0.06)	0.114 (± 0.014)	*In-situ* (32 h; n=2)
HE 154	24. – 30.09. 2001	53°50´N, 7°45´E	Medium	26.27 (± 3.26)	43.2 (± 1.4)	299 (± 3)	16	16	0.61 (± 0.03)	0.023 (± 0.003)	On-board (12 h, 25 h, 72 h; n=1) + *in-situ* (20 h; n=2)
		53°49.5´N, 7°44.5´E	Coarse	77.24 (± 14.36)	41.1 (± 1.6)	672 (± 37)	14	16	0.61 (± 0.03)	0.032 (± 0.003)	On-board (20 h; n=1)

Experiments

Both *in-situ* and on-board experiments were carried out in acrylic cylindrical chambers (31 cm height, 19 cm inner diameter), which were covered by black foil preventing any light penetration to the incubated water and sediments. The water inside each chamber was stirred by a horizontal disk (17 cm diameter), rotating approximately 10 cm above the sediment surface with 20 rpm. The rotating water generates a pressure gradient (ca. 1.5 Pa cm^{-1}), comparable to the pressure gradient at a sediment ripple interacting with bottom currents (Huettel & Rusch 2000). This pressure gradient creates advective pore water flows in permeable sediments.

The chambers were deployed and recovered by divers, and for the *in-situ* experiments the algae were directly injected into the chambers by the divers. At the end of the incubation time of 2 × 32 h (fine sand, HE 148) and 2 × 20 h (medium sand, HE 154), the chambers were closed at the bottom with sealing lids and brought back to R.V. Heincke. The sediment for the on-board incubations was cored and recovered by the divers using the same benthic chambers. On board, the chambers were kept at *in-situ* temperature, and stirring was started immediately. The on-board experiments ran for 2 × 12 h, 2 × 30 h and 2 × 132 h (fine sand, HE 145); for 12 h, 25 h and 72 h (medium sand, HE 154) and 20 h (coarse sand, HE 154). During this time, water samples for diatom numbers, DOC and bacterial numbers were taken at regular time intervals. For the *in-situ* experiments, these samples were only taken at the end of the incubation time. For the assessment of background values, bottom water was collected 2 m above the seafloor with a rosette equipped with 10 L Niskin bottles at the beginning of the *in-situ* experiments.

At the end of all experiments, the entire cores were sliced at intervals of 10 × 1 cm and 2 × 2.5 cm. Every depth interval was carefully mixed and samples for diatom numbers and ^{13}C of particulate organic carbon ($PO^{13}C$) were taken. In order to assess the background $PO^{13}C$ values without organic matter addition, 3 (fine and medium sand) or 1 (coarse sand) additional sediment cores were taken with a multicorer for each experiment. These cores were sliced and analyzed in the same manner as described for the chamber cores.

Analytical techniques

Water samples for diatom numbers were preserved with hexamethylenetetramine buffered formaldehyde (end concentration 2%) and Lugol solution (end concentration 1%) and kept refrigerated in dark glass bottles until analysis. To separate the algae from the sand grains, 1 ml sediment was resuspended two times in 5 ml 0.2 µm filtered seawater, containing formaldehyde and Lugol in the same final concentrations as for the water samples. The supernatant was collected after 30 s of deposition time and filtered on black membrane filters (0.2 µm). All diatom cells of 20 randomly chosen counting grids of three parallel filters per sample were counted under a Zeiss™ Axiophot epifluorescence microscope (excitation wave length 510-560 nm, magnification 1300 ×). Diatom species were identified (Drebes 1974, Pankow 1990) by a Zeiss™ inverted microscope using the method ofUtermöhl (1958) and a magnification of 400 ×.

To test the extraction efficiencies, a known concentration of a *D. brightwellii* culture was added to the various sediments and incubated for 1 day in the dark. Diatom cells were extracted with 0.2 µm filtered seawater as described above. Extraction efficiencies were: 76 ± 5% (fine sand), 82 ± 14% (medium sand) and 79 ± 9% (coarse sand).

For the dry mass determination of the *D. brightwellii* culture, 1 ml sample was filtered on precombusted (500°C, 6 h), pre-weighed GF-F filters, rinsed with distilled water to remove the sodium chloride, dried for 24 h at 60°C and weighed again.

Samples for the carbon content of the culture were filtered on precombusted GF-F filters, pre-treated with 0.1 N HCl for 2 h to remove the bicarbonate and dried at 60°C. Filters were then transferred into tin cups. The particulate organic carbon was measured using a Fisons™ NA1500 elemental analyzer.

For the assessment of the label efficiency of the culture, samples were combusted in a CE Instruments™ CHN-Analyzer and the evolved CO_2 was passed online via a ThermoFinnigan™ interface to a ThermoFinnigan™ isotope-ratio mass spectrometer (IRMS) in a continuous flow of helium.

Samples for the $\delta^{13}C$ values and concentration of the sediment POC were stored frozen in precombusted dark glass vials until processing. About 2 g sediment was dried for 48 h at 60°C and pre-treated with approximately 10 ml 2 M HCl overnight to remove the bicarbonate. Sediments were then centrifuged (2800 **g**, 10 min), washed 3

times with distilled water, centrifuged and dried again. Approximately 100 mg of the sediment were exactly weighed into tin cups and samples were measured as described for the label efficiency.

Carbon isotope ratios ($^{13}C/^{12}C$) are expressed in the conventional delta notation ($\delta^{13}C$) relative to Vienna PDB ($^{13}C/^{12}C_{VPDB}$ = 0.0112): $\delta^{13}C$ (‰) = $[(R_{sample}/R_{std}) - 1)] \times 1000$, where R_{sample} and R_{std} are the $^{13}C/^{12}C$ of the sample and standard, respectively (Craig 1957). Incorporation of ^{13}C is shown as excess (above background) ^{13}C and is expressed in terms total uptake (*I*). *I* was calculated according to Moodley et al. (2000) as the product of the POC concentration and excess ^{13}C (*E*). *E* is the difference between the fraction (*F*) of the sample and background: $E = F_{sample} - F_{background}$, where $F = {}^{13}C / ({}^{13}C + {}^{12}C) = R / (R + 1)$ and *R* = the carbon isotope ratio. *R* was derived from the measured $\delta^{13}C$ values as $R = (\delta^{13}C / 1000 + 1) \times R_{VPDB}$.

Water samples for DOC were filtered through precombusted GF-F filters into precombusted 4 ml glass vials and stored frozen until analysis. The DOC concentration was measured by high-temperature catalytic oxidation using a Shimadzu™ TOC-5050A analyzer. Three parallels were measured per sample.

For the bacteria counts, water samples were preserved with formaldehyde (end concentration 4%) and kept at 4°C. Bacteria were filtered on black membrane filters (0.2 µm), stained with acridine orange, and 20 randomly chosen counting grids of 3 parallel filters per sample were counted under a Zeiss™ Axiophot epifluorescence microscope (excitation wave length 450-490 nm, magnification 1300 ×).

RESULTS

The distribution of planktonic and benthic diatoms in coastal North Sea sandy sediments of different permeabilities

In general, the medium and coarse sands showed a higher diversity of planktonic and benthic diatom species than the fine sand. Furthermore, the penetration depths of single diatom cells and diatom chains were higher in the coarse-grained sands.

Actinoptychus senarius and *Coscinodiscus* spp. were the dominant centric diatom species in all 3 sands (Fig. 3). The vertical distribution of *A. senarius* was very variable in all 3 sands: 0-2 and 3-4 cm (fine sand), 0-0.5, 1-2 and 6-7 (medium sand), and 0.5-1 and 4-6 cm (coarse sand). The penetration depths of *Coscinodiscus* spp. was

1-2 cm (fine sand), 0-3 cm and 5-7 cm (medium sand) and 4-5 and 7-8 cm (coarse sand). *Biddulphia regia* could only be found in the upper sediment layer of the fine sand (0.5-1 cm).

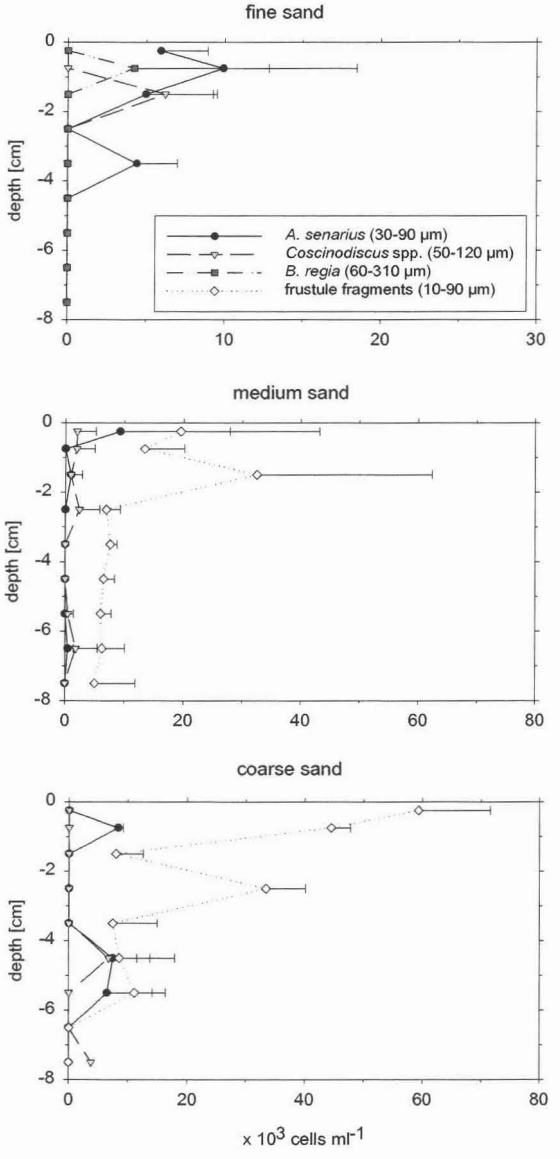

Fig. 3. Vertical distributions and averaged cell numbers (+ s.d.) of centric diatom species in a fine, medium and coarse sand. Sediment cores (fine and medium sand: n = 3; coarse sand: n = 1) were collected in September. Please note different scale for cell numbers.

Besides these centric diatom species, broken parts of diatom frustules from mainly centric species were abundant in relatively high numbers in the medium and coarse sand. The frustule fragments accumulated mainly in the upper 2 cm of the medium sand, whereas in the coarse sand they were mainly found in depths down to 4 cm.

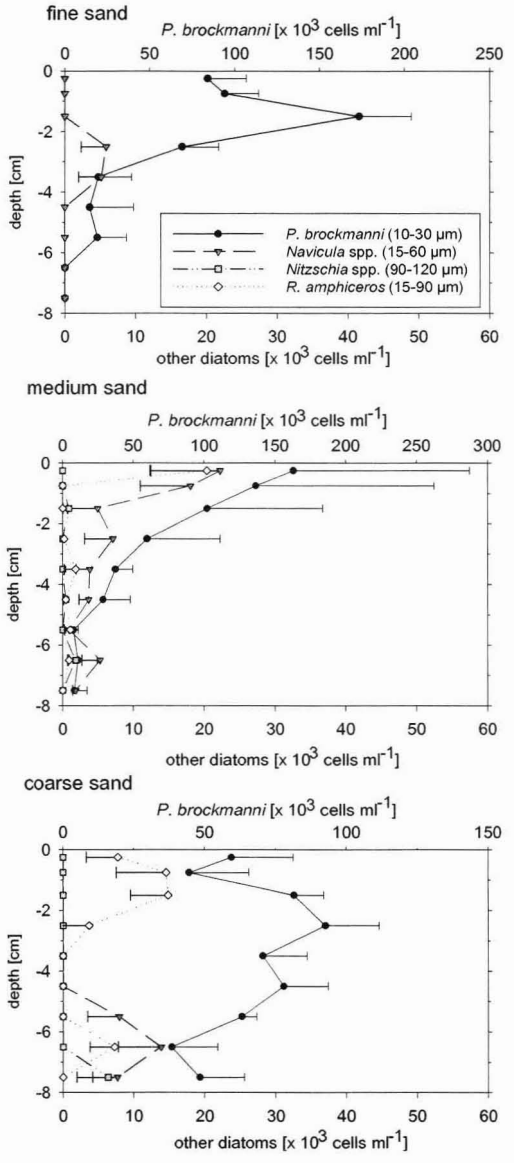

Fig. 4. Vertical distributions and averaged cell numbers of pennate diatom species in a fine, medium and coarse sand. Sediment cores (fine and medium sand: n = 3; coarse sand: n = 1) were collected in September. Please note different scale for *P. brockmanni* numbers (+ s.d.) (upper scale) and other pennate diatoms (- s.d.) (lower scale).

Four different pennate diatom species could be found in the medium and coarse sands (Fig. 4), while in the fine sand only 2 different species occurred. The non-motile diatom *Plagiogramma brockmanni* was the dominant pennate diatom species in all 3 sands, and its abundances were higher compared to the dominant centric diatom species. Maximum penetration depth of *P. brockmanni* also increased with increasing sediment permeability: 6 cm in the fine sand and 8 cm (total sampling depth) in the medium and coarse sands. The maximum cell number united in a chain did not exceed 5 cells for the fine sand, and these chains reached maximum abundance at 2.5 cm sediment depth (Fig. 5). Below 2.5 cm only single cells of *P. brockmanni* were found. In the medium sand, highest cell numbers occurred at the sediment surface and numbers decreased with depth. The maximum cell number per chain amounted to 9 cells in the surface layer of the medium sand. A subsurface maximum with 6 cells chain^{-1} was located at 3.0 cm depth. In the coarse sand, *P. brockmanni* numbers were very homogeneous over total sediment depth, with slightly lower numbers at the sediment surface (0-2 cm) and 6-8 cm depth. The maximum cell number per chain reached 10 cells and was located at 3.5 cm. Chains of 4 cells were even found at 8 cm depth.

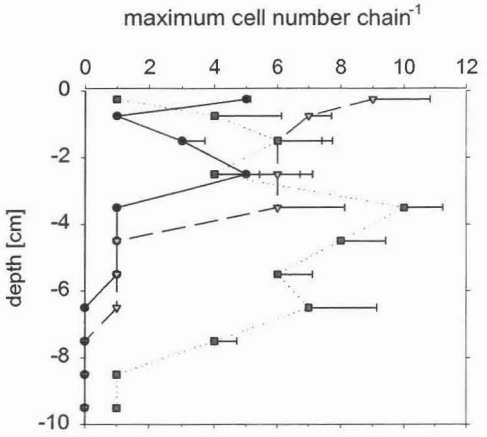

Fig. 5. Maximum cell number united in chains (+ s.d.) of the dominant diatom species *P. brockmanni* in a fine (circle), medium (triangle) and coarse sand (square).

Raphoneis amphiceros, the other non-motile diatom species could only be found in the medium and coarse sand in depths of up to 7 cm.

The motile diatom *Navicula* spp. was present in all 3 sands, but numbers were substantially lower than the cell numbers of the non-motile diatom species. The other motile diatom species *Nitzschia* spp. was only sporadically present with low numbers in the medium and coarse sand.

Transport of ^{13}C-labeled diatoms into sandy sediments of different permeabilities

In all incubations we observed higher penetration depths of *D. brightwellii* cells into the sediments with increasing permeability. This result was supported by the excess ^{13}C data, which showed enhanced transport of algal carbon into deeper layers of the coarse-grained sands.

The transport of *D. brightwellii* cells into the fine sand was restricted to the upper 2 cm of the sediment, with most cells accumulating in the upper centimeter (Fig. 6). Algal penetration depth did not increase with increasing incubation time. Highest cell numbers were also observed in the upper sediment centimeter in the incubations with medium sand, but with increased incubation time (72 h) more cells were found in the 1 to 2 cm layer. In the two *in-situ* experiments with medium sand (Fig. 7), some cells were transported down to 3 cm. In the experiment with coarse sand algae were transported on average 3 cm into the sediment within 20 h (data not shown).

Flux of *D. brightwellii* cells from the water column into or onto the sediment increased with increasing sediment permeability (Table 2), from -1070×10^3 cells m^{-2} d^{-1} (fine sand) to -1552×10^3 cells m^{-2} d^{-1} (coarse sand). No cells could be detected in the chamber water after the first day.

The chamber experiments with different duration showed that, after an incubation time of 12 h, total uptake of excess ^{13}C into the fine sand (Figs. 6-7) was mainly restricted to the upper 2 cm of the sediment. With increasing incubation time (30 to 132 h), more excess ^{13}C could be detected in deeper sediment layers (2 to 6 cm), but the bulk of diatom carbon still accumulated in the surface layer. In the 12 h incubation with medium sand, highest amounts of excess ^{13}C were also detected in the upper 2 cm, but more algal carbon could be found in 2 to 4 cm depth compared to the fine sand incubation. With increasing incubation time (20 to 72 h) excess ^{13}C was

transported deeper into the sediment (Fig. 6). After 72 h, high amounts of labeled diatom carbon were found at 6 to 12 cm depth. In the incubation with coarse sand (20 h) the labeled algal carbon was found in depths of up to 3 cm (data not shown).

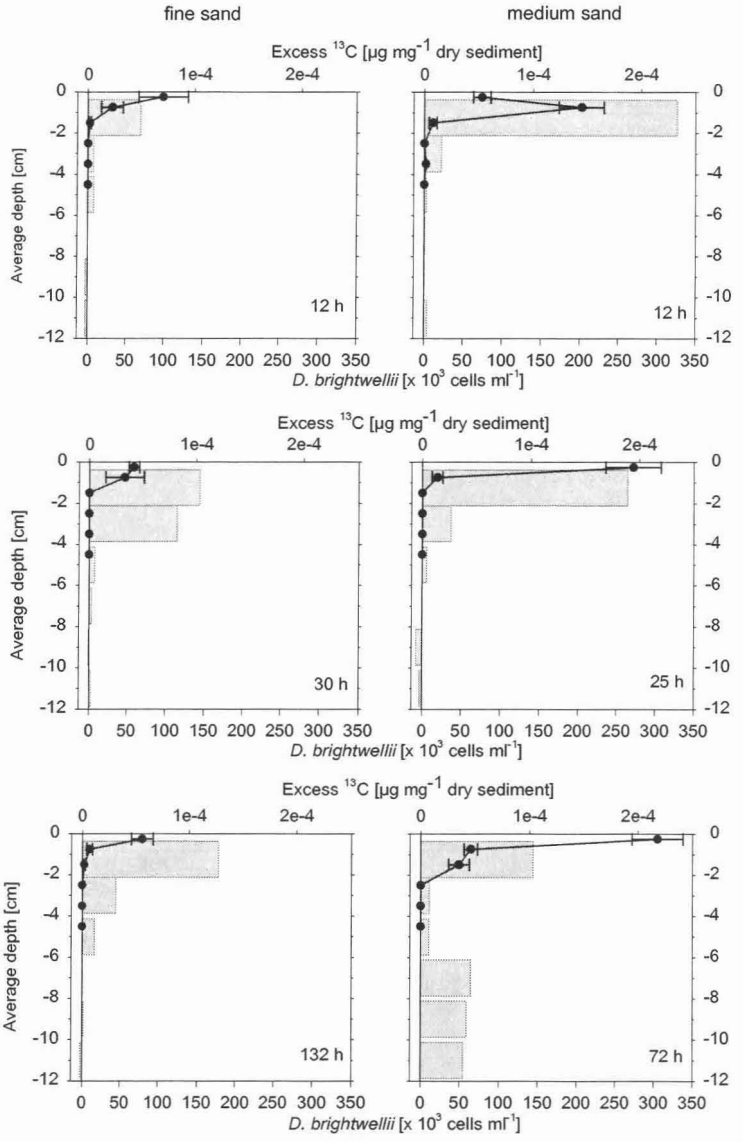

Fig. 6. On-board experiment: Total uptake of ^{13}C-labeled diatoms into fine and medium sand after different periods of incubation. Upper scale: PO^{13}C, plotted without upper 0.5 cm. Lower scale: *D. brightwellii* cells. Fine sand: n = 2; medium sand: n = 1. For the controls, 3 cores were analyzed, and no *D. brightwellii* cells could be detected in any of the sediments.

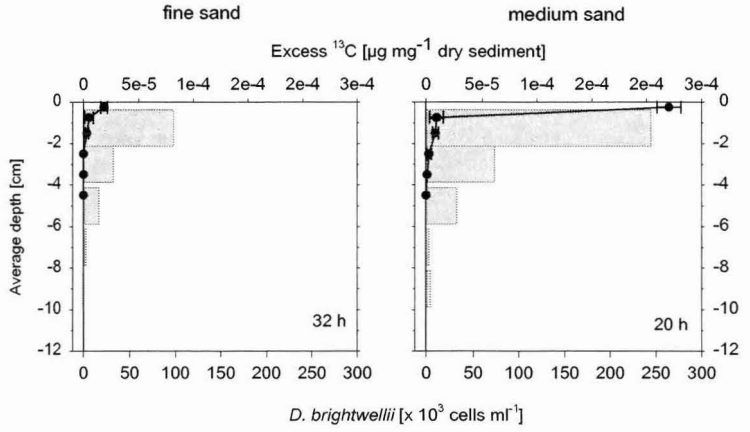

Fig. 7. *In-situ* experiment: Total uptake of ^{13}C-labeled diatoms into a fine (32 h) and medium sand (20 h). Upper scale: PO^{13}C, plotted without upper 0.5 cm. Lower scale: *D. brightwellii* cells. Both experiments were conducted with 2 replicate chambers. For the controls, 3 cores were analyzed, and no *D. brightwellii* cells could be detected in any of the sediments.

Table 2. Flux of *Ditylum brightwellii* cells into or onto the sediment, increase of bacteria, DOC flux and pH changes, measured in the water column of all on-board incubations. The change of cell numbers is given for the first 24 hours of the experiment. pH values are given for the total incubation time. Positive values represent increase; negative values indicate decrease. The pH at the beginning of the experiment was approximately 8.

Sand type	*D. brightwellii* ($\times 10^3$ cells m^{-2} d^{-1})	Bacteria ($\times 10^5$ cells ml^{-1} h^{-1})	DOC (µmol m^{-2} d^{-1})	pH (pH units d^{-1})
Fine sand	-1070	1.35	-1306 (first 72h) + 7183 (72-132 h)	-0.07
Medium sand	-1208	0.55	-1326 (72 h)	-0.05
Coarse sand	-1552	1.02	-1728 (20 h)	-0.09

DOC, pH and bacterial counts

DOC in the water (Table 2) was consumed in all experiments (approx. -1500 µmol m^{-2} d^{-1}), except for the long-time incubation with fine sand, where DOC concentrations increased after 72 h until the end of the experiment (+7183 µmol m^{-2} d^{-1}). During the incubation, pH values in the water column (Table 2) changed only slightly in all experiments (less than -0.1 d^{-1}). Lowest decrease of pH was observed for the medium sand, which also had the lowest bacterial growth in the water during the first day. Highest increase in bacterial numbers within the first day occurred in the water of the fine sand incubations.

DISCUSSION

The incorporation of suspended pelagic diatoms into the sediment usually requires the settling of the algae onto the sediment surface, and then the transfer of the deposited material into deeper layers by biological (Huettel 1990) or hydrodynamical sediment mixing (Jenness & Duineveld 1985). Flow-induced advective transport may additionally enhance the deposition of particles into permeable sediments (Huettel et al. 1996) by direct transfer of suspended algae from the boundary layer into the sediment.

Planktonic diatom species, dominated by *Coscinodiscus* spp., were present in all investigated sands. The two major taxonomic divisions, centric (Centrales, Fig. 3) and pennate diatoms (Pennales, Fig. 4), also reflect a major ecological difference, as Pennales are mainly benthic and Centrales are mainly planktonic (Schrader & Schuette 1981). This division was applicable for most species we identified, with the exception of *P. brockmanni*, *Nitzschia* spp. (Pennales) and *A. senarius* (Centrales), which have been reported as both, benthic and planktonic forms (Drebes 1974). During the spring bloom in 2001, high numbers of *Nitzschia* sp. were present in the plankton of our study site (Ehrenhauß et al. unpublished data), but were only present in the medium and coarse sand in September with relatively low numbers (Fig. 4). Broken parts of diatom frustules from mainly centric species as *Coscinodiscus* spp. and *Thalassiosira* spp., (the latter dominated the diatom spring bloom in 2001 (Ehrenhauß et al. unpublished data)), were abundant in the medium and coarse sands. This may indicates fast breakdown and decomposition of the trapped cells due to mechanical stress in these dynamic sediments. The maximum penetration depth of the dominant planktonic diatom *Coscinodiscus* spp. increased with sediment

permeability: 2 cm, 7 cm and 8 cm (total sampling depth) for the fine, medium and coarse sand, respectively (Fig. 3). This indicates enhanced advective transport of these planktonic diatoms into the highly permeable sands, as could be confirmed by our *in-situ* and on-board experiments.

The diatom *D. brightwellii* (Drebes 1974) is a common species in the German Bight, and was also abundant during the spring bloom in 1998 near our station (53°53 N, 7°32 E) as reported by Lo (1999). The experiments showed fast decrease of the number of added diatom cells in the water (Table 2), resulting from gravitational settling and transport of suspended *D. brightwellii* cells into deeper layers of the permeable sediments (Figs. 6-7). Higher flux of cells into the sediment with increasing permeability demonstrates the greater filtration capacity of coarse-grained sediments.

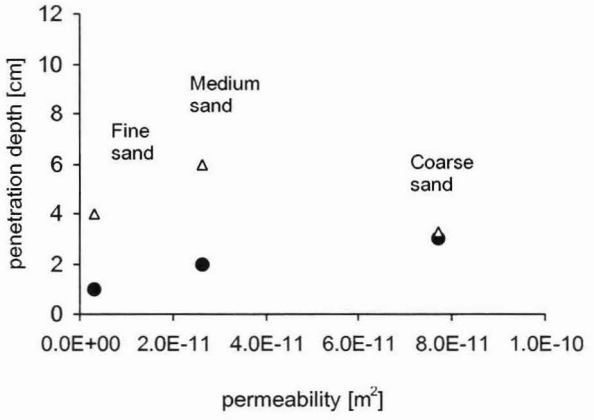

Fig. 8. Penetration depth of *D. brightwellii* cells (circles) and $PO^{13}C$ (triangles) depending on the sediment permeability. Please note different incubation times: 30 h (fine sand) and 20 h (medium and coarse sand). This means that the higher penetration depth of algal cells with increasing permeability was obtained in less time.

Diatom uptake into the sediment correlated with sediment permeability and sand grain size. The deposition and main penetration depths of *D. brightwellii* cells were higher in the coarse (3 cm, data not shown) and medium sands (2 cm) compared to the fine sand (1 cm) (Figs. 6-8). The lower penetration depth of *D. brightwellii* compared to *Coscinodiscus* spp. may be caused by the relatively short incubation time of the experiments, the different cell shapes and cell surface characteristics of both species,

and lower advective pore water flows in the experiments compared to *in-situ* conditions. The pressure gradient in our stirred chambers is comparable to the pressure gradient at sediment ripples of 2 cm height interacting with bottom currents of 10 cm s^{-1} at 10 cm above the sediment surface (Huettel & Rusch 2000). Bottom current velocities at our study site are in the range of 30 to 60 cm s^{-1} at 100 cm above the sediment surface, which could lead to an underestimation of the advective transport of the diatoms in our experiments compared to the natural environment.

Table 3. Transport rates of *D. brightwellii* cells (% of total added algal cells) into the different sediments. The recovery rate of the total algal cells in the sediment was between 10 to 36% (fine sand), 50 to 82 % (medium sand) and 43% for the coarse sand.

Time (h)	Fine sand	Medium sand	Coarse sand
0-0.5 cm depth	(% ± s.d.)	(% ± s.d.)	(% ± s.d.)
12	22.2 ± 7.2	12.0 ± 1.8	
20		70.6 ± 3.5	22.4 ± 2.8
25		44.1 ± 5.8	
30	13.4 ± 1.6		
32	5.9 ± 0.9		
72		49.4 ± 5.3	
132	17.8 ± 3.2		
0.5-4 cm depth			
12	13.6 ± 6.3	60.9 ± 9.9	
20		11.8 ± 6.0	21.0 ± 10.3
25		5.6 ± 2.0	
30	18.5 ± 10.0		
32	4.6 ± 3.0		
72		32.2 ± 6.1	
132	4.9 ± 2.2		

With increasing incubation time (72 h), more cells, corresponding to 32% of the added diatom cells, were transported below 0.5 cm depth of the medium sand (Table 3). After an incubation time of 132 h, the bulk of diatom cells was still found in the uppermost 0.5 cm of the fine sand and only 5% of the added diatoms were found below 0.5 cm. Highest transport rates were recorded in the coarse sand where 21 % of the added algae were found below 0.5 cm after 20 h incubation time. With increasing grain size of the sand bed, a larger volume of water is forced through the sediment. Due to increasing interfacial flows and the larger interstices between the sand grains, the medium and coarse sands were larger sinks for diatom cells than the fine sand. Particles trapped in deeper sediment layers cannot easily be removed again from the sediment by upwelling pore water, as the flow velocity decreases with depth, and

relatively high pore water flows are needed to dislocate trapped material again (Huettel & Rusch 2000).

The pennate diatom species were dominated by *P. brockmanni* in all 3 sands (Fig 4). *P. brockmanni* belongs to the non-motile epipsammic diatom species (Schrader & Schuette 1981), and the single cells are united in long chains (Drebes 1974). In sandy sediments exposed to waves and currents, attached benthic diatoms generally dominate over motile ones (Rusch et al. 2001). *P. brockmanni* has also been reported as being abundant during the spring bloom in the plankton near the Frisian Islands (Drebes 1974). Lo (1999) could also observe high numbers of *P. brockmanni* in the plankton near our station in March (54°02´N, 8°14´E) and April 1998 (54°11´N, 7°21´E). Thus, we do not know if the *P. brockmanni* cells we found lived as benthic form in the sediment or originated from the water column. Under epifluorescence microscopy, chlorophyll autofluorescence was present in the bulk of cells, indicating their living state, however, the non-growing vegetative cells of many diatoms have a long survival time in dark and cold environments (Smayda & Mitchell-Innes 1974). No data are available on the light intensity reaching the sediments, but the sea floor in the southern North Sea is a relatively low light environment (Jerlov 1951). Nevertheless, light may reach the sea floor occasionally in these shallow depths, e.g. during bright summer days.

Studies on the continental shelf of the South Atlantic Bight (14-40 m) revealed that benthic microalgae, which were dominated by diatoms (Nelson et al. 1999), contributed an average of 37 % to the total primary production (Jahnke et al. 2000). Thus, further studies on light penetration to the North Sea floor, benthic primary production and sedimentation rates of phytoplankton will be needed to enlighten these processes.

The vertical distribution of *P. brockmanni* in the fine sand with a subsurface maximum at 1.5 cm may be caused by algal growth, or can be explained by the incorporation of the diatoms by moving sediment ripples (Jenness & Duineveld 1985), which causes typical stripes in up to 5 cm depth in the sediment at the base of the ripples. The vertical distribution of *P. brockmanni* in the medium and coarse sand did not show stripes, but rather a typical distribution as caused by advection. Laboratory chamber experiments, where ripple migration was excluded, showed very similar profiles of advective diatom transport into the sediment (Ehrenhauß & Huettel unpublished data). The maximum penetration depth of *P. brockmanni* was higher in

the medium and coarse sands, indicating that the advective transport of cells was effective down to 8 cm depth (total sampling depth). Furthermore, the depth in which the longest diatom chains could be found and the maximum chain lengths recorded in the sediment increased with permeability (Fig. 5). The average pore sizes in the sediment increase with sediment permeability and sand grain size, therefore the advective transport of diatom cells is more effective in coarser sediments, and the maximum penetration depths of single cells (10 cm) and chains (8 cm) were much higher in the coarse sand compared to the fine and medium sand. For the medium sand, maximum penetration depths of single cells (7 cm) and chains (4 cm) were lower. The smaller pores of the fine sand may have limited the transport of longer *P. brockmanni* chains (>5 cells) into the sediment, and may also have been responsible for the lower penetration depth of chains (3 cm) and single cells (6 cm). These results indicate a positive relationship between the sediment permeability and sand grain size with the maximum penetration depth of single *P. brockmanni* cells or chains (Fig. 9). A negative relationship between the proportion of fine sediments and benthic microalgal biomass in shallow water ecosystems has been shown by Cahoon et al. (1999).

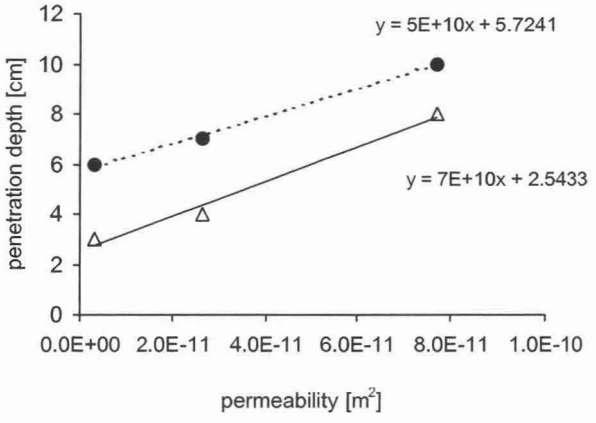

Fig. 9. Maximum penetration depth of *P. brockmanni* cells (circles) and chains (triangles) depending on the sediment permeability.

Besides *P. brockmanni*, three other pennate diatom species occurred: the non-motile epipsammic diatom species *R. amphiceros*, and the motile epipelic diatom species *Navicula* spp. and *Nitzschia* spp.. The fine sand had the lowest diversity of pennate diatom species with *P. brockmanni* and *Navicula* spp., whereas all four pennate species were found in the medium and coarse sand. *Nitzschia* spp. and *R. amphiceros* are relatively big diatom species with a maximum cell size of 120 µm and 90 µm, respectively, which could explain their absence in the fine sand. Higher permeabilities and ensuing higher filtration rates may explain the higher abundance of benthic diatoms in the medium and coarse sands. Another reason could also be deeper penetration of light, if present, in coarse-grained sands than in finer grained sediments (Kühl et al. 1994).

Our results are in agreement with Huettel & Rusch (2000), who demonstrated a higher flux of algal cells (*Dunaliella* sp.) into the sediment with increasing permeability. Pilditch et al. (1998) also observed that coarser sediments can be a larger sink for diatoms, when boundary flows interact with biogenic structures. Laboratory chamber experiments with sieved sediments of different permeabilities (Ehrenhauß & Huettel unpublished data) confirmed the higher filtration capability of coarser sands in trapping planktonic diatoms (*Skeletonema costatum* and *Thalassiosira rotula*). In these experiments, transport of diatoms into the sediment was clearly an effect of advective transport processes, as the algae in the stagnant control chambers mainly accumulated at the sediment surface. Maximum penetration depths of the algae in the stirred chambers were 1 cm, 2 cm and 5 cm for permeable fine, medium and coarse sand comparable to those in this study. The maximum penetration depths are therefore in the same range as in our *in situ* experiments. Higher diatom penetration depth in the coarse sand of the laboratory experiment with a grain size of 1000-500 µm may be attributed to the fact that the natural sediments were not as well sorted as the laboratory sediment. 58% of the coarse sand in our *in-situ* study had a grain size between 1000-500 µm, but the remaining sediment had a lower (33%) or higher (9%) sand grain size (Janssen & Witte in prep.). Therefore, the open pore space was reduced, which may have limited the transport of cells into the sediment. Penetration depth is additionally determined by the size, shape and surface characteristics of the diatom cells (Huettel & Rusch 2000). *S. costatum* and *T. rotula* have both a discoidal shape and a maximum cell size of 10 or 55 µm respectively. *D. brightwellii* has an elongated, prismatic shape with a long spine on both sides and a maximum cell length

of 100 µm (Fig. 2), which most likely caused the lower penetration depth compared to the other diatom species.

Sediment mixing associated with the feeding activities of benthic macrofauna may have also accounted for particle transport into the sediment. Laboratory chamber experiments on the fine sand with *Fabulina fabula* (Tellinidae), the dominant macrofauna species at our fine sand station, revealed that *F. fabula* was responsible for the deposition of algal material down to 5 to 7 cm depths (Kamp 2002). In our *in-situ* study, *D. brightwellii* cells were found only in the uppermost sediment layers (0-2 cm) of the fine sand, but excess ^{13}C was found in depths up to 6 cm (Figs. 6-7). Excess ^{13}C includes not only diatom cells, but also broken parts of the cells, which could not be detected by microscopic observations, and also the incorporation of algal ^{13}C into bacteria and meiofauna. Incorporation of ^{13}C into bacterial phospholipid-derived fatty acids was detectable after 12 h in up to 3 cm depth, and increased with depth after 30 h (Buehring et al. unpublished data). The distribution of excess ^{13}C in the medium sand also exceeded maximum penetration depth of diatom cells, especially in the long-time incubation, where excess ^{13}C was found over the total sampling depth of 12 cm. Maximum detection depth of excess ^{13}C in the sediment also correlated with sediment permeability, except for the coarse sand where excess ^{13}C was only found in the upper 3 cm (Fig. 8). This may be caused by local sediment inhomogeneities. According to Huettel & Gust (1992) advective transport processes may have been limited to the upper 2 cm of the fine sand, whereas this pressure-driven pore water flow can be effective to more than 8 cm depth in the medium and coarse sand. This explains the higher transport of algal cells and excess ^{13}C into deeper sediment layers (below 0.5 cm) of the medium sand compared to the fine sand (Tables 3-4). As macrofauna abundance usually decreases in highly turbulent areas with coarse-grained sediments (Jenness & Duineveld 1985), bioturbation seems to be less important for solute and particle transport in the medium and coarse sand. Pore water nutrient profiles of all 3 sands (Ehrenhauß et al. unpublished data) revealed that advective solute exchange led to reduced silicate, phosphate and ammonia concentrations with increasing sediment permeability. Therefore, the coarse sand had the lowest nutrient concentrations, despite POC concentrations comparable to those in the medium sand (Table 1). Marinelli et al. (1998) found that advection also was the dominant solute transport process in the upper sediment layers of sandy sediments on

the South Atlantic Bight, which had a comparable permeability and sand grain size as our medium and coarse sand.

Table 4. Transport rates of $PO^{13}C$ (% of total added algal $PO^{13}C$) into the different sediments. The recovery rate of the total $PO^{13}C$ in the sediment was between 1.2 to 1.5% (fine sand), 2.4 to 5.2% (medium sand) and 4.9% (coarse sand).

Time (h)	Fine sand	Medium sand	Coarse sand
0-0.5 cm depth	(% ± s.d.)	(% ± s.d.)	(% ± s.d.)
12 h	1.17 ± 1.65	1.87	
20 h		0.76 ± 0.04	4.15
25 h		4.21	
30 h	0.13 ± 0.18		
32 h	0.33 ± 0.13		
72 h		3.41	
132 h	0.46 ± 0.41		
0.5-12 cm depth			
12 h	0.31 ± 0.66	1.17 ± 2.58	
20 h		1.65 ± 2.32	0.75 ± 2.26
25 h		0.97 ± 2.10	
30 h	1.05 ± 1.53		
32 h	0.89 ± 1.36		
72 h		1.14 ± 0.95	
132 h	0.92 ± 1.61		

In our chamber experiments, a DOC increase due to the degradation of the added algal carbon could not be observed during the first 3 days (Table 2). This indicates fast remineralization of the algal material. DOC, thus, did not accumulate in the chamber water within the first three days, because it was effectively used by the increasing bacteria population in the water (Table 2) and sediment (Buehring et al. unpublished data). In laboratory chamber experiments (Ehrenhauß & Huettel unpublished data), we also observed a decrease of DOC concentrations in the water (-1300 to -3900 µmol m^{-2} d^{-1}) after diatom addition during the first days. However, CO_2 concentrations increased immediately after the food pulse (3700 to 6400 µmol m^{-2} d^{-1}), indicating fast degradation of the added algal carbon. The high DOC increase in the chambers with fine sand after the third day (7183 µmol m^{-2} d^{-1}, corresponding to 28% of the added algal carbon), reveals that the diatom carbon was rapidly decomposed. This may also explains the low amounts of $PO^{13}C$ (between 1.2 to 5.2%), that could be recovered from the sediment of the chambers (Table 4). Diatom frustules were still abundant in the sediment (Table 3), as the dissolution of opal by mainly inorganic dissolution is relatively slow. Nevertheless, laboratory chamber

experiments revealed higher dissolution rates of trapped diatom frustules in coarse-grained permeable sediments compared to fine-grained sediments (Ehrenhauß & Huettel unpublished data). Advective solute exchange in highly permeable sediments prevents the build up of silicate concentrations in the pore water, thereby ensuing highest opal dissolution rates.

CONCLUSIONS

Our study area is characterised by high bottom current velocities (Antia 1993) and a distinct sea bed topography, e.g. biogenic structures and sediment ripples. Therefore, advective transport processes take place in these permeable sands, providing an effective pathway for the periodic input of fresh phytodetritus into deeper sediment layers. Stoeck & Kröncke (2001) reported a subsurface chlorophyll a maximum of fresh algal material in sediments of the hydrodynamically high energetic Dogger Bank (North Sea), and concluded that this fresh phytodetritus was recently deposited due to advective transport. Our study supports the view that permeable sediments have a high filtration capability, trap suspended planktonic diatoms and thus prevent the resuspension by strong bottom currents and waves. Trapped in the sediment, these algae are most likely rapidly degraded, as shown by Boon et al. (1998), who demonstrated that a substantial part, up to 40%, of the primary production was buried and subsequently degraded in non-depositional areas of the southern and central North Sea. Further studies are needed to resolve these processes, which are a major issue for carbon and nutrient recycling in shelf sediments.

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Chapter 4

Decomposition of diatoms and nutrient dynamics in permeable North Sea sediments

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ABSTRACT

This study addresses the decomposition of sedimented diatoms in highly-permeable North Sea sand beds. During 3 cruises in 2001 to the southern German Bight, the regeneration of nutrients after the experimental deposition of organic matter corresponding to a typical spring diatom bloom was assessed in *in-situ* and on-board chamber experiments for 2 different permeable North Sea sand sediments. The diatom pulse was followed by a rapid and high regeneration of nutrients during the first day: 5 to 10% d^{-1} of the added nitrogen was converted to NH_4^+, up to 0.64% d^{-1} of the added opal was dissolved to $Si(OH)_4$ and -5 to -6% d^{-1} of the added organic phosphorus was probably rapidly bound to the grains or consumed by bacteria. These results are used to interpret the response in nutrient pore water concentrations in 3 different permeable North Sea sands to seasonal nutrient and phytoplankton dynamics in the water column. The rapid advective solute exchange in these permeable sediments reduces accumulation of regenerated nutrients, as can be concluded from the decrease in $Si(OH)_4$, PO_4^{3-} and NH_4^+ pore water concentrations with increasing permeability of the 3 investigated sands. The dissolution rate of the deposited opal is accelerated as high flushing rates prevent the build up of $Si(OH)_4$ in the pore water. All sands were characterized by relatively high NO_3^- concentrations down to 10 cm depth, indicating that the upper sediment layers are oxidized by advective flushing of the bed. Our results demonstrate that permeable sediments are an important site for organic matter mineralization and nutrient recycling in coastal areas.

KEY WORDS

Diatoms - Nutrient cycles - Permeable sediments - Sediment-water exchange – Advection - North Sea

INTRODUCTION

About 30% of the oceanic primary production takes place in shelf and coastal environments, which cover only a tenth of the ocean area (Jørgensen 1996). This high biological productivity is caused by a variety of factors, including the input of nutrients from rivers, upwelling of nutrient-rich deep waters and the close coupling of benthic and pelagic systems (Wollast 1991). In shelf areas of the northern temperate latitudes, as the North Sea, large and intense phytoplankton spring blooms can provide the bulk of the annual food supply to the benthos (Conley & Johnstone 1995). The typical seasonal succession in the North Sea starts with a diatom-dominated phytoplankton community in spring. $Si(OH)_4$ (dissolved silica) is an essential nutrient for diatoms to synthesize their solid (SiO_2) frustules. In comparison to other nutrients as P and N, the remineralization of particulate silica is relatively slow, as the dissolution rate is mainly controlled by the state of saturation of the surrounding water (Kamatani & Riley 1979). Other factors affecting the dissolution are pH, temperature, the protective organic coating and the content of metals, especially aluminum, incorporated into the silica frustules (Lewin 1961, Hurd 1972).

Due to the shallow nature of shelf areas, up to 50% of the primary production can settle through the water column (Jørgensen et al. 1990), and most of this particulate organic material is remineralized in the sediment. Consequently, the pore water is enriched in nutrients compared to the overlying water column (Rutgers van der Loeff 1980). This concentration gradient leads to a continuous release of nutrients from the sediment to the water by molecular diffusion, which represents the main transport process for solutes in muddy, cohesive sediments (Huettel et al. 1998).

In permeable sediments, however, which cover approximately 70% of the shelf area (Emery 1968), pressure-driven advective transport processes gain significance (Huettel et al. 1998). In such non-cohesive sandy sediments, pore water flows are generated when bottom currents interact with sediment topography (Huettel et al. 1996). This advective exchange facilitates a close coupling between the production process in the water column and the mineralization process in the sediment. Laboratory flume experiments have demonstrated that advective pore water flows can enhance the nutrient efflux (Huettel et al. 1998) and the oxic sediment volume (Forster et al. 1996) of permeable sediments. Advective pore water flows also provide a fast pathway for the transport of particles, like phytoplankton cells, into sandy sediments (Huettel & Rusch 2000). As a result of the effective pore water exchange,

the decomposition of this organic material may be enhanced. Laboratory studies have shown that the dissolution of opal (biogenic silica) increases with sediment permeability (Ehrenhauß & Huettel unpublished data). Therefore, we propose that effective solute exchange due to advection leads to enhanced remineralization rates of diatoms within the sediment matrix. This enhanced opal dissolution may be linked to increased organic matter turnover rates in permeable sediments (Shum & Sundby 1996).

Besides diffusion and advection, bioturbation and bioirrigation are important transport processes for solutes in permeable sediment (Huettel 1990).

In-situ studies of nutrient profiles in permeable shelf sediments (Marinelli et al. 1998, Jahnke et al. 2000) and of nutrient fluxes and pore water concentrations in sandy North Sea sediments (Rutgers van der Loeff 1980, van Raaphorst et al. 1990, Nedwell et al. 1993, van Duyl et al. 1993) revealed that organic-poor sands can have relatively high mineralization rates. Laboratory studies supported these findings, indicating that nutrient regeneration in such sandy sediments may be comparable to those of fine-grained deposits (Hansen & Kristensen 1998, Huettel et al. 1998). These studies demonstrated that the common perception of coastal sand beds being zones of limited sedimentary decomposition activity has to be revised.

This study focuses on nutrient regeneration in North Sea sands with 3 different permeabilities, that were investigated during 3 cruises to the German Bight (Spiekeroog Island) in April, June and September 2001. The study shows the response of the nutrient pore water concentrations in the sandy sediments to the seasonal nutrient and phytoplankton dynamics in the water column. In order to directly compare the remineralization in sediments with different permeabilities, we also quantified the regeneration of nutrients in *in-situ* and on-board chamber experiments in a fine and medium sand after the sedimentation of a simulated diatom bloom. Our study reveals that in permeable North Sea sediments, advective pore water flow increase the transport of particles and solutes into the bed and enhances organic matter remineralization and nutrient release, while pore water solute concentrations remain low compared to muddy sediments.

MATERIALS AND METHODS

Study area

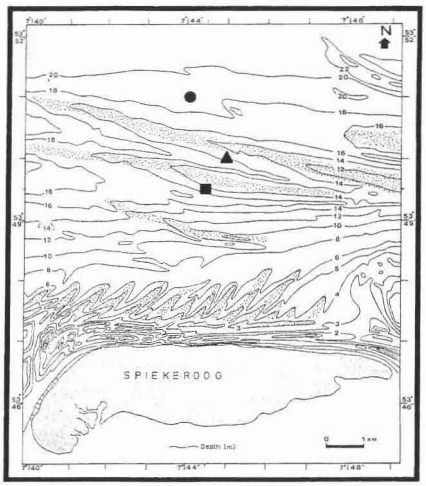

Fig. 1. Bathymetry of the Spiekeroog shoreface in the German Bight, as given by Antia (1993), and locations of the 3 stations. A circle indicates the station with the fine sand, a triangle the medium and a square the coarse sand.

The study site is located seaward of Spiekeroog Island, at the south-east corner of the German Bight (Fig. 1). This coastal area is a high-energy environment and sediment transport is strongly influenced by bottom currents due to tides, waves and storm events (Antia 1995). Mean tidal range at the study site is 2.5 m and current velocities at 1 m above the sea-bed are in the range of 30 to 60 cm s^{-1} (Antia 1993). Salinity varied between 31 and 32.

Measurements and experiments were carried out during 3 cruises of R.V. Heincke in April (HE 145), June (HE 148) and September 2001 (HE 154) on well-studied fine, medium and coarse subtidal sands (Antia 1993, Antia 1995, Janssen & Witte unpublished data), all located within a radius of 2500 m (Table and Fig. 1).

Background sampling

In order to characterize the dynamics of the nutrient concentrations and the diatom bloom situation in the overlying water column, water samples were collected on each cruise with a rosette equipped with 10 L Niskin bottles. The samples were taken at low, incoming, high and outgoing tide in the surface water (2 m depth) and 2 m above the seafloor (April and June: n = 2; September: n = 1).

To compare the interstitial nutrient concentration of the 3 different sands, sediment cores were taken during the September cruise at all 3 stations (fine and medium sand: n = 3; coarse sand: n = 1).

To assess seasonal variations in the pore water nutrient concentrations, sediment cores were taken with a multicorer at the station with fine sand on all cruises. The cores were sliced at intervals of 1 cm, and subsequently the pore water from the individual slices was extracted by centrifugation.

Experiments

In two *in-situ* and two on-board chamber experiments (Table 1), we quantified the impact of organic enrichment on nutrient dynamics in permeable sands (fine and medium sand) using diatoms as organic substrate.

To produce these diatoms, we cultured a clone of *Ditylum brightwellii* (Bacillariophyceae, Biddulphiales) at 25°C in sterile artificial seawater with a salinity of 33 (Grasshoff et al. 1999) enriched with f/2 medium (Guillard & Ryther 1962). The algal material was harvested by centrifugation (404 **g**, 4 min), rinsed 3 times with an isotonic sodium chloride solution and centrifuged again. From this concentrated material samples for dry mass, particulate organic carbon and nitrogen (POC and PON), cell numbers and nutrient concentrations were taken, and then the algae were stored frozen until use.

The cell numbers of *D. brightwellii* added per chamber were $14571 \pm 2453 \times 10^3$ cells L^{-1} (HE 145), $10720 \pm 548 \times 10^3$ cells L^{-1} (HE 148) and $8765 \pm 1876 \times 10^3$ cells L^{-1} (HE 154). With a C:N ratio of 7.79, the amount of carbon and nitrogen of algae added to each chamber corresponded to 25810 µmol C m^{-2} and 3313 µmol N m^{-2} (HE 145), 29973 µmol C m^{-2} and 3848 µmol N m^{-2} (HE 148) and 41629 µmol C m^{-2} and 5344 µmol N m^{-2} (HE 154). Assuming an average N:Si:P mole ratio of 16:16:1 for marine diatoms (Brzezinski 1985), the quantity of silicon added to each chamber was equivalent to the nitrogen addition, and the added phosphorus corresponded to 207 µmol P m^{-2} (HE 145), 240 µmol P m^{-2} (HE 148) and 334 µmol P m^{-2} (HE 154).

Both *in-situ* and on-board experiments were carried out in cylindrical chambers made of acrylic (31 cm height, 19 cm inner diameter). To avoid photosynthesis of local microphytobenthos, all chambers were covered by black foil preventing any light penetration to the incubated water and sediments. The water inside each chamber was stirred by a horizontal disk (17 cm diameter), rotating approximately 10 cm above the sediment surface at 20 rpm. The rotating water column generates a radial pressure gradient of approximately 1.5 Pa cm^{-1} with lowest pressures in the center and highest

at the outer rim of the chamber, comparable to the pressure gradient at sediment ripples of 2 cm height interacting with bottom currents of 10 cm s^{-1} at 10 cm above the sediment-water interface (Huettel & Rusch 2000). This pressure gradient causes advective pore water flows in permeable sediments.

For the *in-situ* experiments, the chambers were deployed and recovered by divers, and the algae were directly injected into the chambers. For the assessment of background values, bottom water was collected 2 m above the seafloor with a rosette at the beginning of the experiment. At the end of the incubation time of 2×32 h (fine sand, HE 148) and 2×20 h (medium sand, HE 154), samples from the chamber water were taken. For the second set of chamber experiments on board of R.V. Heincke, the sediments were cored by the divers using the same benthic chambers. In contrast to the *in-situ* experiment, the chambers with sediment then were closed at the bottom with sealing lids and brought back to R.V. Heincke in order to permit a tighter sampling pattern for the flux measurements. On board, the chambers were kept at *in-situ* temperature, and stirring was started immediately. The on-board experiments ran for 2×12 h, 2×30 h and 2×132 h (fine sand, HE 145) and for 12 h, 25 h and 72 h (medium sand, HE 154). During these incubation periods, water samples for nutrients were taken at regular time intervals. The on-board experiments were first incubated for 12 h without algae, to study the nutrient fluxes prior to the organic matter addition. At the end of all experiments, the entire cores were sliced at intervals of 10×1 cm and 2×2.5 cm. All macrofauna individuals were collected from each layer to quantify macrofauna abundance (Kamp 2002), and the sediment of each slice then was carefully mixed. 20 cm^3 subsamples for pore water nutrient analyzes were taken. In order to assess the pore water nutrient concentrations without organic matter addition, 3 additional sediment cores were taken with a multicorer on the fine and medium sand for every experiment. These cores were sliced and analyzed in the same manner as described for the chamber cores.

Table 1. Positions, sediment and water characteristics of the study sites. The permeability k and the POC concentration of the sediments are taken from (Janssen & Witte unpublished data). For the permeability and POC values, averages (± s.d.) are given. Additionally to the experimental sediment cores retrieved by divers, sediment cores were taken with a multicorer (fine and medium sand: n=3; coarse sand: n=1). n.a.: not analyzed

Cruise	Date	Position	Sand type	k ($10^{-12}m^2$)	Average water depth (m)	Water temperature (°C)	Bottom water POC (mg L^{-1})	Bottom water PON (mg L^{-1})	Bottom water C:N ratio	Sediment POC (% dry mass)	Chamber experiment with algae
HE 145	08. – 18.04.01	53°51´N, 7°44´E	Fine	3.02 (± 1.66)	19	9	0.96 (± 0.02)	0.13 (± 0.00)	7.38	n.a.	On-board (12 h, 30 h, 132 h; n=2)
HE 148	07. – 15.06.01	53°51´N, 7°44´E	Fine	3.02 (± 1.66)	19	13	1.22 (± 0.06)	0.15 (± 0.01)	8.13	0.114 (± 0.014)	*In-situ* (32 h; n=2)
HE 154	24. – 30.09.01	53°51´N, 7°44´E	Fine	3.02 (± 1.66)	19	16	0.61 (± 0.03)	0.07 (± 0.00)	8.71	0.129 (± 0.041)	-
HE 154	24. – 30.09.01	53°50´N, 7°45´E	Medium	26.27 (± 3.26)	16	16	0.61 (± 0.03)	0.07 (± 0.00)	8.71	0.023 (± 0.003)	On-board (12 h, 25 h, 72 h; n=1) + *in-situ* (20 h; n=2)
HE 154	24. – 30.09.01	53°49.5´N, 7°44.5´ E	Coarse	77.24 (± 14.36)	14	16	0.61 (± 0.03)	0.07 (± 0.00)	8.71	0.032 (± 0.003)	-

Analytical procedures

Water column samples for nutrient analyzes were filtered (0.2 µm) and preserved with mercury chloride solution to an end concentration of 0.01% and kept refrigerated at 4°C until processing. Pore water was obtained by centrifugation (2800 **g**, 10 min) of 20 cm^3 of each sediment slice using centrifuge vials with 2 compartments separated by cellulose-acetate filters (0.2 µm), and treated as described for the water column samples.

Silicate ($Si(OH)_4$; 810 nm), phosphate (PO_4^{3-}; 880 nm), ammonia (NH_4^+; 630 nm), nitrate and nitrite (NO_3^- and NO_2^-; 540 nm) in the seawater were determined spectrophotometrically with a Skalar™ 5-channel Continuous-Flow-Analyzer according to the reactions described in Grasshoff et al. (1999).

For dry mass determination of the *D. brightwellii* culture, 1 ml sample was filtered onto pre-combusted (500°C, 6h), pre-weighed GF-F filters, rinsed with distilled water to remove the sodium chloride, dried for 24 h at 60°C and weighed again.

Samples for POC/PON also were filtered onto pre-combusted GF-F filters, pre-treated with 0.1 N HCl for 2 h to remove the bicarbonate and dried at 60°C. The particulate carbon and nitrogen content was measured using a Fisons™ NA1500 elemental analyzer.

Water samples for diatom abundances were preserved with hexamethylenetetramine buffered formaldehyde (end concentration 2%) and Lugol solution (end concentration 1%), and kept refrigerated in dark glass bottles until analysis.

Diatom species were identified (Drebes 1974, Pankow 1990) by a Zeiss™ inverted microscope using the method of Utermöhl (1958) and a magnification of 400 ×.

For the assessment of abundance, a sample aliquot was filtered onto black membrane filters (0.2 µm). All intact fluorescent diatom cells of 20 randomly chosen counting grids of three parallel filters per sample were counted under a Zeiss™ Axiophot epifluorescence microscope (excitation wave length 510-560 nm, magnification 400 ×).

RESULTS

Seasonal dynamics of nutrient concentrations and diatom abundances in the water column

On all 3 cruises, the measurements over a whole tidal cycle did not show any vertical gradients or significant temporal differences in the nutrient concentrations and diatom abundances.

During the April cruise, concentrations of $Si(OH)_4$, PO_4^{3-} and NH_4^+ in the water column at the study site were low, approx. 0.8 µM, 0.1 µM and 0.4 µM, respectively, whereas NO_3^- concentrations exceeded 20 µM (Table 2). In June and September, NO_3^- concentrations were lower, while $Si(OH)_4$, PO_4^{3-} and NH_4^+ were higher.

Table 2. Average nutrient concentrations and diatom numbers (± s.d.) in the water column. NO_2^- concentrations remained below the detection limit of the method (0.6 µM). As nutrient concentrations and diatom numbers did not significantly differ, neither between surface and bottom water, nor within the tidal cycle, they were averaged. In April, many zooplanktonic larvae and the following diatoms were sporadically present in the plankton: *Thalassionema nitzschioides*, *Biddulphia* spp., *Eucampia zoodiacus* and *Stephanopyxis turris*.

Nutrient concentration (µM)	April 2001 (n = 2)	June 2001 (n = 2)	September 2001 (n = 1)
$Si(OH)_4$	0.81 (± 0.21)	2.64 (± 0.27)	8.02 (± 0.35)
PO_4^{3-}	0.10 (± 0.00)	0.19 (± 0.04)	0.60 (± 0.00)
NH_4^+	0.36 (± 0.15)	6.52 (± 0.82)	5.82 (± 0.37)
NO_3^-	23.04 (± 2.09)	10.19 (± 0.74)	4.21 (± 0.50)
Frequently occurring diatoms ($\times 10^3$ cells L^{-1})			
Thalassiosira sp.	5937 (± 816)	242 (± 106)	65 (± 113)
Rhizosolenia setigera	2277 (± 392)	90 (± 33)	3 (± 5)
Chaetoceros spp.	2069 (± 679)	0	0
Nitzschia sp.	2024 (± 661)	0	0
Skeletonema costatum	1729 (± 420)	1349 (± 477)	0

During all seasons investigated, the phytoplankton community was dominated by diatoms (Table 2). The highest diatom numbers and diversity were found in April, with *Thalassiosira* sp. being the dominant genus. Other important diatoms were *Rhizosolenia setigera*, *Chaetoceros* spp., *Nitzschia* sp. and *Skeletonema costatum*. With exception of *R. setigera*, the community was dominated by small (2-40 µm), chain-building diatoms. In June diatom numbers and diversity had decreased, only 3 species could be found. The dominant diatom was *S. costatum*. In September only 2

diatom species, *Thalassiosira* sp. and *R. setigera*, were sporadically present in the plankton.

The particulate organic carbon and nitrogen content of the bottom water showed the highest concentrations in April and June (Table 1). In September these concentrations had decreased to roughly half the amount (0.61 and 0.07 mg L^{-1}). The C:N ratio increased from 7.38 in spring to 8.71 in autumn.

Seasonal variations in the pore water nutrient concentrations of the fine sand

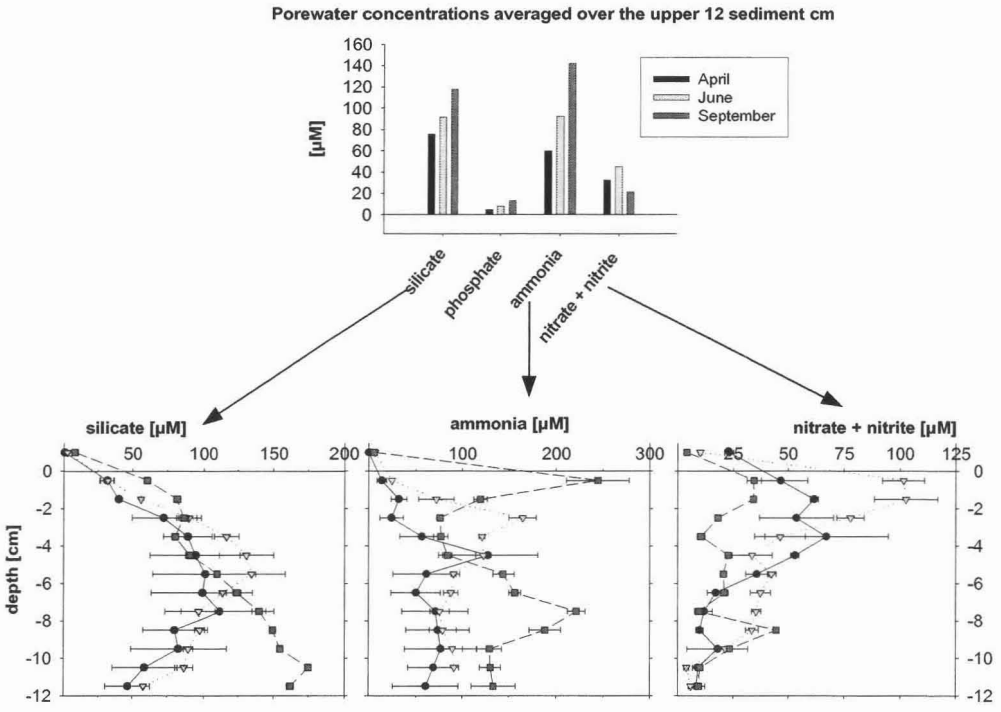

Fig. 2. Pore water nutrient concentrations averaged over the upper 12 sediment cm, and nutrient profiles in the fine sand (n = 3) in April (circles), June (triangles) and September (squares).

Pore water nutrient concentrations were always higher than the concentrations in the overlying water (Fig. 2). $Si(OH)_4$, PO_4^{3-} and NH_4^+ concentrations were increasing from April to September, while the NO_3^- and NO_2^- concentrations reached highest values in summer and were lowest in fall. In the upper 7 cm, $Si(OH)_4$ showed very similar profiles in all seasons with concentrations increasing with depth (Fig. 2). PO_4^{3-}

(data not shown) remained relatively low and homogenous over the sediment depth investigated (2-14 µM). In autumn, very high NH_4^+ concentrations were found in the upper centimeter (240 µM). NO_3^- and NO_2^- were present in all cores down to 12 cm, and in general, the concentration decreased with depth.

Nutrient fluxes in the on-board experiments and pore water concentrations (*in-situ* and on-board) in the 3 North Sea sands with different permeabilities

With permeabilities exceeding 10^{-12} m^2 (Table 1), advective transport processes took place in all 3 sediments (Huettel & Gust 1992). The content of particulate organic carbon in the fine sand was significantly higher than in the medium and coarse sand, which had comparable POC concentrations (Janssen & Witte unpublished data). Fluxes could be measured only for the fine and medium sands.

The $Si(OH)_4$ profiles (Fig. 3) showed low and homogeneous concentrations in the medium (approx. 50 µM) and especially in the coarse sand (approx. 25 µM). In the upper 4 cm of the fine sand, $Si(OH)_4$ reached 60 to 80 µM and increased with depth to 215 µM at 14 cm. The $Si(OH)_4$ fluxes for the fine and medium sand (Table 3) were directed out of the sediment and about 40 µmol m^{-2} d^{-1} higher for the medium sand.

PO_4^{3-} pore water concentrations were relatively low and homogeneous (2-14 µM) over total depth for all sediments (data not shown). PO_4^{3-} fluxes were low for the fine sand or not detectable for the medium sand (Table 3).

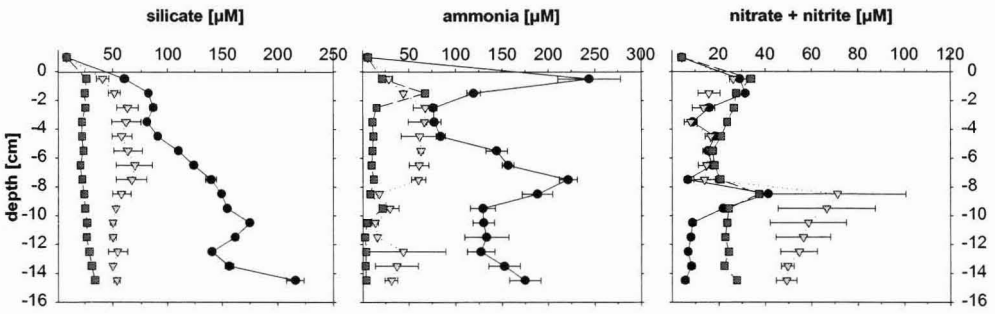

Fig. 3. Nutrient profiles in the fine (circles), medium (triangles) and coarse sand (squares) in September. 3 replicate cores were taken for the fine and medium sand, 1 core for the coarse sand.

The fine sand stood out by the highest average NH_4^+ concentration over total depth, with up to 250 µM in the surface layer and at 8 cm depth. In contrast NH_4^+ concentrations in the medium sand never exceeded 80 µM, and lowest values were found at the sediment surface. The coarse sand was characterized by the lowest and most homogeneous NH_4^+ concentration over total depth. The NO_3^- and NO_2^- profiles of the fine and coarse sand were very similar, with relatively homogeneous concentrations over total depth (<40 µM). In the upper 8 cm of the medium sand, NO_3^- and NO_2^- concentrations were also in the same range as in the other sediments, but underneath the concentration exceeded 70 µM. The fine and medium sand behaved differently in their dissolved inorganic nitrogen sediment-water exchange rates. The fine sand was a source for NH_4^+ and a sink for NO_3^-, whereas the medium sand consumed NH_4^+ and released NO_3^- at relatively high fluxes.

Table 3. Calculated flux of nutrients out of the sediment in the on-board experiments with (+) and without (-) addition of diatoms. Positive fluxes represent net transport from sediments to the overlying water; negative fluxes indicate net transport from the seawater to the sediment. The sediment-water exchange rates were obtained from the nutrient concentration changes in the water with time and the fluxes were calculated from the slope of a linear regression curve. $Si(OH)_4$ fluxes showed a significant linear trend ($R^2>0.9$) for all sediments. This trend could not be observed for PO_4^{3-} ($0.3<R^2>0.9$). All NH_4^+ fluxes showed a clear linear trend ($R^2>0.90$), except for the medium sand incubation with algae ($R^2<0.1$). With the exception of the fine sand with algae addition ($R^2<0.1$), all NO_3^- fluxes were significant linear ($R^2>0.9$). NO_2^- concentrations remained below the detection limit of the method (0.6 µM).

Sand type	fine	fine	medium	medium
Organic enrichment	-	+	-	+
$Si(OH)_4$ (µmol m^{-2} d^{-1})	+ 228.4	+ 300.5	+ 269.4	+ 220.1
PO_4^{3-} (µmol m^{-2} d^{-1})	- 1.8	- 32.7	0.0	- 61.2
NH_4^+ (µmol m^{-2} d^{-1})	+ 98.1	+ 542.4	- 327.4	+ 33.3
NO_3^- (µmol m^{-2} d^{-1})	- 199.3	+ 44.9	+ 1161.2	+ 299.6

Influence of organic enrichment on nutrient fluxes in permeable sediments of the on-board experiments

We observed an immediate response to the simulated diatom bloom in the sediment-water exchange rates that was most pronounced in the inorganic nitrogen components (Table 3). Conversion of the added opal to $Si(OH)_4$ (Table 4) was very slow and amounted to +0.64% d^{-1} of the added silica for the fine sand, and here the efflux

slightly increased (Table 3). In the chambers with the medium sand dissolved silica was consumed or adsorpted (-0.27% d^{-1} of the added opal), and the efflux decreased. Both sands consumed more PO_4^{3-} after the diatom addition. The NH_4^+ efflux from the fine sand increased nearly 6-fold after the algal addition (10.40% d^{-1} of the added organic nitrogen), whereas the direction of the NO_3^- flux changed from consuming to releasing NO_3^- to the water column (1.66% d^{-1} of the added organic nitrogen). In the chambers with medium sand, the conversion of the added nitrogen to NH_4^+ amounted to 5.23% d^{-1} and the sand became a source of NH_4^+, while NO_3^- fluxes were reduced after the food pulse.

Table 4. Calculated daily conversion (% d^{-1}) of the added organic material into inorganic nutrients and release to the overlying water in the on-board chamber experiments. Rates were obtained from the differences between the nutrient fluxes before and after the addition of diatoms (Table 3) and calculated as percentage of the maximum concentrations and fluxes assuming complete conversion of the added algae into inorganic nutrients. Positive values represent mineralization into nutrients and release to the overlying water; negative fluxes indicate consumption by organisms or adsorption of the released nutrients.

Sand type	fine	medium
$Si(OH)_4$	+ 0.64	- 0.27
PO_4^{3-}	- 4.87	- 5.98
NH_4^+	+ 10.40	+ 5.23
NO_3^-	+ 1.66	- 3.64

Influence of organic enrichment on pore water nutrient profiles in permeable sediments (on-board and *in-situ* experiments)

After the addition of diatoms, we observed changes in the nutrient pore water profiles (Figs. 4-5). In general, $Si(OH)_4$ decreased in the fine and medium sand relative to the control cores (Fig. 4). Also, total PO_4^{3-} concentrations (data not shown) were slightly reduced in the fine and medium sand compared to the control.

Addition of algal material had no clear influence on the NH_4^+ profiles (Fig. 5) of the fine sand, but reduced the concentration in all incubations with the medium sand. Although the NO_3^- and NO_2^- profiles (Fig. 5) in the 12 h and 30 h on-board incubation on the fine sand did not show any significant trend, pore water concentrations were reduced to a third of the control values after 132 h. This contrasts with the doubled pore water concentrations in the *in-situ* experiments in the fine sand after 32 h. In all

chambers with the medium sand, the food pulse was followed by an increase of the NO_3^- and NO_2^- concentrations in the upper 8 cm.

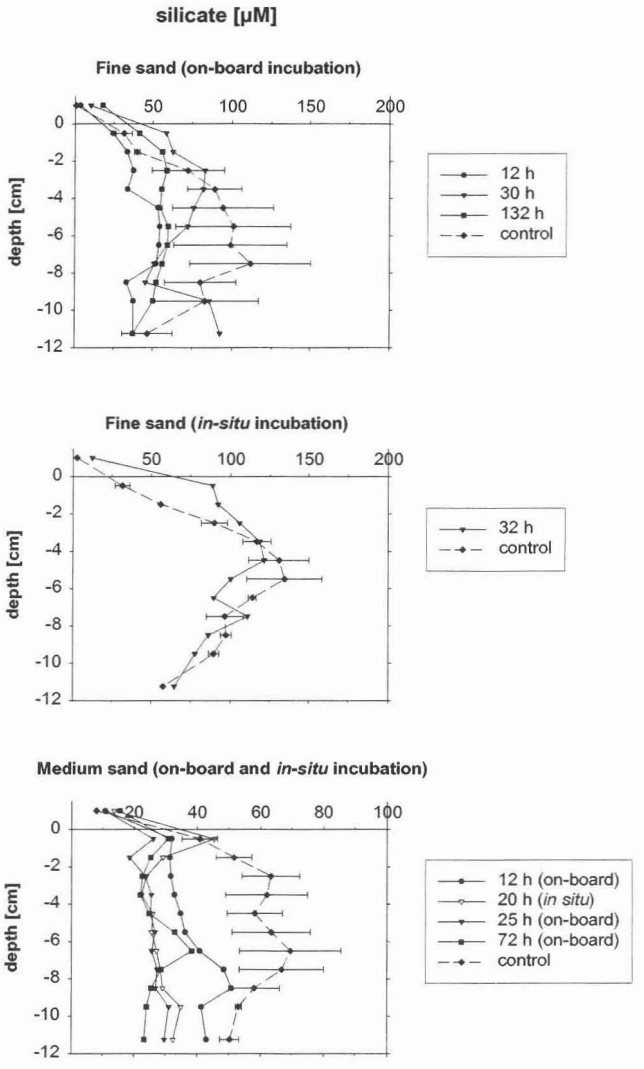

Fig. 4. $Si(OH)_4$ pore water concentrations in the enrichment experiments after 12 h (circles), 20-32 h (triangles) and 72-132 h (squares). Fine sand (on-board and *in-situ*): n = 2; Medium sand: on-board: n = 1 and *in-situ*: n = 2. For the controls (diamonds), 3 cores were analyzed.

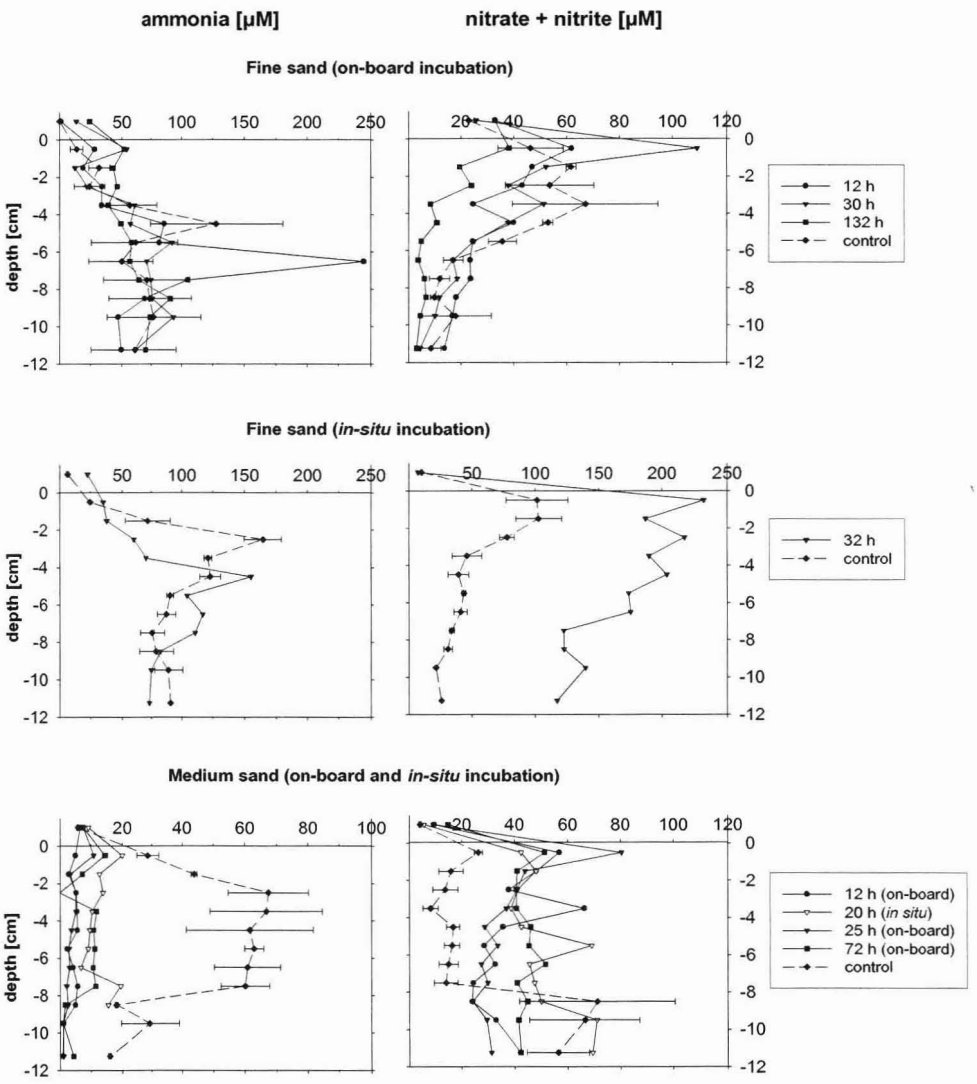

Fig. 5. NH_4^+, NO_3^- and NO_2^- pore water concentrations in the enrichment experiments after 12 h (circles), 20-32 h (triangles) and 72-132 h (squares). Fine sand (on-board and *in-situ*): n = 2; Medium sand: on-board: n = 1 and *in-situ*: n = 2. For the controls (diamonds), 3 cores were analyzed.

Macrofauna abundances in the chambers with the fine sand

The total dry mass of the macrofauna found in the chambers (Table 5) increased from 14959 ± 10090 mg m^{-2} in April to 36903 ± 22418 mg m^{-2} in June. Also the macrofauna abundances were higher in June (971 ± 113 individuals m^{-2}) than in April (610 ± 347 individuals m^{-2}). The bivalve *Fabulina fabula* (Tellinidae) was the dominant macrofauna species with an average abundance of 34 to 64% of all individuals. Thus, the fine sand can be characterized as *Fabulina fabula* community, which has been reported as most frequently occurring macrofauna community in the German Bight (Salzwedel et al. 1985). Besides, 12 other species could be determined, with *Nephtys* spp. (Nephtyidae) as the most frequently observed polychaete, *Urothoe poseidonis* (Haustoriidae) as the most abundant crustacean, and *Echinocardium cordatum* (Spatangidae) with the highest numbers for Echinodermata. Sporadically occurring species with high biomass were the polychaetes *Lanice conchilega* (Terebellidae) and *Nereis* sp. (Nereididae).

Table 5. Macrofauna abundances (N m^{-2}) and dry mass (DM in mg m^{-2}) in the cores of the on-board and *in-situ* experiments (fine sand).

		on-board (HE 145)						*in-situ* (HE 148)	
		12 h (n = 2)		30 h (n = 2)		132 h (n =2)		32 h (n = 2)	
		N	DM	N	DM	N	DM	N	DM
Bivalvia	*Fabulina fabula*	127	1968.2	334	4968.2	287	1821.7	621	16047.8
	Montacuta bidentata	64	6.4	303	35.0	16	3.2	64	6.4
	Montacuta ferruginosa	-	-	16	6.4	-	-	48	98.7
	Spisula sp.	-	-	-	-	-	-	16	22.3
Polychaeta	*Nephtys caeca + hombergii*	80	162.4	48	350.3	48	1353.5	143	16630.6
	Lanice conchilega	-	-	32	3143.3	32	1420.4	48	4082.8
	Magelona mirabilis	16	6.4	-	-	143	172.0	-	-
	Nereis sp.	-	-	16	17812.1	-	-	-	-
	Eumida bahusiensis	-	-	-	-	-	-	16	22.3
Crustacea	*Urothoe poseidonis*	-	-	207	101.9	-	-	16	3.2
	Crangon crangon	-	-	16	789.8	-	-	-	-
Echinodermata	*Echinocardium cordatum*	16	1968.2	16	1203.8	-	-	-	-
Cnidaria	*Actinaria*	-	-	-	-	16	7582.8	-	-
Macrofauna	N and DM per m^2	303	4111.5	987	28410.8	541	12353.5	971	36914.0

DISCUSSION

Seasonal dynamics of nutrient concentrations and diatom abundances in the water column

In mixed turbulent nearshore waters of the German Bight diatoms usually dominate over dinoflagellates (Hesse et al. 1995). In April a typical spring situation was found at our study site: a diatom bloom, dominated by *Thalassiosira* sp., had decreased the $Si(OH)_4$ and PO_4^{3-} concentration in the water column (Table 2), whereby total primary production was limited. Low PO_4^{3-} concentrations can limit primary production in coastal areas (Bauerfield et al. 1990, Woodward & Owens 1990). NH_4^+ also was almost depleted, but NO_3^- concentrations were still high. This NO_3^- probably originated to a large extent from the input of the rivers Weser and Elbe (Raabe et al. 1997). Lo (1999) observed very similar water column nutrient concentrations close to our station (53°53N, 7°32E) in April 1998, (1.6 µM $Si(OH)_4$, 0.3 µM PO_4^{3-}, and 16.2 µM NO_3^-). The diatoms *Thalassiosira* sp., *Rhizosolenia* spp. and *Chaetoceros* spp. were also dominating the spring bloom in 1998, suggesting that the situation we found during our investigations is not uncommon.

After spring until autumn, remineralization processes increased the concentrations of $Si(OH)_4$ and NH_4^+ in the water column, whereas PO_4^{3-} remained at very low concentrations. NO_3^- decreased, reflecting reduced input from the rivers Weser and Elbe (Beddig et al. 1997) or enhanced uptake by phytoplankton (new production), as NH_4^+ concentrations were approx. 5 µM in autumn and algae prefer NH_4^+ for their nitrogen supply only as long as its concentration exceeds 5 µM (Strickland et al. 1969). The C:N ratio of the suspended particulate organic material indicated a marine origin of the organic matter. In all cruises the ratio lied between 7 and 8 (Table 1), a ratio typical for phytoplankton that in our case was dominated by diatoms (Hansen & Kristensen 1998). The C:N ratio increased from spring to autumn, reflecting the preferred mineralization of nitrogen over carbon in fresh organic matter (Officer & Ryther 1980).

Seasonal variations in the pore water nutrient concentration of the fine sand

The nutrient concentration in the sediment is controlled by transport (sediment-water exchange), nutrient release (by fauna, bacteria and dissolution) and uptake (by plants, bacteria and adsorption) (Asmus 1986).

The observed increasing $Si(OH)_4$ concentrations with depth (Fig. 2) are a result of biogenic silica dissolution in the sediment, $Si(OH)_4$ uptake by diatoms at the surface (Ehrenhauß et al. unpublished data) and advective transport processes removing dissolved silica from the surface layer. The $Si(OH)_4$ concentrations averaged over the investigated sediment depth increased from spring to autumn, reflecting dissolution of biogenic silica due to the decay of diatoms grown during spring bloom and summer (Table 2), and enhanced dissolution rates due to higher temperature and bacterial activity in fall (Table 1) (Lewin 1961). Bacteria can enhance the dissolution of opal by several mechanisms that include the degradation of the protective organic coating (Bidle & Azam 1999) and the excretion of metabolites like organic acids, which accelerates the dissolution (Assmy 1999).

The average NH_4^+ concentration in the sediment also increased from April to September, indicating an increase of remineralization of organic matter and macrofaunal activity (incl. excretion of NH_4^+ (Henriksen et al. 1983)) from spring to autumn. The average POC concentration in the fine sand was slightly higher in September compared to June (Table 1), but significantly higher only in the uppermost cm (Janssen & Witte unpublished data). The NH_4^+ values in the upper 1 cm also were very high in September, indicating enhanced mineralization activity due to recently deposited material. Higher remineralization and temperature in September led to lower oxygen concentration in the sediment, as could be concluded from the NO_3^- and NO_2^- profiles with relatively low concentrations in autumn. Decreasing oxygen can lead to enhanced release of PO_4^{3-} from the particulate fraction (Sundby et al. 1986), and this may also have contributed to the higher PO_4^{3-} concentrations in autumn.

In spring and early summer the NH_4^+ concentrations in the upper sediment layer were very low, whereas NO_3^- concentrations were high. NO_3^- concentrations in the pore water of the upper 6 cm always exceeding those in the overlying water column revealed nitrification in the upper sediment layers. In all seasons NO_3^- and NO_2^- decreased from the sediment surface downwards, reflecting decreasing oxygen concentration and nitrification, and increase in NO_3^- reduction with depth. Significant assimilation of NO_3^- by local microphytobenthos is unlikely, because the NH_4^+ concentration never dropped below 5 μM.

Marinelli et al. (1998) also observed an increase of pore water $Si(OH)_4$ and NH_4^+ concentrations in permeable sediments of the South Atlantic Bight continental shelf from spring to autumn. These results imply that pore water concentrations are "reset"

to relatively low concentrations during winter, as a result of decreasing temperature and increasing storm activities. The same mechanism can be assumed for the North Sea, where the nutrient concentrations in the water column also are characterized by an annual cycle (Radach & Pätsch 1997).

Nutrient fluxes in the on-board experiments and pore water concentrations (*in-situ* and on-board) in the 3 North Sea sands with different permeabilities

The 3 stations are located within a radius of 2500 m (Fig. 1). This implies that all 3 stations are exposed to similar water column characteristics and tidal currents. Nevertheless, the pore water nutrient concentrations differed in the 3 sands (Fig. 3), indicating that the different sediment characteristics, e.g. the permeability, and faunal abundance affected the nutrient concentrations in the bed. The fine and medium sand also acted differently as sources and sinks for nutrients, which can be related to their different permeabilities (Table 3).

Based on the observations of Huettel & Gust (1992), the main transport processes for solutes in highly permeable sediments like those investigated in this study are advection in the uppermost sediment layer followed by bioturbation and diffusion below that layer. The depth ranges of the different processes are dependent on sediment permeability. In the fine sand with a permeability of 3.0×10^{-12} m^2, advective transport processes may have been limited to the upper 2 cm of the sediment (Huettel & Gust 1992). In the medium and coarse sand, the pressure-driven pore water exchange can be effective in up to 8 cm depth (Marinelli et al. 1998).

This is also visible in the $Si(OH)_4$ and NH_4^+ profiles of the 3 different sands (Fig. 3). Efficient advective pore water exchange may have been responsible for the lower $Si(OH)_4$ and NH_4^+ concentrations in the coarse sand compared to the medium sand, despite comparable POC concentrations (Table 1). The profile of the fine sand with relatively low $Si(OH)_4$ concentrations in the upper 4 cm and increasing concentrations with depth below that layer, reveals that pore water exchange due to advection here was restricted to the upper sediment layer. Comparing the $Si(OH)_4$ effluxes of the fine and medium sand (Table 3), more $Si(OH)_4$ was released from the medium sand indicating enhanced pore water exchange and dissolution of particulate silica in this sand. Gehlen et al. (1995) also demonstrated reduced $Si(OH)_4$ pore water concentrations with increasing permeability in their study on 3 different permeable

sediments in the southeastern North Sea (mud, fine and medium sand), but in contrast to our study their $Si(OH)_4$ fluxes were reduced with increasing permeability. Benthic diatoms, like *Navicula* spp., were present in all 3 sands (Ehrenhauß et al. unpublished data). The average benthic diatom numbers did not differ in the medium and coarse sands (approx. 12.0×10^3 cells ml^{-1}), but were lower in the fine sand (4.9×10^3 cells ml^{-1}). As benthic diatoms can be a sink for regenerated nutrients in the sediment (Marinelli et al. 1998), the uptake of nutrients should have lied in the same order of magnitude for the medium and coarse sand, but should have been lower in the fine sand. This also may contribute to the higher nutrient concentration in the fine sand compared to the other two sands. Macrofauna was abundant in the fine sand (Table 5), indicating that bioturbation here may be an important transport process for solutes. As macrofauna abundance decreases in coarse-grained sediments (Jenness & Duineveld 1985), bioturbation is probably less important for solute and particle exchange in the medium and coarse sand. The biogenic activity of benthic macrofauna increases the release of inorganic nitrogen from the sediment, mainly in the form of NH_4^+ (Henriksen et al. 1983), what probably contributed to the NH_4^+ release from the fine sand.

The NO_3^- and NO_2^- concentrations were relatively high and in the same order of magnitude in all 3 sands over the total sampling depth (15 cm), revealing that pore water exchange, at least sometimes, can reach down to these deeper sediment layers. With these pore water flows, NO_3^- could be carried deeper into the sediment or oxygen transported by this water could enhance nitrification in the deeper layers. Ziebis et al. (1996) demonstrated that advective transport processes could enhance the oxygen penetration depth about 2-fold in permeable sediments of the North Sea ($K = 5 \times 10^{-12}$ m^{-2}). For the fine sand, NH_4^+ was by far the dominant form of fixed nitrogen. In the medium sand NH_4^+ and $NO_3^- + NO_2^-$ concentrations were of the same order of magnitude, while in the coarse sand, NO_3^- and NO_2^- were dominant over NH_4^+ (Fig. 6). These results indicate the enhanced advective transport of oxygen into the sediment with increasing permeability, which results in higher nitrification and NO_3^- concentration. This hypothesis is supported by the relatively high NO_3^- flux from the medium sand.

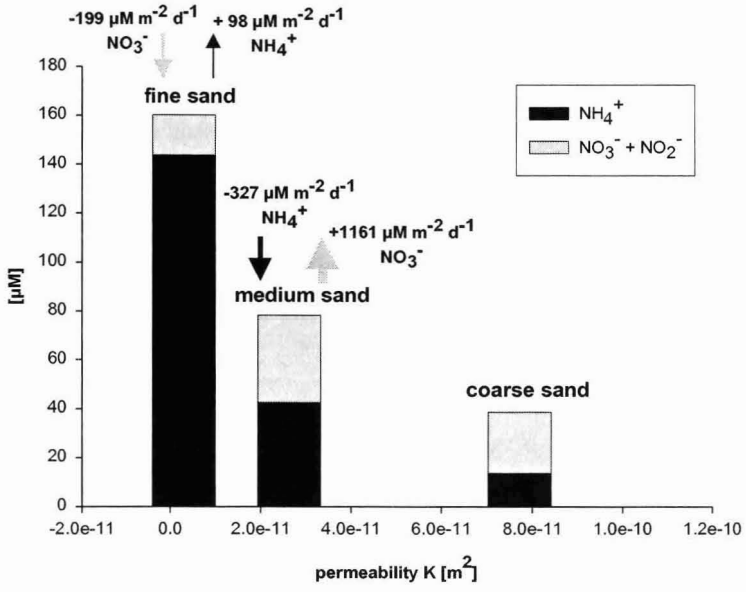

Fig. 6. DIN pore water concentrations (µM) averaged over the upper 15 sediment cm for the fine, medium and coarse sand, and sediment-water exchange rates (µmol m^{-2} d^{-1}) for the fine and medium sand.

PO_4^{3-} fluxes were low for the fine sand or not detectable as for the medium sand. In oxic sediments, more PO_4^{3-} is bound to iron-rich particles than in anoxic sediments (Gunnars & Blomqvist 1997), leading to low PO_4^{3-} concentrations and reduced exchange rates. Besides, benthic heterotrophic bacteria have been reported to be a sink for PO_4^{3-} in sandy North Sea sediments (van Duyl et al. 1993).

Marinelli et al. (1998) found relatively low and nearly vertical $Si(OH)_4$ (<80 µM) PO_4^{3-} (<8 µM) and NH_4^+ (<80 µM) profiles in permeable South Atlantic Bight sediments with a median grain size ranging from 200 to 700 µm. The median grain sizes of the sands we studied were 164, 299 and 672 for the fine, medium and coarse sand, respectively (Janssen & Witte unpublished data). The medium and coarse sand, which had comparable medians as the sands investigated by Marinelli et al. (1998), showed very similar profiles for $Si(OH)_4$, PO_4^{3-} and NH_4^+ as those found in the South

Atlantic Bight. Previously reported sediment-water nutrient fluxes in sandy North Sea sediments (van Raaphorst et al. 1990, Lohse et al. 1993, van Duyl et al. 1993) were in the range of 55 to 701 μmol m^{-2} d^{-1} $Si(OH)_4$, -6 to 67 μmol m^{-2} d^{-1} PO_4^{3-}, -2 to 745 μmol m^{-2} d^{-1} NH_4^+ and 72 to 724 μmol m^{-2} d^{-1} NO_3^-. The $Si(OH)_4$ and PO_4^{3-} fluxes measured in our study were comparable, but the inorganic nitrogen fluxes were quite different. The medium sand was a greater sink for NH_4^+ (-327 μmol m^{-2} d^{-1}), but released instead more NO_3^- (1161 μmol m^{-2} d^{-1}), indicating higher nitrification in this sand. High nitrification rates in sediments of the North Sea have been described by several authors (Rutgers van der Loeff 1980, van Raaphorst et al. 1990). The relatively low release of NH_4^+ from the fine sand and the high uptake observed in the medium sand may be attributed to the uptake of NH_4^+ by bacteria (van Duyl et al. 1993) or benthic diatoms (Marinelli 1992). Nutrient uptake by benthic microalgae led to no measurable light and dark nutrient fluxes in permeable sediments of the South Atlantic Bight despite advective pore water transport (Jahnke et al. 2000).

Compared to muddy sediments, our permeable sediments were characterized by relatively high NO_3^- concentrations and low, nearly constant $Si(OH)_4$, PO_4^{3-} and NH_4^+ concentrations over depth, with average concentrations that decreased with increasing permeability. The fine sand behaved differently compared to the medium and coarse sand, because advective transport processes were limited to the upper 2-4 cm of the sediment and, thus $Si(OH)_4$, PO_4^{3-} and NH_4^+ concentrations below the surface layer were much higher than in the coarser sands. Compared to the fine sand, the medium sand was a greater source for $Si(OH)_4$ and NO_3^- and not a sink for PO_4^{3-}, stressing the importance of this highly permeable sand for nutrient regeneration. An *in-situ* study at the same site, using the novel autonomous chamber system "Sandy" for permeable sediments, confirmed a significant release of NH_4^+ only for the fine sand, whereas the medium and coarse sand released high amounts of NO_3^- and NO_2^- (Janssen & Witte unpublished data).

Influence of organic enrichment on nutrient fluxes and pore water nutrient profiles in permeable sediments (on-board and *in-situ* experiments)

The typical seasonal succession in the North Sea starts with a diatom dominated phytoplankton community in spring. The planktonic diatom *D. brightwellii* used in our study is a common species in the North Sea and has been reported to form blooms in spring (Raabe et al. 1997). The C:N ratio of the added diatoms was 7.8, and lied in

the same order of magnitude as the C:N ratio of the particulate organic matter in the bottom water of the study area (Table 1). The amount of POC added (between 0.31 and 0.50 g C m^{-2}) is roughly half of the daily export production to the sediment in the North Sea (Southern Bight), which was given by Wollast (1991) as 170 g C m^{-2} yr^{-1}. The added *D. brightwellii* numbers ranged from 8765 to 14571 $\times$ 10^3 cells L^{-1}, which are in the same order of magnitude as the diatom numbers in the water of the study site in April (around 14000 $\times$ 10^3 cells L^{-1}; Table 2). Thus, conditions in our bloom simulation experiment are similar to natural conditions in the German Bight.

The response of sediments to increases in the deposition rate of organic matter may vary depending upon a variety of factors including differences in sediment type (van Raaphorst et al. 1992) and the abundance of benthic macrofauna (Aller 1982).

In this study, the fine and medium sand showed different responses to the food pulse. With exception of PO_4^{3-}, nutrient fluxes and pore water concentrations changed differently in both sands.

$Si(OH)_4$ fluxes from the fine sand increased after the bloom event (Table 3) and the pore water $Si(OH)_4$ concentrations decreased (Fig. 4). This indicates that the addition of organic material was followed by an enhanced activity of the macrofauna, which flushed $Si(OH)_4$ from the sediment. Therefore, the increased $Si(OH)_4$ concentration in the water (+0.64% d^{-1} of the added opal; Table 4) can not be linked to the dissolution of the added diatoms only. Burrowing species, like *Lanice conchilega* and *Nereis* sp. and to some extent *Nephtys hombergii*, were present in the fine sand (Table 5), and enhanced $Si(OH)_4$ fluxes resulting from bioturbation by *Nereis* sp. were reported before (Asmus 1986).

The lower $Si(OH)_4$ concentrations in the pore water of the medium sand were not balanced by an increase in the efflux. One possible explanation for this unexpected result could be the enhanced uptake of $Si(OH)_4$ by benthic diatoms, that were PO_4^{3-}-limited before the food pulse. Therefore, we made a rough estimation of the $Si(OH)_4$ uptake potential of the benthic diatom population, which was dominated by *Navicula* spp. (Ehrenhauß et al. unpublished data) using the total benthic diatom abundance and a $Si(OH)_4$ uptake rate of 21-62 pM $\times$ 10^6 $cells^{-1}$ min^{-1}, reported for a exponentially grown culture of *Navicula pelliculosa* (Sullivan 1977). Assuming that all cells we counted were alive, the benthic diatoms in the chambers with medium sand could be responsible for a reduction of the $Si(OH)_4$ flux by roughly 32-94 µmol m^{-2} d^{-1}. Due to

lower abundances of benthic diatoms in the fine sand, the potential $Si(OH)_4$ uptake was lower and could have reduced the $Si(OH)_4$ flux by 10-31 μmol m^{-2} d^{-1}. The results of these estimates demonstrate that the $Si(OH)_4$ uptake by the benthic diatoms can be an explanation for the lower $Si(OH)_4$ release from the medium sand, as well as for the lower $Si(OH)_4$ pore water concentration.

The addition of algae to the fine and medium sand was followed by an enhanced uptake of PO_4^{3-} in both sediments, corresponding to 4.87 and 5.98% d^{-1} of the added organic phosphorus for the fine and medium sand respectively (Table 4). In the oxidized sands, PO_4^{3-} resulting from the mineralization rapidly was adsorbed to the iron-coated sand grains or taken up by bacteria in the water and the incubated sediment, as could be concluded from the decrease of the PO_4^{3-} pore water concentrations in both sediments (data not shown). Bacteria counts from the overlying water (Ehrenhauß et al. unpublished data) showed an increase in bacterial numbers even in the short-time incubations. An estimation of bacterial biomass in the sediment from analysis of bacteria-specific fatty acids (Buehring et al. unpublished data) could also confirm enhanced bacterial production in the sediment even after 12 h.

The addition of algal material enhanced the NH_4^+ fluxes from both sands: 10.40% d^{-1} (fine sand) and 5.23% d^{-1} (medium sand) of the added algal nitrogen was converted into NH_4^+ and released to the overlying water. The pore water concentration in the fine sand (Fig. 5) did not change significantly, indicating that most of the added material was mineralized at the sediment surface. Microscopic counts and TOC samples from the incubated sediments revealed that the added diatoms accumulated in the upper sediment centimeter of the fine sand, and the penetration depth for the added diatom carbon did not exceed 6 cm (Ehrenhauß et al. unpublished data). Measurements of pore water CO_2 revealed that the total remineralization of the algal carbon to CO_2 was restricted to the upper sediment layer (Witte et al. unpublished data).

Due to the higher permeability of the medium sand, maximum penetration depth of intact diatom cells were 2 cm, and the added algal carbon was found in depths up to 12 cm. The remineralization of the added organic matter, therefore, was shifted into deeper sediment layers, resulting in changes of the NH_4^+ pore water profiles. Also CO_2 release from the added algal carbon took place over the total depth of 12 cm (Witte et al. unpublished data). The NH_4^+ pore water concentration decreased but NO_3^- and NO_2^- increased (Fig. 5), suggesting that the mineralization products

enhanced sedimentary nitrification. However, NO_3^- fluxes from the medium sand were reduced after the food pulse (approx. 3.64% d^{-1} of the added algal nitrogen), but release of NH_4^+ increased (approx. 5.23% d^{-1} of the added algal nitrogen).

NO_3^- fluxes from the fine sand were enhanced as a result of increasing NH_4^+ production at the sediment surface corresponding to 1.66% d^{-1} of the added algal nitrogen. The NH_4^+ release stimulated nitrification in the water column. Such an initial enhancement of nitrification after the addition of organic material was also reported by Caffrey et al. (1993). NO_3^- and NO_2^- pore water concentrations in the fine sand (Fig. 5) were generally unaffected by the addition of algae, except during the *in-situ* incubation and the long-time incubation on-board. Again, this indicates that most of the added material was degraded on the sediment surface. In the 132 h incubations, however, NO_3^- pore water concentrations dropped, probably resulting from the extended enhanced oxygen consumption at the sediment surface. Consequently, nitrification decreased within the sediment and denitrification may also have contributed to this drop. In laboratory flume experiments with comparably permeable North Sea sediments ($k = 5 \times 10^{-12}$) by Forster et al. (1996), the addition of fresh algal carbon (0.72 g C m^{-2}) led to a decrease in water column oxygen by 43% over a period of 6 d, demonstrating the lasting effect of such additions on the oxygen in the overlying water. In the 32 h *in-situ* incubations, the food pulse was followed by a doubling of the NO_3^- pore water concentrations. The *in-situ* experiments were carried out in June, when NO_3^- pore water concentrations were already high compared to April (Fig. 2), indicating enhanced mineralization in a well oxygenated sediment.

Many studies have addressed the effects of organic matter addition on sediment nutrient recycling processes in muddy and sandy sediments (Jensen et al. 1990, Caffrey et al. 1993, Enoksson 1993, Conley & Johnstone 1995, Hansen & Kristensen 1998, Huettel et al. 1998, Tuominen et al. 1999) but in most cases with the addition of relatively high amounts of organic material. After the addition of 6.9 g diatom C m^{-2} to muddy Baltic Sea sediments (Conley & Johnstone 1995), 0.52, 0.37, 0.35 and 0.02% of this organic material was remineralized to $Si(OH)_4$, PO_4^{3-}, NH_4^+ and NO_3^- respectively per day. Compared to the percentage of added diatoms remineralized in our experiment on the fine sand, slightly more $Si(OH)_4$, but 30-fold more NH_4^+ and 80-fold more NO_3^- was regenerated from the organic matter. The released PO_4^{3-} from the algae was rapidly consumed by organisms or adsorbed.

In the incubations with the medium sand, the regeneration of NH_4^+ was 15-fold higher than the rates reported by Conley & Johnstone (1995), however, all the other inorganic nutrients released in our experiments were more rapidly consumed or adsorped as observed in their experiments.

After the addition of 62.72 g C m^{-2} macroalgal detritus to sandy, as well as muddy sediments, Hansen & Kristensen (1998) reported that 1.04 to 1.31% (sand) and 0.11 to 0.39% (mud) of the added nitrogen was remineralized to NH_4^+ per day. These findings support our hypothesis that the mineralization in permeable sands can exceed that in impermeable sediments. In our experiment, 4 to 10-fold more NH_4^+ was regenerated compared to the sandy sediment investigated by Hansen & Kristensen (1998), and even 10 to 100-fold more compared to their muddy sediment, stressing the high ability of our permeable sediments to regenerate nitrogen.

High NH_4^+ effluxes (1500 to 6714 µmol m^{-2} d^{-1}) and high NO_3^- uptake rates (-457 to -2428 µmol m^{-2} d^{-1}) by sediments after addition of organic material was observed by many scientists in sandy (Caffrey et al. 1993, Hansen & Kristensen 1998), as well as in muddy sediments (Jensen et al. 1990, Hansen & Kristensen 1998, Tuominen et al. 1999). In contrast, both sands investigated in our study released NH_4^+ and NO_3^- after the addition of algae, indicating that nitrification still took place.

CONCLUSIONS

Our measurements and experiments show that permeable sediments are capable of intensive organic matter mineralization causing high release rates of nutrients. The regeneration of nitrogen exceeded rates reported from fine-grained deposits (Conley & Johnstone 1995, Hansen & Kristensen 1998), revealing the high ability of nitrogen regeneration in permeable sediments.

The high flushing rates in sands also accelerated the remineralization of particulate silica, because the dissolution rate is mainly controlled by the state of saturation of the surrounding water (Kamatani & Riley 1979). Laboratory experiments have shown that the remineralization of deposited opal increases with sediment permeability (Ehrenhauß & Huettel unpublished data). Enhanced PO_4^{3-} uptake by fine and medium sand and reduced $Si(OH)_4$ and NO_3^- fluxes from the medium sand after addition of organic matter indicate that the microbial community in these sands is PO_4^{3-} limited. However, both sands have a large potential for mineralization activity that is not always fully used but can react when possible, e.g. after settling of a bloom.

We conclude that in coastal areas, where primary production can be limited by $Si(OH)_4$, the decomposition of diatom blooms in permeable sandy sediments may be an important process for maintaining high primary production rates.

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Chapter 5

Hydrodynamical impact on biogeochemical processes in aquatic sediments

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ABSTRACT

Boundary layer flow characteristics and sediment permeability control pathways and magnitude of material exchange in the surface layer of aquatic sediments. In fine-grained cohesive beds, bottom currents and sediment microtopography shape the diffusive boundary layer and locally produce areas where the interfacial solute fluxes are increased or reduced. Where sediment permeabilities exceed 10^{-12} m^2, advective pore water flows driven by boundary flow-topography interaction dominate the sediment-water exchange of matter, with transport rates that exceed those of molecular diffusion by two orders of magnitude and more. The curved paths of the advective pore flows through the surface layers of such sandy beds generate complex three-dimensional biogeochemical patterns with extreme spatial and temporal variability ranging from millimeters to decimeters and seconds to seasons. High filtration rates, a bacterial community firmly attached to the mineral grains, rapidly changing biogeochemical zonations and winnowing of the sediment surface layers by frequent resuspension convert these beds into effective biocatalytical filter systems.

KEY WORDS

Boundary flow – sediment – permeability - solute flux - mineralization

Transport mechanisms at the sediment-water interface

In shallow aquatic environments, the sediment bed is the most important site for accumulation, storage and biogeochemical transformation of organic matter and contaminants (Wainright et al. 1992, Canfield et al. 1993, Villar et al. 1999). The extent to which the sedimentary processes are linked to the overlying water column is determined by transport mechanisms that carry particulate and dissolved substances into and out of the bed (Berner 1976, Vanrees et al. 1996). In most aquatic environments, the most important transport processes are molecular diffusion, gravitational settling, bioturbation and bioirrigation, pore water advection and burial due to lateral sediment transport (Aller 1982, Shum & Sundby 1996, Vaughn & Hakenkamp 2001). All these mechanisms are strongly affected by boundary layer flows making water currents, surface gravity waves and turbulence dominant factors controlling benthic-pelagic coupling.

Boundary flows and diffusive sediment-water exchange

Where the boundary flows are weak, fine-grained sediments can accumulate producing deposits with organic matter and solute concentrations that exceed those in the overlying water column by far (Berner 1980, Ignatieva 1996). Due to the resulting concentration gradients and the relatively low hydraulic conductivity of these deposits, molecular diffusion in such beds usually is the most important mechanism for the transport of dissolved substances across the sediment-water interface. In such environments, the boundary layer hydrodynamics govern the biogeochemistry of the sediment surface layers by controlling the solute concentration gradients at the sediment water interface (Jørgensen 1994, Golosov & Ignatieva 1999). These gradients are not only shaped by the characteristics of the boundary layer flow (e.g. laminar or turbulent) but also by the interaction of the flow with the microtopography of the sediment. Jørgensen & Des Marais (1990) observed the compression and dilatation of oxygen concentration isolines due to locally accelerating or decelerating contour flows at microtopography of a microbial mat. In their recent microscale studies of oxygen distribution at the surface of a silty bioturbated sediment, Røy et al. (2002) demonstrated that flow-microtopography interaction affects also the diffusive boundary layer and oxygen flux in fine-grained marine sediments. At sub-millimetre scale, the sediment surface appears as a three-dimensional structure where the concentration gradients that loosely follow the topography support fluxes not only in

vertical but also in horizontal direction (Fig. 1). A one-dimensional measuring approach may underestimate oxygen flux in such settings by 5 to 15% revealing the importance of flow, topography and the ensuing three-dimensional nature of the sediment water exchange.

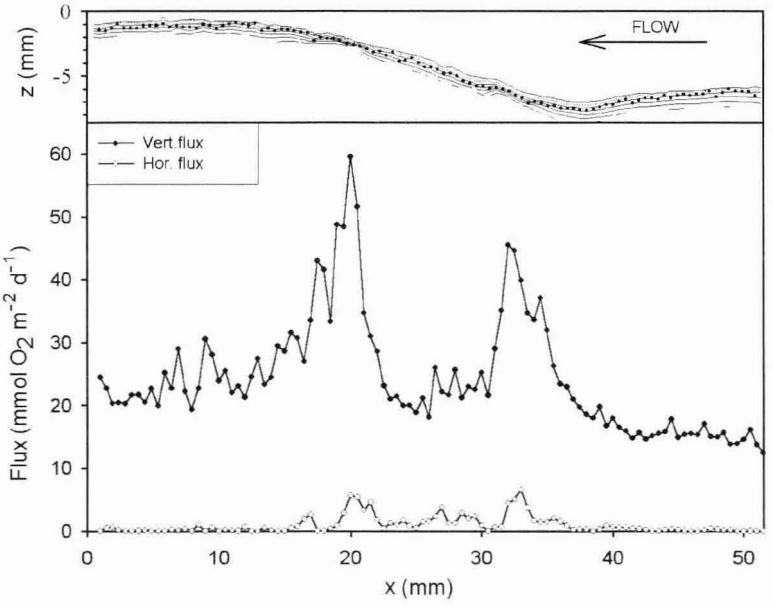

Fig. 1. Upper pane: Cross-section of a fine grained sediment that was inhabited by oligochaetes (interface indicated by dotted line) and the oxygen concentration isolines that are shaped by the interaction of the microtopography, hotspots and boundary layer flow. The isolines were derived from oxygen profiles measured with a microsensor at a spatial resolution of 250 μm and 100 μm in horizontal and vertical direction, respectively. The isolines reveal compression of the diffusive boundary layer (DBL) and enhanced oxygen flux at microtopography and two hotspots (at x = 20 mm and x = 32 mm, lower pane). The latter were caused by fresh faecal pellets deposited on the surface by oligochaetes. The elevated flux between 10 and 30 mm relative to the flux between 40 and 50 mm can be attributed to the compression of the DBL due to the hydrodynamical compression of the DBL. Median grain size 6.3 μm, permeability $k = 1.5 \times 10^{-13}$ m^2, porosity = 0.8, organic content = 2.9%, shear velocity $u^* = 0.09$ cm s^{-1}.

Advective filtering in permeable sediments exposed to flow

The importance of boundary flows for the metabolic activities in the sediment increases with increasing intensity of the flow near the sediment-water interface (Berninger & Huettel 1997, Migne & Davoult 1998). In river and shallow coastal environments, strong bottom currents frequently resuspend and winnow the sediment resulting in coarse-grained beds with relatively high hydraulic conductivities and low content of organic matter (Li & Amos 1999). Nevertheless, such sediments can have oxygen consumption rates similar to those recorded for fine-grained beds rich in organic matter suggesting that these beds efficiently mineralize organic material originating from the overlying water column (Andersen & Helder 1987, Lohse et al. 1996). However, strong currents and turbulence exceeding the settling velocities of organic matter and fine particles by far require other processes than gravitational settling for the uptake of such substances into the sediments. The boundary layer hydrodynamics again are the key factor controlling the transfer of matter into these sediments. In such high-energy environments, advective pore water flows and lateral sediment transport control the transfer of matter into the permeable bed.

Interfacial advective flows are driven by small lateral pressure gradients (ca. 1-3 Pa cm^{-1}) that result from the interaction of unidirectional or oscillating boundary layer flows with sediment topography (Huettel & Gust 1992). Obstruction of the flow by protruding structures causes local increase of pressure that forces water and suspended particles into porous sediments, while the acceleration of flow when passing over these protrusions results in a pressure decrease that draws pore water from the sediment (Savant et al. 1987, Thibodeaux & Boyle 1987, Huettel et al. 1996)(Fig. 2). In typical coastal settings this transport reaches to approximately 15 cm sediment depths. Because there is no river or sea bed that is perfectly smooth, all natural sediments with a permeability exceeding 10^{-12} m^2 function as effective filter systems when exposed to boundary layer flow.

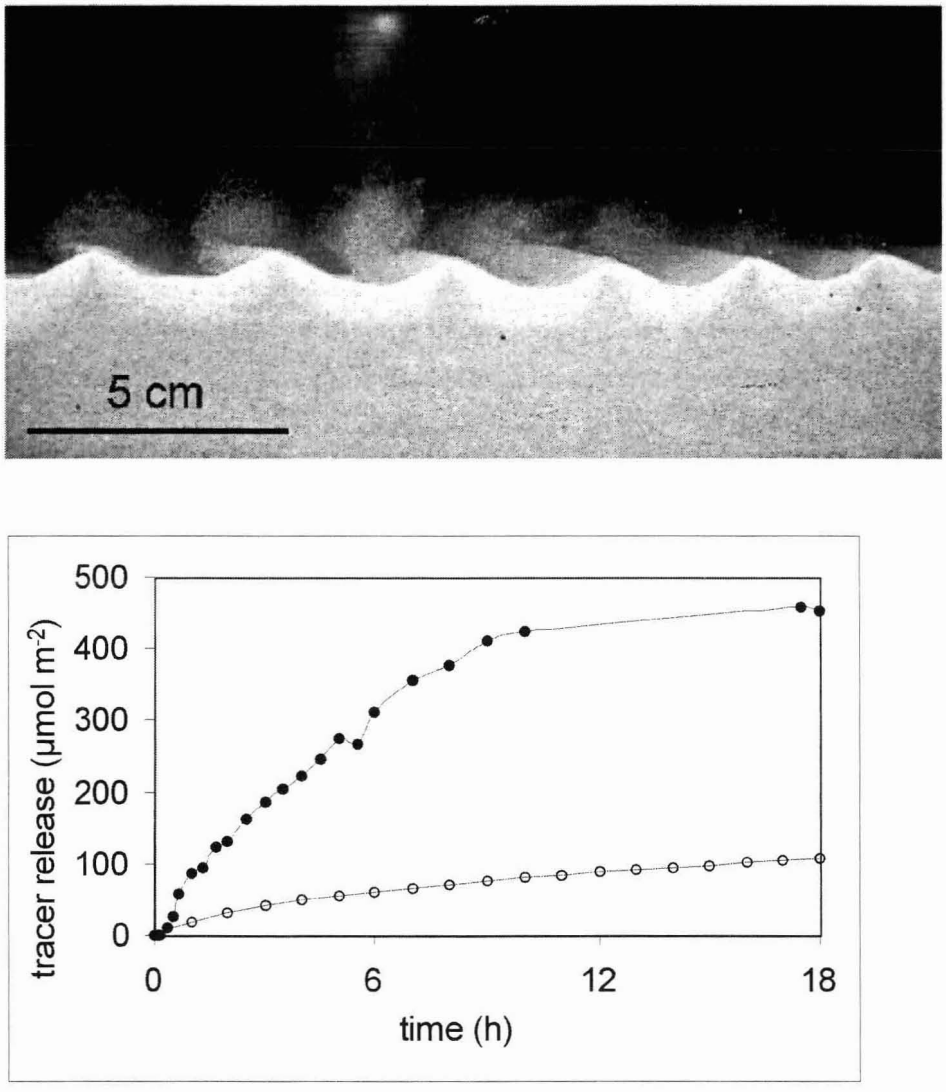

Fig. 2. Upper pane: Advective pore water exchange due to oscillating boundary currents interacting with ripple topography generated by waves. Stained pore water is released to the water column at the ripple crests, while unstained water intrudes the sediment in the ripple troughs. Experimental settings: median grain size: 250 µm, k: 2.9×10^{-11} m^2, water depth in wave tank: 20 cm, wave amplitude: 10 cm, wavelength: 120 cm, av. u* = 0.12 cm s^{-1}, filtration rate: 90 L m^2 d^{-1}. Lower pane: Comparison of advective and diffusive release of solute tracer from the same sediment under stagnant flow conditions and exposed to the waves. Advective release due to waves in this case increased solute flux by factor 10 relative to diffusion.

The ecological relevance of the interfacial advective water flows is linked to the transport of reactive materials into permeable sediments. Laboratory and *in-situ* experiments showed that phytoplankton cells, bacteria and organic detritus particles are transported several centimetres into the sediment within 12 to 24 h (Pilditch et al. 1998, Huettel & Rusch 2000, Rusch et al. 2001)(Fig. 3). This process causes rapid particulate matter uptake in environments where strong boundary currents prevent the gravitational deposition of organic matter.

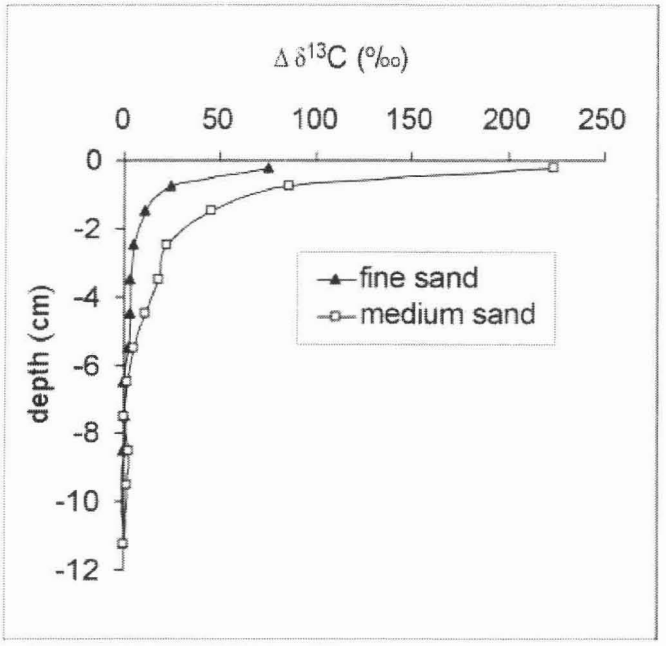

Fig. 3. Results of an *in-situ* experiment on transport of ^{13}C-labeled *Ditylum brightwellii* diatom cells into North Sea sediments of different grain size and permeability. Fine sand: $k = 3 \times 10^{-12}$ m^2, penetration time 32 h, medium sand: $k = 26 \times 10^{-12}$ m^2, penetration time 20 h. Interfacial water flows carried labeled diatoms down to 3 cm in the fine sand and down to 6 cm in the medium sand. In the latter this transport distance was covered in less than one day.

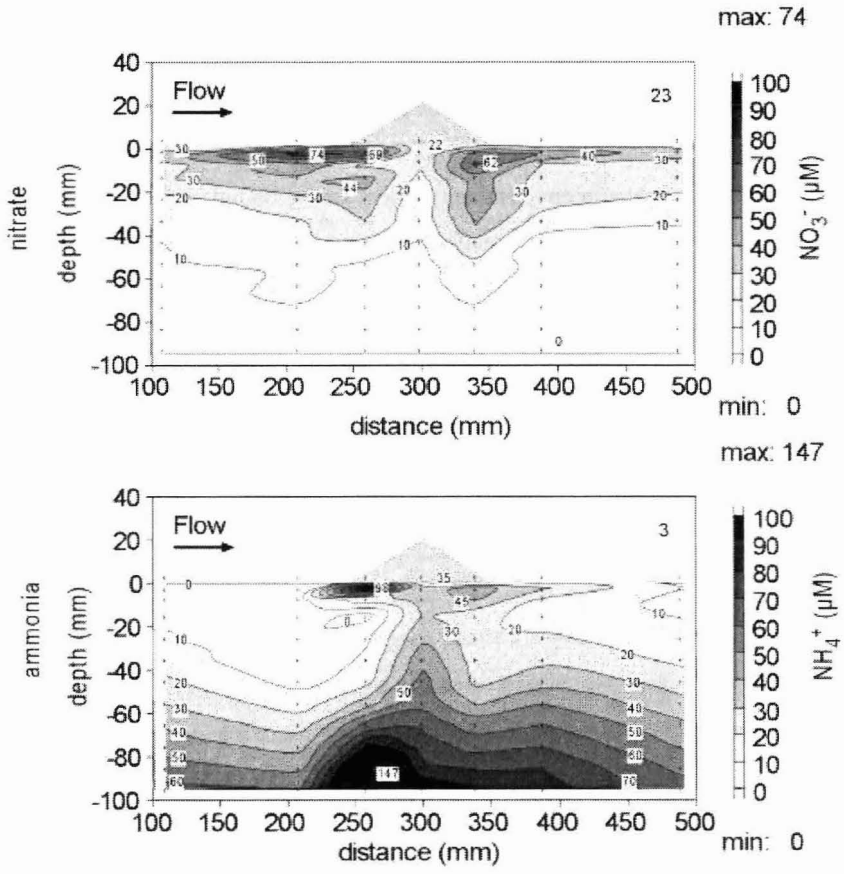

Fig. 4. Zones of enhanced nitrification are generated up- and downstream of protruding surface structures (in this case a small mound of 2.5 cm height, upper pane), while pore water rich in ammonia is drawn to the surface underneath the protrusion creating steep gradients between aerobic and anaerobic sediment zones (lower pane). Here ammonium-oxidizing bacteria find ideal growing conditions. Likewise metals are affected by the advective pore water flows. Dissolved ferrous iron and dissolved manganese are drawn from deeper anoxic sediment layers to the surface. The upwelling pore water flows, thus, create a pathway of reduced metals through the oxidized surface layer of the sediment permitting the release of these substances to the water column. Pollutants can be released from such sediments in the same manner. Median grain size 350 µm, permeability $k = 5.1 \times 10^{-11}$ m^2, porosity = 0.4, organic content = 0.2%, shear velocity $u^* = 0.38$ cm s^{-1}. (Modified after Huettel et al. 1998)

Concurrent with the transport of organic particles into the bed, water rich in oxygen and other electron acceptors (e.g. nitrate, sulfate) is forced into the sediment and, because the fluid experiences less friction than the particulate matter, passes through the layers where the intruding particles accumulate within the bed (Huettel et al. 1998). The pore water flow field associated with sediment topography dictates a directed flow from the area of intrusion to the release zone providing an efficient exchange mechanism for pore water and dissolved metabolites. More than 90% of the bacterial cells in sandy sediments are attached to the mineral grains (Rusch et al. 2001). When water rich in organic matter and electron acceptors is flushed through sand beds, the bacterial community converts these beds into efficient biocatalytical filters (Fig. 4).

Spatial and temporal heterogeneity in sedimentary biogeochemical processes due to boundary flow-topography interaction

Because in natural environments sediment topography as well as the boundary layer flow characteristics change on time scales ranging from seconds to seasons, the fast advective transport of particles and fluid caused by the topography-flow interaction generates a rapidly changing biogeochemical zonation of complex three-dimensional structure (Huettel et al. 1998)(Fig. 5). These rapid spatial and temporal changes further enhance the biocatalytical activity of permeable aquatic sediments and accelerate the transformation of matter in these beds (Aller 1994). A low content of reactive materials in such beds, thus, cannot be interpreted as low metabolic activity but rather is the consequence of rapid turnover and high exchange rates.

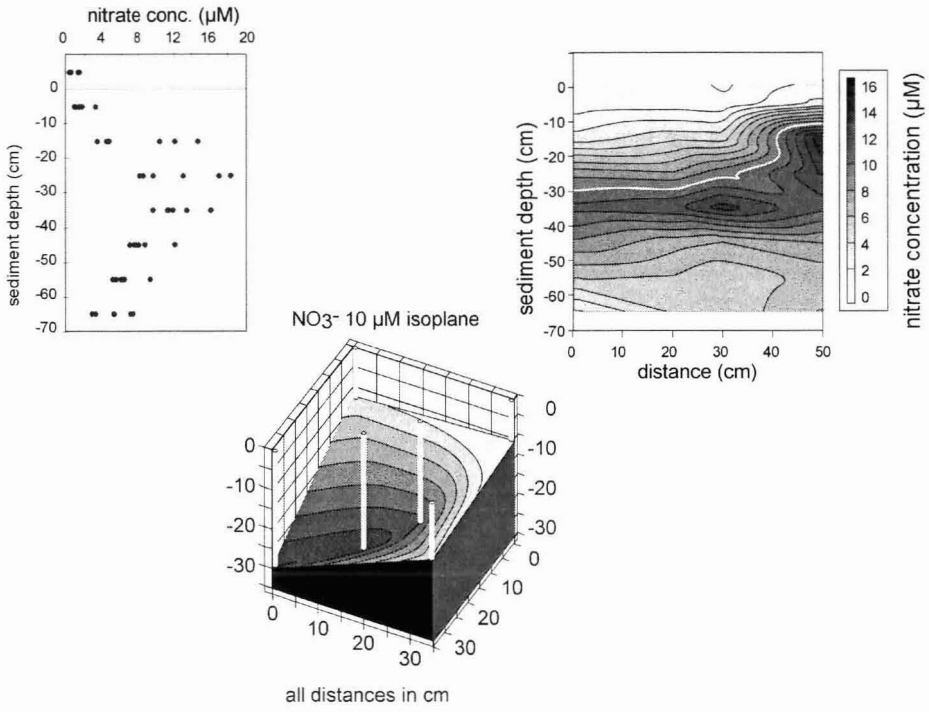

Fig. 5. The same set of nitrate pore water profiles originating from permeable carbonate sediment (Kaneohe Bay/Oahu, permeability $k = 5 \times 10^{-11}$ m^2 – 9×10^{-11} m^2) depicted in one- (upper pane), two- (middle pane), and three-dimensional (lower pane) plots. In permeable sediments the variation of concentrations between single vertical profiles may be caused by the complex three-dimensional nature of the biogeochemical zonation. By collecting horizontal spatial information with the vertical profiles, this three-dimensional structure can be shown.

CONCLUSIONS

The hydrodynamical boundary flow conditions and the permeability of the sediment define whether diffusion or advection dominates the exchange of substances between aquatic sediments and the overlying water column. When sediment permeability exceeds 10^{-12} m^2, advective transport surpasses diffusion (Fig. 6). In natural environments, this picture is complicated by the activity of benthic meio- and macrofauna organisms that enhance interfacial transport of solutes and particles by bioturbation and bioirrigation. In coastal permeable beds, this biological transport locally can be as efficient as advective exchange, however, the biological activity is also controlled by the boundary hydrodynamics (e.g. due to supply of oxygen).

Exchange of solutes and particles in aquatic environments is controlled by the hydrodynamic conditions at the sediment-water interface, and measurements attempting to quantify the interfacial exchange have to take the variability of the boundary flows and sediment permeability into account.

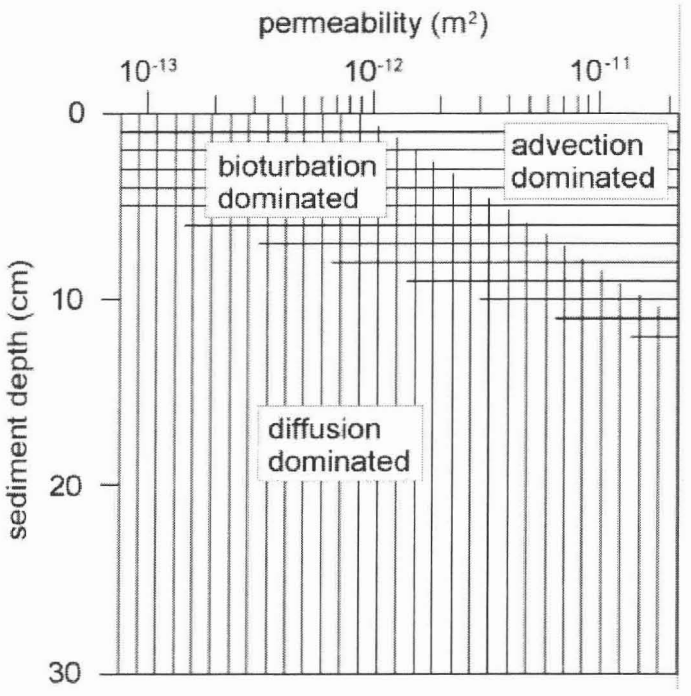

Fig. 6. The permeability and depth ranges of the main transport mechanisms in aquatic environments. The zone where bioturbation is dominant is depicted for marine coastal environments (modified after Huettel & Gust 1992).

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Chapter 6

Summary

Zusammenfassung

SUMMARY

This thesis demonstrates the importance of permeable sediments for the carbon and nutrient cycling in shelf areas. The high biological productivity of shelf environments is mostly supported by diatoms, and large amounts of this primary production are degraded in the shelf sediments. In this study we investigated the possible importance of permeable shelf sediments for the degradation of diatom blooms with focus on the associated silicate regeneration. The main working hypothesis postulates that permeable sediments can filter diatoms from the water column and that the diatoms are rapidly degraded in the sediment due to the enhanced advective pore water exchange in these sand beds.

The first study (Chapter 2), based on laboratory chamber experiments, demonstrates that permeable sediments ($k>7 \times 10^{-12}$ m^2) exposed to boundary flows can filter coastal bloom diatoms from the water column. We observed rapid transfer of fresh organic material into sediment layers as deep as 5 cm within 72 h. The penetration depth of diatoms depended on sediment permeability and diatom chain length. Maximum penetration depth decreased with increasing chain length. Thus, chain formation of coastal diatoms counteracts benthic filtration and may also be an adaptation to avoid this fate. High advective solute exchange in coarse sand enhanced the dissolution of the trapped diatom frustules by a factor of 5 compared to very fine sand. Thus, total dissolution of the added opal would take more than 2 years in very fine sand, but less than half a year in coarse sand. The effective pore water exchange that increases with increasing permeability prevents the accumulation of dissolved silica in the pore water, thereby promoting high opal dissolution rates. Advective pore water exchange enhanced the algal carbon degradation in medium sand by a factor of 3 and in coarse sand by a factor of 8, relative to sediment where diffusion dominated the solute exchange. High flushing rates also stimulated benthic oxygen consumption by a factor of 1.3 or 1.5 in medium sand or coarse sand, respectively, as well as sedimentary nitrification. These results suggest that the advective filtration of planktonic diatoms into permeable sediments can boost remineralization and cycling of organic matter in the shelf.

In-situ experiments on fine, medium and coarse North Sea sands (Chapter 3 and 4) support our laboratory results. Benthic chamber deployments in the coastal North Sea demonstrated enhanced advective transport of diatom frustules and ^{13}C-

labeled diatom carbon into sandy sediments with increasing permeability. Highest diatom transport rates were observed on the coarse sand where 21% of the added diatom frustules were found below 0.5 cm sediment depth after 20 h. The trapped diatom carbon was rapidly degraded with DOC release rates of 7200 μmol C m^{-2} d^{-1} (corresponding to 28% of the added algal carbon) after only three days of incubation time. The diatom food pulse was followed by a fast and high regeneration of nutrients during the first day: 5 to 10% of the added nitrogen was converted to NH_4^+ and up to 0.64% of the added opal was dissolved to $Si(OH)_4$. The regeneration rates of nitrogen exceeded rates reported from fine-grained sediments. Enhanced PO_4^{3-} uptake (-5 to -6% d^{-1} of the added organic bound phosphorus) by the sediments after addition of organic matter indicate that the microbial community in these sands is phosphate limited or that a large fraction of the phosphate released is adsorbed within the sediment. However, these sands have a large potential for mineralization which is activated fast when conditions become favourable, e.g. after settling of a diatom bloom.

Under natural conditions all sands were characterized by high NO_3^- pore water concentrations down to 10 cm depth, indicating that the upper sediment layers are oxidized by advective flushing of the bed. This hypothesis is supported by the relatively high NO_3^- flux (+1161 μmol m^{-2} d^{-1}) from the medium sand. Higher advective solute exchange further enhanced the $Si(OH)_4$ efflux from the medium sand by a factor of 1.2 compared to fine sand. A seasonal study on fine sand without organic matter addition demonstrated increasing $Si(OH)_4$ and NH_4^+ pore water concentrations from spring to autumn. These results imply that pore water concentrations are "reset" to relatively low concentrations during winter. Thus, sandy sediments do not accumulate organic material, but rather represent filter systems, where organic matter is rapidly degraded, and regenerated nutrients are effectively recycled and resupplied to the primary production in the water column. Broken frustule parts of *Thalassiosira* sp., which dominated the diatom spring bloom in 2001, were abundant in the medium and coarse sand in autumn 2001. This indicates that advective transport and to a limited extent also bioturbation deposits phytoplankton into sandy sediments, where strong bottom currents theoretically would prevent the sedimentation of this low-density material. The organic content of the trapped cells is rapidly degraded, leaving the empty frustules behind. High flushing rates in sandy,

permeable sediments further enhanced the dissolution of the diatom frustules as demonstrated by our laboratory experiments.

This study reveals that advective transport provides an effective pathway for the periodic input of fresh phytoplankton into deeper sediment layers of sandy, permeable sediments. Permeable sediments, which cover extensive areas of the continental shelves, represent expansive coastal filter systems, where high advective flushing rates boost remineralization of trapped diatom cells. These processes result in a fast recycling of nutrients back to the water column and thus may be important for maintaining high primary production rates in shelf environments.

ZUSAMMENFASSUNG

Die vorliegende Doktorarbeit unterstreicht die Bedeutung permeabler Sedimente für den Kohlen- und Nährstoffkreislauf in Schelfgebieten. Diatomeen sind die dominierenden Primärproduzenten in nährstoffreichen Küstengewässern, und ein Großteil der von ihnen produzierten Biomasse wird direkt in den Schelfsedimenten abgebaut. Diese Arbeit beschäftigt sich mit dem Beitrag, den permeable Schelfsedimente zum Abbau von Diatomeenblüten leisten, wobei ein Schwerpunkt auf der damit verbundenen Regenerierung von Silikat liegt. Die wichtigsten Arbeitshypothesen hierbei sind, dass permeable Sedimente Diatomeen aus der Wassersäule filtrieren, und dass der hohe advektive Porenwasseraustausch in diesen Sanden den Abbau der Diatomeen im Sediment beschleunigt.

In Laborexperimenten (Kapitel 2) konnte gezeigt werden, dass permeable Sedimente ($k>7 \times 10^{-12}$ m^2) durch Interaktion mit Bodenströmungen Diatomeen aus der Wassersäule filtrieren. Frisches organisches Material wird dadurch innerhalb von nur 72 h in bis zu 5 cm Sedimenttiefe transportiert. Die Sedimenteindringtiefe der Diatomeen hängt dabei sowohl von der Permeabilität des Sediments, als auch von der Kettenlänge der Diatomeen ab. Die maximale Eindringtiefe nimmt mit zunehmender Kettenlänge ab. Die Kettenbildung, die ein typisches Merkmal küstennaher Diatomeen ist, wirkt somit einer möglichen Filtration durch permeable Sedimente entgegen, und stellt eventuell auch eine Anpassung dar, um dieses Schicksal zu vermeiden. Im Vergleich zur Auflösung in Feinsanden, wurde durch den hohen advektiven Wasseraustausch in Grobsanden die Auflösung der Diatomeenschalen um das 5-fache erhöht. Folglich würde die komplette Auflösung der Diatomeenschalen in feinem Sand mehr als 2 Jahre dauern, während das gesamte Silikat bei einer Auflösung der Schalen in grobem Sand nach weniger als einem halben Jahr wieder zu Verfügung stehen würde. Der effiziente Porenwasseraustausch, der sich mit zunehmender Permeabilität des Sediments erhöht, verhindert eine Anhäufung des gelösten Silikats im Porenwasser und fördert somit hohe Auflösungsraten der Diatomeenschalen. Im Vergleich zu Sedimenten, in denen Diffusion den Stoffaustausch dominiert, wurde der Abbau des Diatomeenkohlenstoffs durch advektiven Porenwasseraustausch um das 3-fache (Mittelsand) bzw. um das 8-fache (Grobsand) erhöht. Hohe Durchflussraten förderten sowohl die Sauerstoffzehrung in Mittelsanden um das 1.3-fache und in Grobsanden um das 1.5-fache, als auch die Nitrifikation im

Sediment. Diese Ergebnisse belegen, dass die advektive Filtration von planktischen Diatomeen in permeable Sedimente die Remineralisierung und den Umsatz in Schelfgebieten ankurbelt.

Die Laborergebnisse wurden durch Felduntersuchungen an feinen, mittleren und groben Nordseesanden bestätigt (Kapitel 3 und 4). In benthischen Kammerversuchen wurde ein erhöhter advektiver Transport von Diatomeenschalen und ^{13}C-markiertem Diatomeenkohlenstoff mit zunehmender Permeabilität des Sediments festgestellt. Die höchste Transportrate der Diatomeenschalen wurde im groben Sand beobachtet, wo sich 21% der zugegebenen Diatomeen nach nur 20 Stunden in Sedimentschichten unter 0.5 cm befanden. Der dadurch im Sediment eingelagerte Kohlenstoff wurde effektiv zu DOC abgebaut, mit Remineralisierungsraten von 7200 µmol C m^{-2} d^{-1} nach dreitägiger Inkubationszeit, was einem Anteil von 28% des zugegebenem Kohlenstoffs entsprach. Die Freisetzung von Nährstoffen aus dem zugebenen Algenmaterial setzte bereits am ersten Tag ein. 5 bis 10% des zugegebenen Stickstoffs wurde am ersten Tag als NH_4^+ freigesetzt, und bis zu 0.64% des zugegebenen biogenen Silikats wurde zu $Si(OH)_4$ gelöst. Die Freisetzung von Stickstoff übertrifft somit die Raten, die in feinkörnigen Sedimenten gemessen wurden. Nach Zugabe des organischen Materials wurde eine erhöhte Aufnahme von PO_4^{3-} durch die Sedimente beobachtet, die 5 bis 6% des zugegebenen Phosphors pro Tag entsprach. Dies könnte ein Indiz dafür sein, dass die mikrobielle Gemeinschaft in diesen Sanden phosphatlimitiert ist, oder, dass ein großer Anteil des freigesetzten Phosphats in den Sedimenten adsorbiert wird. Dennoch zeigen diese Sande eine hohe Remineralisierungskapazität, die schnell aktiviert werden kann, wenn sich günstige Bedingungen einstellen, z.B. nach dem Absinken einer Diatomeenblüte.

Die untersuchten Sande waren unter natürlichen Bedingungen durch eine hohe NO_3^- Porenwasserkonzentration in den oberen 10 cm charakterisiert. Dies ist ein Hinweis darauf, dass die oberste Sedimentschicht durch advektiven Porenwasseraustausch oxidiert ist. Diese Hypothese wird durch den relativ hohen Nitratfluss aus dem mittleren Sand bekräftigt (+ 1161 µmol m^{-2} d^{-1}). Der höhere advektive Wasseraustausch im Mittelsand erhöhte zudem die Freisetzung von $Si(OH)_4$ um das 1.2-fache, relativ zu der Freisetzung im Feinsand. In einer saisonalen Studie an feinem Sand ohne Zugabe von organischem Material, konnte eine Zunahme von $Si(OH)_4$ und NH_4^+ im Porenwasser vom Frühjahr zum Herbst beobachtet werden. Diese Ergebnisse weisen darauf hin, dass die Porenwasserkonzentrationen im Winter auf sehr niedrige

Werte zurückfallen. Demnach akkumulieren sandige Sedimente kein organisches Material. Sie repräsentieren vielmehr Filtersysteme, in denen organisches Material schnell abgebaut wird, freigesetzte Nährstoffe effizient regeneriert werden und somit wieder der Primärproduktion in der Wassersäule zur Verfügung stehen. Im Herbst 2001 konnten Schalenfragmente von *Thalassiosira* sp., der dominanten Diatomeenart der Frühjahrsblüte 2001, im mittleren und groben Sand gefunden werden. Das weist darauf hin, dass advektive Transportprozesse und im begrenzten Maße auch Bioturbation zur Ablagerung von Phytoplankton in Sanden führen können, in denen starke Bodenströmungen die Sedimentation dieses leichten Materials theoretisch verhindern würden. Der organische Anteil der abgelagerten Zellen wird effizient abgebaut. Hohe Durchflussraten in sandigen, permeablen Sedimenten erhöhen zudem die Auflösung der Diatomeenschalen, wie wir in unseren Laborexperimenten demonstrieren konnten.

Diese Arbeit zeigt, dass advektiver Transport einen effektiven Weg für den periodischen Eintrag von frischem Phytoplankton in tiefere Sedimentschichten sandiger, permeabler Sedimente darstellt. Permeable Sedimente, die weite Teile des Kontinentalschelfs bedecken, stellen somit ausgedehnte küstennahe Filtersysteme dar, in denen hohe advektive Durchflussraten die Remineralisierung von abgelagerten Diatomeenzellen beschleunigen. Diese Prozesse führen zu einer schnellen Rückführung von Nährstoffen aus dem Sediment in die Wassersäule und sind dadurch möglicherweise von großer Bedeutung zur Aufrechterhaltung der hohen Primärproduktionsraten in Schelfgebieten.

LIST OF PUBLICATIONS

Publications presented in this thesis

1) Ehrenhauß S. and Huettel M.

Advective transport and decomposition of chain-forming planktonic diatoms in permeable sediments. This article has been submitted to Journal of Sea Research.

2) Ehrenhauß S., Witte U., Buehring S.I. and Huettel M.

Effect of advective pore water transport on distribution and degradation of diatoms in permeable North Sea sediments. This article has been submitted to Marine Ecology Progress Series.

3) Ehrenhauß S., Witte U., Kamp A., Janssen F. and Huettel M.

Decomposition of diatoms and nutrient dynamics in permeable North Sea sediments. This article has been submitted to Continental Shelf Research.

4) Huettel M., Røy H., Precht E. and Ehrenhauß S.

Hydrodynamical impact on biogeochemical processes in aquatic sediments. This article has been accepted for publication in Hydrobiologia.

Further publications

1) Kamp A., Buehring S.I., Ehrenhauß S. and Witte U.

The importance of macrofauna for carbon flux in permeable sediments (North Sea): Experiments with ^{13}C labeled phytoplankton, in prep.

2) Witte U., Moodley L., Ehrenhauß S., Kamp A. and Buehring S.I.

Degradation of particulate organic carbon in sandy North Sea sediments of different permeabilities, in prep.