Vol. 21: 265–273, 2000 | AQUATIC MICROBIAL ECOLOGY
Aquat Microb Ecol | Published June 15

Dynamics of phyto- and bacterioplankton in a high Arctic lake on Franz Joseph Land archipelago

Michaela Panzenböck[1,*], Britta Möbes-Hansen[1], Roland Albert[1], Gerhard J. Herndl[2]

[1]Institute of Ecology, Althanstr. 14, 1090 Vienna, Austria
[2]Dept of Biological Oceanography, Netherlands Institute for Sea Research (NIOZ), 1790 AB Den Burg, The Netherlands

ABSTRACT: Pelagic food web processes with focus on phyto- and bacterioplankton dynamics were followed in a high Arctic lake on Ziegler Island, Franz Joseph Land archipelago, during July and August 1996. The oligotrophic, permanently ice-covered lake is characterized by a rather short pelagic food web with rotifers representing the highest trophic level. Phytoplankton biomass and net primary production averaging 1.8 µg chl *a* l^{-1} and 22 µg C l^{-1} d^{-1}, respectively, decreased during the investigation period. Photosynthetic extracellular release (P_{er}) corrected for bacterial uptake was high and contributed between 31% (July) and 96% (August) of total primary production. The abundance of bacteria (9.3 to 17.3 × 10^5 ml^{-1}) and flagellates (7.8 to 17.3 × 10^2 ml^{-1}) varied within a narrow range. Bacterioplankton production ranging from 1.2 to 3.9 µg C l^{-1} d^{-1} and bacterial growth rates (0.1 to 0.3 d^{-1}) increased with increasing % P_{er}, indicating that algal exudates are the major carbon source for bacterioplankton. Bacterial carbon demand (assuming a 50% growth efficiency) amounted to 19% of gross pelagic primary production (P_{part} + P_{er}) and 31% of P_{er} during the investigation period. Evidence was found that bacterioplankton metabolism responds quickly to slight increases in temperature (1.2 to 2.0°C) with increased growth. Overall, production rates of phyto- and bacterioplankton in this high Arctic lake are similar to other Arctic lakes studied thus far, and the food web structure is even simpler than in most lakes at similar latitudes.

KEY WORDS: Arctic lake · Bacterioplankton · Phytoplankton · Bacterial activity · Primary production

INTRODUCTION

High latitude freshwaters, both Arctic and Antarctic, have received considerable attention over the last decades. They are now recognized as highly adapted ecosystems which are expected to be very sensitive to global climatic change (Wharton et al. 1989). Therefore, knowledge on the carbon and energy flux in these habitats, where the impact of climatic changes is most pronounced, may also lead to a better understanding of the impact of climatic changes in temperate aquatic systems where the food web structure is more complex.

High latitude lakes are characterized by low diversity of the biota due to the combination of extreme physical or environmental factors. Extreme radiation conditions, generally low nutrient input and permanently low water temperatures determine biodiversity and activity of these communities (Moore 1978), food web structure (Kling et al. 1992) and biogeochemical cycling between different trophic levels (Laybourn-Parry & Bayliss 1996). Consequently species richness declines with increasing latitude (Chengalath & Koste 1989, Laybourn-Parry et al. 1991). Larger planktonic organisms are rare in polar lakes (Parker et al. 1982, Kling et al. 1992) and, if present, not very abundant (Hobbie et al. 1999). In Antarctic lakes, the pelagic food web is comprised primarily of microbial plankton (Laybourn-Parry et al. 1991). In fact, microbial plankton, which is now known to be important for the functioning of aquatic ecosystems (Azam et al. 1983), seems to play a key role in the retention and recycling of nutrients especially in such oligotrophic waters where allochthonous input is negligible (Stockner & Porter 1988).

*E-mail: micha@pflaphy.pph.univie.ac.at

A number of studies concerning autotrophic and heterotrophic pico- and microplankton have been conducted in Antarctic lakes (e.g. Ellis-Evans 1991, Laybourn-Parry et al. 1995). Studies on Arctic lakes have focused primarily on physical and chemical parameters (Schindler et al. 1974, de March 1975, Whalen & Cornwell 1985), on bacterioplankton (Morgan & Kalff 1972, Hobbie et al. 1983), or on algae (Kalff 1967, Miller et al. 1986). However, there have been only a few investigations in Arctic lakes, focusing on the coupling between autotrophic and heterotrophic processes within the microbial food web (O'Brien et al. 1992).

We investigated the interactions between phyto- and bacterioplankton activity in a high Arctic lake on the Franz Joseph Land archipelago. This paper presents data on phyto- and bacterioplankton dynamics during the Arctic summer of 1996. Simultaneous measurements of phytoplankton and bacterioplankton production and nutrient concentrations (nitrate, nitrite, ammonium, phosphate, silicate, DOC) were carried out in an attempt to determine the interactions within different members of the microbial community. In order to detect possible predator-prey interactions we also included the dynamics of flagellates and rotifers, because it has been stressed that especially in Arctic oligotrophic systems bottom-up regulation is of higher importance than top-down control (Hobbie et al. 1999).

This high Arctic lake was chosen for investigation because of its permanent ice-cover, which prevents the input of allochthonous material from terrestrial sources and atmospheric deposition. Small glacier creeks are the only source of allochthonous input. Furthermore, there is no significant benthic primary production in this lake. Thus, the lake is characterized by a relatively simple food web. Rotifers represent the highest trophic level of the pelagic food web: no cladocerans, pelagic copepods or fish inhabit this lake.

MATERIALS AND METHODS

Study site and sampling. The investigated freshwater lake is located at the westernmost part of Ziegler Island, Franz Joseph Land archipelago (81.04° N, 56.17° E, Fig. 1). The surrounding catchment is characterized by basalt rocks and glaciers. Some small glacier creeks feed the lake during snow- and ice-melt. A single outflow drains the lake into the nearby sea (Fig. 1). The lake covers an area of about 82 000 m^2 and has a mean depth of 9 m. This unnamed lake is covered with a thick ice-sheet of up to 2.4 m; it only becomes ice-free

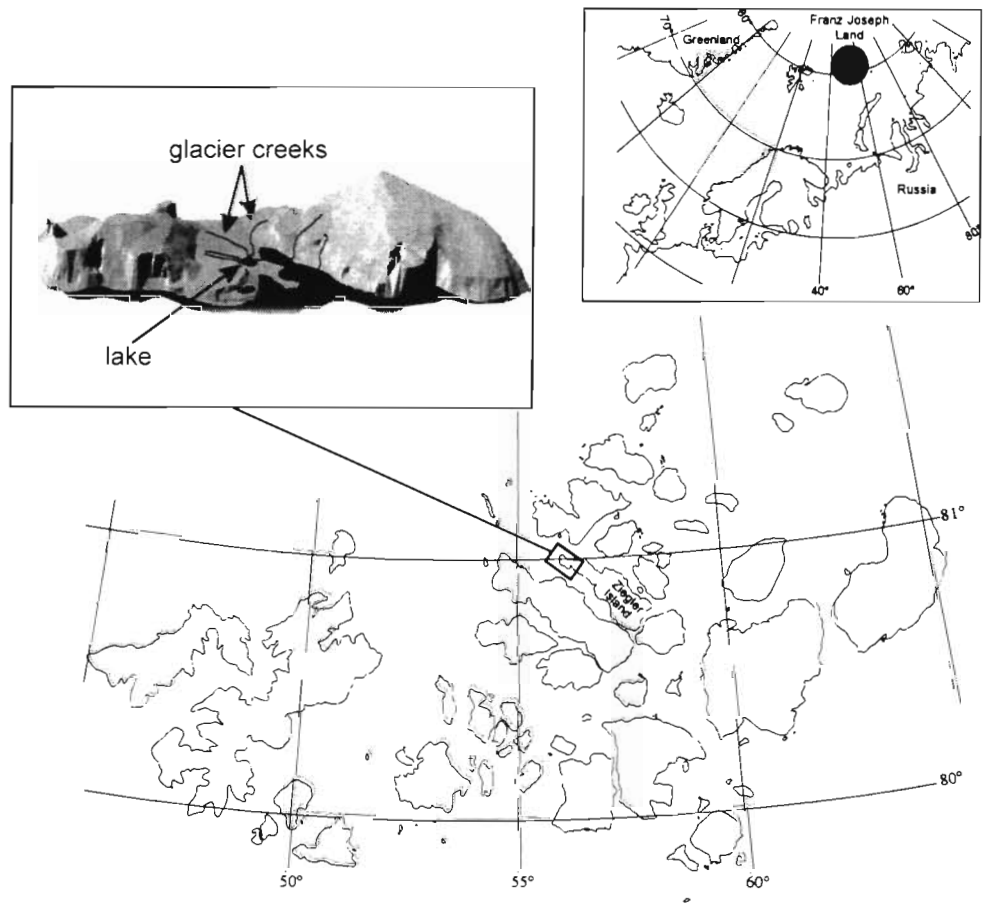

Fig. 1 Location of the study site on Ziegler Island, Franz Joseph Land

near the inlets in summer (8% of the lake area was ice-free in July and August 1996).

From 15 July to 14 August 1996, the lake was sampled at 3 d intervals (with the exception of one 4 d interval) through a hole in the ice, using a 1.8 l Niskin bottle. Water samples (10 l) were taken from a depth of 5 m. The water column of the lake was homogenously mixed during the investigation period. Additional water samples (8 to 10 l) for zooplankton enumeration and identification were filtered through a 40 µm net and fixed in 4% formaldehyde. During sampling, water temperature was measured. The water samples were brought back to the nearby field laboratory within 30 min for enumeration and incubations as outlined below. More detailed and complex analyses were performed at the Institute of Ecology, University of Vienna.

Phytoplankton biomass and primary production. Phytoplankton biomass was determined by measuring the chlorophyll *a* (chl *a*) content of 1 l of lake water filtered onto glass fiber filters (Whatman GF/F, 47 mm filter diameter) and kept frozen until analysis. Then, the filters were extracted in 10 ml of 90% (v/v) acetone for 12 h; thereafter the solution was filtered again through a Whatman GF/F filter to remove any particles. Chl *a* concentrations were estimated spectrophotometrically as described in Parsons et al. (1984).

Primary production was estimated via the incorporation of radiolabeled ^{14}C-sodium bicarbonate into organic carbon (Parsons et al. 1984). We differentiated particulate production (P_{part}) from photosynthetic extracellular release (P_{er}). Subsamples (100 ml) were filled into BOD flasks, rinsed with lake water prior to incubation and 1 ml of 1 µCi ml^{-1} ^{14}C-sodium bicarbonate (specific activity 55 mCi $mmol^{-1}$, Amersham) was added. Incubation of duplicate subsamples at 4 different radiation levels (10, 30, 50 and 100% of surface radiance) and 2 dark controls were performed at *in situ* temperature for 24 h, which was found to be appropriate for oligotrophic Arctic lakes (Kalff & Welch 1974, Miller et al. 1986). After incubation, samples were filtered onto 0.45 µm pore size cellulose nitrate filters (Millipore HA, 25 mm diameter filter) by applying a suction pressure not exceeding 20 mbar. Filters were rinsed twice with 0.2 µm filtered lake water, placed in scintillation vials and 100 µl concentrated HCl was added to remove any remaining inorganic ^{14}C. Before rinsing the filters, 4 ml of the filtrate was transferred into scintillation vials, acidified with 100 µl concentrated HCl and left open for 24 h (Niemi et al. 1983). Filters and filtrates were stored at 4°C until further analysis at the Institute of Ecology, University of Vienna. There, filters were dissolved in 1 ml ethylacetate and after 10 min, 8 ml scintillation cocktail (Packard Insta-Gel) was added to the filters and the filtrate samples. Radioactivity was measured in a liquid scintillation counter (Canberra Packard, TriCarb 2000) after 14 h. Quenching was corrected by the external standard ratio. Since radiation measurements under ice were not possible because of logistical problems, primary production was estimated by using the mean of the 4 different light treatments, which showed only small variations. Photoinhibition or generally less production at lower irradiances could not be observed. For calculations of P_{part}, the disintegration per min (DPM) values of the dark incubations were subtracted from the radiation-exposed samples.

Furthermore, primary production values were corrected for bacterial uptake of P_{er} during the incubation as follows:

net PP_{tot} = P_{part} + net P_{er} (apparent in filtrate)
gross PP_{tot} = P_{part} + gross P_{er}
gross P_{er} = net P_{er} + BCD
BCD = BP (thymidine incorporation) + respiration (assuming a growth efficiency of 50%)
gross% P_{er} = (gross P_{er}/gross PP_{tot}) × 100

where PP_{tot} is total primary production, BCD is bacterial carbon demand and BP is bacterial production.

Bacterial and flagellate abundance. The abundance of bacteria and heterotrophic flagellates was determined by DAPI (4',6-diamidino-2-phenylindole) staining and enumeration under an epifluorescence microscope (Hobbie et al. 1977). Subsamples (5 ml for bacteria, 40 ml for flagellates) were fixed with 0.2 ml of 0.2 µm filtered concentrated formaldehyde and stained with DAPI for 15 min (Porter & Feig 1980). After filtration onto black polycarbonate filters (Nuclepore, 25 mm diameter filters; 0.2 µm pore size for bacteria, 0.8 µm pore size for flagellates), the filters were embedded in Nikon immersion oil and viewed under a Leitz Laborlux microscope equipped with a Ploemopak epifluorescence unit. At least 300 bacteria and 100 flagellates were counted per sample.

Bacterial production. Immediately upon return to the field laboratory, bacterial production was estimated by measuring the incorporation of [^3H]-thymidine (specific activity 83.9 Ci $mmol^{-1}$; final conc. 5 nM). Triplicate subsamples (10 ml) and 2 formalin-killed blanks were incubated in gamma-radiated test tubes (Greiner, Inc.) in the dark at *in situ* temperature for 2.5 h. Thereafter, the samples were filtered onto cellulose nitrate filters (Millipore HA, 0.45 µm pore size, 25 mm diameter) and extracted with 10 ml ice-cold 5% trichloroacetic acid (Sigma Chemicals) for 10 min. The filters were transferred into scintillation vials and stored at 4°C until further analysis at the Institute of Ecology, University of Vienna. There, the filters were dissolved in 1 ml ethylacetate, 8 ml scintillation cocktail (Packard Insta-Gel) added and the radioactivity was measured in a liquid scintillation counter (Can-

berra Packard, Tricarb 2000) after 14 h. Thymidine incorporation was converted into bacterial carbon production by using a conversion factor of 1.1×10^{18} cells mol^{-1} thymidine incorporated (Riemann et al. 1987) and assuming a carbon content of 10 fg $cell^{-1}$ (Bratbak & Dundas 1984). Specific growth rates were calculated as described by Coveney & Wetzel (1995): $\mu = [\ln (B_0 + P) - \ln B_0]/T$, where B_0 was initial cell number, P was production of cells (estimated by thymidine incorporation) and T was incubation time for the thymidine assay.

Dissolved oxygen, pH, inorganic nutrients, DOC and irradiance. Dissolved oxygen concentrations of the lake water were measured using Winkler titration (Wetzel 1995). For pH measurements, a WTW pH 91 electrode was used and for estimating the amount of inorganic nutrients (phosphate, nitrate, nitrite, ammonium), 250 ml of Whatman GF/F-filtered lake water was filled in acid-rinsed bottles and stored frozen until analysis. Concentrations of inorganic nutrients except for nitrate were determined using the conventional spectrophotometric methods described in Parsons et al. (1984); nitrate was measured by HPLC analysis (Winter et al. 1992). Alkalinity was estimated by HCl titration (Wetzel 1995).

Subsamples (5 ml) for DOC were filtered through Whatman GF/F filters, filled in combusted (450°C for 4 h) glass ampoules and stored frozen until analysis. DOC content was determined using a Shimadzu TOC-5000 after sparging the samples with CO_2-free air. Standards were prepared with potassium hydrogen phthalate (Kanto Chemical Co, Inc.); a platinum catalyst on quartz was used.

All nutrient analyses were performed in duplicate. The photosynthetic active radiation (PAR, 400 to 700 nm) of the surface solar radiation was measured with a Skye quantum sensor.

RESULTS

Physical and chemical parameters

The water column of the lake was well mixed as indicated by the constant temperatures throughout the water column. During the investigation period, water temperature increased from 1.1°C to a maximum of 2°C (Fig. 2A). Because the ice-cover largely prevented direct solar heating of the water column, the glacier creeks entering the lake with a water temperature of up to 6°C primarily influenced the heat budget of the lake. Dissolved oxygen concentration increased during the investigation period as well (Fig. 2A) and oxygen saturation averaged 99%. Nutrient concentrations (nitrate, nitrite, ammonium, phosphate, DOC, silicate)

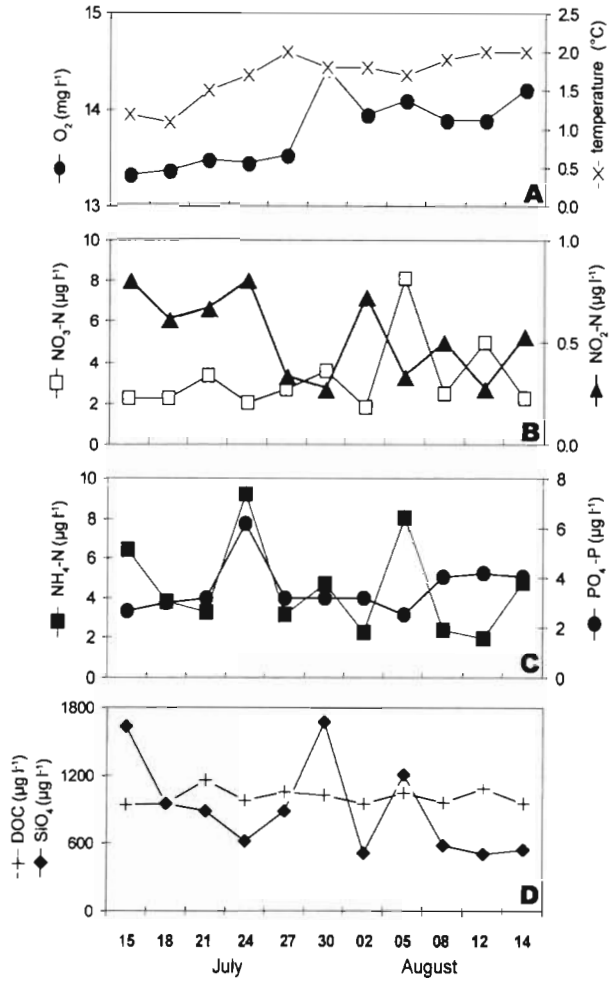

Fig. 2. Chemical and physical parameters of lake water during the investigation period. (A) Oxygen concentration, temperature. (B) NO_3-N, NO_2-N. (C) NH_4-N, PO_4-P. (D) DOC, silicate

of the lake were generally low, fluctuating somewhat during the investigation period, but showing no trend (Fig. 2B to D). However, organic nitrogen and phosphorus content was not measured. DOC concentrations in the glacier creeks were slightly higher (1.3 to 1.6 mg l^{-1}) than in the lake water (0.9 to 1.2 mg l^{-1}). The PAR at the ice-surface ranged between 50 and 600 µE m^{-2} s^{-1}, pH and alkalinity ranged between 5.6 and 6.1 and 0.4 and 0.8 meq l^{-1}, respectively.

Phytoplankton production

The representative groups of the phytoplankton were Chrysophyceae (with the dominant alga of the lake: *Dinobryon* sp.), Chlorophyceae, Desmidiaceae and diatoms.

Primary production varied between 7.8 and 41.5 µg C $l^{-1}d^{-1}$ (Table 1). P_{part} fluctuated during the investiga-

Table 1. Summary of particulate (P_{part}) and net and gross dissolved (P_{er}) primary production. Total net primary production (net PP_{tot}) = P_{part} + net P_{er}; gross PP_{tot} = P_{part} + gross P_{er}; net P_{er} = apparent P_{er}; gross P_{er} = net P_{er} + bacterial carbon demand (BCD); BP = bacterial production (via thymidine incorporation); BCD = BP + respiration (assuming a growth efficiency of 50%); gross % P_{er} = (gross P_{er}/gross PP_{tot}) × 100; % BCD of gross P_{er} = (BCD/gross P_{er}) × 100; % BCD of gross PP_{tot} = (BCD/gross PP_{tot}) × 100

Date	Net PP_{tot}	Gross PP_{tot}	P_{part}	Net P_{er}	Gross P_{er}	BP	BCD	Gross %P_{er}	BCD of gross P_{er}	BCD of gross PP_{tot}
	($\mu g\ C\ l^{-1}\ d^{-1}$)							(%)		
Jul 15	35.4	38.1	20.6	14.8	17.5	1.4	2.7	46	16	7
Jul 18	15.1	18.6	4.9	10.2	13.7	1.7	3.5	74	25	19
Jul 21	41.5	47.0	32.7	8.8	14.3	2.7	5.5	31	38	12
Jul 24	25.6	28.0	16.3	9.3	11.8	1.2	2.5	42	21	9
Jul 27	10.6	17.8	1.0	9.6	16.8	3.6	7.2	94	43	40
Jul 30	21.8	27.5	10.5	11.3	17.0	2.9	5.7	62	34	21
Aug 02	17.3	24.1	2.4	14.9	21.7	3.4	6.8	90	31	28
Aug 05	30.3	35.7	13.0	17.2	22.6	2.7	5.4	63	24	15
Aug 08	21.0	24.1	8.5	12.5	15.6	1.6	3.1	65	20	13
Aug 12	7.8	15.7	0.6	7.2	15.1	3.9	7.9	96	52	50
Aug 14	15.4	20.4	7.1	8.3	13.3	2.5	5.0	65	37	24
Mean	22.0	27.0	10.7	11.3	16.3	2.5	5.0	60	31	19
(±SD)	(±9.9)	(±9.3)	(±9.2)	(±3.0)	(±3.2)	(±0.9)	(±1.8)	(±20)	(±11)	(±13)

tion period, whereas the rate of apparent P_{er} (net P_{er}) remained relatively constant (Table 1). On average, net P_{er} was similar to P_{part}; however, when corrected for bacterial uptake of carbon released by phytoplankton, the contribution of P_{er} (gross P_{er}) was higher than P_{part} (Table 1). In 3 samplings during the initial phase of the investigation, P_{part} dominated over net P_{er}. In all other samplings, extracellular release (gross P_{er}) comprised >60% of total primary production (Table 1). Chl *a* concentrations showed a decreasing trend during the investigation period (Fig. 3A). However, specific productivity (net primary production per biomass) fluctuated greatly, following primarily the production rates of phytoplankton (net PP_{tot}) (compare Fig. 3A and Table 1).

Microheterotrophic biomass and bacterial production

Bacterial and flagellate numbers ranged from 9.3 to 17.3×10^5 and from 7.8 to 17.3×10^2 cells ml^{-1}, respectively, exhibiting no pronounced temporal trend (Fig. 3B). Bacteria were dominated by small cocci and very small rods. Bacterial production varied between 1.2 and 3.9 $\mu g\ C\ l^{-1}\ d^{-1}$ (Fig. 3C). The peaks in bacterial production corresponded with lowest primary production (July 27 and August 12) (compare Table 1 and Fig. 3C); however, there is no clear relationship discernible between primary and bacterial production. Bacterial growth rates varied between 0.1 and 0.3 d^{-1} (Fig. 3C) and were primarily determined by changes in production rates. The abundance of rotifers and rotifer eggs increased during the investigation period from 90 to 234 ind. l^{-1} and from 48 to 511 rotifer eggs l^{-1} (Fig. 3D).

DISCUSSION

This oligotrophic lake on Franz-Joseph-Land is characterized by very low inorganic nutrient concentrations (Fig. 2B to D) comparable to other Arctic lakes, e.g. Toolik Lake (Whalen & Cornwell 1985), Char Lake (Schindler et al. 1974) and Barrow ponds (Prentki et al. 1980) and to the ultra-oligotrophic Lake Tahoe (Paerl et al. 1975). The DOC content of the lake (Fig. 2D) is also at the lower end of reported DOC concentrations of Arctic lakes and ponds, which range from <90 (Schindler et al. 1974) to 15500 $\mu g\ l^{-1}$ (Prentki et al. 1980). However, compared with alpine lakes the DOC content of this Arctic lake is in the upper range: Sommaruga et al. (1999) found mean DOC concentrations of 390 $\mu g\ l^{-1}$ in glacier-fed lakes and 700 $\mu g\ l^{-1}$ in lakes not fed by glaciers. Although the investigated Arctic lake is fed by glacier melt-water, even higher DOC concentrations than in the lake itself were found in the glacier creeks which supplied the lake with allochthonous DOC. This DOC seems to be leached from tundra vegetation covering the drainage basin (about 200 m in length).

In the lake, autochthonous DOC production is exclusively based on phytoplankton production since there is no benthic vegetation present. Primary production has to take place under ice due to the permanent ice-cover, leaving only a small area ice-free where warmer glacier creek water enters the lake. During the Arctic summer, the transparent ice cover, which is free of snow and partly formed of candle-ice, allows PAR penetration (Bolsenga et al. 1991). A number of studies have quantified primary production under ice without snow cover (e.g. Kalff 1967, Miller et al. 1986), which is

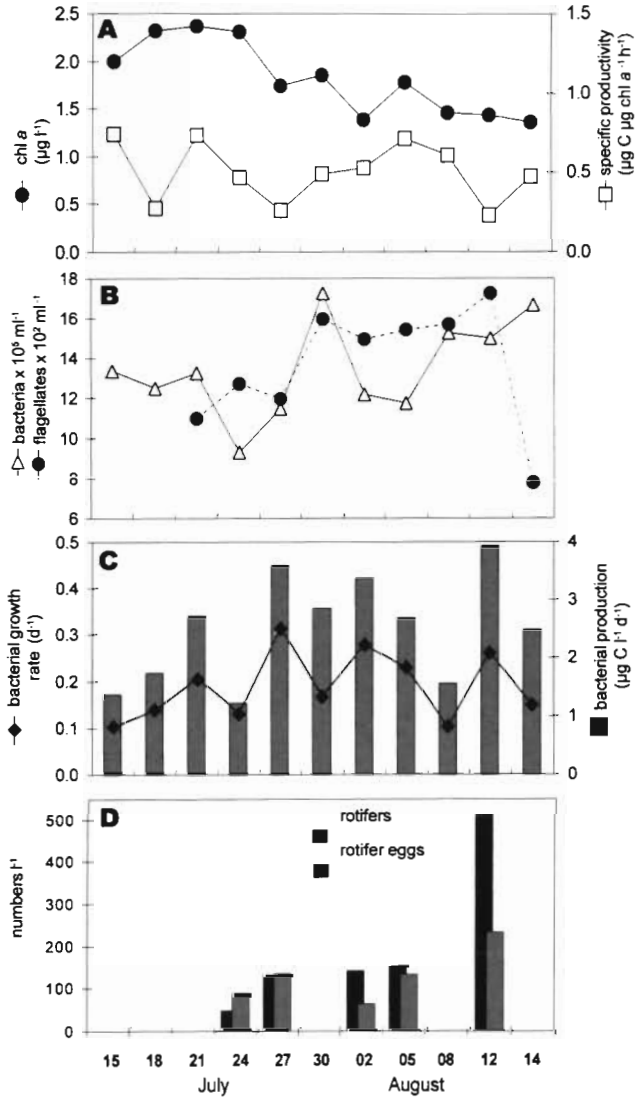

Fig. 3. (A) Chlorophyll *a* concentration and specific productivity (net PP_{tot}/biomass) of phytoplankton. (B) Bacterioplankton and flagellate numbers. (C) Bacterial production (thymidine incorporation) and bacterial growth rate. (D) Number of rotifers and rotifer eggs

supported by the nutrient input during the snow-melting period (Whalen & Cornwell 1985). Nutrient availablility rather than irradiation seems to be the limiting factor for primary production in most high latitude freshwater systems (Whalen & Cornwell 1985); however, in the investigated lake, we found no clear relationship between algal biomass or primary production with nutrient concentrations.

During the investigation phytoplankton biomass declined more or less continuously (Fig. 3A) while primary production fluctuated without any trend over time (Table 1). Mean net primary production amounted to 22 µg C l^{-1} d^{-1} and mean phytoplankton biomass was 1.8 µg l^{-1} chl *a*. Thus, the measured biomass and primary production are also within the order of magnitude reported for high mountain lakes (Reche et al. 1996, Sommaruga et al. 1999). Pelagic primary production in polar lakes and ponds ranges from 0.072 to 240 µg C l^{-1} d^{-1} (Kalff 1967, Kalff & Welch 1974, Parker et al. 1982, Ellis-Evans 1991). Most of these studies measured only particulate primary production and may therefore underestimate total primary production rates. Interestingly, comparing pelagic primary production rates in different Arctic lakes, it becomes obvious that higher phytoplankton production rates are found in lakes without bottom vegetation (Whalen & Cornwell 1985, Miller et al. 1986, this study). In lakes with benthic algae, mosses and macrophytes, the pelagic primary production is low, and benthic primary production contributes between 80 and 87% to total primary production (Welch & Kalff 1974, Ramlal et al. 1994).

Specific productivity of phytoplankton (net primary production/biomass) with a mean of 0.5 mg C (mg chl *a*)$^{-1}$ h^{-1} (Fig. 3A) is higher than in most other Arctic and Antarctic lakes (exception: Lake Sombre; Ellis-Evans 1991). The specific productivity in Char Lake was 0.22 mg C (mg chl *a*)$^{-1}$ h^{-1} (Kalff & Welch 1974), and for Antarctic lakes, 0.023 to 0.137 mg C (mg chl *a*)$^{-1}$ h^{-1} has been reported (Vincent 1981, Parker et al. 1982). However, a specific productivity of as high as 6.3 mg C (mg chl *a*)$^{-1}$ h^{-1} for the oligotrophic Lake Sombre was reported by Ellis-Evans (1991). Although primary production is depressed by low temperature (Rigler 1978), specific productivity in the investigated lake is similar to that of the temperate oligotrophic Lake Almind (Søndergaard et al. 1988). It is important to note that higher specific productivity is reported in studies where the photosynthetic extracellular release was included in the measurements (Søndergaard et al. 1988, Ellis-Evans 1991, this study). Calculating specific primary production only from the particulate production, we found a specific productivity of 0.02 to 0.6 mg C (mg chl *a*)$^{-1}$ h^{-1}, which is similar to the specific productivity found for other polar lakes (Kalff & Welch 1974, Vincent 1981, Parker et al. 1982).

P_{er} is known to be of higher importance in oligotrophic than eutrophic lakes (Cole et al. 1982, Baines & Pace 1991). The contribution of P_{er} to total primary production in oligotrophic lakes ranges from 12 to >90% (Parker et al. 1977, Tilzer & Horne 1979, Søndergaard et al. 1988), with the highest % P_{er} recorded from Lake Bonney-East, Antarctica (Parker et al. 1977). This corresponds to our data with a gross P_{er} ranging from 30 to 96% of total phytoplankton production (Table 1). We observed an increasing contribution of P_{er} during the course of the investigation period. Similar trends were found by others following the succession of phyto-

plankton blooms (Storch & Saunders 1978, Larsson & Hagström 1979). This increasing contribution of P_{er} to total primary production has been related to the senescent stage of the phytoplankton community (Nalewajko & Schindler 1976, Hino 1988) as indicated in our study by the inverse relation between gross % P_{er} and phytoplankton biomass ($r = -0.65$, $p < 0.05$, $n = 11$) and specific productivity ($r = -0.72$, $p < 0.005$, $n = 11$), respectively. Rotifers were also found to enhance extracellular release by 'sloppy feeding' (Lampert 1978). However, rotifer numbers, although increasing during the investigation period (Fig. 3D), did not correlate with % P_{er}.

In our study, P_{er} contributed, on average, about 50% to the total primary production. Bacteria readily take up this extracellular carbon (Larsson & Hagström 1979, Chrost & Faust 1983). Thus, the net P_{er} reported here is likely to be underestimated, especially if the long incubation time is considered. Therefore, we estimated the gross % P_{er} (% P_{er} of total primary production) assuming bacterial production equals approximately the bacterial assimilation of P_{er} (Bell & Kuparinen 1984, Søndergaard et al. 1988). A bacterial growth yield of 50% was used for calculations of the gross % P_{er} (Jensen et al. 1985, Coveney & Wetzel 1989). Extracellular release taking the bacterial carbon uptake during the incubation into account gives us the gross P_{er}, averaging ~60% of total carbon fixation (gross PP_{tot}) (Table 1). About 31% of the carbon released (gross P_{er}) is required to meet the bacterial carbon demand, or in other terms, 19% of total primary production (gross PP_{tot}) is channeled directly into bacteria (Table 1). This is at the lower end of the range of estimates (Larsson & Hagström 1979, Coveney 1982). However, our estimates of the bacterial carbon demand are conservative since the assumed bacterial yield of 50% is, although widely used, at the high end of estimates reported for freshwater bacterioplankton. If we use the more likely bacterial growth yield of 20%, then the bacterioplankton would take up about 53% of the gross P_{er} and 36% of the gross PP_{tot}. This relatively low P_{er} assimilation efficiency may be affected by the low temperature (Bell & Kuparinen 1984, Scavia & Laird 1987).

In our study, gross % P_{er} correlated well with bacterial production ($r = 0.67$, $p < 0.05$, $n = 11$) and bacterial growth rate ($r = 0.65$, $p < 0.05$, $n = 11$), indicating the importance of the P_{er} as a substrate for bacteria. This has also been concluded in a number of other studies on lakes of lower latitudes (e.g. Nalewajko & Schindler 1976, Coveney & Wetzel 1995). Coveney (1982) suggested that P_{er} is not an important loss factor for phytoplankton while it is an important substrate for bacterioplankton. Cole et al. (1982) speculated that phytoplankton-derived extracellular matter is capable of partly regulating bacterial growth in oligotrophic waters. Our findings confirm this assumption for this particular high Arctic lake.

The abundance of bacteria reported for Arctic and Antarctic lakes ranges from 0.1 to 80×10^5 ml^{-1} with maxima in late summer and autumn (Morgan & Kalff 1972, Laybourn-Parry et al. 1995, Ramaiah 1995). In the present study, bacterial numbers varied within a small range without any clear trend (Fig. 3B) while bacterial production increased slightly during the investigation period (Fig. 3C). Bacterial production rates of the investigated lake are comparable to Antarctic lakes (Ellis-Evans 1991, Laybourn-Parry et al. 1995) and also to high mountain lakes (Sommaruga & Psenner 1995, Reche et al. 1996).

The impact of temperature on bacterial production and growth has been extensively discussed (White et al. 1991, Wiebe et al. 1992, Felip et al. 1996), including the temperature range <4°C (Pomeroy & Deibel 1986, Rivkin et al. 1996). Christian & Wiebe (1974) observed a 1.8 times higher growth rate and a 4.4 times higher respiration rate for bacteria when temperature increased from 1 to 4°C which may have a very dramatic effect in view of the predicted temperature increase over polar regions (Wiebe et al. 1992). We found that bacterial production was positively correlated with temperature ($r = 0.64$, $p < 0.05$, $n = 11$) even over a rather narrow temperature range. Growth rates of bacterioplankton in the present study are low although comparable to Antarctic lakes (Ellis-Evans 1991) and to those obtained for temperate lakes in winter (e.g. Coveney & Wetzel 1995).

As temperature is assumed to greatly influence bacterial production especially at the low temperature range, at higher temperatures substrate availability becomes the major factor controlling bacterial growth (Scavia & Laird 1987, Felip et al. 1996). This might lead to the paradox that in cold environments, during periods of high primary production, bacterial production is probably limited by low temperature (Pomeroy & Deibel 1986, Wiebe et al. 1992), while towards the end of the phytoplankton bloom more suitable temperatures favour bacterial production. Although Cole et al. (1988) found significant correlations between bacterial and primary production and chl *a*, respectively, across freshwater and seawater ecosystems they also referred to outliers obtained in early spring (Riemann et al. 1982, Bell & Kuparinen 1984) when temperature was low. In general, our results indicate an inverse relation between primary production and bacterial production. The ratio primary production:bacterial production declined from 28 to 4 during the investigation period ($r = 0.59$, $p < 0.05$, $n = 11$). Thus, in the investigated lake bacterial growth seems to be primarily influenced by temperature and nutrient supply; predation effects could not be observed (Fig. 3B).

In conclusion, in this high Arctic lake the increasing contribution of P_{er} to total phytoplankton production coincided with increased bacterial productivity, bacterial growth rates and slightly higher temperatures, indicating a close coupling of primary and bacterial production via extracellular release during the investigation period.

Acknowledgements. We thank W. Richter for organizing the expedition, G. Müller-Niklas, N. Queric and K. Reiter for valuable help and 3 anonymous reviewers for improvements to the manuscript. This study was supported by the Austrian Science Foundation (P11686-BIO). This work is part of the fulfillment of the requirements towards a PhD degree at the University of Vienna by M.P.

LITERATURE CITED

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

Baines SB, Pace ML (1991) The production of dissolved organic matter by phytoplankton and its importance to bacteria: patterns across marine and freshwater systems. Limnol Oceanogr 36:1078–1090

Bell RT, Kuparinen J (1984) Assessing phytoplankton and bacterioplankton production during early spring in Lake Erken, Sweden. Appl Environ Microbiol 48:1221–1230

Bolsenga SJ, Herdendorf CE, Norton DC (1991) Spectral transmittance of lake ice from 400–850 nm. Hydrobiologia 218:15–25

Bratbak G, Dundas I (1984) Bacterial dry matter content and biomass estimations. Appl Environ Microbiol 48:755–757

Chengalath R, Koste W (1989) Composition and distributional patterns in arctic rotifers. Hydrobiologia 186/187:191–200

Christian RR, Wiebe WJ (1974) The effects of temperature upon the reproduction and respiration of a marine obligate psychrophile. Can J Microbiol 20:1341–1345

Chrost RH, Faust MA (1983) Organic carbon release by phytoplankton: its composition and utilization by bacterioplankton. J Plankton Res 5:477–493

Cole JJ, Likens GE, Strayer DL (1982) Photosynthetical produced dissolved organic carbon: an important carbon source for planktonic bacteria. Limnol Oceanogr 27: 1080–1090

Cole JJ, Findlay S, Pace ML (1988) Bacterial production in fresh and saltwater ecosystems: a cross-system overview. Mar Ecol Prog Ser 43:1–10

Coveney MF (1982) Bacterial uptake of photosynthetic carbon from freshwater phytoplankton. Oikos 38:8–20

Coveney MF, Wetzel RG (1989) Bacterial metabolism of algal extracellular carbon. Hydrobiologia 173:141–149

Coveney MF, Wetzel RG (1995) Biomass, production, and specific growth rate of bacterioplankton and coupling to phytoplankton in an oligotrophic lake. Limnol Oceanogr 40:1187–1200

de March L (1975) Nutrient budget for a high arctic lake (Char lake, N.W.T.). Verh Int Ver Limnol 19:496–503

Ellis-Evans JC (1991) Numbers and activity of bacterio- and phytoplankton in contrasting maritime Antarctic lakes. Verh Int Ver Limnol 24:1149–1154

Felip M, Pace ML, Cole JJ (1996) Regulation of planktonic bacterial growth rates: the effects of temperature and resources. Microb Ecol 31:15–28

Hino S (1988) Extracellular release of organic matter associated with the physiological state of freshwater blue-green algae. Arch Hydrobiol 113:307–317

Hobbie JE, Daley RJ, Jasper S (1977) Use of Nuclepore-filters for counting bacteria by fluorescence microscopy. Appl Environ Microbiol 33:1225–1228

Hobbie J, Corliss T, Peterson B (1983) Seasonal patterns of bacterial abundance in an Arctic lake. Arctic Alp Res 15(2):253–259

Hobbie J, Bahr M, Rublee PA (1999) Controls on microbial food webs in oligotrophic arctic lakes. Arch Hydrobiol Spec Issues Adv Limnol 54:61–76

Jensen LM, Jorgensen OG, Sondergaard M (1985) Specific activity. Significance in estimation release rates of extracellular dissolved organic carbon (EOC) by algae. Verh Int Ver Limnol 22:2893–2897

Kalff J (1967) Phytoplankton dynamics in an arctic lake. J Fish Res Board Can 24:1861–1872

Kalff J, Welch HE (1974) Phytoplankton production in Char Lake, a natural polar lake, and in Meretta lake, a polluted polar lake, Cornwallis Island, N.W.T. J Fish Res Board Can 31:621–636

Kling GW, O'Brien WJ, Miller M, Hershey A (1992) The biogeochemistry and zoography of lakes and rivers in arctic Alaska. Hydrobiologia 240:1–14

Lampert W (1978) Release of dissolved organic carbon by grazing zooplankton. Limnol Oceanogr 23:831–834

Larsson U, Hagström A (1979) Phytoplankton exudate release as an energy source for the growth of pelagic bacteria. Mar Biol 52:199–206

Laybourn-Parry J, Bayliss P (1996) Seasonal dynamics of the planktonic community in Lake Druzhby, Princess Elizabeth Land, Eastern Antarctic. Freshw Biol 35:57–67

Laybourn-Parry J, Marchant HJ, Brown P (1991) The plankton of a large oligotrophic freshwater Antarctic lake. J Plankton Res 13:1137–1149

Laybourn-Parry J, Bayliss P, Ellis-Evans JC (1995) The dynamics of heterotrophic nanoflagellates and bacterioplankton in a large ultra oligotrophic Antarctic lake. J Plankton Res 17:1835–1850

Miller MC, Hater GR, Spatt P, Westlake P, Yeakel D (1986) Primary production and its control in Toolik Lake, Alaska. Arch Hydrobiol 74(Suppl):97–131

Moore J (1978) Some factors influencing the diversity and species composition of benthic communities in twenty arctic and subarctic lakes. Int Rev Ges Hydrobiol 63:757–771

Morgan KC, Kalff J (1972) Bacterial dynamics in two high arctic lakes. Freshw Biol 2:217–228

Nalewajko C, Schindler DW (1976) Primary production, extracellular release, and heterotrophy in two lakes in the ELA, Northwestern Ontario. J Fish Res Board Can 33: 219–226

Niemi M, Kuparinen J, Uusi-Rauva A, Korhonen K (1983) Preparation of algal samples for liquid scintillation counting. Hydrobiologia 106:149–156

O'Brien WJ, Hershey AE, Hobbie JE, Hullar MA, Kipphut GW, Miller MC, Moller B, Vestal JR (1992) Control mechanisms of arctic lake ecosystems: a limnocorral experiment. Hydrobiologia 240:143–188

Paerl HW, Richards RC, Leonard RL, Goldman CR (1975) Seasonal nitrate cycling as evidence of complete vertical mixing in Lake Tahoe, California-Nevada. Limnol Oceanogr 20:1–8

Parker BC, Hoehn RC, Paterson RA, Craft JA, Lane LS, Stavros RW, Sugg HG, Whitehurst JT, Fortner RD, Weand BL (1977) Changes in dissolved organic matter, photosyn-

thetic production, and microbial community composition in Lake Bonney, Southern Victoria Land, Antarctica. In: Llano GA (ed) Adaptations within Antarctic ecosystems. Gulf Publishing Co, Houston, TX, p 873–890

Parker BC, Simmons GM, Kenneth GS, Cathey D, Allnutt FCT (1982) Comparative ecology of plankton communities in seven Antarctic oasis lakes. J Plankton Res 4:271–284

Parsons T, Maita Y, Lalli C (1984) A manual of chemical and biological methods for seawater analysis. Pergamon Press, Oxford

Pomeroy L, Deibel D (1986) Temperature regulation of bacterial activity during the spring bloom in Newfoundland coastal waters. Science 233:359–361

Porter KG, Feig YS (1980) The use of DAPI for identifying and counting aquatic microflora. Limnol Oceanogr 25:943–948

Prentki RT, Miller MC, Barsdate RJ, Alexander V, Kelley J, Coyne P (1980) Chemistry. In: Hobbie JE (ed) Limnology of tundra ponds. Dowden, Hutchinson and Ross, Stroudsburg, PA, p 76–178

Ramaiah N (1995) Summer abundance and activities of bacteria in the freshwater lakes of Schirmacher Oasis, Antarctica. Pol Biol 15:547–553

Ramlal PS, Hesslein RH, Hecky RE, Fee EJ, Rudd JW, Guildford SJ (1994) The organic carbon budget of a shallow Arctic tundra lake on the Tuktoyaktuk Peninsula, N.W.T., Canada. Biogeochemistry 24:145–172

Reche L, Pugnetti A, Cruz-Pizaarro L, Carrillo P (1996) Relationship between bacteria and phytoplankton in a high-mountain lake: importance of the organic carbon released by pelagic algae for bacterioplankton. Arch Hydrobiol Spec Issues Adv Limnol 48:31–38

Riemann B, Søndergaard M, Schierup HH, Bosselmann S, Christensen G, Hansen G, Nielsen B (1982) Carbon metabolism during a spring diatom bloom in the eutrophic Lake Mossø. Int Rev Ges Hydrobiol 67:145–185

Riemann B, Bjørnsen PK, Newell S, Fallon R (1987) Calculation of cell production of coastal marine bacteria based on measured incorporation of [^{3}H] thymidine. Limnol Oceanogr 32:471–476

Rigler FH (1978) Limnology in the high arctic: a case study of Char Lake. Verh Int Ver Limnol 20:127–140

Rivkin RB, Anderson MR, Lajzerowicz C (1996) Microbial processes in cold oceans. I. Relationship between temperature and bacterial growth rate. Aquat Microb Ecol 10: 243–254

Scavia D, Laird GA (1987) Bacterioplankton in Lake Michigan: dynamics, controls, and significance to carbon flux. Limnol Oceanogr 32:1017–1033

Schindler DW, Welch HE, Kalff J, Brunskill GJ, Kritsch N (1974) Physical and chemical limnology of Char Lake, Cornwallis Island (75°N Lat.). J Fish Res Board Can 31: 585–607

Sommaruga R, Psenner R (1995) Trophic interactions within the microbial food web in Piburger See (Austria). Arch Hydrobiol 132:257–278

Sommaruga R, Psenner R, Schafferer E, Koinig KA, Sommaruga-Wögrath S (1999) Dissolved organic carbon concentration and phytoplankton biomass in high-mountain lakes of the Austrian Alps: potential effect of clinatic warming on UV underwater attentuation. Arctic Alp Res 31(3):247–253

Søndergaard M, Riemann B, Jensen LM, Jørgensen NOG, Bjørnsen PK, Olesen M, Larsen JB, Geertz-Hensen O, Hansen J, Christofferson K, Jespersen AM, Andersen F, Bosselmann S (1988) Pelagic food webs in an oligotrophic lake. Hydrobiologia 164:271–286

Stockner JG, Porter KG (1988) Microbial food webs in freshwater planktonic ecosystems. In: Carpenter SD (ed) Complex interactions in lake communities, Springer, New York, p 69–84

Storch TA, Saunders GW (1978) Phytoplankton extracellular release and its relation to the seasonal cycle of dissolved organic carbon in a eutrophic lake. Limnol Oceanogr 23: 112–119

Tilzer MM, Horne AJ (1979) Diel patterns of phytoplankton productivity and extracellular release in ultra-oligotrophic Lake Tahoe. Int Rev Ges Hydrobiol 64(2):157–176

Vincent WF (1981) Production strategies in Antarctic inland waters: phytoplankton eco-physiology in a permanently ice-covered lake. Ecology 62:1215–1224

Welch HE, Kalff J (1974) Benthic photosynthesis and respiration in Char Lake. J Fish Res Board Can 31:609–620

Wetzel RG (1995) Limnological analyses. Springer, New York

Whalen SC, Cornwell JC (1985) Nitrogen, phosphorus and organic carbon cycling in an arctic lake. Can J Fish Aquat Sci 42:797–808

Wharton R, Simmons G, McKay C (1989) Perennially ice-covered Lake Hoare, Antarctica: physical environment, biology and sedimentation. Hydrobiologia 172:305–320

White PA, Kalff J, Rasmussen JB, Gasol JM (1991) The effect of temperature and algal biomass on bacterial production and specific growth rate in freshwater and marine habitats. Microb Ecol 21:99–118

Wiebe WJ, Sheldon WM, Pomeroy LR (1992) Bacterial growth in the cold: evidence for an enhanced substrate requirement. Appl Environ Microbiol 58:359–364

Winter K, Richter A, Engelbrecht B, Posada J, Virgo A, Popp M (1992) Effect of elevated CO_2 on growth and crassulacean-acid-metabolism activitry of *Kalanchoë pinnata* under tropical conditions. Planta 201:389–396

Editorial responsibility: Karel Šimek, České Budějovice, Czech Republic

Submitted: October 12, 1999; Accepted: February 29, 2000
Proofs received from author(s): May 25, 2000