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Viability of bacteria from different aquatic habitats. I. Environmental conditions and productivity

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ABSTRACT: Various freshwater, estuarine and coastal stations of the Southern Baltic Sea were comparatively studied to evaluate pelagic bacterial performance. Inner coastal waters (so-called bodden or lagoons) are highly productive systems and dominate the coast of the Southern Baltic Sea. Due to high nutrient loads up to the 1990s in combination with an enhanced primary production, increased amounts of particulate (POC) and dissolved organic carbon (DOC) accumulated in these waters. In the Darß-Zingst bodden chain, POC < 16 and DOC < 13 mg C l^{-1}, and C:N ratios of 9 to 11 in particulate matter were measured in winter and spring samples. Due to high POC concentrations, the average ratio of DOC:POC was 1.1:1, which is very low compared to other aquatic systems. Bacterial abundance and activities were rather high and reached 24×10^6 ml^{-1} and 18 µg C l^{-1} h^{-1}, respectively. Although 2 of the 3 investigated freshwater systems were classified as eutrophic, the highest measured POC concentrations, bacterial abundance and production were much lower (1.6 mg C l^{-1}, 11×10^6 bacteria ml^{-1}, 4.4 µg C l^{-1} h^{-1}) than in the bodden. In contrast to that, the DOC load was as high as in these inner coastal waters (<12 mg C l^{-1}). The coastal stations of the Baltic Sea, classified as mesotrophic, were not severely loaded with organic matter and bacteria (POC < 0.8, DOC < 5.5 mg C l^{-1}, bacteria < 3×10^6 ml^{-1}). Bacterial production again was lower than at all other stations; however, levels did reach an exceptional 4.6 µg C l^{-1} h^{-1}, which is comparable to values of the freshwater systems. Compared to the other investigated marine and freshwater systems, the bodden were heavily loaded with organic matter, especially particulate organic matter (POM). The origin of this material is assumed to be mainly autochthonous as it is known not to be transported by rivers into these estuaries. Although dissolved inorganic nitrogen (DIN) concentrations were high at least in winter, POM was of poor quality; this was reflected by high C:N ratios and a low contribution of phytoplankton carbon to POC. However, this is particularly surprising, because nitrogen should be readily available at all bodden sites by resuspension from the sediment caused by frequent winds in these very shallow systems of <2 m depth.

KEY WORDS: Organic matter · Bacterial production · Hydrolytic enzymes · Marine systems · Brackish systems · Freshwater systems

INTRODUCTION

Bacteria are the most important decomposers of organic matter in the pelagial and especially in the sediments of aquatic systems (e.g. Chróst et al. 1986). Hydrolytic enzymes, produced mainly by bacteria, play a key role in the degradation of particulate (POM) and dissolved organic matter (DOM) (e.g. Münster et al. 1992). These enzymes are a prerequisite in the transformation of dissolved or colloidal polymeric material to oligo- and monomers, which can then be taken up and metabolised. Therefore, it is useful to compare rates of bacterial production, respiration and hydrolytic enzyme activity in various aquatic systems. Comparisons between bacterial activities and concentrations of organic matter along with dissolved inorganic nitrogen (DIN) and phosphorus in different systems should help to elucidate the coupling of

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organic matter input and decomposition, and subsequently reveal the most important regulating factors of bacterial activity.

Besides nutrient availability, grazing as a top down control factor regulates bacterial biomass and species composition (e.g. Berninger et al. 1991). Protozoa, especially heterotrophic nanoflagellates, are an important, or often the dominating, loss factor for bacterial standing stock in pelagic systems (e.g. Jürgens et al. 1997). Because protozoan grazing pressure influences bacterial standing stock and may modulate bacterial cell specific activity, data on the main grazers are also important to understand organic matter transformations. Other important regulating factors of bacterial biomass and production can be cell lysis by viruses and photoinhibition by ultraviolet radiation (Wilhelm & Smith 2000).

In this study, different waters were investigated with respect to their organic matter loading, inorganic nutrient status, bacterial biomass and bacterial and protozoan activity. Three freshwater stations, which were classified as meso- to eutrophic, 4 mesotrophic coastal Baltic Sea stations and 5 estuarine locations, ranked between eu- and hypertropic, were compared. The inner coastal waters of the Southern Baltic Sea coast are phytoplankton-dominated systems due to high nutrient influx up to the 1990s. High primary production rates (Wasmund & Kell 1991) led to enhanced microbial biomasses, including bacteria, phytoplankton, proto- and metazoa. Due to the intensive primary production and the microbial turnover of organic matter, high concentrations of POM and DOM with low nitrogen contents accumulated in these waters (Schumann et al. 2001). In contrast to many other aquatic systems, the POM in the semi-enclosed Darß-Zingst bodden (lagoon) cannot be washed out substantially into the Baltic Sea due to hydrodynamic and geomorphological factors. In contrast, POM from the river Oberwarnow and its estuary Unterwarnow and from the outer coastal stations is easily transported to the open sea, or in the case of the stratified lake Tiefer See is deposited permanently. Moreover, POM in the bodden is frequently resuspended by wind-induced mixing (Rieling et al. 2000), and processed photochemically and by aerobic micro-organisms. The high C:N ratio in POM and the high percentages of non-carbohydrate and non-proteinaceous material (cf. Schumann et al. 2001) may be the result of these processes and the permanent contribution of sediment material to pelagic seston.

Samples were taken once in winter (January/February), when high concentrations of DIN were present in all the eutrophicated systems, and once in spring (April/May) at higher water temperatures and lower DIN concentrations. Thus, the growth limiting factor in winter can be assumed to be temperature. This 'limited' situation is compared to the beginning of the phytoplankton spring bloom, where inorganic nutrients for primary production were still 'unlimited' and readily usable organic substances from phytoplankton exudates were already abundant (Schumann 1994).

The aims of this study were: (1) to describe the special environmental conditions of semi-enclosed and extremely shallow estuaries—the bodden—compared to freshwater systems and locations at the outer coast of the Baltic Sea; (2) to relate their effects on organic matter quality and quantity as well as micro-organisms in the pelagial; and (3) to give the data a basis for investigations on bacterial viability and its possible dependence on environmental factors (cf. Schumann et al. 2003, this issue). The following questions are addressed: Does a high organic load result in a high bacterial standing stock as a bottom-up control? Is the high bacterial biomass controlled effectively by protozoa as top-down regulation? Why are the bacteria very active (hydrolytic enzyme activity) but not productive (thymidine and leucine uptake)?

The selected locations provide a broad range of environmental factors. They are situated in an important industrialised region in central Europe and were, until the early 1990s, heavily polluted by fertilisers, pesticides and agricultural wastes. The rivers transported certain other pollutants introduced by the industry, e.g. heavy metals, into the Baltic Sea. However, in the last years, serious action has been taken against this pollution. Phosphorus, pesticide and heavy metal input have been considerably reduced. Additionally, all investigated aquatic systems here are situated in a region primarily used for tourism but also for sustainable and environmentally friendly agriculture. The coastal Baltic Sea stations are in actual fact bathing beaches, and the bodden belong to the Vorpommersche Boddenlandschaft national park. The river Oberwarnow provides drinking water for the town of Rostock.

Although these systems have been investigated for several decades, there are only few data sets published and discussed in scientific journals, especially on micro-organism activity, and most results constitute summarised data given in non-public reports. Hence, it is crucial to evaluate the data from the time of increasing eutrophication and pollution and to follow the process of restoration of these different aquatic systems. The results concerning microbial activities in biogeochemical cycling of organic matter will help (1) to estimate the ecosystem's potential for self-purification; (2) to plan measures for their rehabilitation; and (3) to suggest possibilities for new sustainable industry and agriculture.

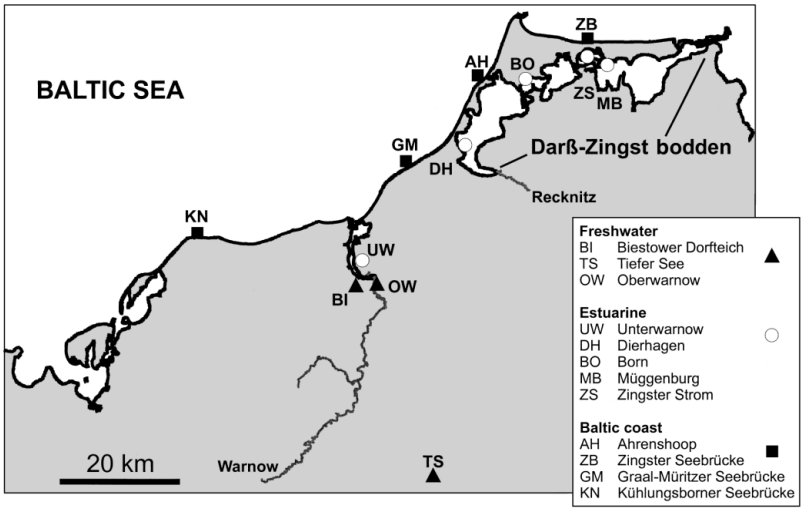

Fig. 1. Investigation area of the southern Baltic Sea coast (■), the estuarine stations (○) and the sampled freshwater systems (▲)

MATERIALS AND METHODS

Sampling. Different pelagic systems including 3 freshwater, 5 estuarine and 4 coastal stations of the Southern Baltic Sea (Fig. 1) were sampled once in winter at water temperatures below 5°C and once during spring at temperatures between 6 and 17°C (Table 1). From the upper 50 cm, 10 l samples were taken and transported in a cold box to the laboratory within 1 h. They were incubated for activity measurements and processed immediately for all other determinations. Samples were kept at *in situ* temperature for all viability staining procedures, which were performed within the next 5 h.

Abiotic parameters. Salinity was determined with a LF 197 electrode and expressed as psu (wtw, Wissenschaftlich-technische Werkstätten GmbH). Ammonium, nitrate and nitrite were each estimated spectrophotometrically in Whatman GF/F filtrates after the methods described in Rohde & Nehring (1979) and summed to DIN. Soluble reactive phosphorus (SRP) was analysed in GF/F filtrates by applying the molybdenum blue method in a flow-through system (Malcolm-Lawes & Wong 1990).

Seston and organic matter. The amount of suspended particulate matter (seston) was measured by filtering 20 to 400 ml water onto precombusted (450°C for 4 h) and pre-weighed glass-fibre filters (25 mm in diameter, Whatman GF/F). After drying the filters overnight at 60°C, they were weighed again on an electronic microbalance (M2P, Sartorius). Standard errors of 3 replicates were rather high (1 to 35%) due to sediment particles, which occurred at some very shallow stations under stormy conditions in winter. For the quantification of total organic carbon (TOC), unfiltered subsamples were analysed with a total organic carbon analyser (TOC 5000 A, Shimadzu) equipped with a suspended particle kit after catalytic high temperature oxidation (Sugimura & Suzuki 1988). The corresponding filtrate through precombusted GF/F filters was measured for dissolved organic carbon (DOC). Both results were corrected for inorganic carbon (IC). Particulate organic carbon (POC) was calculated as the difference between TOC and DOC. Organic carbon was analysed in 3 replicates with a SE <2%. For estimating the C:N ratio of POM, 20 to 400 ml was filtered onto Whatman GF/F and dried at 60°C. IC was expelled in a HCl atmosphere for 20 min. The filters were packed air-tight in tin foil and measured in an elementar analyser (vario EL, Elementar) for carbon and nitrogen following Verardo et al. (1990). Triplicates had a maximum SE of 16%.

Micro-organisms. Total bacterial cell numbers were counted in unfixed samples after staining with DAPI (Roth) according to Porter & Feig (1980). Replicate sub-

Table 1. Sampling dates in 2000 of the 3 freshwater, 5 estuarine and 4 Baltic Sea coast stations (see Fig. 1 for station abbreviations). T_W: water temperature (°C); Secchi: Secchi depth (cm); SRP: soluble reactive phosphorus (µmol l^{-1}); nd: not determined because too shallow to measure Secchi depth

Stn	Winter samples				Spring samples			
	Date	T_W	Secchi	SRP	Date	T_W	Secchi	SRP
Freshwater								
BI	03 Feb	4.0	nd	32.2	04 May	15.0	nd	22.5
TS	15 Feb	3.3	190	0.1	18 Apr	8.5	220	0.5
OW	18 Jan	2.9	70	1.0	07 Apr	8.0	60	0.2
Estuaries								
UW	25 Jan	0.0	105	0.9	28 Apr	12.5	115	0.5
DH	17 Feb	1.5	27	0.1	27 Apr	12.0	25	0.4
BO	12 Jan	2.0	40	0.1	19 Apr	9.5	25	0.3
MB	01 Feb	4.0	30	0.1	17 Apr	8.0	45	0.1
ZS	24 Feb	1.0	30	0.1	02 May	17.4	20	0.5
Baltic Sea coast								
AH	27 Jan	3.0	nd	0.5	12 Apr	5.5	nd	0.4
ZB	22 Feb	0.5	450	0.5	10 Apr	6.0	450	0.3
GM	10 Feb	4.0	nd	0.7	05 Apr	5.5	nd	0.1
KN	08 Feb	5.0	120	0.4	03 Apr	5.5	200	0.1

samples of 0.5 to 2.0 ml were filtered onto black stained 0.2 µm Isopore™ polycarbonate filters (Sigma-Aldrich) and stained separately (1 mg DAPI in 100 ml phosphate buffer, pH 7.6, 29 µM final concentration) for 10 min. An Olympus BH2-RFCA was used (1250-fold magnification, filter set UG-1). Biovolume was calculated with an individual cell volume of 0.15 μm^3 (unpubl. data).

Protozoa >10 µm were counted in rafter chambers containing 0.5 to 1.0 ml of water sample in duplicates using a light microscope (BH-2, Olympus) at a magnification of 50-fold. Smaller protozoa (6-fold per sample) were counted in a Bürker blood counting chamber at a magnification of 125×. All animals were counted alive at the day of sampling (Dale & Burkill 1982) and kept at *in situ* temperature until examination. Pigment absence was checked by epifluorescence illumination applying green light (BP 545) and a higher magnification if necessary. Biovolume was calculated from measured diameters assuming geometrically objects, e.g. spheres, spheroids or cylinders.

Chlorophyll *a* (chl *a*) was extracted with 90% acetone and measured spectrophotometrically (Jeffrey & Humphrey 1975).

Bacterial production and community respiration. Bacterial production was measured by the incorporation of ^{3}H-thymidine according to Fuhrman & Azam (1982). Methyl-^{3}H-thymidine (185 GBq $mmol^{-1}$, Amersham) was added to 3 ml subsamples to give a final concentration of 60 nM and samples were incubated for 30 min at *in situ* temperature. Thymidine incorporation was stopped by adding formaldehyde (final concentration 4%). Subsequently, nucleic acids of the samples were extracted with 3 ml of 5% trichloric acid (TCA) and filtered onto 0.2 µm cellulose acetate filters. The filters were rinsed 7-fold with 1 ml of 5% ice cold TCA. Each filter was then transferred into 10 ml of scintillation cocktail (Ultima Gold, Sigma) and measured in a liquid scintillation counter (Wallac 1410, Pharmacia). Bacterial production was calculated using a thymidine conversion factor of 1.1×10^{18} cells mol^{-1} (Riemann et al. 1987) and a carbon conversion factor for eutrophic waters of 2.5×10^{-14} g C $cell^{-1}$ (Bell 1993).

Bacterial production was additionally measured following the ^{3}H-leucine incorporation (1 nM) into bacterial protein, which is insoluble in TCA (Kirchman et al. 1985). To estimate total leucine uptake by the bacterial community, *in situ* concentrations of leucine were measured by high pressure liquid chromatography after derivatisation with *o*-phthaldialdehyde (Lindroth & Mopper 1979, modified according to Hubberten 1994) and related to the turnover rates of the radioactively labelled leucine pool. Total leucine incorporation was converted into biomass production according to Simon & Azam (1989) assuming a fraction of 7.3% leucine in bacterial protein and a cellular carbon per protein ratio of 0.86. Intracellular isotope dilution of leucine by *de novo* synthesis was assumed to be 2. We measured 5 replicates per sample with a SE of 29% on average. The measured low leucine uptake rates, especially at winter *in situ* temperatures, were the reason for this poor reproducibility.

To measure photosynthesis (data not shown) and community respiration the samples were concentrated by 4- to 90-fold by centrifugation (5000 rpm, $4500 \times g$) and were kept in the dark at *in situ* temperature for at least 30 min. An 8 ml aliquot was transferred into the measuring cuvette (Illuminova). Oxygen concentration was measured by a Clark-type electrode MI-730 (response time <20 s, Microelectrodes), inserted at the back of the cuvette. Prior to each measurement, the system was calibrated against air-saturated seawater at experimental temperature (= 100% oxygen saturation) and against an oxygen-free sodium dithionite solution (= 0% oxygen). The oxygen concentrations in the concentrated samples were followed for 10 min in darkness to determine the respiration rate. At the beginning of the respiration measurements, the initial oxygen saturation was >80% in most samples. All measured data (oxygen concentration and changes with time, temperature, velocity of the stirrer) were recorded every 4 s. Respiration was calculated as the slope of the linear regression of the oxygen decline with time. A respiratory quotient of 0.88 was applied for the conversion into carbon (Robinson et al. 1999).

Hydrolytic enzyme activity. Total esterase and peptidase activities were measured as the enzymatical hydrolysis of 4-methylumbelliferyl butyrate (MUF-butyrate) and L-leucine-4-methyl-7-coumarinylamide hydrochloride (Leu-MCA) (Sigma-Aldrich), respectively. The procedure followed Hoppe (1983), with minor adaptations. The artificial substrates were dissolved in 100% ethanol and added to 2 ml subsamples at a final concentration of 91 µM. All samples were buffered at a pH of 8.2 with Tris buffer (1 ml 50 mM Tris/HCl per 10 ml sample). Three replicates per sample were incubated at room temperature (21°C) and recorded for the fluorescent hydrolysis product 3-fold within 2 h for esterase and 3 to 9 h for peptidase activities in a Hitachi F4010 fluorometer (excitation 365 nm, emission 451 nm, bandpass 1.5 nm, response 2 s, averaged over 2 s). Blanks of sterile-filtered, distilled water and the fluorogenic substrates were treated the same way to correct the results for non-enzymatic hydrolysis, which could be substantial for the MUF-butyrate at the chosen pH of 8.2. The linear increase of fluorescence over time represents the hydrolytic enzyme activity. Standards of 1 to 100 µM 4-MUF (=7-hydroxy-4-methylcoumarin) and 7-amino-4-methylcoumarin (AMC) in 50 nM Tris-buffer, pH 8.2 were measured at each sampling date to calibrate

hydrolysis rates from relative fluorescence units. The same procedure was carried out with filtrates through 0.2 µm cellulose acetate membranes of each sample to quantify the amount of free dissolved enzyme activity.

Statistical analysis. To prove associations between abiotic factors, organic material, micro-organisms and their activities a Spearman rank order correlation analysis was performed on the whole data set. A critical p-value of <0.05 was always applied. Differences between average concentrations found at the freshwater, the Darß-Zingst bodden and the Baltic Sea stations were detected by 1-way ANOVA if the data passed normality test. In that case, average concentrations are the arithmetic means. However, the majority of data was not distributed normally and therefore variances were analysed by Kruskal-Wallis 1-way analysis on ranks. Hence, the medians serve as average values. A critical p-value of <0.05 was always applied. The all pairwise multiple comparison Dunn's method was used to isolate the significantly differing values.

RESULTS

Environmental conditions

The 3 freshwater systems (Fig. 1) include very different water types: the shallow and slow running eutrophic river Warnow (with sampling location Oberwarnow, OW: cf. Schumann et al. 1992, Hübener et al. 1996, Schlungbaum & Selig 1996), a small, shallow village pond (BI), and the 31 m deep dimictic meso- to eutrophic lake Tiefer See (TS: cf. Gewässergütebericht Mecklenburg-Vorpommern 1996/1997). The estuarine stations (UW and the 4 Darß-Zingst bodden stations DH, BO, MB and ZS) are more similar concerning morphological data, especially since 4 of the 5 are situated very close together in the same inner coastal water system. However, they are quite different regarding their eutrophication status (Schmidt 1989, Schiewer et al. 1991, Wasmund & Kell 1991). The Unterwarnow estuary is the least eutrophicated estuary, because of its intensive water exchange with the Baltic Sea. The Darß-Zingst bodden stations are hypertrophic in the inner western parts, because the water exchange with the Baltic is very restricted there, and eutrophic in the east. The outer coastal stations of the Baltic Sea (AH, ZB, GM and KN) are mesotrophic (Wasmund et al. 2000). Maximum water depth at the sampling points was about 5 m. Secchi depths of the mesotrophic stations were greater than 120 cm (Table 1). The eutrophic inner coastal stations had very low Secchi depths of only 20 to 45 cm.

In the estuarine systems, i.e. the inner coastal stations, salinity ranged from 1.5 to 7.7 psu. In the outer coastal Baltic Sea stations, salinity was significantly higher (9.5 to 17.0 psu). The sampling stations are lined up in each figure with increasing salinity measured in the winter samples (cf. Fig. 2a).

Of the limnetic systems only the eutrophic river Oberwarnow (OW) had rather high DIN concentrations, predominantly as nitrate. Besides lower water temperatures in winter, only the DIN concentrations dropped clearly between winter and spring, by 16% in freshwater and by 67 and 62% in the brackish and Baltic Sea samples, respectively (Fig. 3). All other abiotic parameters did not change significantly between the 2 sampling periods. At all sampling dates, SRP concentrations were very low except in the village pond (BI; Table 1).

There were significant negative correlations between micro-organisms—measured as bacterial numbers, chl *a* concentrations and protozoan biomass—and salinity. DIN was positively correlated with the micro-organisms and bacterial production, determined via thymidine incorporation (Table 2).

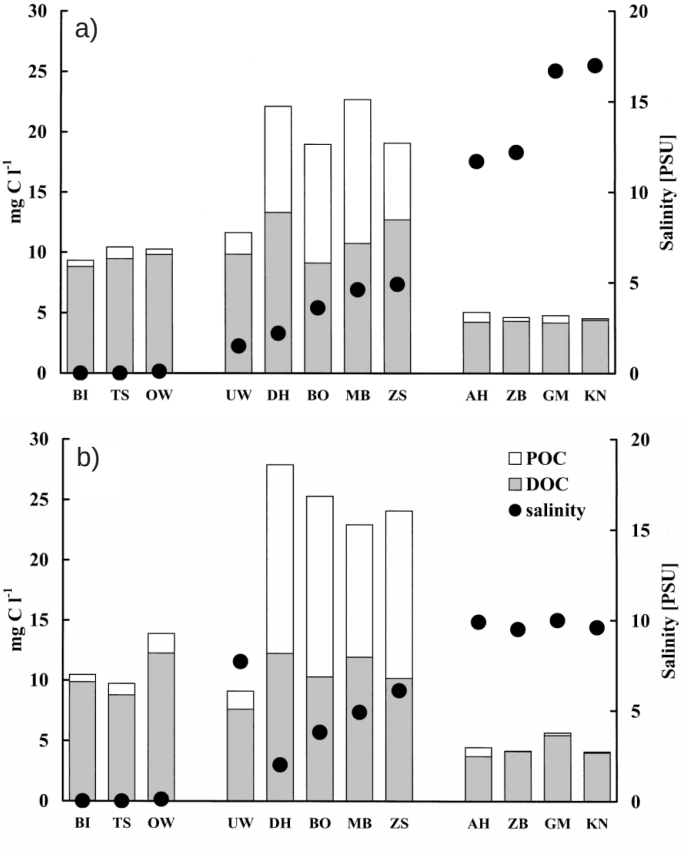

Fig. 2. Dissolved (DOC) and particulate organic carbon (POC) (mg C l^{-1}) at the freshwater, estuarine and Baltic Sea stations (see Fig. 1 for station abbreviations) lined up by increasing salinity (psu) in (a) winter and (b) spring (see Table 1 for sampling dates)

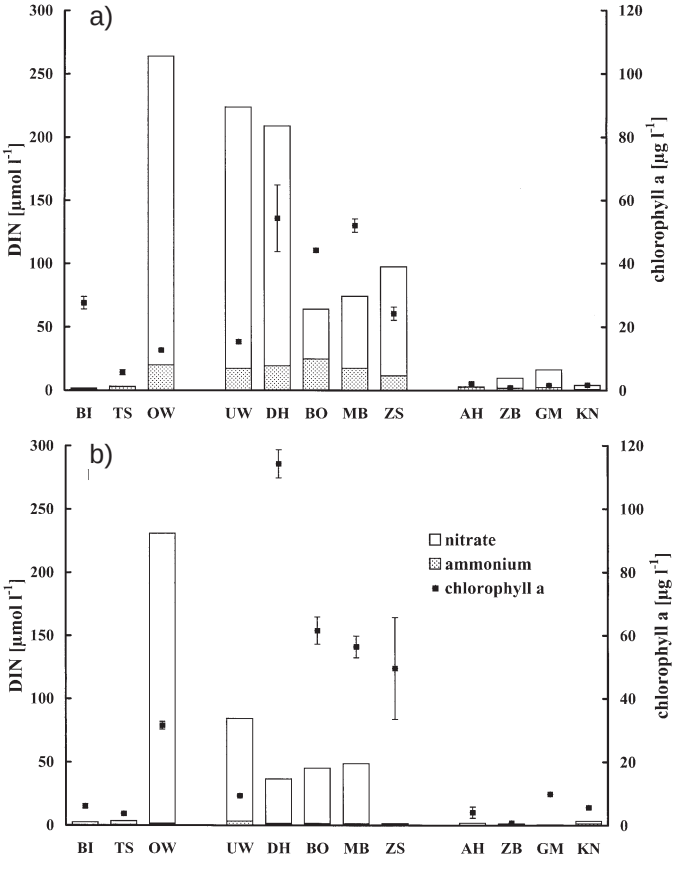

Fig. 3. Dissolved inorganic nitrogen (DIN) (µmol l^{-1}) and chlorophyll *a* (chl *a*) concentrations (µg l^{-1}) in (a) winter and (b) spring. Stations are arranged as in Fig. 2 (see Fig. 1 for station abbreviations). Error bars of chl *a*: SD of 3 replicate measurements

Organic material

DOC concentrations were high at the freshwater and estuarine stations (8 to 13 mg C l^{-1}). The POC concentrations in the freshwater systems were low (<2 mg C l^{-1}), so that the ratio between DOC and POC was on average 14:1. The POC contents were 2 to 16 mg C l^{-1} and were highest in the brackish samples, resulting in DOC:POC ratios of only 2:1. In the Baltic Sea, DOC and POC amounts were both much lower and the ratio between them was 35:1 on average (Fig. 2).

The C:N ratio was lowest in the freshwater systems (7.4 on average) and moderate in the estuarine samples (9.2). The occasional resuspension of mineral sediment material into the pelagial of the rather shallow Baltic Sea stations resulted in high seston amounts (not shown), but not enhanced POC (cf. Fig. 2). The C:N ratio of POM was highly variable and reached a maximum of 23.1 (Fig. 4).

While the freshwater stations exhibited chl *a* concentrations ranging from 4 to 32 µg l^{-1} in spring, all estuarine locations developed up to 114 µg l^{-1} and the Baltic Sea stations only 10 µg chl *a* l^{-1} maximum (Fig. 3). On average, 9 mol C (g chl *a*)$^{-1}$ was rather high for the freshwater systems, but average values at the estuarine stations were nearly twice as high (17 mol C [g chl *a*]$^{-1}$). While 3 out of the 4 Baltic Sea sampling sites showed POC:chl *a* ratios of 31 mol C (g chl *a*)$^{-1}$, the other Baltic Sea site (KN) averaged at 5 mol C (g chl *a*)$^{-1}$. These high POC:chl *a* ratios in the winter samples may have been the result of interfer-

Table 2. Spearman rank order correlation between salinity (psu), water temperture (T_W) (°C), dissolved inorganic nitrogen (DIN) (µmol l^{-1}), dissolved organic carbon (DOC) (mg C l^{-1}), seston (mg dry wt l^{-1}), the C:N ratio in particulate organic matter (C:N in POM) and bacteria (10^6 ml^{-1}), chlorophyll *a* (chl *a*) (µg l^{-1}), protozoan biomass (mg C l^{-1}), bacterial production measured by thymidine and leucine uptake (µg C l^{-1} d^{-1}), community respiration (µmol O_2 l^{-1} h^{-1}), esterase and peptidase activity (µmol l^{-1} h^{-1}). Data from all stations: n = 24; r_S: correlation coefficient; p: error probability; *: significantly correlated with $p < 0.05$

		Salinity	T_W	DIN	DOC	Seston	POC	C:N in POM
Bacteria	r_S	−0.48*	0.12	0.51*	0.71*	0.43*	0.84*	0.07
	p	0.02	0.59	0.01	0	0.04	0	0.74
Chl *a*	r_S	−0.45*	0.09	0.43*	0.82*	0.53*	0.81*	0.21
	p	0.03	0.68	0.03	0	0.01	0	0.33
Protozoan biomass	r_S	−0.69*	−0.10	0.41*	0.70*	0.24	0.62*	−0.03
	p	0	0.64	0.04	0	0.26	0	0.89
Thymidine uptake	r_S	−0.27	−0.36	0.48*	0.71*	0.46*	0.72*	0.31
	p	0.21	0.09	0.02	0	0.03	0	0.14
Leucine uptake	r_S	−0.11	0.18	0.24	0.45*	0.61*	0.59*	0.38
	p	0.60	0.42	0.26	0.03	0	0	0.06
Respiration	r_S	−0.08	−0.22	0.36	0.58*	0.70*	0.71*	0.42
	p	0.73	0.34	0.10	0.01	0	0	0.05
Esterase	r_S	−0.37	0.29	0.28	0.77*	0.64*	0.85*	0.17
	p	0.07	0.18	0.18	0	0	0	0.43
Peptidase	r_S	−0.54*	0.28	0.30	0.84*	0.53*	0.85*	0.13
	p	0.01	0.19	0.15	0	0.01	0	0.55

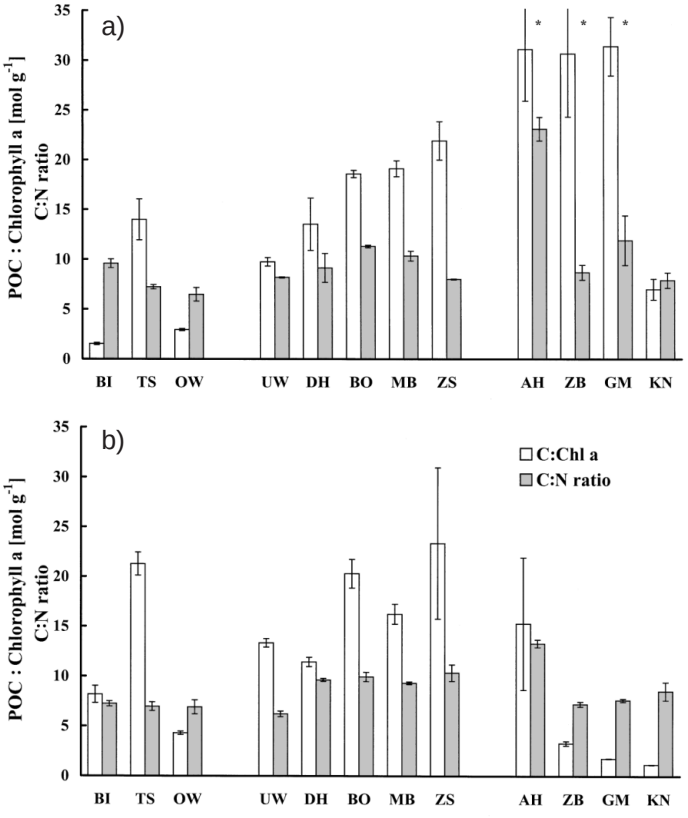

Fig. 4. POC:chlorophyll *a* (chl *a*) (mol g^{-1}) and C:N ratios of particulate matter (mol:mol) in (a) winter and (b) spring. Stations are arranged as in Fig. 2 (see Fig. 1 for station abbreviations). Error bars: SD of 3 replicate measurements. *Samples with resuspended sediments excluded from statistical analyses

ence with resuspended material, because they were taken during or immediately after storms. The ratios were considerably smaller in spring (Fig. 4).

POC and DOC were strongly correlated with biomass and activities of all micro-organisms. Community respiration, hydrolytic enzyme activities and bacterial production were all also significantly correlated to organic matter quantities. However, there was no correlation to the C:N ratio of POM (Table 2).

Heterotrophic organisms

Bacteria in the freshwater systems reached between 4.4 and 10.9×10^6 cells ml^{-1} and were exceeded 2-fold by cell numbers in the estuarine samples. In contrast, bacteria in the Baltic Sea samples were 7-fold lower than in the estuaries. Differences between cell numbers in winter and spring were not significant.

In winter, up to 19 ciliates were counted per ml. Heterotrophic flagellates averaged 782 ml^{-1} in freshwater and 1510 ml^{-1} in estuarine samples. Flagellates were then completely absent in the Baltic Sea. In ¾ of the samples, protozoan abundance was much higher in spring, with ciliates increasing to 43, 60 and 8 ml^{-1} in freshwater, estuaries and the Baltic Sea, respectively. Heterotropic flagellates increased to 2170, 4670 and 360 ml^{-1} in freshwater, estuaries and the Baltic Sea, respectively (Fig. 5).

Bacteria dominated heterotrophic biovolume at 82% on average at all stations. Ciliates accounted for 12% of biovolume because of their much higher individual volume in comparison to flagellates. Heterotrophic flagellates, most of them in the 'nano' size class between 2 and 20 µm in diameter, reached only 6% on average and up to 29% maximum of total heterotrophic biovolume. While differences between stations and seasons were insignificant, bacteria, protozoa and phytoplankton were significantly correlated (Table 3).

Heterotrophic activities

The limnetic waters were characterised by comparably low bacterial production rates (average 51 µg C l^{-1} d^{-1}). At nearly all estuarine stations, the bacterial carbon production was higher than in the other envi-

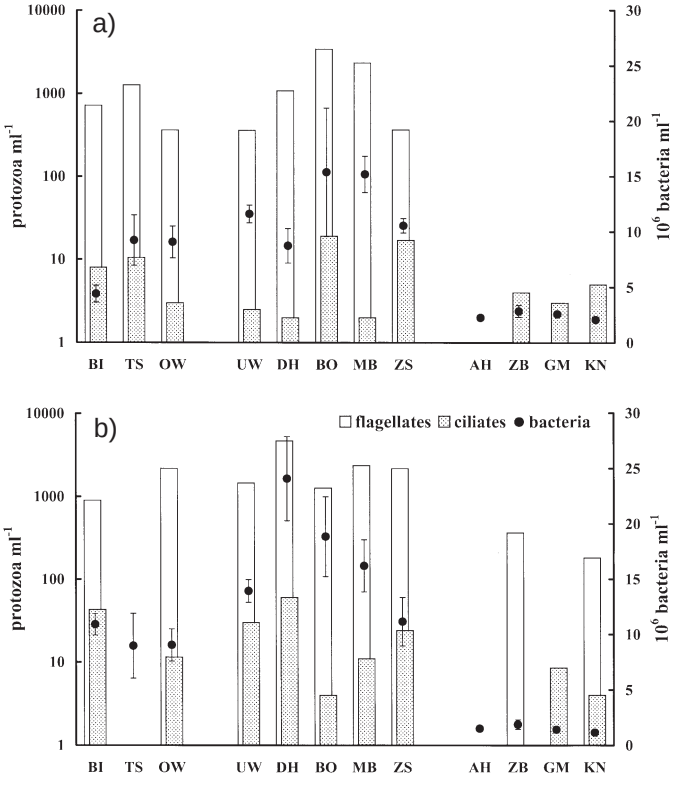

Fig. 5. Abundances of heterotrophic micro-organisms (ind. ml^{-1}) in (a) winter and (b) spring. Stations are arranged as in Fig. 2 (see Fig. 1 for station abbreviations). Error bars of bacterial abundance: SD of 4 replicate measurements

Table 3. Spearman rank order correlation between bacteria (10^6 ml^{-1}), chlorophyll *a* (chl *a*) (µg l^{-1}), protozoan biomass (mg C l^{-1}) and bacterial production measured by thymidine (T) and leucine (L) uptake (µg C l^{-1} d^{-1}), bacterial productivity calculated as ratios between production and biomass (P:B) on the basis of T and L incorporation (µg C µg C^{-1} d^{-1}) community respiration (µmol O_2 l^{-1} h^{-1}), esterase and peptidase activity (µmol l^{-1} h^{-1}), cell specific enzyme activities (fmol l^{-1} h^{-1}) calculated from bacterial abundances, portions of free-dissolved enzyme activities (%). Data from all stations: n = 24; r_S: correlation coefficient; p: error probability; *: significantly correlated with $p < 0.05$

		Bacteria	Chl *a*	Protozoan biomass
Thymidine uptake	r_S	0.65*	0.77*	0.59*
	p	0	0	0
P:B ratio (T)	r_S	−0.12	0.25	0.04
	p	0.59	0.23	0.84
Leucine uptake	r_S	0.63*	0.62*	0.36
	p	0	0	0.08
P:B ratio (L)	r_S	−0.23	−0.02	−0.27
	p	0.28	0.91	0.20
Respiration	r_S	0.77*	0.71*	0.48*
	p	0	0	0.03
Esterase activity	r_S	0.80*	0.80*	0.65*
	p	0	0	0
Cell specific esterase	r_S	0.72*	0.69*	0.70*
	p	0	0	0
Portion of free esterase	r_S	−0.76*	−0.78*	−0.78*
	p	0	0	0
Peptidase	r_S	0.80*	0.92*	0.68*
	p	0	0	0
Cell specific peptidase	r_S	0.78*	0.90*	0.74*
	p	0	0	0
Portion of free peptidase	r_S	−0.35	−0.39	−0.20
	p	0.09	0.06	0.34
Bacteria	r_S	–	0.73*	0.68*
	p		0	0
Chl *a*	r_S		–	0.68*
	p			0

ronments (200 µg C l^{-1} d^{-1}). Lowest production rates occurred at the Baltic Sea stations (29 µg C l^{-1} d^{-1}; Fig. 6). The productivity, expressed as production per biomass per day (P:B) based on thymidine uptake reached 0.3 for the freshwater bacteria, 0.6 at the estuarine stations and 0.5 in the Baltic Sea. In only 4 samples did bacterial production rates increase at higher water temperatures in spring (Fig. 6). The molar ratio between leucine and thymidine uptake was on average 6 for the freshwater stations, 3 for the estuarine and 4 for the Baltic Sea samples.

The freshwater samples had low community respiration rates (average 130 µg C l^{-1} d^{-1}). Respiration was highest in the estuarine samples (913 µg C l^{-1} d^{-1}) and lowest in the Baltic Sea (103 µg C l^{-1} d^{-1}). Higher water temperatures in spring did not result in significantly higher respiration rates (Fig. 6).

Esterase and peptidase activities were moderate in the freshwater systems and highest at the estuarine stations. At the Baltic Sea stations, the esterase activity was on average 4-fold lower than at the estuarine stations, but the peptidase activity was even lower (34-fold) (Fig. 7). In the limnetic and brackish samples, the esterase exceeded the peptidase activity by 3- to 15-fold. Because of the very low peptidase activities in the Baltic Sea samples, this ratio ranged from 21- to 91-fold. The portion of free-dissolved esterase was, even at 38%, rather high in fresh and estuarine waters, but much higher at the Baltic Sea stations (79%). In contrast, free-dissolved peptidase was not significant, contributing only up to 8% of the total activity. At all stations, spring values were on average only 1.5-fold higher for esterase and 2.3-fold higher for peptidase compared to the winter activities.

Bacterial production and hydrolytic enzyme activities increased significantly with bacterial abundance. The bacterial activities were also significantly correlated to phytoplankton and protozoa, but because micro-organism abundance or biomass were also correlated, it is impossible to prove direct interrelationships between bacterial production and phytoplankton or protozoa. Bacterial productivity (P:B ratio) did not change with bacteria or any other biomass parameter (Table 3). In contrast, hydrolytic enzyme activity normalised to bacterial cells was higher in samples with high bacterial abundance. Community respiration was correlated to all micro-organism biomass parameters (Table 3).

DISCUSSION

Darß-Zingst bodden—rich in POM

Salinity, DOC:POC ratios and the concentrations of each were chosen as the main parameters to group the sampled stations. At the freshwater sites, DOC was as high as at the estuarine bodden locations, but POC was much lower. At the Baltic Sea stations, both POC and DOC were lower than at any other investigated station (cf. Fig. 2). In contrast, the POC concentrations of the limnetic and marine sites were well in the range of values reported for other freshwater or marine systems, respectively. POC in the bodden was rather high in comparison to other estuaries (cf. overview in Schumann et al. 2001). DOC concentrations of the meso- to

eutrophic freshwater sampling sites were similar to those of other eutrophic lakes. The DOC content in the Darß-Zingst bodden was rather moderate, although they are hypertrophic. There are several large estuaries and hypertrophic or humic lakes with maximum DOC concentrations about twice as high. DOC concentrations in the open ocean peak at about 3 mg l^{-1}. In different parts of the Baltic Sea, up to 4.8 mg DOC l^{-1} was observed, which is similar to the maximal 5.5 mg C l^{-1} we measured at the outer coastal stations (Table 4). These values are the result of the important freshwater influx by rivers transporting organic matter into the almost completely enclosed Baltic Sea (Zweifel et al. 1995; cf. Fig. 2 for salinities). The range of DOC:POC ratios of 1 to 2 in the Darß-Zingst bodden chain (cf. Fig. 2) is at the lower end of reported values for polluted or eu- to hypertrophic waters (Table 4). The origin of the high POC levels in the Darß-Zingst bodden, which lowers the DOC:POC ratios so drastically, is assumed to be mainly autochthonous (Schumann et al. 2001) and is produced mainly by phytoplankton (Meyercordt et al. 1999).

There were DIN concentrations of up to 290 µmol l^{-1} at the estuarine stations and in the river Oberwarnow (cf. Fig. 3), so that a N-limitation of phytoplankton growth can be excluded at least for these sites and sampling dates. Nevertheless, their average C:N ratio of 9.1 was not lower than the average of all stations (cf. Fig. 4). However, for samples with a C:N ratio above 8.3, a moderate N-limitation of phytoplankton growth is assumed (Hecky et al. 1993). C:N ratios of marine phytoplankton growing with sufficient nitrogen are far lower, ranging between 3.5 and 6.9 (Jørgensen et al. 1991). While C:N ratios of flagellates exhibit similar values (Eccleston-Parry & Leadbeater 1995), bacteria can have C:N ratios as low as 1.2 (Kuipers et al. 2000), but on the other hand can reach 13 when they grow very slowly (Goldman & Dennett 2000). However, the average C:N ratio of the Darß-Zingst bodden samples (median = 9.8, n = 8) was significantly higher than that of the freshwater samples (median = 7.1, n = 6, p = 0.02). In the bodden, up to 90% of POC does not belong to the biomass of micro-organisms, but represents refractory material with obviously little nitrogen content. Moreover, substantial parts of POC are not protein or carbohydrates (Schumann et al. 2001). Although the C:N ratio is not extraordinarily high, most POM is not readily degradable and may persist in the system. The biochemical composition of POM and its accessibility to micro-organisms, e.g. large mucus envelopes, particle sizes, aggregation status, limit its degradation additionally to nitrogen concentrations. Therefore, C:N ratios are not sufficient to assess the remineralisation rate of organic matter or explain its limitation by a single element, such as nitrogen.

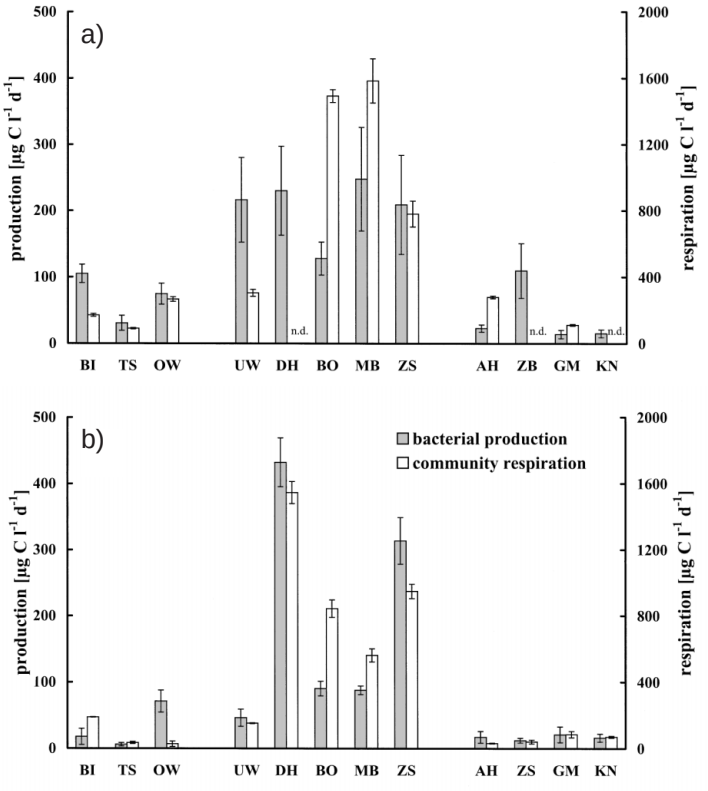

Fig. 6. Bacterial production calculated from ^{3}H-thymidine uptake and community respiration (µg C l^{-1} d^{-1}) in (a) winter and (b) spring. Stations are arranged as in Fig. 2 (see Fig. 1 for station abbreviations). Error bars: SD of 5 replicate measurements for bacterial production and SE of the slope (linear regression of oxygen consumption over time). nd: not determined

The POC:chl *a* ratios of up to 23 mol C (g chl *a*)$^{-1}$ also seem to indicate nutrient-limited growth of phytoplankton in ¾ of all samples, if the indicator value of 4.2 to 8.3 for moderate and >8.3 for severe nutrient depletion is applied (Hecky et al. 1983). The POC:chl *a* ratios of the Darß-Zingst bodden samples were all >11, but not significantly different from the freshwater and marine sites (cf. Fig. 4). However, POC:chl *a* ratios of phytoplankton are strongly species specific, increase significantly with light (Falkowski et al. 1985) and decrease with nitrogen availability (e.g. Riemann et al. 1989) or under mixotrophic growth (Laliberté & de la Noüe 1993). As there are so manifold influential factors on cellular chl *a* content, direct conclusions cannot be drawn from POC:chl *a* ratios. The high ratios, especially in the Darß-Zingst bodden, should better be interpreted as a small contribution of phytoplankton carbon to POM unless biovolumes are quantified and converted to carbon.

The high C:N ratio, the low chl *a* content along with the high percentages of non-carbohydrate and non-

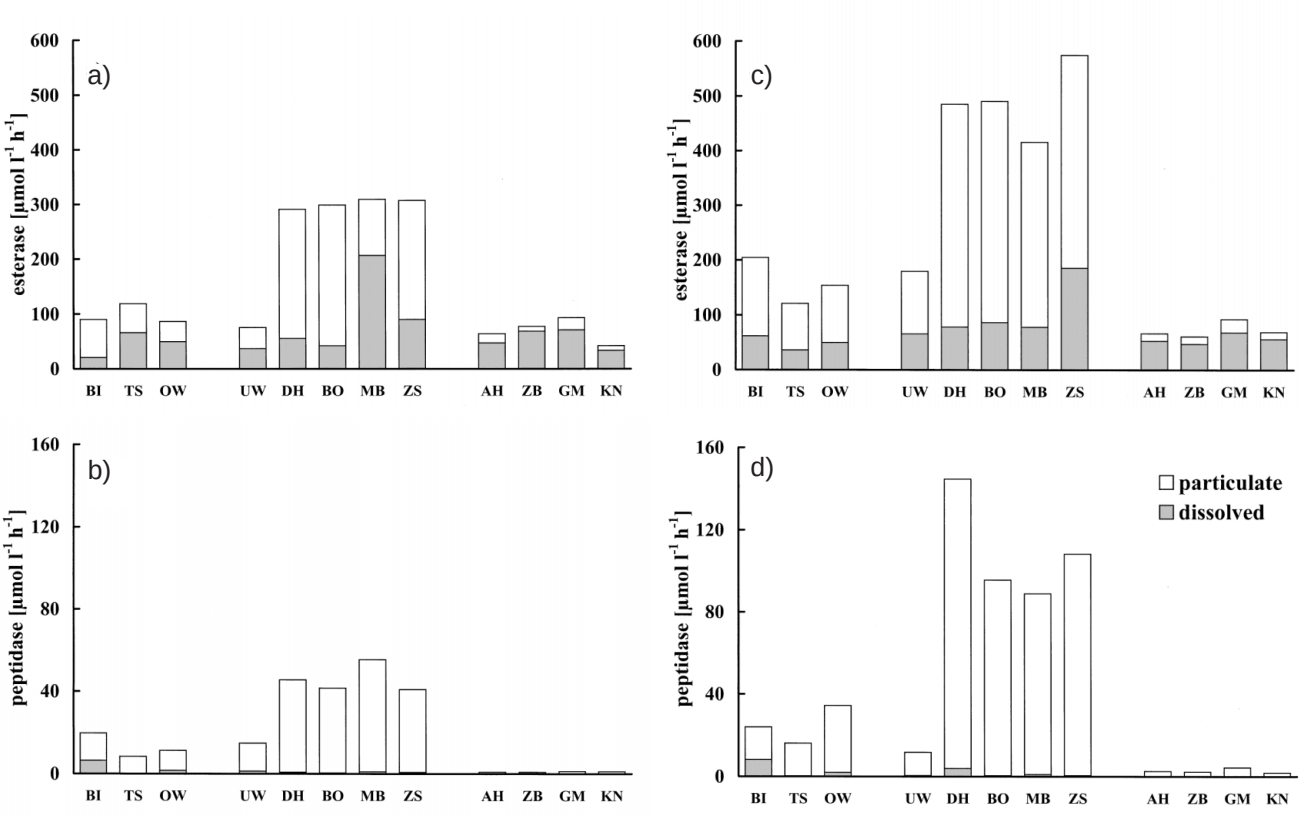

Fig. 7. (a) Particle-associated and free-dissolved esterase and (b) peptidase activity (µmol l^{-1} h^{-1}) in winter and (c) esterase and (d) peptidase activity in spring. Stations are arranged as in Fig. 2 (see Fig. 1 for station abbreviations)

protein material (Schumann et al. 2001) in POM of the Darß-Zingst bodden chain indicate a high contribution of refractory material to POM. The small rivers and brooks entering the bodden chain carry only a small load of POM, but high amounts of DOM (unpubl. data). Additionally, only 10% of water influx is freshwater (Schlungbaum et al. 1994). Therefore, rivers cannot be an important source for the high POM values in the bodden. The low contribution of phytoplankton biomass to POM measured on a volume and carbon concentration basis (Schumann et al. 2001), which is also reflected by the high POC:chl *a* ratios, leads to the conclusion that most of the POM is not 'new' material, but strongly degraded. This degradation takes place mostly in the sediments. Due to frequent wind-induced resuspension of the upper sediment particles, this decomposed material is mixed into the pelagial (Rieling 2000). The narrow connection to the Baltic Sea in the east (cf. Fig. 1) restricts the exchange with the Baltic Sea, so that the water exchange rates are about 6- to 7-fold yr^{-1} in the innermost Saaler Bodden at Stn DH and 55-fold in the Barther Bodden at Stn MB (Schlungbaum et al. 1994). The POM export from the bodden into the Baltic Sea must be small.

Darß-Zingst bodden—high abundance of heterotrophic micro-organisms

Bacterial abundance was highest in the hypertrophic Darß-Zingst bodden (cf. Fig. 5), but did not reach the extreme values of up to 46×10^6 ml^{-1} reported for these systems in Klinkenberg & Schumann (1995). Bacterial numbers in the limnetic samples of 4 to 11×10^6 ml^{-1} are typical for many other freshwater systems of all trophic grades. There are several reports of higher bacterial cell numbers in the Baltic Sea than we quantified in our samples (cf. overview in Klinkenberg & Schumann 1995). This may be due to the low water temperatures of up to 5.5°C even in the spring samples (cf. Table 1).

Heterotrophic ciliate abundance in the Darß-Zingst bodden chain was in the range of that reported for earlier years (Schumann & Schiewer 1994). Since 1991/1992, ciliates have been dominated by small species (<40 µm diameter) of the orders Oligotrichida, Hymenostomatida and Cyclotrichida. Similar high abundances were only found in eu- and hypertrophic lakes (cf. overview in Foissner et al. 1999) or in the Rhode river estuary (Dolan & Gallegos 1991), especially if minute or nanociliates prevailed as in the Darß-

Zingst bodden. Such small ciliates are predominantly bacterivorous (Šimek et al. 1990, Sommaruga & Psenner 1995).

The abundance of heterotrophic flagellates, most of them in the 'nano' size class, peaked at a comparably high value of 4700 ml^{-1} in the Darß-Zingst bodden (cf. overview in Sanders et al. 1992), and exceeded that in several other estuaries (Dolan & Gallegos 1991, Laybourn-Parry et al. 1992, El Serehy & Sleigh 1993) and some lakes (Carlough & Meyer 1991, Vörös et al. 1996). Heterotrophic nanoflagellates were not so abundant at the limnetic stations and in the Baltic Sea (cf. Fig. 5) although they are the main grazers of bacterioplankton in most aquatic systems. The abundance of both bacteria and flagellates related mainly to the trophic status and not to salinity (Sanders et al. 1992). Since bacterial and flagellate abundances are positively correlated, if data of various systems are considered (Berninger et al. 1991), the supply of bacteria as flagellate food seems to control their growth from bottom-up. How-

Table 4. DOC concentrations (mg C l^{-1}) and DOC:POC ratios in marine, estuarine and limnetic waters

	Characteristics	DOC	DOC:POC	Source
Marine				
Georges Bank	Continental shelf	0.6–1.0		Chen et al. (1996)
Middle Atlantic Bight		0.6–1.1		Guo et al. (1995)
Arctic ice		1.3		Amon et al. (2001)
Bedford Basin, Nova Scotia	Small coastal bay	0.8–1.9		Kepkay et al. (1993)
Gulf of Mexico		0.5–2.6		Guo et al. (1994, 1995)
Baltic Sea (Bothnian Sea)		3.0–4.8		Zweifel et al. (1995)
Baltic Sea (Kattegat)	Coastal area	Averages: 2.4–4.3		Middelboe & Søndergaard (1995)
Southern Baltic Sea	Mesotrophic coastal area	3.7–5.5	5–138	This study
Southern Baltic Sea		Averages: 5.7–5.9		Ferrari et al. (1996)
Alexandria Harbour	Highly polluted		2.5	Abdel Moati et al. (1991)
Gulf of Trieste (Adriatic Sea)		1–10		Herndl & Malacic (1987)
Estuarine				
Pawcatuck River Estuary	Polluted	Averages: 2–7		Doering et al. (1994)
Unterwarnow	Polluted	7.6–9.8	5–6	This study
2 Florida salt marshes		3.0–12.1		Coffin et al. (1993)
Darß-Zingst boddens	Eu- to hypertrophic	9.1–13.3	1–2	This study
Massachusetts estuaries		2.4–14.4		Peterson et al. (1994)
Delaware Bay salt marsh		1.5–15.5		Roman & Daiber (1989)
5 Florida estuaries		4.3–29.6		Coffin et al. (1993)
Limnetic				
Lago Maggiore		Averages: 0.8–1.5		Bertoni & Callieri (1992)
Lake Constance	Mesotrophic	1.4–2.3		Weiss & Simon (1999)
Lake Klintsjön	Oligotrophic clearwater	3.1		Tranvik & Jørgensen (1995)
Paraná River		1.3–5.5	4–18	Depetris & Kempe (1993)
River Öre		Averages: 6.0–6.9		Wikner et al. (1999)
20 lakes in southern Québec		Averages: 2.7–7.5		del Giorgio & Peters (1994)
Lake Kjelsåsputten	Small, humic	7.5	4	Hessen (1992)
Esrum Sø	Mesotrophic	Averages: 5.1–8.3		Middelboe & Søndergaard (1995)
Lake Skärshultsjön	Oligotrophic humic	10.3		Tranvik & Jørgensen (1995)
Bastrup Sø	Eutrophic	Averages: 11.0–11.4		Middelboe & Søndergaard (1995)
3 freshwaters (NE Germany)	Meso- to eutrophic	8.8–12.2	8–22	This study
Chillisquaque Creek system	Fed by a eutrophic pond	4.9–13.7		Ciaio & McDiffett (1990)
River Meuse	Polluted	ca. 3–14	1–12	Descy & Gosselain (1994)
Frederiksborg Slotsø	Hypertrophic	Averages: 10.3–15.2	ca. 2–4	Middelboe & Søndergaard (1995), Søndergaard et al. (1995)
Grib Sø	Humic	Averages: 16.6–19.7		Middelboe & Søndergaard (1995)
River Kiiminkijoki	Humic	7.8–21.3	3–22	Heikkinen (1989)
River Krutynia	Lake-river system	6.5–23.8	>3	Radwan et al. (1992)
Hartbeespoort Dam	Hypertrophic reservoir	5.0–24.8		Robarts et al. (1990)
Lake Mekkojärvi	Acid, polyhumic	8.0–25.0		Münster et al. (1992)

ever, there is also evidence of a strong top-down control of the flagellate biomasses (Gasol et al. 1995). Nevertheless, heterotrophic nanoflagellates remove substantial parts of bacterial production (up to 21% bacteria d^{-1}; Šimek et al. 1990). Moreover, they seem to graze especially on the active portion of bacterioplankton (del Giorgio et al. 1996). Therefore, data on nanoflagellates should always be included in the discussion of bacterial activity.

Although the abundances of heterotrophic nanoflagellates were high in the bodden, bacterial cell numbers were also high (cf. Fig. 5) and could have sustained many more flagellates (Berninger et al. 1991). The top-down control of the main bacterial grazers does not seem to be strong enough to reduce their cell numbers further. This could have been caused by a high grazing pressure on flagellates performed by ciliates. Abundances of almost 400 ind. ml^{-1} were observed earlier in the bodden (Schumann & Schiewer 1994), but not during the investigation period in 2000. Such high abundances of 200 ciliates ml^{-1} were found only occasionally in some hypertrophic lakes (Foissner et al. 1999). In contrast to the high protozoan biomasses in the bodden, at the Baltic Sea locations, nanoflagellates were often absent. Ciliate abundances were well in the range of mesotrophic lakes (Foissner et al. 1999). Nevertheless, bacterial abundance remained low, indicating a bottom-up limitation of bacteria, probably simply by temperature (cf. T_W in Table 1 and bacterial production in Fig. 6). However, since we could not estimate grazing rates of flagellates on bacteria, feeding modes and preferred food types of ciliates, we cannot prove that ciliates regulate flagellate development or if ciliates themselves feed substantially on bacteria. This open question also demonstrates the importance of thorough investigations on aquatic protozoa. Unfortunately, protozoa are not part of any European or national monitoring program, which include phytoplankton, macrozoo- and macrophytobenthos, and sometimes metazooplankton. Aquatic bacteria are investigated solely with respect to human pathogenity. Data on bacteria, protozoa and microbial turn-over of organic matter can therefore only be derived from basic research of universities or research institutions, which often cannot sustain long-term or large-scale research strategies.

Darß-Zingst bodden—high microbial activities, but low bacterial productivity

The freshwater and Baltic Sea samples had production rates higher than the average of freshwater or marine systems, respectively. However, from eutrophic and polluted freshwater sites there are occasional reports of higher maximal production rates (Chrzanowski & Hubbard 1989, Hudson et al. 1992, Servais & Garnier 1993). Although bacterial production in the Darß-Zingst bodden was enhanced compared to the other investigated systems (cf. Fig. 6), it was in the typical range for estuarine and coastal locations (cf. overview in White et al. 1991). Compared to the high standing stock of bacterioplankton in the bodden (Klinkenberg & Schumann 1995), bacterial production is rather low, which is reflected by a low productivity of 0.6 d^{-1} (0.1 to 0.8 d^{-1}). Bacterial productivity at the investigated freshwater and Baltic Sea stations was even lower (0.3 and 0.5 d^{-1}).

Community respiration was low at the investigated freshwater stations (28 to 267 µg C l^{-1} h^{-1}) and at the Baltic Sea coast (32 to 279 µg C l^{-1} h^{-1}). The daily respiration in the Darß-Zingst bodden was in the range of eutrophic lakes (e.g. Schwaerter et al. 1988) and reached, at a maximum (up to 1585 µg C l^{-1} h^{-1}), values of a fertilised fish pond (Szyper et al. 1992). Because the contribution of bacteria to the community respiration was not investigated, we cannot conclude something about bacterial specific activity. The high protozoan abundance, especially in the bodden, suggests a high contribution of these heterotrophic organisms to the community respiration. The respiration of the high phytoplankton biomass in the bodden (Schumann et al. 2001) may substantially contribute to total community respiration in the dark, not only at night, but also due to a very low light penetration during the day (Sagert & Schubert 1999).

The activity of leucine-aminopeptidase of 0.9 to 4 µmol l^{-1} h^{-1} measured in the Baltic Sea samples is very high compared to published values. Only in the Adriatic Sea were similar high values of 0.1 to 1.7 µmol l^{-1} h^{-1} found (Karner et al. 1992). Peptidase activities measured in the fresh and brackish water samples were at least 6-fold higher than those we found in the literature for highly eutrophic systems (e.g. Hoppe et al. 1998). These comparatively high values could be the result of some of the methodological conditions we chose. We used almost optimal pH and temperature conditions for aminopeptidases (cf. Chróst 1992). The linear increase of the fluorescent hydrolysis product was surveyed in every sample. The incubation time was adjusted accordingly. We dissolved the only slightly water-soluble fluorogenic substrates in a very strong organic solvent like Hoppe et al. (1988), which insures that all fluorogenic substrate molecules are available to the enzymes. On the other hand, most of the samples were taken from very shallow waters, where much resuspended material from the sediment surface can be found in the pelagic zone (cf. POC in Fig. 2). Therefore, particle-associated micro-organisms from the benthal and their enzymes were included in

the measurements of the plankton samples, which may have contributed substantially to total enzyme activity. However, it remains unclear why we could not measure higher cell-specific bacterial production rates. One reason may be that the oxygen-saturated pelagic conditions suppress the growth rates of anaerobic and facultatively aerobic bacteria from the anoxic sediments if they are resuspended. The high free-dissolved esterase activity we measured in all pelagial samples (Fig. 7a,c) is, on a volume basis, well within the range measured for the upper cm of sediments in neighbouring coastal waters (Köster et al. 1997). This may be due to resuspension of material or even dissociation of enzyme molecules into the water column from the sediments. Unfortunately, quantitative data for esterase activities in different pelagic systems are very rare, because most researchers concentrate on peptidases, chitinases, glucosidases and phosphatases (e.g. Hoppe et al. 1998). All parameters of microbial activity measured in this study, increased significantly with POC, DOC and bacterial abundances (Tables 2 & 3). Unlike the P:B ratios of bacteria, the cell-specific enzyme activities were significantly correlated with bacterial cell numbers. This suggests that samples with high concentrations of organic matter and bacteria had not only more bacteria but more hydrolytically active bacteria. However, this interpretation of ratios and correlations holds true only if the assumption is made that bacteria are the sole or predominant source of hydrolytic enzyme activities in water samples, which may not be always the case (cf. Schumann et al. 2003).

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