MICROBIAL ECOLOGY

Microb Ecol (2000) 39:101–115
DOI: 10.1007/s002480000007

Bacterioplankton Production in Humic Lake Örträsket in Relation to Input of Bacterial Cells and Input of Allochthonous Organic Carbon

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Received: 24 May 1999; Accepted: 8 November 1999; Online Publication: 29 March 2000

Abstract

In order to compare riverine bacteria input with lake water bacterial production and grazing loss with output loss, a bacterial cell budget was constructed for humic Lake Örträsket in northern Sweden. The riverine input of bacterial cells in 1997 represented 29% of the number of bacterial cells produced within the layer of the lake affected by inlet water. A large share of the *in situ* lake bacterial production was consumed by grazers, mainly flagellates, which stresses the importance of bacteria as energy mobilizers for the pelagic food web in the lake. The bacterial production in Lake Örträsket, which is almost entirely dependent on humic material as an energy source, was clearly stimulated by high flow episodes which brought high amounts of little degraded material into the lake. During base flow condition the bacterial production in the inlet rivers was high, which led to an input of more degraded material to the lake. This material did not stimulate the lake bacterial production. Internal factors that determined the utilization of the allochthonous DOC in the lake were the retention time and the exposure to light and high temperatures. Thus, the potential for *in situ* production of bacteria in Lake Örträsket was to a large extent a function of how precipitation and runoff conditions affected terrestrial losses and river transport of humic material.

Introduction

Humic lakes have chemical and physical characteristics that directly or indirectly affect the environment for planktonic organisms. Humic substances absorb light and restrict the amount of light energy available for primary producers [2, 21, 41]. The humic material also serves as a carrier of nitrogen (N) and phosphorus (P) and thereby restricts the bioavailability of these nutrients for plankton [19, 20, 22, 46]. Humic lakes have, therefore, been characterized as having low productivity [52], which was also stressed by the early classification of humic lakes as "dystrophic" [45].

The composition of the planktonic community in humic lakes is different from that in oligotrophic clear-water lakes. Since humic material is an energy and carbon source for

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bacteria [36, 48], the bacteria in humic lakes are not as dependent on phytoplankton to receive carbon as in other lake types [12, 18]. Consequently, the biomass of pelagic bacteria is positively correlated with the humic content of the water [11, 47], and the microplankton community is often dominated by bacterioplankton [17, 42, 48]. Because of the high input of allochthonous carbon, the bacterioplankton in humic lakes are not energy limited but rather nutrient limited [13, 17]. The bacterial production may also be several times higher than the planktonic primary production [18, 50], and high ratios of respiration to primary production indicate the presence of an important carbon source in addition to that supplied by primary producers [6, 21, 42]. Thus, the dissolved humic material (DHM) promotes heterotrophic production [7, 18], and humic lakes can have a heterotrophic base for total production [12, 18].

The share of the allochthonous dissolved organic carbon (DOC) that is readily available for bacterial breakdown is usually about 10% or less [36, 47, 57]. However, the input and the quality of the humic material may vary over the season, which may affect the availability of the DHM for the bacteria [34]. Moreover, the bioavailability of DHM seems to increase after exposure to sunlight. Photo-oxidation degrades the dissolved organic matter into a number of biologically labile photoproducts [4, 37] which can stimulate bacterial growth [29, 53].

River DOC has been shown to be more photolabile than lake DOC [35]. It was suggested by the authors that the difference was due to the fact that river DOC was recently exported from surrounding peatlands, while the lake DOC had extensive previous exposure to sunlight, consuming large parts of the photolabile DOC [35]. For the same reason epilimnetic water can be less photolabile than hypolimnetic water [43]. Depending on season and age in the aquatic systems, the DOC may thus have different availability to lake water bacteria. However, bacterial degradation of allochthonous DOC not only depends on the supply and the character of the substrate, but is also regulated by access to limiting nutrients (N and P) [13, 17] and by temperature [55].

It can be hypothesized that the bacterial utilization of allochthonous DOC in humic lakes could be highly variable depending on the supply and the character of inflowing DOC, as well as on the prehistory of the DOC both in the inlet rivers and in the lake itself. In addition, it must also be taken into account that a high bacterial biomass and a high bacterial production in humic lakes may not necessarily depend on *in situ* production. It may also be the result of an import of a high number of active bacterial cells together with the allochthonous humic material [48].

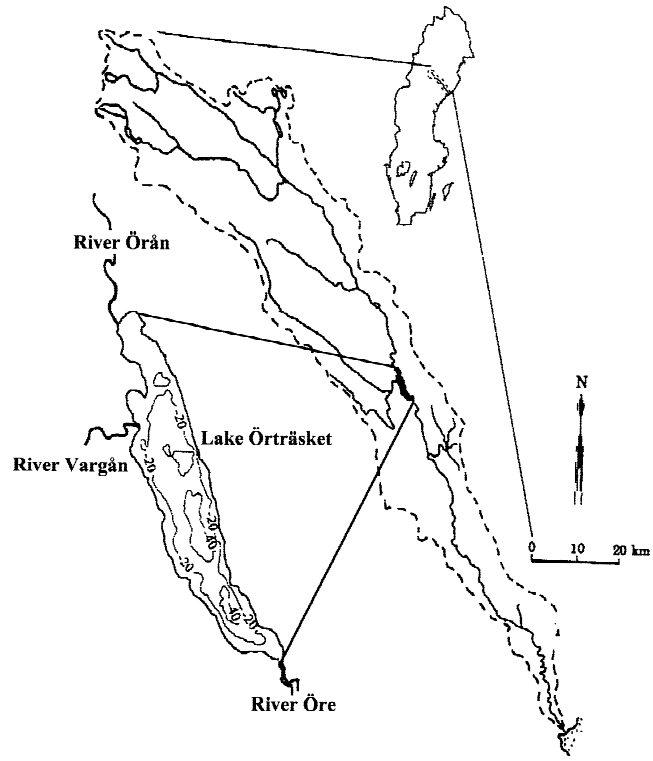

Fig. 1. The River Öre catchment and Lake Örträsket.

In order to elucidate the roles of the allochthonous carbon and the bacterial cell import for the lake bacterial production and biomass, a study was carried out in Lake Örträsket, a large humic lake in northern Sweden. The main objectives were to investigate the role of imported bacterial cells versus lake internal production of cells and how the lake internal production was controlled by the amount and quality of inflowing organic substrates and factors that determined bacterial utilization of such substrates.

Methods

Study Area

Lake Örträsket (64°10′N, 18°55′E), situated in the northern part of Sweden (Fig. 1), is a large lake (7 km^2) with a maximum depth of 64 m and a mean depth of 23 m. The water color is approximately 80 mg Pt L^{-1} and the mean secchi depth is 2.5 m [17]. The drainage area is 2174 km^2 and consists of coniferous forest and mires [17]. The drainage area is sparsely populated and the anthropogenic influence on the water quality is negligible [9]. The dominant bedrocks are granite and gneiss [16]. The lake has two inlets, River Örån and River Vargån, and one outlet, the River Öre (Fig. 1). A

majority of the inflowing water comes from River Örån (75%) and River Vargån (21%). Diffuse inlets have a minor share of the total amount of water that enters the lake [24]. The theoretical water retention time for Lake Örträsket is about 100 days and ranges, depending on season, between 20 and 250 days. The lake is ice covered from December to early May. Thermal stratification usually develops in the beginning of June and lasts until the end of September. The metalimnion is situated between 10 and 20 m during most of the stratification period.

Sampling Procedure

Sampling was conducted every week in May, and every second week during June to mid-October 1997. On each occasion, water samples were collected from the inlets (River Örån and River Vargån) and the outlet (River Öre), as well as from the lake (epilimnion and hypolimnion). In addition, lake data were used from sampling occasions in March, April, and December 1996, and in February 1998, in order to utilize data that corresponded to the winter period.

Water from the inlets and the outlet was collected using a Ruttner sampler. Samples were taken in the middle of the rivers at a depth of 0.5 m and poured into acid-rinsed bottles. Composite samples from the epilimnion and hypolimnion of the lake were collected according to the procedure described by Jansson et al. [17]. The lake water was collected with a tube sampler (2m long, 2-liter vol) at three stations in the lake, and each 2-m layer was sampled in proportion to the relative volume of this layer in the whole lake. The water was then mixed to give composite samples of 50 liters [17]. The samples were thus composed so that chemical and biological data from the epilimnion and the hypolimnion of the lake were representative for the average condition within each stratum.

Hydrology

Discharge in the inlets (River Örån and River Vargån), and in the outlet (River Öre) were determined during the observation period by continuous registration of the water level, and by subsequent calculation of discharge using previously established water level/discharge relationships [23]. Volumetric changes of the lake used for bacterial budget calculations (see below) were calculated using previously established discharge/volumetric relationships (Jonsson, unpublished data).

Analyses

Water for chemical analyses was frozen within 1 h after sampling. All samples were analyzed for DOC (filtered through pre-ignited Whatman GF/F-filters). DOC analyses were performed at Umeå Center for Marine Sciences with a Shimadzu TOC 5000. Absorbance was determined on filtered water (pre-ignited Whatman GF/F-filters) with a quartz cuvette (5 cm) at wavelength 420 nm, using a Hitachi U-1100 Spectrophotometer. N and P were analyzed in the epilimnetic lake samples from June 13 until September 3 in 1997, by standard methods at the Institute of Limnology in Uppsala. Soluble reactive phosphorus (SRP) was analyzed according to Murphy and Riley [38] after filtration through 0.45-μm membrane filters (Sartorius). Total phosphorus was analysed according to Menzel and Corwin [33]. NH_4-N, NO_2-N+NO_3-N, and Kjeldahl-N were analyzed according to Chaney and Marbach [5], Wood et al. [58], and Jönsson [26], respectively.

Samples for bacterial biomass determination were fixed with formaldehyde (final concentration 4%). Bacteria were counted and measured with acridine orange staining and epifluorescence microscopy [3]. At least 20 randomly selected squares and 400 cells were counted in each sample. Cell sizes were decided for at least 100 cells in each sample. Bacterial biomass was calculated assuming a biovolume to carbon biomass factor of 0.308 pgC μm^{-3} [10]. The bacterial biomass was determined in all samples from the lake and the rivers. Bacterial production (BPP) was determined immediately after sampling by measuring incorporation of ^{3}H-leucine (specific activity 6.1 MBq $nmol^{-1}$). Then, 1.2 ml of water was added with ^{3}H-leucine to a concentration of 30 nM and incubated for 60 min at *in situ* temperature in the dark. Measurements of ^{3}H activity were made with a Beckman LS 1801 scintillation counter. A detailed description of the procedure is given by Jansson et al. [17]. The bacterial production was determined in all samples from the lake and the rivers.

The ratio between BPP and DOC (BPP/DOC) was calculated for all samples and used as an indicator of the bioavailability of DOC [34]. In order to estimate changes in the chemical quality of the DOC, the ratio between absorbance at 420nm and DOC (ABS_{420}/DOC) was determined. The BPP/DOC ratio and the ABS_{420}/DOC ratio were calculated both for the lake (epi- and hypolimnion) and for the rivers (River Örån, River Vargån, and River Öre). In the epilimnetic samples the C:N ratio was further used to characterize the dissolved organic matter. The ratio was calculated as DOC divided with DON, where the DON was defined as the difference between the concentration of Kjeldahl-N and NH_4-N.

Primary production was measured in the epilimnion (June 13–September 3) as *in situ* $H^{14}CO_3$ uptake according to the procedure given by Drakare et al. [8]. Water was collected with a Ruttner sampler at depths 0.1, 0.2, 0.4, 0.8, 1.6, 3.2, and 6.4 m and added together with a sodium bicarbonate solution containing ^{14}C (Amersham CFA3, specific activity 3.7 MBq $mmol^{-1}$, final conc. 800 Bq per ml sample) to 125-ml borosilicate bottles. Triplicates plus one dark bottle were incubated at the original sampling depths between 1000 and 1400 h. After incubation, the samples were filtered, and the total production was assumed to be represented by particles collected on 0.2 μm (polycarbonate, MSI MicronKlear) filters. The ^{14}C activity was counted in a scintillation counter. The production rates were calculated using the equation of Wetzel and Likens [54] and expanded to daily values assuming that productivity is directly proportional to light [54].

Species composition and biomass of phytoplankton and zooplankton was determined in the epilimnetic samples from June 13

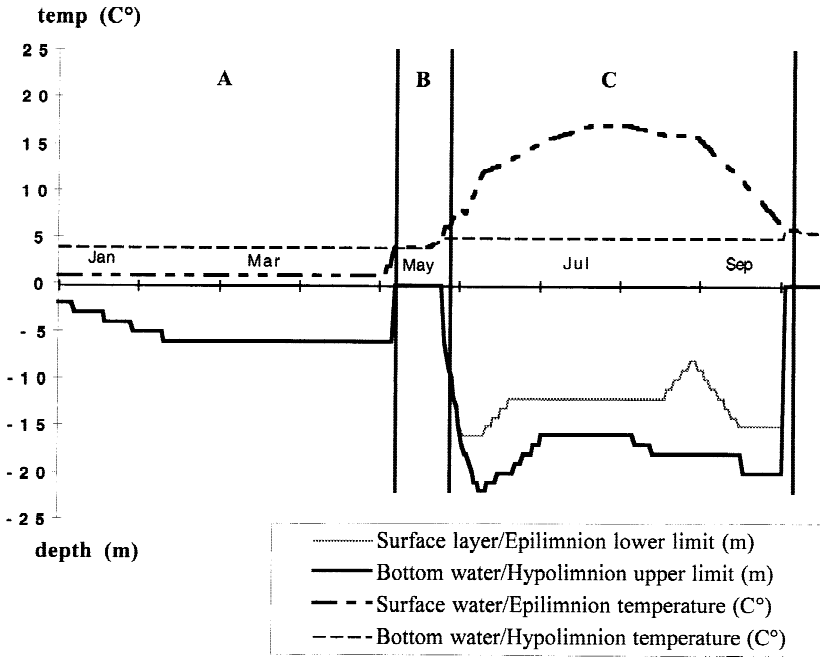

Fig. 2. Temperature and stratifications depths for the surface layer and the bottom water during winter stratification, and for the epilimnion and hypolimnion during summer stratification, in Lake Örträsket in 1997.

until September 3. The water samples were preserved with Lugol's solution [40]. Phytoplankton samples were counted using an inverted phase-contrast microscope after overnight sedimentation [40]. The characterization of phytoplankton species was carried out according to Jansson et al. [17] and Isaksson et al. [14]. Zooplankton species were counted from concentrated samples counted in their entirety. The characterization of zooplankton species was carried out according to Jansson et al. [18].

Bacterial Cell Budget

A bacterial budget was constructed in order to compare the number of bacterial cells flowing into the lake via the inlets to the number leaving the lake via the outlet, and to the number of bacteria produced within the lake. Bacterial concentrations multiplied by discharge from the inlets and the outlet were used to calculate the magnitude of this exchange. During circulation, the inflowing water and the bacterial cells therein were assumed to mix with the whole lake volume. Inflowing water was assumed to mix with the cold surface water during winter stratification, and the epilimnetic water during summer stratification. The bottom water during winter stratification and the hypolimnetic water during summer stratification were regarded as closed systems. Changes of the bacterial concentrations within the lake were calculated from measured lake bacterial concentrations and lake bacterial production. Linear interpolation between the sampling occasions was used to get values for each day of the study period. Temperature and stratification depths are shown in Fig. 2 for 1997 for the surface layer and the bottom water of Lake Örträsket during winter stratification, and for the epilimnion and the hypolimnion during summer stratification.

The budget was calculated for four major periods (A–D), defined and characterized as follows:

Period A (December 1–May 9): Winter stratification. The hydrology was characterized by a low and stable discharge (Fig. 3) which mixed with the cold surface water of the lake.

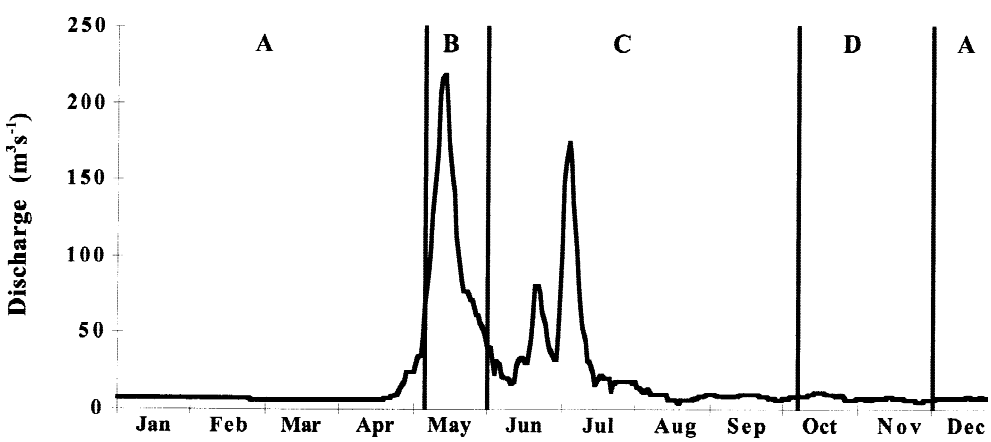

Fig. 3. The daily discharge at the outlet of Lake Örträsket 1997.

Period B (May 10–May 28): Spring circulation. The hydrology was characterized by a pronounced spring flood (Fig. 3), which mixed with the whole water volume and renewed all water in the lake.

Period C (May 29–October 7): Summer stratification. The hydrology was characterized by one small and one pronounced summer episode, after which the discharge was low (Fig. 3). The inflowing water was mixed with epilimnetic water, and the hypolimnion was regarded as a closed system.

Period D (October 8–November 30): Autumn circulation. The hydrology was characterized by a low and stable discharge (Fig. 3), which mixed with the whole water volume in the lake.

The net change of bacterial cells in Lake Örträsket, during stratification and during circulation, was calculated as the difference in bacterial cell concentration between the first day and the last day of each period (with the exception of period D, which was only sampled once). The net bacterial production of bacterial cells in the lake (BPP_{net}) for the different periods was calculated from the lake bacterial production measurements and the lake bacterial biomass estimates. Elimination of bacteria for each period was calculated as (Input + BPP_{net}) − (Output + Net change) (with the exception of period D, which was only sampled once). The elimination of bacterial cells during summer (period C), caused by flagellate and zooplankton grazing, was determined by using clearance rates from grazing experiments (flagellates), and by using data on clearance rates from literature data (zooplankton). Grazing experiments with phagotrophic flagellates were carried out using fluorescent microspheres (FLM) according to the procedure given by Isaksson et al. [14]. The experiments were conducted from June 13 until September 3 in 1997, and were run in duplicate. The FLM (diameter of 0.51 μm) were added to a final concentration representing 20–50% of ambient bacterial concentration. The species composition and individual numbers of zooplankton were determined in the epilimnion from June 13 until September 3 according to Jansson et al. [18] (cf. above). Zooplankton bacterivory was calculated for ciliates (individual clearance rates from Isaksson et al. [14]), rotifers (individual clearance rates from Sanders et al. [44]), and cladocerans (individual clearance rates from Kankaala [27]). Copepods were not included, as they are assumed to be incapable of feeding on bacteria [28].

Modeling of Bacterial Production in the Rivers

A model was constructed for each of the rivers (River Örån, River Vargån, and River Öre) in order to test how the bacterial production (BPP) in these systems was affected by DOC concentration, light exposure, and temperature. This simple model was utilized because temperature, insolation, and DOC concentrations showed weak but better correlation with river BPP than any other single parameter. The daily insolation (W $m^{-2}s^{-1}$) was measured at the Umeå Center for Marine Science, some 100 kilometers from the lake. A mean daily insolation (MDI) (W $m^{-2}s^{-1}$) light dose for 5 days (including the day of measurement and the 4 preceding days) was calculated and used in the model, as this light dose was found to best predict the BPP. The Q_{10} value for bacterial activity temperature dependence was set to 2.5. The epilimnion temperature was used to estimate the Q_{10} value, since the rivers and the epilimnion of the lake have approximately the same water temperatures during the summer season (unpublished data). A constant (k) was used to adjust predicted values to measured values for each station. The formula used to predict BPP (μgC $L^{-1}d^{-1}$; $BPP_{predicted}$) from DOC concentrations (mg L^{-1}), temperature (°C; Q_{10}-corrected) and insolation (MDI; W $m^{-2}s^{-1}$) was

$$BPP_{predicted} = DOC \times Q_{10}\text{-corrected} \times MDI \times k$$

Results

Chemical and Biological Lake Data

Nutrient concentrations, C:N ratios, primary production and phytoplankton and zooplankton biomass of the epilimnion during summer in 1997 are shown in Table 1. Phytoplankton biomass and production increased up to the end of August and then decreased. The zooplankton biomass peaked in late July (Table 1). The C:N ratio increased from June until September from 30 to 53, as did the NH_4-N concentration, from 7 to 19 μg L^{-1}. The SRP and the NO_2 + NO_3-N concentrations were fairly stable throughout the summer stratification. The total-P concentration ranged be-

Table 1. Chemical and biological characteristics of the epilimnion in Lake Örträsket in summer of 1997

	June 13	June 26	July 8	July 26	August 8	August 22	September 3
SRP (μg L^{-1})	2	2	2	4	3	3	0
Total-P (μg L^{-1})	20	18	20	31	22	18	16
NH_4-N (μg L^{-1})	7	6	8	8	13	15	18
NO_2+NO_3-N (μg L^{-1})	5	11	11	14	13	13	14
Kjeldahl-N (μg L^{-1})	344	283	405	412	313	348	259
Total-N (μg L^{-1})	349	294	507	484	366	399	293
C:N-ratio	30	36	38	39	47	41	53
Phytytoplankton biomass (μgC L^{-1})	14	15	10	29	40	37	9
Primary production (μgC $L^{-1}d^{-1}$)	3	7	1	6	9	15	1
Zooplankton biomass (μgC L^{-1})	37	19	12	49	31	20	17

tween 16 and 31 μg L^{-1} with a peak in late July. The total-N concentration ranged between 200 and 500 μg L^{-1} (Table 1).

Hydrology

After a low runoff during winter (period A), the spring flood started in the end of April and lasted until the beginning of June (period B) (Fig. 3). During summer stratification (period C) two episodes occurred: a small one in the end of June (Fig. 3), and a pronounced one in the beginning of July (Fig. 3). From the end of July until the end of September, the runoff was low (Fig. 3). The autumn circulation (period D) and the winter stagnation in December were both characterized by a low discharge (Fig. 3). The intensity of the spring flood occuring simultaneously with the spring circulation replaced the whole lake volume with spring flood water. The summer episode in July replaced the whole epilimnion volume while the hypolimnion was more or less unaffected. After an episode the episode water was slowly replaced by base flow water, and during winter when the water flow was low the volume of the lake consisted mainly of base flow water (Fig. 3).

Bacterial Biomass

The bacterial biomass and the bacterial concentrations were lowest during winter stratification (Table 2). A marked peak in lake bacterial biomass was shown during spring circulation, when the lake bacterial biomass was as high as 72 μgC L^{-1} (Table 2). During summer, both the bacterial biomass and the bacterial concentration were significantly higher in the River Örån (one-way ANOVA, $p < 0.05$, Tukey's post hoc test), in comparison with the other stations. In the River Vargån and the River Öre, the bacterial biomass and concentrations were similar to the lake bacterial biomass and concentrations (Table 2). The average cell volume (ACV) (Table 2) was not significantly different between the lake and the rivers during the investigated period (one-way ANOVA, log transformed data; $p > 0.05$).

Bacterial Production

The bacterial production (BPP) in the surface water was low in February but increased in April in combination with the onset of the spring flood (Figs. 3 and 4A). In late April the spring flood water did not mix with the warmer bottom water because of its cold temperature [51], and thus the BPP in the bottom water remained low (Fig. 4B). After the spring flood the BPP in the epilimnion (Fig. 4A) declined until the high flow episode in early July, after which the highest value during the observation period occurred. After the July high flow episode the BPP in the epilimnion decreased rapidly. In the hypolimnion (Fig. 4B) the BPP increased in combination with the spring circulation, after which the BPP slowly decreased until the end of the year.

The highest BPP in the epilimnion of Lake Örträsket was clearly registrated in connection with high flow DOC input (Figs. 3 and 4A). The highest BPP was found in July when the epilimnion consisted mainly of summer episode water and the second highest when it consisted only of spring flood water in the beginning of June (Figs. 3 and 4A). The highest BPP in the hypolimnion occurred after the spring circulation, when all of the hypolimnion water consisted of spring flood water (Fig. 4B). During summer stratification, when the hypolimnion had been cut off from exposure to inlet water, the BPP clearly decreased, although the DOC remained fairly constant (Fig. 4B). A weak relationship was found between DOC concentration and BPP in the epilimnion ($r^2 = 0.4$, $p < 0.05$) (Fig. 4A), but not in the hypolimnion ($r^2 = 0.001$; $p > 0.05$) (Fig. 4B). No relationships were found with ABS_{420}/DOC ratios (Table 2) or C:N ratios or nutrient concentrations (Table 1). Therefore, it appears as if hydrological variations have a crucial impact on the lake water BPP. Surprisingly, the BPP in river water expressed different intensity and different temporal variation than in the lake.

During summer, the BPP was significantly higher in the inlet rivers than in the lake (one-way ANOVA, $p < 0,05$; Tukey's post hoc test) (Table 2). The outlet BPP during summer was lower than the inlet's BPP (Table 2). In contrast to the lake, the highest BPP in all rivers were recorded during low flow in late July and the lowest during spring flood (Table 2). During summer a relationship between BPP and DOC concentration was found for River Vargån ($r^2 = 0.6$, $p > 0.05$), but not for the River Örån ($r^2 = 0.2$, $p > 0.05$), or the River Öre ($r^2 = 0.3$, $p > 0.05$). During this period, the BPP in the rivers was not related to the ABS_{420}/DOC ratios nor, in contrast to the lake, to the discharge (cf. Table 2). However, the BPP in the rivers could be well explained by the model, including variations in DOC concentration, temperature, and light insolation. When DOC concentration, temperature, and insolation were high, the highest BPP was seen in all rivers (Fig. 5). The relationships between predicted bacterial production ($BPP_{predicted}$) and measured bacterial production ($BPP_{measured}$) were all statistically significant (linear regression analysis, $p < 0.05$) (Fig. 5), and the

Table 2. Mean values for Lake Örträsket and its tributaries for bacterial production (BPP), bacterial biomass and concentration, average cell volume of bacteria (ACV), DOC concentration, and BPP/DOC and Absorbance (ABS)/DOC ratios during 1997[a]

Period	Sample station	Bacterial production ($\mu gC\ L^{-1}d^{-1}$)	Bacterial biomass ($\mu gC\ L^{-1}$)	Bacterial concentration ($10^6\ ml^{-1}$)	ACV (μm^3)	DOC ($mg\ L^{-1}$)	BPP/DOC	ABS/DOC
	R.Örån	9.1 (0.7–17.4)	26 (7–44)	1.4 (0.6–2.2)	0.050 (0.035–0.065)	6.4 (5.6–7.1)	1.3 (0.1–2.5)	0.02360 (0.02339–0.02380)
	R.Vargån	9.6 (2.6–16.5)	16 (11–21)	1.0 (0.8–1.2)	0.052 (0.045–0.058)	11.7 (7.4–15.9)	0.7 (0.4–1)	0.02730 (0.02365–0.03095)
Winter stratification	L.Örträsket S.Layer	2.9 (0.6–5.2)	24 (18–29)	1.4 (1.1–1.7)	0.054 (0.052–0.056)	8.3 (7.9–8.7)	0.4 (0.1–0.7)	0.02104 (0.02011–0.02196)
	L.Örträsket B.Water	0.6 (0.2–1)	17 (11–23)	1.0 (0.8–1.2)	0.053 (0.047–0.059)	8.8 (8.7–8.9)	0.1 (0.02–0.1)	0.2019 (0.01971–0.02067)
	R.Öre	1.1 (0.6–1.5)	15 (11–19)	1.1 (0.8–1.5)	0.044 (0.043–0.044)	8.2 (8.1–8.2)	0.2 (0.1–0.2)	0.02108 (0.2–0.02216)
	R.Örån	7.4 (3.5–12.4)	36 (32–38)	1.8 (1.5–1.9)	0.065 (0.063–0.069)	12.8 (12–13.4)	0.6 (0.5–0.9)	0.02127 (0.2031–0.02242)
Spring circulation	R.Vargån	11.2 (4.9–17.7)	33 (31–37)	1.3 (1.3–1.4)	0.081 (0.073–0.094)	14.7 (12.6–17.9)	0.8 (0.3–1.3)	0.02177 (0.2071–0.02299)
	L.Örträsket	3.8*	72*	2.9*	0.082*	11.4*	0.3*	0.0236*
	R.Öre	5.6 (3.3–8.1)	37 (36–39)	2.0 (1.9–2.2)	0.061 (0.055–0.046)	12.4 (10.7–14.6)	0.5 (0.3–0.8)	0.02234 (0.2127–0.02308)
	R.Örån	17.0 (2.8–34.2)	46 (33–59)	3.3 (2.5–4.2)	0.046 (0.039–0.059)	10.4 (6.5–18.7)	1.7 (0.4–3.1)	0.02225 (0.1950–0.02477)
	R.Vargån	16.0 (3.5–42.7)	31 (22–45)	2.3 (1.8–3.2)	0.044 (0.039–0.055)	14.2 (11.7–23)	1.1 (0.3–2)	0.02636 (0.2224–0.03088)
Summer stratification	L.Örträsket Epi	5.1 (0.4–11.8)	31 (24–39)	2.5 (1.6–4.0)	0.043 (0.032–0.059)	12.6 (10–15.6)	0.4 (0.03–0.8)	0.02197 (0.1930–0.02523)
	L.Örträsket Hypo	2.7 (1.1–4.7)	28 (21–34)	2.1 (1.6–3.4)	0.045 (0.031–0.059)	11.7 (10.9–13)	0.2 (0.1–0.4)	0.02117 (0.01992–0.02193)
	R.Öre	10.0 (2.3–23.7)	32 (22–48)	2.5 (1.5–3.8)	0.046 (0.031–0.084)	12.5 (10.3–15.2)	0.8 (0.2–1.6)	0.02159 (0.01960–0.02307)
	R.Örån	5.8*	40*	2.7*	0.048*	7.9*	0.7*	0.02139*
	R.Vargån	3.7*	29*	2.2*	0.042*	12.2*	0.3*	0.02795*
Autumn circulation	L.Örträket	0.3*	31*	1.8*	0.055*	10.8*	0.03*	0.02093*
	R.Öre	1.7*	28*	2.2*	0.041*	10.4*	0.2*	0.02154*

* One sampling occasion.

[a] Ranges are given within parentheses. (S.Layer = Surface layer; B.water = Bottom water; Epi = Epilimnion; Hypo = Hypolimnion).

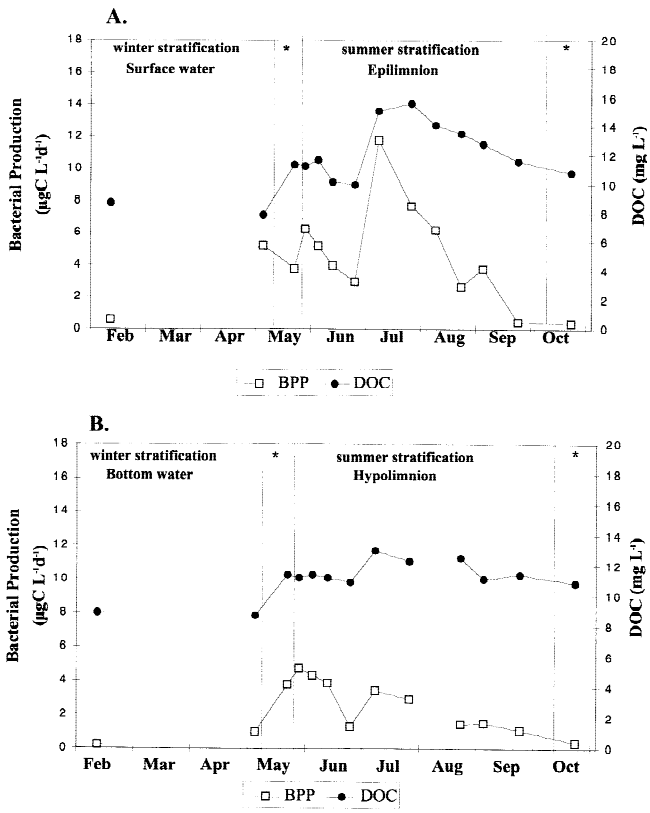

Fig. 4. Bacterial production (open squares) and DOC concentration (filled circles) during winter stratification, during spring and autumn circulation (marked with an *), and during the summer stratification. (A) The surface layer, the whole lake volume (*), and the epilimnion. (B) The bottom layer, the whole lake volume (*), and the hypolimnion.

River Örån was best predicted by the model. In contrast to the rivers, the BPP in the epilimnion and in the hypolimnion of Lake Örträsket could not be modeled by using DOC concentration, temperature, and light insolation. Thus, it is obvious that the BPP in the rivers and in the lake were regulated in different ways.

BPP/DOC Ratios

The BPP/DOC ratios for the epilimnion and the hypolimnion were plotted over time from May 29 until September 22, where May 29 was set as day number 1 (Fig. 6). As the epilimnion was exposed twice to large episodes (Fig. 3), the relationship between BPP/DOC ratios and time were examined after each episode (Epilimnion A: May 29–June 25, Epilimnion B: July 7–September 22) (Fig. 6). The highest BPP/DOC ratios in Lake Örträsket were found in the epilimnion after the spring flood (day 1) and after the high flow

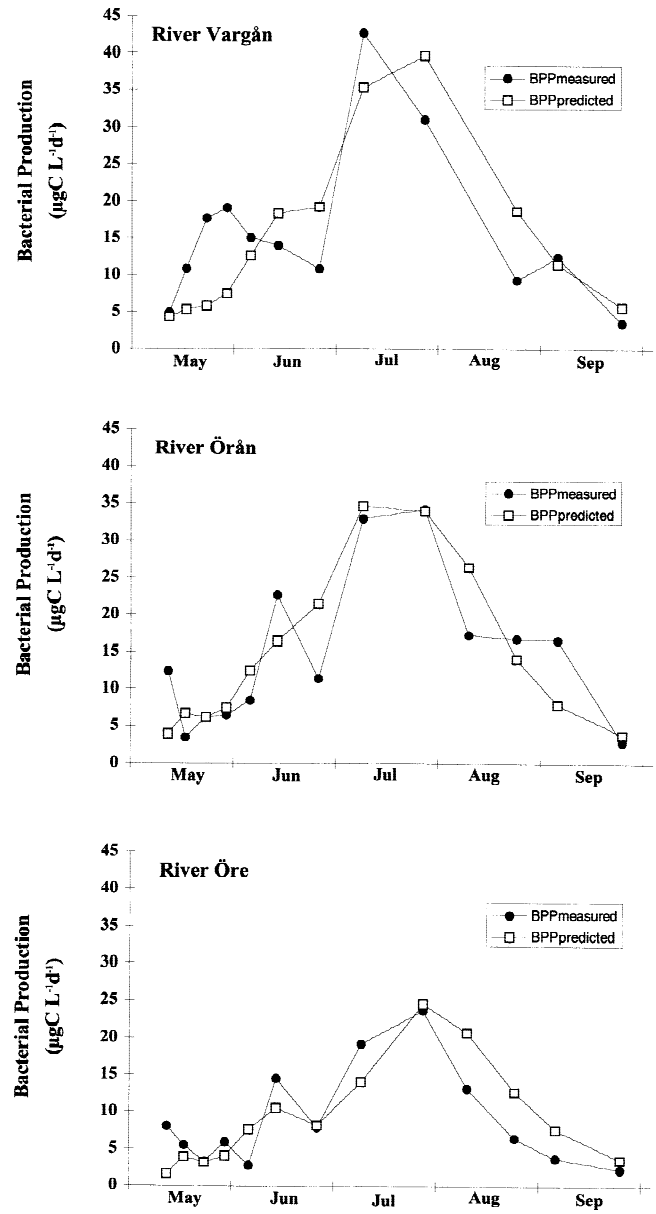

Fig. 5. The predicted bacterial production ($BPP_{predicted}$) modeled by variations in DOC concentration, temperature, and light insolation for the River Örån, the River Vargån, and the River Öre, respectively. The equations used in the models in order to predict the bacterial production ($BPP_{predicted}$) were: River Örån $BPP_{predicted}$ = DOC × Q_{10}-corrected × MDI × 0.003; River Vargån $BPP_{predicted}$ = DOC × Q_{10}-corrected × MDI × 0.0025; River Örån $BPP_{predicted}$ = DOC × Q_{10}-corrected × MDI × 0.0016. The relationships between $BPP_{predicted}$ (open squares) and measured bacterial production ($BPP_{predicted}$) (filled circles) were all statistically significant for the rivers (linear regression analysis; Stat View Student); River Örån, $r^2 = 0.77$; $p = 0.002$; River Vargån, $r^2 = 0.62$; p = 0.003; River Öre, $r^2 = 0.65$; $p = 0.001$.

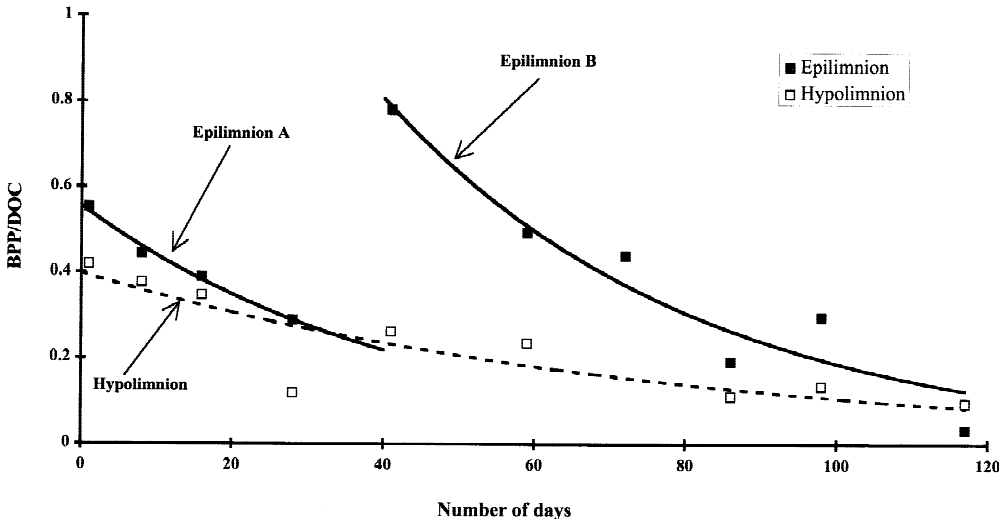

Fig. 6. The decline in the BPP/DOC ratio over time in the epilimnion and in the hypolimnion of Lake Örträsket in 1997. Day number 1 for each relationship is set to times when almost 100% of the epilimnion or the hypolimnion consisted of high flow episode water, respectively. The relationship between BPP/DOC ratio and time (nonlinear relationship, Excel 5.0) for the hypolimnion is described by the equation BPP/DOC = 0.398 $\times$ $e^{(-0.0131\times\text{Number of days})}$ (r^2 = 0.77; p = 0.002). The first relationship between BPP/DOC ratio and time in the epilimnion (A) is described by the equation BPP/DOC = 0.555 $\times$ ($e^{(-0.0232\times\text{Number of days})}$) ($r^2$ = 0.99; p = 0.006), and the sec ond (B) by the equation BPP/DOC = 0.807 $\times$ $e^{(-0.0242\times\text{Number of days})}$ (r^2 = 0.91; p = 0.003).

episode in July (day 40). In the hypolimnion the highest value was found after the spring circulation (day 1) (Fig. 6). No clear relationships between the BPP/DOC ratio and temperature (Fig. 2), insolation, ABS_{420}/DOC or C:N ratios, or nutrient concentrations (Tables 1 and 2) were found in the lake water. Thus, the BPP/DOC ratio could not be coupled to single chemical characteristics of DOC or to single environmental factors with a possible influence on the DOC utilization.

There was a regular variation of the BPP/DOC ratios in relation to the high flow events, both in the epilimnion and in the hypolimnion of Lake Örträsket. After both high flow episodes in the epilimnion, the decrease of the ratio followed the same exponential expression. The decline in the hypolimnion was also exponential but slower (Fig. 6). The BPP/DOC ratio in the hypolimnion was unaffected by the summer episode when the inflowing water was mixed only with epilimnion water. The "half-lives" for the BPP/DOC ratio in the epilimnion and in the hypolimnion was estimated as 30 days and 53 days, respectively.

In the inlet rivers, the BPP/DOC ratios were statistically higher than in the lake (one-way ANOVA, p < 0,05, Tukey's post hoc test), and as for bacterial production, the inlet BPP/DOC ratios and the outlet BPP/DOC ratios did not differ statistically (Table 2). When the flow weighted inlet BPP/DOC ratios, outlet BPP/DOC ratio (River Öre), and hypolimnion BPP/DOC ratios were divided with epilimnion BPP/DOC ratios (Fig. 7), it was clearly seen that the BPP/DOC ratios were higher in the running waters than in the epilimnetic lake water (one-sample t-test; $p < 0.05$). There were also clear differences between the inlets and the outlet and between the hypolimnion and the epilimnetic values, though hypolimnion did not differ statistically from the epilimnion ratios (one-sample t-test; $p > 0.05$). The difference

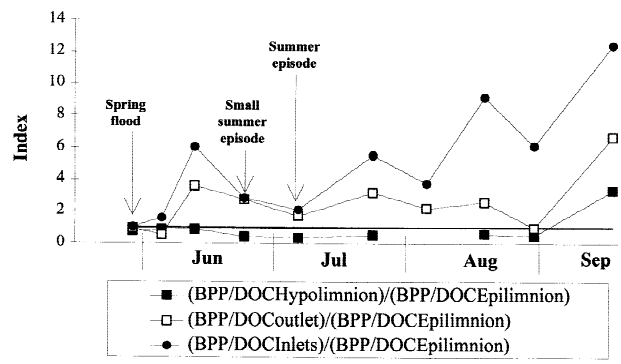

Fig. 7. The BPP/DOC ratios for flow weighted inlet, the outlet, and the hypolimnion divided by the BPP/DOC ratios in the epilimnion during the summer stratification in 1997. A value of 1 indicates identical conditions with the epilimnion. The inlet and outlet BPP/DOC ratios were statistically higher than the epilimnion BPP/DOC ratios (one-sample t-test; $p < 0.05$). The hypolimnion BPP/DOC ratios were usually lower than the epilimnetic ratios, but did not differ statistically from the epilimnetic ratios (one-sample t-test; $p > 0.05$).

Table 3. Results from the bacterial cell budget constructed for different time periods (A–D) in Lake Örträsket during 1997[a]

Period	Water layer	Input (cells × 10^{20})	Output (cells × 10^{20})	Net change (cells × 10^{20})	BPP_{net} (cells × 10^{20})	Elimination (cells × 10^{20})	Predation flagellates/ elimination (%)	Predation zooplankton/ elimination (%)	Input/ BPP_{net} (%)
A									
Winter stratification	Surface water	1.27	1.10	0.54	3.97	3.6	n.m.	n.m.	32
	Bottom water			-0.85	6.19	n.m.	n.m.	n.m.	n.m.
B									
Spring circulation	Circulation	4.24	4.29	-0.01	5.99	5.95	n.m.	n.m.	71
C									
Summer stratification	Epilimnion	8.68	9.07	0.97	40	38.64	23	13	22
	Hypolimnion			-1.45	17.6	n.m.	n.m.	n.m.	n.m.
D									
Autumn circulation	Circulation	0.68	0.65	n.m.	1.65	n.m.	n.m.	n.m.	41

[a] Net change of bacterial cells was calculated as the difference in bacterial cell concentration between the first day and the last day of each period for each stratum in the lake. The net bacterial production (BPP_{net}) represents the number of bacterial cells produced within the lake strata during the different time periods. The elimination of bacterial cells during each period was calculated as (Input+BPP_{net})-(Output+Net change). Elimination of bacterial cells due to flagellate grazing was determined from grazing experiments, and the elimination of bacterial cells caused by zooplankton was determined by using clearance rates from literature data. (n.m. = not measured.)

in BPP/DOC ratios between running water and epilimnetic water decreased markedly during high flow events (Fig. 7), because of the combined effect of a higher ratio of the epilimnetic DOC during high flow events and a lower ratio of the DOC in the rivers. Thus, rivers and lakes seemed to respond differently to high flow episodes regarding the bacterial utilization of allochthonous DOC.

Bacterial Cell Budget

The results from the bacterial cell budget are shown in Table 3. The input of bacterial cells was highest in combination with high flow events. During all periods the number of bacterial cells produced within the surface water, during circulation, and in the epilimnion of the lake was higher than the input of bacterial cells via the inlets. The number of bacterial cells produced within the epilimnion was higher than the production in the hypolimnion. During winter stratification, the production of bacterial cells was higher in the bottom water than in the surface water. The input of bacterial cells ranged between 20 and 70% of the production of bacterial cells in the surface water, in the epilimnion, and during circulation in the lake for periods A–D. The elimination of bacterial cells was also higher than the input of bacterial cells via the inlets, further indicating the importance of the *in situ* lake production in comparison with inlet input of bacterial cells. Predation loss during summer, due to grazing by flagellates, represented 23% of the elimination of bacterial cells. The estimated loss due to zooplankton grazing was 13% of the elimination during this period (Table 3). The elimination of bacterial cells caused by other factors than grazing was thus high.

Discussion

The bacterial biomass and the bacterial production (BPP) in Lake Örtäsket were mainly based on *in situ* production (Table 3). The input of bacterial cells for the whole study period represented approximately 30% of the total number of bacterial cells that were produced within the layer of the lake affected by inlet water. In comparison with the total lake production of bacterial cells in Lake Örtäsket during 1997, the input of cells was only 20%. However, even if the input of cells was low compared to lake production, the imported bacteria could have served as an inoculum to the lake. If imported bacterial cells grew and divided in the lake, they may actually have been responsible for a substantial part of the net bacterial production measured in the lake. It is not possible to elucidate from this study the extent to which the bacteria that grew in the lake should be regarded as riverine bacteria or lake-specific bacteria. What we can conclude is that, by number, the input of bacterial cells via the inlets was substantially lower than the net production of cells in the lake.

The budget (Table 3) also demonstrated a high elimination of bacterial cells in the lake. The elimination was during all periods considerably higher than the input of cells and quite similar to the production of cells in the lake. This result stresses that the turnover of cells in Lake Örträsket was rather independant of inlet input and outlet losses of cells. A large part of this elimination was due to grazing. Measured flagellate predation removed about 20–30% of the BPP, and the estimated bacterivory by zooplankton removed at the most another 15% of the BPP in the epilimnion (Table 3). Thus, bacterivory by flagellates and zooplankton removed up to 45% of the BPP in the epilimnion in 1997 (Table 3). The relatively high amount of bacterial cell lost due to flagellate grazing may be an effect of the relatively high bead-to-bacteria ratio (20–50%) used in the grazing experiment. If the bacterivores were dependent upon particle concentrations, this may have lead to an overestimation of the ingestion rates [32]. However, in other years the flagellate predation can be higher and amount to 100% of the epilimnion BPP [14]. Other possible causes of elimination of bacterial cells from the epilimnion of Lake Örträsket may be sedimentation of bacterial cells attached to flocculated humic matter [49] or viral lysis [30, 56]. Even if grazing did not explain the total elimination of bacterial cells in 1997, the large share of the total BPP that was consumed by grazers stresses the importance of the energy mobilization by bacteria for the energy economy of higher trophic levels in this lake. Since the grazing on bacteria depended on the bacterial cells produced within the lake, and not to any larger extent on imported cells (cf. above), it is important to discuss how the BPP in the lake is regulated.

Bacterial growth depends on the supply of oxidizable carbon compounds of allochthonous or autochthonous origin. The BPP in Lake Örträsket has been shown to be almost entirely dependent on the utilization of allochthonous DOC during summer [18, 25]. Therefore, variations in DOC input, DOC quality and factors influencing the bacterial utilization of DOC could be suspected to influence the BPP in the lake. However, the seasonal variation in BPP in Lake Örträsket or in the rivers showed no simple relationship with DOC concentration, simple DOC characteristics (ABS_{420}/

DOC or C:N ratios), or environmental factors such as temperature and nutrient concentrations. Moreover, the BPP in the inlets and the lake itself showed different seasonal variation (Figs. 4 and 5) and were obviously controlled by different factors or by that some regulating factors were expressed differently in river water and lake water.

The seasonal variation in BPP in the rivers was well explained by a model including temperature, daily light insolation, and DOC concentration (Fig. 5). This type of dependence is reasonable because temperature is a strong determinant of bacterial growth in freshwater systems [55], and as several investigators have demonstrated that light degradation of humic compounds is important, by rapidly modifying the organic material to forms readily available to bacterial degradation [4, 29, 53]. The temperature and insolation had a greater effect on the BPP variation than DOC concentrations in this model, since the predicted BPP was nearly as good in all rivers if DOC was excluded.

However, no relationship similar to that in Fig. 5 could be found for the epilimnion or the hypolimnion of the lake. Other differences between the rivers and the lake were that the BPP in the river water was higher than in the lake (Table 2), and that river production was highest during low flow situations (Fig. 5), while the highest production in the lake was recorded during high flow situations (Figs. 3 and 4). These discrepancies between river-water and lake-water BPP may offer a key to an explanation of how lake-water BPP can be regulated by substrate availability.

Since the high bacterial utilization of the allochthonous DOC in the rivers was positively correlated with light exposure, it is reasonable that the BPP in the epilimnion of Lake Örträsket can be lower than in the rivers (Table 2). The epilimnion is quite deep in Lake Örträsket (Fig. 2), and the light penetrates only one-fifth of the depth of the epilimnion. Thus, the epilimnetic effective light climate [41] is low, ranging between 10 and 20 $\mu E\ m^{-2}\ s^{-1}$ for an average summer day (unpublished data from L. Örträsket). Even though the photo degradation of DOC in the epilimnion of Lake Örträsket is significant [25], the light exposure of DOC must be considerably less in the epilimnion than in the shallow and turbulent rivers. This should, in turn, affect the amount of bacterial substrate produced from photodegradation [4, 29, 53]. The long residence times of DOC in the lake compared with DOC in the rivers should, in addition to low photodegradation, contribute to lower BPP in lake water than in river water. Bacterial degradation should successively deplete the lake water DOC of available substrates, resulting in a lower mean substrate availability in lakes than in rivers which contain younger, less processed, DOC [35]. Ageing of the lake DOC during passage through the lake was reflected by the fact that the BPP in the outlet water was only half of that in the inlet water (Table 2 and Fig. 5).

Besides that the BPP in the lake showed seasonal variations that were quite different from those of the river water, there were also pronounced differences between the production in the epilimnion and the hypolimnion (Figs. 4A,B). All these variations can be discussed using the BPP/DOC ratio, which can be used as an estimator of the *in situ* availability of the DOC [34].

The seasonal variations in BPP and BPP/DOC ratio in the epilimnion were clearly dependent on the discharge variation and input of episode water in the epilimnion (Figs. 4A,B and 6). The high values during high flow episodes (Fig. 6) could theoretically have been caused by increased input of limiting nutrients, permitting a higher bacterial utilization of allochthonous DOC than during low-flow events. However, nutrient enrichment experiments have demonstrated that stimulation of BPP by limiting nutrient (P) additions was particularly pronounced during high flow events in Lake Örträsket [18]. Similar results were obtained by Hessen et al. [13], who found the BPP responded most to N and P additions in Norwegian humic lakes after high flow events in spring and autumn. Much as nutrient-limited phytoplankton grow faster at optimal light conditions than at low light conditions [1], the bacteria should be able to show higher growth rates when the energy supply in the form of DOC is favourable. P-limitation should then restrict BPP differently at different organic substrate concentrations, but decreased nutrient limitation could not explain the BPP peaks in the lake during the high flow events.

We therefore, suggest that the lake water bacteria were stimulated by an input of relatively "young," less degraded, allochthonous DOC during high flow events (Fig. 6). With time, the bioavailability of the allochthonous DOC decreased because of bacterial degradation and photodegradation. During base flow conditions, the lake BPP was not stimulated by the riverine input of allochthonous DOC (Fig. 6), partly because the input of allochthonous DOC was small relative to the DOC content of lake water, and partly because the inflowing DOC during a base flow period should have been quite degraded before reaching the lake. The higher BPP/DOC ratio in the inlets compared to the epilimnion during low flow situations (Fig. 7) probably reflects that the bacterial utilization can proceed in a faster rate because of light (cf. above). The similar BPP/DOC ratio in the inlets and in the lake during high flow may be interpreted so that

the fast transport of river water during high flow events does not permit the bacterial substrate to be degraded to the same degree as during low flow before entering the lake.

The summer episode gave a higher BPP/DOC ratio in the epilimnion than the spring flood episode (Fig. 6). The result indicates that the higher water temperature in the epilimnion (Fig. 2), or a better substrate quality, allowed a higher bacterial utilization of the allochthonous DOC at this time. The difference in effective light climate between the events was small and should not have had any great influence on substrate production. It is possible that rainstorms in summer, in contrast to the spring situation, wash out a mix of plant exudates and bacterial degradation products from surface soils [31, 39], which may be less degraded than the DOC from spring- and base flow water [15]. This possibility was given some support by the fact that the BPP value of the inlets during the summer episode was higher than the value predicted from temperature, insolation, and DOC concentration (Fig. 5). On the other hand, the BPP/DOC ratio in the epilimnion declined exponentially also after the summer episode, with identical kinetics as after the spring episode in the epilimnion (Fig. 6). Together, these facts indicate that the summer episode contained a larger amount of suitable bacterial substrates than the spring episode, but that the substrates were of a similar quality during both events.

The BPP/DOC ratio also reflects how the allochthonous carbon was processsed in the lake. The ratio increased considerably from the winter base flow values of 0.1 to about 0.5 (Table 2) in both the epi- and hypolimnion when the lake began to stratify, and when the whole lake volume consisted of spring flood water. During the summer stratification the hypolimnion was sealed from the influence of inlet water (Fig. 4B and 6). The slow exponential decline of the BPP/DOC ratio in the hypolimnion during summer (Fig. 6) then shows how the bacterial degradation affected the bioavailability of allochthonous DOC over time, when temperature was constant (Fig. 2) and light exposure was absent [25]. In the epilimnion the decrease in bioavailability was more rapid (Fig. 6), indicating that, temperature and perhaps light exposure, were important in regulating the bacterial utilization of the DOC. Calculations based on experimental results on photodegradation of Lake Örträsket DOC (Graneli et al.; unpublished data), indicate that photodegradation of DOC represents approximately 20% of total DOC degradation in the epilimnion of Lake Örträsket, in spite of the poor light climate [25]. Since the temperature difference between the epi- and the hypolimnion in June was small (Fig. 2), and both water layers consisted of spring flood water containing the same kind of DOC (cf. above), the faster decline in the epilimnion in comparison with the hypolimnion (Fig. 6) at this time could have been due to photodegradation. The faster degradation in the epilimnion means that the "aging" was a faster process in the epilimnion than in the hypolimnion (Fig. 6), and that the development toward a more recalcitrant composition of the lake DOC pool was faster in the epilimnion than in the hypolimnion.

The likely answers to the question regarding what mainly regulates the production of bacteria in Lake Örträsket to a great extent include the prehistory of the DOC that enters the lake. High input of relatively undegraded material such as occurs during high flow episodes clearly stimulates the lake BPP. Base flow conditions lead to input of more degraded material which does not stimulate lake production. The potential for *in situ* production of bacteria during summer in Lake Örträsket was, therefore, largely a function of precipitation and runoff conditions. Internal factors that determine the utilization of the allochthonous DOC in Lake Örträsket are the retention time in the lake and the exposure to light and high temperatures. Phosphorus limitation probably restricts the rate at which the DOC can be processed by bacteria. Considering the great importance of bacteria as energy mobilizers for the pelagic food web in Lake Örträsket [18] and in other humic lakes [12, 28, 48], this study demonstrates possible links between climatological and weather conditions, and the productivity of boreal forest ecosystems via terrestrial export of organic carbon.

Acknowledgments

We thank Lars-Inge Karlsson, Anneli Ågren, and Stina Drakare for technical assistance during fieldwork, Jan Johansson for counting the bacteria, and Anders Jonsson for comments on the manuscript. Financial support was provided by the Swedish Natural Science Research Council (NFR).

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