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ORIGINAL ARTICLE

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Tidal impact on planktonic primary and bacterial production in the German Wadden Sea

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Abstract Tidal variation of biological parameters was studied at three anchor stations in selected inlet channels of the northern German Wadden Sea in May and July 1994. Concentrations of bacteria, chlorophyll a and suspended matter as well as primary and bacterial production were assessed over a period of 25 h in the surface and in the bottom water. Diurnal variation in primary production was found both under in situ light conditions and under constant illumination. Tidal turbulence caused the introduction of detritus, bacteria and pigments from the sediment into the water column. The impact of sediment resuspension was most evident in the bottom water, leading to tidally oscillating bacterial production rates which were high during high stream velocity and low during the slack times. Estimations of the areal daily phytoplankton production and corresponding bacterial carbon demands were unbalanced. Primary production accounted for only 25–45% of the total bacterial carbon requirement. This discrepancy is due to the shallow euphotic depth in the Wadden Sea, allowing net primary production only in the upper 2–3 m of the water column, while the relatively high levels of bacterial activity do not show a vertical decline. Assuming that the specific biological activities in the water columns over the tidal flats are similar to those found in the inlet channels, it was found that production processes dominate in shallow areas whereas decomposition processes dominate in the deep channels. Moreover, the predominance of heterotrophic processes in the inlet channels means that additional organic carbon sources must contribute to the heterotrophic metabolism in the deep parts of the Wadden Sea, and that the horizontal flux of material is important in this turbid mesotidal ecosystem.

Key words Tidal variation · Wadden Sea · Production and decomposition

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Introduction

The Wadden Sea differs from other land/ocean interfaces in its melting pot-like function for products of terrestrial, limnetic and marine processes. Strong tidal currents, high wind speeds and a shallow water column are the main physical vectors that stimulate fast transport, dispersion and mixing of materials deriving from the various sources of biological production and decomposition in the region. With respect to primary production, the effect of high nutrient inputs by terrestrial runoff is counteracted by high turbidity levels deriving from intense sediment resuspension due to tidal turbulence and by fast flushing rates, at least in the estuarine parts of the region. In contrast to this, the significant amounts of suspended organic matter that enter the system from adjacent areas, as well as the high nutrient concentrations, may stimulate bacterial decomposition. Some authors emphasize that the frequently occurring summer maxima of orthophosphate in the Wadden Sea – at a time when other nutrients are locally depleted – are an expression of excess remineralization of imported organic material (Jonge and Postma 1974; Hesse et al. 1995). The balance between primary production and bacterial carbon demand may therefore be a key parameter, resulting from the fundamental physicochemical properties and scales which characterize the Wadden Sea system. This key ratio may be a useful indicator in the evaluation of the ecological status of the Wadden Sea by future monitoring programs, such as the Trilateral Monitoring and Assessment Program of the Wadden Sea (CWSS 1992). However, planktonic catabolism and anabolism are, especially in the Wadden Sea, subject to strong temporal and spatial variability. With respect to short temporal scales, interfering phases of diurnal and tidal cycles, as the variable constellation of the daily sun cycle versus tidal period (water depth and turbulence), may considerably influence the relative intensity of those processes.

These problems present difficulties for present monitoring programmes because of missing covariance and lack of adequate information. The case study presented

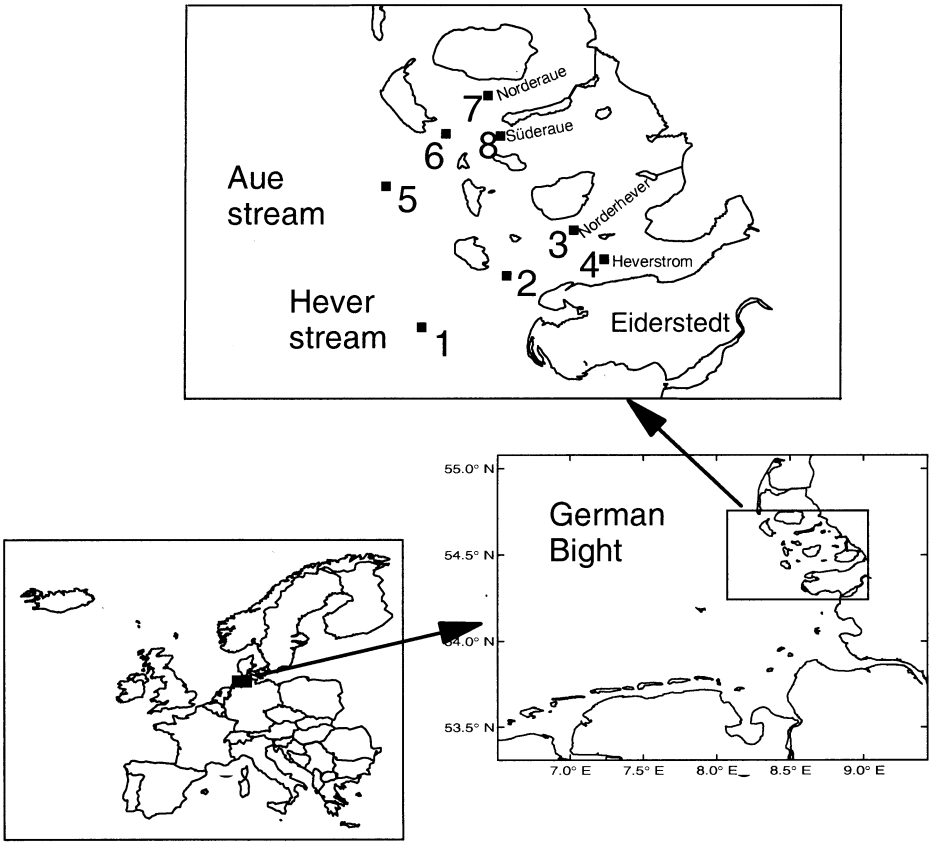

Fig. 1 Study site; station 4 (Heverstrom) was sampled on 13 May, station 3 (Norderhever) on 16 July, and station 7 (Norderaue) on 17 July

here focuses on the impact of the tidal and diurnal cycle on bacterial activity and primary production in the Wadden Sea. The aim of this study was to improve the sampling strategy in order to gain data which are both relevant and reliable. Since tidal variations can be detected only by performing repeated measurements on a short time scale, we conduct our experiments with hourly samplings over a period of 25 h. As far as we know, this is the first time that such measurements have been performed with such a high frequency in the Wadden Sea. Based on data from three tidal experiments performed in spring and summer, an estimation of the balance between autochthonous primary formation of organic material and bacterial consumption as well as an extrapolation over the whole Wadden Sea were carried out.

Materials and methods

The positions of the stations are shown in Fig. 1. The first experiment was conducted on 13/14 May 1994 at station 4 in the Heverstrom from aboard the R.V. Littorina. Average water depth at the sampling site was about 13 m. The second and third experiments were carried out on 16/17 and 17/18 July 1994, respectively, at station 3 in the Norderhever and station 7 in the Norderaue, respectively, from aboard the R.V. Victor Hensen. Both stations were, on an average, about 20 m deep. Comparing these locations with the whole Wadden Sea, the sampling sites lay at relatively deep positions. The mean water depth of the study area fluctuates between 3.22 m (low water) and 3.92 m (high water) (S. Dick, BSH Hamburg, personal communication).

Water samples were taken every hour from 1-m water depth and from the bottom layer (2 m above the seafloor) over a period of 25 h using a 5-l Niskin bottle. Subsamples for biological and suspended matter (SPM) analysis were immediately taken, assuring a homogeneous suspension of particulate material by slightly shaking the Niskin sampler.

Subsamples (100 ml) for bacterial counts were placed in brown-glass bottles, preserved with formaldehyde (final conc. 0.8%), and stored dark and cool. Bacterial numbers were determined using epifluorescence microscopy according to Daley and Hobbie (1975). About 2–5 ml of the sample was filtered through a 0.2-µm Poretics black polycarbonate membrane (VKI, Denmark). The cells on the filter were stained with a 10% acridine orange solution (Merck) for 3 min and washed with citrate buffer (0.056 M Na-citrate, 0.056 M NaOH, 0.044 M HCl, pH 4). Twenty random fields were counted per sample under 1250-fold magnification.

For chlorophyll a (Chl-a) determinations, 100–1000 ml of the sample was filtered through a Whatman GF/C filter. Filters were immediately deep-frozen and stored at –20°C until analysed according to the spectrophotometric method of Lorenzen (1967). Determination of suspended matter (SPM) was carried out by filtering 200–1000 ml of the sample through a pre-weighed Whatman GF/C-filter. Filters were washed with distilled water in order to remove salt and then they were deep-frozen. Prior to weighing, filters were dried in a desiccator.

Primary production (PP) measurements were restricted to the surface samples. Subsamples of 30 ml were put in polycarbonate tubes (Oak Ridge centrifuge tubes, Nalgene), supplemented with 2.7 µCi $NaH^{14}CO_3$ and incubated. One set of tubes was used for incubation under simulated in situ conditions on deck. Tubes were fixed in a box cooled to in situ temperatures by running seawater and exposed to natural sunlight. Another set of tubes was installed in a laboratory incubator under in situ temperatures controlled by running seawater and exposed to artificial light (OSRAM D-light) to give a PAR intensity of 150 µE m^{-2} s^{-1} inside the tubes. For

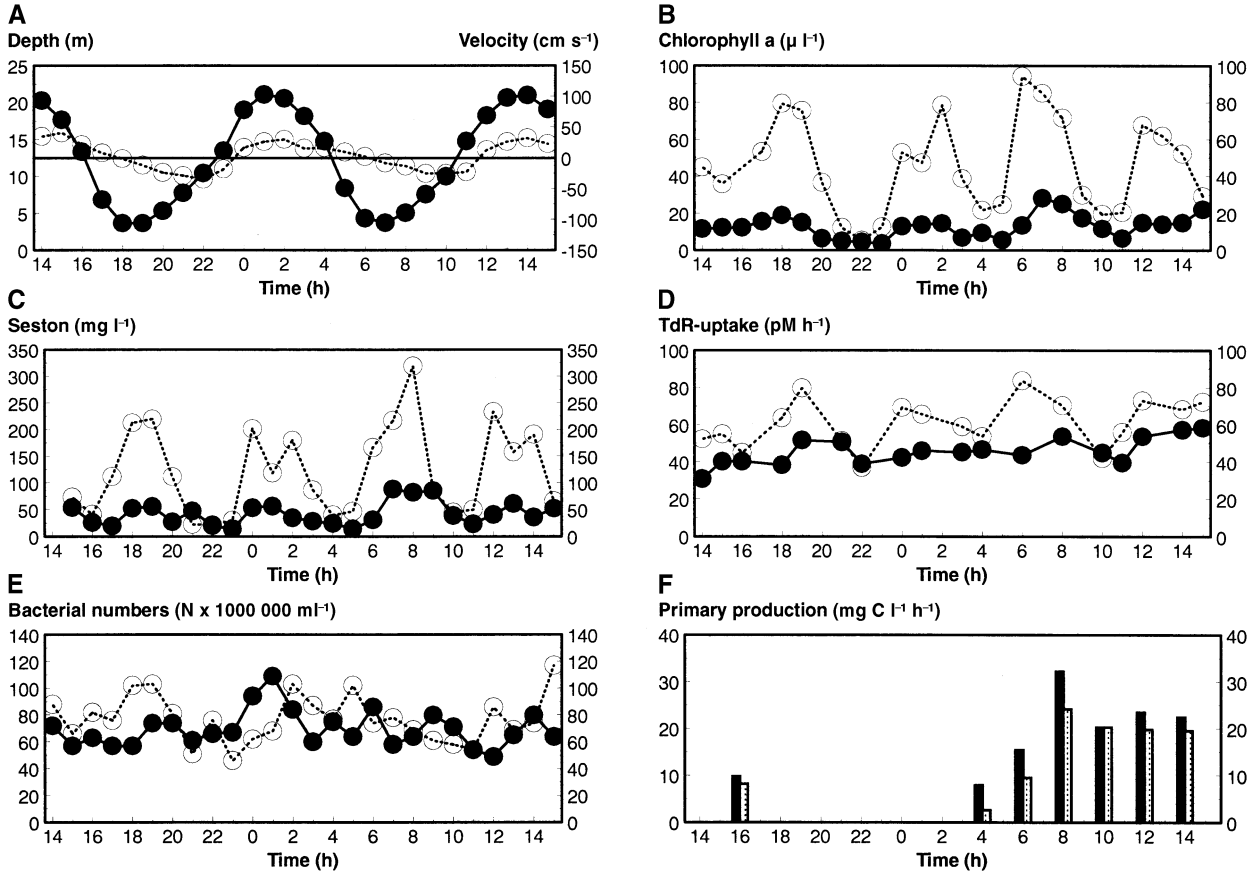

Fig. 2A–F Heverstrom in May 1994. Variation of: **A** water depth (*dotted line*) and stream velocity at the surface (*solid line*); **B** chlorophyll-a concentration; **C** SPM concentration; **D** TdR-uptake; **E** bacteria concentration; and **F** primary production. *Solid lines* in **B–E** show data of surface samples and *dotted lines* show data of bottom water samples. *Filled bars* in **F** show results of assays performed under constant light conditions, and *open bars* show those of experiments run under in situ illumination

each measurement, a dark bottle served as control and was later used as t_0 value. After an incubation time of 3 h, the sample was filtered through a 0.2-µm cellulose acetate filter. The filter was washed twice with 10 ml of prefiltered seawater (0.2 µm), which was adjusted to pH 4, and transferred to 6-ml vials. After addition of the scintillation cocktail (Lumagel, Packard), a 2-day storage allowed for dissolution of the filters. Scintillation was counted in a Packard LSC. Particulate PP was determined taking alkalinity into account. Dark bottle blanks were subtracted. Daily PP was calculated by summing up the values of the 24 h of a day.

For determination of bacterial production (BP), subsamples of 10 ml were supplemented with (^{3}H)-methyl-thymidine (TdR purchased from NEN Dupont, specific activity 80 mCi µmol^{-1}) to a final concentration of 5.95 nM (the pre-checked saturation concentration) and incubated in a water bath under in situ temperatures on board. Each determination consisted of three replicates and one formaldehyde-fixed control. After 1 h, incubation was stopped by adding 200 µl of 35% formaldehyde. In the laboratory, samples were filtered through 0.2-µm polycarbonate membranes. The filters were rinsed once with cooled, pre-filtered (0.2 µm) seawater and five times with 2 ml of a cooled solution of 5% trichloroacetic acid (TCA) before being transferred to 6 ml vials. Scintillation counting was done in a Packard LSC after a 2-day storage in the scintillation cocktail (Lumagel, Packard). Calibration with a known amount of labelled thymidine allowed the calculation of incorporated thymidine. Bacterial carbon biomass production was estimated by using a conversion factor of 1.5×10^{18} cells mol^{-1} thymidine (Admiraal et al. 1985) and 20 fg C cell^{-1} (Lee and Fuhrmann 1987). Daily BP was calculated by summing up the hourly assessments of the day.

Data for stream velocities were provided by W. Schönfeld (BSH, Hamburg), who used a dispersion model, taking the current meteorological and thermodynamic conditions during the experiment into account. The model is described elsewhere (Dick and Schönfeld 1996). Since we expected that stream velocity would be the best indication of the tidal phases, possible tidal variations of plankton data were checked by testing the significance of Pearson product-moment correlations between the data.

Results and discussion

Tidal dynamics of the plankton parameters are shown in Figs. 2–4. Corresponding mean values as well as maxima and minima are listed in Table 1. Most values showed variations of >50% around their mean. When compared with the other inlets, the Heverstrom (station 4) always exhibited the highest bacterial abundance, Chl-a and SPM concentrations. The same holds true for the magnitude of differences between data from the surface and bottom water. This phenomenon may be explained by a higher erosion intensity in the Heverstrom due to the shallower water depth (13 m) at the station compared with the other sampling sites (20 m) situated in the Norderhever (station 3) and Norderaue (station 7).

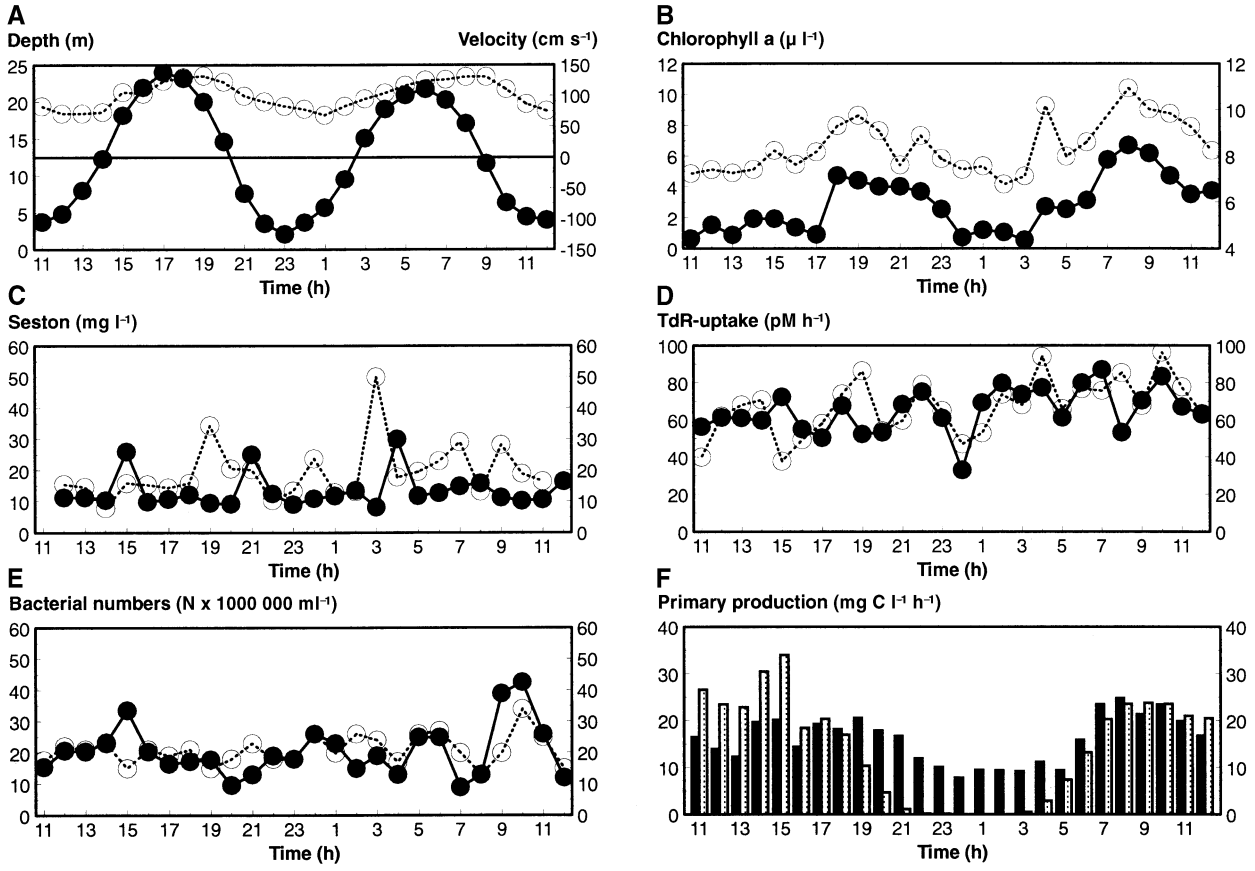

Fig. 3A–F Norderhever in July 1994. See legend to Fig. 2 for further details

Table 1 Variability of planktonic data during the anchor stations: maxima, minima and means ±SD

	Heverstrom (May 1994)		Norderhever (July 1994)		Norderaue (July 1994)	
	Sampled water layer		Sampled water layer		Sampled water layer	
	Surface	Bottom	Surface	Bottom	Surface	Bottom
Bacterial numbers (100,000 N ml^{-1})						
Maximum	109	117	43	26	37	42
Mean	69±13	77±18	21±8	21±5	24±8	26±8
Minimum	49	46	9	13	16	14
TdR incorporation (pM h^{-1})						
Maximum	59	84	87	96	89	97
Mean	46±7	61±13	65±12	67±15	59±14	74±15
Minimum	31	37	33	38	28	38
Chl-a (µg l^{-1})						
Maximum	28.2	85.1	8.5	10.4	14	18.2
Mean	13±6	46±25	6±1	7±2	8±2	10±3
Minimum	3.6	5.4	4.4	4.7	5.2	5.7
SPM (mg l^{-1})						
Maximum	88	220	30	50	20	50
Mean	43±21	118±82	13±6	19±9	13±4	29±12
Minimum	14	22	8	8	5	9
Illumination	Constant	In situ	Constant	In situ	Constant	In situ
PP (µg C l^{-1} h^{-1})						
Maximum	32	24	25	31	49	78
Mean	19±9	15±8	16±5	14±11	26±9	24±23
Minimum	8	3	8	0	15	0

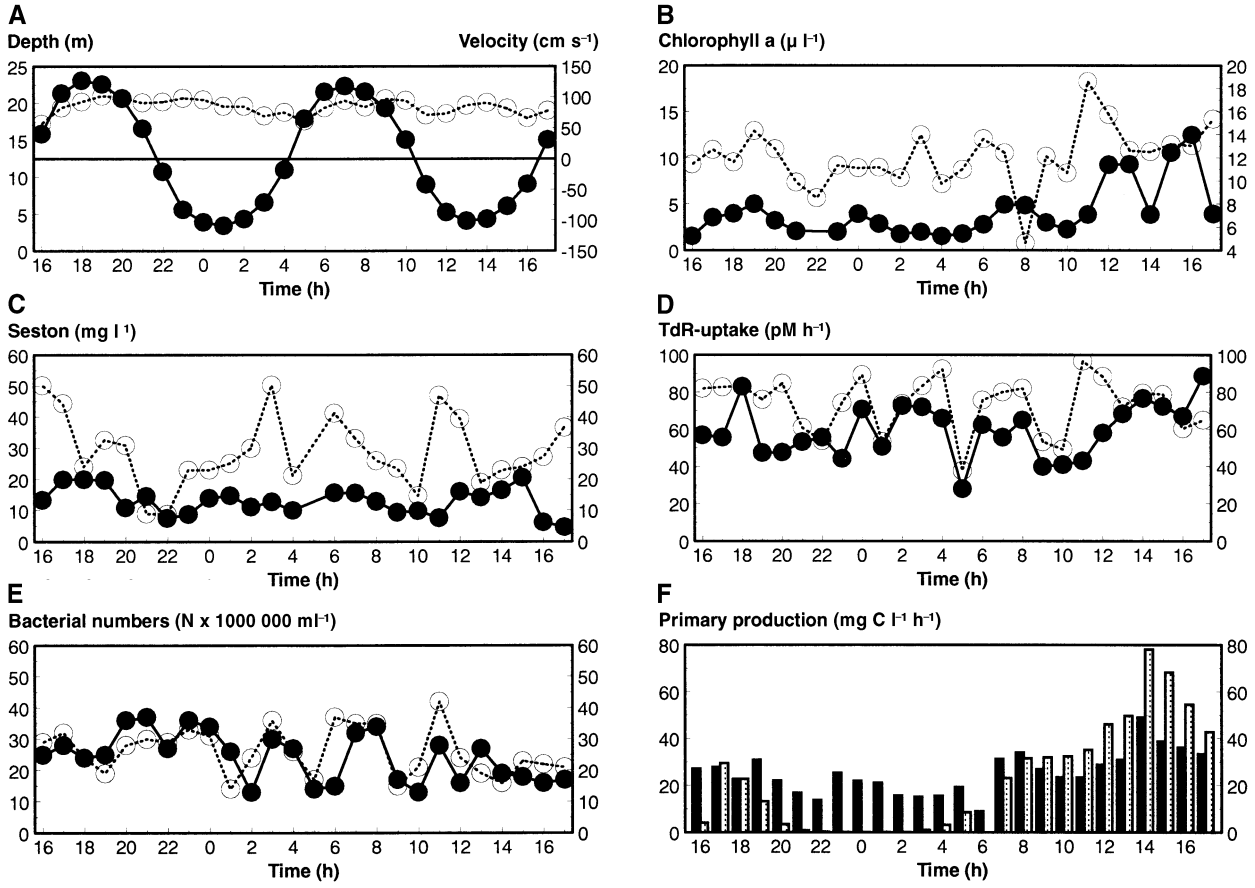

Fig. 4A–F Norderaue in July 1994. See legend to Fig. 2 for further details

Two types of oscillation were observed: a diurnal one for PP and a tidal one for SPM and other planktonic parameters.

Diurnal variation

A clear diurnal day/night oscillation in PP was observed in the incubation series under natural (in situ) illumination on deck, as was expected, but it was not expected that this diurnal rhythm would also be displayed under constant light conditions. While the mean production rates in the Heverstrom, Norderhever and Norderaue were 19, 16 and 26 µg C l^{-1} h^{-1} during daytime, the rates declined to 8, 9 and 15 µg C l^{-1} h^{-1} during night despite unaltered light conditions. This means a reduction in activity of 42–58%. The observed variation cannot merely be a biomass signal but is probably either a sign of light stress to the dark-adapted algae sampled in the night or is due to cell division happening during night. In contrast to production rates, Chl-a curves did not show any diurnal rhythm. Night ratios of Chl-a and PP, as measured in the incubator, decreased by about 20–50% compared to daytime values (data not shown here), although light was not the limiting factor in these series.

One has to be aware, however, that in a dynamic system like the Wadden Sea, algal composition may change rapidly, due to advection. It may therefore be that changes in the population structure as well as light inhibition contributed to the observed diurnal variation in specific PP. The knowledge of possible shifts in the parameters of the P-vs-I curve would have contributed to a better understanding.

In contrast to phytoplankton production, BP did not exhibit any diurnal rhythm, indicating that it is not influenced by short-term changes of photosynthetically produced material.

Tidal variation

Stream velocity

The strength and direction of the stream velocities indicated the tidal phases. The stream velocities at the bottom (not shown in the figures) were generally lower than at the surface (in the Norderhever approx. 30% of the surface value, 42% in the Heverstrom, and 93% in the Norderaue) and the slack lagged at the bottom always slightly behind the surface (Norderaue: approx. 5 min, Norderhever: 15 min, Heverstrom: 60 min). Compared with velocity, the water depth indicated the tidal phases far less. The position of the ship was obviously not stringently fixed but circled around the anchor line.

Table 2 Pearson product-moment correlation (r) for the parameter set of the Heverstrom (station 4) in May 1994. *n.s.* Not significant ($P>0.05$); *n.d.* not determined

		Velocity	SPM	Bacteria	Chl-a	TdR uptake	PP
Velocity	Surface		0.52	n.s.	0.56	n.s.	n.s.
	Bottom		0.77	n.s.	0.84	0.77	n.d.
SPM	Surface	0.52		n.s.	0.56	n.s.	0.88
	Bottom	0.77		n.s.	0.84	0.77	n.d.
Bacteria	Surface	n.s.	n.s.		n.s.	n.s.	n.s.
	Bottom	n.s.	n.s.		n.s.	n.s.	n.d.
Chl-a	Surface	0.56	0.77	n.s.		n.s.	0.86
	Bottom	0.84	0.42	n.s.		0.60	n.d.
TdR-uptake	Surface	n.s.	n.s.	n.s.	n.s.		n.s.
	Bottom	0.77	n.s.	n.s.	0.60		n.d.
PP	Surface	n.s.	0.88	n.s.	0.86	n.s.	
	Bottom	n.d.	n.d.	n.d.	n.d.	n.d.	

Suspended matter (SPM)

The SPM content in the bottom water was mostly closely related to the tidal phase. High values generally occurred in periods between high and low tide, when high absolute values of stream velocity were found. An exception was the Norderhever, where nearly every correlation between the parameter measured was absent. It is likely that the SPM variation in the other inlets was caused by sediment resuspension and by selective sedimentation of heavier material during slack. On the other hand, Cadée (1982) performed similar experiments in the Marsdiep (Dutch Wadden Sea) and found no correlation between current velocity and SPM. However, his study was restricted to surface samples, whereas the data set shown here includes also bottom water samples, which most probably show a stronger impact by erosion processes than surface samples. So, for monitoring purposes one should keep in mind that the deeper the depth at which a sample is taken, the stronger the possibility of an intense site-specific erosion.

Chlorophyll a

The Chl-a concentration showed a high affinity to the SPM content in the Heverstrom (Table 2), as can be traced by the highly significant correlation coefficients at this station. It can therefore be concluded that the pigment variation in the water of this site is mainly determined by tidally induced resuspension events from the sediment. In the other two channels, these relationships were less distinct or even absent (Tables 3, 4), which may be explained by a lower erosion intensity at these stations.

Primary production

Chl-a showed high correlation with PP (incubation under constant illumination) at all stations including the Norderhever. This relationship indicates that most of the pigments were actively involved in photosynthesis and that nutrient limitation was unlikely to occur. This is in accordance with the dissolved nutrient status during the experiments (U. Brockmann, IBCM Hamburg, personal communication). The different ratios of PP versus Chl-a (Heverstrom about 1.5; Norderhever about 2.7; Norderaue about 3.6) were probably caused by changes in the species composition of the algal assemblages. Mesoscale patchiness, spatially separated algal blooms and short-term tidal variation of species composition in the Wadden Sea have been reported several times (Hesse et al. 1992, 1995).

Bacterial numbers

While bacterial cell concentrations in the Heverstrom and the Norderhever did not exhibit any sound relationship with other parameters (Tables 2, 3), some significant correlation with SPM and bacterial activity (TdR-uptake) existed in the bottom water of the Norderaue (Table 4), whereas corresponding correlations were missed for the surface water. This suggests that sediment resuspension has caused the bacterial fluctuations by introducing benthic bacteria into the water column.

Bacterial activity

TdR uptake was correlated with Chl-a in the bottom water samples of each station (Tables 2–4), while no correlation was found in the surface water. Therefore it may seem, at first sight, that the observed fluctuations in bacterial activity were due to an increase in bacterial biomass as a result of tidally induced resuspension (see above). However, this cannot be the only reason, because bacterial concentrations varied much less than did the SPM content, and the TdR-uptake was less correlated with bacterial numbers than with the SPM concentration. Moreover, the correlation between TdR-uptake and bacterial numbers (and SPM) was significant only in the Heverstrom (Table 2) but not in the other channels. So, it is more likely that the specific TdR-uptake activity had been stimulated. Wainright (1987) observed an increase in bacterial growth and mean biovolume in mesocosms with artificial resuspension as well as in studies with intact sediment cores from 6- and 18-m depth (Wainright 1990).

Table 3 Pearson product-moment correlation (r) for the parameter set of the Norderhever in July 1994. See legend to Table 2 for further details

		Velocity	SPM	Bacteria	Chl-a	TdR uptake	PP
Velocity	Surface		n.s.	n.s.	n.s.	n.s.	n.s.
	Bottom		n.s.	n.s.	n.s.	n.s.	n.d.
SPM	Surface	n.s.		n.s.	n.s.	n.s.	n.s.
	Bottom	n.s.		n.s.	n.s.	n.s.	n.d.
Bacteria	Surface	n.s.	n.s.		n.s.	n.s.	n.s.
	Bottom	n.s.	n.s.		n.s.	n.s.	n.d.
Chl-a	Surface	n.s.	n.s.	n.s.		n.s.	0.69
	Bottom	n.s.	n.s.	n.s.		0.62	n.d.
TdR-uptake	Surface	n.s.	n.s.	n.s.	n.s.		n.s.
	Bottom	n.s.	n.s.	n.s.	0.62		n.d.
PP	Surface	n.s.	n.s.	n.s.	0.69	n.s.	
	Bottom	n.d.	n.d.	n.d.	n.d.	n.d.	

Table 4 Pearson product-moment correlation (r) for the parameter set of the Norderaue in July 1994. See legend to Table 2 for further details

		Velocity	SPM	Bacteria	Chl-a	TdR uptake	PP
Velocity	Surface		n.s.	n.s.	n.s.	n.s.	n.s.
	Bottom		n.s.	n.s.	n.s.	n.s.	n.d.
SPM	Surface	0.68		n.s.	n.s.	n.s.	n.s.
	Bottom	n.s.		0.41	0.58	0.54	n.d.
Bacteria	Surface	n.s.	n.s.		n.s.	n.s.	n.s.
	Bottom	n.s.	0.41		n.s.	0.57	n.d.
Chl-a	Surface	n.s.	n.s.	n.s.		n.s.	0.57
	Bottom	n.s.	0.58	n.s.		n.s.	n.d.
TdR uptake	Surface	n.s.	n.s.	n.s.	n.s.		n.s.
	Bottom	n.s.	0.54	0.57	0.60		n.d.
PP	Surface	n.s.	n.s.	n.s.	0.57	n.s.	n.s.
	Bottom	n.d.	n.d.	n.d.	n.d.	n.d.	n.d.

Observations that bacteria inhabiting the bottom water layer demonstrate a higher activity were reported by Ritzrau and Graf (1992). Poremba (1995) found that microbial stimulation, most probably caused by sediment resuspension, reached up to 60 m above the bottom of a 3700-m-deep submarine canyon. In the present study, the correlation coefficients between TdR uptake and SPM decrease in the order of stations from Heverstrom to Norderaue and Norderhever, according to the decreasing amount of SPM resuspended at the different sites of investigation.

Balance of production and decomposition

The balance between autochthonous PP of organic material and bacterial decomposition may be a key process for the functional evaluation of the subsidiary Wadden Sea system. The data were converted to common units using a number of assumptions. The measured PP values were increased by 10% to account for dissolved production. Losses due to algal respiration – generally estimated to be in the range of 10% (cf. Karrasch et al. 1996) – were not considered.

The bacterial carbon demand (BCD) was calculated by assuming a 50% growth efficiency and doubling the value of BP (Jahnke and Craven 1995). Since lower efficiencies of about 25% have also been reported for the Wadden Sea (van Duyl and Kop 1988), the magnitude of the BCD reported here should represent a lower limit rather than an overestimation. We prefer an overestimation of PP and an underestimation of decomposition in view of the statement at the end of this section.

Since there was no pronounced vertical gradient in BP, it was possible to calculate water column production using the correspondent mean values between the surface layer and the bottom water. PP in the euphotic zone was estimated (Cadée and Hegemann 1974, 1979), i.e. by multiplying the surface value by a factor of 1.5 and the corresponding Secchi-depth.

In May, particulate PP in the Heverstrom increased from 0 during night to 24 µg C l^{-1} h^{-1} at noon (Table 1), resulting in a total PP of 230 µg C l^{-1} day^{-1} in the surface water (Table 5). Daily areal PP for the whole water column was estimated to be 345 mg C m^{-2} day^{-1} (Table 5). Mean BP rates at the same station accounted for 54 pM TdR h^{-1} (46 pM h^{-1} at 1-m depth and 61 pM h^{-1} at the bottom; see Tables 1 and 5), corresponding to a daily BP of 40.8 µg C l^{-1} day^{-1}. Based on these data, a daily areal BCD in the whole water column of about 985 mg C m^{-2} was calculated.

In July, particulate photosynthetic production amounted to 25 µg C l^{-1} h^{-1} in the Norderhever and 49 µg C l^{-1} h^{-1} in the Norderaue. Total PP at the surface was estimated to be 372 µg C l^{-1} day^{-1} in the Norderhever and 591 µg C l^{-1} day^{-1} in the Norderaue, corresponding to a daily PP in the whole water column of 558 and 887 mg C m^{-2}, respectively. The mean BP rates were nearly the same at both sites, accounting for 67 pM TdR h^{-1} or 48 µg C l^{-1} day^{-1}, which resulted in

Table 5 Daily primary production and bacterial production

	Heverstrom (May 1994)	Norderhever (July 1994)	Norderaue (July 1994)
Particulate primary production in the surface water ($\mu g\ C\ l^{-1}\ h^{-1}$)[a]	8.7	14.1	22.4
Total primary production in the surface water ($mg\ C\ m^{-2}\ day^{-1}$)[b]	230	372	591
Total pelagic primary production in the water column ($mg\ C\ m^{-2}\ day^{-1}$)[c]	345	558	887
Bacterial production (mean of water column and day) ($fmol\ TdR\ ml^{-1}\ l^{-1}\ h^{-1}$)[d]	54	66	67
($mg\ C\ m^{-2}\ day^{-1}$)[e]	493	992	930
Total bacterial consumption in the water column ($mg\ C\ m^{-3}\ day^{-1}$)[f]	82	85	96
($mg\ C\ m^{-2}\ day^{-1}$)[g]	985	1984	1860

[a] Determined in samples from 1-m depth during shipboard incubations under in situ illumination and temperature; calculated means of the 24 measurements of 1 day
[b] Taking additional 10% for produced and exuded dissolved organic carbon into account
[c] Assuming that the whole pelagic production is the production at 1 m depth×1.5 Secchi depth – here 1 m (mean)
[d] Mean of measurements from the headwater and from 2 m above the bottom
[e] Taking a mean water depth of 12.8 m in the Heverstrom, 20.9 m in the Norderhever, and 19.5 m in the Norderaue
[f] Assuming an efficiency of 50%
[g] Calculated for the whole water column (depth according to footnote e)

an estimation of daily carbon demand of about 2000 mg C m^{-2}.

Although a number of crude estimations had to be made, these data suggest a considerable imbalance between autochthonous production and decomposition. On a daily basis, total BCD in the whole water column was higher by a factor of 3–4 than PP. The latter was just sufficient to fuel the BCD down to a water depth of 4.2 m (Heverstrom) to at best 9.2 m (Norderaue), representing only 25–45% of the actual BCD in the water column of these tidal channels. The discrepancy proliferates, if one keeps in mind: (1) that bacteria preferably use the dissolved phase of PP; (2) that other heterotrophic compartments (e.g. zooplankton and fungi) have not been taken into account in the budget; and (3) that growth efficiencies of 50% range at the upper end of bacterial efficiencies reported (usually between 10 and 60%; Jahnke and Craven, 1995).

The idea that the coastal margin is a region of net heterotrophy, in which respiration exceeds PP, has been assumed before (Smith and Mackenzie 1987; Jong et al. 1993; Deegan et al. 1994), and Smith and Hollibaugh (1997) spoke about a “donor system” at shallow sites compared to a “recipient system” at deep ones. In the present study, the sink of organic carbon via bacteria alone exceeds the local source of primary material. As a consequence, this imbalance has to be balanced by additional carbon sources contributing to the food requirements of the bacterial community in the deep Wadden Sea. This additional material may be derived from terrestrial discharge or be imported into the system by tidal action from adjacent sites of more intense phytoplankton growth. These sites may be situated in the less turbid and stratified (in summer) open German Bight, and part of the organic matter produced may be advected into the Wadden Sea. However, there may also be a transport of materials with the ebb stream, which drains the inner parts of the Wadden Sea. These shallow areas may be net producers and exporters of primary material, because light and nutrient conditions favour planktonic and benthic PP, starting here early in the season, while pelagic bacterial concentrations per square meter are much less than in the channels.

Conclusion

Variation of SPM in inlet channels of the northern German Wadden Sea is closely related to the tidal phase, especially in the bottom water, indicating resuspension processes. Together with sediment particles, Chl-a is introduced into the water column. Resuspension affected bacterial numbers and bacterial activity predominantly at the shallowest site in the Heverstrom. Sampling in monitoring programs, usually focusing on water quality assessment and long-term trends, should therefore be performed at either high tide or low tide in order to keep variations in tidal disturbance to a minimum. In the assessment of PP under simulated conditions (incubation under constant light), water sampled during night can lead to underestimations; therefore the natural endogenous day/night rhythms of photosynthesis should also be taken into account. The imbalance between PP and BP suggests that the heterotrophic compartments in the tidal channels are sustained by a considerable import of additional organic material entering the system from seaward sources, from terrestrial runoff or from the very shallow inner parts of the Wadden Sea. Especially the latter site is held to be an area of net production because more favourable light and nutrient conditions stimulate PP with regard to heterotrophic activity. So, if the specific biological activities of the planktonic organisms over the tidal flats are similar to those in the channels, the Wadden Sea can be structured in compartments with respect to the ratio of these two processes.

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