

Tidal dynamics of dissolved and particulate matter and bacteria in a tidal flat ecosystem in spring and fall

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Abstract

Tidal flat ecosystems are highly dynamic environments with tremendous short-term and long-term changes in physical, chemical, and biological properties. We measured salinity, temperature, oxygen, dry weight (dry wt), inorganic (PIC) and organic carbon (POC) fractions of suspended particulate matter (SPM), and chlorophyll *a* (Chl *a*); counted numbers of free-living and particle-associated bacteria; and measured dissolved amino acids and carbohydrates, and ectoenzymatic activities throughout tidal cycles in the Spiekeroog tidal flat system of the German Wadden Sea in November 1999 and May 2000. Bacterial production was measured only in May 2000. In November, high sediment resuspension, as indicated by increased amounts of SPM, PIC, and POC, mainly controlled bacterial dynamics and led to enhanced numbers of aggregate-associated bacteria. In contrast, in May, phytoplankton-related processes mainly influenced bacterial dynamics. Increased concentrations of oxygen, Chl *a*, and dissolved combined neutral monosaccharides resulted in high numbers of free-living bacteria, elevated β -glucosidase activities, and high bacterial production rates. The introduction of foreign water masses, either from the open North Sea or adjacent tidal basins, as reflected by different signatures of SPM and the mole percent composition of particulate combined amino acids, appeared to be a regular event in this highly dynamic system and rapidly changed physical, chemical, and biological processes.

Tidal flats are among the most productive ecosystems in the world and exhibit great biodiversity. They constitute unique interfaces between land and sea and are strongly influenced by interactions between physicochemical and biological processes. Sandbanks, reefs, and islands near the coast reduce the kinetic energy from the open sea, thus increasing the deposition of sand and clay particles and fine particulate organic material in these ecosystems (Dittmann 1999). Tidal flats comprise substances of terrestrial, limnetic, and marine origin. Strong currents and shallow water depths

stimulate fast transport, dispersion, and mixing of dissolved and particulate material from various sources (Poremba et al. 1999a). The strength of tidal currents is not only dependent on the tidal cycle, but also on the cycle of spring and neap tide (e.g., from neap to spring tide, current velocity increases) and on wind direction and strength (Niesel 1999). The coastal section of the North Sea between Den Helder (Netherlands) and Esbjerg (Denmark)—the Wadden Sea—is the largest tidal flat ecosystem globally and is of general importance for land–sea interactions of the North Sea.

Most of the suspended particulate matter (SPM) in tidal flats is composed of microaggregates of <500 μm , which undergo pronounced changes and restructuring during current velocity changes. Studying tidal cycles in the Ems estuary, van Leussen (1996) found SPM maxima and minima when current speed was highest and lowest, respectively. Changes in particle size distribution, with largest particles occurring around high and low tide (Eisma and Li 1993), result in frequent changes of the biogeochemical composition of SPM throughout each tidal cycle (van Leussen 1988).

Supply of labile organic matter in tidal systems occurs mainly via phytoplankton and benthic primary production (van Duyl et al. 1999; Tillmann et al. 2000; Wolfstein et al. 2000). Seasonal variations of pelagic and benthic primary production and the deposition of phytoplankton biomass determine bacterial decomposition rates. In general, tidal flat

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systems can be regarded as net heterotrophic, and microbial mineralization renders particulate organic and inorganic matter available to the whole food web (Poremba et al. 1999a). In addition, microbial degradation of organic matter in the sediment releases dissolved degradation products into the sediment pore water and further into the overlying water (Villebrandt et al. 1999). Changes in concentration of dissolved organic matter (DOM) and SPM greatly influence microbial processes in the water column (Postma 1984). Heterotrophic bacteria produce high-quality food as biomass or DOM and decompose high-molecular mass substances into smaller compounds that can then be further used by other organisms (Alongi and Hanson 1985). The quality of organic matter has often been recognized to affect rates of organic matter remineralization by bacteria (e.g., Grossart and Ploug 2000), but factors determining organic matter quality in these highly variable systems remain elusive, and possible relationships between DOM, SPM dynamics, and microbial processes still have to be explored.

Although dissolved inorganic and organic matter is flushed rapidly into and out of estuaries and tidal flat systems, SPM remains entrapped much longer and its organic fraction is degraded extensively by particle-associated bacteria. In the Columbia River estuary, high microbial activities in the water column were mainly associated with particles 3–10 μm in size (Crump and Baross 2000). These authors demonstrated that this particle size fraction supported 87% of bacterial biomass production but contained only 38% of total particulate organic carbon (POC) and 38% of SPM. Whether this is also the case in other shallow marine ecosystems has not yet been studied.

In this study, we focus on tidal dynamics of SPM in the Wadden Sea and how they affect abundances and activities of particle-associated and free-living bacteria at two contrasting seasonal situations: November, with low biological productivity and enhanced inorganic loading, and May, with high biological productivity but low inorganic loading. The goal of this study was to examine whether bacterial processes in the Wadden Sea are linked to quantity and quality of SPM (e.g., resuspension of particulate organic matter from the benthos) (McCandliss et al. 2002) and whether these processes are of importance for organic matter cycling.

Materials and methods

Study site and sampling—The study site was located in the German Bight of the North Sea in the tidal flat system near the East Frisian island of Spiekeroog in a tidal channel with a maximum water depth of 15 m (Fig. 1). The average tidal range in this area is 2.7 m (Eitner 1994), and tidal current velocities range up to 1.5 m s^{-1} , which reflects typical conditions in the Wadden Sea (Niesel 1999). Surface water (0.5–1 m) was collected with a Niskin bottle from onboard RV *Senckenberg* every hour on 18–19 November 1999 (over 19 h) and on 17–18 May 2000 (over 22 h). The sampling campaign in November 1999 was 2 d before peak spring tide and in May 2000 during peak spring tide. At both sampling dates, wind speed was moderate (3.5–5.4 m s^{-1}) and had been low for 5 d prior to our sampling (data pro-

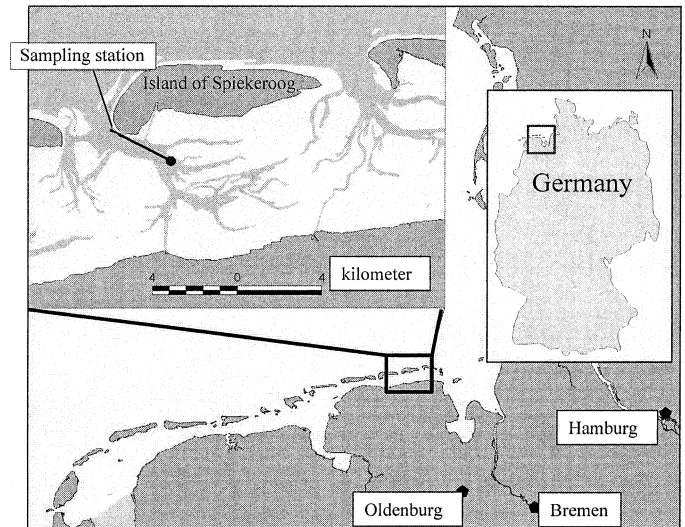


Fig. 1. Location of sampling site in Wadden Sea near the East Frisian island Spiekeroog, Northern Germany.

vided by the German meteorological service). Thus, the hydrodynamic situations in November and May were comparable. For the analysis of POC and chlorophyll *a* (Chl *a*), 0.5–1 liter of seawater was filtered immediately onto pre-combusted and weighed glass fiber filters (GF/F, Whatman). Samples for dissolved amino acid and carbohydrate analyses were prefiltered through 0.2- μm Acrodisc syringe filters (Gelman) and 0.2- μm Nuclepore membranes, respectively. For the analysis of particulate combined amino acids (PCAA) and carbohydrates (PCCHO), 100 ml of sample was filtered onto weighed and precombusted glass fiber filters (GF/F, Whatman). All samples were stored at -20°C in the dark until further analyses in the laboratory within 8 weeks. For enumeration of free-living and particle-associated bacteria, 100-ml water samples were fixed with formalin (4%) and stored at 4°C .

Hydrographic data—At each sampling, water temperature, salinity, pH, and oxygen were measured by probes (LF 196, pH192, OXI 196, WTW). On 18–19 November 1999, we continuously monitored turbidity with a multiprobe (Applied Microsystems Inc.), and on 17–18 May 2000, water temperature, salinity, current speed, and direction were measured with a CTD probe built and provided by the Environmental Physics Lab of the University of Oldenburg, Germany.

Inorganic and organic nutrients—Soluble reactive phosphorus (SRP), ammonium, nitrite, nitrate, and silica ($\text{Si}(\text{OH})_4$) were determined on samples stored at 4°C following the techniques outlined in Liebezeit and Velimirov (1984). Particulate organic phosphorus (POP) was determined according to Liebezeit (1991).

Bacterial and algal counts—For enumeration of bacteria, 1 ml of fixed seawater was filtered onto a black 0.2- μm pore size Nuclepore membrane and stained with DAPI (4',6'-diamidino-2-phenylindole) according to Porter and Feig (1980).

To reduce the background fluorescence of inorganic matter, filters were counterstained with a 0.1% acridine orange solution (Crump et al. 1998). Free-living and particle-associated bacteria were counted in the same sample by epifluorescence microscopy (Axioplan, Zeiss) at $\times 1,000$ magnification. Algal cell numbers of individual species were counted in Lugol-fixed samples by the Utermöhl (1958) technique.

Chlorophyll a—GF/F filters were extracted in hot (75°C) 100% ethanol, and concentration of Chl *a* was measured by the monochromatic method according to Schwoerbel (1986). The concentration of Chl *a* was determined photometrically by measuring extinction at a wavelength of 655 nm before (Chl *a* and pheopigments) and after (pheopigments) acidification with 2 mol L⁻¹ HCl.

Dry weight and particulate carbon—After drying the GF/F filters at 110°C for 1 h, the filters were weighed on a microbalance (Sartorius). Because filters were not rinsed to remove salt, dry weight (dry wt) was corrected for salt remaining on the dried filter by a regression analysis between dry wt of filters containing salt (unrinsed) versus filters rinsed with distilled water on an extra set of samples. Total particulate carbon (TC) was measured in a Coulometrics instrument (UIC) by titration with barium perchloride, pH 10. Particulate inorganic carbon (PIC) was measured in a Coulomat 702-SO (Ströhlein Instruments) by titration with perchloric acid. POC was determined as the difference of TC and PIC.

Amino acid and carbohydrates—Concentrations of dissolved free amino acids (DFAA) were analyzed by high-performance liquid chromatography (HPLC) after *o*-phthalaldehyde derivatization according to Lindroth and Mopper (1979). Dissolved combined amino acids (DCAA) were hydrolyzed with 6 mol L⁻¹ HCl at 155°C for 1 h and analyzed as DFAA. Concentrations of dissolved free neutral monosaccharides (DFCHO) were analyzed by HPLC with a CarboPac PA 10 column (Dionex) and pulsed amperometric detection according to Mopper et al. (1992). NaOH (20 mol L⁻¹) was used as eluent. Prior to analysis, samples were desalted by ion-exchange chromatography (Borch and Kirchman 1997). Dissolved combined neutral monosaccharides (DCCHO) were analyzed by HPLC as DFCHO after 20 h of hydrolysis with 0.09 mol L⁻¹ HCl at 100°C.

PCAA and PCCHO were analyzed in the filtered samples that were used for dry wt determinations. A quarter of these filters was subjected to acid hydrolysis in the same manner as for DCAA and DCCHO. Samples were diluted up to 100-fold; thus, desalting of samples for monosaccharide analysis was not necessary.

Bacterial production—Rates of bacterial biomass production were measured on 17–18 May 2000 only by the incorporation of [¹⁴C]-leucine (Simon and Azam 1989). Triplicates and a formalin-killed control were incubated with [¹⁴C]-leucine (10.8 GBq mmol⁻¹, Hartmann Analytic) at a final concentration of 50 nmol L⁻¹, which ensured saturation of uptake systems of both free-living and particle-associated

bacteria. Incubation was performed in the dark at in situ temperature for 1 h. After fixation with 2% formalin, samples were filtered onto 0.45- μ m nitrocellulose filters (Sartorius) and extracted with ice-cold 5% trichloroacetic acid (TCA) for 5 min. Thereafter, filters were rinsed twice with ice-cold 5% TCA, dissolved with ethylacetate, and radioassayed by liquid scintillation counting. Biomass production was calculated according to Simon and Azam (1989). Standard deviation of triplicate measurements was usually <15%.

Hydrolytic enzyme activities—Aminopeptidase and β -glucosidase activities of bacteria were measured with the use of L-leucine-methyl coumarinyl amide (Leu-MCA) and methyl-umbelliferyl- β -D-glucoside (β -D-Gluc-MUF) as substrate analogs according to Hoppe (1983). Three samples (including resuspended particles) and a formalin-killed control were incubated in rotating vials at in situ temperature in the dark for 1 h. Final concentrations of substrate analogs were 100 μ mol L⁻¹, which ensured maximum hydrolysis as determined by saturation kinetics. Fluorescence of both fluorochromes was measured in a TD 700 fluorometer (Turner Design), with filters ranging from 300–400 nm (excitation) and 410–610 nm (emission).

Statistical analysis—To test for tidal dependency and for seasonal differences, least squares analyses were performed by the program JMP 4.01 (SAS Institute Inc.). In May, the last three data points of all measured parameters were excluded from statistical analyses because they were taken from an entirely different water mass, presumably originating from adjacent tidal flats (see Results). The temporal parameter used was “hours from high tide.” Because high tidal currents in fall occurred approximately 1 h prior to slack water, we additionally tested the temporal parameter “hours from 1 h before low or high tide.” Linear regression analyses were calculated to test for dependency between all measured parameters for November and May separately.

Results

Hydrographic data—Water temperature in November 1999 was around 5°C, with slightly higher values at high tide when more saline and warmer water from the North Sea was introduced into the tidal flat system (Fig. 2). In contrast to temperature and salinity, oxygen saturation did not show any tidally dependent variability and ranged around 95% (Fig. 2).

In May, temperature and salinity were higher than in November (up to 18°C and 32.5 psu, respectively; Fig. 2; Table 1). In contrast to November, salinity remained constant, but temperature showed inverse tidal patterns, with highest values at low tide and lowest values at high tide (Fig. 2) because of the introduction of colder North Sea water at high tide. Oxygen saturation was higher than in November and exhibited tidal variations with highest values at high tide, presumably because in the incoming North Sea water, the ratio of photoautotrophic to heterotrophic processes was higher than in the Wadden Sea water (Fig. 2; Table 1).

A dramatic change in current direction and in the σ_T value

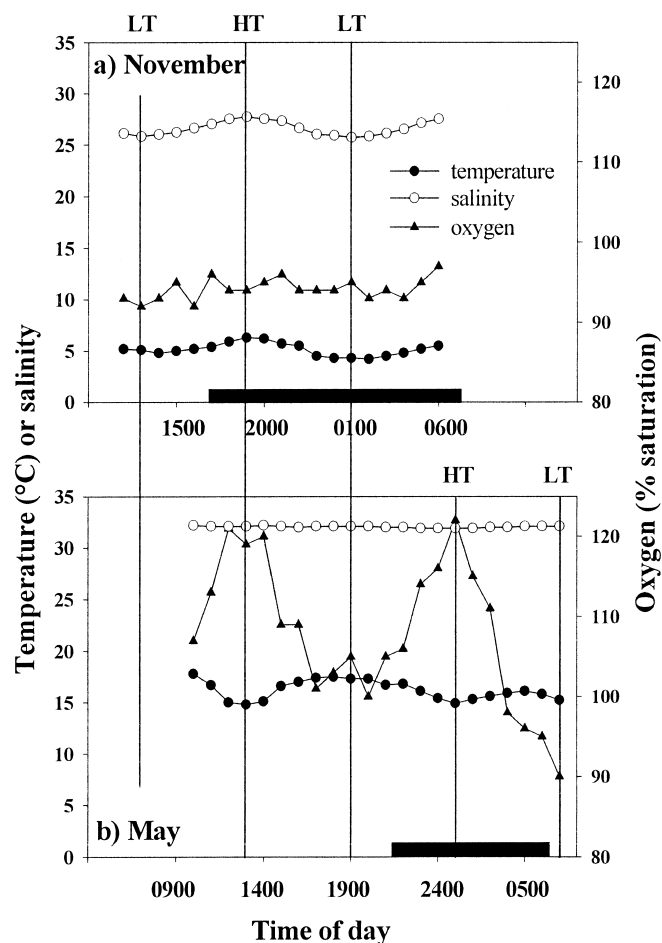


Fig. 2. Temperature, salinity, and oxygen saturation during tidal studies with hourly measurements (a) 18–19 November 1999 and (b) 17–18 May 2000. Calculated time of high (HT), and low tide (LT) for the island of Spiekeroog. Dark bars represent dark periods at night.

occurred from 0400 until 0600 h on 18 May (data not shown). This occurrence, along with shifts of almost all parameters measured (e.g., dry wt, PIC, POC, Chl *a*, amino acids, and bacterial activities; Figs. 2–7), indicates the appearance of an entirely different waterbody at that time, presumably from the neighboring tidal flats. Thus, these data points were excluded from the statistical analyses.

Inorganic and organic nutrients—Concentration maxima of dissolved and particulate inorganic and organic nutrients (SRP, POP, dissolved inorganic nitrogen, NH_4^+ , $\text{Si}(\text{OH})_4$, NO_2^- , NO_3^- ; Table 2) were always higher in November than in May. There were no pronounced tidal patterns for any of the nutrients except for silica in May, which showed highest concentrations at low tide and lowest concentrations at high tide. Highest POP concentrations on 18 May appeared between 0400 and 0600 h, when a different water mass was sampled (see Results: Hydrographic Data).

Phytoplankton—In November, phytoplankton abundance was low, and benthic as well as benthic-pelagic diatoms such

Table 1. Difference of measured parameters between the two sampling dates (least squares analysis). +, month at which a value was higher. For abbreviations, see text.

Parameter	November	May	Significance level
Salinity		+	<0.0001
Temperature		+	<0.0001
Oxygen		+	<0.0001
Dry wt	+		0.0013
Chl <i>a</i>		+	<0.0001
TC	+		<0.0001
POC	+		0.0028
PIC	+		<0.0001
% POC			ns
POC/PIC		+	<0.0001
Free bacteria		+	<0.0001
Particulate bacteria	+		<0.0001
Protease			ns
Cell-specific protease	+		<0.0001
β -glucosidase		+	0.0002
Cell-specific β -glucosidase		+	0.0473
DCCHO		+	<0.0001
DFAA			ns
DCAA	+		<0.0001
PCAA			ns

ns, not significant.

as *Paralia sulcata* and *Trigonium alternans* dominated. In addition, *Thalassiosira* spp., *Odontella* spp., and *Chaetoceros* spp. were present. In contrast, microalgae in May were primarily of planktonic origin and greatly dominated by the diatom *Guinardia delicatula*, which contributed >90% to total phytoplankton biomass.

Dry weight, Chl *a*, and particulate carbon—Dry wt, Chl *a*, and the particulate carbon fractions showed pronounced tidal patterns in November, with maxima 1 h before slack water when the current velocity was highest (Figs. 3, 4a). All these parameters were significantly correlated with each other and tide (Tables 3, 4). Maxima before high tide were higher than those before low tide. In May, dry wt and Chl *a* concentrations did not show any tidal pattern (Fig. 3), but

Table 2. Range of concentrations ($\mu\text{mol L}^{-1}$) of particulate organic phosphorus (POP), soluble reactive phosphorus (SRP), dissolved inorganic nitrogen (DIN), ammonium (NH_4^+), silica ($\text{Si}(\text{OH})_4$), nitrite (NO_2^-), and nitrate (NO_3^-) during the tidal cycles in November 1999 and May 2000.

	Concentration ($\mu\text{mol L}^{-1}$)	
	November	May
POP	1.6–6.1	<0.1–1.8
SRP	0.9–1.7	<0.1–1.0
DIN	16.5–26	<0.1–17
NH_4^+	5.5–15.4	<0.1–13.8
$\text{Si}(\text{OH})_4$	17–26	1.4–16
NO_2^-	4–7	<0.1–4
NO_3^-	5–6	<0.1–5

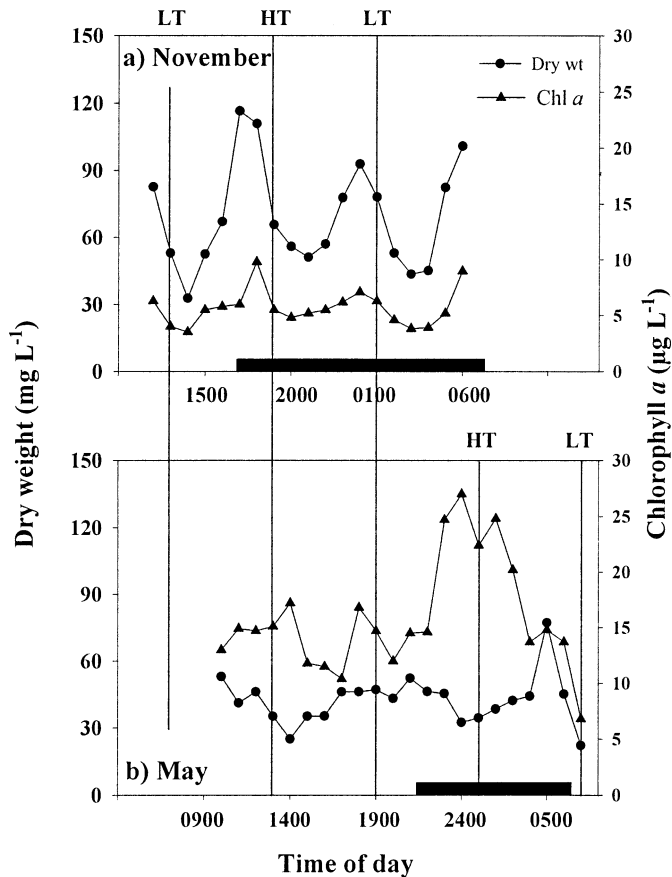


Fig. 3. Tidal course of dry wt and Chl *a* 18–19 November 1999 and 17–18 May 2000. For abbreviations, see Fig. 2.

highest and lowest concentrations of Chl *a* were measured shortly before high tide during night and at low tide in early morning, respectively. Chl *a* was positively correlated with oxygen saturation (Table 3). Concentrations of dry wt were significantly lower in May than in November, whereas those of Chl *a* were much higher (Table 1). Concentrations of TC and POC were enhanced 1–2 h before high tide but were generally lower than in November, PIC in particular (Fig. 4b). In May, parameters characterizing SPM were neither significantly correlated with each other nor with tide (Tables 3, 4). PIC was significantly reduced at high tide.

POC as a percentage of dry wt (percent POC) ranged between 2.0% and 3.8% in November and between 2.2% and 6.8% in May. In November, only minor changes occurred over the tidal cycle, and the POC : PIC ratio remained almost constant (Fig. 4c). In May, however, percent POC increased around high tide and covaried with the POC : PIC ratio, but only PIC dynamics showed a tidal pattern (Fig. 4d).

Free-living and particle-associated bacteria—In November, numbers of free-living and particle-associated bacteria were in the same range (Fig. 5), but the latter fluctuated much more during the tidal cycle. They were significantly correlated with concentrations of dry wt, Chl *a*, TC, and POC, but not with PIC (Table 3). In contrast, numbers of

free-living bacteria were negatively correlated with concentrations of dry wt, TC, and POC (Table 3).

In May, numbers of free-living bacteria were much higher, and numbers of particle-associated bacteria were significantly lower than in November (Fig. 5; Table 1). Abundance of free-living bacteria was enhanced in the evening, 1–2 h before nightfall, but numbers of both free-living and particle-associated bacteria were reduced at high tide. Abundances of free-living and particle-associated bacteria were positively correlated with each other and temperature, but negatively correlated with oxygen saturation and high tide (Tables 3, 4). The abundance of particle-associated bacteria was positively correlated with dry wt and PIC but negatively correlated with POC : PIC (Table 3).

Bacterial ectoenzymatic activities and production—Protease and β -glucosidase activities showed significant tidal patterns in November (Fig. 6a; Tables 3, 4). Highest protease activity occurred at high tide, whereas peaks of β -glucosidase activity occurred 1 h before slack water, concurrently with enhanced concentrations of dry wt and TC. In May, protease activity was in the same range as in November but did not vary with tide (Fig. 6b). In contrast, β -glucosidase activity was much higher in May than in November, with pronounced peaks around high tide (Figs. 6a,b; Table 1). It was negatively correlated with PIC but positively with POC : PIC (Table 3). Bacterial production, measured only in May, showed not a tidal, but a diurnal, pattern, with high rates during the day and reduced values at night (Fig. 6b).

To assess tidal dynamics of normalized hydrolytic activities, we calculated protease, β -glucosidase, and bacterial production rates per cell, assuming all DAPI-counted cells were active. In November, cell-specific protease did not covary with tide, whereas cell-specific β -glucosidase activity did (Fig. 6c), being positively correlated with concentrations of dry wt, Chl *a*, TC, POC, and PIC (Table 3). In May, cell-specific protease and β -glucosidase activity were more variable and correlated with each other (Fig. 6d; Table 3). Maxima occurred around high tide and minima around low tide. Cell-specific bacterial production exhibited patterns similar to volume-based rates (Fig. 6d).

Dissolved free and combined neutral monosaccharides—Concentrations of dissolved neutral monosaccharides did not exhibit any tidal pattern. In November, concentrations of DFCHO were always below detection limit ($<10 \text{ nmol L}^{-1}$), and concentrations of DCCHO ranged between 0.5 and 1.8 $\mu\text{mol L}^{-1}$ of monosaccharide equivalents (Fig. 7a). Glucose (25–30 mol%) and mannose (18–25 mol%) constituted highest percentages and fucose, rhamnose, arabinose, and galactose lower fractions (10–15 mol% each) of DCCHO.

In May, concentrations of DFCHO did not exhibit tidal variations, and the mean value was $42 \pm 15 \text{ nmol L}^{-1}$. Glucose was the dominant monomer (80 mol%) and mannose, fucose, rhamnose, and arabinose contributed $<5 \text{ mol\%}$ each. Concentrations of DCCHO in May were also higher than in November, ranging between 2.0 and 7.6 $\mu\text{mol L}^{-1}$, with glucose and mannose being the dominant monomers. Highest values occurred during night at enhanced Chl *a* concentra-

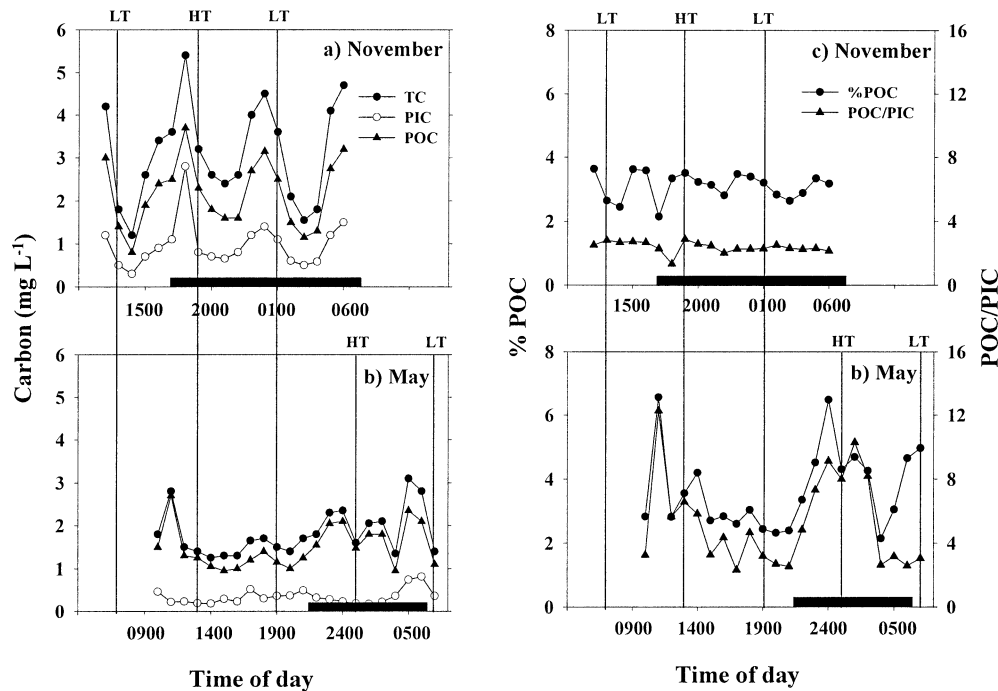


Fig. 4. Tidal course of (a, b) total carbon, inorganic carbon, and organic carbon and (c, d) percentage of organic carbon of total dry wt (% POC) and ratio of organic carbon to inorganic carbon (POC:PIC) in November and May, respectively. For further abbreviations, see Fig. 2.

tions (Fig. 7b). Both parameters were positively correlated (Table 3).

Amino acids—Concentration ranges of DFAA were similar at both sampling dates (Fig. 7c,d) and varied between the detection limit ($0.002 \mu\text{mol L}^{-1}$) and $1.7 \mu\text{mol L}^{-1}$ in November and between 0.02 and $1.0 \mu\text{mol L}^{-1}$ in May. Concentrations of DCAA ranged from 1.9 to $10 \mu\text{mol L}^{-1}$ and 0.3 to $3 \mu\text{mol L}^{-1}$ in November and May, respectively; those of PCAA ranged from 4 to $25 \mu\text{mol L}^{-1}$ (Fig. 7c,d). Concentrations of DCAA and PCAA were positively correlated with tide, salinity, dry wt, Chl *a*, TC, POC, PIC, and total protease activity in November, but not in May (Tables 3, 4). At the latter date, only concentrations of PCAA correlated with cell-specific protease activity.

The mole percent composition of DFAA, DCAA, and PCAA showed pronounced differences between November and May (Fig. 8). Proportions of aspartate and glutamate in all amino acid fractions were higher in May than in November (Fig. 8). Highest mole percentage of aspartate and glutamate occurred in the PCAA in May and accounted for 35, 47, and 55 mol% at low tide, high tide, and the current velocity maximum, respectively. Proportions of both amino acids decreased at midnight and early morning (0400–0600 h) when an entirely different waterbody had reached the sampling station (data not shown). PCAA contributed 10–32% and 12–55% to POC in November and May, respectively. In November, highest percentages of PCAA were detected during and shortly after high tide, whereas PCAA concentrations were more variable in spring.

Discussion

Our study focused on two typical and contrasting seasonal situations in the Wadden Sea: the late spring bloom in May, with high inputs of organic matter, and November, after the end of the growing season with a low input of freshly produced organic matter and enhanced resuspension of inorganic matter. Our results demonstrate that SPM dynamics were related to two major processes: (1) resuspension of the surface sediment and (2) phytoplankton growth. In addition, the introduction of foreign water masses, either from the open North Sea or from adjacent tidal basins, appears to be a typical feature of the Wadden Sea. These water masses exhibited different SPM signatures compared with those of the SPM of the tidal basin we studied, such as on the early morning of 18 May.

In November, concentrations of SPM and particulate carbon fractions covaried directly with tidal dynamics. SPM appeared to be mainly of benthic origin, as indicated by enhanced PC and POC, but low Chl *a* concentrations compared with May, despite rather similar current velocities. Resuspension of the benthic layer appeared of minor importance in May, presumably because the surface of the benthic layer is more firm during the growing season from epibenthic microalgae (Noffke et al. 2001). In May, SPM rich in organic matter and Chl *a* was mainly of phytoplankton origin and also was introduced from the open North Sea, as indicated by higher values around high tide. In line with SPM and phytoplankton dynamics, abundances and activities of attached and free-living bacteria greatly varied between No-

Table 3. Significance levels of linear regression analysis of all measured parameters on 18–19 November 1999 (below the diagonal) and on 17–18 May 2000 (above the diagonal). For abbreviations, see text. Bacterial production was not correlated with any of the measured parameters in May 2000.

	Salinity	Temp.	O ₂	Dry wt	Chl <i>a</i>	TC	POC	PIC
Salinity	X	ns	ns		<i>0.0236</i>	ns	ns	ns
Temperature	< 0.0001	X	< <i>0.0001</i>	0.0177	ns	ns	ns	0.0026
O ₂	ns	ns	X	<i>0.0247</i>	0.0345	ns	ns	<i>0.0006</i>
Dry wt	ns	ns	ns	X	ns	ns	ns	0.0011
Chl <i>a</i>	ns	ns	ns	0.0009	X	ns	ns	ns
TC	ns	ns	ns	0.0001	< 0.0001	X	< 0.0001	ns
POC	ns	ns	ns	0.0001	< 0.0001	< 0.0001	X	ns
PIC	ns	ns	ns	0.0012	< 0.0001	< 0.0001	< 0.0001	X
% POC	ns	ns	ns	0.0034	0.0015	< 0.0001	< 0.0001	0.0104
POC : PIC	ns	ns	ns	ns	<i>0.0466</i>	ns	ns	<i>0.0335</i>
Free bacteria	ns	ns	ns	<i>0.0444</i>	ns	<i>0.0221</i>	<i>0.0423</i>	ns
Particulate bacteria	ns	ns	ns	0.0289	0.0343	0.0098	0.0068	ns
Protease	0.0004	<i>0.0022</i>	ns	ns	ns	ns	ns	ns
β-glucosidase	ns	ns	ns	0.0083	0.0008	0.0008	0.0008	0.0026
DCCHO	ns	ns	ns	ns	ns	ns	ns	ns
DFAA	ns	ns	ns	ns	ns	ns	ns	ns
DCAA	0.0064	ns	ns	0.0105	0.0293	0.0391	0.0406	0.0190
PCAA	0.0114	ns	ns	0.0172	0.0050	0.0046	0.0051	0.0031

ns, not significant; bold, positive correlation; italic, negative correlation.

vember and May, with enhanced numbers of free-living and reduced numbers of particle-associated bacteria in May and similar numbers of both fractions in November. This situation indicates that bacterial decomposition responded to the enhanced input of organic matter and were more tightly coupled to phytoplankton growth in May. Large seasonal variations in algal and bacterial biomass have been observed frequently in tidal flat systems (e.g., Admiraal et al. 1985; Poremba et al. 1999b) and presumably are related in similar ways, as we found, to dynamics of biological and sedimentological processes.

Factors controlling suspended matter and microbial dynamics—Sediment resuspension: Sedimentation and resuspension of particulate matter are the most characteristic features of the Wadden Sea (Eisma et al. 1991). Both processes are greatly controlled by current velocity, which in turn is controlled by tides, wind, or both (van Leussen 1996). Increasing current velocity leads to high shear forces, resulting in increased resuspension of the upper benthic layer. In contrast, decreasing current velocity leads to low shear forces and allows aggregation and sedimentation of SPM (van Leussen 1988). Our studies in November and May both were performed at moderate wind speed at spring tide, when tidal dynamics and current velocities are highest. Hence, tidal currents could be expected to be the most important hydrodynamic factor of SPM dynamics in this study. In November, resuspension of sediment and benthic algae was highest at the current velocity maximum. This pattern was found even though we solely sampled surface water roughly 13 m above the sediment. This effect is presumably more pronounced further down in the water column, because highest SPM concentrations occur closely above the sediment at the highest shear rates (Eisma et al. 1991). Chl *a* dynamics covaried with dry wt and POC, leading to a rather constant POC : PIC

ratio throughout the tidal cycle. The increasing percent POC shortly before the current velocity maxima in November, however, can be attributed to resuspension of the organic matter-rich benthic layer, as has been reported by McCandliss et al. (2002) from the coastal North Sea in the Netherlands. The relatively high percent POC during high tide presumably resulted from the preferential removal of fast-settling inorganic particles (Liebezeit et al. 1994). High resuspension of the benthic surface layer yielded extremely high concentrations of DCAA and PCAA shortly before high tide. The covariation of numbers of particle-associated bacteria with dry wt and the particulate carbon fractions in November and higher numbers compared with May are a further indication that resuspended material dominated SPM dynamics in this situation. The significance of resuspension and vertical exchange for tidal dynamics of SPM, particle-associated bacteria, and pheopigments as an index of decaying algae was reported also for the Weser estuary, situated farther east of our study area (Schuchardt and Schirmer 1991).

In May, an enhanced fraction of the organic matter was derived from phytoplankton, also partly imported from the North Sea, as indicated by the higher values of percent POC and the POC : PIC ratio at high tide during night. The low Chl *a* concentrations but high POC : PIC ratios at the current velocity maximum at 1100 h on 17 May before high tide and at 0500 h on 18 May before low tide, however, indicate that resuspension of freshly settled benthic material also contributed to suspended POC. Microscopic examinations and the PCAA mole percent composition indicated that the SPM rich in organic matter at the latter time point resulted from resuspension of benthic material from a different water mass, presumably from the adjacent tidal flats. The observed increase in the POC : PIC ratio is in good agreement with the inverse relation between percent POC and total SPM found

Table 3. Extended.

% POC	POC : PIC	Free bacteria	Particulate bacteria	Protease	β -glucosidase	DCCHO	DFAA	DCAA	PCAA
ns	ns	ns	ns	ns	ns	0.0071	0.0340	ns	0.0353
ns	0.0290	0.0165	0.0013	ns	<0.0008	ns	ns	ns	ns
ns	0.0038	0.0026	0.0001	ns	ns	0.0032	ns	ns	ns
ns	ns	ns	0.0212	ns	ns	ns	ns	ns	ns
0.0241	0.0091	ns	ns	ns	ns	0.0001	ns	ns	ns
0.0001	0.0256	ns	ns	ns	ns	ns	ns	ns	ns
< 0.0001	0.0020	ns	ns	ns	ns	ns	ns	ns	ns
ns	0.0027	ns	0.0047	ns	ns	ns	ns	ns	ns
X	< 0.0001	ns	ns	ns	ns	ns	ns	ns	ns
ns	X	ns	0.0298	ns	ns	ns	ns	ns	ns
0.0475	0.0039	X	< 0.0001	ns	ns	ns	ns	ns	ns
0.0025	ns	ns	X	ns	ns	ns	ns	ns	ns
ns	ns	ns	ns	X	ns	ns	ns	ns	ns
0.0086	ns	0.0375	0.0123	ns	X	ns	ns	ns	ns
ns	ns	ns	ns	ns	ns	X	ns	ns	ns
ns	ns	ns	0.0414	ns	0.0305	ns	X	ns	ns
ns	ns	ns	ns	ns	ns	ns	ns	X	ns
0.0340	ns	ns	ns	0.0154	ns	ns	ns	0.0041	X

by Hickel (1984) and Liebezeit et al. (1994) in the German Wadden Sea. A higher percent POC frequently has been found during slack water in tidally affected coastal areas when heavy inorganic particles settle out and large aggregates form (Eisma and Li 1993; van Leussen and Cornelisse 1993; Liebezeit et al. 1994; McCandliss et al. 2002).

Phytoplankton-related processes: Our results provide evidence that in May, phytoplankton-related processes were important for dynamics of the organic fraction of SPM. Higher concentrations of Chl *a*, a higher POC : PIC ratio, low concentrations of inorganic nutrients, and higher numbers of free-living bacteria indicate that autotrophic processes in the

Table 4. Tidal dependency of measured parameters (least squares analysis). Tide 1 is hours from high tide; tide 2 is hours from 1 h before low or high tide.

Parameter	November		May	
	Tide 1	Tide 2	Tide 1	Tide 2
Salinity	+<0.0001	ns	ns	ns
Temperature	+<0.0001	ns	-<0.0001	ns
Oxygen	ns	ns	+<0.0001	ns
dry wt	ns	+0.0066	-0.0221	ns
Chl <i>a</i>	ns	+0.0319	ns	ns
TC	ns	+0.0094	ns	ns
POC	ns	+0.0072	ns	ns
PIC	ns	+0.0131	-0.0057	ns
% POC	ns	ns	ns	ns
POC : PIC	ns	ns	+0.0090	ns
Free bacteria	ns	ns	-0.0005	ns
Particulate bacteria	ns	ns	-<0.0001	ns
BPP	nd	nd	ns	ns
Cell-specific BPP	nd	nd	ns	ns
Protease	+0.0003	ns	ns	ns
Cell-specific protease	ns	ns	+0.0004	ns
β -glucosidase	+0.4550	+0.0158	+0.0178	ns
Cell-specific β -glucosidase	ns	+0.0144	+0.0005	ns
DCCHO	ns	ns	ns	ns
DFAA	ns	ns	ns	ns
DCAA	+0.0040	ns	ns	ns
PCAA	+0.0097	+0.0418	ns	ns

ns, not significant; nd, not determined; +, positive correlation, -, negative correlation; BPP, bacterial protein production.

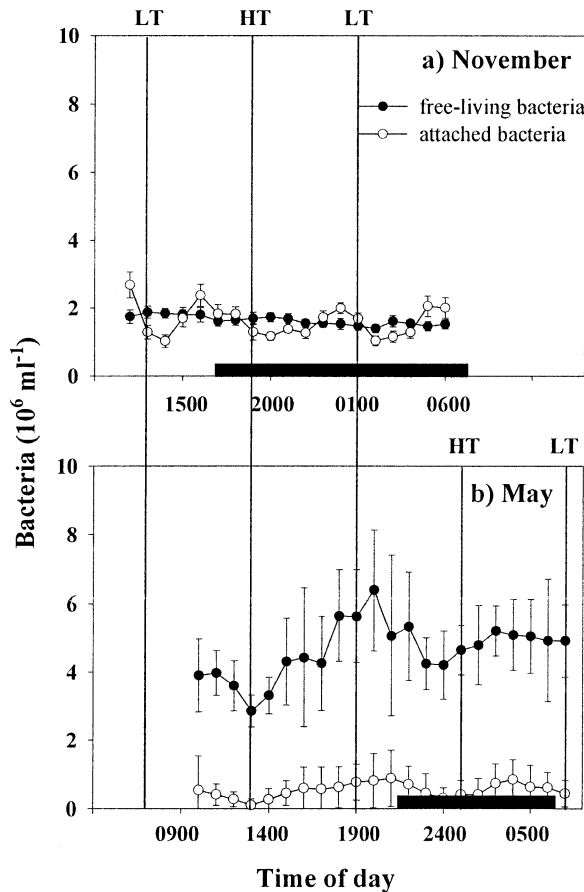


Fig. 5. Tidal dynamics of the abundances of free-living and attached bacteria in November and May.

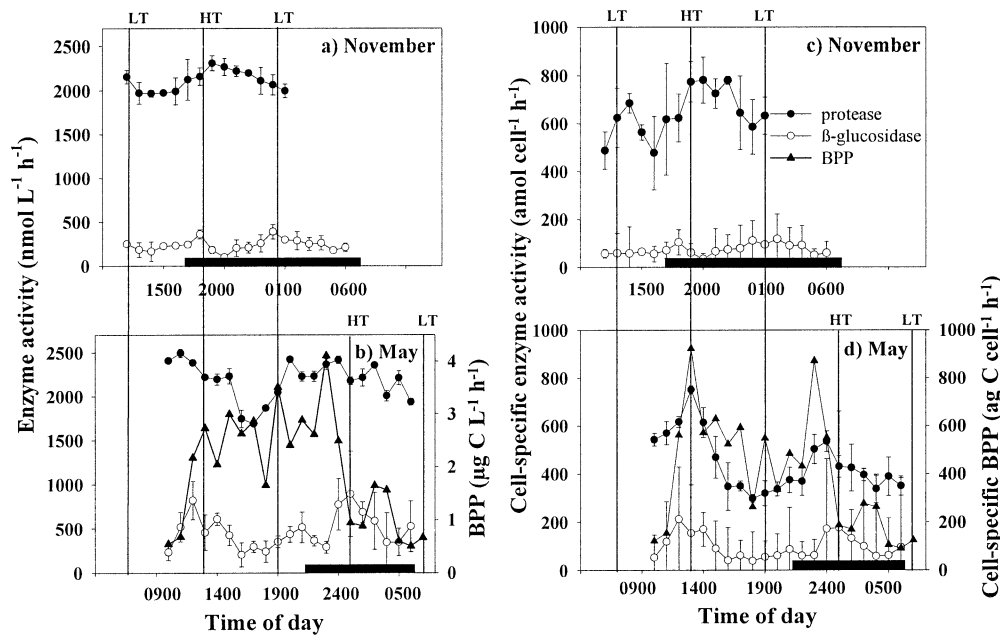


Fig. 6. Tidal dynamics of (a, b) total protease, β -glucosidase activity, and bacterial protein production and (c, d) cell-specific protease, β -glucosidase activity, and bacterial protein production in November and May, respectively. Bacterial production was only measured in May. For further abbreviations, see Fig. 2.

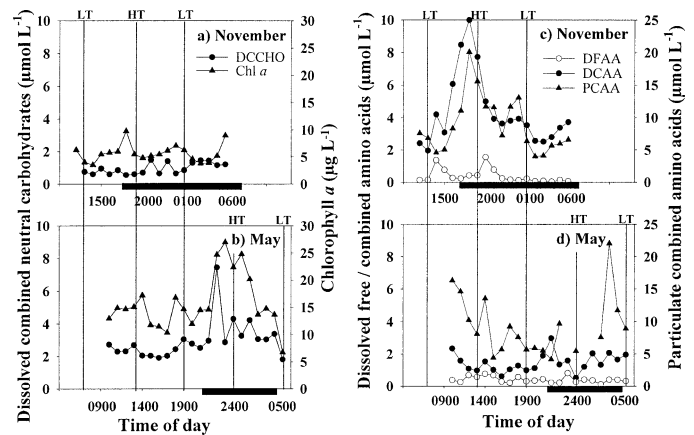


Fig. 7. (a, b) Tidal dynamics of dissolved combined neutral monosaccharides (DCCCHO) and Chl *a* and (c, d) dissolved free (DFAA), dissolved combined (DCAA), and particulate combined amino acids (PCAA) in November and May, respectively. For further abbreviations, see Fig. 2.

water column were more important in this month compared with November. Concentrations of DCCCHO and β -glucosidase activities were also higher in May, suggesting an enhanced release by algae and a higher bacterial turnover. These effects were most pronounced around high tide during the night, when phytoplankton-rich North Sea water was introduced. Enhanced DCCCHO concentrations during a phytoplankton spring bloom have been reported from the North Sea (Ittekkot et al. 1981), as well as higher β -glucosidase activities during the bacterial breakdown of phytoplankton-derived carbohydrates (Agis et al. 1998). Dry wt concentra-

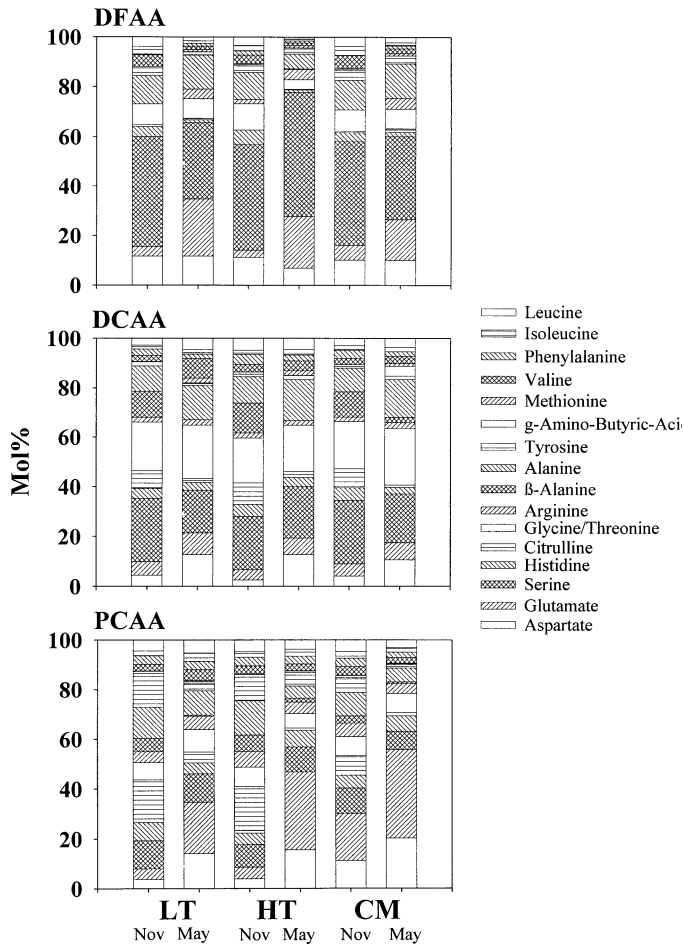


Fig. 8. Comparison of mole percent composition (mol%) of dissolved free (DFAA), dissolved amino acids (DCAA), and particulate combined amino acids (PCAA) at low tide (LT), high tide (HT), and maximum current velocity (CM) in November and May.

tions were lower in May than in November and POC tended to constitute a higher percentage of dry wt, even though it was still a minor percentage. The positive correlation between concentrations of Chl *a*, percent POC, and the POC: PIC ratio and the lower values of dry wt in May further suggest that phytoplankton-related processes dominated POC dynamics at this time, independent of a still substantial background of resuspended inorganic SPM. The dynamics of Chl *a*, TC, and POC, which were independent of the tide in May (Table 4), and the low contribution of benthic algae to phytoplankton biomass also provide evidence for this relationship.

Sinks of the phytoplankton algae in the Wadden Sea include grazing by zooplankton (Niesel and Günther 1999), aggregation, and sedimentation, but also breakup by high shear rates in the tidal channels and during inflow from the North Sea through the outlet when current velocities of up to 1.5 m s⁻¹ are reached. All these processes lead to the release of DOM, including DCCHO and DCAA, and result in the production of particulate detritus, both of which can be utilized by heterotrophic bacteria. Microscopic inspection of SPM confirmed that substantial fractions of the algae were

broken up in May. The similar mole percent composition of PCAA and DCAA also confirmed that the latter was of phytoplankton origin.

In contrast to DCCHO, concentrations of DFAA were not significantly different between May and November, and concentrations of DCAA were even higher in November. This might appear surprising because protein is a major constituent of the phytoplankton biomass. The mole percent composition of particulate and dissolved amino acids in both months showed pronounced differences, suggesting different sources. Increased mole percentages of aspartate and glutamate in PCAA and DCAA in May point to a phytoplankton origin (Lee and Cronin 1984; Grossart et al. 2003). Higher mole percentages of serine, tyrosine, and γ -amino butyric acid suggest a more refractory nature of the PCAA in November (see Lee and Cronin 1984).

Our results demonstrate that the dynamics of SPM and its organic fraction and microbial processes exhibit pronounced seasonal differences in the German Wadden Sea and, presumably, in similar tidal flat systems. In May, dynamics of the organic SPM fraction were mainly controlled by phytoplankton-related processes, despite a rather high background of inorganic SPM. These processes stimulated bacterial decomposition of the organic matter, as shown by high concentrations of DCCHO, β -glucosidase activity, and the dominance of free-living bacteria. In November, resuspension of benthic material was the main source of SPM and POC in the water column, leading also to high numbers of particle-associated bacteria in the water column. We also found evidence that introduction of foreign water masses, either from the open North Sea or adjacent tidal basins, could rapidly change physical, chemical, and biological processes in the Wadden Sea. These changes have profound consequences for the coupling of SPM and microbial dynamics. Further studies on microbial processes in tidal flat systems should include experimental setups to distinguish between the effects of current speed and mixing of water masses, as well as those of temporal and seasonal variability of substrate dynamics on relevant microbial parameters.

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