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Bacterioplankton in a subarctic estuary: the Gulf of Bothnia (Baltic Sea)

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ABSTRACT: The magnitude and control of the bacterioplankton standing stock and its growth in the Bothnian Bay and Bothnian Sea, 2 basins in the Gulf of Bothnia, a subarctic estuary, were evaluated by measuring bacterial numbers, biovolumes, thymidine incorporation rate and turnover time of the biomass during 4 cruises. Cell numbers averaged 0.84×10^6 cells ml^{-1} in winter, 1.66×10^6 cells ml^{-1} in June and 1.60×10^6 cells ml^{-1} in August. Thymidine incorporation rates were 0.17, 5.0 and 7.8 pmol l^{-1} h^{-1} respectively (all depths included). Mean cell volumes were within the ranges 0.026 to 0.090 μm^3 in winter, 0.029 to 0.129 μm^3 in June and 0.018 to 0.051 μm^3 in August. The shortest turnover time was ca 1 mo in winter and ca 5 d in June and August. Bacterial numbers and thymidine incorporation rate showed a positive correlation to temperature. Thymidine incorporation rate (growth) and temperature did not correlate with mean cell volume. The results indicated that part of the bacterioplankton production in the Bothnian Bay was supported by allochthonous sources. In addition, the bacterial cell volumes in August were probably controlled by predators. However, it is suggested that in the Gulf of Bothnia the available resources control bacterioplankton.

INTRODUCTION

Several abiotic and biotic factors (e.g. supply and quality of organic matter, nutrient concentrations and ratios, predation) control the standing stock and growth of bacterioplankton. It is essential to know these factors to be able to understand the bacterioplankton dynamics of an estuarine system.

In estuarine ecosystems the flow of organic matter is based on both the autochthonous primary production and the allochthonous matter supplied by rivers. The large amounts of allochthonous matter may enable the formation of food webs that are based more on detritus than on primary production (Moran et al. 1988, Smith et al. 1989, Findlay et al. 1991). Thus bacterioplankton production would be higher than predicted on the basis of phytoplankton primary production.

Classically, bacteria have been viewed as the major remineralizers of nutrients in aquatic environments, but the role of heterotrophic flagellates and microzooplankton has been emphasized during the past decade (Williams 1981, Azam et al. 1983). In ecosystems with considerable quantities of allochthonous matter the role of bacteria as remineralizers is probably more important, and they are less of a sink for nutrients than in ecosystems based only on primary production (Findlay et al. 1991).

The Gulf of Bothnia is a subarctic estuary consisting of the Bothnian Bay and the Bothnian Sea (Fig. 1). The Bothnian Bay and the Bothnian Sea are 2 of the 3 major basins in the Baltic Sea. The deepest point in the Bothnian Sea is ca 250 m and in the Bothnian Bay ca 150 m. The water balance of the Gulf of Bothnia is positive and is regulated completely by the large discharge of river water (Fonselius 1986). The river inflow to the Bothnian Bay is roughly twice the river inflow to the Bothnian Sea (Mikulski & Falkenmark 1986). The lowest inflow is in March and the maximum inflow in the Bothnian Bay is in May and in the Bothnian Sea in June (Mikulski 1986). During winter the Gulf of Bothnia is frequently ice-covered and the average number of real ice days ranges from ca 30 d in the southern Bothnian Sea to 190 d in the northernmost part of the Bothnian Bay (Seinä & Peltola 1991). Vertical salinity stratification is weak, but strong thermoclines usually develop during the summer. Salinity increases from north to south from ca 1 to 6 ppt in the surface water, and from ca 3 to 7 ppt in deep water (Kullenberg 1981).

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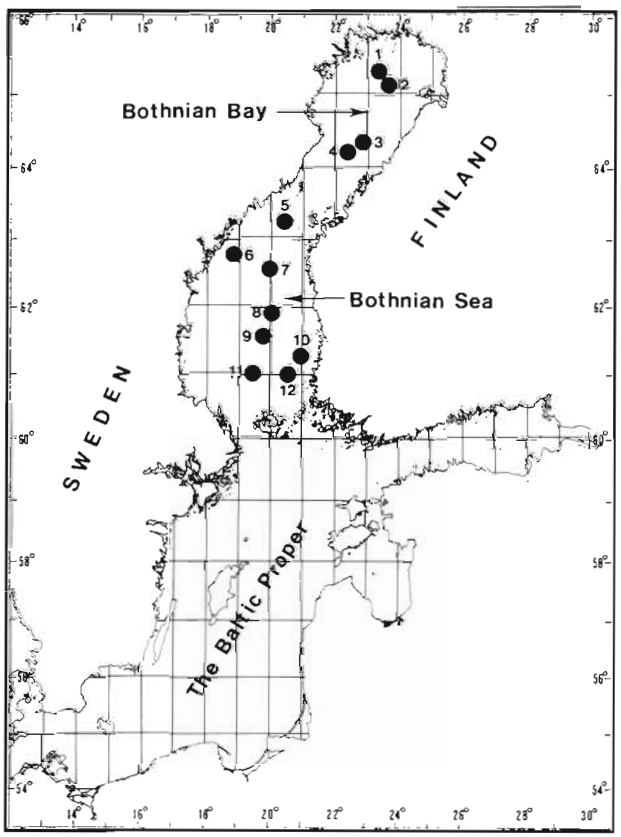

Fig. 1. Location of the sampling stations in the Gulf of Bothnia. (1): 65° 23' N, 23° 28' E; (2): 65° 14' N, 23° 34' E; (3): 64° 25' N, 22° 55' E; (4): 64° 18' N, 22° 21' E; (5): 63° 19' N, 20° 17' E; (6): 62° 51' N, 18° 52' E; (7): 62° 35' N, 19° 59' E; (8): 61° 59' N, 20° 04' E; (9): 61° 37' N, 19° 48' E; (10): 61° 14' N, 20° 59' E; (11): 61° 05' N, 19° 35' E; (12): 61° 05' N, 20° 36' E

Phytoplankton primary production in the Gulf of Bothnia is lower than that in the other areas of the Baltic Sea, and in the Bothnian Bay it is about one-third of that in the Bothnian Sea (Lassig et al. 1978). In the Bothnian Sea the vernal phytoplankton maximum is in April–May, but in the Bothnian Bay it is in June (Lassig et al. 1978, Valtonen et al. 1978). The Bothnian Bay is more oligotrophic than the other areas of the Baltic Sea, and is considered to be phosphorus-limited (Wulff et al. 1990). The allochthonous matter in the Gulf of Bothnia is mainly of terrestrial origin and thus is highly refractory. Even if the bacterioplankton is adapted to utilize allochthonous compounds, degradation is probably slow. However, allochthonous matter is an energy input into the aquatic food webs.

In this study bacterial numbers, biovolumes, thymidine incorporation rate and biomass turnover time were analysed during 4 cruises in order to evaluate the magnitude and control of the bacterioplankton standing stock and its growth in the Gulf of Bothnia, a subarctic estuary.

MATERIAL AND METHODS

Sampling. Samples were taken during 4 cruises of RV 'Aranda'. The cruises took place 13–18 January, 23–27 February, 17–23 June and 2–10 August 1988. Sampling in January and February was done only in the Bothnian Sea. One 2 l water sample was taken from each depth at the sampling stations. The sampling depths of bacterioplankton parameters are shown in Appendix and the sampling depths of other parameters are shown in Table 1. The locations of the sampling stations are shown in Fig. 1.

Chemical and phytoplankton variables. In August some chemical variables and chlorophyll *a* (chl *a*) were also measured. Dissolved oxygen and nutrients were determined according to Grasshoff et al. (1983). Dissolved inorganic phosphate, nitrite, and nitrate were analysed on a Technicon autoanalyzer. Silicate-silicon and ammonia were analysed on an Akea autoanalyzer. Chl *a* was extracted in 90 % acetone and measured fluorometrically (Edler 1979). Particulate phytoplankton primary productivity was measured in an incubator at *in situ* temperature using the ^{14}C technique (Steemann Nielsen 1952, BMEPC 1984). Samples (30 ml) were illuminated for 2 h with fluorescent tubes (Philips TLD 18 W/33); the irradiance conditions ensured photosynthetic saturation. After incubation the samples were filtered (Sartorius cellulose nitrate filters, 0.45 µm). The filters were placed in glass vials and 100 µl acid (0.5 M HCl) added to remove unincorporated ^{14}C. Particulate primary productivity was measured at 6 stations in the Bothnian Bay and at 12 stations in the Bothnian Sea (depths: 0, 2, 5, 10, 15, 20 m).

Numbers and biovolumes of bacteria. Subsamples (20 ml) were fixed with particle-free formalin (200 µl, 39 %), stained with particle-free acridine orange (1 mM, Chroma), and bacterial numbers and volumes measured under an epifluorescence microscope (Hobbie et al. 1977). The January and February samples were measured using a Leitz Laborlux D microscope, and the June and August samples using a Leitz Aristoplan microscope. At least 200 cells and 20 fields were counted when estimating the numbers. The lengths and widths of 100 cells from each sample were measured with a Patterson Globe and Circle G1 grid (Graticules Ltd.) to estimate the mean volume of bacteria (Patterson & Cawood 1936).

Thymidine incorporation. In January and June 3 subsamples (20 ml) and 3 controls, in February 5 subsamples and 5 controls, and in August 3 subsamples and 1 control from each depth were incubated with a final concentration of 11 to 16 nM of [methyl-^{3}H]thymidine (40 Ci mmol^{-1}, Amersham International). The controls were killed with formalin before the addition of [^{3}H]thymidine in order to obtain blank values.

Incubation was started immediately after sampling and was carried out in polystyrene boxes in the dark at *in situ* temperature. In January, February and June the subsamples were incubated for 120 min, except for the June samples taken above the thermocline in the Bothnian Sea which were incubated for 60 min. In August the subsamples were incubated for 30 min. Incubation was stopped by the addition of formalin, and 5 ml of a subsample extracted with 10 % trichloroacetic acid (TCA) and filtered through 0.20 µm filters (Asypor membrane, Domnick Hunter Ltd.). The filters were rinsed with 5 % TCA. Extraction and filtration were done in ice-cold conditions. The radioassay was performed using a 1217 Rackbeta liquid scintillation counter (LKB Wallac) after adding 10 ml of scintillator (Lumagel, Lumac).

For calculating the turnover times of the biomass, the bacterial productivity was estimated by the thymidine incorporation technique (Fuhrman & Azam 1982) using a conversion factor of 1.1×10^{18} cells mol^{-1} (Riemann et al. 1987). The mean cell volume was obtained by microscopy and the carbon content of 0.35 pg C μm^{-3} was obtained from the literature (Bjørnsen 1986).

RESULTS

The cell numbers (mean: 0.84×10^6 cells ml^{-1}) and thymidine incorporation rate (mean: 0.17 pmol l^{-1} h^{-1}) were clearly lower during the 2 winter cruises in the Bothnian Sea than during the summer cruises (see Appendix). The thymidine incorporation rate was negligible and at about the same level at all depths, apart from the higher surface (0 m) value recorded at Stn 8 in February. The mean cell volumes were evenly distributed within the range 0.026 to 0.090 μm^3. Due to the low productivity the shortest calculated turnover time was ca 1 mo. Water temperatures measured at stations ranged from 0 to 3 °C.

During the cruise in June the vernal phytoplankton bloom was probably still continuing in the Bothnian Bay but not in the Bothnian Sea (Lassig et al. 1978). The measured bacterioplankton variables were distinctive in the Bothnian Bay and the Bothnian Sea. Thymidine incorporation rates in the Bothnian Sea were ca 2 to 3 times higher than in the Bothnian Bay (see Appendix). The difference in the thymidine incorporation rate between the surface and other depths was drastic, especially at Stn 5, where the highest thymidine incorporation rate of the whole study (26 pmol l^{-1} h^{-1}) was recorded. Cell numbers were higher in the Bothnian Sea than in the Bothnian Bay, and the turnover times were shorter. The only measured variable which did not differ between these 2 basins in June, or between the winter data and June data, was mean cell volume. The surface water temperatures at stations in the Bothnian Sea were slightly higher than those in the Bothnian Bay.

The differences in bacterioplankton variables between the 2 basins levelled off in late summer (2–10 August) when the fourth cruise was made. Thymidine incorporation rates were, however, slightly higher in the Bothnian Sea than in the Bothnian Bay. In both basins the cell numbers increased in June and August when the thymidine incorporation rate increased (Fig. 2). The most striking result of the August cruise was that mean cell volumes at all stations and at all sampling depths were 0.05 μm^3 or less (see Appendix). The average mean cell volume in August was 50 % of that in June, and 67 % of that in winter. In the Bothnian Bay the thymidine incorporation rate and the cell numbers were higher than in June. The turnover time was amazingly similar at all depths and was shorter than in June, except for the surface samples of the Bothnian Sea. The water column was strongly temperature stratified and the surface temperature averaged 16 °C. The particulate primary productivity averaged 3.2 mg C h^{-1} m^{-3} in the Bothnian Bay and 6.6 mg C h^{-1} m^{-3} in the Bothnian Sea.

The results of chemical variables and chl *a* at some representative stations measured during the August cruise are listed in Table 1. We did not measure winter concentrations, but some have been measured in previous studies (1979–1989): Bothnian Sea surface water (0 to 12 m) nitrate: 2 to 6 mmol m^{-3}, phosphate: 0.1 to 0.5 mmol m^{-3}; 100 m depth nitrate: 2 to 7 mmol m^{-3}, phosphate: 0.2 to 0.8 mmol m^{-3} (BMEPC 1990, Rosenberg et al. 1990). Bothnian Bay surface water (0 to 5 m) nitrate: 4 to 6 mmol m^{-3}, phosphate: 0.1 to 0.2 mmol m^{-3}; 100 m depth nitrate: 5 to 9 mmol m^{-3}, phosphate: 0.1 to 0.3 mmol m^{-3} (Rosenberg et al. 1990).

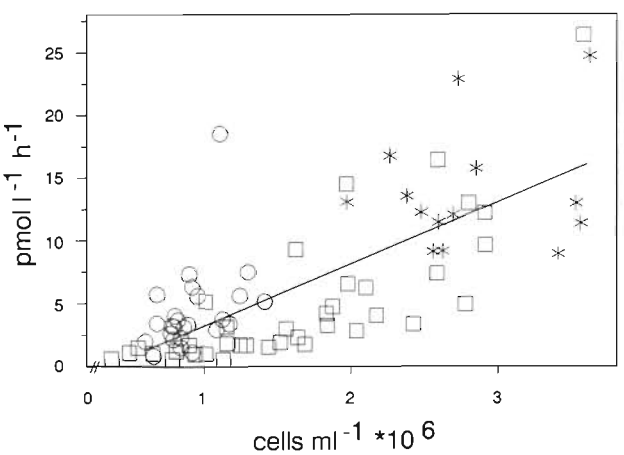

Fig. 2. Thymidine incorporation rate (pmol l^{-1} h^{-1}) vs cell numbers (cells ml^{-1}) and the estimated regression line (r^2 = 0.54). (□) June; (*) August (below the thermocline); (○): August (above the thermocline)

DISCUSSION

The results were comparable to earlier studies carried out in the Gulf of Bothnia, except for the shorter turnover time of the biomass (Andersson et al. 1986, Rheinheimer et al. 1989, Heinänen 1991, Andersson, Lundberg & Hagström unpubl.). The shorter turnover times were due to the lower biomasses recorded in this study. The results were also in the range of published values for other areas of the open Baltic Sea (Virtanen 1985, Gast & Gocke 1988, Kuosa & Kivi 1989, Autio 1990, Heinänen & Kuparinen 1991).

However, the mean cell volumes are likely to be underestimates, because only 100 randomly selected cells from a sample were measured and the large, very rare cells are not represented quantitatively. 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. The conversion of biovolume into carbon is also problematic, because published values for the Baltic Sea bacterioplankton are lacking and a carbon conversion factor available for another area(s) (0.35 pg C μm^{-3}; Bjørnsen 1986) had to be chosen. Future work will reveal how much this error influenced the productivity and biomass estimates. However, the same carbon conversion factor and mean cell volume were used for both the productivity and the biomass estimates in this study, thus they have no effect on the general conclusions made concerning the relationship of productivity and biomass.

Cells of a size close to the detection limit of light microscopes (ca 0.2 µm) are difficult to measure, as a result of the halo effect and, of course, because they are so small. The number of the cell volume measurements is usually limited by the time the measurements require. In theory it is possible to increase the number of measured cells within a given time by using image analysis combined with epifluorescence microscopy. However, the exact sizing of the smallest cells is at present difficult with image analysis, because the problem of the halo effect around the fluorescent particles is accentuated.

Areal bacterioplankton productivity in the Bothnian Sea (310 mg C m^{-2} d^{-1}) in August was 1.9 times higher than in the Bothnian Bay (160 mg C m^{-2} d^{-1}). However, the average depth of the stations sampled in the Bothnian Sea was 155 m and in the Bothnian Bay 90 m. The areal bacterioplankton productivities in these 2 basins were equal when proportioned to average depth. When compared to the concentrations of chl *a* and the primary productivity (double in the Bothnian Sea compared to the Bothnian Bay), this indicated that part of the bacterioplankton production in the Bothnian Bay was supported by allochthonous sources. There is also a possibility that this difference between the 2 basins was due to the higher growth efficiency of bacterioplankton in the Bothnian Bay than in the Bothnian Sea. This, however, seems less likely because of the highly refractory nature of the allochthonous matter supplied by the rivers. A further question is, how much of the carbon

Table 1. Concentration of dissolved oxygen (ml l^{-1}), chl *a* (mg m^{-3}), PO_4, NO_2, NO_3, NH_4 and dissolved inorganic silicate (Si) (mmol m^{-3}) at some stations of the fourth (August) cruise. –: not measured; bd: below detection limit of the method

Stn	Depth (m)	Oxygen	Chl *a*	PO_4	NO_2	NO_3	NH_4	Si
1 (8 Aug)	0	6.6	1.6	0.01	0.15	2.9	–	33
	15	7.1	1.1	0.01	0.20	3.9	–	32
	20	8.3	0.7	0.01	0.30	6.1	–	31
	60	7.8	–	0.01	0.01	8.5	–	34
	75	7.4	–	0.04	0.01	8.9	–	36
4 (7 Aug)	0	6.8	1.2	bd	0.05	1.5	–	29
	5	6.9	1.1	bd	0.05	1.9	–	30
	20	8.9	0.6	bd	0.15	5.5	–	36
	60	7.9	–	bd	0.16	5.7	–	33
	105	7.7	–	0.02	0.14	6.2	–	33
5 (7 Aug)	0	6.2	3.2	0.02	bd	0.06	–	5.5
	20	6.2	2.7	0.02	bd	0.08	–	5.3
	60	7.7	–	0.11	0.07	4.2	–	19
	94	6.7	–	0.48	0.03	6.0	–	26
7 (6 Aug)	0	6.7	2.7	0.01	bd	0.03	0.11	9.9
	10	6.7	1.6	bd	bd	0.03	0.14	9.4
	20	8.3	0.6	0.01	0.36	0.35	0.09	11
	80	6.8	–	0.40	0.03	5.8	–	26
11 (5 Aug)	0	6.4	1.8	0.04	0.01	0.14	0.26	4.0
	20	6.8	1.7	0.03	bd	0.60	0.32	3.0
	40	8.8	–	0.03	0.32	0.36	0.32	3.8
	100	6.4	–	0.05	0.20	6.2	0.12	29
	120	5.8	–	0.28	0.12	6.7	1.9	40

originating from allochthonous sources is transferred to higher trophic levels?

A positive relationship existed between the bacterial numbers (r^2 = 0.67) and temperature, and between thymidine incorporation rate (r^2 = 0.71) and temperature. Similar relationships between temperature and the bacterioplankton variables have been recorded earlier both in the Baltic Sea and elsewhere (Väätänen 1980, Virtanen 1985, Coffin & Sharp 1987, Iriberri et al. 1987, Joint & Pomroy 1987, Li & Dickie 1987, White et al. 1991). It has been, however, hypothesized that the low concentration of labile substrates usually present rather than temperature limits bacterial metabolism and production in cold waters (Wolter 1982, Li & Dickie 1987, Pomeroy et al. 1991, Wiebe et al. 1992). Thus the positive relationship found may be a result of interacting seasonal phenomena, especially phytoplankton blooms, which are an important source of labile dissolved organic carbon for bacterioplankton.

Temperature did not correlate with the bacterioplankton biomass. The highest biomasses occurred in June not in August owing to the small mean cell volumes in August. In June the growth of the bacterioplankton assemblage resulted in an increase in both biovolume and numbers, but in August only in an increase in numbers.

Variation in the mean cell volume is often explained by temperature, growth rate and predation. An increase in temperature leads to smaller cell volume (Hagström & Larsson 1984, Chrzanowski et al. 1988, Bjørnsen et al. 1989), and an increase in growth rate leads to larger cell volume (e.g. Pritchard & Tempest 1982). A shift in mean cell volume due to temperature could be primarily an intrinsic property of aquatic bacteria (Chrzanowski et al. 1988). However, the development of a different assemblage with smaller cell forms could also occur as a result of predation pressure on large cells (Turley et al. 1986) or as a seasonal shift in the dominant species of the bacterioplankton assemblage. The high surface to volume ratio of small cells is an adaptation for good growth in low nutrient concentrations (van Gemerden & Kuenen 1984).

In this study the thymidine incorporation rate (growth) and temperature did not correlate with the mean cell volume (r^2 = 0.04 and 0.05 respectively). The proportion of variation in the mean cell volume explained by temperature remained negligible, even when the data from different cruises and the data above or below the thermocline were examined individually.

It is well known that the richer the growth medium, the larger the size of the bacterial cells (e.g. Pritchard & Tempest 1982). Thus an increase in the biovolume in June implied that there was plenty of substrates available for bacterioplankton growth and bottom-up control dominated over top-down control. However, the importance of different carbon and nutrient sources for bacterioplankton growth is unresolved in the Baltic Sea. The results also agreed with the observations made by Billen et al. (1990) that bacterial biomass is proportional to the richness of the environment, and the turnover of bacterial biomass appears to be largely independent of the richness of the environment. Accordingly, during the regenerated production period in August the biomasses were low in spite of the short turnover time of the biomass.

Predation was not directly investigated in this study. Current methods are not adequate to determine the time scales over which bacterial growth and predation balance in the sea (McManus & Fuhrman 1988). However, predation control of bacterioplankton has been confirmed in the Baltic Sea (Andersson et al. 1986, Kuosa & Marcussen 1988, Kuosa & Kivi 1989, Kuuppo-Leinikki 1990, Kuuppo-Leinikki & Kuosa 1990, Wikner et al. 1990, Wikner & Hagström 1991). This gives justification to focus on some specific features in the data with regard to predation. Due to low bacterioplankton numbers and water temperature, the bacterioplankton were probably little affected by predation in winter. If size-selective predation changes the size distribution of bacterioplankton cells (Andersson et al. 1986, Turley et al. 1986, Coffin & Sharp 1987, Gonzalez et al. 1990, Kuuppo-Leinikki 1990, Monger & Landry 1991), firstly, in June predation could not compensate for the bottom-

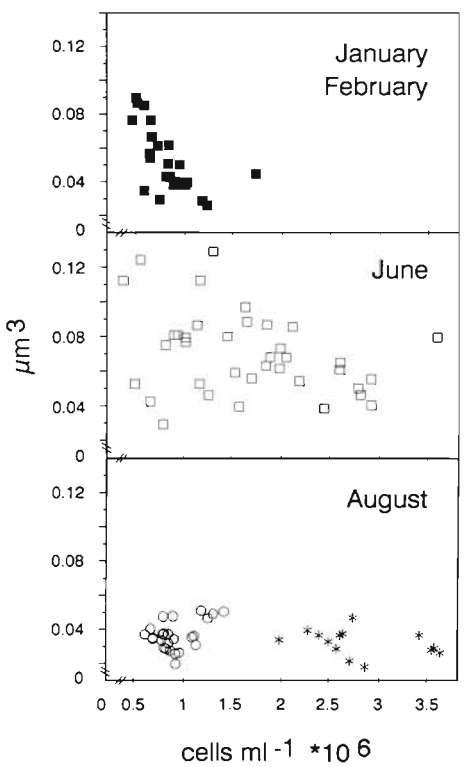

Fig. 3. Mean cell volumes (μm^3) vs cell numbers (cells ml^{-1}); (■): winter (January–February); other symbols are as in Fig. 2

up control and, secondly, a preference for large cells could explain the small cell volumes in August (Fig. 3).

In addition, the higher thymidine incorporation rate per cell and the shorter turnover time of the biomass in August (mean: 10 d) than in June (mean: 25 d) indicated that the small cells in August were not dormant nor had a low growth rate, but were a dynamic component of the ecosystem.

In conclusion, the results suggested that part of the bacterioplankton production in the Bothnian Bay was supported by allochthonous sources. The bacterial cell volumes were probably controlled by predators in August. However, bacterioplankton in the Gulf of Bothnia seemed to be controlled by the resources (inorganic nutrients, carbon) available rather than by predators.

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Appendix. Temperature (Temp.; °C), thymidine incorporation (Tdr; pmol l^{-1} h^{-1}), mean cell volume (Vol.; μm^3), numbers (N; cells $ml^{-1} \times 10^6$) and turnover time (T; d) at sampling stations

Stn (date)	Depth (m)	Temp.	Tdr	Vol.	N	T
1st cruise (13–18 Jan 1988)						
10 (16 Jan)	0	1.5	0.17	0.038	1.01	55
	10	1.5	0.15	0.045	1.73	110
	20	1.5	0.15	0.040	1.00	60
	40	1.0	0.14	0.029	1.18	75
	50	0.5	0.18	0.039	0.89	50
11 (16 Jan)	0	1.5	0.36	0.055	0.65	18
	10	2.0	0.13	0.044	0.81	60
	20	2.0	0.22	0.030	0.75	35
	40	2.0	0.27	0.040	0.90	30
	80	3.0	0.25	0.040	1.03	40
	120	2.5	0.18	0.035	0.58	30
2nd cruise (23–27 Feb 1988)						
7 (26 Feb)	0	0	0.10	0.062	0.83	80
	20	0	0.09	0.087	0.52	55
	60	2.0	0.07	0.062	0.73	100
	100	2.5	0.08	0.057	0.64	75
	181	2.0	0.14	0.067	0.66	45
8 (26 Feb)	0	1.0	0.73	0.051	0.83	105
	20	0.5	0.07	0.039	0.92	130
	40	0.5	0.09	0.086	0.59	60
	70	2.5	0.08	0.077	0.46	55
	131	2.5	0.11	0.077	0.65	60
11 (25 Feb)	0	0.5	0.11	0.090	0.51	45
	20	1.0	0.09	0.039	0.90	95
	40	1.0	0.11	0.051	0.95	80
	80	2.5	0.11	0.026	1.23	105
	118	2.5	0.16	0.043	0.85	50
3rd cruise (17–23 Jun 1988)						
2 (20 Jun)	0	8.5	4.2	0.063	1.84	16
	20	2.5	1.0	0.077	1.01	35
	40	1.0	0.97	0.081	0.94	35
	71	1.5	0.50	0.029	0.79	60
3 (19 Jun)	0	4.0	2.3	0.088	1.64	25
	20	3.5	2.0	0.059	1.52	30
	40	3.0	1.6	0.080	1.44	35
	82	1.0	0.34	0.086	1.13	125
4 (20 Jun)	0	6.0	5.2	0.079	1.01	7.4
	20	3.5	1.7	0.081	0.90	20
	40	2.0	1.0	0.043	0.65	25
	107	0.5	1.2	0.075	0.81	25
5 (19 Jun)	0	12.5	26	0.080	3.58	5.2
	20	5.0	6.6	0.073	1.98	12
	40	1.0	1.7	0.129	1.29	30
	100	2.0	1.9	0.112	1.16	25

Appendix (continued)

Stn (date)	Depth (m)	Temp.	Tdr	Vol.	N	T
6 (21 Jun)	0	11.0	15	0.061	1.97	5.2
	20	5.5	9.3	0.097	1.63	6.6
	50	1.0	1.5	0.124	0.55	14
	100	2.5	0.60	0.112	0.37	25
	197	2.5	1.1	0.053	0.49	18
7 (18 Jun)	0	9.5	12	0.055	2.91	9.0
	20	5.0	6.3	0.086	2.11	13
	40	2.0	1.8	0.056	1.69	35
	100	1.5	1.7	0.046	1.25	25
9 (18 Jun)	0	8.5	16	0.065	2.59	6.0
	20	5.0	4.8	0.068	1.88	12
	40	2.5	3.3	0.087	1.84	20
	82	1.5	4.1	0.054	2.18	20
11 (17 Jun)	0	8.5	13	0.046	2.80	7.8
	20	5.5	7.4	0.061	2.59	13
	50	2.0	2.9	0.068	2.04	25
	124	2.5	3.2	0.053	1.16	14
12 (17 Jun)	0	9.5	10	0.040	2.91	11.0
	20	6.5	5.0	0.050	2.78	20
	40	3.0	3.4	0.039	2.43	25
	74	1.5	3.0	0.040	1.56	20
4th cruise (2–10 Aug 1988)						
1 (08 Aug)	0	15.5	14	0.036	2.39	6.6
	15	10.0	9.2	0.037	2.63	11
	30	2.5	3.4	0.051	1.18	13
	60	1.5	2.6	0.033	0.77	11
	77	1.5	2.1	0.047	0.79	14
2 (08 Aug)	0		12	0.021	2.70	8.4
	10		9.2	0.028	2.56	11
	50		1.5	0.032	0.84	20
	70		2.0	0.037	0.60	12
4 (07 Aug)	0	15.5	9.0	0.037	3.41	15
	5	11.5	11	0.029	3.56	12
	30	3.0	5.7	0.046	1.25	8.4
	60	4.0	5.2	0.050	1.41	10
	105	3.0	3.8	0.031	1.13	11
5 (07 Aug)	0	17.0	17	0.039	2.27	5.1
	30	9.0	6.3	0.026	0.92	5.5
	60	1.5	3.3	0.047	0.89	11
	94	1.5	2.3	0.037	0.84	14
6 (06 Aug)	0	15.0	25	0.026	3.62	5.5
	15	14.0	13	0.034	1.98	5.7
	40	2.0	3.0	0.035	1.09	14
	100	2.0	0.83	0.040	0.66	30
	150	2.5	3.1	0.027	0.86	11
	195	2.5	1.1	0.020	0.92	30
7 (06 Aug)	0	15.5	23	0.047	2.73	4.5
	11	10.0	12	0.033	2.48	7.7
	40	2.5	19	0.036	1.11	2.3
	100	1.5	3.2	0.038	0.80	9.5
	150	2.0	3.2	0.037	0.78	9.2
	195	2.0	3.4	0.034	0.68	7.4
11 (05 Aug)	0	16.5	13	0.028	3.53	10
	20	10.5	12	0.037	2.60	8.5
	50	2.0	3.7	0.029	0.82	8.5
	100	2.5	5.7	0.035	0.68	4.6
	120	2.5	7.3	0.034	0.90	4.7
12 (05 Aug)	0	16.0	16	0.018	2.85	6.8
	20	6.0	7.5	0.049	1.30	6.5
	50	2.0	4.0	0.029	0.80	7.4
	77	2.0	5.6	0.026	0.96	6.7

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