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Pore-water advection and solute fluxes in permeable marine sediments (II): Benthic respiration at three sandy sites with different permeabilities (German Bight, North Sea)

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Abstract

This contribution presents total oxygen uptake (TOU) rates and nutrient fluxes of organically poor permeable shelf sands of the German Bight. Measurements have been made in situ with the novel autonomous benthic chamber system *Sandy* under controlled conditions of advective pore-water exchange. Average oxygen consumption rates of 31.3 ± 18.2 mmol m^{-2} d^{-1} measured in this study were relatively high as compared with rates reported from shelf sediments with much higher organic contents. TOU of highly permeable medium and coarse grained sands was substantially enhanced in the presence of advection. This indicates that advective oxygen supply contributed significantly to respiration in these sediments and that advection has to be considered when assessing oxygen consumption and organic matter mineralization in shelf areas. In fine-grained, less permeable sands, no effect of advection could be measured. A lower advective oxygen supply in these sediments is in agreement with a release of ammonium instead of nitrate and a shallower oxygen penetration depth. Scaled up to the entire German Bight, the results imply that in 40% of the area an effect of advection on benthic oxygen uptake and other advection-related processes can be largely excluded, while in the remaining 60% significant pore-water advection potentially takes place. However, because permeabilities of the sediments investigated in this study were widely spaced, a significant effect on oxygen supply was only verified for highly permeable sands that are likely to cover approximately 3% of the area.

Until the 1980s the biogeochemistry of coastal sands has received relatively little attention. Because organic matter content generally decreases with increasing grain size, it seemed that coarse grained sandy deposits lack the substrate to sustain significant biological activity. Sands were therefore considered to be biogeochemical deserts that did not significantly contribute to the cycling of organic matter (Boudreau et al. 2001).

A new perception of sandy sediments developed when systematic investigations increased the understanding of solute transport in these sediments (Savant et al. 1987; Thibodeaux and Boyle 1987; Huettel and Gust 1992*a*). Permeabilities in excess of 10^{-12} m^2, as common for sandy sediments, were found to permit pore-water advection, i.e., the flow of water through the interstices of the sediment. While transport in silty and muddy deposits is restricted to molecular diffusion, bioturbation, and bioirrigation, advective pore-water flow represents an additional solute transport mechanism in sandy sediments. The main driving forces of advection are pressure gradients along the sediment surface. These develop whenever unidirectional or oscillating bottom flows are deflected by topographical features of the sediment surface (e.g., ripple and mounds) (Huettel and Gust 1992*a*; Precht and Huettel 2003). Other factors that can lead to pore-water flow include undulating pressures at the seafloor due to the passage of surface gravity waves (''wave pumping''), groundwater seepage, fluid venting, gas bubble emergence, and temperature or salinity gradients (*see* Huettel and Webster 2001 and references therein).

Horizontal pressure differences induced locally by roughness elements at the seafloor are expected to be in the range of a few Pascal only (Thibodeaux and Boyle 1987; Huettel et al. 1996). Nevertheless, they can lead to pore-water transport down to >10 cm sediment depth and to solute exchange at rates exceeding those of molecular diffusion by up to three orders of magnitude (Huettel and Gust 1992*a*; Huettel et al. 1996). This enhances the supply of electron acceptors, such as O_2 and SO_4^{2-}, that may limit the mineralization rates of benthic heterotrophs (Jørgensen and Sørensen 1985; Enoksson and Samuelsson 1987). At the same time, waste products such as reduced electron acceptors and remnants of organic matter mineralization (carbon dioxide and nutrients) are efficiently removed (e.g., McLachlan et al. 1985). Furthermore, advection may contribute to the supply of fresh par-

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ticulate organic matter to the sediment, even if the hydrodynamic forces prevent any gravitational settling of particles. By means of advective pore-water flow, unicellular algae, bacteria, and organic detritus can be carried down several centimeters into the sediment, where they become trapped (Huettel et al. 1996; Pilditch et al. 1998). The advective transport of solutes and particles in combination with the biogeochemical reactions within the sediment result in a complex distribution of biologically relevant substances such as oxygen, nutrients, heavy metals, and organic matter (Ziebis et al. 1996; Huettel et al. 1998; Precht et al. 2004). The resulting biogeochemical transition zones (e.g., the redox discontinuity layer) are larger than those of horizontally laminated beds and highly dynamic since they are coupled to current speed and direction and to sediment surface topography, all of which continuously change on time scales from seconds to seasons (Huettel et al. 2003). Such transition zones, particularly if oscillating, are considered to be sites of intense metabolic activity (Aller and Aller 1998).

On account of these findings, sands are nowadays envisioned as potential sites of high metabolic activity that are likely to play an important role for the cycling of organic matter in the natural environment (Boudreau et al. 2001; Huettel and Webster 2001; Huettel et al. 2003). Since sandy sediments cover approximately two-thirds of the continental shelf seafloor (Emery 1968), they represent the dominant sediment type in a particularly productive part of the oceans, where up to one-third of the entire pelagic primary production is thought to take place (Jørgensen 1996), and additional organic matter is supplied through benthic primary production (Cahoon 1999).

In order to evaluate the role of sands in the cycling of matter on the continental shelf, the metabolic activity of natural sandy sediments needs to be addressed. As the biogeochemistry of sands is most likely closely linked to advection-related processes, the applied methods should allow for pore-water advection in order to give reasonable results. Bag or slurry incubations that are often used in muddy sediments (Hansen et al. 2000) are of limited applicability for sands, since they do not account for advective exchange. Column experiments may be an alternative, since they allow the percolation of water through the sediment as a surrogate of pore-water advection (Reimers et al. 2004). Still, unidirectional flushing at a uniform rate throughout the sediment column strongly deviates from pore-water circulation patterns that are produced by current- and topography-induced advection (Huettel et al. 1996). A more natural representation of pore-water advection can be obtained within benthic chambers. The stirrer-induced pressure distribution in cylindrical chambers with a rotating stirrer disc results in an advective pore-water circulation pattern that shows strong similarities to what is produced by flow-topography interactions (Huettel and Rusch 2000). Since the pressure gradient magnitude is a function of stirrer speed, benthic fluxes can be studied under defined conditions of advective transport. Changing the stirrer speed further allows the effect of advection rates on benthic fluxes to be evaluated.

Based on this chamber design, the autonomous chamber system *Sandy* was developed to conduct flux studies in permeable sands in situ (*see part I of this series;* Janssen et al. 2005). In this part of the study, the total oxygen uptake (TOU) and nutrient fluxes of sandy sediments were determined in order to investigate benthic respiration rates and to characterize the metabolic processes taking place in these sands. Measurements were performed in the presence of moderate stirrer-induced pressure gradients that were assumed to reasonably represent natural conditions in the area. To evaluate the significance of advection for the oxygen supply of the sediments, oxygen uptake rates in the presence of advective pore-water exchange were compared with rates measured subsequently in the absence of advection. In order to assess the effect of permeability on oxygen and nutrient fluxes, the chambers were deployed on fine, medium, and coarse North Sea shelf sands located in close proximity to each other.

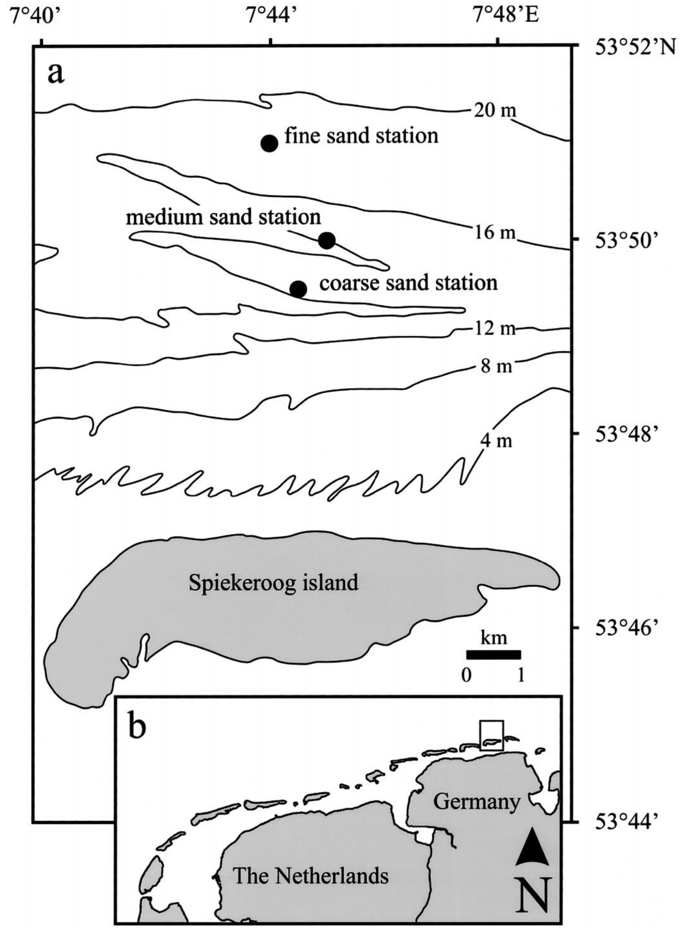

Fig. 1. (a) Location of the three stations and the bathymetry of the area (redrawn after Antia 1993). (b) The chain of West and East Frisian Islands. The box marks the area around the Island of Spiekeroog.

Material and methods

Study area—Investigations were carried out at three stations seaward of the barrier island of Spiekeroog in the southeastern North Sea. The distance between the northernmost and southernmost station was 2.8 km (Fig. 1). The

Table 1. Station data and sediment characteristics.*

Sediment type	Position	Water depth (m)	Permeability (10^{-11} m²)	Bulk sediment characteristics† Median grain size (μm)/sorting‡	Porosity/solids density (g cm^{-3})	TOC (% DW)/ TOC : TN)§
Fine	53°51.0′N 7°44.0′E	19	0.30±0.17	163±20/ 0.58±0.03	0.37 ± 0.009/ 2.70 ± 0.02	0.122 ± 0.023/ 8.0 ± 2.6
Medium	53°50.0′N 7°45.0′E	16	2.63±0.33	299 ± 8/ 0.46±0.02	0.34 ± 0.006/ 2.68 ± 0.02	0.023 ± 0.002/ 7.4 ± 2.6
Coarse	53°49.5′N 7°44.5′E	16	7.46±1.34	672 ± 78/ 0.80 ± 0.11	0.33 ± 0.006/ 2.71 ± 0.02	0.030 ± 0.006/ 8.8 ± 2.8

* Sediment samples were taken in polycarbonate cores of 36 mm inner diameter by means of a miniaturized multiple corer. Sediments were fractionated by dry sieving after rinsing the sediment on a 63-μm mesh for the determination of the silt and clay fraction. Grain size parameters were determined graphically (Lindholm 1987). Porosity and solid fraction density was inferred from weight (wet and after drying at 60°C) and water displacement of the samples. Total organic carbon (TOC) and total nitrogen (TN) were measured by automated combustion (Fisons Instruments NA 1500 elemental analyzer) of freeze dried and ground samples that were previously acidified within the silver sample cups to remove carbonates.
† Averages ± SD of three (grain size parameters, physical properties) and six replicates (TOC and TN).
‡ Sorting (i.e., the graphic SD) is given in phi units.
§ Molar ratio.

study area is located in a mesotidal high-energy environment with a mean tidal range of 2.5 m (Postma 1982). During calm weather conditions, tides result in average bottom flow velocities of approximately 20 cm s^{-1}, with peak flow velocities of up to 35 cm s^{-1} (measured 15 cm above the seafloor; Janssen unpubl. data). Wind and wave-driven currents add to the water motion above the bed. Significant wave heights of 1–2 m, as they are typically encountered in the area, are expected to result in maximum oscillatory current velocities of 56 ± 25 and 18 ± 12 cm s^{-1} at water depths of 10 and 20 m, respectively (calculated from wave recordings by means of Airy wave theory; Antia 1993).

Most of the seafloor within the study area is covered with quaternary silicate sands (Figge 1981). Hydrodynamic forces and animal activity leads to the formation of ripples and discrete topographical features such as mounds or pits at the sediment surface. Heights of roughness elements as measured in 0.5 m long sediment surface scans at all three stations were typically in the range of 10–20 mm with maximum elevations of 30–35 mm (Janssen unpubl. data). The three stations were selected for their different sediment properties (Table 1). Median grain sizes increased from the northern to the southern station by more than a factor of four. According to Wentworth (1922), the sediments at the three stations are classified as fine, medium, and coarse sand, and the respective stations are subsequently referred to as "fine", "medium", and "coarse sand station." The permeabilities reflect the differences in grain size (Fig. 2). Relative to the fine sand station, the resistance to water transport through the pore space was approximately 9 and 25 times less at the medium and the coarse sand station, respectively. The total organic carbon (TOC) content (Table 1) was generally low but significantly higher at the fine sand station as compared with both other stations ($p = 0.005$; Wilcoxon two-group test). In contrast to the grain size median that was almost constant within the upper sediment layer at all three stations, the TOC content tended to decrease with sediment depth (Fig. 3).

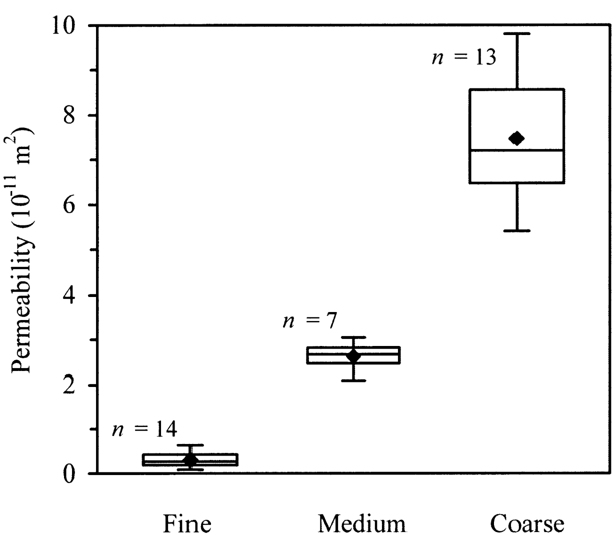

Fig. 2. Permeabilities of the surficial sediments at the three stations as determined on board using 80–190 mm long cores of 36 mm inner diameter. Measurements took place at in situ temperature with the constant head method (Klute and Dirksen 1986). The diamond represents the mean, the median is given by the horizontal line. The box marks the upper and lower quartile, the whiskers the total range of values.

Chamber deployments—Oxygen and nutrient fluxes at the three stations were determined with the chamber system *Sandy*, which is based on a cylindrical chamber with a central stirrer disc similar to the chamber described by Huettel and Gust (1992*b*). Stirring results in a radial pressure gradient along the sediment surface that scales with the stirring rate (Glud et al. 1996). As the chamber isolates the sediment from all natural hydrodynamic forces, this permits exposure to the enclosed sediment to defined and reproducible pressure gradients. If the permeability is sufficiently high, the pressure gradient causes an advective circulation of chamber water through the sediment pore space along curved paths from the outer region of the chamber toward a relatively small central outflow area. A detailed description of the system and a characterization of the hydraulic properties of the

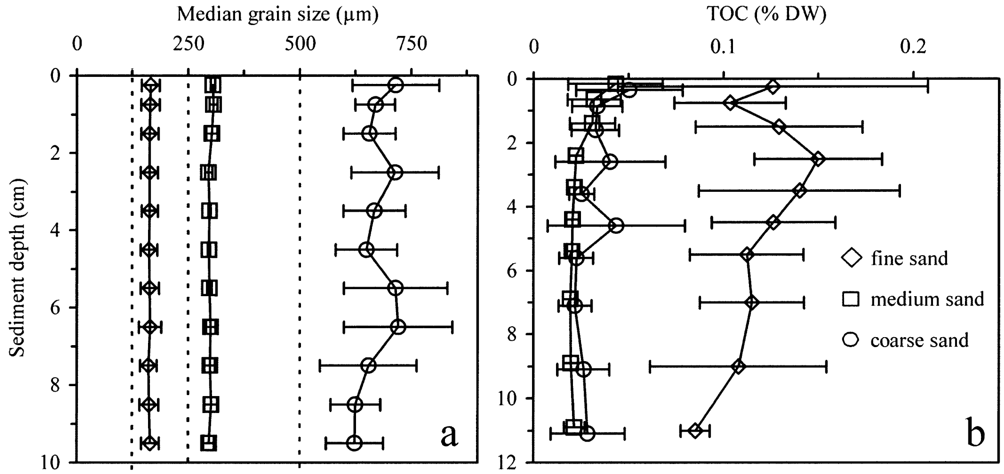

Fig. 3. (a) Median grain size, and (b) total organic carbon content (TOC) versus sediment depth. Marks represent the average (whiskers, SD) of three (grain size) and six replicates (TOC), respectively. Points are positioned in the center of the respective sediment layer. Depth intervals: 0–1 cm in 0.5-cm steps, 1–10 cm in 1-cm steps (grain size); 0–1 cm in 0.5-cm steps, 1–6 cm in 1-cm steps, 6–12 cm in 2-cm steps (TOC). Dotted lines in (a) represent the lower limits of the Udden-Wentworth size classes: fine, medium, and coarse sand (from left to right). In (b) points have been slightly shifted vertically to facilitate discrimination between the respective data series.

chamber can be found in Janssen et al. (2005). Further details of flow and pressure fields in cylindrical chambers may be found in Khalili et al. (1997).

Sandy deployments took place during four cruises with the research vessels *Heincke* and *Uthörn* (Table 2). Two chambers with controlling electronics were mounted to a three-legged frame that was deployed and recovered by means of a rope with an attached surface marker buoy (Janssen et al. 2005). After the *Sandy* system was lowered to the seafloor, the stainless steel chambers (200 mm inner diameter) were driven into the sediment. Each chamber was equipped with one or two syringe water samplers with seven sampling and one injection syringe (~45 ml volume per syringe). The injection syringe was used to add a neutrally buoyant sodium bromide solution to the chamber water at the beginning of the deployments (1.2–1.5 g NaBr per chamber). The bromide concentration of the first syringe sample permitted the determination of the enclosed water volume (on average [± SD] 3.3 ± 0.6 liters in all chamber incubations that were used to quantify TOU). The remaining syringe samples were withdrawn at preset intervals over the time course of the deployment. Three fiberoptic oxygen sensors (optodes) (Klimant et al. 1995) continuously measured the oxygen concentration in the overlying water of each chamber. The optodes as well as the ports, where the syringe sampling tubes inserted, were not placed directly in the chamber but in a gastight water circuit that was permanently flushed with the overlying chamber water by means of a peristaltic pump.

The oxygen uptake of the sediments was determined at two different stirrer settings that were applied consecutively within each of the deployments. During the first half of the deployment (1.5 to 2.5 h) the stirrer was run at 40 rpm to induce a pressure gradient and hence an advective circulation of pore water through the enclosed sediment (''advective stirrer setting''). Given an average distance (± SD) of 85 ±

Table 2. Cruise and deployment data. The right column specifies the number of chamber incubations of the respective cruises that are included in the TOU and nutrient flux measurements presented in this study.

Vessel (cruise ID)	Date	Water temp. (°C)	Stations of *Sandy* incubations and number of replicates presented in this study
Heincke (148)	07–15 Jun 2001	13	fine: TOU (n = 5), NH_4^+ (n = 4), NO_3^- (n = 5), PO_4^{3-} (n = 5), SO_4^{4-} (n = 4) coarse: TOU (n = 3), NH_4^+ (n = 4), NO_3^- (n = 3), PO_4^{3-} (n = 4), SiO_4^{4-} (n = 3)
Heincke (154)	24–30 Sep 2001	16	fine: NH_4^+ (n = 3), NO_3^- (n = 2), PO_4^{3-} (n = 3), SiO_4^{4-} (n = 3) medium: TOU (n = 2), NH_4^+ (n = 3), NO_3^- (n = 3), PO_4^{3-} (n = 3), SiO_4^{4-} (n = 2) coarse: NH_4^+ (n = 3), NO_3^- (n = 3), PO_4^{3-} (n = 1), SiO_4^{4-} (n = 3)
Uthörn	22–27 Oct 2001	14	fine: TOU (n = 1), NH_4^+ (n = 2), NO_3^- (n = 1), PO_4^{3-} (n = 2), SiO_4^{4-} (n = 2) medium: TOU (n = 4), NH_4^+ (n = 5), NO_3^- (n = 5), PO_4^{3-} (n = 7), SiO_4^{4-} (n = 7) coarse: TOU (n = 1), NH_4^+ (n = 4), NO_3^- (n = 4), PO_4^{3-} (n = 4), SiO_4^{4-} (n = 4)
Uthörn	10–13 Nov 2001	11	fine: NH_4^+ (n = 2), NO_3^- (n = 2), PO_4^{3-} (n = 2), SiO_4^{4-} (n = 2) medium: TOU (n = 2) coarse: TOU (n = 1), NH_4^+ (n = 1), PO_4^{3-} (n = 1), SiO_4^{4-} (n = 1)

Table 3. Rates of TOU (averages with standard deviations) as measured at the advective and nonadvective stirrer setting and differences between the respective rates.

		TOU (mmol m^{-2} d^{-1}), average ± SD		
Sediment type	Replicates	Advective setting	Nonadvective setting	Difference
Fine	8	29.2±12.2	28.8±12.0	0.4±4.8
Medium	6	37.3±28.5	26.1±18.3	11.2±10.6
Coarse	5	27.7±11.5	17.0±12.8	10.7±3.4
All sediments	19	31.3±18.2	24.8±14.5	6.5±8.5

19 mm between the stirrer disc and the sediment surface in all deployments (as inferred from the average chamber water volume), the differential pressure between the outer rim and the center of the enclosed sediment was 2.9 ± 0.5 Pa with a maximum radial pressure gradient of 0.044 Pa mm^{-1} at $r = 62$ mm (*see* Janssen et al. 2005). At the beginning of the second half of the deployment the stirrer setting was changed to intermittent stirring at 20 rpm (15 s clockwise, 15 s pause, 15 s counterclockwise, 15 s pause, etc.). Pressure gradients were absent and pore-water advection stopped at this ''nonadvective setting,'' restricting the interfacial solute transport to diffusion and bioirrigation (Janssen et al. 2005).

Sample analysis and data treatment—Subsamples for oxygen, nutrients, and bromide were taken from the syringes immediately after retrieval of the *Sandy* system. Oxygen concentrations of the samples were determined on board via Winkler titration. The optodes were calibrated by fitting a modified Stern-Volmer equation (Holst et al. 1997) to the oxygen concentrations of the samples versus the luminescence lifetime readings of the optodes that were recorded at the time of sampling. Samples from several successive deployments were included in the calibrations in order to improve accuracy.

Bromide and nutrient samples were filtered (Minisart® 0.2-μm cellulose acetate syringe filters) and either frozen (bromide) or kept at 4°C (nutrients) after addition of mercury chloride (110 ppm final concentration). Bromide was measured with an Ion Chromatograph (Sykam anion column LC A14 and UV detector S 3200). Nutrient concentrations (ammonium, nitrite, nitrate + nitrite, phosphate, and silicate) were determined with a continuous flow autoanalyzer (Skalar SanPlus) following the methods given by Grasshoff (1999).

Oxygen, nutrient, and bromide concentrations of the syringe samples were corrected for concentrations in the dead volume of the sampling tubes (2.6 ml deionized water). TOU and nutrient fluxes were determined from linear regressions of concentrations of oxygen (averages of 2–3 optodes) and nutrients (syringe samples) versus time. TOU in the presence and absence of advection was calculated separately based on the oxygen decrease during the last 1–1.5 h the stirrer was run at the advective setting and the first 1–1.5 h directly after switching to the nonadvective setting. In the case of nutrient fluxes, all samples that were taken in the time course of the deployment were included in the regression since changes in the nutrient concentrations were relatively small and poorly resolved by the small number of samples taken during the first and second part of the incubations, respectively. Nutrient fluxes thus do not differentiate between the respective stirrer settings but focus on general station characteristics. Flux determination was restricted to deployments where no evidence of chamber leakage (most likely due to chamber washout) was found in the bromide data (i.e., no sudden decrease in concentration at some point of the deployment). TOU was only determined in incubations where oxygen at both stirrer settings decreased linearly with time. Nutrient fluxes were only used if any visually discernible trend (i.e., increase, decrease, or stagnancy) was recognized in the syringe sample concentrations. Oxygen and nutrient fluxes were statistically analyzed for differences between stations using the software package JMP 4.0.0 (SAS Institute Inc.). Simultaneous comparisons between all three stations were carried out with the Kruskal-Wallis test. The Wilcoxon two-group test was used for pairwise comparisons.

Results

TOU in the presence and absence of advection—Sediment oxygen uptake rates in the presence of pressure gradients (i.e., at the advective stirrer setting) were highest at the medium sand station with an average of 37.3 mmol m^{-2} d^{-1} as compared with 29.2 and 27.7 mmol m^{-2} d^{-1} at the fine and coarse sand station, respectively. The deviations in TOU between the individual deployments were relatively large (Table 3). Consequently, differences between stations were statistically insignificant ($p > 0.05$ in pairwise and simultaneous comparisons).

Two examples of oxygen concentration time series that cover the entire deployment time and include the consecutive incubations at the advective and nonadvective stirrer setting are presented in Fig. 4. In graph a from the fine sand station, the change from the advective to the nonadvective stirrer setting at $t = 150$ min did not affect the rate of oxygen decrease in the chamber water, while in graph b from the coarse sand station, the rate clearly decreased immediately after switching to the nonadvective stirrer setting. Examples of the oxygen decrease as measured 90 min before and after the change in stirrer setting at all three stations are given in Fig. 5a–f to facilitate a direct comparison of the respective oxygen uptake rates. A clear difference between uptake rates in the presence and absence of advection can be seen in the examples from the coarse and also, though less obvious, in those from the medium sand station (Fig. 5e,f and c,d). In contrast, no difference is discernible in the results from the fine sand station. In order to compare the stirring effect on TOU in all deployments at the different stations, the ratio of

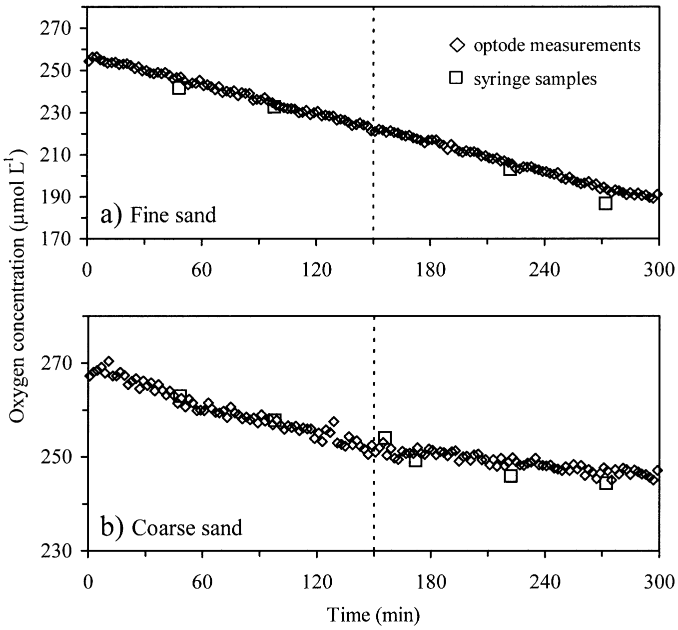

Fig. 4. Examples of oxygen depletion with time at (a) the fine, and (b) the coarse sand station. Diamonds represent the optode measurements, squares the oxygen concentrations of the syringe samples. The dotted lines at $t = 150$ min indicate the shift from the advective to the nonadvective stirrer setting.

$TOU_{advective}/TOU_{nonadvective}$ was calculated for each deployment. Despite the large variability of TOU between replicate deployments and the sometimes relatively large scatter in the oxygen measurements, the ratios between the rates that were measured at the advective and nonadvective stirrer settings within the same deployments confirmed pronounced differences between stations (Fig. 6). TOU at the advective stirrer setting at the fine, medium, and coarse sand station was enhanced by a factor of 1.02 (0.88; 1.19), 1.38 (1.17; 1.64), and 1.91 (1.39; 2.63) as compared with the nonadvective stirrer setting (geometric mean of ratios calculated separately for each chamber incubation; values in brackets represent upper and lower limits of the 95% confidence interval calculated on the basis of the log-transformed ratios). The difference between TOU ratios at the medium and coarse sand station to the ratio at the fine sand station was statistically significant ($p = 0.03$ and 0.01, respectively), while no significant difference existed between the medium and coarse sand station ($p = 0.17$). Expressed as absolute oxygen uptake rates, differences in TOU between the advective and nonadvective setting were similar at the medium and coarse sand station (11.2 and 10.7 mmol m^{-2} d^{-1}, respectively; Table 3).

Nutrient fluxes—The nutrient fluxes showed a considerable variability between replicate deployments (Fig. 7, Table 4). Nevertheless, some differences between stations could be identified. A pronounced release of ammonium was only found at the fine sand station, with fluxes being significantly larger than those at the medium and coarse station ($p = 0.04$ and 0.01, respectively). The differences between ammonium fluxes at the medium and the coarse sand station were statistically insignificant ($p = 0.46$). Nitrate fluxes, on the contrary, were highest at the coarse sand station, with averages being two and three times higher than those at the medium and fine sand station, respectively. These differences, however, proved to be statistically insignificant ($p > 0.05$ in pairwise and simultaneous comparisons). Nitrite fluxes seemed to be of minor importance as compared with fluxes of the other nitrogen species (Table 4). However, the nitrite data have to be treated with caution, since nitrite concentrations in the chamber water were mostly close to or even below the detection limit of the method (0.6 μmol L^{-1}). Phosphate fluxes, being also relatively small, showed no significant differences between stations. Silicate fluxes were highest at the fine sand station, but significant differences were only detected between the fine and the coarse sediment ($p = 0.04$).

Discussion

Quantification of oxygen fluxes in sands—The total oxygen uptake of sediments has been widely studied as a measure of benthic metabolic activity and organic matter mineralization (*see* Viollier et al. 2003, and references therein). TOU was also chosen for the purpose of this study, since oxygen may be measured with sensors at high accuracy, which facilitated the detection of differences in fluxes in response to changes in advective pore-water transport. Since oxygen represents the terminal electron acceptor, TOU principally comprises not only aerobic carbon degradation but also anaerobic decay (indirectly as oxygen demand for the reoxidation of reduced electron acceptors) (Rowe et al. 1988). This is based on the assumption that no significant efflux of reduced electron acceptors (like S^{2-}, Mn^{2+}, or Fe^{2+}) occurs, which typically applies for sediments that are, like the sediments in this study, underlying well-oxygenated waters (Thamdrup and Canfield 2000). Further, it is required that formation and reoxidation of reduced compounds are in steady state during measurements and that no net precipitation of reduced compounds (mainly through pyrite formation) takes place. The question, whether these assumptions are valid, can be addressed by comparing the oxygen uptake with the efflux of dissolved inorganic carbon (DIC), which represents a more direct measure of organic matter mineralization (Anderson et al. 1986). In incubations of sandy sediments from the North Sea intertidal and in situ chamber deployments in subtidal South Atlantic Bight sands, oxygen uptake and DIC release were in good agreement with a respiratory quotient (i.e., the molar ratio of DIC evolved or carbon mineralized per oxygen consumed) of typically close to one (Kristensen et al. 1997 and Jahnke pers. comm.). This implies that TOU may be a reasonable measure of mineralization in sands. However, it cannot be ruled out that differences exist between different sandy environments and seasons. In addition, results will depend on experimental conditions during measurements, since in permeable sediments the obtained fluxes (including a potential efflux of accumulated reduced electron acceptors and DIC from deeper sediment layers) will depend on the rates of advection (*see below*).

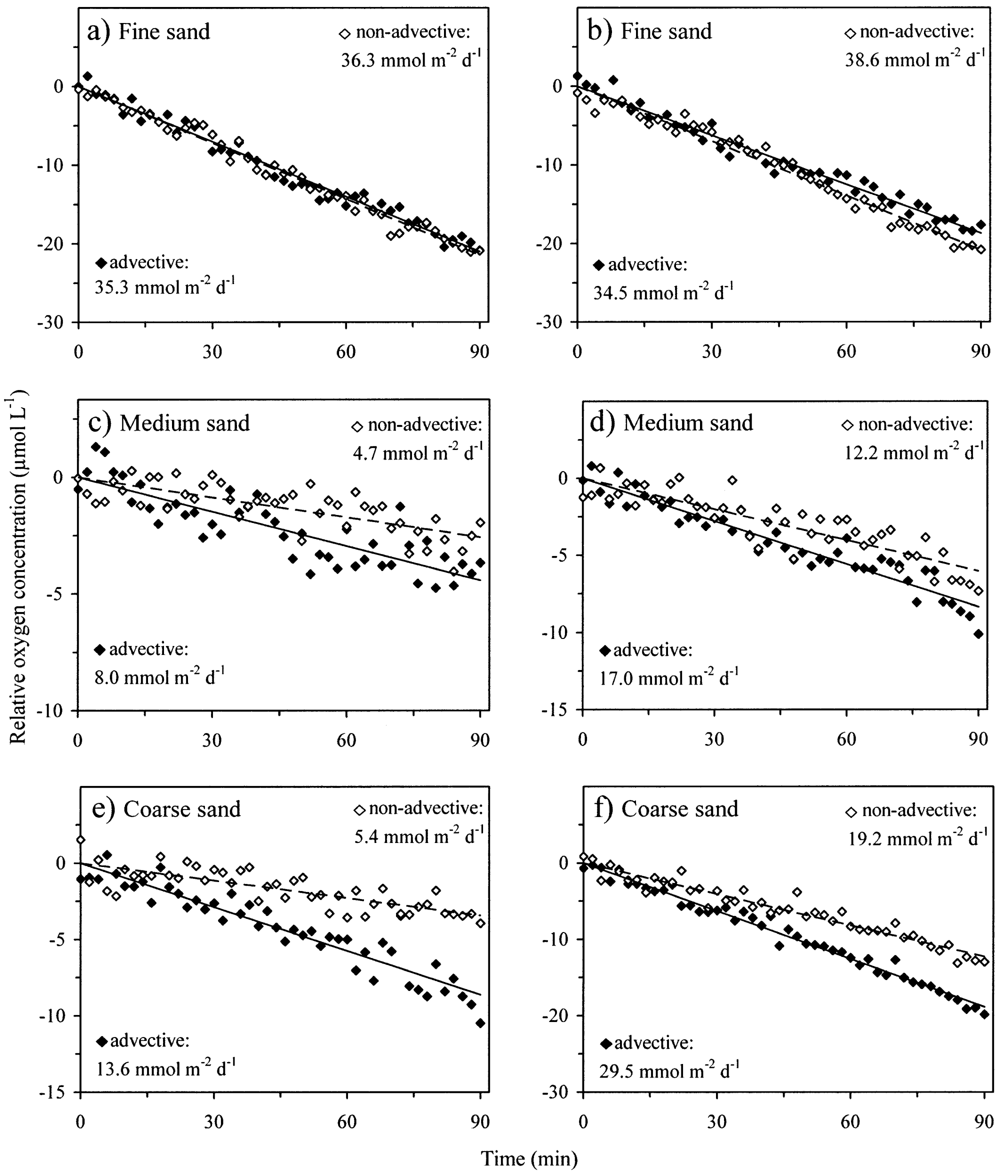

Fig. 5. Six examples of oxygen concentration time series at the (a, b) fine, (c, d) medium, and (e, f) coarse sand station. Oxygen concentrations are normalized to the same initial concentration and originate from the last 90 min of the advective (filled diamonds) and the first 90 min of the nonadvective stirrer setting (open diamonds). The trend lines represent linear regressions to oxygen depletion during the advective (solid line) and nonadvective stirrer setting (dashed line). The corresponding TOU values are indicated in the graphs.

Studies of benthic fluxes in the natural environment are expected to result in more realistic flux estimates as compared with ex situ incubations since disturbance of the sediment structure is minimized and changes in biogeochemical zonation due to sampling and ageing prior to the incubations are ruled out. As an alternative to benthic chamber incubations, in situ fluxes may be determined based on profiles of solute concentration above or below the sediment–water interface. This approach, however, works only in spatially homogenous muddy sediments, where one-dimensional concentration profiles may reasonably represent conditions of diffusive transport. In order to quantify the net flux in sands, measurements would have to integrate over separated inflow and outflow areas since they are created by advective porewater circulation (Ziebis et al. 1996; Precht et al. 2004). Even more important, basic knowledge of the rates of advection is missing and an appropriate mathematical representation of advective solute transport is not yet available (Boudreau et al. 2001). Recently, an attempt has been made to infer oxygen fluxes from a combination of laboratory measurements of volumetric respiration rates and in situ time series of oxygen penetration depth (de Beer et al. 2005). Another promising technique for the quantification of TOU in permeable sediments in situ is the eddy correlation tech-

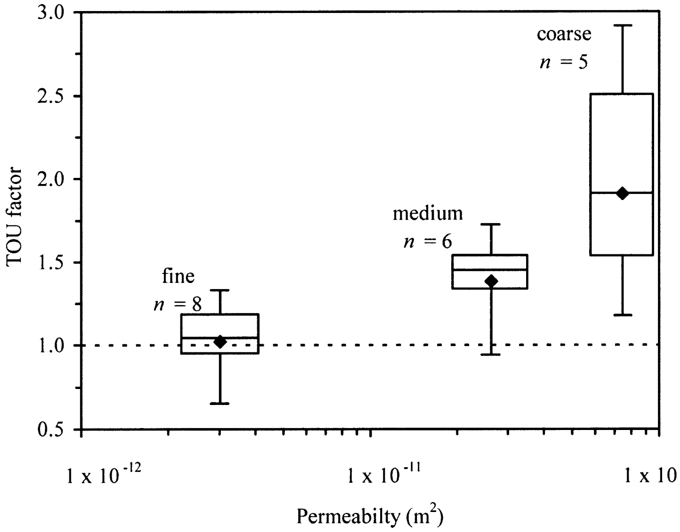

Fig. 6. Factor between total oxygen uptake rates (TOU) in the presence and absence of advection at the three stations (calculated separately for each chamber incubation). The diamond represents the geometric mean. The median is given by the horizontal line. The box marks the upper and lower quartile, the whiskers the total range of values.

nique that is based on simultaneous measurements of flow and oxygen concentration in the benthic boundary layer (Berg et al. 2003).

Chamber-derived fluxes of permeable sands depend on the hydrodynamic properties within the chamber, since these determine the pressure gradients at the sediment surface, and hence the rates of advective solute exchange (Booij et al. 1991; Glud et al. 1996; Jahnke et al. 2000). Most available chamber designs include some kind of rotating stirrer to prevent stagnation of the chamber water (Tengberg et al. 1995). Since any rotation of the water column results in pressure gradients (Tengberg et al. in press), it is likely that at least some advective pore-water exchange is included in most existing chamber-derived solute flux estimates from permeable sandy sites. However, in order to compare fluxes obtained at different sites and by different investigators, a characterization of the pressure distribution in the chamber and information on the permeabilities should be considered as a minimum requirement for future flux studies in permeable sands. This study presents the first flux data from permeable sites that were obtained under defined conditions of advective pore-water exchange in situ. Furthermore, the change in stirrer-induced pressure gradients during chamber deployments allows an investigation of the effect of advection on TOU in natural sandy sediments.

Oxygen fluxes in the presence of advection—In order to obtain oxygen fluxes that are representative for a specific environment, knowledge of natural pressure gradients within the area under consideration is needed in order to adjust the pressure gradients in the chamber accordingly. Pressure gradients and advection in excess of natural conditions would result in an artificially deep oxygenation of the enclosed sediment and could draw reduced pore waters from below the regularly flushed layer to the sediment surface. This would lead to reoxidation of accumulated reduced solutes and would violate the above mentioned steady state assumption

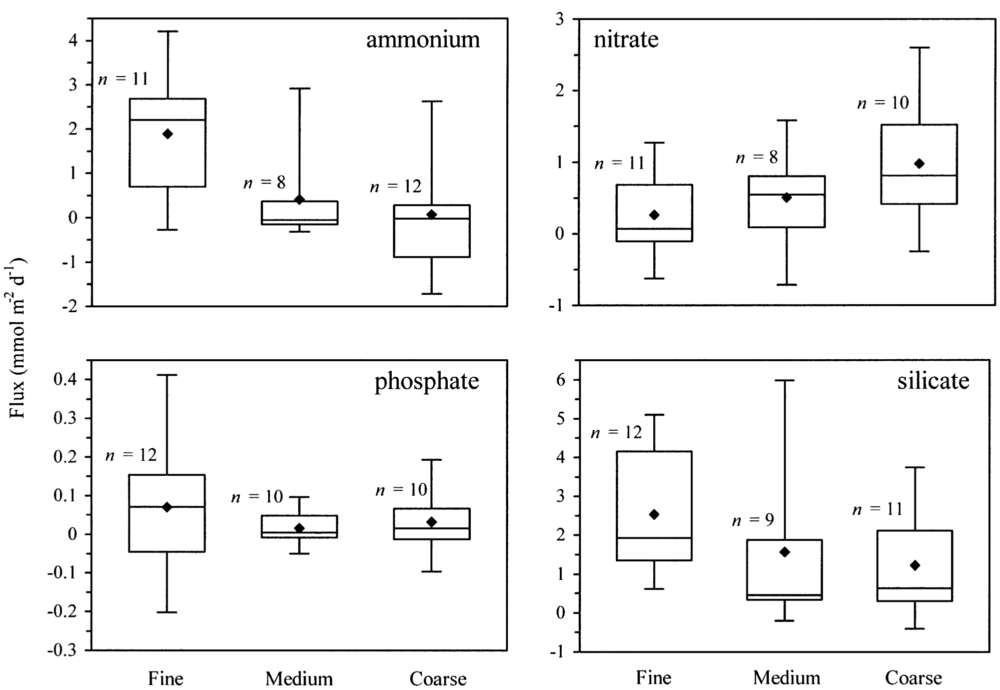

Fig. 7. Box plot of ammonium, nitrate, phosphate, and silicate fluxes. The diamond represents the mean, the median is given by the horizontal line. The box marks the upper and lower quartile, the whiskers the total range of values.

Table 4. Nutrient fluxes (averages with standard deviations) obtained at the three stations. Numbers of replicates are indicated in Fig. 7.

Sediment type	Nutrient fluxes (mmol m^{-2} d^{-1}), average $\pm$ SD				
	Ammonium	Nitrate	Nitrite	Phosphate	Silicate
Fine	1.89±1.49	0.26±0.58	0.09±0.14	0.07±0.16	2.54±1.67
Medium	0.41±1.10	0.51±0.74	0.06±0.18	0.02±0.05	1.57±2.25
Coarse	0.07±1.30	0.98±0.89	0.06±0.29	0.03±0.09	1.22±1.44

between their production and reoxidation, resulting in an overestimation of oxygen fluxes and mineralization rates. Huettel and Gust (1992*a*) and Huettel et al. (1996) found that horizontal pressure gradients in current-exposed sediments increase exponentially with bottom flow velocity and roughness element height. In these studies, pressure gradients similar to those induced at the advective stirrer setting (2.9 Pa overall pressure differential between the center and the circumference, 0.044 Pa mm^{-1} maximum gradient) were found to develop across mounds of 10 mm height that were exposed to unidirectional bottom flow of roughly 20 cm s^{-1} (measured 10 cm above the sediment surface). These values correspond to average roughness heights and flow velocities as they have been measured in the area. Maximum sediment elevations (35 mm) and peak tidal bottom flows (35 cm s^{-1}), however, proved to be much higher. Still, they are most likely well below the true maximum values in this area since measurements took place at calm weather conditions and larger topographical features like dunes or ridges cannot be recognized in the 0.5 m long topography profiles. Therefore, the pressure gradients at the advective stirrer setting are considered to be representative of normal conditions, while maximum gradients in the area are expected to be much higher.

Huettel and Rusch (2000) emphasized that the radial pressure gradient and the resulting pore-water flow field within the enclosed sediment have strong similarities to conditions at current-exposed topographical features with respect to pore-water flow trajectories, velocities, and penetration depth. Nevertheless, the pore-water circulation pattern will most likely change upon enclosure, since the former natural pressure distribution is replaced by the stirrer-induced gradient. Initially, the oxygen concentration of the pore water that leaves the sediment in the central low pressure region of the chamber therefore represents the remains of preenclosure oxygen supply and consumption. With ongoing deployment time, the oxygen distributions within the sediment gradually adjust to the new advective pattern, as has been observed in laboratory flumes and chambers (Booij et al. 1991; Ziebis et al. 1996; Precht et al. 2004). Pore water emerging from the sediment then starts to reflect these changes. However, this transition in response to chamber conditions is not expected to introduce substantial artifacts to flux estimates. Shifting pore-water transport pathways can be expected to be common in natural permeable sands, where direction and speed of tidal bottom flows permanently change and alterations of sediment topography take place due to currents and bioturbation (e.g., Wheatcroft 1994). This implies that changes in pore-water flow fields as they result from sediment enclosure can be viewed as a normal scenario. In addition, the flux determinations were restricted to deployments where oxygen decrease was linear, i.e., where a pronounced effect of such a transition on oxygen fluxes was not detectable. In summary, the incubation at the advective stirrer setting is assumed to reasonably represent environmental conditions with respect to pressure gradient magnitude and pore-water circulation patterns, including the general pattern as well as possible transitions following the enclosure. Therefore, conditions of oxygen transport and reaction in the chamber should resemble those in the environment, and oxygen uptake rates inside the chamber are expected to be a realistic approximation of natural fluxes.

TOU at the advective stirrer setting proved to be in a similar range in all three sediments with an average of 31.3 mmol m^{-2} d^{-1} for all incubations. These fluxes are relatively high as compared with values reported from other shelf environments. Based on a compilation of 60 studies of carbon oxidation rates in shelf sediments, Canfield and Teske (1996) reported a median oxygen uptake rate of 13.7 mmol m^{-2} d^{-1}. The average organic carbon content of the sediments is given as 0.65 wt% (i.e., 5, 28, and 22 times that of the fine, medium, and coarse sand, respectively), indicating that their data set also included organically rich deposits. The fact that oxygen uptake rates measured in the organically poor sediments of this study were substantially higher confirms that total organic matter content is an inappropriate measure of sediment activity and that oxygen uptake rates of sandy sediments are not necessarily small but can be in the same order than those of finer, organically rich deposits (Andersen and Helder 1987; Cammen 1991).

With respect to the organic matter content of these organically poor sediments, it has to be stated that even at the organically poorest but most active medium sand station, the organic carbon contained in the sediment (0.023% dry weight) amounts to a standing stock that is still relatively large in relation to the observed oxygen uptake rate (37.3 mmol m^{-2} d^{-1}). At the actual porosity of only 0.34, 1 ml of wet sediment contains as much as 1.8 g of solids and 0.41 mg of organic carbon. Assuming a respiratory quotient of one, the organic matter contained in the top 5 cm of the sediment (20.3 g or 1.7 mol C per square meter) could sustain benthic respiration for 45 d. At the coarse and fine sand station, the respective turnover times would amount to 82 and 296 d.

The significance of advection for sediment oxygen uptake—In order to investigate the effect of advective transport on oxygen consumption, we compared TOU in the presence and absence of advection. Switching to the nonadvective stirrer setting resulted in a pronounced drop in TOU by a factor of 1.38 and 1.91 at the medium and coarse sand station, while TOU remained unchanged at the fine sand station. The difference between factors at the medium and coarse sand station should be treated with caution because of the large variability of the data. A clear and statistically significant difference, however, existed between factors at both of these stations and that of the less permeable fine sand station (1.02).

Benthic macrofauna has to be considered as a potential cause for the observed drop in TOU at the medium and coarse station. This would require a reduction in bioirrigation activity (Forster et al. 1999) taking place in response to the stirring mode change. All stations lie within a region that is characterized by the ''*Tellina-fabula* macrofauna association'' (Salzwedel et al. 1985). A significant contribution of the macrofauna at the medium and coarse sand station thus seems unlikely since at least some change in TOU would have been expected to occur at the fine sand station, too.

Assuming that bioirrigation remained unaffected by stirring, the drop in TOU must have been due to the lack of advective pore-water transport at the nonadvective stirrer setting. This indicates that at the advective stirrer setting advection supplied a significant proportion of the oxygen that was consumed within the sediment. An enhanced sediment oxygen uptake in the presence of advection is in agreement with the flume study of Forster et al. (1996), who found that TOU in permeable sediments with topographically rough surfaces scaled with bottom flow velocity. Because the increase in TOU corresponded to the estimated increase in oxygenated sediment volume due to advection, they concluded that it was the advective supply with oxygen that allowed for the additional TOU.

The combined oxygen transport by diffusion and bioirrigation at the nonadvective stirrer setting proved to be insufficient to satisfy the sediment oxygen demand that existed in the presence of advection. Low rates of diffusive uptake are likely to be connected to an enhanced sediment oxygenation by means of advection. Stirrer-induced pressure gradients lead to an inflow of chamber water in most of the enclosed sediment surface area, while the pore-water outflow is restricted to a relatively small central region (Huettel and Rusch 2000). Similar patterns with large inflow areas and relatively small corresponding outflow areas are characteristic also for topography-induced advective pore-water flow fields (Huettel and Gust 1992*a*; Huettel et al. 1996). This inflow of oxygen-rich water in the majority of the enclosed sediment area will keep oxygen gradients relatively small, as was observed in response to stirring in cylindrical laboratory chambers (Booij et al. 1991). When the stirrer setting is changed and advection ceases, oxygen diffusion along these small gradients will take place at relatively low rates, which explains the observed immediate drop in TOU.

The difference in TOU between both settings represents the proportion of the oxygen consumption that was based on advective oxygen supply at the advective stirrer setting. How much of this supply was actually used within the sediment can be assessed by comparing the differences in TOU between both stirrer settings with rates of advective pore-water exchange. At the coarse sand station, advective exchange rates of approximately 90 L m^{-2} d^{-1} have been estimated from the progressive depletion of an inert tracer dye that was added to the chamber water (Janssen et al. 2005). According to the relationship between advective exchange and permeability reported by Glud et al. (1996), the advective exchange at the medium sand station can be expected to be 40% lower, i.e., 54 L m^{-2} d^{-1}. The net advective oxygen transport into the enclosed sediment equals the pore-water exchange rate multiplied by the difference in oxygen concentration between the chamber water that enters the sediment (218.4 $\pm$ 25.4 [SD] μmol L^{-1} at the time of the stirring mode change) and the pore-water that is released. Thus, a minimum exchange rate of 50 L m^{-2} d^{-1} is needed to allow for the advection-related TOU enhancement of roughly 11 mmol m^{-2} d^{-1} at the medium and coarse sand station. Given the above pore-water exchange rate of 54 L m^{-2} d^{-1}, this calculation suggests that almost all oxygen (93%) was removed from the pore water during the passage through the medium sand. At the coarse sand station, according to the same calculation, 44% of the oxygen was still present in the emerging pore water. This would have allowed for an additional oxygen demand of the coarse sediment of 8.7 mmol m^{-2} d^{-1}. In the case of the medium sand station it seems that, at the applied pressure gradients, oxygen consumption rates were still limited by the rates of advective transport. At higher pressure gradients (e.g., in the presence of strong wind- or wave-driven currents or large roughness elements) the oxygen uptake that is accounted for by advection may thus be even higher. The calculated incomplete oxygen removal at the coarse sand station indicated that at moderate, stirrer-induced advection the supply with oxygen exceeded the demand of the biological and chemical processes taking place in the sediment. However, this also implies that under normal conditions, advection could sustain oxygen consumption in excess of the rates measured in this study given a sufficient supply of labile organic matter. Such conditions can be expected during phytoplankton blooms, when fresh organic particles are abundant in the water column and transported into the sediment by means of advection (Pilditch et al. 1998; Huettel and Rusch 2000; Rusch et al. 2001).

Implications for the natural environment—Based on the assumption that the stirrer-induced pressure gradients were in the same range as those encountered in the environment, it is likely that under natural conditions, too, a significant proportion of the oxygen needed for respiration in the medium and coarse sands is supplied by advection. In the less permeable sediments of the fine sand station, advective oxygen supply is probably of minor importance. Since the oxygen demand proved to be roughly similar at all three stations, a reduced advective oxygen supply in the fine sand is expected to result in a shallower oxygen penetration as compared with the other stations. This is confirmed by in situ oxygen microprofile time series that indicated average oxygen penetration depths ($\pm$ SD) of 9 $\pm$ 3 and 26 $\pm$ 12 mm, at the fine and medium sand station, respectively (Werner unpubl. data). A reduced oxygen penetration in the fine sand also agrees with the release of ammonium at that station since it would restrict nitrification to the uppermost sediment horizon. By contrast, at the medium and coarse sand station, higher rates of advective oxygen supply and deeper oxygen penetration most likely allow for a quantitative nitrification of ammonium within the sediment. The general pattern of dissolved inorganic nitrogen (DIN) species released at the three stations is also in agreement with fluxes that were measured by Ehrenhauss et al. (2004) in incubations of sands from the same three stations.

Assuming that all oxygen uptake measured at the three stations was due to organic matter mineralization, the corresponding rates of carbon oxidation can be related to the chamber-derived DIN fluxes (i.e., $JNH_4^+ + JNO_3^- + JNO_2^-$). If the sediment TOC : TN ratio was representative of the organic matter that was mineralized and the respiratory quotient equaled one, the respective DIN fluxes at the fine, medium, and coarse sand station were 1.6, 5.0, and 2.6 times smaller than expected from the organic matter composition. A possible sink for DIN is the uptake by growing bacteria. Van Duyl et al. (1993) observed that DIN fluxes in sandy sediments were lowest when bacterial production was highest. The relatively low DIN fluxes, especially in the medium and coarse sand, suggest that bacterial populations in these sediments have the potential to grow if nutrients and organic matter become available. This might be envisioned as an indication for a high activity of bacteria at these stations. Another indication of an intensified microbial activity in the medium and coarse sands as compared with the fine sand can be inferred from the respective bacterial biomasses. Based on bacteria-specific fatty acids, the bacterial biomass in the fine sand was estimated to exceed that in the medium and coarse sand by a factor of 4 and 9, respectively (Bühring et al. 2005). The fact that the rates of TOU were in the same range at all three stations indicates that the microbial metabolism was higher per unit of biomass at the medium and coarse sand station.

An enhanced metabolic activity of the sediment bacteria in the medium and coarse sand may be explained by the presence of significant advection at these stations. As highlighted in the introduction, a number of advection-related processes are thought to create favorable conditions for microbial activity and organic matter mineralization in permeable sediments. These include trapping of suspended organic particles resulting in a better availability of fresh organic matter, an enhanced supply with electron acceptors, an efficient waste product removal, and the formation of enlarged and spatiotemporally dynamic biogeochemical transition zones. Since all of these processes are directly coupled to advection, it can be expected that not only the oxygen supply is intensified in the medium and coarse sand but that the whole range of advection-related processes applies to these sediments with all consequences for the sediment biogeochemistry and the supply and mineralization of organic matter.

Several studies identified sediment permeability as the key factor that determines whether or not advection-related processes are significant relative to diffusive transport, bioturbation, and bioirrigation. The studied processes include the quantification of pore-water exchange (Huettel and Gust 1992*a*; Glud et al. 1996), the filtration of suspended particles and microalgae (Huettel et al. 1996; Huettel and Rusch 2000), and the transport and consumption of oxygen as determined with enclosures and microsensors (Forster et al.

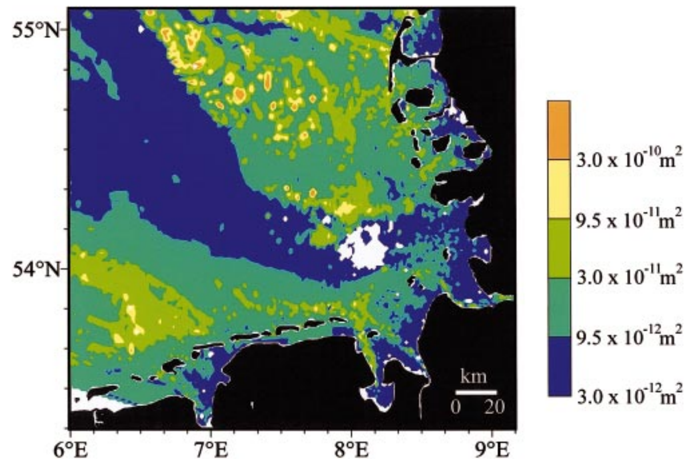

Fig. 8. Contour plot of the permeabilities of the German Bight as calculated based on grain size measures according to Krumbein and Monk (1943) using the median grain sizes and standard deviation in phi units. The standard deviation was inferred from the reported 25th and 75th percentile (data source: Marine Environmental Data Base, Federal Maritime and Hydrographic Agency of Germany). The permeablities of the individual samples are transferred to an approximately 1×1 km^2 grid by triangulation with linear interpolation. Gridding and contour plotting were done with the software Surfer 6.01 (Golden Software Inc.). Blank parts in the plot mark areas that were not covered by samples (lower left corner) or where median grain sizes were below the sand size range (e.g., muddy area around 54°N, 8°E).

1996; Ziebis et al. 1996). Despite the diversity of the investigated processes and experimental approaches (flumes and chambers, in the laboratory and on tidal flats), all studies agree that sediment permeabilities between 10^{-11} and 10^{-12} m^2 are the minimum requirement for a significant effect of advection on the respective processes. In the present study, the permeability threshold for an effect of advection on TOU in natural shelf sediments proved to lie between 3×10^{-12} and 2.6×10^{-11} m^2 (i.e., between the permeabilities of the fine and medium sand station) and thus agrees with the thresholds reported in the previous studies. These results provide field evidence that the effect of advection on sedimentary processes does not apply to sandy sediments in general but is restricted to sites of high permeability. Estimating the significance of advection-related processes in sandy areas further is complicated because the reported permeability thresholds are dependent on the pressure gradients that have been applied in the respective studies. The above mentioned permeability thresholds were generally obtained under low to moderate energy conditions (i.e., stirring at relatively low rates with flows below the erosion threshold and subcritical flume flows). It can thus be expected that under natural environmental conditions with stronger boundary layer flows as frequently present on the shallow shelf, significant advective transport may also occur in less permeable sands.

Significance of advection for oxygen supply in German Bight sediments—Approximately 98% of the surficial sediment of the German Bight area is composed of sands (all colored area in Fig. 8). While permeability measurements in

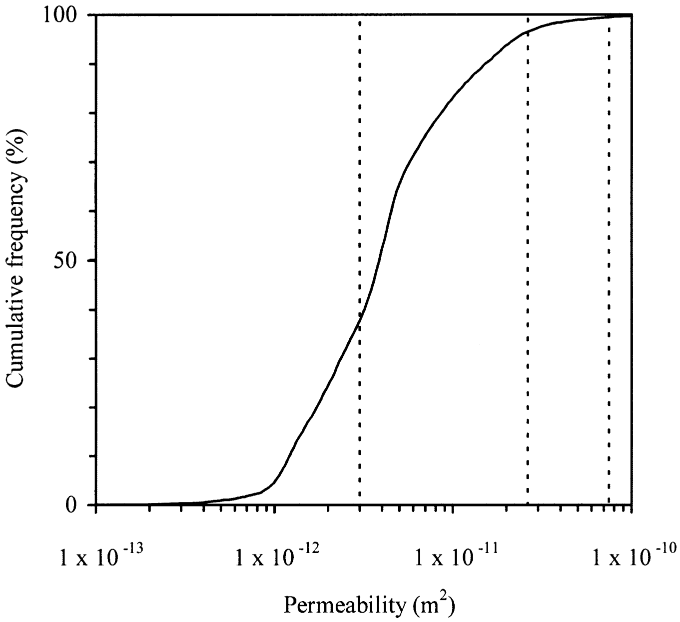

Fig. 9. Cumulative frequencies of the permeabilities of the German Bight according to the 1 × 1 km^2 grid (*see legend of Fig. 8*). Apart from minute errors that result from the simplifying equidistant cylindrical projection, the frequencies equal the proportion of the total seafloor area of Fig. 8 (approximately 29,000 km^2) that is covered by sands of the respective permeabilities. The dashed vertical lines represent the permeabilities at the fine, medium, and coarse sand station (from left to right).

the area are largely missing, rough estimates may be obtained based on granulometric data. Rusch et al. (2001) found that permeabilities calculated from median grain size and sorting of intertidal sands according to the relationship of Krumbein and Monk (1943) overestimated the actual permeabilities by a factor of 3.87 ± 2.21 (SD). A likely reason for this discrepancy is that the relationship was determined in sieved sands with a Gaussian grain size distribution and does not account for distribution skewness and kurtosis or biological clogging of the pores. An overestimation by a factor of 2.03 ± 0.94 was also observed at the three sites of this study. Figure 8 shows permeability estimates for the entire German Bight as calculated from median grain size and sorting of a total of approximately 16,000 surface sediment samples (Marine Environmental Data Base, Federal Maritime and Hydrographic Agency of Germany). The values were reduced by a factor of three to account for the effects mentioned above. Figure 9 shows the areal coverage of the sediment permeabilities as a cumulative frequency plot.

Sediments with permeabilities below that of the fine sand station (i.e., all blue areas in Fig. 8) are estimated to cover roughly 40% of the total surface area. Based on the chamber results, an impact of advection on oxygen fluxes, at least under calm conditions, can be largely excluded in these areas. In the remaining 60% of the German Bight, permeabilities are within a range, where significant advective pore-water exchange is expected to occur (Huettel and Gust 1992*a*; Glud et al. 1996). It thus seems likely that in these regions advection contributes to oxygen uptake to an extent that gradually increases with increasing permeability. Direct evidence for such an effect was restricted to the medium and coarse sand station. Sands with such high permeabilities (i.e., 2.6×10^{-11} m^2 or higher), however, are only expected to occur in 3% of the German Bight seafloor. The areal coverage of sediments, where advection significantly contributes to oxygen uptake, thus remains largely unresolved. Further uncertainties arise from the fact that this estimate is based on permeability only and does not take the spatial distribution and temporal changes of hydrodynamic conditions and sediment topography into account. More detailed studies are needed to increase our knowledge of advection-related processes in natural environments in order to gain insight into the relevance of permeable sediments for carbon cycling on the shelf. Main topics to be addressed include the factors controlling advective pore-water flow and solute exchange in natural environments (i.e., permeabilities, topographies, and hydrodynamics), as well as the impact that advective exchange has on processes that are connected to organic matter mineralization in these beds.

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