

# Spatio-temporal dynamics of suspended matter properties and bacterial communities in the back-barrier tidal flat system of Spiekeroog Island

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**Abstract** Back-barrier tidal flat systems are characterized by basins and inlets through which water is exchanged with the coastal sea by tidal water movements. The hydrographic and morphometric properties at the inlets and in the basins vary considerably, but there is little information available how biogeochemical properties in the water column at these different sites respond to these differences. Therefore, we investigated tidal dynamics of suspended particulate matter (SPM), particulate and dissolved organic carbon (DOC), chlorophyll *a*, phaeopigments, numbers of particle-associated (PA) and free-living bacteria (FL), bacterial biomass production, and concentrations of dissolved manganese (Mn). Samples were taken at the surface, a mid-depth and 1 m above the bottom at a fixed station at the inlet and in the basin of the Spiekeroog back-barrier tidal flat system in the German Wadden Sea. Five tidal cycles representative for typical seasonal situations, January (winter), April and May (late spring bloom), July (summer), and November (late fall) were studied in 2005 and 2006. In July, processes related to phytoplankton dynamics and

bacterial decomposition were much more enhanced in the basin, whereas in April, these processes were enhanced at the inlet but were particularly low within the basin itself. The low values within the basin were a result of the settled phytoplankton spring bloom and represent a rather short period at the decline of this bloom. In November and January, differences were much less pronounced than during the growing season and restricted mainly to SPM and PA bacteria, exhibiting higher values in the basin. FL bacteria, DOC, and dissolved Mn exhibited different patterns and much less differences between the two stations, indicating that biogeochemical processes in the dissolved phase were controlled by different factors than PA biogeochemical processes. These differences reflect the retentive properties of the basin for particles and PA biogeochemical processes, particularly during the growing season, and in general emphasize the high productivity of back-barrier tidal flat systems.

**Keywords** Suspended matter · Chlorophyll · Bacteria · Bacterial production · DOC · Tidal flats

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## 1 Introduction

Tidal flat systems occur in wide and shallow coastal areas at the transition zone between land and coastal seas. They are structured by tidal channels and intertidal banks and accumulate particulate matter, which settles out at sites of reduced kinetic energy. Tidal flats may be exposed to pronounced tidal currents and wave action, the dynamics of which may cause intense sedimentation and resuspension of particulates, resulting in permanently turbid water masses with high loads of suspended particulate matter (SPM). Inputs of inorganic nutrients and organic matter from both

terrestrial and marine sources result in high productivity and turnover of organic matter and thus make tidal flats one of the most productive marine ecosystems (Alongi 1998). Because of the high input of organic matter, mainly in spring and summer, tidal flat ecosystems are usually net-heterotrophic and act as a sink for organic matter (Cadée 1980, Postma 1981). They are, together with estuaries, of prime importance in land–sea interactions.

Tidal flat systems are either wide and open to the sea (macrotidal) or protected by barrier islands (micro- to mesotidal). In open systems, a gradual transition from the coastal sea to the tidal flats exists, with water exchanging along the entire front. In systems with barrier islands, back-barrier tidal flats may develop, which have somewhat different features. The islands, often occurring in a chain separated by inlets of different size, channelize water exchange between the open sea and the back-barrier area, which results in the formation of distinct tidal basins with rather different hydrographic and biological properties as compared to open tidal flat systems.

The Wadden Sea, which occupies the coastal region of the North Sea between Den Helder (The Netherlands) and Skallingen (Denmark), is the largest continuous tidal-flat ecosystem in the world and hence of general importance for land–sea interactions in this region. Large areas, i.e., the West, East, and parts of the North Frisian Wadden Sea, are structured as back-barrier tidal flat systems. Water exchange between the basins and the open sea is mainly funneled through the inlets and the main tidal channels between the islands. In addition, there is some water exchange across the tidal watersheds between individual tidal basins (Stanev et al. 2003). It is well known that the tidal currents and the general hydrographic conditions affect resuspension and the settling behavior of suspended matter, leading to a fractionation of settling aggregates and thereby affecting sediment properties (Van Leussen 1996; McCandliss et al. 2002; Lunau et al. 2004; Chang et al. 2006; Bartholomä et al. 2009). It is, however, not known whether, and if so, how the biogeochemical properties of suspended matter and the heterotrophic microbial processes in the water column are affected by the varying hydrographic conditions in different areas of the back-barrier basins. For example, are the tidal dynamics of these parameters and processes similar in the inlets and within the back-barrier basins, or does the morphometry of the basins lead to a different tidal response in different parts of the basins? Furthermore, is the seasonality of these parameters and processes similar in the basins and the inlets, i.e., do they basically reflect the processes of the open coastal sea beyond the islands? There is some information available on these issues, e.g., modeling results on ecosystem dynamics and cycling of inorganic nutrients in various parts of the back-barrier tidal flat system of Spiekeroog Island, East Frisian Wadden Sea,

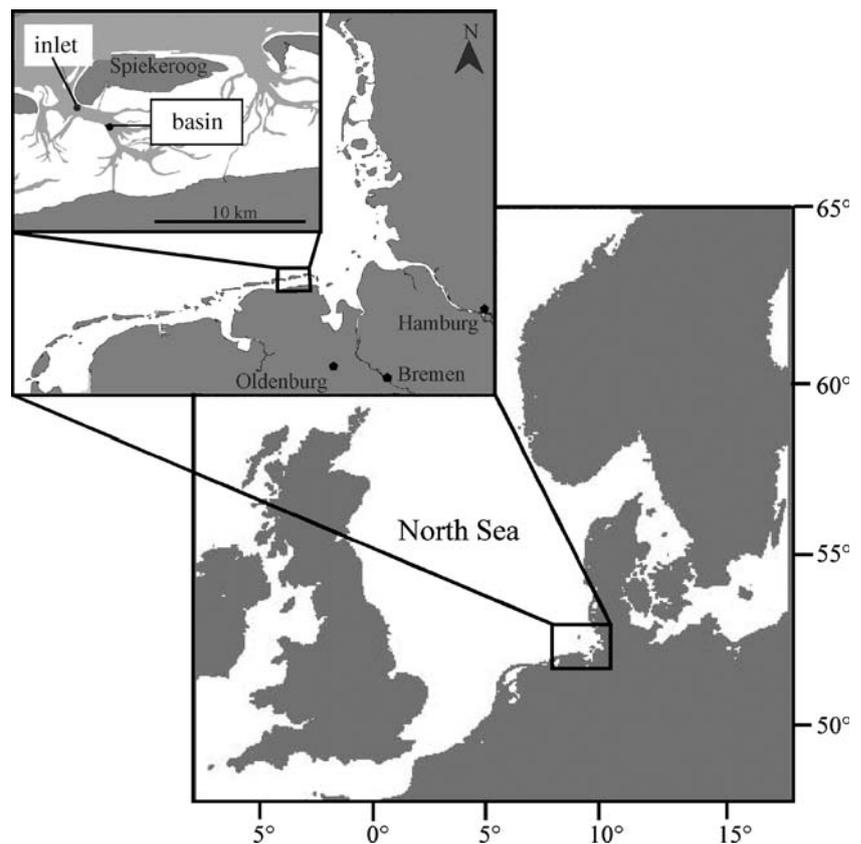
Germany (Kohlmeier and Ebenhöf 2007). However, these results are mainly based on data assimilated from other tidal flat systems, and there is therefore a need to complement and validate the model by data generated in the system itself. To better understand the biogeochemical characteristics of back-barrier tidal flat systems and to identify differences relative to open coast and estuarine tidal flat systems, it is important to examine these properties, not only by modeling approaches but also by measuring typical biogeochemical properties of the particulate and dissolved phases.

In order to examine whether, and if so, how the different hydrographic conditions at the inlets and in the basins affect biogeochemical properties at these contrasting locations, we investigated tidal dynamics of parameters associated with the particulate phase as well as the dissolved phase at the inlet and at a central station within the basin located in the main tidal channel of the Spiekeroog back-barrier tidal flat system, East Frisian Wadden Sea (Fig. 1). We hypothesized that the hydrographic conditions affect the particulate phase differently and more pronounced than the dissolved phase. SPM, particulate organic carbon (POC), chlorophyll, dissolved organic carbon (DOC) and manganese (Mn), numbers of free-living (FL) and particle-associated (PA) bacteria, and biomass production of heterotrophic bacteria were investigated in the entire water column during five tidal cycles typical for spring (April, May), summer (July), fall (November), and winter (January).

## 2 Materials and methods

Samples were collected in the year 2005 (11–12 January, 26–27 April, 19–20 July, 16–17 November) and 2006 (3–4 May) at hourly intervals from the surface, mid-depth (6–7 m) and 1 m above the channel bed (11–13 m) from aboard the RV Senckenberg. Stations were located in the inlet of the main tidal channel of the back-barrier area southwest of the barrier island of Spiekeroog (Otzumer Balje, station OB9; 53°44.9' N, 07°40.0' E; Fig. 1) and at a central station of the back-barrier basin near Neuharlingersiel (station OB18; 53°43.4' N, 07°43.3' E). In May 2006, only surface samples were collected. The mean tidal range is 2.6 m, and the mean depth at OB9 was 15 m. At OB18, the maximum depth varied, depending on the position of the ship. In January and November, it was 16 and 13 m, respectively, whereas in April and July, it was 11 m. Thirteen samples were collected per tidal cycle, by bucket at the surface, and by Niskin bottles mounted on a rosette sampler at mid-depth and 1 m above the channel bed. Temperature and salinity were determined by a CTD system (Model OTS 1500, ME Meerestechnik-Elektronik, Kiel, Germany). Subsamples for all further analyses were

**Fig. 1** Map of the study area with sampling sites (inlet, basin) in the back-barrier tidal basin of Spiekeroog Island, German Wadden Sea



immediately withdrawn and further processed. Sampling always started and ended at high tide. The exact sampling time was derived from a hydrographical model for the German Bight and the adjacent Wadden Sea (Bundesamt für Seeschifffahrt und Hydrographie, Hamburg, Germany) and water-level recordings from a time-series station (University of Oldenburg, <http://las.physik.uni-oldenburg.de/wattstation/>) located directly at station OB9. At this station, hydrographical, meteorological, and water chemistry data are being continuously recorded (Grunwald et al. 2007).

SPM, POC, and chlorophyll were determined as described in detail in Lunau et al. (2006). Briefly, SPM and POC subsamples were filtered onto precombusted and preweighed Whatman GF/F filters, rinsed with distilled water, and kept frozen at  $-20^{\circ}\text{C}$  until further analysis in the lab. Filters for SPM were dried and weighed again for gravimetric analysis, and POC subsamples were analyzed with a FlashEA 1112 CHN-analyzer (Thermo Finnigan). Before analysis, POC filters were exposed to hydrochloric acid fumes to remove carbonates. Samples for chlorophyll *a* (Chl *a*) and phaeopigments (phaeo) were filtered onto Whatman GF/F filters, immediately wrapped into aluminum foil, and kept frozen at  $-20^{\circ}\text{C}$  until spectrophotometric analysis in the shaded lab within 1 week. Filters were mechanically hacked and extracted in hot ethanol ( $75^{\circ}\text{C}$ )

for 1 h in the dark. Concentrations of chlorophyll *a* and phaeopigments, after acidification with HCl, were determined spectrophotometrically and calculated according to von Tuempling and Friedrich (1999).

Bacterial numbers were enumerated by epifluorescence microscopy after SybrGreen I staining according to Lunau et al. (2005). Subsamples were filled into 5 ml cryovials (Sarstedt) on board ship, preserved with 2% (final concentration) glutaraldehyde, and stored at  $-20^{\circ}\text{C}$  in the dark until further processing. For enumeration of FL bacteria, samples were centrifuged ( $\text{RCF}=190\text{ g}$ ) to separate bacteria from other particulates. An aliquot of 500 to 1,000  $\mu\text{l}$  of the supernatant was filtered through a black 0.2- $\mu\text{m}$  polycarbonate filter, stained with a SybrGreen I-moviol solution directly on a glass slide and enumerated thereafter. To determine total bacterial numbers, PA bacteria were detached from the particles by treatment with methanol and sonication and further processed as samples for FL bacteria. Numbers of PA bacteria were calculated as the difference of total minus FL bacteria. For further details, see Lunau et al. (2005).

Rates of bacterial production were determined by the leucine method (Simon and Azam 1989). Triplicates and a formalin-killed control were incubated with  $^{14}\text{C}$ -leucine ( $10.8\text{ GBq mmol}^{-1}$ , Hartmann Analytic, Germany) at a final concentration of 70 nM, which ensured saturation of

uptake systems. Five-milliliter samples were incubated in 8-ml plastic test tubes in the dark at in situ temperature for 1 h on a plankton wheel to avoid sedimentation. After fixation with 2% formalin, samples were filtered onto 0.45- $\mu\text{m}$  nitrocellulose filters (Sartorius, Germany) 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 radio-assayed by liquid scintillation counting. Biomass production was calculated according to Simon and Azam (1989) assuming a twofold intracellular isotope dilution. Standard deviation of triplicate measurements was usually <15%.

Dissolved Mn was analyzed by inductively coupled plasma mass spectroscopy in 25-fold diluted samples, prefiltered through 0.45- $\mu\text{m}$  surfactant-free cellulose acetate syringe filters, as described in Dellwig et al. (2007a) and Rodushkin and Ruth (1997).

Concentrations of DOC were determined after high-temperature oxidation by a multi N/C 3000 analyzer (Analytik Jena, Germany). Therefore, subsamples of 50 ml were filtered through precombusted GF/F filters on board ship and stored at 4°C in brown glass bottles after acidification to pH 2 by HCl until analysis within 1 week (Dellwig et al. 2007a).

Similarities between the parameters at both stations were tested by *t* test by comparing the tidal mean values of each parameter at both stations. The means were defined as significantly different when  $P < 0.05$  and as a different trend when  $P < 0.1$ . To examine tidal covariations at both stations, Pearson product-moment analyses were performed on tidal dynamics of each parameter at both stations. These analyses were performed using SigmaStat 2.03 (Systat).

### 3 Results

The tidal cycles in April and May were typical for the late and decaying spring bloom, the one in July for a summer situation, and those in November and January for late fall and winter, as shown by the concentration ranges of SPM and Chl *a*, which were comparable to previous years (Lunau et al. 2006). The tidal dynamics of the particulate phase (SPM, POC, and Chl *a*) typically exhibit maxima 1 h after the current velocity maximum at mean tide and minima at high and low tide (Lunau et al. 2006; Bartholomä et al. 2009). Tidal dynamics of the dissolved phase are much less pronounced than that of the particulate phase (Lunau et al. 2006; Dellwig et al. 2007b).

#### 3.1 Hydrography

The five tidal cycles exhibited pronounced differences with respect to temperature and salinity. Temperatures ranged

between  $\sim 7^\circ\text{C}$  in January and  $\sim 19^\circ\text{C}$  in July and salinities between 29.76 and 32.51 in November and April, respectively (Table 1). Mean differences of the tidal temperature and salinity between the inlet and basin remained always below  $0.9^\circ\text{C}$  and below 0.5, respectively.

#### 3.2 Suspended particulate matter

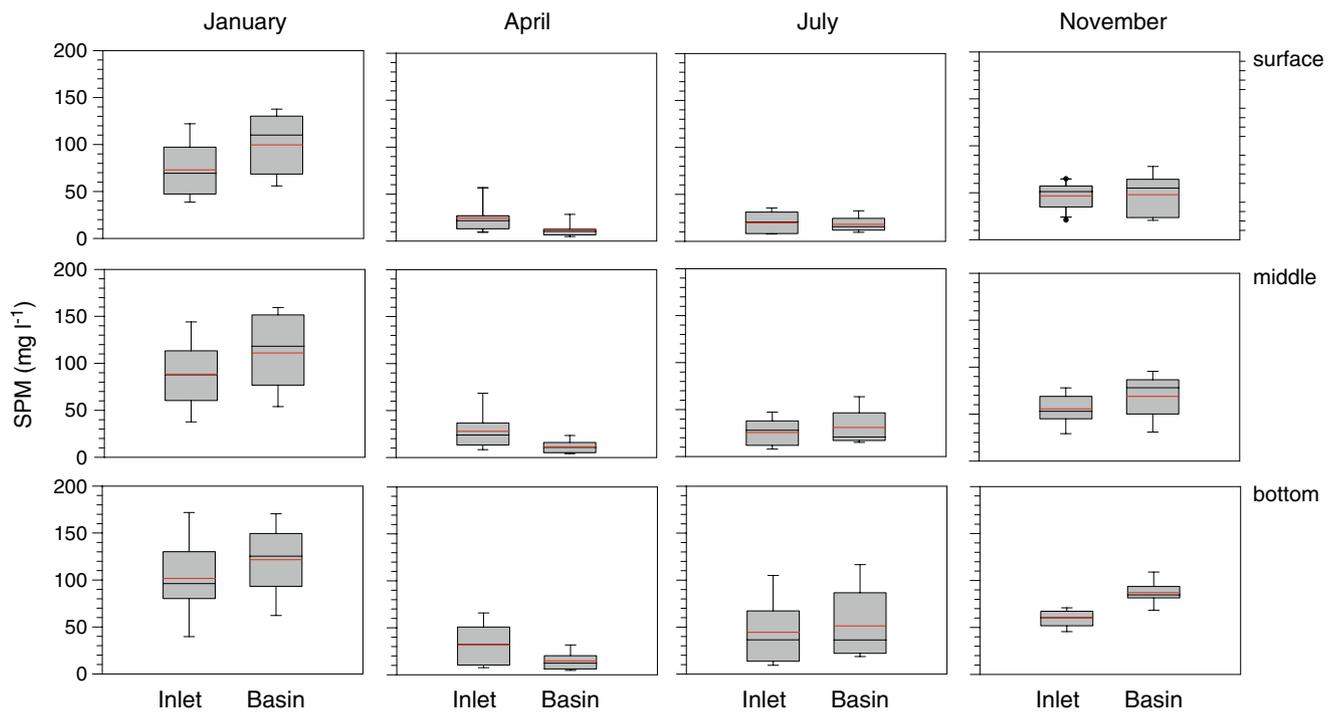
Concentrations of SPM were highest in January and much lower in April and July at both stations (Fig. 2). In January, April, and November, there were no vertical differences of SPM concentrations in the water column, whereas in July, concentrations near the bottom were substantially higher than further up in the water column. Tidal variations were highest in January and near the bottom in July. In January and November, SPM concentrations in the basin were higher and more variable than at the inlet. Mean concentrations in the basin, however, were only significantly higher than at the inlet in January at the surface and in November at the bottom (Table 2). By contrast, in April, SPM concentrations were significantly higher at the inlet than in the basin. Tidal dynamics of SPM at both stations were only positively correlated in July (Table 3) when tidal means were not significantly different at the two stations.

#### 3.3 Particulate organic carbon and C/N ratio

Concentrations of POC were highest in January and lowest in April (Fig. 3). As for SPM, vertical differences occurred only in July when POC concentrations near the bottom were substantially higher than in the water column above. Tidal variations were most pronounced in January and July. In January and November, and in contrast to SPM, POC concentrations at the inlet and in the basin were not significantly different (Table 2, Fig. 3). In April and May, POC concentrations were higher at the inlet than in the basin with significant differences at the surface and the mid-depth. In July, the situation was reversed with higher concentrations in the basin. Tidal dynamics of POC at both stations correlated in July and November at the surface and the mid-depth (Table 3).

**Table 1** Temperature and salinity at the inlet and basin stations in the back-barrier tidal basin of Spiekeroog Island during the tidal cycles studied in 2005

	Temperature ( $^\circ\text{C}$ )		Salinity	
	Inlet	Basin	Inlet	Basin
January	7.25	6.93	30.83	31.30
April	9.91	10.42	32.51	32.31
July	19.69	18.87	31.97	31.77
November	8.85	8.74	29.84	29.76



**Fig. 2** Box-whisker plots of the tidal means (*dotted line*) and median (*solid line*) of suspended particulate matter (SPM) at the surface, mid-depth (*middle*) and 1 m above the bottom (*bottom*) at the inlet and

basin stations in the back-barrier tidal basin of Spiekeroog Island, German Wadden Sea. *Error bars* indicate the 5 and 95 percentiles and the *boxes* the 25 and 75 percentiles

The C/N ratio varied between 6 and 11 with highest values and greatest variability in November at the inlet and lowest values in April in the basin. Significant differences between the two stations, however, only occurred in January

at the surface, in April near the bottom, in November at the mid-depth, and the bottom with lower values in the basin (Table 2). Tidal dynamics between the two stations covaried only in July at the surface, albeit inversely (Table 3).

**Table 2** Comparison of the tidal means of the parameters indicated between the inlet and basin stations in the back-barrier basin of Spiekeroog Island during the studied tidal cycles

		SPM	POC	C/N	Chl	Phaeo	Phaeo%	PA-Bac	FL-Bac	BP	Mn	DOC
Jan 05	Surface	0.036*	ns	0.003*	ns	ns	ns	ns	0.002*	ns	ns	
	Middle	ns	ns	ns	ns	0.032*	0.002*	ns	<0.001*	ns	ns	ns
	Bottom	ns	ns	ns	ns	0.014*	<0.001*	<0.001*	<0.001*	ns	ns	ns
Apr 05	Surface	0.008*	0.010*	ns	0.004*	ns	ns	0.038*	ns	ns	0.036*	
	Middle	0.010*	0.020*	ns	<0.001*	ns	ns	ns	0.071**	ns	ns	
	Bottom	0.041*	0.064**	0.004*	<0.001*	ns	ns	ns	0.026*	ns		
Jul 05	Surface	ns	0.065**	ns	<0.001*	0.003*	ns	<0.001*	ns	0.040*	ns	
	Middle	ns	0.004*	ns	<0.001*	0.001*	ns	<0.001*	ns	0.073**	ns	ns
	Bottom	ns	0.004*	ns	ns	0.007*	0.005*	<0.001*	ns	ns	ns	ns
Nov 05	Surface	ns	ns	ns	ns	ns	ns	0.031*	<0.001*	ns	ns	
	Middle	0.095**	ns	0.004*	0.006*	ns	ns	0.003*	0.008*	ns	ns	
	Bottom	<0.001*	ns	0.04*	0.055**	0.002*	ns	0.014*	<0.001*	ns	ns	
May 06	Surface	ns	<0.001*	ns	<0.001*	ns	0.021*	ns	0.001*	0.022*	<0.001*	

Given are the *P* values of Student's *t* test

ns non significant (*P*>0.10)

\**P*<0.05; \*\**P*<0.10

**Table 3** Correlation analysis of tidal dynamics of the parameters indicated at the inlet and basin stations in the back-barrier basin of Spiekeroog Island during the tidal cycles studied in 2005

	Depth	January	April	July	November
SPM	Surface	ns	ns	0.753	ns
	Middle	ns	ns	0.692	ns
	Bottom	ns	ns	0.846	ns
POC	Surface	ns	ns	0.672	0.631
	Middle	ns	ns	0,6	0.616
	Bottom	ns	ns	ns	ns
C/N	Surface	ns	ns	-0.562	ns
	Middle	ns	ns	ns	ns
	Bottom	ns	ns	ns	ns
Chl <i>a</i>	Surface	ns	0.748	0.797	ns
	Middle	ns	ns	0.798	ns
	Bottom	0.598	ns	ns	ns
Phaeopigments	Surface	ns	ns	ns	ns
	Middle	ns	ns	0.615	ns
	Bottom	ns	ns	0.771	ns
Phaeopigments (%)	Surface	ns	ns	ns	ns
	Middle	ns	ns	ns	ns
	Bottom	ns	ns	0.647	ns
FL Bacteria	Surface	ns	ns	ns	ns
	Middle	ns	ns	ns	ns
	Bottom	0.578	ns	ns	ns
PA Bacteria	Surface	ns	ns	0.718	ns
	Middle	ns	0.609	0.658	ns
	Bottom	ns	ns	ns	ns
BPP	Surface	ns	ns	0.640	ns
	Middle	ns	ns	0.700	ns
	Bottom	0.858	ns	0.780	ns
DOC	Surface	0.637	ns	ns	ns
	Middle	ns	ns	0.628	ns
	Bottom	ns	ns	ns	ns
Mn	Surface	0.725	0.898	ns	ns
	Middle	ns	0.960	0.714	ns
	Bottom	Ns	0.933	0.641	ns

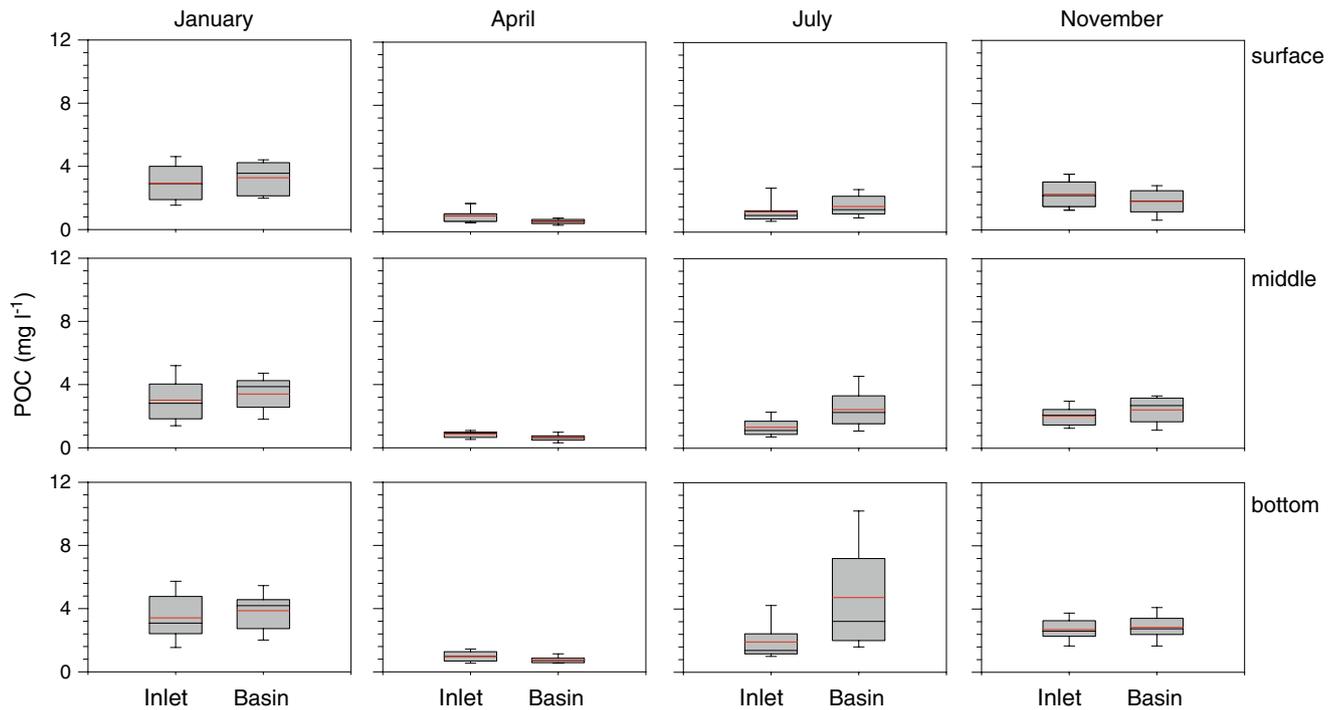
Given are the correlation coefficients of a Pearson Product-Moment analysis ( $P$  value  $\ll 0.05$ )

*ns* not significant

### 3.4 Chlorophyll

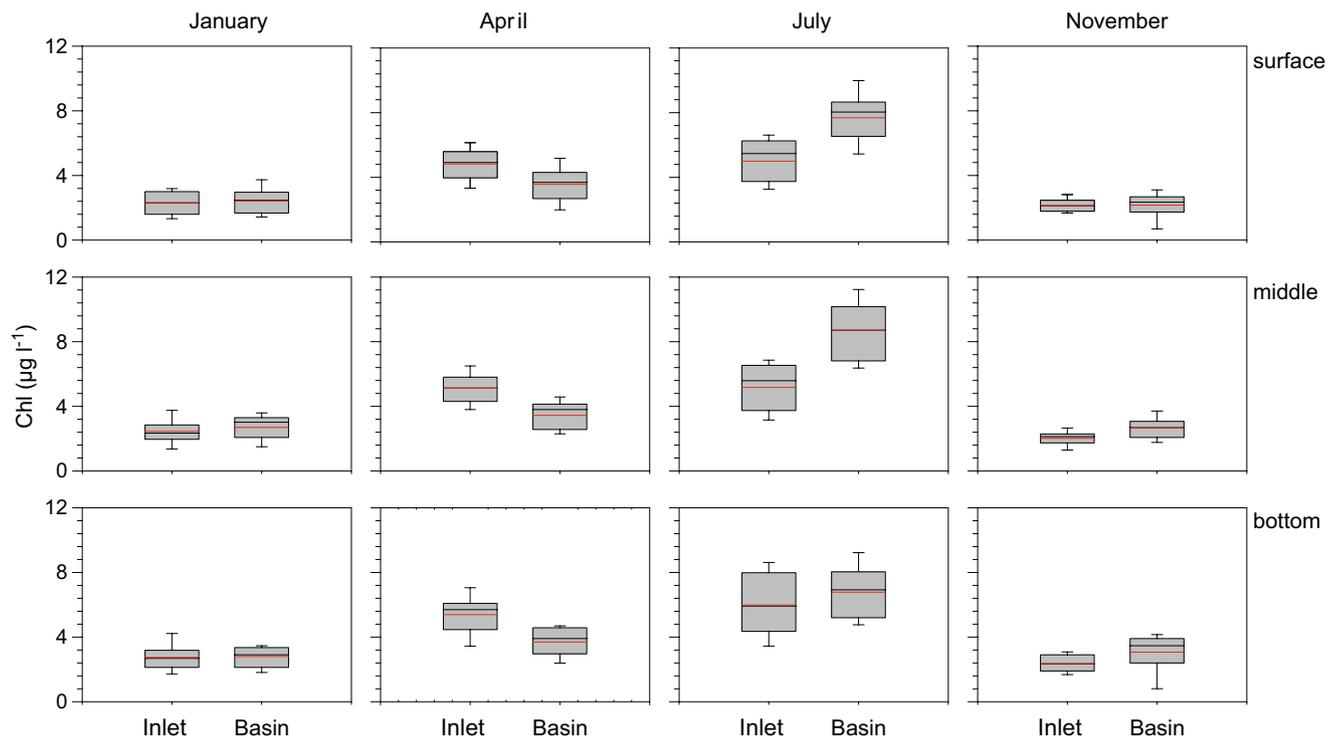
Seasonal dynamics of Chl *a* concentrations were substantially different than those of SPM and POC, with higher concentrations in April and July. In April, concentrations of Chl *a* were significantly higher at the inlet than in the basin in the entire water column and in May at the surface. In July, the situation was reversed, with significantly higher concentrations and maximum values occurring in the basin at the surface and mid-depth (Fig. 4, Table 2). In November, an even vertical distribution of Chl *a* occurred at the inlet, whereas enhanced Chl *a* concentrations occurred at mid-depth and near the bottom in the basin. Tidal dynamics at both stations covaried significantly in April and July at the surface and mid-depth (only July) and in January near the bottom (Table 3).

Patterns of phaeopigment concentrations in general covaried with those of Chl *a*. The phaeopigments, expressed as a percentage of total Chl, were 20–40% in April, 40–50% in July, except near the bottom where they ranged up to 70%, and reached 60–80% in January and November, indicating pronounced seasonal differences of the physiological state of the phytoplankton (Fig. 5). Significantly higher concentrations in the basin as compared to the inlet occurred in January at mid-depth and near the bottom, in July in the entire water column, and in November near the bottom (Table 2). In April, there were no significant differences between the two stations because of large tidal variations in the basin. Phaeopigments, expressed as a percentage of Chl, however, were only significantly higher in the basin than at the inlet in January at the mid-depth and near the bottom, in May at the surface,



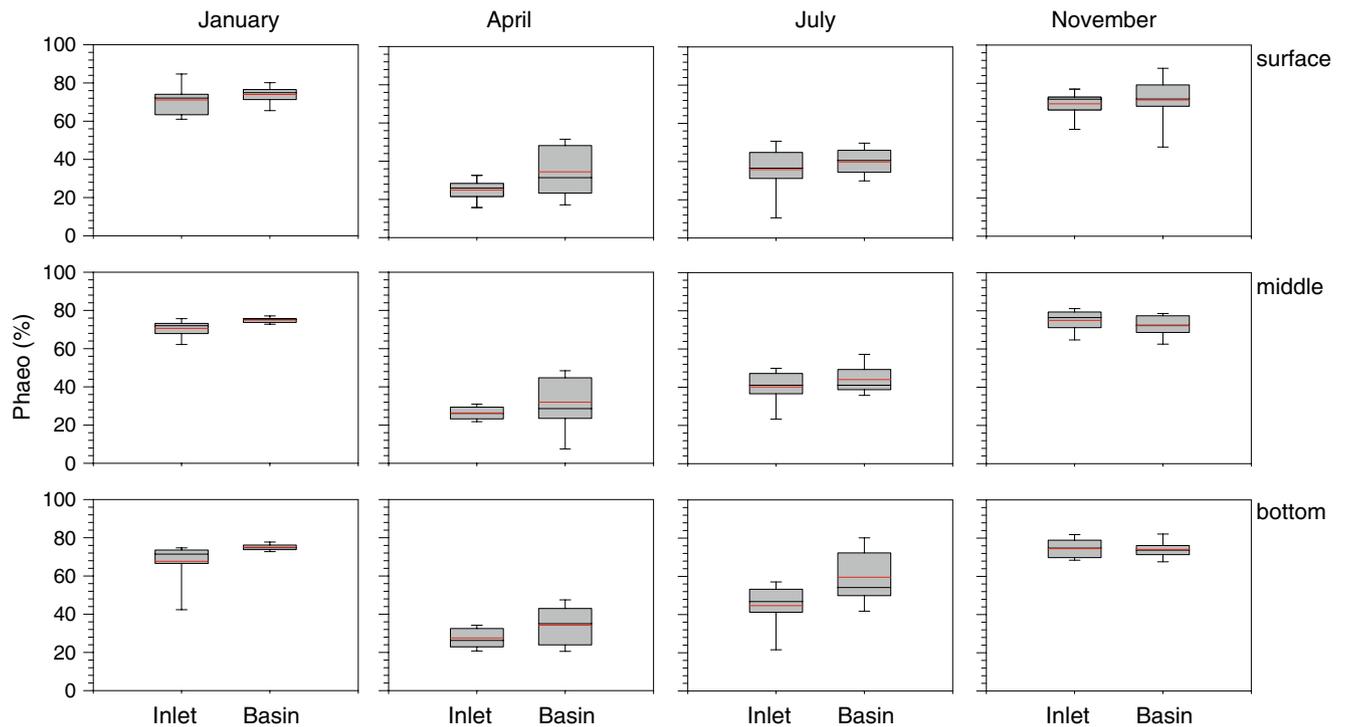
**Fig. 3** Box-whisker plots of the tidal means (*dotted line*) and median (*solid line*) of particulate organic carbon (POC) at the surface, mid-depth (*middle*) and 1 m above the bottom (*bottom*) at the inlet and

basin stations in the back-barrier basin of Spiekeroog Island, German Wadden Sea. *Error bars* indicate the 5 and 95 percentiles and the boxes the 25 and 75 percentiles



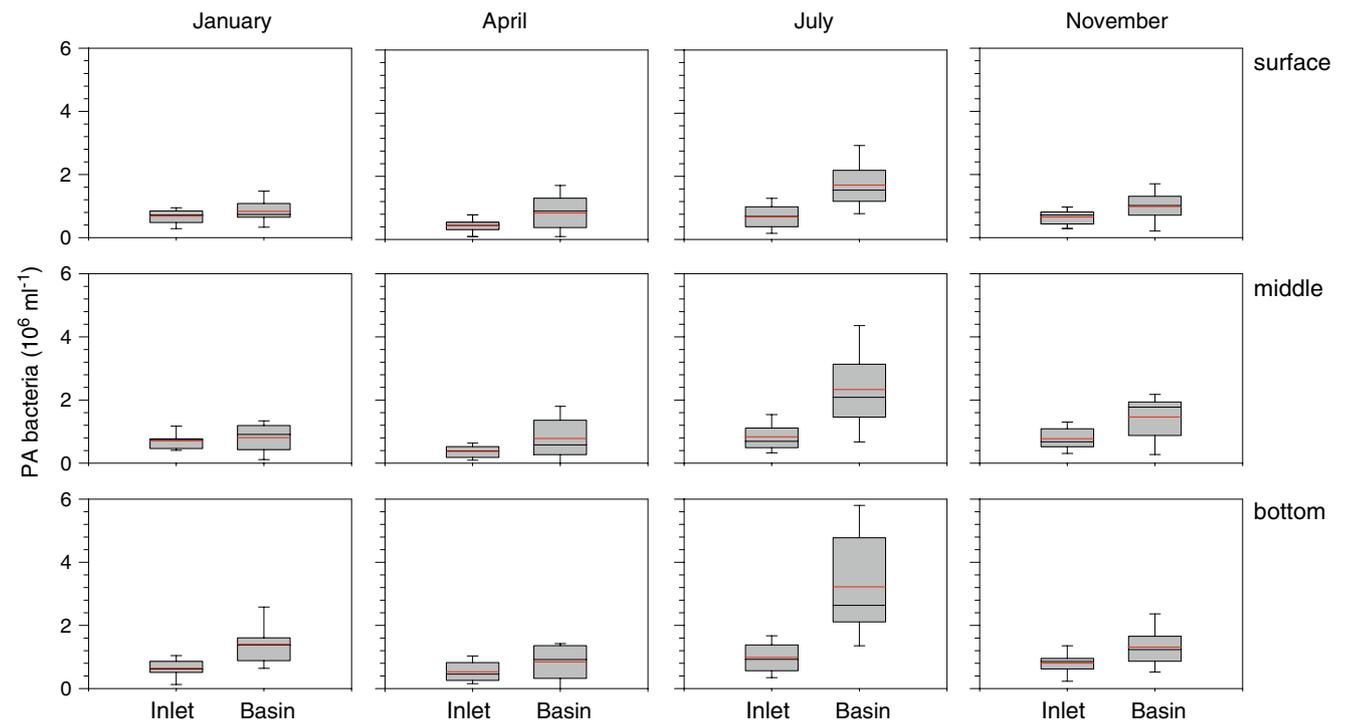
**Fig. 4** Box-whisker plots of the tidal means (*dotted line*) and median (*solid line*) of chlorophyll a (Chl) at the surface, mid-depth (*middle*) and 1 m above the bottom (*bottom*) at the inlet and

the back-barrier basin of Spiekeroog Island, German Wadden Sea. *Error bars* indicate the 5 and 95 percentiles and the boxes the 25 and 75 percentiles



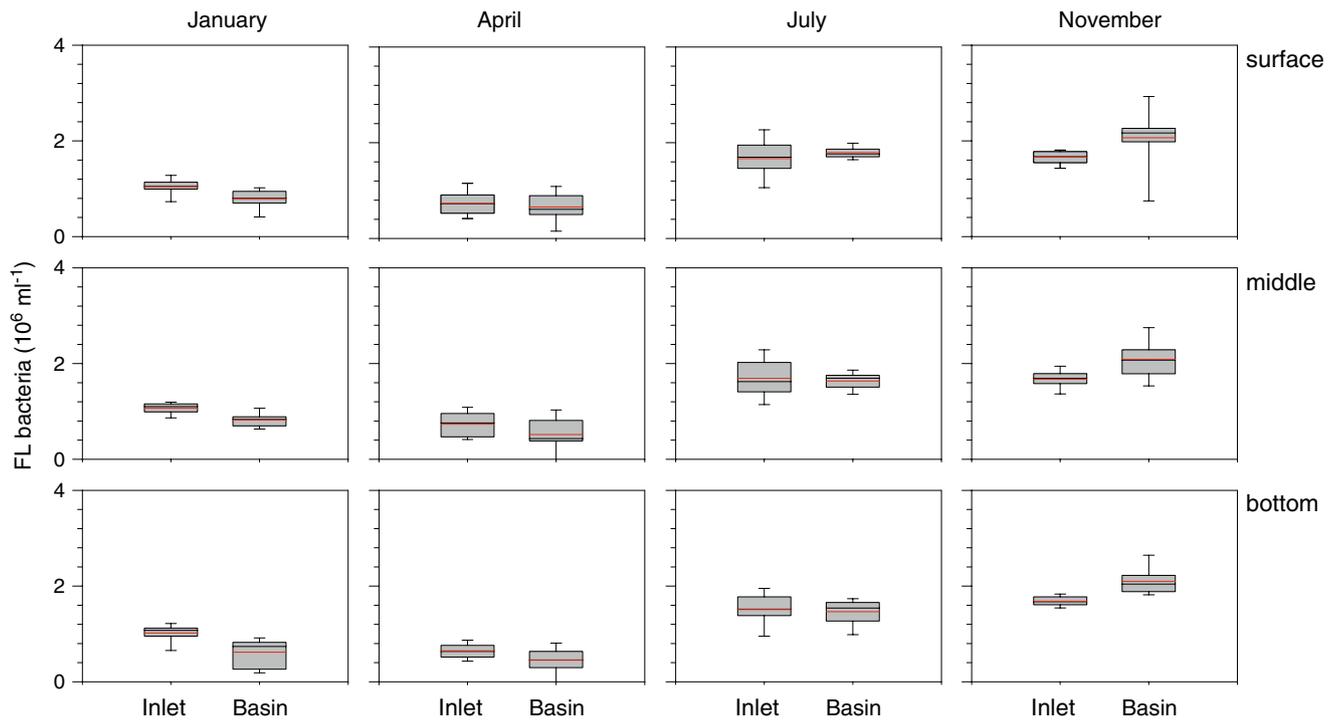
**Fig. 5** Box-whisker plots of the tidal means (*dotted line*) and median (*solid line*) of phaeopigments as percent of total chlorophyll at the surface, mid-depth (*middle*) and 1 m above the bottom (*bottom*) at the

inlet and basin stations in the back-barrier basin of Spiekeroog Island, German Wadden Sea. *Error bars* indicate the 5 and 95 percentiles and the *boxes* the 25 and 75 percentiles



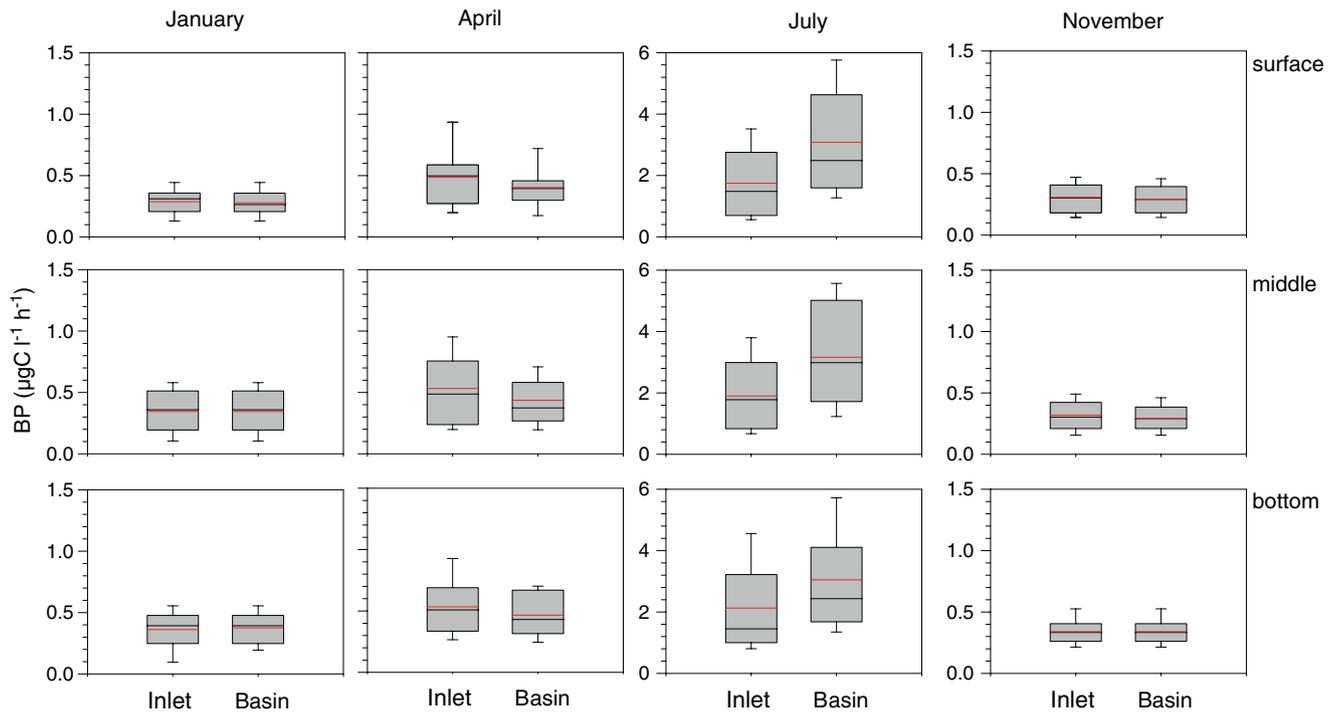
**Fig. 6** Box-whisker plots of the tidal means (*dotted line*) and median (*solid line*) of numbers of particle-associated bacteria (PA bacteria) at the surface, mid-depth (*middle*) and 1 m above the bottom (*bottom*) at

the inlet and basin stations in the back-barrier basin of Spiekeroog Island, German Wadden Sea. *Error bars* indicate the 5 and 95 percentiles and the *boxes* the 25 and 75 percentiles



**Fig. 7** Box-whisker plots of the tidal means (*dotted line*) and median (*solid line*) of numbers of free-living bacteria (FL bacteria) at the surface, mid-depth (*middle*) and 1 m above the bottom (*bottom*) at the

inlet and basin stations in the back-barrier basin of Spiekeroog Island, German Wadden Sea. *Error bars* indicate the 5 and 95 percentiles and the *boxes* the 25 and 75 percentiles



**Fig. 8** Box-whisker plots of the tidal means (*dotted line*) and median (*solid line*) of bacterial biomass production (BP) at the surface, mid-depth (*middle*) and 1 m above the bottom (*bottom*) at the inlet and basin stations in the back-barrier basin of Spiekeroog Island, German

Wadden Sea. Note the different scaling of the y-axes. *Error bars* indicate the 5 and 95 percentiles and the *boxes* the 25 and 75 percentiles

and in July near the bottom (Table 2). Tidal dynamics of phaeopigment concentrations and percentages at the two stations correlated only in July at mid-depth and the bottom (Table 3).

### 3.5 Particle-associated bacteria

Numbers of PA bacteria were highest in July in the basin and lowest in April at the inlet (Fig. 6). Numbers and the tidal variations in the basin were always higher than at the inlet and differences were significant in July and November in the entire water column, in January near the bottom, and in April at the surface (Table 2). Tidal dynamics of PA bacteria at the two stations covaried significantly in April at mid-depth and in July at the surface and mid-depth (Table 3).

### 3.6 Free-living bacteria

Numbers of FL bacteria exhibited different patterns than those of PA bacteria and any other parameter of the particulate phase. They were much higher in July and November as compared to January and April. In January, numbers of FL bacteria at the inlet were significantly higher in the entire water column than in the basin (Fig. 7, Table 2). This was also the case near the bottom in April

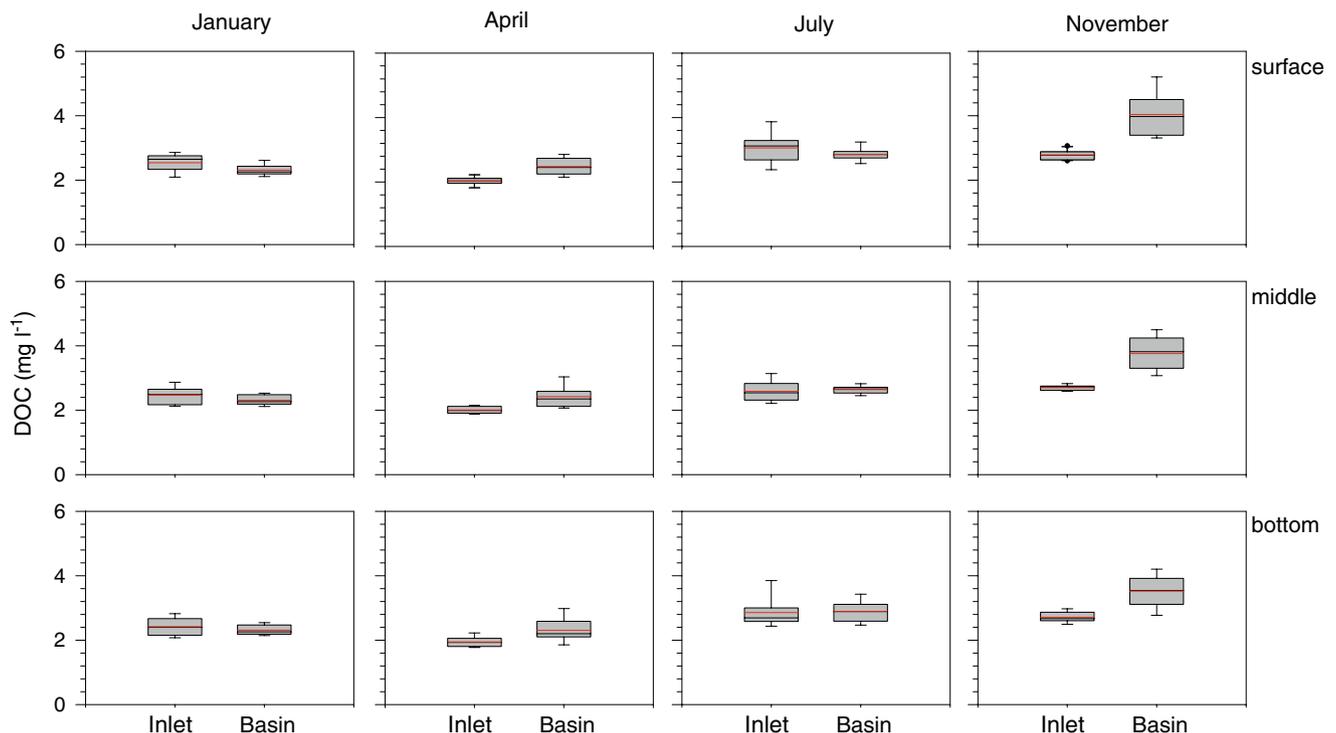
and at the surface in May 2006. In July, numbers at the inlet and in the basin were similar, whereas in November, numbers in the basin were significantly higher, reversing the situation in January. Tidal variations of FL bacteria were lower than those of PA bacteria. Numbers of FL bacteria did not covary tidally at the two stations, except in January near the bottom (Table 3).

### 3.7 Bacterial biomass production

Rates of bacterial biomass production were low in January and November and without vertical and spatial differences between the two stations (Fig. 8 and Table 2). In April, enhanced values and a higher tidal variability occurred at the inlet. In July, the highest values and the highest tidal variability were recorded, and tidal means were systematically higher in the basin than at the inlet. Differences, however, were only significant at the surface (Table 2). In July, tidal dynamics of BP rates at both stations correlated significantly (Table 3).

### 3.8 Dissolved organic carbon

Concentrations of DOC ranged between 2 and 4 mg C l<sup>-1</sup>, with lowest concentrations in April and highest concentrations in November and an even distribution in the entire



**Fig. 9** Box-whisker plots of the tidal means (*dotted line*) and median (*solid line*) of dissolved organic carbon (DOC) at the surface, mid-depth (*middle*) and 1 m above the bottom (*bottom*) at the inlet and

basin stations in the back-barrier basin of Spiekeroog Island, German Wadden Sea. *Error bars* indicate the 5 and 95 percentiles and the *boxes* the 25 and 75 percentiles

water column (Fig. 9). In January and July, both stations exhibited similar concentrations, whereas in April and November, concentrations in the basin were significantly higher than at the inlet (Table 2). Significant correlations between tidal dynamics of DOC concentrations at the two stations existed only in January at the surface and in July at mid-depth (Table 3). As numbers of FL bacteria, seasonal dynamics of DOC did not reflect those of any parameter of the particulate phase (Fig. 9).

### 3.9 Dissolved manganese

Tidal mean concentrations of dissolved Mn ranged between 48 nM in January and 331 nM in April. For further details, see also Dellwig et al. (2007a, b). Despite these pronounced seasonal variations, concentrations at the two stations were not significantly different, except in April and May, at the surface when concentrations in the basin were higher (Table 2). Tidal dynamics at both stations, however, were significantly correlated in January at the surface, in April in the entire water column, and in July at the mid-depth and near the bottom (Table 3).

## 4 Discussion

To our knowledge, no comparable detailed studies from other tidal flat systems exist, in which biogeochemical properties of at least two stations displaying different hydrography and morphometry, and being located in rather close proximity to each other, have been compared. Admiraal et al. (1985) investigated the seasonal dynamics of bacterioplankton and phytoplankton growth in the Ems–Dollart estuary, an embayed and much wider tidal flat system than the one we studied but only with a single sample per week at incoming tide during the growing season. In the same system, tidal dynamics of SPM were only studied on a transect from the outer estuary to the River Ems (Van Leussen 1996), showing a clear gradient of increasing SPM concentrations upstream with highest values in the turbidity maximum zone. In the North Frisian Wadden Sea, Poremba et al. (1999) studied tidal dynamics of SPM, chlorophyll, phytoplankton primary production, and bacterioplankton abundance and production at two stations, however, of similar hydrographic properties but in tidal areas 20 km distant from each other. These authors did not find significant differences of the tidal means of the parameters measured, neither at the surface nor in the bottom layer.

Our results of comparing two stations of contrasting hydrography in the back-barrier tidal flat system of Spiekeroog Island show that distinct differences in biogeochemical properties in the water column exist between the

inlet and the basin in particular seasons. The basis for this comparison were the tidal means and covariations of the various parameters representing typical properties of the particulate, i.e., settling phase, and the dissolved, i.e., non-sinking phase, including FL bacteria. Most striking was that in July, Chl *a* and bacterial biomass production exhibited higher values in the basin, whereas in April, these parameters were enhanced at the inlet while being particularly low in the basin. In late fall and winter, i.e., November and January, differences were much less pronounced than during the growing season, and restricted mainly to SPM and PA bacteria, exhibiting higher values in the basin. FL bacteria, DOC, and dissolved Mn, representing the dissolved and non-sinking phase, exhibited different patterns and much less differences between the two stations, indicating that processes related to these variables, such as hydrolysis and uptake of dissolved organic matter by FL bacteria, were controlled by different factors than PA biogeochemical processes at the two stations.

In order to understand these differences at the two stations, it is important to determine the local sediment composition, hydrographic similarities and dissimilarities, and how biogeochemical properties respond to these features. The sediment properties at both stations are rather similar. Only at locations of generally lower kinetic energy within this basin is the sediment of much finer grain size (Chang et al. 2006). The tidal currents and general circulation field of the back-barrier system of the East Frisian Wadden Sea is very stable (Stanev et al. 2003), and storm events may only perturbate the system for short periods. The mean residence time of the water in the Spiekeroog back-barrier area is around six to eight tidal cycles, i.e., 3–4 days (E. Stanev, personal communication). The residence time of the water in the basin is longer than at the inlet (Kohlmeier and Ebenhöf 2007) where it is more readily mixed and thus diluted with North Sea water. Hence, growth rates of the phytoplankton, PA and FL bacteria, size, density, sedimentation, and resuspension rates of aggregated SPM and POC affect the residence time of these parameters in the basin. High biological activities, e.g., phytoplankton biomass and rates of bacterial biomass production, associated to the particulate phase in the water column, high aggregation rates of SPM, and rapidly sinking aggregates exceeding shear-induced resuspension, keep the SPM and organic matter in the basin. By contrast, low biological activity, in particular, associated with the dissolved phase, low aggregation rates of SPM, and the dominance of non-sinking particles such as small phytoplankton cells, bacteria and micro-aggregates, and high shear and turbulence favor large-scale mixing and the transport and exchange of SPM, POC, and suspended microbial cells between the basin and the inlet and further out to the coastal North Sea.

A situation with high biological activity associated with the particulate phase is typical for summer, as recorded in July when concentrations of Chl *a*, POC, phaeopigments, numbers of PA bacteria, and rates of bacterial biomass production were higher in the basin than at the inlet, indicating more favorable conditions for phytoplankton growth and bacterial decomposition of organic matter in the basin. In addition to the features mentioned above, these conditions include continuous inputs of inorganic nutrients at low tide from the freshwater drainage system of the hinterland through a tidal sluice at Neuharlingersiel, remineralization of organic matter near the bottom and in the sediment, and release of nutrients from the sediment (Dellwig et al. 2007a, b). As indicated by Chl *a*, autotrophic processes in the basin were more enhanced toward the surface, whereas decomposition processes were more enhanced near the bottom, as shown by enhanced concentrations of POC, phaeopigments, and PA bacteria. Resuspension of settled organic material certainly contributed to these high values near the bottom. At the inlet, less favorable conditions and tidal mixing with North Sea water obviously resulted in lower PA biogeochemical activities and no significant vertical difference in these properties. Interestingly, numbers of FL bacteria and concentrations of DOC were similar at both stations, indicating that the dissolved and non-sinking particulate phases were well mixed and decoupled from PA processes. It is noteworthy, though, that despite these differences at the two stations, tidal dynamics of most parameters at both stations covaried, as shown by quite a few positive correlations in July (Table 3). In other seasonal situations, much less positive correlations were found.

During late fall and winter, the seasons of low biological activity, differences between the two stations were mainly related to SPM, phaeopigments, DOC, and PA and FL bacteria. SPM concentrations were generally enhanced but more so in the basin than at the inlet. The mean size of suspended aggregates is significantly smaller in this part of the year than during the growing season, and numbers of microaggregates in the water column are higher by one order of magnitude (Lunau et al. 2006; Bartholomä et al. 2009). In November, concentrations of SPM and DOC and numbers of FL and PA bacteria in the basin were higher than at the inlet, either in the entire water column or below the surface. For SPM and PA bacteria, these differences are presumably related to the generally high abundance of small aggregates in the water column and are rather similar to the situation in January. For phaeopigments, the difference probably points to resuspension of stale algal debris. For FL bacteria and DOC, the situation in November and January is different. The enhanced DOC concentrations in November are presumably a result of sustained and substantial DOC release from the sediment,

continuously decreasing in the course of the unproductive season and leading to an even distribution across the entire tidal flat system in winter. In November, numbers of FL bacteria appear to reflect the enhanced DOC concentrations, both appearing to be still enhanced because the months of September and October were rather warm as compared to previous years. In January, the reduced numbers of FL bacteria were presumably a result of scavenging bacteria utilizing the SPM, which exhibited the highest concentrations of the entire study at that time.

In April, concentrations of SPM, POC, and Chl *a* were higher at the inlet than in the basin, and SPM and POC exhibited the lowest concentrations recorded in this study. These patterns were opposite to those found in the other seasonal situations when values in the basin were higher or not different (POC). These data were collected near the end of the spring bloom, i.e., toward its decline and sedimentation. Settling conditions for aggregated SPM and POC in the basin obviously were more favorable than at the inlet, leading to a higher elimination of SPM and POC from the water column and resulting in an efficient retention of nutrients and accumulation of organic matter in the basin. Interestingly, in this situation, the processes between the inlet and the basin appeared to be rather uncoupled, as only Chl *a* at the surface and PA bacteria at mid-depth exhibited significant correlations (Table 3). Obviously, in such a situation of high sedimentation and low resuspension rates, biogeochemical microbial processes in the water column of the basin are not favored, being instead shifted more toward the sediment. According to our observations in the course of several years, such situations are rather rare and mainly occur in spring but even then for short periods only. The mineralization of organic matter and release of mineralized nutrients from the sediment into the water column obviously occurs with a time lag of several weeks (Dellwig et al. 2007b).

These results indicate that, except for a short period in spring, the hydrographic and ecological conditions favor SPM-associated biogeochemical processes in the basin during the growing season, including growth of the phytoplankton, and presumably also of the phyto-benthos, and accumulation of organic matter and, in particular, its microbial decomposition in the water column and the sediment. The general tidal patterns of aggregation, settling, and resuspension of particulates and of bacterial turnover of organic matter, however, are rather similar in the entire system (Lunau et al. 2006; Lemke et al. unpublished results) but do not necessarily covary at both stations. The energetic conditions and the current field lead to a fractionation of the settling material and structuring the sediment (Chang et al. 2006), which is also a result of the gradient in biogeochemical activity and tidal dynamics from the inlet to the basin and further toward the shallow

tidal flat areas. Our findings provide good evidence for the assumption that the general productivity of back-barrier tidal flat systems is favored as compared to open tidal flat systems due to the retaining properties with an enhanced residence time of the water masses and accumulation and settling out of particulate organic matter and SPM. The fact that the Wadden Sea largely consists of back-barrier tidal flats certainly contributes to its high productivity and its utmost importance as a resting and overwintering place for migrating water fowl.

PA bacterial communities play an important role in the biogeochemical processes, which exhibit the differences between the two stations. Therefore, it would be interesting to examine whether the composition of these communities also exhibits differences between the stations. Even though we do not have experimental evidence for such differences, some evidence exists, from various investigations at different stations in the Spiekeroog tidal basin and other places of the East Frisian Wadden Sea, that these communities are rather similar throughout the Wadden Sea. Applying denaturing gradient gel electrophoresis of polymerase chain reaction-amplified 16S rRNA gene fragments with primers of various specificities, no pronounced tidal or spatial but rather seasonal differences at various sampling sites have been found (Rink et al. 2007, 2008; Stevens et al. 2005; Selje and Simon 2003). Pronounced differences between the composition of PA, FL, and surface sediment-associated bacterial communities indicate that the composition of these communities is controlled by different environmental factors.

As a conclusion, our results show that properties related to the particulate phase in the water column, such as SPM, POC, phytoplankton, and PA bacteria, show pronounced differences at the inlet and in the central basin of the Spiekeroog tidal flat system. These differences point to enhanced microbial activity in the basin during summer and reduced activity only during a short period in the late phase of the spring phytoplankton bloom. The enhanced residence time and retaining properties of the back-barrier tidal basin favor microbial processes associated with the particulate phase. Properties associated with the dissolved phase and non-sinking microaggregates exhibit fewer differences between the two stations, indicating that they are differently controlled in that they escape the accumulation and retaining properties of the back-barrier tidal basin.

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