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Bacterial numbers, biomass and productivity in the Baltic Sea: a cruise study

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ABSTRACT: Bacterial numbers, biomass and productivity were studied during 2 cruises in the Baltic Proper, Gulf of Finland and the Bothnian Sea. Bacterial populations in the open sea area had longer turnover times and lower productivity than in coastal areas, comparable to those found in the open ocean, but their biomass and abundance were as high as in the coastal areas of the Baltic Sea. High bacterial productivity in the aphotic water layer in the Gulf of Finland is suggested to indicate eutrophication of this area.

INTRODUCTION

Bacteria have been recognized as a key component in the trophic dynamics of pelagic marine ecosystems (Azam et al. 1983). This has created an urgent need to quantify the flow of organic matter and energy through bacteria. Despite the generally accepted view of the importance of bacterioplankton in pelagic marine food-webs, there are few data available on microbial parameters in the open Baltic Sea. As early as 1969, Seppänen & Voipio (1971) studied the vertical distribution of different types of bacteria at the Gotland Deep (250 m) in the Central Baltic Sea, and found a correlation between bacteriological and physico-chemical parameters. This interesting area with distinctive hydrographical characteristics – oxic water down to a depth of about 100 m, with an underlying transition zone and anoxic water – was also studied by Gast & Gocke (1988). They demonstrated the change in the bacterial population associated with the transition from oxic to anoxic conditions.

Total bacterial numbers, viable counts and maximum glucose uptake velocity in the Bornholm Basin, Danzig Deep and Gotland Deep were studied by Gocke (1977). Väätänen (1980a) compared abundances of certain micro-organisms in the Northern Baltic Proper and in the Gulf of Finland. Both Gocke and Väätänen suggested that phytoplankton blooms are important for offshore microbial populations, since the open Baltic areas are only indirectly influenced by allochthonous organic matter. Väätänen (1980b) found that organic matter, water temperature, chlorophyll *a* and salinity had the greatest effect on microbial populations off the southern coast of Finland. Community respiration and development of bacterial numbers and productivity were followed by Lahdes et al. (1988) during the vernal growth period in the open northern Baltic Proper. They found that almost 70% of bacterial production and consumption took place in the 0 to 30 m water layer, and bacteria accounted for about 13% of the net primary production in the same water layer. The depth at the sampling site was 158 m. Bölter & Rheinheimer (1987) studied the microbial and chemical characteristics of the central and western Baltic Sea and were able to distinguish geographical zones on the basis of statistical analysis of the data. Rheinheimer et al. (1989) compared hydrographic conditions and microbiological variables in the Baltic Proper and Gulf of Bothnia. Although there were large differences among particular areas, there were also common features: the number and activity of bacteria were always highest in the photic zone and lowest in the zone between the thermocline and the halocline, which is often called 'winter water'.

In this study bacterial numbers, biomass and productivity, as well as other biological and physico-chemical characteristics, were measured during 2 cruises in the Baltic Proper, Gulf of Finland and the Bothnian Sea. The purpose of this paper is to review these results and to examine the relationships between the measured parameters.

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MATERIAL AND METHODS

Study area. The Baltic Sea is the largest brackish water area in the world. A prominent feature of the Baltic Sea is salinity stratification, with low-salinity surface water caused by freshwater affluents, and high salinity in deep and bottom waters due to the inflow of North Sea water. Salinity is lowest in the Gulf of Bothnia (1 to 6‰ in surface water and 3 to 7‰ in deep water) and in the Gulf of Finland (3 to 6‰ and 5 to 9‰ respectively), and higher in the Baltic Sea proper (6 to 9‰ and 10 to 13‰ respectively) (Kullenberg 1981). Salinity increases from east to west and from north to south. In summer the thermocline is sharp and the euphotic zone is about 20 m deep in most parts of the Baltic Sea. Another characteristic feature is that the Baltic Sea is partly covered with ice during the winter.

Sampling. Water samples were taken during 2 cruises of RV 'Aranda' in summer 1987. The first cruise, proceeding from the Gulf of Finland to the Bothnian Sea, took place from 14 to 22 July (Stns LL7, IU3, Eros20, Kns, Eros23, TKH37 and X1), and the second to the Gulf of Finland and to the Baltic Proper from 24 August to 3 September (Stns LL3a, LL11, LL15, BY31, BY38, BCSIII12, HBP215, HBP139 and GDR113). Samples were taken when the research vessel arrived on station, but always between sunrise and sunset. The earliest sampling time was 08:00 h and the latest 18:50 h (+3 GMT). During the first cruise bacterial parameters were measured in the surface water layer, and during the second cruise also at one aphotic depth. The same bacterial parameters were measured during both cruises, but physico-chemical parameters, except for temperature, salinity, and phytoplankton parameters, were only measured during the second cruise. The positions of the sampling stations are shown in Fig. 1.

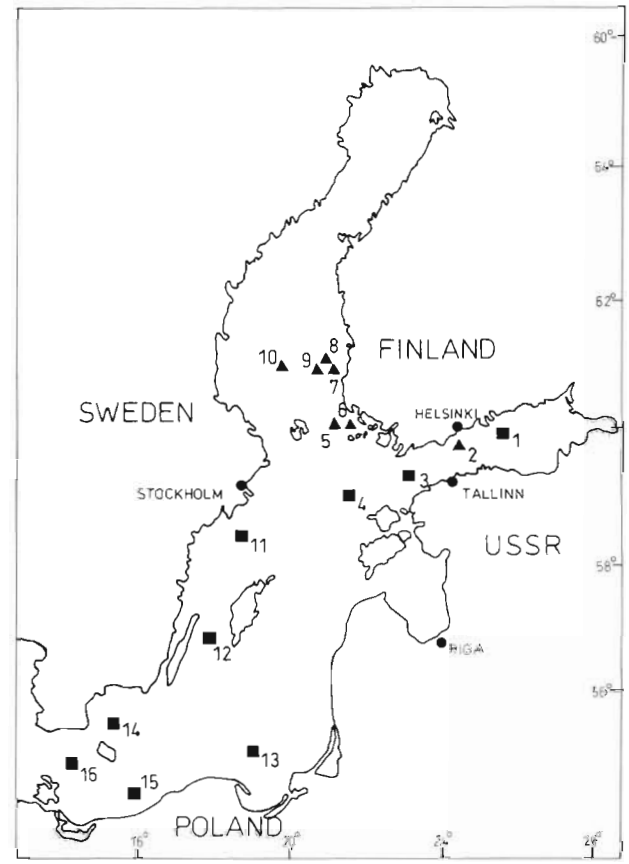

Fig. 1. Positions of sampling stations in the Baltic Sea. First cruise (▲): 2 = LL7 (59°51'N, 24°50'E), 5 = IU3 (60°20'N, 21°07'E), 6 = X1 (60°21'N, 21°36'E), 7 = Eros20 (61°15'N, 20°51'E), 8 = TKH37 (61°19'N, 20°47'E), 9 = Eros23 (61°15'N, 20°39'E) and 10 = Kns (61°18'N, 19°20'E). Second cruise (■): 1 = LL3a (60°04'N, 26°20'E), 3 = LL11 (59°35'N, 23°18'E), 4 = LL15a (59°13'N, 21°37'E), 11 = BY31 (58°35'N, 18°14'E), 12 = BY38 (57°07'N, 17°40'E), 13 = BCSIII12 (55°15'N, 18°43'E), 14 = HBP215 (55°37'N, 14°52'E), 15 = HBP139 (54°27'N, 15°45'E) and 16 = GDR113 (54°55'N, 13°57'E)

Hydrographical, chemical and phytoplankton variables. Temperature and conductivity were measured with a CTD-sonde (Mark III, Neil Brown) and salinity was computed from the data according to UNESCO (1981). Dissolved oxygen, pH and nutrients were determined according to Grasshoff et al. (1983). Dissolved inorganic phosphate, total phosphorus, nitrite, nitrate and total nitrogen were analysed on a Technicon autoanalyzer. Silicate-silicon and ammonia were analysed on an Akea autoanalyzer. Particulate phytoplankton primary productivity was measured in an incubator at in situ temperature using the ^{14}C technique (Steemann Nielsen 1952, Baltic Marine Environment Protection Commission 1984). Samples (30 ml) were illuminated for 2 h by tubes (Philips TLD 18 W/33); irradiance conditions ensured photosynthetic saturation. After the incubation the samples were filtered (Sartorius cellulose nitrate filters, pore size 0.45 µm). The filters were placed into glass vials and 100 µl acid (0.5 M HCl) was added to remove unincorporated ^{14}C. Chlorophyll *a* was assayed in 90% acetone and measured fluorometrically (Edler 1979).

Microbiological variables.

Bacterial abundance and biomass: Total number and biovolumes of bacteria were determined by the acridine orange direct count method (Hobbie et al. 1977), the measurements being carried out with a Leitz Laborlux D epifluorescence microscope and a Patterson Globe and Circle G1 grid (Graticules Ltd). At least 20 fields (about 10 to 20 cells field^{-1}) were counted and 60 cells measured per sample. A conversion factor of 0.35 pg C µm^{-3} (Bjørnsen 1986) was used to calculate biomass from cell volumes.

Estimation of bacterial productivity: Bacterial productivity was measured by the thymidine incorporation method (Fuhrman & Azam 1982). Preliminary experiments indicated that the thymidine uptake systems are

saturated at ca 5 nM in these areas and this time of year. Uptake was linear for at least 4 h. For practical reasons (methyl-^{3}H)thymidine (41 to 46 Ci mmol^{-1}, Amersham International) was added to 20 ml subsamples to give a final concentration of 10 nM, and the subsamples were incubated for 60 min. The incubations were started immediately after sampling and were carried out at in situ temperature in polystyrene boxes filled with water from the respective sampling depths. Incubation was terminated by adding formalin. Subsamples were extracted in 10 % TCA (5 ml) without delay and filtered (Asypor membrane filters, pore size 0.2 µm, Domnick Hunter Ltd). The filters were rinsed 5 times with 1 ml of 5 % TCA. Extraction and filtration were done in ice-cold conditions. The filters were kept in vials at +4 °C prior to addition of 10 ml of scintillation cocktail (Lumagel, Lumac), and the radioactivity retained on the filters assayed on a liquid scintillation counter (1217 Rackbeta, LKB Wallac). The assay was always carried out within 2 wk after sampling. Blank values from controls killed with formalin varied from 2 to 8 % of total incorporation for samples from the surface water, and from 11 to 36 % for samples from the aphotic water layer.

Bacterial productivity was estimated using a conversion factor of 1.1×10^9 cells nmol^{-1} (Riemann et al. 1987), carbon content of 0.35 pg C µm^{-3} (Bjørnsen 1986) and the mean cell volume. The mean cell volume of each sample was obtained by measuring 60 cells.

RESULTS

Bacterial abundance, biomass and production

During the first cruise surface water temperature was 14 °C at Stns 2, 5, 7, 9 and 10, 15 °C at Stn 8, and 19 °C at Stn 6. Salinity was within the range 5.4 to 6.3 ‰. The highest bacterial biomass (about 80 mg C m^{-3}) was found in the Bothnian Sea (Stns 7, 8, 9 and 10; Table 1). In the Gulf of Finland (Stn 2) and in the Archipelago Sea (Stns 5 and 6) the biomass was only half this. Bacterial numbers varied less than biomass, and ranged from 3.06 (Stn 10) to 5.70×10^6 cells ml^{-1} (Stn 2) (Table 1). Bacterial productivity was lowest in the Archipelago Sea (1.8 to 2.1 mg C m^{-3} d^{-1}, Stns 5 and 6) and highest (6.1 mg C m^{-3} d^{-1}, Stn 7) in the Bothnian Sea (Table 1).

Table 1. Thymidine incorporation (TdR; pmol l^{-1} h^{-1}), cell volume (V; µm^3), numbers (N; cells ml $\times 10^6$), bacterial productivity (P; mg C m^{-3} d^{-1}), biomass (B; mg C m^{-3}) and turnover time (T; days) at different sampling stations

Cruise stn	Stn no.	Depth (m)	TdR	V	N	P	B	T
1st cruise (14–22 Jul 1987)								
LL7	2	0	28.72	0.023	5.70	5.37	45.01	8.3
IU3	5	0	7.35	0.027	3.79	1.83	36.04	20
X1	6	0	10.93	0.021	4.10	2.12	29.94	14.3
Eros20	7	0	12.30	0.054	4.17	6.13	79.34	12.5
TKH37	8	0	7.00	0.050	4.66	3.24	81.98	25
Eros23	9	0	11.41	0.046	5.40	4.85	86.20	16.7
Kns	10	0	6.69	0.072	3.06	4.72	77.14	16.7
2nd cruise (24 Aug–3 Sep 1987)								
LL3a	1	0	14.36	0.039	3.45	5.17	47.43	9.1
		50	1.89	0.062	0.60	1.08	13.00	12.5
LL11	3	0	9.38	0.046	3.46	3.99	55.22	14.3
		50	0.85	0.049	0.45	0.38	7.72	20
LL15a	4	0	16.00	0.019	2.82	2.81	19.12	6.7
		50	0.25	0.040	0.40	0.09	5.58	50
BY31	11	0	11.37	0.029	4.36	3.05	43.72	14.3
		50	1.30	0.047	0.36	0.57	5.95	10
BY38	12	0	18.24	0.035	3.49	5.90	42.64	7.1
		50	1.89	0.044	0.50	0.77	7.75	10
BCSIII12	13	0	18.57	0.026	3.69	4.46	33.09	7.7
		50	1.79	0.049	0.38	0.81	6.43	7.7
HBP215	14	0	16.13	0.024	3.30	3.58	28.20	7.7
		50	1.85	0.027	1.15	0.46	10.99	25
BHP139	15	0	13.26	0.014	3.21	1.72	16.02	9.1
		40	1.65	0.016	0.75	0.24	4.18	16.7
GDR113	16	0	18.86	0.019	3.32	3.31	22.38	6.7
		40	3.13	0.014	2.21	0.41	11.19	25

During the second cruise the highest bacterial biomasses were found in surface water in the Gulf of Finland (Stns 1 and 3) with 47 and 55 mg C m^{-3} (Table 1). Bacterial biomass was lowest at Stn 4 (19 mg C m^{-3}) located in the northern Baltic Proper. From Stn 11 to the south as far as Stn 16, biomasses decreased from 44 to 16 mg C m^{-3}. Bacterial biomasses below the euphotic water layer were low, usually less than 10 mg C m^{-3}.

Bacterial numbers in the surface samples varied from 2.82 to 4.36×10^6 cells ml^{-1} (Table 1). Both Stn 11, which had the maximum abundance, and Stn 4, with minimum abundance, are located in the northern Baltic Proper. Bacterial numbers below the euphotic layer varied from 0.36 to 2.21×10^6 cells ml^{-1}.

Bacterial productivity in the surface water layer was highest (5.9 mg C m^{-3} d^{-1}) in the western Gotland Basin (Stn 12) and lowest at Stn 15 (1.7 mg C m^{-3} d^{-1}) in the southern Baltic Proper (Table 1). In the Gulf of Finland bacterial productivity decreased towards the entrance of the Gulf. Productivity was low in samples taken from depth 40 or 50 m, and was highest at Stn 1 (1.08 mg C m^{-3} d^{-1}). The results for physico-chemical parameters, chlorophyll *a* and primary productivity are listed in Table 2.

Turnover time

During the first cruise the turnover time of the bacterial population at Stn 2 in the Gulf of Finland was much shorter (8.3 d) than that at Stns 5 to 10 (from 12.5 to 25 d) in the Archipelago and Bothnian Seas (Table 1). This may reflect the coastal influence at Stn 2, e.g. more dissolved and particulate organic matter.

The turnover time of the surface sample bacterial populations during the second cruise was rather constant, except for Stn 3 in the Gulf of Finland and Stn 11 in the northern Baltic Proper, where it was much longer (14.3 d) than at the other stations (Table 1). The shortest turnover time (6.7 d) was recorded at Stn 4, in the northern Baltic Proper, and at Stn 16, in the southern Baltic Proper. The other area with a long turnover time (Landsort Deep, Stn 11) was also studied in July–August 1982 (Sörensson & Sahlsten 1987). The results indicated that bacteria play a minor role, having a low growth rate and a very low biomass. In the aphotic water layer, turnover time varied greatly from 7.7 d (Stn 13) to 50 d (Stn 4). The turnover time was usually longer in the aphotic water layer. Exceptions are 10 d in the aphotic water layer at Stn 11 compared to 14.3 d in the surface water layer and 7.7 d in both layers at Stn 13.

Relationships between parameters

Although the scarcity of the data does not permit comprehensive statistical analysis, correlation analysis was carried out on the surface sample data from the second cruise. There was significant correlation between bacterial abundance and the concentration of dissolved oxygen ($p < 0.05$), and between average bacterial cell volume and the concentration of chlorophyll *a* ($p < 0.05$). This may be because they were controlled by the same environmental factors.

Table 2. Depth (m), temperature (°C), salinity (‰), concentration of dissolved oxygen (mg l^{-1}), pH, concentration of chlorophyll *a* (mg m^{-3}), primary productivity (Pp; mg C m^{-3} h^{-1}), concentrations of PO_4, total phosphorus (TP), NO_2, NH_4, total nitrogen (TN) and dissolved inorganic silicate (Si) (mmol m^{-3}) at stations of the second cruise. bd: below detection limit

Stn	Depth	Temp.	Sal.	Oxyg.	pH	Chl	Pp	PO_4	TP	NO_2	NO_3	NH_4	TN	Si
1	0	14.6	4.12	7.1	8.4	3.9	11.9	0.03	0.4	0.03	0.03	0.11	24.8	1.4
	50	2.4	7.49	4.1	7.6			1.7	1.8	0.08	10	0.08	28	31
3	0	13.7	6.36	7.2	8.4	4.8		0.02	0.5	0.02	0.01	0.12	23.1	5.9
	50	3.1	7.20	7.0	7.9			0.8	1.0	0.43	6	0.14	23	18
4	0	14.0	7.01	6.2	8.4	3.2	9.4	0.01	0.5	bd	0.06	0.20	21.5	6.8
	50	3.0	7.39	7.5	8.1			0.4	0.7	0.24	1.1	0.6	20	10
11	0	13.0	6.14	7.6	8.3	3.5	9.3	0.03	0.2	0.01	0.16	0.55	19.4	7.6
	50	2.0	7.38	8.3	8.0			0.5	0.8	0.20	1.7	0.68	19	12
12	0	13.1	6.68	7.2	8.4	2.7	3.1	0.03	0.3	bd	0.04	0.20	20.0	8.0
	50	2.3	7.73	6.3	7.8			1.0	1.5	0.30	6	0.7	22	30
13	0	14.9	7.28	6.7	8.4	2.8		0.04	0.6	bd	0.03	0.08	19.1	6.6
	50	2.9	7.70	8.1	8.2			0.3	0.8	0.14	0.7	1.3	10	9
14	0	13.9	6.71	7.2	8.4	2.5	3.7	0.08	0.3	bd	0.06	0.54	20.0	8.8
	50	2.4	10.00	6.0	7.8			0.7	0.9	0.18	4	0.3	19	19
15	0	14.8	7.04	6.7	8.3	2.9		0.02	0.4	0.01	0.03	0.14	20.1	6.7
	40	2.4	8.79	6.3	8.0			0.5	0.6	0.30	2	2.0	21	15
16	0	14.8	7.44	7.0	8.4	3.5	7.3	0.05	0.4	0.05	0.03	0.1	22.3	8.2
	40	11.7	13.7	3.0	7.8			1.0	1.2	0.25	7	1.0	24	40

Table 3. Component loadings of the first and second principal component. Loadings which explain 40% or more of total variation of the principal component in question are in bold type

	PC 1	PC 2
Bacterial biomass	0.531	**0.725**
Bacterial numbers	–0.376	**0.703**
Bacterial production	0.654	0.247
Average cell volume	**0.726**	0.540
Chlorophyll *a*	**0.707**	0.320
Primary productivity	**0.647**	0.301
Salinity	**–0.747**	–0.468
Temperature	0.319	**–0.726**
Dissolved oxygen	–0.102	**0.881**
pH	0.518	–0.297
PO_4	–0.398	0.051
Total phosphorus	0.352	**–0.716**
NO_2	0.571	0.021
NO_3	–0.546	**0.630**
NH_4	**–0.643**	0.585
Total nitrogen	**0.919**	0.029
Dissolved inorg. silicate	**–0.884**	–0.088

Principal component analysis was also done on the same data set (Table 3). In this analysis new variables called principal components are formed from the original variables. The advantage of this type of analysis is that the number of variables is reduced, and the new variables do not correlate with each other. The first principal component formed in the analysis expressed the growth of bacterio- und phytoplankton and was positively correlated with total nitrogen and negatively correlated with salinity, NH_4 and dissolved inorganic silicate. It was characterized by a high positive loading for bacterial productivity and average cell volume, phytoplankton primary productivity and the concentration of chlorophyll *a*. The loading depicts how strongly the variable affects the structure of the component. The connection between the first principal component and both phyto- and bacterioplankton growth and total nitrogen and NH_4 indicates the key role of nitrogen for plankton communities in the Baltic Sea (Tamminen 1982, Tamminen et al. 1985). The second principal component expressed the size of the bacterial population and was positively correlated with dissolved oxygen and NO_3 and negatively correlated with temperature and total phosphorus. It was characterized by a high positive loading for bacterial biomass and abundance. The first 2 principal components explained 63% of the variation in the original data.

A sampling unit (station) component score was calculated for each principal component using the original values of the variables. When the component scores of the first and second principal components were plotted (Fig. 2) the stations formed 3 clusters, except for Stn 11 in the northern Baltic Proper. The first group in the Gulf

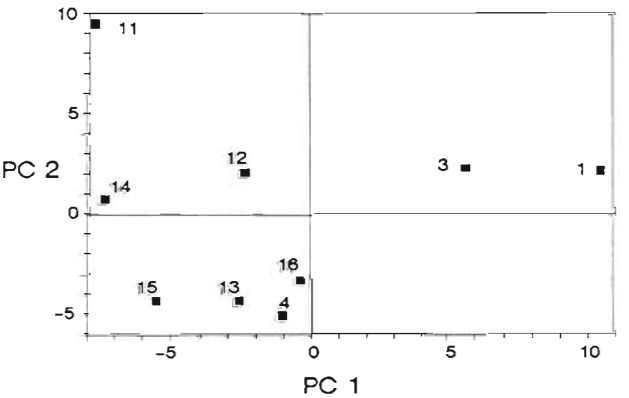

Fig. 2. Component scores of first (PC 1) and second (PC 2) principal components

of Finland is explained by the strong influence of river water, which causes lower salinity and a higher concentration of total nitrogen. By late summer, when this cruise was carried out, almost all the inorganic nutrients in the euphotic water layer were fixed in the biomass. Both stations in the second group are situated in the western part of the Baltic Proper. Primary productivity and the concentration of chlorophyll *a* are low. The concentration of dissolved inorganic silicate is high and those of NH_4 and PO_4 are also high, especially at Stn 14. Although bacterial numbers at both stations are almost the same, bacterial productivity is higher and average cell volume (0.035 μm^3) larger at Stn 12. All the stations in the third group are situated in the eastern and southern sides of the basins of the Baltic Proper. They have moderate or low bacterial productivity compared to the other stations, and the lowest biomasses despite the fairly high primary productivity. The bacterial cell volumes, ranging from 0.014 to 0.026 μm^3, were much lower than the average value of 0.029 μ^3 for surface samples from all stations. The high salinity, a typical feature within stations of this group, is created by the general horizontal circulation pattern of surface waters in the Baltic Sea (Fonselius 1971).

DISCUSSION

Bacterial communities

If the levels of measured bacterial parameters are compared to the relevant published data (Table 4), it can be seen that the bacterial abundance and biomass are in most cases higher and the productivity lower than in comparable studies. For example, Virtanen (1985) found that the shortest turnover time of the bacterial population at a site in the Gulf of Finland (Tvärminne area) in July and August 1980 was 1 d [productivity measured by the FDC (frequency of

Table 4. Estimates of mean bacterial cell volume (μm^3), number ($\times 10^6$ cells ml^{-1}), biomass (mg C m^{-3}) and production (Prod.; mg C m^{-3} d^{-1}), in the surface water layer

Sea area and source	Volume	Number	Biomass	Prod.
Baltic Sea Larsson & Hagström (1982)				10–15 (FDC)
Baltic Sea Virtanen (1985)	0.021	1.6–4.5	3.8–10.5[a]	max. 4.2 (FDC)
Irish Sea Turley & Lochte (1985, 1986)	0.11–0.12			12.7 (FDC)
Sargasso Sea Fuhrman et al. (1989)	0.051[b]	0.47–2.1[b]	9.3–41.2[b]	2.7–6.2[c] (TdR)
Baltic Sea Kuosa & Kivi (1989)				0.17–7.2[d, e] (TdR)

[a] Conversion factor 10 % C of wet weight
[b] Recalculated from the given data
[c] Thymidine conversion factor 4×10^9 cells $nmol^{-1}$
[d] Carbon conversion factor 0.27 pg C μm^{-3}
[e] Thymidine conversion factor 1.1×10^9 cells $nmol^{-1}$

dividing cells) technique]. In the same area in July and August 1986 at a depth of 0 to 5 m the bacterial productivity, measured by the TdR incorporation technique, was at about the same level. However, it was one order of magnitude lower than that found in normal summers by this technique owing to the unusually low water temperature in July–August (Kuosa & Kivi 1989, Kuosa pers. comm.). When Larsson & Hagström (1982) studied the eutrophication gradient in the northern Baltic Proper (FDC technique), productivity at their control station was even higher than at any of the stations in this study. In the Irish Sea in July (FDC technique), the doubling time of the bacterial population was 0.9 d (Turley & Lochte 1985, 1986) and in the Sargasso Sea in July at a depth of 10 m (TdR incorporation technique) the doubling time ranged from 5.0 to 12.4 d (Fuhrman et al. 1989).

In this study the cell number and mean volume were determined simultaneously on each sample. Because only 60 randomly selected cells from a sample were measured, it is clear that the accidental presence or absence of unusually large cells would have a strong effect on the estimate of the bacterial mean cell volume, used to calculate both biomass and productivity. However, the mean cell volumes obtained in this study are in accordance to published values from the Baltic Sea. Virtanen (1985) calculated a mean cell volume of 0.021 μm^3 in the Gulf of Finland in July and August 1980. In the northern Baltic Proper bacterial mean volumes varied between 0.033 and 0.125 μm^3 (SEM technique) in April, May and June 1982 (Lahdes et al. 1988). During the vernal phytoplankton bloom, mean cell volumes ranged from 0.032 to 0.112 μm^3 at a coastal site in the Gulf of Finland (Kuparinen 1988). In the Norrby Archipelago, which is situated in the northern part of the Bothnian Sea, the median bacterial volume during the spring was 0.17 μm^3 and during the summer 0.11 μm^3 (Andersson et al. 1985). When these figures are compared to the mean cell volumes of this study, it should be remembered that the mean cell volumes in the Baltic Sea are higher during the vernal phytoplankton bloom than during summer (Andersson et al. 1985, Virtanen 1985) and because of factors not yet properly known (e.g. terrestrial matter carried by the rivers) bacterial cells in the Bothnian Sea tend to be larger than in the other areas of the Baltic Sea. When more data is available from the Baltic Sea, it will be possible to see if the mean cell volumes are really very low or if the published values are biased because of difficulties in measuring the actual size of the cells.

The conversion of bacterial biovolume into carbon is also problematic. This is usually done using the factors available in the literature, such as the value of 0.35 pg C μm^{-3} (Bjørnsen 1986) used in this study. A factor of 0.121 pg C μm^{-3} (Watson et al. 1977) was earlier used widely, but today values as high as 0.56 pg C μm^{-3} (Bratbak 1985) are used. Because the same carbon conversion factor and mean cell volume were used for both the productivity and biomass estimates in this study, they have no effect on the general conclusions made concerning the productivity per biomass ratio.

One possible explanation for the discrepancy between results from the above-mentioned studies and this study is that the cell volumes in this study were small (average of all surface samples 0.033 μm^3). Because the cell volume is also used to calculate bio-

mass, this only partly explains the discrepancy between the long turnover times obtained in this study. Another explanation could be that the thymidine estimates are underestimates and/or the FDC estimates are overestimates (Pedros-Alio & Newell 1989). However, such underestimation should also bias the other results obtained by the TdR technique in the same way, and thus can only partly explain the discrepancy.

The conversion factor of 1.1×10^9 cells produced per nmol thymidine incorporated (Riemann et al. 1987) was used to calculate thymidine incorporation because it is based on a larger data set than the other published conversion factors. The factor in question is low compared to other published values (e.g. Fuhrman & Azam 1982, Ducklow & Hill 1985), and thus gives conservative productivity values.

Recent results indicate that many actively growing cells do not take up thymidine (Davis 1989, Pedros-Alio & Newell 1989), and that thymidine uptake also occurs in the absence of cell division (Davis 1989). If this is the case then results would have a different bias in different environments because uptake would depend on the population in question. This feature should be taken into account when the thymidine technique is applied to estimate bacterial productivity. However, there are not much data available about the species composition of bacterial populations in the Baltic Sea.

Present results suggest that bacterial populations in the open sea area in the Baltic Sea have a longer turnover time and lower productivity than those in the coastal areas of the Baltic Sea, comparable to those found in the open ocean. However, the biomass and abundance are comparable to those of coastal areas. More intensive studies are needed in the open sea area of the Baltic Sea to clarify this controversial finding.

Variable associations

Contrary to the summer and early autumn results of Virtanen (1985) and Kuosa & Kivi (1989) in the northern Baltic Proper, the bacterial productivity and water temperature were not intercorrelated. In the coastal waters of the same area Väätänen (1980b) also found temperature to be a significant variable explaining the variation in microbiological parameters. In the Kiel Bight, however, no direct relationship was found between bacterial parameters and temperature, and the hydrographical changes and input of labile organic material were more important determinants of bacterial activity (Gocke et al. 1987). Similar to these results, environmental factors other than temperature had a more direct effect on the intensity of bacterial productivity during our cruises.

Offshore and onshore effects

Stn 10 is equivalent to Stn G sampled in August 1982 by Rheinheimer et al. (1989). The bacterial numbers followed the same trend during both cruises, i.e. slightly lower at this station than at the other stations. The bacterial activities measured in 1982 were the lowest in the range they found. This was also the case for the thymidine incorporation activity measured during our cruise. The results support the conclusion made by Rheinheimer et al. (1989) that, in the Gulf of Bothnia, substantial amounts of terrestrial plant material and humic compounds have resulted in the bacterial populations becoming especially adapted to substances that are difficult to degrade. If the length of the turnover time indicates activity, then this also supports the other conclusion they made in that a larger proportion of the population is inactive than in the Baltic Proper.

In the study by Larsson & Hagström (1982), bacterial productivity in the atrophic layers was considerably higher at eutrophicated stations than at the control station. During the second cruise at Stn 1, the easternmost station in the Gulf of Finland, and at Stn 16 in the southern Baltic Proper, bacterial productivity in the atrophic water layer was about double the average. This probably indicates eutrophication of these areas. Bacterial biomasses in the Gulf of Finland were also higher than those in the Baltic Proper owing to the larger mean cell volumes. However, the turnover time was near average. In the absence of information about bacterial substrate utilization and the effect of grazing, it is impossible to define the most important causes of the increased bacterial productivity and biomass in the aphotic layer, e.g. whether it was the increased amount of sedimenting particles, increased concentration of dissolved organic matter and/or decreased grazing. Experimental studies would be useful in clarifying eutrophication processes in the aphotic water layer.

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