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ORIGINAL ARTICLE

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Distribution patterns of bacterioplankton and chlorophyll-a in the German Wadden Sea

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Abstract In a first synoptic evaluation, the temporal and spatial distribution of bacterioplankton and chlorophyll-a were determined in the German Wadden Sea. Three surveys were undertaken in winter, spring, and summer of 1994 using up to eight ships simultaneously between the river Ems and Sylt island. Despite intensive hydrodynamic mixing of the Wadden Sea water, spatial gradients were obvious. The abundance of bacterioplankton ranged from 0.4 to 26×10^5 ml^{-1} and chlorophyll-a varied between <0.1 and 79 $\mu g\ l^{-1}$. In winter, relatively homogeneous distribution patterns of both parameters with small gradients were found. Highest chlorophyll-a values connected with a highly patchy structure were observed in spring, while in summer both total chlorophyll-a values and the complexity of the distribution pattern had decreased. In contrast, bacterial numbers increased steadily from January to July with the highest bacterial densities and greatest patchiness observed in summer. Moreover, in some regions of the Wadden Sea, a trophic succession of algae as carbon producers and bacteria as consumers was evident. Correlation analysis verified the relationship between bacteria and chlorophyll a, indicating bottom-up control of bacterial abundance in the northern part of the German Wadden Sea. Since the observed regression slope is remarkably low (0.12–0.46) compared to literature values (0.5–0.8), we suggest that the link between phytoplankton and bacteria found here is a special characteristic of the Wadden Sea as a transition zone between the coastal region and the outer North Sea.

Key words Bacterioplankton · Distribution patterns · Wadden Sea

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Introduction

Early models of the ecological structure of the marine environment suggested that all primary production would either be consumed by herbivorous zooplankton or sink to the sea floor (Steele 1974). These early models ignored the impact of microbes. Recent models not only emphasize that bacteria constitute the largest part of the total biomass in the sea but also stress their role as consumers of dissolved organic matter deriving from exudation or autolysis of phytoplankton (Azam et al. 1983). Thus, it was predicted that control of bacterial numbers in the sea is not usually mediated by top-down control of bacterivorous grazing (McQueen et al. 1986; McManus and Peterson 1988), but mainly attributed to bottom-up control of the nutrient supply derived from primary production (Cole et al. 1988; Billen et al. 1990; Ducklow and Carlson 1992). Numerous studies along the coasts of Belgium (Lancelot and Billen 1984; Billen and Fontigny 1987) and Holland (Laanbrooek et al. 1985; Veldhuis et al. 1986), in Lake Constance (Simon and Tilzer 1987), in the northern North Sea (Wanderschneider 1983), and in the North Atlantic (Ducklow et al. 1993) have shown that the development of phytoplankton blooms and bacterial cell density are tightly coupled, and that the equation [log bacterial number ($N\ ml^{-1}$)=5.87+0.78 log chlorophyll a ($\mu g\ l^{-1}$)] fits well (Bird and Kalff 1984), although bacterial multiplication usually lags behind phytoplankton development by about 1 week. Again, this general prediction is possibly inaccurate for the Wadden Sea, because the vast majority of studies have been conducted in lakes or in the open ocean. The C budget of these so-called autotrophic systems is mainly fuelled by autochthonous primary production (De Jong et al. 1993). Microbial degradation depends on this autochthonously produced material.

These autotrophic systems are distinguished from heterotrophic systems, whose budgets receive significant inputs of exogenous food sources from rivers, the atmosphere or the adjacent sea. While an autotrophic system is clearly seasonally triggered by levels of irradiance and

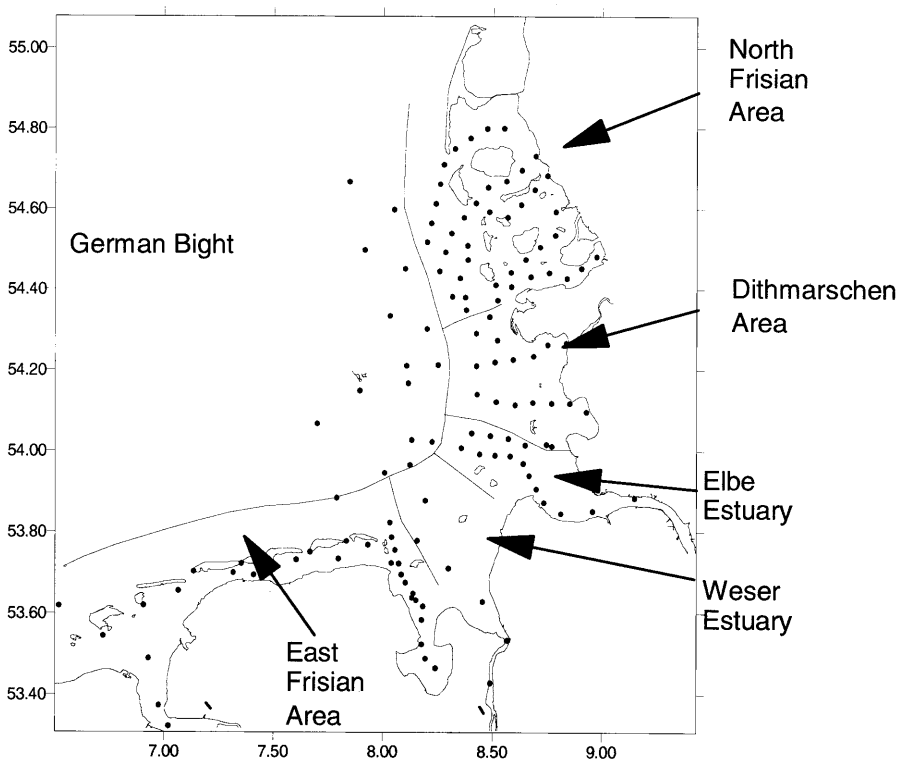

Fig. 1 Study site with position of stations. The area is divided into several sections: the offshore part of the German Bight and nearshore subregions of the Wadden Sea proper

water temperature, a heterotrophic system is influenced more by fluctuations in wastewater discharge, precipitation or currents. Coastal waters and especially estuaries are heterotrophic systems and mostly characterized by a larger gross respiration rate than primary production (Vadstein and Olsen 1989). Indeed, recent investigations in the estuary of the Delaware (Coffin and Sharp 1987), the St. Lawrence (Painchaud and Therriault 1989), and in the Hudson River (Findlay et al. 1991) demonstrated that the algae–bacteria link is not statistically detectable when additional C sources are available for mineralization.

The Wadden Sea is an example of a transition zone between the autotrophic system of the North Sea and the heterotrophic systems of estuaries. The first intensive attempt to biologically characterize this area and distinguish it from the central North Sea was undertaken by the program SYNDWAT (Synoptic Data Management of Nutrient and Phytoplankton Budgets of the Wadden Sea) in 1989–1991. Several synoptic surveys conducted during this project showed that the phytoplankton community successively develops through the year, creating distinct seasonal distribution patterns with respect to the heterodynamic hydrographic structure of the environment, influxes of river plumes and the distribution of nutrients (Hesse et al. 1992, 1994, 1995). In 1994, TRANSWATT (Transport, Transfer and Transformation of Biomass Components in Wadden Seas) continued the working package of SYNDWAT with the introduction of bacterial abundance as an additional parameter. The work presented in this paper is the first comprehensive dataset of bacterioplankton in the German Wadden Sea, which provides information on whether there are spatial gradients even though the area is intensively hydrodynamically mixed. For example, the flushing times in the tidal basins of the study site (the time needed to renew the water by 60%) are 2–9 days (Dick and Schönfeld 1996), so that a homogeneous distribution could also be expected. Moreover, since the Wadden Sea usually possesses high nutrient loading, which facilitates algae growth, but also receives additional organic matter imported from the adjacent sea and from terrestrial runoff, we also compared bacterial abundance with chlorophyll-a, so that we could test whether the algae–bacteria link is different from those reported in the literature.

Materials and methods

A map of the area studied is shown in Fig. 1. The Wadden Sea extends between the Dutch Den Helder and the Danish Sallingen peninsula with a total area of about 8000 km^2, of which 4600 km^2 belongs to Germany. The German Wadden Sea encloses a 2100-km^2 area extending from the western East Frisian area (EF) between the rivers Ems and Elbe, and a northeastern part (2500 km^2) extending from the Elbe to Sylt island. Between both areas the estuaries of the river Weser (WE) and the river Elbe (EE) can be distinguished. The northern Wadden Sea can be separated into the northern North Frisian area (NF; 1200 km^2) and the southern Dithmarschen area (DI; 1300 km^2). The separation of the Wadden Sea into these subregions, according to the major areas of influence of riverine or marine waters, corresponds to the suggestion of the Common Wadden Sea Secretariat (CWSS 1993, p. 31). The area situated offshore is called the German Bight proper (GB). The tidal amplitude of >3 m in the DI area is too big to let islands exist between the Elbe and Eiderstedt peninsula, while several islands occur in the NF and the EF area with the moderate tidal amplitude

Table 1 Time schedule of the cruises and the corresponding conditions

Season	Winter 1994	Spring 1994	Summer 1994
Date	30 Jan–1 Feb	10–11 May	19–20 July
Wind speed	5–7 Bft.	2–3 Bft.	0–2 Bft.
Water temp.	2–5°C	10–14°C	20–23°C

of 2–3 m. The dry falling flat areas of the German Wadden Sea exceed 50% of the total area, so that about 60% of the total water body flows out of the basins during ebb tide (Hesse et al. 1992).

Only minor freshwater discharges (<15 $m^3 s^{-1}$) flow into the NF area. The water body of the NF area is drained by the three main tidal watersheds Hörnumtief, Aue, and Hever. The Hörnumtief drains the area between the islands Sylt, Föhr, and Amrum (857×10^6 m^3), the Aue drains the area between Amrum, Föhr, Langeneß, and Pellworm (544×10^6 m^3), and the Hever drains the area between Pellworm, Nordstrand, and Eiderstedt (1644×10^6 m^3). The DI area is affected by the river plumes of Eider (mean: 20 $m^3 s^{-1}$) and Elbe (between 500 $m^3 s^{-1}$ in July and 1000 $m^3 s^{-1}$ in March 1994) and its main watersheds are the Eider out-stream (draining 152×10^6 m^3), the Piep (draining 622×10^6 m^3), and the Elbe out-stream (draining 1612×10^6 m^3). The EF area is affected by the rivers Elbe and Ems, but also by the residual circulation of North Sea water masses directed toward the east. For more information, see Hesse et al. (1994), Brockmann et al. (1995), and Otto et al. (1990).

In 1994, three synoptic sampling surveys were conducted using up to eight ships simultaneously (Table 1). The station grid included five transects within NF, three transects within DI, and one transect in EF (Fig. 1). The stations were in the main inlet channels. The mean distance between the stations was about 5 km. To reduce errors in the evaluation of the distribution patterns of plankton organisms caused by shifting water masses, the samplings started 2 h before high tide at the most nearshore station and finished 2–2.5 h later at the seaside position. One additional transect was made within the Weser estuary (WE) and in the Elbe estuary (EE). Here, the inner station was near the town of Brunsbüttel, where a turbidity maximum of the Elbe is located. For the sake of comparison, a limited number of stations were in nearshore parts of the German Bight (Fig. 1).

The samples were taken at 1-m water depth using a 5-l Niskin bottle. Subsamples were taken after shaking the sampler to avoid settling of particles and to prevent a possible unequal distribution of them in the subsample flasks. The subsamples (100 ml) for bacterial numbers were poured into brown glass bottles, preserved with 0.8% formaldehyde (final concentration), and stored in the dark and cool. Compared to the literature, our preservative concentration lies within the range of 0.1–10% used by others (Kepner and Pratt 1994). Bacterial numbers were determined by epifluorescence microscopy according to Daley and Hobbie (1975). Since the Wadden Sea samples always contain much suspended material, care was taken in diluting the sample so that not more than 50% of the microscope field was covered by particles. This means that an amount of about 2–5 ml was filtered onto a 0.2 µm Nuclepore polycarbonate membrane (Costar GmbH, Bodenheim, Germany), which was prestained with Sudan black (Sigma, 40 ml 50% ethanol l^{-1}). The cells on the membrane were stained with AO (acridine orange, Merck, 100 ml aqua dest. l^{-1}) for 3 min and washed with citrate buffer (0.056 M Na-citrate, 0.056 M NaOH, 0.044 M HCl, pH 4). Counting of cells was carried out with a Leitz Aristoplan epifluorescence microscope under 1250-fold magnification fitted with the objective NPL Fluotar 100/1.32 Oil, an HB0-50 W high-pressure mercury burner, blue 470–490 nm excitation, and a 520-nm barrier filter. The particle content of the samples mentioned above made the identification of bacteria difficult. Here, we counted the orange–red and greenish fluorescing particles possessing a size of 0.2–2 µm and showing the typical distinct shape of a cocci, rod, vibrio or spirillum. No correction for particle masking of bacteria was performed. Forty microscopic fields were counted per sample. To reduce problems of observer subjectivity, one person processed and counted all the samples.

Table 2 Average abundances (±SD) of phyto- and bacterioplankton

Area	Chl-a (µg l^{-1})		
	Winter	Spring	Summer
NF	3.18±2.39	14.33±7.60	11.39±5.55
DI	2.00±1.25	37.14±26.35	15.69±12.36
EE	2.32±1.60	12.60±5.67	11.67±7.28
WE	1.97±0.49	14.35±5.03	18.65±6.65
EF	3.86±2.00	29.86±16.17	12.24±6.61
GB	1.19±1.68	12.27±7.33	8.43±3.80
Total dataset	2.261±2.07	20.83±18.24	12.21±7.61
	Bacteria (N * 10^5 ml^{-1})		
Area	Winter	Spring	Summer
NF	3.64±1.70	5.35±1.92	9.12±3.79
DI	13.76±33.1	6.86±3.12	12.76±–6.31
EE	1.28±0.69	1.25±1.22	4.06±2.35
WE	6.41±4.63	2.84±4.27	0.45±0.33
EF	3.81±3.83	2.58±1.92	5.05±6.28
GB	2.17±1.38	1.59±1.44	2.22±2.71
Total dataset	4.29±11.13	4.86±2.93	7.80±5.73

For chlorophyll-a (Chl) measurement, between 100 and 1000 ml water was filtered through a GF/C-Whatman filter. The filters were immediately frozen and stored at –20°C. In the laboratory, Chl was quantified photometrically according to Lorenzen (1967). The distribution patterns of bacteria and Chl were calculated and plotted using the program Surfer (Golden Software Inc., Golden, USA). The data were interpolated by linear kriging and presented as 2-D isoplet plots.

Statistic analysis was performed using the program Statistica, Vers. 5.0 (StatSoft. Inc., Tulsa, USA). The validity of separating the study area into the subregions suggested by the CWSS (1993) was tested by performing a one-way MANOVA test on the regions as independent factor and checking the homogeneity of the data variances and the probability of post-hoc tests.

Results

Only every second station was sampled in the NF area because of rough weather conditions during the January/February campaign. During the May campaign, no samplings were performed in EF, but during the July campaign all planned 108 stations were covered. Details are shown in Table 1.

The winter values for bacterio- and phytoplankton (as Chl) were generally low (Table 2). The mean values were 4.3×10^5 bacteria ml^{-1} and 2.6 µg Chl l^{-1}. The distribution patterns of the two groups showed slightly higher Chl values in EF compared to the other sites, while DI and WE showed relatively higher bacterial numbers (Figs. 2, 3).

In May, phytoplankton had bloomed, reaching a 4.7-fold higher mean of 12 µg Chl l^{-1} compared to winter. The maximal values were 79 µg Chl l^{-1} in DI and 65 µg Chl l^{-1} in EF. The bacterial densities had also increased,

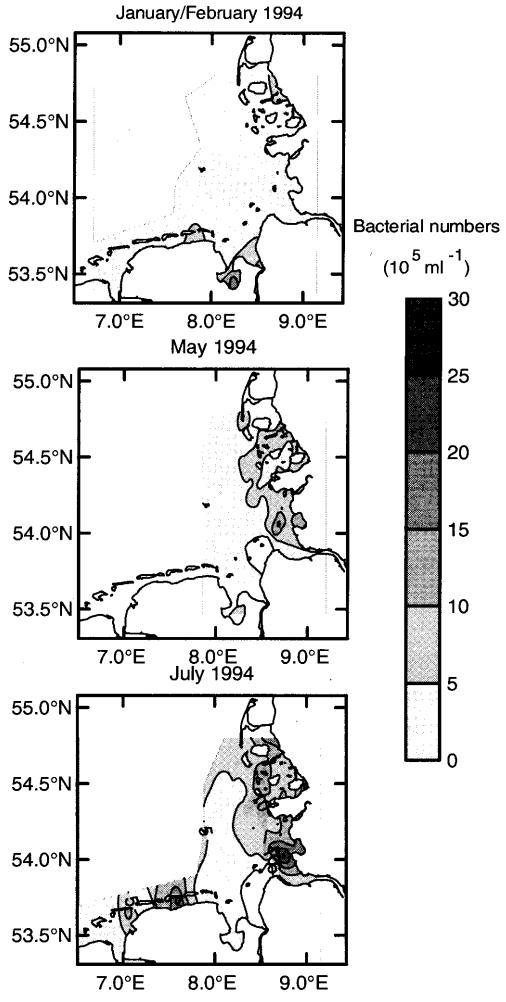

Fig. 2 Distribution patterns of bacteria (N×10^5 ml^{-1}); no samplings in the East Frisian (EF) region

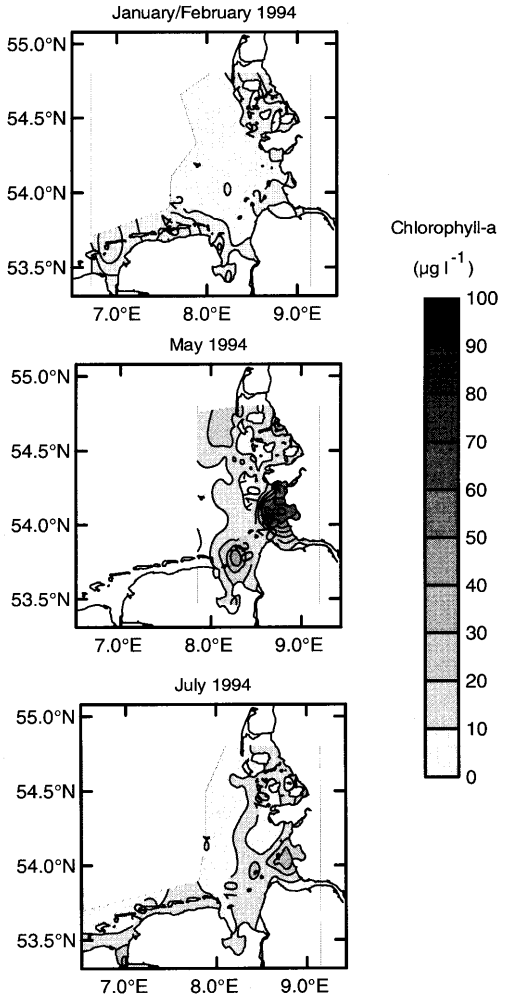

Fig. 3 Distribution patterns of chlorophyll a (µg l^{-1}); no samplings in the EF region

but only 1.2-fold compared to winter. The mean was 4.9×10^5 ml^{-1} and the highest numbers were found in the NF and DI, where concentrations of up to 14×10^5 ml^{-1} were observed. The bacterial tongue coming out of the inner NF area, which was shown by the data in winter, was still present in spring, and Chl showed a very patchy distribution pattern, especially in NF, where two minimum zones were present.

In July, the bacterial numbers had further increased, reaching a 1.8-fold higher mean value (7.8×10^5 ml^{-1}) than measured in winter, and still showed relatively high densities in NF and DI (Table 2). In contrast, the Chl values had decreased compared to spring and were only 4.7-fold higher than in winter. The distribution of Chl was not as patchy as it was in spring. The spring bloom event in DI was still present, but the Chl concentrations reached maximum values of only 41 µg l^{-1}. Comparing the distribution pattern of May and July, the two patches of low Chl concentration mentioned in spring had extended and flowed together in summer.

Since the study area was split into subregions according to the suggestion of the CWSS (1993), it was tested whether it is possible to distinguish these clusters from each other by comparing the variances of our plankton data. To check the probability of the following tests, the homogeneity of data variance was validated for each of the three cruises by univariate and Levene's tests (P<0.05). Then, a Spjotvoll/Stoline test was applied to show which regions can be differentiated from the others. As indicated in Table 3, the two plankton fractions could support the separation in many cases but not in all. In winter, only DI, EF, and partly GB were different from one another, DI mainly due to its specific bacterial numbers and EF and GB due to the Chl values. So, the separation of subregions could be validated by the Chl values alone and the values of Chl and bacteria together (P<0.0005), but not by using the data of bacteria numbers alone (P=0.137). In spring, Chl was strongly responsible for the spatial differences, while the bacterial data could mainly explain the difference of NF and DI. The total effect as well as the single effect on the MANOVA statistics were strong (P<0.05) for each factor combination. In summer, the impact of bacterial data had increased further (P<0.05 for bacteria alone as well as for

Table 3 Spjotvoll/Stoline test for checking the possibility of differenting spatial subregions on the basis of Chl or bacteria data. Only the cases with significant probability ($P<0.05$) are shown

	Chl						Bacteria					
	NF	DI	EE	WE	EF	GB	NF	DI	EE	WE	EF	GB
Winter 1994												
NF	–					C	–	B				
DI		–			C		B	–	B		B	B
EE			–		C			B	–			
WE				–	C					–		
EF		C	C	C	–	C		B			–	
GB	C				C	–		B				–
Spring 1994												
NF	–	C			C		–	B			B	B
DI	C	–		C		C	B	–	B	B	B	B
EE			–					B	–			
WE		C		–				B		–		
EF	C				–	C	B	B			–	
GB		C			C	–	B	B				–
Summer 1994												
NF	–	C					–	B	B		B	B
DI	C	–				C	B	–	B	B	B	B
EE			–				B	B	–			
WE				–				B		–		
EF					–		B	B			–	
GB		C				–	B	B				–

bacteria and Chl together), but that of Chl had declined, so that Chl reached an (insignificant) impact probability factor of only 0.2.

Discussion

Concentrations of Chl and bacterioplankton

The reported values of Chl might seem to be relatively high while the values for bacterial density are relatively low. For example, Admiraal et al. (1985) described an annual cycle from four stations of the Ems-Dollard where 50 µg Chl l^{-1} was found, compared to the 79 µg l^{-1} of our study. More striking is the difference in the bacteriological data: Admiraal et al. (1985) found 10 (February) – 100 (May)×10^5 bacterioplankton ml^{-1} compared to 0.4–26 in our study. Since 60% higher Chl concentrations might be possible due to accumulation of particulate matter in the inner German Bight, one would not expect in the same region and time bacterial densities that were lower by a factor of 4. In another study, van Duyl and Kop (1988) determined total bacterial numbers of monthly sampled surface waters to be 2 (January) and 94 (May)×10^5 ml^{-1} for the western Wadden Sea between the Dutch mainland and the islands of Texel and Terschelling. Again, the highest bacterial abundance occurred in May and not in late summer as in our study. In the adjacent North Sea, Vosjan et al. (1992) found about 7–10×10^5 ml^{-1} between Helgoland and the western border of our Wadden Sea station net in July 1987. Billen et al. (1990) reported in their review paper a range of 1–10×10^5 bacteria ml^{-1} in surface waters of the North Sea.

Since we cannot explain our generally low bacterial values per se, we tentatively suggest that they are due to the relatively long storage period (2–4 months caused by the high number of samples) before the samples were analysed. Turley and Hughes (1992) reported a strong decrease in cell number (mean: 39%) and shrinkage of cell sizes during the first 40 days of storage, and supposed that cells had attached to the inner surface of the storage bottle. Gunderson et al. (1996) could reduce the loss from 50% (after 29-day storage) to 18% by adding a protease inhibitor prior to the addition of the preservative, concluding that remaining protease activity may be the major cause of bacterial loss in preserved seawater samples. Therefore, the bacterial numbers determined here must be treated with care and may be compared with caution to those calculated in other investigations; but within this Wadden Sea study the comparison of data is valid.

Distribution patterns and seasonal succession of the plankton community

The three distribution patterns suggest that the communities of algae and bacteria not only develop and decline in our study site; the organisms were also obviously able to form spatial gradients, which were unexpected because of the intensive mixing of the water masses in the area. For example, Dick and Schönfeld (1996) have recently estimated the flushing time within the tidal basins to be 2–9 days. Moreover, we also found indications that the development of bacteria lags behind that of the algae, which was even more unexpected since the hydrodynamic turbulence should not only prevent the establishment

Table 4 Correlation analysis of bacterial abundance (log N ml^{-1}) and Chl (log µg l^{-1}). Only significant cases ($P<0.05$) are shown

Area			
	TW-1: January / February 1994		
NF	Log bacterial numbers=5.320+0.462×log Chl	r^2=0.313	P=0.0012
GB	Log bacterial numbers=5.195+0.122×log Chl	r2=0.228	P= 0.0376
Total data set	log bacterial numbers=5.313+0.193×log Chl	r^2=0.149	P=0.0002
	TW-2: May 1994		
NF	Log bacterial numbers=5.402+0.274×log Chl	r^2=0.196	P=0.0024
DI	Log bacterial numbers=5.236+0.385×log Chl	r^2=0.480	P=0.0007
Total data set	log bacterial numbers=5.176+0.292×log Chl	r^2=0.054	P=0.0209
	TW-3: July 1994		
NF	Log bacterial numbers=5.470+0.447×log Chl	r^2=0.239	P=0.0006
DI	Log bacterial numbers=5.705+0.338×log Chl	r^2=0.469	P=0.0012
EE	Log bacterial numbers=6.468–1.086×log Chl	r^2=0.610	P=0.0022

of distinct communities but should also uncouple the link between bacteria and algae.

Succession of phytoplankton and bacteria in the German Wadden Sea was apparent because: (1) in winter, Chl showed the first local production sites in the North Frisian area while bacteria were widely equal in numbers and (2) in spring, bacteria had grown in areas where algae had been found in January. Simultaneously, algae bloomed in the Dithmarschen area and declined in the North Frisian area – possibly caused by herbivore grazing. Unfortunately, we have no idea of the plankton development in the East Frisian Wadden Sea, where peaks of Chl were found in winter. In summer, bacteria showed a patchy distribution, similar to that of Chl in spring, but their seasonal highest abundance while phytoplankton was still in its declining phase.

This trophic succession has been proposed by several authors. For example, Billen and Fontigny (1987) showed a delayed development of bacteria with respect to phytoplankton. The authors performed high frequency sampling and were able to show that this delay caused a typical anticlockwise cycle of the ratio between bacteria and algae (see also Billen et al. 1990). In contrast to this study, our three synoptic campaigns provide instantaneous data only on the seasonal development of phyto- and bacterioplankton. Much of the temporal dynamics occurred between the cruises. Moreover, the samples collected on the three cruises definitely did not belong to the same water masses, so that a trophic link between producers and consumers may be unlikely – especially since their link is also temporarily delayed. On the other hand, the observation of spatial gradients in the study area despite the hydrodynamic mixing indicates that the plankton communities within the Wadden Sea are obviously able to establish distinct populations. So, the observations of a trophic succession become more likely, although the arguments for this succession can be backed up only by weak evidence.

Correlation between bacterial abundance and Chl

We tested the degree of metabolic coupling of photoautotrophic and chemo-organo-heterotrophic processes in the Wadden Sea. Since bacteria are considered to be near the base of the food chain, the idea of a bottom-up control of bacteria by resource supply is generally favoured against a top-down control of them by bacterivore grazing (Ducklow 1984; Ducklow and Carlson 1992).

Although numerous marine surveys have included both bacterial and algal quantification, statistical tests of a bacterio-/phytoplanktonic correlation have not been routinely made. For Wadden Sea studies, Admiraal et al. (1985) only described small delays in the developments of bacteria compared to Chl, but they did not calculate regressions between both parameters.

The data were split in spatial clusters, as suggested by the CWSS (1993), according to their hydrodynamic differences. These separations could generally be validated by comparing the variances of plankton data (one-way MANOVA), thereby indicating that the organism's distribution patterns follow the hydrodynamic structure.

Table 4 shows the results of linear regression of our dataset. In winter, all 85 data points and the 17 points of the North Frisian area are significant. In spring, the significant correlation extends southwards to the Dithmarschen area. The positive slope of the relation indicates that bacterial growth depends on Chl as food supply, suggesting bottom-up control. In contrast to this, we found a significant negative slope in summer in the Elbe estuary, which may indicate a depression of bacterial growth by phytoplankton. An explanation may be that the estuarine water was rich in inorganic particulate matter, which supported bacterial growth but reduced light penetration and algal growth, so that the correlation between bacteria and Chl remained but was reversed. Regarding the other numerous cases, where no correlation could be found, this may mean that bacteria do not stringently depend either on phytoplankton or on allochthonous material.

In summary, it can be concluded that a relationship can be observed between the two planktonic members in a heavily mixed and hydrodynamically well-disturbed ecosystem like the Wadden Sea, and that topographically separated areas possess distinct distribution patterns of phyto- and bacterioplankton. Moreover, a relationship

between algae and bacteria exists in winter also, when algae activity is depressed to its seasonal minimum. This relationship is maintained in the northern Wadden Sea area, and the link extends to spring from the NF area southwards to the DI area, against the expected water circulation along the coast of the German Bight from southwest to northeast.

A more detailed interpretation may be possible using the regression's slope of our calculations and comparing the latter with others obtained from the literature. Bird and Kalff (1984) took 27 references of marine and freshwater habitats into account and calculated slopes of bacteria (log of number per millilitre) and Chl (log of micrograms per litre) between 0.78 and 0.84. Cole et al. (1988) summarized 70 foreign datasets and found a mean slope of 0.52. Ducklow and Carlson (1992) listed in their overview several slopes, half of them significant, and reported a range of 0.5–0.8, a part from a study from the Antarctic Weddel Sea (Cota et al. 1990; slope=0.11) and another from the Benguela upwelling (Linley et al. 1983; slope=1.05). Except for these two unusual values, the slopes of our study in the Wadden Sea are always smaller.

Here are some possible explanations for the small slopes. Intense bacterivore grazing may have limited the development of high bacterial abundance, so that the bottom-up control shown here masked an existing top-down control from grazers. We did not test such a top-down control. Perhaps microflagellate abundance would have correlated better with bacterial numbers than Chl. However, the question must arise, what enabled the high Chl values if grazing was so intense. Secondly, the phytoplankton cells in the Wadden Sea possess a higher ratio of Chl versus organic C compared to algae living in the open sea, which may be interpreted as an adaptation to the lower light conditions. This would indicate that increased Chl in the Wadden Sea does not necessarily mean increased organic matter available for bacterial utilization. Preliminary evidence exists for a higher Chl/organic C ratio in the Wadden Sea (Brockmann et al. 1995). Thirdly, algae populations in the Wadden Sea often consist of *Phaeocystis*, which may be harmful to bacteria due to its acrylic acid (Sieburth 1960). Organic matter derived from this species is less nutritive and may be inhibitory for bacterial development. Fourthly, the Wadden Sea is strongly influenced by tidal water exchange, which includes the export of microphytobenthic material from the flat areas into the deep channels. Perhaps the microphytobenthic material is partly pre-degraded, so that the specific content of easily degradable compounds per unit Chl is lower than in fresh marine phytoplankton. A less nutritive content of degradable material must mean less material for bacterial development, as a correlation between substrate "freshness" and bacterial growth efficiency had already been reported (Goldman et al. 1987; Turley and Lochte 1990; Jahnke and Craven 1995). Possibly this phenomenon caused our unusually low slope between bacteria and Chl.

Conclusions

We present here a first synoptic evaluation of bacterial and Chl concentrations in the German Wadden Sea. These concentrations displayed a graduated distribution pattern, which was surprising, considering the intense tidal mixing in the Wadden Sea. Moreover, there was evidence of a trophic succession between the two plankton fractions, which was best proven for the Dithmarschen Wadden Sea area, but an algae–bacteria link was also evident in the whole northern area, where an algae spring bloom occurred. However, there was also evidence that this link could turn into an inverse relationship. The unusually low regression slopes found here, compared to those reported in the literature, suggest that bacteria and phytoplankton in the Wadden Sea are differently linked, compared to other systems, but since our study examined only three moments of the seasonal cycle, more frequent observations would be advantageous to be able to understand the whole site-specific plankton dynamics. Unfortunately, this will be hard to realize due to logistic problems.

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References

Admiraal W, Beukema JJ, Es FB van (1985) Seasonal fluctuations in the biomass and metabolic activity of bacterioplankton and phytoplankton in a well mixed estuary: the Ems-Dollard (Wadden Sea). J Plankt Res 7:877–890

Azam F, Fenchel T, Gray JG, Meyer-Reil L-A, Thingstad F (1983) The ecological role of water column microbes in the sea. Mar Ecol Prog Ser 10:257–263

Billen G, Fontigny A (1987) Dynamics of *Phaeocystis*-dominated spring bloom in Belgian coastal waters. II Bacterioplankton dynamics. Mar Ecol Prog Ser 37:249–257

Billen G, Joiris C, Meyer-Reil L-A, Lindebloom H (1990) Role of bacteria in the North Sea. Neth J Sea Res 26:265–293

Bird DF, Kalff J (1984) Empirical relationships between bacterial abundance and chlorophyll concentration in fresh and marine waters. Can J Fish Aquat Sci 41:1015–1023

Brockmann U, Hentschke U, Baraniok B, Starke A (1995) Stofflüsse und Bilanzen. In: Hesse K-J, Dick S, Hickel W, Schaumann K, Brockmann U (eds) TRANSWATT. Zwischenbericht. Forschungs- und Technologiezentrum Westküste, Büsum, 1:13–165

Coffin RB, Sharp JH (1987) Microbial trophodynamics in the Delaware Estuary. Mar Ecol Prog Ser 41:253–266
Cole JJ, Findlay S, Pace ML (1988) Bacterial production in fresh and salt water ecosystems: a cross-system over-view. Mar Ecol Prog Ser 43:1–10
Cota CF, Kottmeier ST, Robinson DH, Smith WO, Sullivan CW (1990) Bacterioplankton in the margin ice zone of the Weddel Sea: biomass, production and metabolic activities during austral autumn. Deep-Sea Res 37:1145–1167
CWSS (Common Wadden Sea Secretariat) (1993) Quality status of the North Sea, subregion 10, the Wadden Sea. Common Wadden Sea Secretariat, Wilhelmshaven, 174 pp
Daley RJ, Hobbie JE (1975) Direct count of aquatic bacteria by a modified epi-fluorescent technique. Limnol Oceanogr 20:875–882
De Jong F, Bakker CF, Dahl K, Dankers N, Farke H, Jäppelt W, Koßmagk-Stephan K, Madsen PB (1993) Quality status report of the North Sea, subregion 10, the Wadden Sea. Common Wadden Sea Secretariat, Wilhelmshaven, 174 pp
Dick S, Schönfeld W (1996) Water transport and mixing in the North Frisian Wadden Sea – results of numerical investigations. Dtsch Hydrogr Z 48:27–48
Ducklow HW (1984) Geographic ecology of marine bacteria: physical and biological variability at the mesoscale. In: Klig MJ, Reddy CA (eds) Current perspectives in microbial ecology. American Society of Microbiology, Washington, DC, pp 22–30
Ducklow HW, Carlson CA (1992) Oceanic bacterial production. Adv Microb Ecol 12:113–181
Ducklow HW, Kirchman DL, Quinby HL, Carlson CA, Dam HG (1993) Stocks and dynamics of bacterioplankton carbon during the spring bloom in the eastern North Atlantic Ocean. Deep-Sea Res 40:245–263
Duyl FC van, Kop AJ (1988) Temporal and lateral fluctuations in production and biomass of bacterioplankton in the western Dutch Wadden Sea. Neth J Sea Res 22:51–68
Findlay SF, Pace ML, Lints D, Cole JJ, Caraco NF, Peierls B (1991) Weak coupling of bacterial and algal production in a heterotrophic system: the Hudson River estuary. Limnol Oceanogr 36:268–278
Goldmann JC, Caron DC, Dennett MR (1987) Regulation of gross growth efficiency and ammonium regeneration in bacteria by substrate C:N ratio. Limnol Oceanogr 32:1239–1252
Gunderson K, Bratbak G, Heldal M (1996) Factors influencing the loss of bacteria in preserved seawater samples. Mar Ecol Prog Ser 137:305–330
Hesse K-J, Hentschke U, Brockmann U (1992) A synoptic study of nutrients and phytoplankton characteristics in the German Wadden Sea with respect to coastal eutrophication. In: Colombo G, Ferrari I, Ceccherelli VU, Rossi R (eds) Marine eutrophication and population dynamics. Olsen & Olsen, Fredeborg, pp 45–53
Hesse K-J, Tillmann U, Brockmann U, Dick S (1994) SYNDWAT PILOT, Abschlußbericht. Büsum/Hamburg, pp 7–59
Hesse KJ, Tillmann U, Brockmann U (1995) Nutrient–phytoplankton relations in the German Wadden Sea. CM/ICES T8:1–13
Jahnke RA, Craven DB (1995) Quantifying the role of heterotrophic bacteria in the carbon cycle: a need for respiration measurements. Limnol Oceanogr 40:436–441
Kepner RL, Pratt JR (1994) Use of fluorochromes for direct enumeration of total bacteria in environmental samples: past and present. Microbiol Rev 58:603–615
Lancelot C, Billen G (1984) Activity of heterotrophic bacteria and its coupling to primary production during spring phytoplankton bloom in the southern bight of the North Sea. Limnol Oceanogr 29:721–730
Laanbrooek HL, Verplanke JC, De Visscher PRM, de Vuyst R (1985) Distribution of phyto- and bacterioplankton growth and biomass parameters, dissolved inorganic nutrients and free amino acids during a spring bloom in the Oosterschelde basin, The Netherlands. Mar Ecol Prog Ser 25:1–11
Linley EAS, Newell RC, Lucas MI (1983) Quantitative relationships between phytoplankton, bacteria and heterotrophic microflagellates in shelf waters. Mar Ecol Prog Ser 12:77–89
Lorenzen CJ (1967) Determination of chlorophyll and pheo-pigments: spectrophotometric equations. Limnol Oceanogr 12:343–347
McManus GB, Peterson WT (1988) Bacterioplankton production in the nearshore zone during upwelling off central Chile. Mar Ecol Prog Ser 43:11–17
McQueen DJ, Post JR, Mills EL (1986) Trophic relationships in freshwater pelagic ecosystems. Can J Fish Aquat Sci 43:1571–1581
Otto L, Zimmermann JTF, Furnes GK, Mork M, Saetre R, Becker G (1990) Review of the physical oceanography of the North Sea. Neth J Sea Res 26:161–238
Painchaud J, Therriault JC (1989) Relationship between bacteria, phytoplankton and particulate organic carbon in the Upper St Lawrence Estuary. Mar Ecol Prog Ser 56:301–311
Sieburth JMcN (1960) Acrylic acid, an antibiotic principle in *Phaeocystis* blooms in Antarctic waters. Science, New York 132:676–677
Simon M, Tilzer MM (1987) Bacterial response to seasonal changes in primary production and phytoplankton biomass in Lake Constance. J Plankt Res 9:335–352
Steele JH (1974) The structure of marine ecosystems. Blackwell, Oxford, 128 pp
Turley CM, Hughes DH (1992) Effects of storage on direct estimates of bacterial numbers of preserved seawater samples. Deep-Sea Res 39:375–394
Turley CM, Lochte K (1990) Microbial response to input of fresh detritus to the deep-sea bed. Paleogeogr Palaeoclimatol Palaeoecol 89:2–23
Vadstein O, Olsen Y (1989) Chemical composition and phosphate uptake kinetics of limnetic bacterial communities cultured in chemostats under phosphorus limitation. Limnol Oceanogr 34:939–946
Veldhuis MJW, Colijn F, Venekamp LAH (1986) The spring bloom of *Phaeocystis pouchetii* (Haptophyceae) in Dutch coastal waters. Neth J Sea Res 20:37–48
Vosjan JH, Gunkel W, Tijssen SB, Pauptit E, Klings K-W, Bruns K, Poremba K, Hagmeier E (1992) Distribution and activity of microorganisms in coastal waters off the Netherlands and Germany. Neth J Sea Res 29:333–341
Wanderschneider K (1983) Some biotic factors influencing the succession of diatom species during FLEX 1986. In: Sündermann J, Lenz J (eds) North Sea dynamics. Springer, Berlin Heidelberg New York, pp 573–583

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