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**Temporal variations
in microbial carbon
turnover**

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Temporal variations in microbial activities and carbon turnover in subtidal sandy sediments

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Received: 8 September 2008 – Accepted: 14 September 2008 – Published: 6 November 2008

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Published by Copernicus Publications on behalf of the European Geosciences Union.

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Abstract

Temporal dynamics and vertical patterns in bacterial abundances and activities were studied in a shallow subtidal sand flat in the Sylt-Rømø Basin (North Frisian Wadden Sea, Germany.) Extracellular enzymatic activities, bacterial carbon production and community respiration showed strong (factor of 4–5) temporal variations that were mostly related to seasonal temperature change, but also to changes in substrate availability. These temporal patterns in activity were barely reflected in bacterial (200–400 mmol C m⁻²) and microphytobenthic biomass (800–1500 mmol C m⁻²) or the sedimentary carbohydrate inventory (1300–2900 mmol C m⁻²), suggesting that grazing controls the standing stocks of the microphytobenthic and bacterial assemblages. Despite their exposure to strong hydrodynamic forces such as tidal currents and wind-induced wave surge, the subtidal sandy sediments showed persistent vertical gradients in bacterial abundances, bacterial carbon production and extracellular enzymatic activities at all times. The vertical distribution of these parameters was tightly coupled to that of the microphytobenthos, dominated by diatoms. Despite the low organic carbon content typical for surge-exposed sandy sediments, high extracellular enzymatic activities and bacterial carbon production rates indicate a very active heterotrophic bacterial community, with a gross secondary productivity of 30–180 mmol C m⁻², and a biomass turnover time of 2–18 days. Our data suggest that this high activity is supported by the rapid flux of carbohydrates from microphytobenthic primary productivity. Accordingly, the potential activities of enzymes hydrolyzing carbohydrates cover most of the total bacterial carbon demand during all seasons.

1 Introduction

Shelf sediments represent less than 10% of the ocean floor, but they contain the largest pool of particulate organic matter in the marine environment and play a major role in global carbon and nitrogen cycles (Jahnke, 2004). Shallow coastal ecosystems con-

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tribute substantially to oceanic carbon fixation via pelagic and benthic primary productivity (Wollast, 2002; Gattuso et al., 2006). The turnover of carbon in subtidal shelf sediments has been extensively investigated, however most studies focused on organic-rich, silty and muddy seafloors. Sandy sediments have long been considered as biochemically inert due to their low organic carbon content, and hence have been neglected in the marine carbon cycle (Boudreau et al., 2001). However, permeable sands are the dominant sediment type on continental shelves (Emery, 1968; Hall, 2002) and are important from biological, geological, and economic perspectives. Recent studies measured high primary productivity in sandy sediments (Billerbeck et al., 2007), and found that organic matter mineralization rates in sands are comparable to or even higher than rates in fine-grained, organic-rich sediments (D'Andrea et al., 2002; de Beer et al., 2005; Rusch et al., 2006).

The high mineralization rates are driven by photosynthetic production, either in the form of settling phytodetritus or via photosynthetic products excreted by the microphytobenthos (Goto et al., 2001; Rusch et al., 2003). Although burial of phytoplankton detritus has been shown to stimulate benthic microbial activities (Meyer-Reil, 1987; van Duyl et al., 1992; Rooney-Varga et al., 2005), primary productivity by microphytobenthic algae (MPB) is recognized as the main source of organic carbon for benthic life in light-exposed coastal sediments (MacIntyre et al., 1996; Underwood and Kromkamp, 1999).

Carbon flux from microphytobenthic algae to other benthic microorganisms can be significant and rapid, as has been demonstrated by studies using isotope tracer incubations (Middelburg et al., 2000; Cook et al., 2007a). The carbon flux includes large quantities of extracellular polymeric substances (EPS) secreted by the MPB to promote migration, adhesion to sediment particles and sediment cohesion (Hoagland et al., 1993; Underwood and Paterson, 2003). In addition, unbalanced growth under nutrient-depleted conditions may considerably increase the release of carbohydrates by photoautotrophs in order to maintain cell-nutrient balances (Ortega-Calvo and Stal, 1994; Smith and Underwood, 1998). In consequence, up to 70% of the carbon fixed

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may be excreted as EPS, rather than allocated to algal growth (Middelburg et al., 2000; de Brouwer and Stal, 2001). The MPB is often dominated by benthic diatoms, which form biofilms in association with bacteria (Huettel et al., 2003).

Degradation of polysaccharides by bacterial communities plays a key role in the dynamic environment of coastal sands. Previous works on bacteria and their activities in permeable sediments (e.g. Staats et al., 2001a, b; Rusch et al., 2003; de Beer et al., 2005; Misic and Fabiano, 2005; Misic and Harriague, 2007) focused mostly on intertidal areas, and/or had limited time or depth resolution. Therefore, the dynamics of interactions between autotrophic and heterotrophic components of the microbial communities in sandy sediments and the distribution and availability of substrates, including potential variations in carbon inventories with time and depth, and responses to seasonal temperature changes are not well constrained.

We studied a shallow subtidal sand flat (Hausstrand) in the Sylt-Rømø Basin of the North Frisian Wadden Sea, focusing on temporal and temperature-related variations in benthic microbial activity and the MPB-derived carbohydrate inventory. We also examined the extent to which depth gradients in microbial and MPB-related parameters persisted over time in this hydrodynamically active site. During 6 sampling periods over the course of more than a year, covering a water temperature range of 1.5–18°C, we measured bacterial abundances, bacterial carbon production, and potential activities of extracellular exoenzymes using several substrate proxies, and activities of endo-acting enzymes using fluorescently-labeled polysaccharides. We also measured photopigments (as a proxy for primary producer biomass), bacterial biomass, and total sedimentary carbohydrates as well as EDTA-extractable carbohydrates, which are believed to be the quantitatively most important substrates for the benthic microbial community of photosynthetically active sands. The ratio of bacterial turnover of MPB-derived carbon sources was estimated for different seasons, and the effects of temperature, sediment depth and other factors controlling microbial activity were explored by multivariate analysis. This suite of measurements was intended to provide insight into the influence of MPB on carbon cycling by heterotrophic bacteria in a highly dynamic

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environment. We hypothesized that the spatial and temporal distribution of the MPB and their carbohydrates are major controls on bacterial distribution and activity, and quantification of this influence was a goal of our study.

2 Materials and methods

2.1 Study site

2.1.1 Site description

The study site Hausstrand (Fig. 1) is located on the island of Sylt (55°00′47.7″ N, 008°25′59.3″ E; Fig. 1), where the temperature difference between summer and winter can be more than 20°C (Hedtkamp, 2005). The site is characterized by the strong hydrodynamic forces of tides and wind-induced waves, with a tidal amplitude of ~2 m. Water depth ranges between 0.5–2.5 m, depending on weather and the tidal phase. Sediments consist of well to moderately well sorted silicate sand with a medium particle size of 350 μm. The permeability of the upper 15 cm of the sediments ranges between $1.01 \times 10^{-11} \text{ m}^2$ and $3.36 \times 10^{-11} \text{ m}^2$, with higher values in winter and spring compared to summer and autumn (Hedtkamp, 2005). Since the islands of Sylt and Rømø are connected to the mainland by a causeway, the main water exchange takes place through the inlet to the North Sea. However, in comparison to other areas of the North Sea, the entry of fine material is low (Köster and Müller, 1998). The Hausstrand sands are organic matter impoverished, with an average organic carbon concentration of 0.13% (Hedtkamp, 2005). Further information on the Sylt-Rømø Basin (also known as the List Tidal Basin) are given by Gätje and Reise (1998) and van Beusekom and Reise (2008) and references therein.

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2.1.2 Sampling and sample processing

Push cores (3.6 cm inner diameter, 15–20 cm length; cores for laminarin incubations with silicon-covered injection holes) were collected in February, April, July and November 2005, and 1st and 27th March (labeled March I and March II) 2006 during low tide. In April and November, sampling was performed by scuba-diving, due to stormy weather and high water level. In November, the retrieved sediment cores only included the top 10 cm layer. Replicate cores (8.4 cm inner diameter, 30 cm length) were also collected for measurement of benthic oxygen demand.

Ten replicate sediment cores from an area of $<20\text{ m}^2$ were sectioned in 1-cm intervals down to 15 cm depth. Sediment slices from the same depth horizon were pooled and homogenized. The samples were processed in the laboratory adjacent to the Hausstrand field site (AWI station, List on Sylt) immediately after collection. Subsamples for the measurement of photopigments and carbohydrates were frozen immediately and stored at -20°C . The rest of the homogenized sediment was combined in 5-cm intervals (0–5, 5–10, and 10–15 cm). For bacterial cell counts sediment was fixed in 2% formaldehyde/seawater solution; subsamples for the measurement of extracellular enzymatic activities (EEA) and bacterial carbon production (BCP) were processed immediately. Cores used for laminarin incubation were injected with $100\mu\text{l}$ of laminarin ($1.9\mu\text{mol}$ monomer equivalents L^{-1}) at depths of 1, 5, and 13 cm, and incubated at in situ temperature in the dark.

2.2 Rate Measurements

2.2.1 Bacterial carbon production (BCP)

BCP was estimated by measuring the rate of [Methyl- ^3H] thymidine (TdR) incorporation into DNA (Fuhrman and Azam, 1982; Moriarty and Pollard, 1990). Sediment slurries (1:1 sediment: sterile-filtered seawater; $n=4-5$ per depth interval) amended with TdR were incubated for 1.5–4 h at near in situ temperature, and TdR incorporation was

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stopped by adding 100 μl of 37% formaldehyde. Killed controls received formaldehyde prior to incubation. A time course and concentration experiment was conducted at the beginning of the study to ensure that all measurements were carried out in the initial linear period of incorporation of label into DNA and that isotope dilution by *de novo* synthesis of thymidine was insignificant (Moriarty, 1990). Extractions followed a modification of Findley et al. (1984) and Michel and Bloem (1993). BCP was calculated using a conversion factor of 2×10^6 cells produced per pmol thymidine incorporated (Findley, 1993), and a carbon conversion factor of $20 \text{ fg C cell}^{-1}$ (Fuhrman and Azam, 1982).

2.2.2 Extracellular enzyme activities (EEA)

Potential exoenzymatic activity

Hydrolysis rates were measured in slurries using 4-methylumbelliferone- (MUF-) and 4-methylcoumarinyl-7-amide- (MCA-) labeled model substrates, which capture the activities of exoenzymes that cleave the terminal ends of polymer chains. They are widely used (e.g. Hoppe, 1983; Hoppe et al., 1988; Boetius, 1995; Boetius and Lochte, 1996a, b), facilitating comparison between studies, but the extent to which they represent the activities of enzymes on true polymers is uncertain (Warren, 1996). Potential hydrolytic activities of α -glucosidase, β -glucosidase, chitinase, lipase, phosphatase and aminopeptidase were measured using the MUF-labeled substrate analogs MUF- α -D-glucoside, MUF- β -D-glucopyranoside, MUF-N-acetyl- β -glucosamine, MUF-stearate, MUF-phosphate and MCA-labeled leucine (all obtained from Sigma-Aldrich, Munich, Germany), respectively. For each depth interval (0–5, 5–10 and 10–15 cm) and substrate, five replicate 0.5-ml sub-samples of homogenized sediment from 10 pooled cores were diluted 1:10 with sterile filtered seawater. The substrates were dissolved in ethylene glycol monomethyl ether and added to the slurry at a final concentration of 0.5 mM. The samples were then agitated at in situ temperature in the dark. Shortly after the start of the time course experiment, 1 ml of the sample was removed and added

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to 2 ml of sterile-filtered seawater amended with 250 μ l of borate buffer (pH 10.0). After centrifugation, the supernatant was transferred into disposable UV-cuvettes and the fluorescence of the enzymatically released MUF and MCA was measured (445 nm emission, 365 nm excitation). A second measurement was performed after 2–4 h of incubation time. Pre-experiments were conducted prior to the start of the study to confirm that the final concentrations of MUF and MCA substrates generally represented substrate saturation levels and yielded maximum velocities. Hydrolytic activity was calculated from the increase of fluorescence over time calibrated via standards of both MUF and MCA. Since the fractions of the bacterial community that produce specific enzymes are unknown, cell-specific EEA was calculated as extracellular enzymatic activity divided by the total number of cells.

Potential endoenzymatic activity

Fluorescently labeled (FLA-) macromolecules (e.g. polysaccharides) can be used to measure the activities of endoenzymes (mid-chain cleaving enzymes) (Arnosti, 1995), and may better mimic the degradation of complex macromolecules in natural settings. The analytical procedure is time-consuming, however, restricting the number of analyses that can be performed. Here, hydrolysis of laminarin, an energy storage product of diatoms (Lee, 1980; Painter, 1983), was measured using the method of Arnosti (1995, 2003). Laminarin and fluorescenamine (isomer II) were purchased from Sigma, and fluorescently labeled laminarin was synthesized after Glabe et al. (1983) as described in Arnosti (1995, 2003). Potential hydrolysis rates of laminarin were measured in intact sediment cores by injection of 1.9 μ mol monomer equivalents of laminarin at –1 cm, –5 cm and –13 cm depth. These measures were used to extrapolate to the average activity in the 0–5, 5–10 and 10–15 cm layer. One core was left without laminarin and served as a blank sample. All cores were incubated at in situ temperature in the dark in an upright position. After ~24, ~48 and ~72 h incubation at in situ temperature, 2–3 replicate cores were sacrificed and sectioned in 2-cm intervals. Hydrolysis of substrate was found to be nearly complete by 24 h, so all of the rates reported here are derived

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from triplicate 24 h incubations. Pore water was purged from the sediment with nitrogen, as described by Billerbeck et al. (2006), filtered through 0.2 μm pore size filters, and stored at -20°C until analysis. One core was sectioned immediately after injection as the time zero sample. The molecular weight distribution of hydrolyzed polysaccharides was determined via low-pressure gel permeation chromatography (GPC) with fluorescence detection, as described in Arnosti (2003). Potential hydrolysis rates were calculated based on the molecular weight distribution of laminarin hydrolysis products in each sample as described by Arnosti (1995, 2003).

All laminarinase rates in this study may represent minimum potential rates, since the fluorescently labeled substrate compete with naturally occurring laminarin for enzyme active sites. Usually, FLA-laminarin is added equal to 100–500% of the total dissolved carbohydrates in order to measure hydrolysis at substrate saturation level. The concentration of dissolved interstitial carbohydrates in the sands was not measured in this study. FLA-laminarin was added in concentrations of 2.3–5.4 $\text{mmol glucose L}^{-1}$, which represents 200–800% of the pool of EDTA-extractable carbohydrates. However, since total carbohydrate concentrations were rather high (see results below), competition with naturally available laminarin cannot be excluded, especially in the diatom-dominated surface sediments.

Alderkamp et al. (2006) estimated that ca. 13% of the bacteria from North Sea coastal waters are capable of producing laminarinase. However, it is not known if this result also applies to sediments and how this ratio changes with time or location. In order to allow comparison with cell-specific MUF-/MCA-enzymatic activities, cell-specific laminarinase activities were calculated by dividing laminarinase activities by the total number of bacterial cells.

2.2.3 Benthic oxygen consumption

Gross benthic community respiration rates were estimated *ex situ* via incubation of intact sediment cores. The gas- and air-tight cores (“chambers”) were fitted with sampling ports and a magnetic stirrer and contained approximately 1 L sediment and 0.75 L

of overlying water. The cores were maintained at in situ temperature in a dark cold room. The overlying water in the cores was stirred carefully at a speed of ~20 rpm. Oxygen concentrations in the samples were determined by duplicate Winkler titrations (Winkler, 1888; Grasshoff et al., 1983) according to the procedure of Strickland and Parsons (1972), of samples withdrawn from the chambers over a 5-point timecourse. The benthic oxygen consumption rates were calculated from the averages of oxygen decrease over time according to Thorbergsdóttir et al. (2004). As the stirring speed was at the low end of advection of oxygenated water through Hausstrand sands, the rates presented here likely represent an underestimation of in situ respiration rates.

2.3 Bacterial counts and concentration measurements

2.3.1 Cell numbers

Bacterial abundances were estimated by epifluorescence microscopy after staining with Acridine Orange (AO) using a modification of the method of Hobbie et al. (1977). Prior to staining, the fixed samples (0.5 ml sediment per replicate) were centrifuged for 15 min at 4000 rpm and the fixative was removed and set aside. One milliliter of the removed fixative was placed back onto the sample and the slurry was sonicated for 4 min with an ultrasonic disintegrator while keeping the vial on ice (van Duyl and Kop, 1994). After the sand grains settled, the supernatant containing the cells was transferred to another vial. The remaining sediment was washed six times, each time with 1 ml of the fixative, which was thereafter combined with the cell suspension. Two 1-ml sub-samples (1:1000 final dilution) were filtered onto 0.2 μ m black polycarbonate filters and stained with AO solution (final concentration 0.01%) for 3 min. Subsequently, the filters were rinsed with 1 ml of citrate buffer and bacteria enumerated by epifluorescence microscopy (x1000). Final counts represent averages of 6 filters (2 filters from 3 replicate field samples), with 10–20 grids counted on each filter with at least 1000 cells per filter.

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2.3.2 Determination of photopigments

Triplicates of approximately 1 g of freeze-dried and homogenized sediment from each sediment layer were mixed with 7.5 ml of 90% acetone and extracted in the dark at 4°C for 24 h. Prior to measurement, the samples were centrifuged at 4000 rpm for 10 min. The supernatant was transferred to quartz cuvettes and the absorbance of the extract was measured at 665 and 750 nm before and after acidification with 10% HCl. Chlorophyll-*a* and phaeophytine concentrations were calculated according to Lorenzen (1967). Based on known sediment water contents, concentrations were converted to $\mu\text{g cm}^{-3}$ wet sediment. A carbon to chlorophyll-*a* conversion factor of 34 (Dijkman, as cited in Evrard 2007) was used to estimate MPB biomass.

2.3.3 Carbohydrate analysis

Total and EDTA-extractable carbohydrates were quantified using the phenol-sulfuric acid assay (Dubois et al., 1956; Herbert et al., 1971), according to Underwood et al. (1995). All measurements were done in triplicates. For measurement of EDTA-extractable carbohydrates, 100 mg of lyophilized and homogenized sediment was extracted with 5 ml of 0.1 M Na₂-EDTA for 15 min at 20°C. Following centrifugation at 4000 rpm for 15 min, 2 ml of the supernatant was transferred to combusted glass vials and 1 ml of 5% aqueous phenol (w/v) was added, immediately followed by 5 ml of concentrated H₂SO₄. After 10 min, the samples were carefully homogenized and incubated another 30 min. Absorbance was measured against a reagent blank at 485 nm. Measurements were calibrated against a curve made using glucose as a standard, so concentrations are expressed as microgram glucose equivalents. For the measurement of total carbohydrates, 50 mg of lyophilized and homogenized sediment were diluted in 2 ml of distilled H₂O, and then analyzed as above. Based on known sediment water contents, concentrations were converted to $\mu\text{g ml}^{-1}$ wet sediment.

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2.4 Statistical analysis

Error estimates represent standard deviations from the averages, based on replicate measurements as described above for each method. Correlations between all environmental variables were calculated using the Pearson's correlation coefficient for all samples that included carbohydrate measurements. All data, except for depth and temperature, were \log_{10} -transformed to normalize their distribution. Data was normalized to standard mean=0 and a standard deviation of 1 prior to computation of the Pearson's correlation coefficients. P-values were corrected for multiple testing using the Bonferroni correction (Ramette, 2007).

The relationship between environmental variables was studied in more detail by multivariate statistics using the software package CANOCO for Windows 4.5 (terBraak and Šmilauer, 1998). A principal component analysis (PCA) was used to reduce the dimensionality of the complex data set. PCA is an orthogonal linear transformation method that converts a number of potentially correlated variables into a smaller number of independent variables, the so-called principal components, while maintaining most of the original variability in the data. The first principle component accounts for the greatest variability in the data and each succeeding component explains as much of the remaining variability as possible.

3 Results

3.1 Bacterial cell numbers and growth rates

Total cell numbers and bacterial carbon production (BCP) were highest in the upper 0–5 cm sediment layer and decreased with depth (Table 1). Cell numbers ranged between 1.7 and 2.9 10^9 cells cm^{-3} wet sediment in the 0–5 cm layer, representing a bacterial biomass of 2.8–4.8 mmol C L^{-1} , based on a conversion factor of 20 fg C cell⁻¹ (Fuhrman and Azam, 1982). BCP ranged between 0.43 and 2.29 mmol C L^{-1} . Turnover

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time of the bacterial community biomass was calculated to be 2.1–8.6 d in the 0–5 cm layer, with fastest turnover in July and slowest turnover in November. Bacterial biomass and BCP generally followed temperature, with maximum values in July (Fig. 2). However, despite the fact that BCP rates and bacterial turnover time in the upper sand layer were ca. 4 times higher in July than in preceeding or following sampling months, temporal changes in bacterial biomass were less pronounced and varied by less than a factor of 2.

3.2 Potential extracellular enzyme activities

Enzyme activities measured using MUF- and MCA- substrate amended sediment slurries decreased in the order aminopeptidase >phosphatase>chitinase, β -glucosidase> α -glucosidase>lipase. Hydrolysis rates in the upper sediment layer ranged between 0.7–4.5 $\mu\text{mol L}^{-1}$ wet sediment h^{-1} (α -glucosidase), 1.1–7.8 $\mu\text{mol L}^{-1} \text{h}^{-1}$ (β -glucosidase), 1–9.9 $\mu\text{mol L}^{-1} \text{h}^{-1}$ (chitinase) (Fig. 3a–c); 9–40 $\mu\text{mol L}^{-1} \text{h}^{-1}$ (phosphatase), 0.03–0.8 $\mu\text{mol L}^{-1} \text{h}^{-1}$ (lipase) and 13–101 $\mu\text{mol L}^{-1} \text{h}^{-1}$ (aminopeptidase). Similar to bacterial abundances and bacterial growth rates, all EEA showed a clear depth trend. With few exceptions, hydrolytic activities decreased by factors of 1.5 to 6 with increasing sediment depth. The decrease was more pronounced between the middle and deepest layer than between the surface and middle layer. Only for chitinase and lipase activity was this depth trend inverted in a few cases, such that the EEA was higher at 5–10 cm depth than at 0–5 cm depth. All EEA showed strong temporal patterns and generally followed the temperature curve, with highest activities measured in July and lowest activities at winter sampling dates (Fig. 3). However, in the top layers chitinase (0–10 cm) and phosphatase (0–5 cm) activities were lower in April than in February despite a temperature increase of 5.4°C. Cell-specific MUF- and MCA-EEA ranged between 0.2–2.2 $\text{amol h}^{-1} \text{cell}^{-1}$ for chitinase, between 0.12–0.98 $\text{amol h}^{-1} \text{cell}^{-1}$ for α -glucosidase, between 0.18–1.7 $\text{amol h}^{-1} \text{cell}^{-1}$ for β -glucosidase, between 0.02–0.24 $\text{amol h}^{-1} \text{cell}^{-1}$ for lipase, between 1.9–22 $\text{amol h}^{-1} \text{cell}^{-1}$ for aminopeptidase

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and between 1.24 and 8.8 $\text{amol h}^{-1} \text{cell}^{-1}$ for phosphatase, and generally showed comparable temporal and vertical patterns than non-specific rates; however the vertical decrease was less steep.

Enzymatic hydrolysis of laminarin showed depth and seasonal trends comparable to hydrolytic rates of exoenzymes acting on carbohydrates (Fig. 3). Laminarin hydrolysis rates generally decreased with increasing sediment depth except for March II samples, where rates were higher at a depth of 5 cm than at 1 cm. Laminarin hydrolysis also followed the temperature curve and reached maximum values in July, although seasonal differences were not as pronounced as for MUF- and MCA-labeled substrates. Hydrolysis rates ranged between 0.5–1.8 $\mu\text{mol glucose L}^{-1} \text{ wet sediment h}^{-1}$ at 1 cm depth, 0.5–1.7 $\mu\text{mol glucose L}^{-1} \text{ h}^{-1}$ at 5 cm depth and 0–0.7 $\mu\text{mol monomer L}^{-1} \text{ h}^{-1}$ at 13 cm depth. Rates in intact cores were a factor of ~ 4 lower than exoenzymatic activities measured in sediment slurries (e.g. β -glucosidase), in accordance with the factor of 2 to 6 difference in hydrolysis rates in homogenized sediments compared to intact cores (Arnosti and Holmer, 2003). However, a high fraction of the injected FLA-polysaccharide was hydrolyzed after 24 h incubation: 20–70% in surface sediments, 19–68% in mid-depth sediments, and 0–29% in deep sediments, with highest fraction turned over in July and lowest in March. Hence, at least the rates in surface and mid-layer sediments may be significantly underestimated. Cell-specific laminarinase rates ranged between 0.25–0.61 $\text{amol h}^{-1} \text{cell}^{-1}$ at 1 cm depth, 0.44–0.86 $\text{amol h}^{-1} \text{cell}^{-1}$ at 5 cm depth and 0–0.97 $\text{amol h}^{-1} \text{cell}^{-1}$ at 13 cm sediment depth, which is a similar range as for the exo-acting enzymes. No clear trend with depth was observed. Cell-specific laminarinase rates were higher at –5 cm than at –1 cm and in March also higher at –13 than at –5 cm sediment depth, underlining the potentially high competition with naturally occurring substrate at the sediment surface.

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3.3 Chlorophyll pigments and microphytobenthic biomass

As derived from the chlorophyll-*a* concentrations, a high MPB standing stock was present throughout the whole study period, with values ranging between 6.5–9.1 $\mu\text{g cm}^{-3}$ wet sediment in the top centimeter. Based on average chlorophyll-*a* concentrations between 4.5 and 7.5 $\mu\text{g cm}^{-3}$ in the top 5 cm (Fig. 4a), a MPB biomass of 13–21 mmol C L^{-1} was estimated. Highest concentrations were measured in April 2005 and in March (II) 2006. Both these sampling dates occurred at the beginning of a pelagic diatom spring bloom. However, the integrated standing stock in the water column is only 0.5–7% of the integrated standing stock of the MPB (Fig. 2). The benthic chlorophyll-*a* peaks in spring thus most likely resulted from enhanced growth of the MPB rather than from phytodetritus sedimentation and burial. Over the investigated time period, temporal variation remained below a factor of 2 (Fig. 2). The vertical distribution was characterized by constantly decreasing but high chlorophyll-*a* concentrations ($>1.5 \mu\text{g cm}^{-3}$ wet sediment) down to 5–8 cm. In deeper sediment layers chlorophyll-*a* decreased to concentrations below $1.5 \mu\text{g cm}^{-3}$ wet sediment but was still detectable (Fig. 4a).

Phaeophytine also tended to decrease with depth, although there was no clear vertical profile. Concentrations stayed below $0.9 \mu\text{g cm}^{-3}$ wet sediment, and varied especially in the upper 10 cm of sediment. The ratio between chlorophyll-*a* and phaeophytine ranged between 8 and 75:1 in the upper 5 cm of sediment and decreased to ratios between 1.7 and 11:1 in the 10–15 cm layer, indicating the dominance of living algae over phytodetritus. There was no obvious seasonal trend, but concentrations appeared to slightly decrease from the 1st to the last sampling date.

3.4 Benthic oxygen consumption

Total benthic oxygen consumption in dark incubations (gross respiration) was closely coupled to temperature, ranging between 5 and 21 $\text{mmol C m}^{-2} \text{d}^{-1}$ and varying seasonally with highest values in July 2005 (Fig. 2). The total benthic oxygen consumption

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measured here likely significantly underestimated in situ benthic oxygen consumption due to the low stirring speeds applied. Hence, seasonal trends can be compared, but carbon flux calculated from total oxygen consumption is underestimated (see below).

3.5 Carbohydrate inventory

5 Two carbohydrate fractions were measured, total carbohydrates, which include intracellular and extracellular carbohydrates (soluble as well as particle-bound), and the EDTA-extractable carbohydrate fraction that includes all extracellular soluble carbohydrates. Both fractions showed a clear depth trend (Fig. 4). Concentrations of total carbohydrates were highest in the uppermost centimeter (4–6 μmol glucose equivalents cm^{-3} wet sediment) and decreased almost linearly to 10 cm depth (1–3 μmol glucose equivalents cm^{-3}) and 15 cm (0.3–2 μmol glucose equivalents cm^{-3}). There was no seasonal trend (Figs. 2, 4). Rather, total carbohydrate concentrations in the upper 10 cm constantly decreased from February 2005 until end of March 2006. EDTA-extractable carbohydrates followed the same vertical patterns, with values between 0.7–1.4 μmol glucose equivalents cm^{-3} wet sediment in the uppermost centimeter and between 0.2–0.7 μmol glucose equivalents cm^{-3} at 10 cm depth (0.2–0.4 μmol glucose equivalents cm^{-3} at 15 cm depth; Fig. 4). The EDTA-extractable carbohydrates constituted between 13 and 37% of the total carbohydrate pool in the upper 10 cm; this share did not change considerably with increasing sediment depth. The contribution of EDTA-extractable carbohydrates to the total carbohydrate pool was highest in April 2005 and in March (I) 2006, averaging 27% and 37%, respectively. These sampling dates, together with February 2005, were also the ones where the highest concentrations of EDTA-extractable carbohydrates were measured.

3.6 Statistical analysis of spatial and temporal variations

25 The permeable subtidal sands of the island of Sylt in the northern Wadden Sea constitute a highly dynamic environment, exposed to strong tidal currents and frequent storm

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events. Nevertheless, strong and persistent depth-patterns in bacterial abundances, BCP, EEA, and carbohydrate inventories were found over an annual cycle. Despite the low organic carbon content of the sediments, high extracellular enzyme activities and bacterial carbon production showed that the microbial community was very active.

5 These high microbial activities were found to be tightly coupled to the productivity of the microphytobenthos. The dominating factors explaining the spatial (vertical) and temporal variations of bacterial activities were evaluated by Pearson Correlation (Table 4) and Principal Component Analysis (PCA; Fig. 6). Temporal variation was clearly related to temperature changes (1st axis); and spatial variations (vertical gradients) were best explained by the spatial distribution of the microphytobenthos (2nd axis).
10 Bacterial abundances, benthic chlorophyll-*a*, and phaeophytine as well as total and EDTA extractable carbohydrates showed a strong negative relationship with sediment depth (statistically significant only for chlorophyll-*a* and phaeophytine), likely a result of photosynthetic production being confined to the upper few millimeters of the sediment and mixing with depth. Bacterial abundances were significantly correlated with
15 benthic chlorophyll-*a* and hydrolytic activities of most extracellular enzymes (Table 4; Fig. 6). Phosphatase and aminopeptidase activities were also directly correlated with chlorophyll-*a* and phosphatase also with depth, and most enzymes were correlated with each other. Variation in bacterial carbon production was significantly correlated
20 to α -glucosidase, β -glucosidase and lipase activities. Lipase varied mainly temporally and this variation was strongly linked to the water temperature. The nature of the correlations identified via statistical analysis is examined in greater detail below.

4 Discussion

4.1 Benthic primary production and respiration

25 Permeable coastal sediments are characterized by a high biomass of benthic diatoms, which represent the main source of organic matter (Nelson et al., 1999; D'Andrea et

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al., 2004). At the Hausstrand site, benthic net primary productivity exceeds pelagic net primary productivity with rates around $53 \text{ mmol C m}^{-2} \text{ d}^{-1}$ ($\sim 19 \text{ mol C m}^{-2} \text{ yr}^{-1}$; Wenzhöfer, personal communication) compared to $4\text{--}18 \text{ mmol C m}^{-2} \text{ yr}^{-1}$ (integrated over a mean water depth of 2 m) in the water-column of the Sylt-Rømø Basin (Asmus et al., 1998; Loebel et al., 2007). Even assuming a flushing rate between $160\text{--}500 \text{ L m}^{-2} \text{ d}^{-1}$ (de Beer et al., 2005) of the upper 5 cm of sands by the overlying water, the input of the pelagic spring bloom would be only less than a third compared to the microphytobenthic (MPB) standing stock. Furthermore, the MPB standing stock at the Hausstrand is relatively constant throughout the year (Hedtkamp, 2005). It produces large amounts of extracellular polymeric substances (EPS), mainly composed of carbohydrates, which has been suggested to be the main source of energy and labile organic carbon to the bacterial community (MacIntyre et al., 1996; Underwood and Kromkamp, 1999). In addition, the benthic meiofauna may benefit from these exudates (van Oevelen et al., 2006), and may also feed directly on the bacteria and diatoms (Epstein, 1997; Cahoon, 1999). The MPB, bacteria and other microorganisms form a biofilm community in the surface sands, presumably causing a tight coupling between variations in primary productivity, fluxes of exudates and remineralization. This close linkage allows for a particularly rapid carbon flow from the autotrophic to the heterotrophic compartment at sunlight-exposed, sandy sediment sites (Middelburg et al., 2000).

Total benthic carbon metabolism can generally be estimated from rates of benthic oxygen consumption (e.g. Canfield et al., 1993). Because of the high permeability of the sediments and the low stirring speeds used in our chamber incubations, however, oxygen consumption rates in this study were likely underestimated. Previous in situ chamber incubations at the Hausstrand in summer 2004 yielded oxygen consumption rates of $25 \text{ mmol C m}^{-2} \text{ d}^{-1}$ and $56 \text{ mmol C m}^{-2} \text{ d}^{-1}$, when measured at stirring speeds of 20 and 160 rpm, respectively, indicating that oxygen consumption rates under advective conditions may exceed those under diffusive conditions by a factor of 2.3 (Cook et al., 2007b). Applying this factor to the rates measured here ($\leq 21 \text{ mmol C m}^{-2} \text{ d}^{-1}$)

would yield values close to estimates by Cook et al. (2007b); Heip et al. (1990) and Cramer (1991). The latter authors suggested that meiofauna and macrofauna are only responsible for 1–15% of the total benthic respiration in North Sea sediments. Nevertheless, we found a considerable discrepancy between total benthic respiration and our estimate of bacterial respiration (30–180 mmol C m⁻² d⁻¹), assuming a 1:1 ratio between bacterial carbon production and respiration (i.e. carbon assimilation efficiency of 50%). The BCP rates of 0.4–2.3 mmol C L⁻¹ d⁻¹ (for the upper 0–5 cm) measured at Hausstrand are well within the range of rates measured in other, more organic-rich areas of the North Sea (van Duyl and Kop, 1990; van Duyl et al., 1993; van Duyl and Kop, 1994) and in the productive Great Barrier Reef sands (Alongi, 1992). Previous measurements at Hausstrand yielded DIC fluxes that were about a factor of 2 higher than the oxygen consumption rates measured here (Hedtkamp, pers. comm.). These findings may indicate that a substantial fraction of bacterial respiration in the subtidal sands is anaerobic.

4.2 Contribution of sedimentary carbohydrates to benthic metabolism

To estimate the potential turnover of total and EDTA-extractable carbohydrates by extracellular hydrolysis, carbohydrate concentrations were divided by the sum of potential activities of α -glucosidase, β -glucosidase, chitinase and laminarinase in the 0–5, 5–10, and 10–15 cm depth intervals. As shown in Fig. 5a, in July in the 0–5 cm depth interval, 5–15% of the total carbohydrate pool, and almost the entire EDTA-extractable carbohydrate pool could have been hydrolyzed by these enzymes on a daily basis. Even in the 10–15 cm depth interval, a complete hydrolysis of the EDTA-extractable pool would be possible on the order of 5 days. Potential hydrolysis efficiency was considerably lower in March (I) than in July, but still ranged from 4–12% of the EDTA-extractable pool on a daily basis (Fig. 5b). These rapid turnover rates indicate a high flux of EDTA-extractable carbohydrates throughout the year (Table 2). The seasonal variations are most likely explained by the higher hydrolytic activities in summer. Turnover time of total carbohydrates at the Hausstrand is rapid compared to sandy beach sediments of

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the Ligurian Sea (~3–619 days, Mistic and Fabiano, 2005).

Potential hydrolytic activities of extracellular exoenzymes measured in the present study were as high as those observed in muddy, organic-rich sediments of the Kiel Bight (Meyer-Reil, 1986) and Ems-Dollard estuary (van Duyl et al., 1999). Laminarinase activities, although potentially underestimated in the surface layer due to substrate competition (see below), are comparable to rates measured in microbially active, organic-rich sediments in a range of other environments, including the Skagerrak, Cape Lookout Bight NC, and Svalbard (Hoppe et al., 2002; Arnosti and Holmer, 2003; Arnosti and Jørgensen, 2006). A high fraction of the total added FLA-polysaccharides were hydrolyzed within 24 h, resulting in an underestimation of hydrolysis rates, particularly in the surface and mid-depths, especially during the July sampling period. Furthermore, differences in assay method played a role, since a comparison of hydrolysis for a range of FLA-labeled polymers demonstrated that rates were 2–6 times more rapid in homogenized sediments compared to intact cores (Arnosti and Holmer, 2003).

Turnover of different constituents of organic matter ultimately derived from MPB photosynthetic production can also be estimated and related to carbon demand by bacteria and by the whole benthic community. Figure 2 and Table 2 show a comparison of the major carbon inventories in the sands. Assuming a gross phototrophic primary production of $100 \text{ mmol C m}^{-2} \text{ d}^{-1}$ in the top 10 cm of sand by adding up net benthic photosynthesis (Hausstrand data from May 2003, Wenzhöfer et al., unpublished data) and average respiration rates (assuming a bacterial growth yield of 50%), the MPB biomass (on average $1200 \text{ mmol C m}^{-2} \text{ d}^{-1}$) could be turned over in 12 days (neglecting a potential input of pelagic phytodetritus of max. a third of MPB during spring bloom situations; de Beer et al. 2005). On average during the investigated period, in the 0–10 cm interval, bacterial biomass was $300 \text{ mmol C m}^{-2}$. Based on a gross bacterial carbon production (BCP) of $60 \text{ mmol C m}^{-2} \text{ d}^{-1}$; turnover time of the bacterial biomass was 5–6 days. The MPB: bacterial C ratio was approximately 3:1 which is consistent with Evrard (2007), who estimated for the Hausstrand site that living MPB account on average for about 30% of the total organic carbon pool, while bacteria, meio- and

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macrofauna contribute 6, 2 and 0.5% of the total organic carbon pool, respectively. Total carbohydrate concentrations were on average $2000 \text{ mmol C m}^{-2}$, of which ca. 20% were EDTA-extractable carbohydrates. Summing up MPB biomass, bacterial biomass and total carbohydrates (taking into account that up to ca. 30% of algal biomass consist of carbohydrates that are already included in the total carbohydrate pool), and neglecting faunal biomass and organic matter other than carbohydrates, yields a carbon pool of around $3200 \text{ mmol C m}^{-2}$,

Assuming a bacterial growth yield (carbon assimilation efficiency) of 50%, as is commonly used for heterotrophic benthic bacteria in surface sediments (Moriarty et al., 1985), the average total bacterial C demand is $120 \text{ mmol C m}^{-2} \text{ d}^{-1}$ (peaking in summer with up to $360 \text{ mmol C m}^{-2} \text{ d}^{-1}$). On average, this demand could be covered by a daily turnover of 30% of the EDTA extractable carbohydrates (in summer up to 125%), 6% of the total carbohydrates or 11% of the MPB biomass. The sum of the measured potential hydrolytic activities seems to meet this carbon demand. On average, potential extracellular enzymatic hydrolysis of carbohydrates could supply approximately 110% of the total bacterial C demand, as calculated from the combined action of chitinase, α -glucosidase, β -glucosidase and laminarinase activities (Table 2). Since laminarinase activities in the surface layer were most likely underestimated, hydrolysis of carbohydrates could even provide more C than estimated here. Hence, our calculations support the general assumption that EPS could provide most of the substrate required for microbial metabolism (MacIntyre et al., 1996; Underwood and Kromkamp, 1999), but other substrate sources are also available (e.g. DOC, proteinaceous materials), and the activities of enzymes not measured in this study may also play a critical role in microbial nutrition.

4.3 Vertical zonation of bacterial abundances and activities

The strong hydrodynamic forces at the Hausstrand lead to frequent lateral transport and vertical mixing of the upper 5 cm of sediment (Hedtkamp, 2005). In addition, bioirrigation/bioturbation by benthic fauna can mix the upper 10 cm of sediment (Huettel et

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al., 2003). Therefore, we can assume that the top 5 cm are constantly flushed with oxygen-rich water and include considerable amounts of diatom-derived labile organic carbon, while the 5–10 cm layer is less frequently mixed, and the 10–15 cm layer remains relatively undisturbed and is dominated by diffusive solute transport. This picture is supported by the physical characteristics of the sediment. The upper 5 cm of sediment were extremely coarse and yellowish, indicating a zone of strong mixing and oxygenation. The middle layer was greyish and more compact, indicating a transition zone between this oxygen-rich top layer and the diffusion-dominated, deepest layer that was blackish, smelled faintly of sulfide, and contained also small-grained sediments.

Seasonal and short-term changes in wind stress have been shown to influence sediment permeability (Hedtkamp, 2005); thus storm impacts include increased horizontal and vertical sediment mixing. Despite these active physical dynamics of tides and wave forces at the field site, at all sampling dates (including April and November, with strong storm events) distinct depth trends were evident in MPB biomass, chlorophyll-*a*, and phaeopigments, total carbohydrates and EDTA extractable carbohydrates, as well as in bacterial abundances, growth rates, and extracellular enzymatic activities. Concurrent decreases with depth in hydrolytic activities, bacterial abundances, and bacterial carbon production rates suggest a vertical shift in the availability and nutritional quality of organic matter in the sediment.

Bacterial abundances were statistically correlated to hydrolytic activities of α -glucosidase, β -glucosidase, phosphatase and aminopeptidase (r between 0.84 and 0.94, $p < 0.00024$; Table 4), partially explaining the decrease in hydrolytic activities with depth. But even cell-specific hydrolytic enzyme activities showed a distinct decrease with depth, presumably due to the reduced availability and quality of organic substrates. This is also consistent with the lower turnover of carbohydrates with depth (Fig. 5), and the depth-related decrease in BCP. Similar depth trends have been reported from muddy sediment sites, where particulate organic matter mixing into the sediment depends entirely on bioturbation (e.g. Mayer, 1989; Arnosti, 1995). However, distinct depth trends in highly dynamic sandy environments are unusual. In Middle At-

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lantic Bight shelf sediments, a site quite comparable to Hausstrand, Rusch and coworkers (2003) investigated depth-related and seasonal patterns in bacterial and algal cell abundances, exoenzymatic activities and carbon inventory. The bacterial community was found to be highly active, with aminopeptidase and β -glucosidase activities comparable to those measured in the present study; however depth-related patterns were only found during the winter sampling date. Likewise, an investigation of aminopeptidase, β -glucosidase, alkaline phosphatase activities, their natural substrates, bacterial abundances and biomass in two adjacent areas of a sandy beach over one year showed a lack of vertical patterns within the top 15 cm (Misic and Harriague, 2007). An intertidal sandy area close to our sampling site (Musat et al., 2006) also did not reveal the pronounced depth-related changes in bacterial abundances that we found in the subtidal sediments. We assume that the observed depth gradient is mainly due to the distribution of the MPB and the biofilm-like association with the bacterial community. This is supported by the tight correlation between bacterial abundances and benthic chlorophyll-*a* ($r=0.83$, $p<0.00024$). At Hausstrand, most of the benthic diatom biomass is found in the top 0–5 cm layer, but moderately high concentrations could be observed down to a depth of –8 cm, corresponding to the maximal depth of advective transport. At these depths, diatoms are non-active, but able to survive several months without losing their photosynthetic capacity (Sundbäck and Granéli, 1988; Nelson et al., 1999).

4.4 Temperature-related temporal patterns in bacterial activities

Water temperature followed a typical seasonal pattern over the sampling period (Fig. 2a), with winter temperatures close to the freezing point and summer temperatures of up to 20°C. The spring bloom in the water column of Sylt occurs generally in April, but even at the peak of phytoplankton biomass, the integrated carbon concentrations were <7% of the microphytobenthic standing stock in the sands. Although the temporal variation of the MPB and bacterial standing stock was negligible, the entire benthic community was more active at higher temperatures as indicated by the pattern

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of total benthic oxygen consumption (Fig. 2b). Extracellular enzymatic activities and bacterial carbon production clearly also followed the temperature trend (Fig. 2c, d) and reached maximum values in July. The lack of temporal variation in MPB and bacterial biomass (Fig. 2c) contrasted with the changes in activity patterns, and may be due to higher grazing pressure in the summer. Likewise, the lack of a temperature-related pattern in carbohydrate concentrations (Fig. 4) could reflect higher bacterial consumption during times of higher MPB production, since carbohydrate concentrations reflect the net balance between production and consumption.

Higher enzymatic hydrolysis rates may be the result of faster enzyme function and/or of enhanced bacterial enzyme synthesis at higher temperatures. High BCP rates and high benthic oxygen consumption in July provide evidence for a generally enhanced metabolism in summer. Investigating apparent temperature effects on hydrolytic exoenzyme activities at the Hausstrand experimentally yielded Q_{10} values between 1.4 and 1.7 (Table 3), indicating that temperature effects could cause an increase in the activity of enzymes only by less than a factor of 2 when temperature rises by 10°C . In the field, a much higher increase of enzyme activities was observed between winter and summer, suggesting that enzyme synthesis by the benthic bacteria may have changed, possibly due to induction by increased substrate availability in the summer months. Moreover, temperature between July and November dropped by only 7°C while EEA decreased by a factor of up to 5. Temperature has also been found to be an important but not the only influence affecting seasonal variations in extracellular proteolytic enzyme activity in an intertidal mudflat (Mayer, 1989). Since bacterial abundances do not necessarily reflect the state of activity of the microbial community (Créach et al., 2003) and no information is available on variations in the fraction of the community producing specific enzymes, changes in bacterial community structure and composition may also have influenced seasonal changes in hydrolytic rates.

The microphytobenthic standing stock – as derived from chlorophyll-*a* – was generally stable over the entire sampling period, except for minor peaks in spring, in accordance with observations in other shallow sediment ecosystems (Varela and Peñas,

1985; Goto et al., 1998, 2000). The significant temporal changes in microbial activities thus can best be explained by a combination of the effects of temperature and substrate availability. The minor temporal variations in microbial and MPB biomass are typical for biofilm-type communities; they could result from light and space limitation as well as from extensive grazing pressure. Previous investigations suggested that especially the nano- and meiofauna plays an important role for the removal of bacterial and MPB biomass in permeable sands (Epstein, 1997; Cahoon, 1999; Middelburg et al., 2000; Urban-Malinga et al., 2006; Evrard, 2007).

Acknowledgements. Susanne Menger is gratefully acknowledged for assistance in the field and with sample processing. Stefanie I. C. Hedtkamp kindly provided 2005 benthic respiration data. Sherif Gobrial is thanked for the GPC analysis of potential endoenzymatic activities and Gabriele Schüßler is recognized for assistance with ³H-thymidine incorporation measurements. Hannelore Halliger and Reimer Magens supported our work on Sylt logistically and technically. The scientific divers Christian Buschbaum and Patrick Polte are gratefully acknowledged for recovery of sediments samples in April 2005 and November 2005. Aerial photo material was kindly provided by the Wadden Sea National Park Office. This study was financed by the Max Planck society. CA received funding from the National Science Foundation (OCE-0323975), as well as support from the Hanse Institute for Advanced Study and the Alfred Wegener Institute for Polar and Marine Research while the manuscript was being written.



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This Open Access Publication is
financed by the Max Planck Society.

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Table 1. Depth-related and temporal changes in carbon fractions and enzymatic carbon hydrolysis in Hausstrand sediments.

Date	Sed. layer (cm)	Bact. cell numbers ($\times 10^9 \text{ cm}^{-3}$)	Bacterial biomass (mmol CL^{-1}) ^a	Bact. C prod. ($\text{mmol CL}^{-1} \text{ d}^{-1}$)	Bact. turnover time (d)	MPB biomass (mmol CL^{-1}) ^b	Total carbs (mmol CL^{-1})	EDTA extr. carbs (mmol CL^{-1})	C-hydrolysis by Chitinase ($\text{mmol CL}^{-1} \text{ d}^{-1}$) ^c	C-hydrolysis by β -Glucosidase ($\text{mmol CL}^{-1} \text{ d}^{-1}$) ^d	C-hydrolysis by α -Glucosidase ($\text{mmol CL}^{-1} \text{ d}^{-1}$) ^d	C-hydrolysis by Laminarinase ($\text{mmol CL}^{-1} \text{ d}^{-1}$) ^e *
8 Feb 2005 (1.5°C)	0–5	2.4±0.26	4.0	0.62±0.07	6.5	16.4	33±1.1	7.1±0.40	0.38±0.03	0.34±0.01	0.22±0.00	0.13±0.002
	5–10	1.3±0.13	2.2	0.38±0.19	5.8	4.6	25±0.9	4.6±0.31	0.55±0.21	0.14±0.03	0.08±0.02	0.12±0.007
	10–15	0.9±0.07	1.5	0.23±0.07	6.5	2.0	N.A.	N.A.	0.05±0.01	0.03±0.00	0.02±0.01	0
8 Apr 2005 (7°C)	0–5	2.0±0.28	3.3	0.44±0.06	7.5	19.2	25±0.9	6.6±0.59	0.36±0.04	0.47±0.04	0.25±0.06	0.13±0.006
	5–10	1.4±0.13	2.3	0.35±0.05	6.6	7.0	17±0.7	4.6±1.18	0.23±0.02	0.19±0.01	0.09±0.03	0.09±0.003
2 Jul 2005 (18°C)	0–5	0.6±0.08	1.0	0.23±0.05	4.3	1.3	N.A.	N.A.	0.05±0.01	0.05±0.00	0.03±0.01	0.01±0.001
	5–10	2.9±0.17	4.8	2.29±0.34	2.1	18.1	25±2.0	4±0.50	1.89±0.51	1.13±0.08	0.65±0.06	0.26±0.105
	10–15	2.0±0.28	3.3	1.32±0.13	2.5	6.1	19±1.4	1.9±0.72	0.47±0.33	0.67±0.10	0.22±0.03	0.25±0.049
9 Nov 2005 (11°C)	0–5	1.6±0.12	2.7	0.05±0.08	5.4	1.4	14±1.5	1.8±1.01	0.12±0.09	0.18±0.04	0.05±0.03	0.11±0.067
	5–10	2.3±0.14	3.8	0.44±0.02	8.6	17.5	24±1.0	4±0.64	0.68±0.03	0.44±0.05	0.28±0.04	0.2±0.041
	10–15	1.7±0.26	2.8	0.16±0.05	17.5	7.5	18±1.1	2.2±0.27	0.38±0.08	0.31±0.03	0.13±0.01	0.19±0.064
1 Mar 2006 (2°C)	0–5	N.A.	N.A.	N.A.	N.A.	N.A.	N.A.	N.A.	N.A.	N.A.	N.A.	N.A.
	0–5	1.7±0.61	2.8	0.43±0.05	6.5	12.9	17±1.8	5.9±2.23	0.42±0.03	0.15±0.01	0.11±0.03	0.14±0.050
	5–10	0.8±0.07	1.3	0.30±0.10	4.3	3.1	9±1.0	3.6±0.58	0.14±0.02	0.06±0.01	0.03±0.01	0.07±0.004
27 Mar 2006 (4°C)	0–5	0.6±0.06	0.9	0.17±0.06	5.3	1.3	8±0.9	2.9±1.31	0.19±0.03	0.04±0.01	0.01±0.00	0.08±0.047
	0–5	2.1±0.16	3.5	0.46±0.12	7.6	21.3	19±0.9	2.9±0.48	0.19±0.01	0.24±0.01	0.15±0.01	0.07±0.021
	5–10	1.4±0.18	2.3	0.30±0.10	7.7	8.7	11±0.9	1.7±0.13	0.24±0.05	0.06±0.00	0.05±0.00	0.16±0.053
	10–15	0.5±0.04	0.9	0.19±0.06	4.7	1.1	4±0.8	1.2±0.33	0.04±0.01	0.03±0.00	0.01±0.00	0.06±0.057

^a Conversion factor: 20 fg cell⁻¹ (Fuhrman and Azam, 1982)

^b Conversion factor: 34 (Dijkman, as cited in Evrard, 2007)

^c Carbon conversion factor: 8

^d Carbon conversion factor: 6 (Hoppe, 1993)

^e Carbon conversion factor: 6 (Hoppe, 1993)

* Rates measured at 0–2, 2–4 and 12–14 cm

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Table 2. Temporal changes in total bacterial carbon demand and carbon turnover by the benthic bacterial community at the Hausstrand. Areal estimates are based on integration of the top 10 cm.

	8 Feb 2005	8 Apr 2005	2 Jul 2005	9 Nov 2005	1 Mar 2006	27 Mar 2006
MPB Biomass [mmol C m ⁻²]	1045	1309	1211	1249	796	1499
Bacterial biomass [mmol C m ⁻²]	308	283	408	333	208	292
Total carbohydrates [mmol C m ⁻²]	2889	2090	2195	2071	1302	1472
EDTA extractable carbohydrates [mmol C m ⁻²]	586	556	292	309	472	227
Bacterial carbon production [mmol C m ⁻² d ⁻¹]	50	40	180	30	37	38
Total bacterial C demand [mmol C m ⁻² d ⁻¹] ^a	100	79	360	61	73	76
Total potential C generated from hydrolysis of carbohydrates [mmol C m ⁻² d ⁻¹] ^b	98	91	277	130	57	59
Coverage of total bacterial C demand by C hydrolysis of carbohydrates [%] ^a	99	115	77	215	77	78
Total carbohydrate C fraction potentially consumed by bacterial community [% d ⁻¹] ^a	3	4	16	3	6	5
EDTA extractable carbohydrate C fraction potentially consumed by bacterial community [% d ⁻¹] ^a	17	14	124	20	15	34
MPB biomass fraction potentially consumed by bacterial community [% d ⁻¹] ^a	10	6	30	5	9	5

^a Growth yield 50% (Moriarty et al., 1985)

^b Sum of α -glucosidase, β -glucosidase, chitinase and laminarinase

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Table 3. Q_{10} -values of exoacting extracellular enzymes as determined experimentally with Hausstrand sediment. Hydrolysis rates of the respective MUF- and MCA-substrates were measured at 4°C, 16°C and 25°C. Values represent the increase in enzymatic activity when temperature rises by 10°C.

Enzyme	Q_{10} -value
β -Glucosidase	1.7
Lipase	N.A.
Aminopeptidase	1.4
Phosphatase	1.4
α -Glucosidase	1.7
Chitobiase	1.6

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Table 4. Pearson correlation coefficients at the Bonferroni-corrected level. Data comprises all samples that included carbohydrate measurements.

	Depth	Temp	Chl a	Phaeo	Lam	α -glu	β -glu	Chito	Phos	Lip	Pep	Abd	C prd	EDTA	Total
Depth		0.887	0.000	0.000	0.108	0.001	0.014	0.006	0.000	0.664	0.001	0.001	0.073	0.002	0.014
Temp.	0.040		0.865	0.333	0.010	0.052	0.004	0.098	0.065	0.000	0.056	0.070	0.014	0.260	0.963
Chl-a	*-0.968	0.048		0.000	0.069	0.000	0.007	0.007	0.000	0.592	0.000	0.000	0.081	0.012	0.014
Phaeo	*-0.819	-0.268	*0.798		0.270	0.093	0.219	0.056	0.014	0.677	0.032	0.006	0.493	0.004	0.000
Lam.	-0.431	0.644	0.481	0.305		0.002	0.000	0.000	0.001	0.001	0.002	0.005	0.009	0.780	0.269
α -gluc.	-0.763	0.511	0.787	0.449	0.741		0.000	0.000	0.000	0.010	0.000	0.000	0.000	0.073	0.138
β -gluc.	-0.616	0.691	0.663	0.337	*0.802	*0.955		0.000	0.000	0.001	0.000	0.000	0.000	0.240	0.120
Chito.	-0.677	0.443	0.664	0.503	*0.832	*0.887	*0.833		0.000	0.007	0.000	0.001	0.001	0.094	0.181
Phos.	*-0.810	0.488	*0.829	0.617	0.758	*0.944	*0.924	*0.872		0.017	0.000	0.000	0.001	0.074	0.019
Lip.	-0.122	*0.878	0.151	-0.117	0.749	0.638	0.755	0.660	0.603		0.031	0.046	0.000	0.597	0.898
Pep.	-0.783	0.503	*0.852	0.553	0.732	*0.934	*0.933	*0.799	*0.952	0.558		0.000	0.002	0.143	0.033
Abund.	-0.776	0.480	*0.834	0.677	0.689	*0.842	*0.848	0.760	*0.936	0.523	*0.924		0.005	0.095	0.004
Growth	-0.475	0.620	0.464	0.192	0.645	*0.795	*0.820	0.744	0.743	*0.833	0.725	0.686		0.389	0.488
EDTA	-0.734	-0.310	0.631	0.696	0.079	0.475	0.323	0.448	0.474	-0.149	0.397	0.447	0.240		0.011
Total	-0.617	-0.013	0.620	*0.795	0.305	0.401	0.419	0.365	0.595	-0.036	0.551	0.693	0.194	0.637	

Pearson correlation coefficients calculated on standardized data are shown in bold font in the bottom part of the table. P-values of correlations are shown in normal font in the upper part of the table; *denotes significant coefficients at the Bonferroni-corrected level ($p \leq 0.05/105=0.000476$).

Abbreviations: Temp=temperature, Chl-a=benthic chlorophyll-a, Phaeo=benthic phaeophytine, α -glu.= α -glucosidase, β -glu= β -glucosidase, Chito=chitobiase, Phos=phosphatase, Lip=Lipase, Pep=Aminopeptidase, Abd=bacterial abundance, C prd=bacterial carbon production, EDTA=EDTA-extractable carbohydrates, Total=Total carbohydrates.

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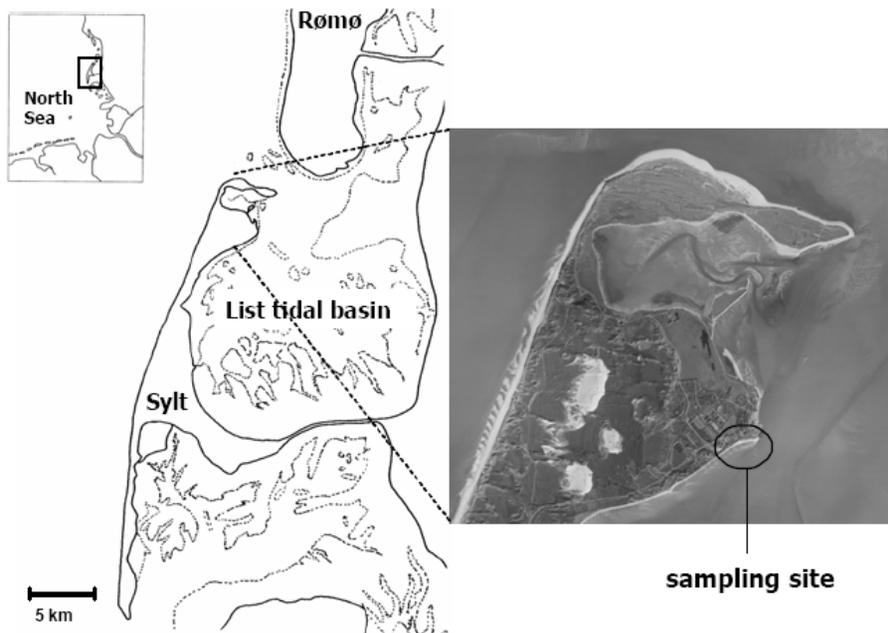


Fig. 1. Map showing the location of the *Hausstrand* sampling site in the Sylt-Rømø Basin (also known as the List tidal basin) close to the island of Sylt in the North Frisian Wadden Sea, Germany (picture obtained from the Wadden Sea National Park Office Schleswig-Holstein).

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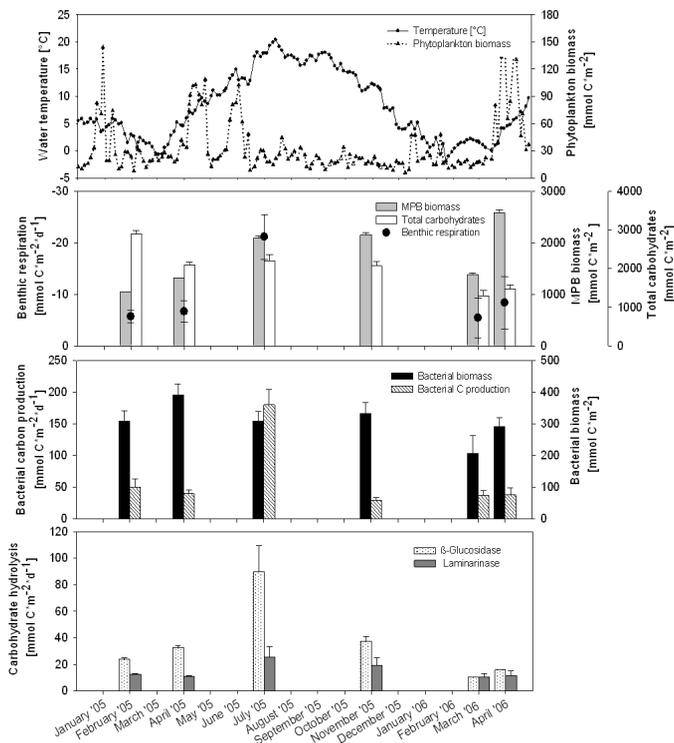


Fig. 2. Seasonal patterns of standing stocks and fluxes in the *Hausstrand* sands. All values were converted to carbon units and integrated over the upper 10 cm of sediment except for the water column data (integrated over the average depth of the water column of 2 m). Error bars represent standard deviations. **(A)** Phytoplankton biomass (triangles) and water temperature (circles). **(B)** MPB biomass (grey bars, $n=3$), total carbohydrates (white bars, $n=3$) and benthic oxygen consumption rates (circles, $n=4$). **(C)** Bacterial biomass (black bars, $n=6$), bacterial carbon production rates measured via thymidine incorporation (striped bars, $n=4-5$). **(D)** C-hydrolysis by β -glucosidase activity (dotted bars, $n=5$) and by laminarinase activity (dark grey bars, $n=2-3$).

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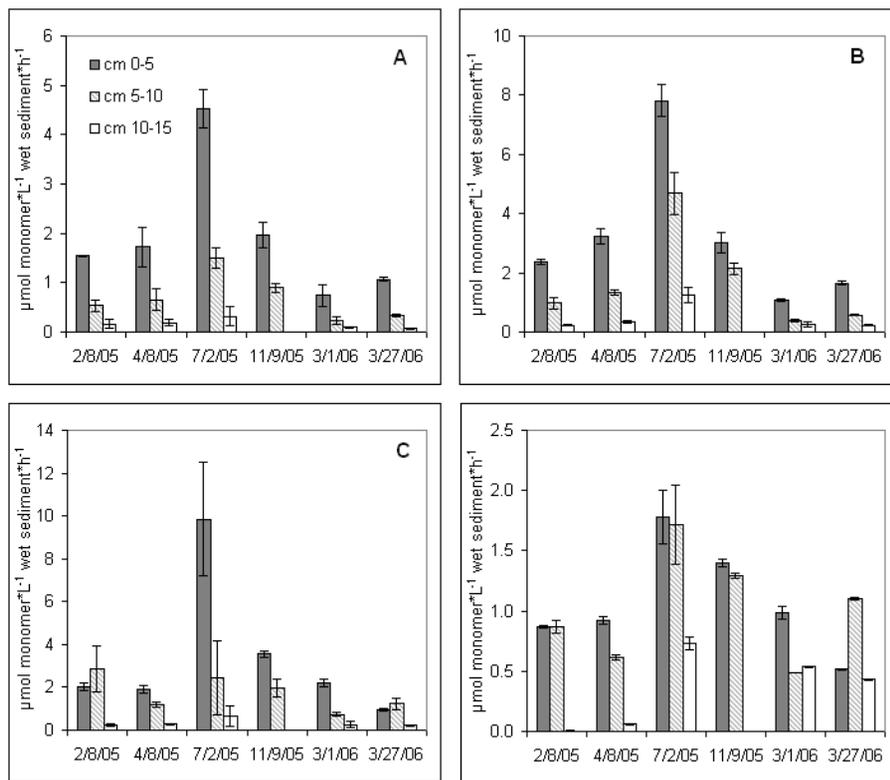


Fig. 3. Depth-related and temporal patterns in potential extracellular enzymatic activities of **(A)** α -glucosidase (MUF- α -D-glucoside), **(B)** β -glucosidase (MUF- β -D-glucoside), **(C)** chitinase (MUF-N-acetyl- β -glucosamine), and **(D)** laminarinase (fluorescently labeled laminarin).

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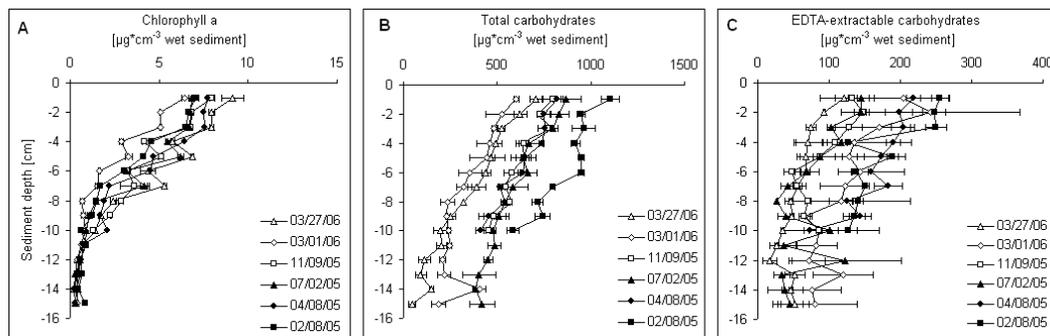


Fig. 4. Depth-related and temporal changes in **(A)** benthic chlorophyll-*a* concentrations; **(B)** total carbohydrate concentrations and **(C)** EDTA-extractable carbohydrate concentrations.

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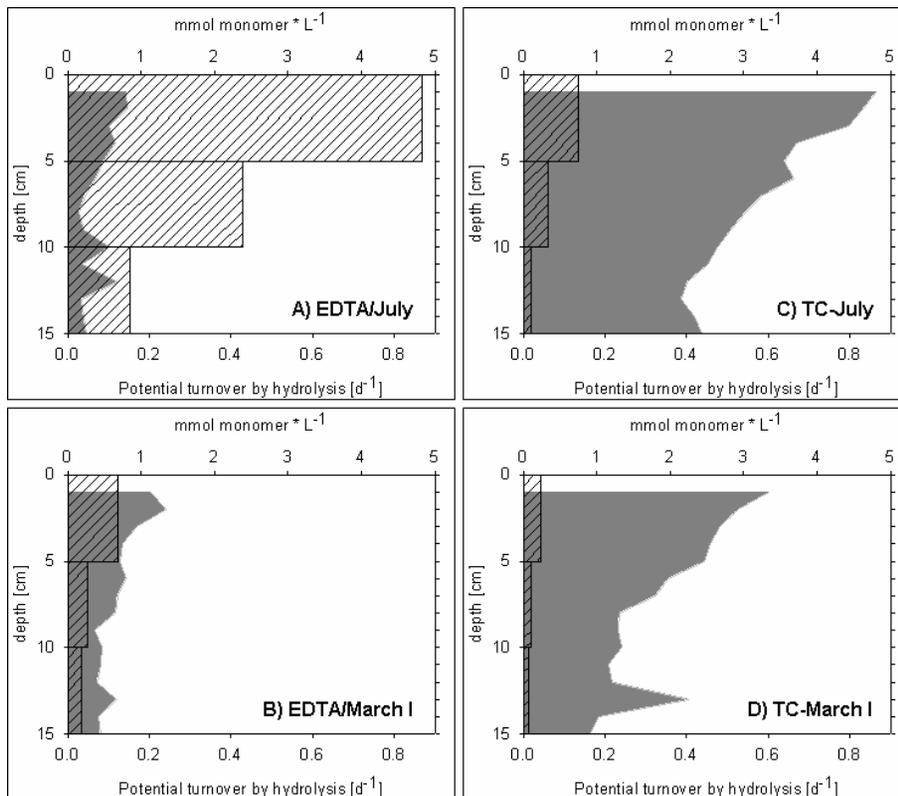


Fig. 5. Potential turnover of (A) EDTA-extractable carbohydrates in July 2005 (B) EDTA-extractable carbohydrates in March I 2006 (C) total carbohydrates in July 2005 and (D) total carbohydrates in March I 2006 in sediment from the Hausstrand. Average carbohydrate concentrations are shown as shaded area; bars represent turnover times based on the sum of laminarinase, α -glucosidase, β -glucosidase and chitinase activities.

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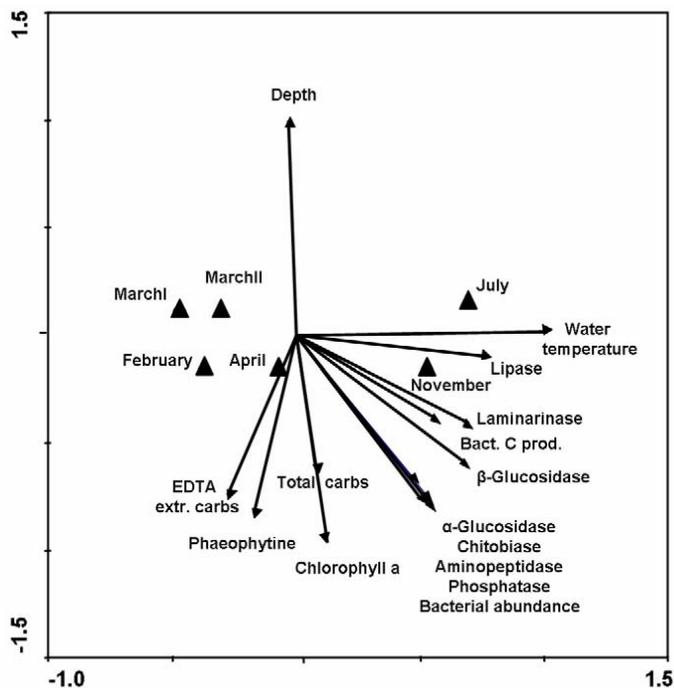


Fig. 6. PCA (Principal component analysis) plot of major environmental variables at the Hausstrand based on an orthogonal linear transformation method that transforms a number of potentially correlated variables into a smaller number of independent variables, the so-called principal components. The magnitude of variation between the variables is depicted in a two-dimensional space. The plot represents 98% of the original variation in the data; axis 1 and 2 explain 76% and 22% of this variation, respectively.

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