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1 Preface

This thesis is based on the papers listed below. They are headed by an introduction and discussion that summarize results of recent literature and personal research on the microbial ecology of alpine and Arctic lakes under the light of ongoing environmental changes. The author's contribution to all three manuscripts includes sampling and field work, laboratory work, data analyses and publication.

MS 1:

Panzenböck M, Möbes-Hansen B, Albert R, Herndl GJ (2000)

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

Aquatic Microbial Ecology 21: 265-273

In this paper we report on the physical, chemical and microbial characteristics of a high Arctic lake on Franz-Joseph-Land including the description of its food web structure. Pelagic primary production counting PER and bacterioplankton production were followed during summer and related to variations of DOC, inorganic nutrients and temperature. A further attempt was to calculate the carbon flux from phytoplankton to bacterioplankton via PER to get an idea about the importance of this carbon source for the bacteria in this permanently ice-covered lake. The results of this study demonstrate that the % PER is relatively high (31-96% of total primary production) hence sufficient to meet the bacterial carbon demand.

MS 2:

Panzenböck M (2007)

Effect of solar radiation on photosynthetic extracellular carbon release and its microbial utilization in alpine and Arctic lakes.

Aquatic Microbial Ecology 48: 155-168

This publication focuses on the contribution of PER to PP and its flux to bacterioplankton in two Arctic and an alpine lake under the impact of radiation (PAR, UVR). The investigation of the alpine lake has been performed over one year including ice-free and ice-covered periods. The seasonal aspect of this study provides additional information on light adaptation and biomass fluctuation (senescence) of the phytoplankton affecting PER. High irradiances increases % PER especially when algae are dark adapted while UVR reduces total primary production, thus lowering PER and carbon flux to bacteria. The UVR impact is greatly related to the DOC concentration identifying the alpine low-DOC lake as more sensitive to higher irradiance levels than the Arctic lakes.

MS 3:

Panzenböck M (manuscript)

Seasonally varying effects of temperature on bacterial production and growth characteristics in alpine and Arctic lakes.

This paper emphasizes the role of temperature on bacterioplankton production and growth characteristics (biomass versus cell production) in lakes of high altitudes and high latitudes predicted to be especially affected by global warming. Temperature manipulation of bacterioplankton at different seasons in an alpine lake shows that bacteria are highly responsive to temperature manipulation in the lower temperature range with resources compensating the negative temperature effects. The bacterial investment strategies vary dependent on both temperature and resource supply that relative importance in controlling bacterial production also differed among variable temperature ranges and seasons. Similar responses of bacterial production and growth characteristics to temperature were detected in two Arctic lakes (Siberia, Russia).

2 General Introduction and Outline



Austria Sund, Franz-Josef Land (M. Panzenböck)

Why research in alpine and Arctic lakes?

Arctic and high alpine regions are harsh environments providing difficult and often unpleasant conditions for researchers. Despite this fact these regions have been recommended as important sites providing simple lentic ecosystems ideally for studies on different trophic levels (Rigler 1978, Hobbie et al. 1999, Vincent et al. 2008). There, lakes experience extreme physical conditions that affect their biogeochemistry and result in a more or less simple food web structure (Hobbie et al. 1999, Straškrabová et al. 1999) allowing, for instance, easier tracking of C- or N- fluxes (Kling et al. 1992). In the past, great attention was paid to abiotic conditions, fish, invertebrates, phyto- and zooplankton communities in alpine and Arctic lakes (e.g. Nauwerck 1966, Kalff 1967, Eppacher 1968, Pechlaner 1971, Holmquist 1973, Tilzer 1973, Schindler et al. 1974, Rigler 1978, Kling et al. 1992), but early research was also done on bacterio- and phytoplankton biomass and production (Hobbie 1964, Morgan and Kalff 1972, Kalff and Welch 1974, Hobbie and Rublee 1975, Miller et al. 1986). For the last decades, researchers focused on investigating structure and population dynamics of the microbial communities in alpine and Arctic lakes (e.g. Pernthaler et al. 1998, Wille et al. 1999, Crump et al. 2007). Reviews on the research of Arctic lakes and ponds are given, for instance, by Vincent and Hobbie (2000), Vincent and Laybourn-Parry (2008) and Rautio et al. (2011).

Alpine and Arctic regions are remote areas with minor anthropogenic influence. However, even lakes there already experienced influx of pollutants mostly derived from atmospheric deposition (Hermanson 1998, Vincent and Hobbie 2000, Wrona et al. 2006 and citations therein, Mladenov et al. 2011). Moreover, these regions are predicted to suffer from greater increases of temperature and ultraviolet radiation (UVR) under the light of global change than other regions (Beniston et al. 1997, Serreze et al. 2000, ACIA 2005, Hinzman et al. 2005, Blumthaler 2007 and citations therein, Allen et al. 2014). Ozone losses in the stratosphere, for instance, are not only observed in the Antarctic but also in the Arctic and mid-latitudes (Rex et al. 1997, Madronich et al. 1998). Additionally, alpine and Arctic lakes are believed to be particularly responsive to UVR increases and temperature related changes such as decreased duration of snow and ice cover, increased evaporation, increased nutrient loading and changes in coloured dissolved organic matter (Vincent and Pienitz 1996, Sommaruga et al. 1999, Levine and Whalen 2001, Thompson et al. 2005, Vincent et al. 2007, Prowse et al. 2011a, Rautio et al. 2011) and may therefore act as sensitive sentinels for climate change (Michelutti et al. 2002, Veillette et al. 2008, Williamson et al. 2008, Mueller et al. 2009, Rose et al. 2009). Thus, limnologists are increasingly interested in investigating the impact of

environmental changes in these areas (e.g. Sommaruga et al. 1999, Schindler and Smol 2006, Wrona et al. 2006, Rose et al. 2009)

Environmental characteristics of Arctic and alpine lakes

Lakes and ponds are especially numerous in the Arctic and show a high diversity concerning their physical, thermal and chemical properties (Vincent et al. 2008). A classification according to the origin and catchment type of Arctic lentic freshwaters was recently given by Rautio et al. (2011). Nevertheless, alpine and Arctic lakes (defined as lakes located above the treeline; Sommaruga 2001) share a lot of properties such as low water temperatures, a short growing season and prolonged ice-coverage accompanied by seasonally greatly fluctuating radiation conditions (Vincent and Hobbie 2000, Sommaruga 2001, Vincent et al. 2008).

Low temperatures strongly dampen biological processes within the microbial food web such as primary and secondary production (e.g. Markager et al. 1999, Adams et al. 2010), growth (e.g. Williamson et al. 2010) and respiration (e.g. Apple et al. 2006). Thus, degradation and nutrient cycling are slowed down in alpine and Arctic lakes (Vincent et al. 2008) where maximum water temperatures rarely exceed 14°C during summer (Table 1). Even in the Arctic where summer brings 24-hour daylight, a substantial amount of the incoming solar radiation is used for ice-melting. Accordingly, warming of the water column is constricted to a short period.

Alpine and Arctic lakes are also indirectly influenced by cold temperatures. Sparse vegetation, poorly developed soils and the presence of permafrost restricting the drainage of the catchment area limit the input of allochthonous material (Hobbie et al. 1999, Sommaruga et al. 1999, Laurion et al. 2000, Sommaruga and Augustin 2006). Some lakes are influenced by loads of suspended sediments of nearby glaciers affecting the underwater light regime and consequently primary production (Sommaruga et al. 1999, Whalen et al. 2006).

Low temperatures also create conditions for an extensive ice cover on the lakes that greatly influences gas transfer and mixis with consequences for the circulation of nutrients (Rouse et al. 1997). Alpine and Arctic lakes are ice-covered for > 8 months (e.g. Miller et al. 1986, Kling et al. 1992, Sommaruga and Psenner 1997, Markager et al. 1999, Hobbie et al. 2000, Belzile et al. 2001, Carrillo et al. 2002). Some Arctic lakes are even permanently ice-covered or thaw irregularly (Schindler et al. 1974, Doran et al. 1996, Veillette et al. 2010, own observation).

Moreover, since ice-coverage controls the input of radiation to the water column, the long duration of ice-coverage greatly constraints the light availability necessary for primary production in the lakes. Especially if snow on top of the ice-cover is present, the incoming radiation is minimized to a great extent (Welch and Kalff 1974, Bolsenga et al. 1991) meaning that snow cover prolongs the darkness of the polar winter for primary producers in Arctic lakes. The amount of this effect, however, seems to depend on age, wetness or density of the snow (Perovich et al. 1998). The photosynthetic active radiation (PAR) transmittance to the water column through the ice-cover itself depends on the type of ice (Bolsenga et al. 1991, Kepner et al. 2000, Belzile et al. 2001). Contrasting to white ice, clear ice allows a large portion of incoming radiation to reach the water column (Bolsenga et al. 1991). Transmittance of incident PAR through snow-free, 1.5 to 2.2-m-thick clear ice was shown to range between 21–35% for high Arctic lakes (Welch and Kalff 1974, Bolsenga et al. 1996). In the Lake Nyagamy (Taymir Peninsula, Siberia), investigated during this study, the transmittance of incoming radiation (PAR) was even 46 – 75 % through 1 - 1.9 m thick clear ice. The attenuation of PAR by the ice-cover was slightly higher than the attenuation by the underlying water (attenuation coefficient K_d ice: 0.67 m^{-1} , K_d water: 0.50 m^{-1}).

There is evidence that a small amount of light penetrating the ice-cover is sufficient to initiate photosynthesis of shade-adapted phytoplankton species in the water column (Tilzer 1973). In Arctic lakes even a notable amount of the yearly primary production seems to occur under ice (Hobbie 1964, Kalff 1967, Welch and Kalff 1974, Rigler 1978) supported by nutrient inputs during the melting process in spring and early summer. Nutrient depletion during the ice-free season, however, may limit primary production despite improved light conditions (Whalen and Cornwall 1985, Miller et al. 1986). In general, in high latitudes and high altitudes the snow- and ice-melting process during spring and early summer acts as important hydrological event serving a significant flush of water and allochthonous material to the lakes (Baron et al. 1991, Hauer et al. 1997). Recent studies also identified storms as contributing factor for nutrient import to Arctic freshwaters (Adams et al. 2015).

During the ice-free period, alpine and Arctic lakes are exposed to high irradiances and in the case of Arctic lakes to continuous light. Photoacclimatization of the phytoplankton to utilize the high PAR intensities received during the ice-free period and the forming of a deep chlorophyll maximum after ice break-up are typical processes observed in alpine and Arctic lakes (Nauwerck 1966, Pechlaner 1971, Tilzer 1973, Kalff and Welch 1974, Sommaruga et al. 1999, Veillette et al. 2010).

Table 1: Overview of limnological parameters in Arctic and alpine lakes. Temperature: water temperature during summer, chl a: chlorophyll a, DOC: dissolved organic carbon, PP: primary production, net PER: net photosynthetic extracellular release, BP: bacterial production, BA: bacterial abundance

	Temperature Summer (°C)	Chl a ($\mu\text{g L}^{-1}$)	DOC (mg L^{-1})	PP ($\mu\text{g C L}^{-1} \text{ h}^{-1}$)	net PER (%)	BP ($\mu\text{g C L}^{-1} \text{ h}^{-1}$)	BA ($\times 10^5 \text{ cells mL}^{-1}$)	References
Arctic sites:								
Lake Peters (Alaska)				0.13				Hobbie 1964
Lake Schrader (Alaska)				0.17				Hobbie 1964
Toolik Lake (Alaska)	14.4	0.14 – 5.0		0.08 – 4.16			1 – 31 (max)	Hobbie et al. 2000, Miller et al. 1986
Pond II + III (Alaska)				2.7 - 10.8				Kalff 1967
4 Ponds (Alaska)							1 – 65	Hobbie and Rublee 1975
Imikpuk Lake (Alaska)	7.7			0.63 – 2.5				Kalff 1967
45 Lakes (Alaska)	5.6 – 20.5	0.3 – 7.6						Kling et al. 1992
7 Lakes (Canada)	1.6 – 7.2	0.04 – 1.24		0.12 – 0.45				Markager et al. 1999
Lake Char (Canada)	5	0.1 – 1.1	3	0.12 – 2.2			0.1 - 2	Kalff and Welch 1974, Morgan and Kalff 1972, Schindler et al. 1974
Meretta Lake (Canada)	7.2	1 - 11		0.6 – 5.4			2 - 80	Kalff and Welch 1974, Morgan and Kalff 1972
5 Lakes (Canada)			1.7 – 3.4					Michelutti et al. 2005
15 Lakes (Svalbard)	8 – 14.8	1 - 3	0.2 – 1.9	0.0008 – 62.5			7 - 57	Ellis-Evans et al. 2001
2 Lakes (Svalbard)	0.6 – 14.4		1.02 – 1.43			0.014 – 0.213	0.47 – 1.27	Mindl et al. 2007

Lake Tvillingvatnet (Svalbard)		0.33 – 1.65		1.02 – 41.6				28.8 (max)	Laybourn-Parry and Marshall 2003
Lake OS (Svalbard)		0.2 – 0.3		0.13 – 1.23				23.6 (max)	Laybourn-Parry and Marshall 2003
Lake FJL (Franz Joseph Land)	1.5 – 2.0	1.4 – 2.4	0.95 - 1.1	0.65 – 1.96	7 – 17	0.05 – 0.16		9.3 – 17.3	this study
LI (Taymir, Siberia)	7.9 - 8.3	1.0 – 1.9	5.9	5.5 – 6.8	14 - 26	0.11 – 0.5		14.7	this study
NYA (Taymir, Siberia)	1.5 – 1.8	0.2 – 1.1	2.5	0.2 - 1.2	41 - 61	0.008 - 0.04		8.5 – 9.5	this study
High mountain lakes:									
La Caldera (Sierra Nevada)	2.6 – 11.8	0.22 – 5.0		0.12 – 3.41	16 – 65	0.003 – 0.145		1.6 – 6.4	Reche et al. 1996, Carrillo et al. 2002
4 Lakes (Sierra Nevada)		0.17 – 0.89	0.4 – 0.8	1.4 – 4.3		0.04 – 0.2			Reche et al. 2001
Lake Redó (Pyrenees)				0.005 – 0.29	5 – 80 *	0.0009 – 0.01			Camarero et al. 1999
7 Lakes (MOLAR project)				0.7 – 2.	5 – 75 *			0.6 - 98	Straškrabová et al. 1999
Vorderer Finstertalersee (Alps)				0.003 – 0.79					Tilzer (1973)
57 high mountain lakes in Austria		0.17 – 10.6	0.24 – 2.48						Sommaruga et al. 1999
Jöri Lake (Alps)	15	0.5 – 5.0				0.01 – 0.03		7 - 17	Hinder et al. 1999
16 Lakes (Alps, Pyrenees)		0.34 – 7.97	0.21 – 1.99						Laurion et al. 2000
GKS (Alps)	2.1 – 15.4	0.4 – 4.9	0.3 – 0.5	0.03 – 2.2	7 – 77	0.002 – 0.2		0.3 – 7.7	Wille et al. 1999, Pernthaler et al. 1998, this study

* gross PER including bacterial assimilation

As a result of the highly varying environmental conditions, primary production in these lakes varies significantly between seasons. In general, pelagic primary production in alpine and Arctic lakes is low compared to lakes situated elsewhere (Table 1). In Arctic lakes and ponds, primary production is often dominated by phytobenthos (Kalff and Welch 1974, Rigler 1978, Hobbie 1984, Vincent and Hobbie 2000, Whalen et al. 2008, Bonilla et al. 2009, Rautio et al. 2011) and similar to Antarctic and alpine lakes, a relative high abundance of mixotrophic organisms can be observed (Roberts and Laybourn-Parry 1999, Straškrabová et al. 1999, Laybourn-Parry and Marshall 2003). Mixotrophy appears to be an important competitive strategy for organisms in ice-covered lakes to survive periods of darkness, thus providing advantage over photoautotrophs.

Presenting an extreme set of conditions for photosynthesis with highly variable radiation and low temperature along with low nutrient concentration, alpine and Arctic lakes are rather unproductive. With few exceptions (i.g Meretta lake) most lakes in these regions are oligotrophic to ultra-oligotrophic (e.g. Kalff and Welch 1974, Ellis-Evans et al. 2001, Levine and Whalen 2001, Antoniadou et al. 2003, Laybourn-Parry and Marshall 2003, Lim and Douglas 2003, Bitušík et al. 2006). Consequently, the pelagic food webs are less complex than elsewhere and dominated by the microbial components widely controlled by available carbon resources (Straškrabová and Šimek 1993, Hobbie et al. 1999, this study: MS1).

Moreover, both alpine and Arctic lakes are systems that receive elevated UVR (Vincent et al. 1998, Vinebrook and Leavitt 1998, Sommaruga 2001). In the Alps and similarly in the Arctic, the combined effect of low aerosol amount and high albedo (reflectivity of the ground) together with altitude, solar zenith angle and atmospheric ozone results in high UV radiation levels in these regions (Blumthaler 2007). Especially in the UVR-wavelengths, a significant increase with altitude can be observed in the Alps (Blumthaler et al. 1997, Schmucki and Philipona 2002). With respect to aquatic environments, UVR transmittance into the water column was found highly related to the quantity and quality of DOC (dissolved organic carbon) with high molecular weight CDOM (chromophoric dissolved organic matter) as main UV-attenuator (e.g. Scully and Lean 1994, Morris et al. 1995, Laurion et al. 2000). Although DOC and CDOM contribution generally decrease with altitude and latitude (Vincent and Pienitz 1996, Sommaruga et al. 1999, Sobek et al. 2007), some alpine lakes contain surprisingly much DOC (Rose et al. 2009). More often, Arctic waters surrounded by meadows or Tundra ponds at lower latitudes greatly influenced by terrestrial inputs (Hamilton et al. 2001) may contain $\text{DOC} > 4 \text{ mg L}^{-1}$ with a high contribution of UVR-absorbing CDOM

(Baron et al. 1991, Laurion et al. 2000, Bonilla et al. 2009, Rautio et al. 2011, own observations).

Most lakes in high latitude and high mountain regions, however, have low DOC concentrations (Table 1). Particularly alpine lakes receive little allochthonous DOC due to the poorly developed soil and sparse vegetation in the catchment (Sommaruga et al. 1999, Reche et al. 2001). Additionally, this DOC flush is largely limited to the period of snowmelt that serves as important pulse of terrestrially derived, aromatic DOC. Thus, in many alpine and high Arctic lakes the predominating DOC derives from autochthonous sources (Hood et al. 2003, Miller et al. 2009). Since the in lake-production of carbon is also limited as discussed before, the low and moreover less coloured DOC allows UVR to penetrate deep into the water column (Baron et al. 1991, McKnight et al. 1997, Vincent et al. 1998, Sommaruga et al. 1999, Laurion et al. 2000, Sommaruga and Augustin 2006). Recently, some authors argued that in highly transparent lakes phytoplankton are even more important than DOC in attenuating UVR (Sommaruga and Psenner 1997, Sommaruga and Augustin 2006).

In lakes with high UVR transparency organisms have to cope with harmful UV doses (Sommaruga 2001, Rose et al. 2009, Rautio et al. 2011). UVR was found to negatively affect growth, production (Helbling et al. 1992, Williamson et al. 2010) and community structure of phytoplankton (Karentz et al. 1991, Xenopoulos and Frost 2003) as well as bacterioplankton activity (Lindell et al. 1996, Sommaruga et al. 1997, Carrillo et al. 2002). The temperature-independent damaging impact of UVR may be even worse in cold lakes (Roos and Vincent 1998, Doyle et al. 2005) concerning the temperature dependence of the enzymatic induced cellular repair mechanisms (Pakker et al. 2000, MacFadyen et al. 2004). Besides temperature, nutrient availability might influence the effects of UVR exposure, though controversial results have been reported to the present. Nutrient depletion was found both to increase (Hiriart et al. 2002) and to decrease the effects of UVR on phytoplankton growth (Xenopoulos and Frost 2003, Doyle et al. 2005).

In general, ice-coverage dependant on the type of ice acts as important UVR screen for the underwater biocoenosis (Kepner et al. 2000, Sommaruga 2001). However, the exclusion of CDOM from the ice-cover during freezing enhances the UVR-transparency of the ice cover (Belzile et al. 2001, 2002). After snow-melting, it may happen that relatively high UV-irradiance reaches the water column inhibiting the still dark-adapted phytoplankton (Neale et al. 1994). However, adaptation to high UVR and increasing assimilation of planktonic photoprotective pigments and mycosporine-like amino acids (MAAs) among other UV-minimizing strategies have been developed by a variety of organisms (Karentz et al. 1991,

Sommaruga 2001, Laurion et al. 2002, Bonilla et al. 2009) keeping the UVR stress of the planktonic community low (Halac et al. 1997) .

In addition, UVR induces photochemical alteration of DOC with controversial effects such as photobleaching of CDOM reducing its attenuating properties (Laurion et al. 2000, Reche et al. 2000) and photohumification of algal DOC increasing the very same (Reche et al. 2001). UVR was also observed to affect the DOC bioavailability (Lindell et al. 1995, Thomas and Lara 1995, Wetzel et al. 1995, de Lange et al. 2003) with the potential to alter the biochemical cycle and the microbial food web structure (Zepp et al. 1998, de Lange et al. 2003, Cooke et al. 2006, Piccini et al. 2009). Results from a recent study even suggest that fulvic acids in Arctic surface waters greatly underly photochemical processes with consequences for their chemical character (Cory et al. 2007).

Predicted impacts of environmental changes on alpine and Arctic lakes

Over the last decades, UVR - especially UVR-B - was found to increase at high altitudes and high latitudes (Blumthaler and Ambach 1990, von der Gathen et al. 1995) associated with changes in stratospheric ozone concentration (Rex et al. 1997, Madronich et al. 1998, Rex et al. 2006). Concerning alpine and Arctic lakes, there may be a different sensitivity to elevated UVR. Clear water lakes on rocky terrain with low DOC are more vulnerable to increasing UVR levels compared to terrestrial influenced lakes with higher DOC content, higher aromaticity of DOC and therefore higher UVR attenuation capacity (Sommaruga et al. 1999, Reche et al. 2001, Michelutti et al. 2002). Moreover, UVR enhancement seems to act synergistically and cumulative with global warming that will have great impacts on alpine and Arctic freshwaters (Rae and Vincent 1998, Wrona et al. 2006, Vincent et al. 2007). The effect of UVR exposure on phytoplankton, for instance, was found to depend on both temperature and nutrient availability (Doyle et al. 2005, Scott et al. 2009).

Along with UVR, predicted global warming is supposed to exhibit greater extensions in alpine and Arctic regions (Overpeck et al. 1997, Allen et al. 2014) with broad impacts on freshwater ecosystems (Sommaruga et al. 1999, Prowse et al. 2006, Wrona et al. 2006, Vincent and Laybourn-Parry 2008, Dokulil et al. 2010). In fact, mean air temperatures in the Alps have already increased by 1°C in the 1980th and 1990th (Beniston 2000) and ongoing temperature increases are expected to change in lake temperatures and ice-cover duration (Thompson et al. 2009). In the Arctic, temperature increased also during the 20th century, however, with regional differences (e.g. Weller 1998, Polyakov et al. 2003). According to the recent IPCC report „the Arctic region will continue to warm more rapidly than the global

mean“ (Allen et al. 2014). Concerning the temperature related characteristics of alpine and Arctic lakes, proposed increases of temperature may have numerous consequences. Some impacts of climate change have been already observed (Hinzmann et al. 2005, Smith et al. 2005, Vincent et al. 2008, Vincent et al. 2009, Loughheed et al. 2011) or reconstructed by paleolimnological approaches (Smol et al. 2005, Michelutti et al. 2007).

Besides increase of water temperatures with predicted impacts on metabolism and structure of the biocoenoses (Rouse et al. 1997, Rae and Vincent 1998, Hobbie et al. 1999, Wrona et al. 2006, Loughheed et al. 2011) and stratification of the water column (Thompson et al. 2009), higher temperatures are supposed to decrease the duration of snow- and ice-coverage (e.g. Doran et al. 1996, Stone et al. 2002). This might have consequences for mixis and the exchange with the atmosphere and the sediments, thus altering nutrient and gas conditions in the lakes (Pechlaner 1971, Hobbie et al. 1999, Vincent et al. 2008, Prowse et al. 2011b).

Studies already reported on earlier dates of ice breakup of alpine and Arctic lakes (Livingstone 1997, Prowse et al. 2011a) and perennially ice-covered lakes that became ice-free during summer (Mueller et al. 2009, Vincent et al. 2009, Veillette et al. 2010). A reduced ice-coverage also prolongs the growing season and modifies the underwater light conditions (Smol et al. 2005) with effects on the microbial biocoenosis as described before. Veillette et al. (2010) witnessed changes in phytoplankton population density and species composition in a perennial ice-covered Arctic lake due to loss of ice during one year. While improved PAR availability supported by increased nutrient influx due to thermally induced melting processes in the catchment may stimulate phytoplankton growth (Pechlaner 1971, Hobbie et al. 1999, Prowse et al. 2006) and increase the productivity of the systems (Michelutti et al. 2005, Michelutti et al. 2007, Vincent et al. 2009), negative impacts of PAR and UVR causing photoinhibition can also be expected. Global warming effects may also lead to shifts in vegetation (Grabherr et al. 1994) as for instance the migration of the tree line (Hauer et al. 1997). An improved development of vegetation and soil cover together with enhanced melting processes in the catchment including melting permafrost soils are supposed to increase the input of allochthonous DOC and particulate material to lakes (Hauer et al. 1997, Rouse et al. 1997, Sommaruga et al. 1999) with the potential to compensate the predicted UVR pollution to a certain amount (Vincent and Hobbie 2000, Sommaruga 2001). Some authors suspect that changes in DOC quantity and quality may have even greater effects on the underwater UVR regime in lakes than stratospheric ozone losses (Schindler et al. 1996, Williamson et al. 1996, Vincent et al. 1998). The complex interaction of temperature and UVR effects complicates the prediction of possible consequences of global warming and stratospheric ozone loss for Arctic

and alpine lakes. To the present knowledge, global warming and UVR increases have the potential to change the microbial metabolism, biogeochemistry and biocoenoses of alpine and Arctic lakes (Perez and Sommaruga 2006, Williamson et al. 2010).

Phytoplankton production, photosynthetical extracellular release and its importance for bacteria in alpine and Arctic lakes (MS 1, MS 2)

Besides the input of humic DOC from catchment soils and vegetation, sources of DOC for aquatic ecosystems include the production of microbially derived humic DOC from biomass (McKnight et al. 1994) and the release of nonhumic microbial and photosynthetical extracellular release (PER) (Giroldo and Vieira 2005, Kawasaki and Benner 2006). Their relative contributions to the DOC pool of a lake are believed to change in response to a changing climate.

Since decades, researchers paid attention to PER (e.g. Fogg 1971, Berman-Frank and Dubinsky 1999, Carlson 2002, Bertilsson and Jones 2003). Its reasons and driving factors, however, are still poorly understood. Among others, the role of PER as barrier for viral attack and support for bacterial remineralization providing inorganic nutrients to the algae has been discussed (Berman-Frank and Dubinsky 1999). A previous study reported PER to contain allelopathic substances (von Elert and Jüttner 1997), others assumed PER and its compounds to act as “chemical cross-talk” between diatom species (Paul et al. 2009). Most studies observed a strong negative relationship between the contribution of PER to total primary production (% PER) and primary production (PP) (Anderson and Zeutschel 1970; Mague et al. 1980, Teira et al. 2001, Moran et al. 2002) supported by the findings that in oligotrophic systems % PER is higher than in eutrophic ones (Teira et al. 2001, Chrost and Siuda 2006). According to Baines and Pace (1991), however, this relationship is restricted to freshwaters.

Especially in lakes with low allochthonous DOC that in addition is recalcitrant to bacterial degradation (Del Giorgio and Davis 2003), the primary producers become increasingly important as carbon provider for bacteria. Several authors reported that during their investigation the removal of algae resulted in a decrease of bacterial production (Aas et al. 1996, Sommaruga et al. 1997, Medina- Sánchez et al. 2002). PER derived from algae and macrophytes is known as highly bioavailable and therefore immediately incorporated by bacteria (e.g. Cole et al. 1982, Chrost and Siuda 2006). A survey of studies covering a wide range of freshwater and marine systems reported that on average 46% of PER is incorporated by bacteria (Baines and Pace 1991). Chrost and Siuda (2006), for instance, observed that in oligo- and mesotrophic lakes a larger amount of PER is utilized by bacteria than in eutrophic lakes supporting the view that PER may be essential as carbon supply in resource poor waters. Recent research also suggests that besides the benefit from PER bacteria may be simultaneously preyed upon by mixotrophic algae resulting in a paradox interaction (Maranon et al. 2004, Medina-Sánchez et al. 2004). In some aquatic ecosystems PER has been found to

meet the bacterial carbon demand (Sundh and Bell 1992, Reche et al. 1996) while in many others it did not (Chrzanowski and Hubbard 1982, Brock and Clynne 1984, Sondergaard et al. 1985, Baines and Pace 1991, Petit et al. 1999a). Moreover, PER was found to modulate the bacterial response to solar radiation (Medina-Sánchez et al. 2002).

Planktonic PP in alpine and Arctic lakes is generally low compared to other lakes (Table 1). The reported estimates, however, often refer to particulate PP or in other words to carbon that is still incorporated in algal cells and retained by the filters after filtration of the labelled sample. Since both filtrate and bacteria contain also a substantial amount of organic matter photosynthesized by phytoplankton (e.g. Camarero et al. 1999), PP values published in many studies are likely to be underestimates. Even in highly productive ecosystems PP is rated too low if PER is neglected (Maranon et al. 2004). The percentage of PER estimated *in situ* in alpine and Arctic lakes is highly variable (Table 1); the bacterial uptake of PER ranges from 1 to 75% of total PP (Reche et al. 1996, Camarero et al. 1999, Straškrabová et al. 1999, Carrillo et al. 2002, Medina- Sánchez et al. 2006).

Three main pathways have been suggested to be responsible for the release of photosynthesized carbon:

I) Lysis of cells due to senescence, viral infection or sloppy feeding by zooplankton (Lambert 1978, Jumars et al. 1989, Murray and Elridge 1994, Nagata 2000) resulting in a complete loss of the cell compounds.

II) Passive diffusion related to cell size and inner-out concentration of cells and the surrounding medium (Bjoernsen 1988).

III) Exudation of actively growing algal cells.

The latter is supported by an often observed positive relationship between total primary production (PP) and PER (Baines and Pace 1991, Teira et al. 2003, Maranon et al. 2004) and the responsiveness of algal exudation to changing environmental conditions. In general, algae appear to release relatively more PER when they are stressed. Nutrient depletion, for instance, has been identified as a factor that may enhance % PER (Fogg 1983, Obernosterer and Herndl 1995, Medina- Sánchez et al. 2006) whereas concerning irradiance contradictory results have been reported to the present. According to some authors, % PER increased with radiation level (Fogg et al. 1965, Wood and Valen 1990) while others found % PER decreasing with irradiance (Berman 1976, Coveney 1982, Maranon et al. 2004). Some other authors observed higher % PER under both, extremely high or low irradiance (Mague et al. 1980, Watanabe

1980, Lee and Rhee 1999) or no relationship between % PER and irradiance (Williams and Yentsch 1976, Lancelot 1983).

Another explanation for the active release of valuable carbon is the result of uncoupling of algal growth under light-saturated but nutrient-depleted conditions that allow photosynthesis but not biomass production (Fogg 1983, Berman-Frank and Dubinsky 1999). This may be particularly relevant for algae under high-light exposure in nutrient-scarce environment as it is the case in alpine and Arctic lakes during summer. Moreover, the impact of UVR – another important stressor in these lakes - on PER is fairly unknown. Since UVR contributes substantially to photoinhibition (Helbling et al. 1992, Milot-Roy and Vincent 1994), UVR can have great effects on the amount of PER in alpine and Arctic lakes. However, there are only few studies that deal with the effect of UVR on PER (e.g. Pausz and Herndl 1999, Carrillo et al. 2002). The radiation impact on the carbon flux from algae to bacteria is even more complicated to detect because of the difficulty to detach between radiation induced photochemical changes of PER affecting its bacterial incorporation (Obernosterer et al. 2001, Reche et al. 2001), changes of PER quantity and quality due to photoinhibition of the algae (Carrillo et al. 2002, Medina- Sánchez et al. 2006) and directly photoinhibited bacteria (Sommaruga et al. 1997, Carrillo et al. 2002, own observation).

The products released by algae include carbohydrates, aminoacids, peptides, organic phosphates, enzymes, vitamins, alditols, carboxylic acids (Fogg 1971, Mykkestad 2000, Bertilsson and Jones 2003 and citations therein), and glycollate as a result of photorespiration (Fogg 1983). While PER is mostly predominated by low molecular products < 700 – 900 Da (Jensen 1983, Maurin et al. 1997) there is evidence that high molecular weight substances can also significantly contribute to PER (Fogg 1977, Nalewajko and Schindler 1976). The amount and quality of PER seem to differ between species, cell size and between stationary and exponential state of growth (Obernosterer and Herndl 1995, Malinsky-Rushansky and Legrand 1996, Kormas 2005, Romera-Castillo et al. 2010). Recently, PER has been reported to contain fluorescent humic-like substances during the exponential growth of phytoplankton cells (Romera-Castillo et al. 2010). The chemical nature of PER, however, is difficult to determine, due to the concurrent bacterial uptake of the biologically labile compounds (Bertilsson and Jones 2003) which is a major methodological problem complicating also the evaluation of total PP, gross PER and its flux to bacteria.

For the presented thesis, I wanted to investigate the contribution of PER to P_{tot} influenced by varying irradiance including UVR and the importance of PER as bacterial carbon supply in alpine and Arctic lakes. As a first attempt, gross PER was calculated by the use of thymidine

incorporation as proxy for bacterial PER uptake (see MS 1). The use of antibiotics reducing the bacterial activity was also tested to estimate total PP, gross PER and its flow to bacteria. In line with the findings of Jensen (1984) bacteria were not completely inhibited irrespective of the type of antibiotics (chloramphenicol, tetracycline, streptomycin) or the range of concentration that were used ($3\ \mu\text{g} - 30\ \mu\text{g mL}^{-1}$) but the antibiotics revealed an inhibitory effect on the primary producers. Thus, the separation of algae and bacteria were done by serial filtration of the ^{14}C -labelled sample through different pore size filters ($> 1.2\ \mu\text{m}$ pore size = “algal”-filter, $> 0.2\ \mu\text{m}$ pore size = “bacterial” – filter) after removal of a liquid subsample for estimating total PP. Similarly, a subsample of the filtrate was used for net PER estimation. To test the reliability of the bacterial PER incorporation values received by serial filtration, bacterial production (BP) was also measured by leucine and thymidine incorporation. This should provide further information about the ability of PER to fulfill the bacterial carbon demand in the studied lakes.

Temperature effects on bacterial growth (MS 1, MS 3)

Since temperature greatly affects biological processes, bacterial metabolism, carbon transfer via the microbial loop and breakdown of organic material is dampened in cold water lakes like alpine and Arctic ones. The slow degradation and nutrient cycling processes due to reduced microbial activity lead to deficiencies in many key nutrients in these ecosystems (Vincent et al. 2008). In turn, slight warming was found to increase the bacterial carbon demand (Kritzberg et al. 2010). Thus, proposed climate warming may have an enormous impact on bacterial mediated carbon and nutrient cycling.

Temperature affects microbial activity in various ways such as regulating bacterial production (Shiah and Ducklow 1994, Adams et al. 2010), growth rate (Nedwell and Rutter 1994), growth efficiency (Apple et al. 2006, Hall and Cotner 2007, Berggren et al. 2010, Kritzberg et al. 2010), cell size of bacteria (Wiebe et al. 1992), community composition (Adams et al. 2010), nutrient use efficiency (Hall et al. 2009) and the proportion of actively respiring bacteria (Rae and Vincent 1998). Moreover, enzyme activity (Privalov 1990, Feller and Gerday 2003), protein synthesis (Araki 1991) and ribosome functioning (Inness and Ingraham 1978) can be impaired by low temperatures. Bacterial growth characteristics describing the bacterial substrate investment into biomass or cell division as estimated by leucine or thymidine incorporation, respectively (Chin-Leo and Kirchman 1988, Servais 1995) were also found to depend on temperature (Tibbles 1996, Shiah and Ducklow 1997, Petit et al. 1999b, Hoppe et al. 2006, Longnecker et al. 2006).

Furthermore, there is growing evidence that temperature and resources act synergistically in influencing bacterial growth (Wiebe et al. 1992, Felip et al. 1996, Nedwell 2000, Pomeroy and Wiebe 2001, Vrede 2005, Hall and Cotner 2007). Cold temperatures lower the uptake capacity as well as the enzymatic regulated processing of substrate. Structural changes of cell membranes due to low temperatures (Russell 1990, Chintalapati et al. 2004) result in reduced substrate affinity and consequently impaired substrate uptake by bacteria (Nedwell and Rutter 1994). Moreover, cold-active enzymes are less stable in order to function at low temperatures to the disadvantage of lowered substrate affinity (Feller and Gerday 2003). However, it was observed that excess substrate can overcome negative temperature effects (Pomeroy et al. 1991, Wiebe et al. 1993). In turn, resource deficiency as often the case in alpine and Arctic lakes might strengthen the constraints due to low temperatures. Therefore, the limitation of bacterial growth in cold water lakes cannot be solely attributed to low temperature because temperature effects depend on resource concentrations, too (Nedwell 2000, Pomeroy and Wiebe 2001, Hall and Cotner 2007, Adams et al. 2015). At the present, contrary results concerning the stimulating effect of resources in dependence of temperature range exist with some authors postulating the effect to be greater at low temperatures (Pomeroy and Wiebe 2001) while others observed greater stimulation by resources at higher temperatures (Kirchman and Rich 1997, Autio 1998, Kirchman et al. 2005).

Bacterioplankton in cold-water lakes like those studied here possess various adaptations to cope with low temperatures such as structural changes of enzymes (Feller and Gerday 2003) and modulation of the membrane fluidity (Russell 1990, Chintalapati et al. 2004) improving the uptake efficiency of substrates (Russell 1990, Nedwell 2000). The latter, however, may result in higher respiratory costs at higher temperatures (Hall et al. 2010). The groups of bacteria that are predominant in cold habitats are psychrophiles with optimal growth temperatures of $< 15^{\circ}\text{C}$ and psychrotolerant bacteria with optimal growth temperatures $< 25^{\circ}\text{C}$ (Morita 1975); both are forced to operate and grow far below their optimum temperature in polar and other cold water systems (Pomeroy and Wiebe 2001, Wallenstein and Hall 2012).

That the responsiveness of bacteria to temperature changes seems to be particularly pronounced in the lower temperature range (Pomeroy and Wiebe 2001, Middleboe and Lundsgaard 2003, Apple et al. 2006, Sand-Jensen et al. 2007, Kirchman et al. 2009, Adams et al. 2010) implicates bacterioplankton in cold water lakes to react very sensitive to predicted global warming even within a narrow range (Wiebe et al. 1992, Vincent and Pienitz 1996).

Since bacteria can affect higher trophic levels via the microbial loop (Azam et al. 1983) and provide important food for protozoans (Sherr and Sherr 1994), environmental changes due to

climate warming such as increase of temperature and nutrient fluxes (Hobbie et al. 1999, Prowse et al. 2006) will likely affect the whole biocoenoses of high altitude and high latitude lakes (e.g. Rouse et al. 1997, Michelutti et al. 2007, Lougheed et al. 2011).

The aim of this study was to detect bacterial responses to increasing temperature in dependence of temperature range and resource supply in alpine and Arctic lakes and to identify the role of temperature and resources in controlling the patterns of bacterial protein versus cell production.

Study sites

The alpine lake (Gossenköllesee) investigated during this study is situated above the timberline in the Stubai Alps (Tyrol, Austria, 47° 13' N, 11°01' E, altitude: 2417 m a.s.l.) Only 10% of its silicious catchment area is covered by soil with alpine meadows. The Gossenköllesee (area: 17 000 m², maximum depth: 9.9 m, mean depth: 4.7 m) is an oligotrophic, di- and holomictic lake and ice-covered for about 8-9 month (Eppacher 1968, Sommaruga and Psenner 1997) with maximum surface temperatures of about 14°C during summer (Nauwerck 1966, Eppacher 1968).

The Gossenköllesee and its biocoenoses is well investigated since the 1930th (e.g. Steinböck 1934, Nauwerck 1966, Eppacher 1968) with current efforts on the investigation of the microbial communities and UVR impacts (e.g. Sommaruga et al. 1997, Sommaruga and Psenner 1997, Pernthaler et al. 1998, Sommaruga 2001, Sommaruga and Augustin 2006, Perez et al. 2010). Since 1977, the Gossenköllesee and its catchment are declared as a UNESCO Man and Biosphere Reserve representing the smallest biosphere reserve worldwide.

In the Gossenköllesee, the bacterial community is dominated by beta-proteobacteria and actinobacteria, also present with seasonally varying importance are alpha-proteobacteria and archaea (Pernthaler et al. 1998, Perez et al. 2010). Filamentous morphotypes, although less abundant, represent a major part of the microbial biomass in this lake due to their length > 10 µm (Pernthaler et al. 1998, Wille et al. 1999). The phytoplankton are dominated by species of green algae, chrysophytes, diatoms, cryptophytes and dinoflagellates (Nauwerck 1966). The zooplankton is dominated by *Cyclops taticus*, *Polyarthra dolichoptera* and *Notholca squamula* (Eppacher 1968). In the 15th or 16th century brown trout (*Salmo trutta F. fario*) was introduced in the Gossenköllesee representing the only fish species in this high mountain lake. Even in the UVR range, the attenuation of surface radiation is very low in GKS due to its low, mainly autochthonous DOC (0.12 –0.65 mg/L) (Sommaruga and Augustin 2006). 10 % of the surface UV-B irradiances were observed to reach almost the bottom of the lake (Sommaruga et al. 1997, Sommaruga and Psenner 1997). This high water transparency especially in the UVR range changes temporarily, decreasing with the development of a deep chlorophyll maximum (Sommaruga and Augustin 2006). Thus, phytoplankton and phytoplankton derived CDOM are suspected as significantly responsible for variations in radiation attenuation (Sommaruga and Psenner 1997, Sommaruga and Augustin 2006).

One of the investigated Arctic lakes is located at the westernmost part of Ziegler Island, Franz Joseph Land archipelago (81.04° N, 56.17 °E). The lake surrounded by basalt rocks and glaciers covers an area of about 82 000 m² and has a mean depth of 9 m. This unnamed lake is

permanently ice-covered (2.4 m thick ice-cover during the investigation in July/August 1996). It only becomes ice-free near the small glacier creeks that enter the lake during snow- and ice-melt. A single outflow drains the lake into the nearby sea.

The other Arctic lakes chosen for this study are located at the Taymir Peninsula, Siberia, and were investigated during an expedition in July 2000. One small unnamed lake (LI, 70°17' N, 88° 30' E, area: 25 000 m², maximum depth: 6 m) was ice-free during the investigation whereas Lake Nyagamia (NYA, 72°42' N, 82°26' E) was still covered by a 1-1.9 m ice sheet in July but becomes irregularly ice-free (Walasova, T., pers. comm.). NYA has an area of about 48 km², the maximum depth is unknown. Whitefish, *Coregonus spp.*, is reported to occur in this lake (Allen-Gil et al. 2003).

Aim and Outline of the thesis

This study aimed at investigating the carbon production and flux within the microbial food of cold water lakes under the impact of predicted environmental changes. I wanted to highlight the influence of radiation (PAR, UVR) on phytoplankton primary production, the contribution of photosynthetic extracellular release and the carbon flux to bacterioplankton via PER. Furthermore I focused on the impact of temperature in concert with resources on growth characteristics and production of bacterioplankton in alpine and Arctic lakes (Fig. 1).

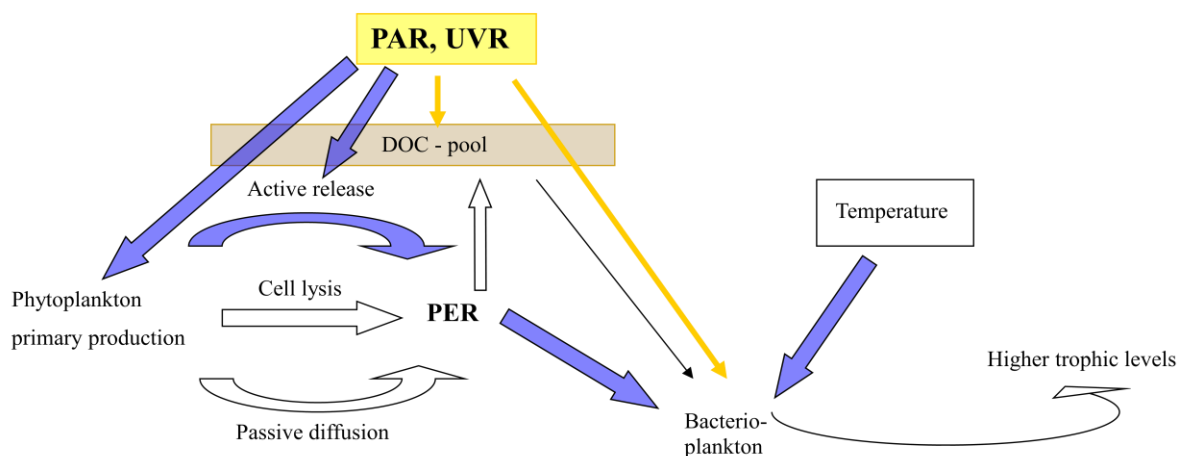


Fig. 1 Simplified outline of the carbon fluxes within the microbial community under the influence of radiation and temperature. Blue arrows indicate the pathways and impacts investigated during this study.

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



Peat bog, Franz Joseph Land (M. Panzenböck)



Little auk colony (*Alle alle*), Franz Joseph Land (M. Panzenböck)

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

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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 $1.8 \mu\text{g chl a l}^{-1}$ and $22 \mu\text{g C l}^{-1} \text{ d}^{-1}$, 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 $17.3 \times 10^5 \text{ ml}^{-1}$) and flagellates (7.8 to $17.3 \times 10^2 \text{ ml}^{-1}$) varied within a narrow range. Bacterioplankton production ranging from 1.2 to $3.9 \mu\text{g C l}^{-1} \text{ d}^{-1}$ 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 ($P_{\text{part}} + P_{\text{er}}$) 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).

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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 m² 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

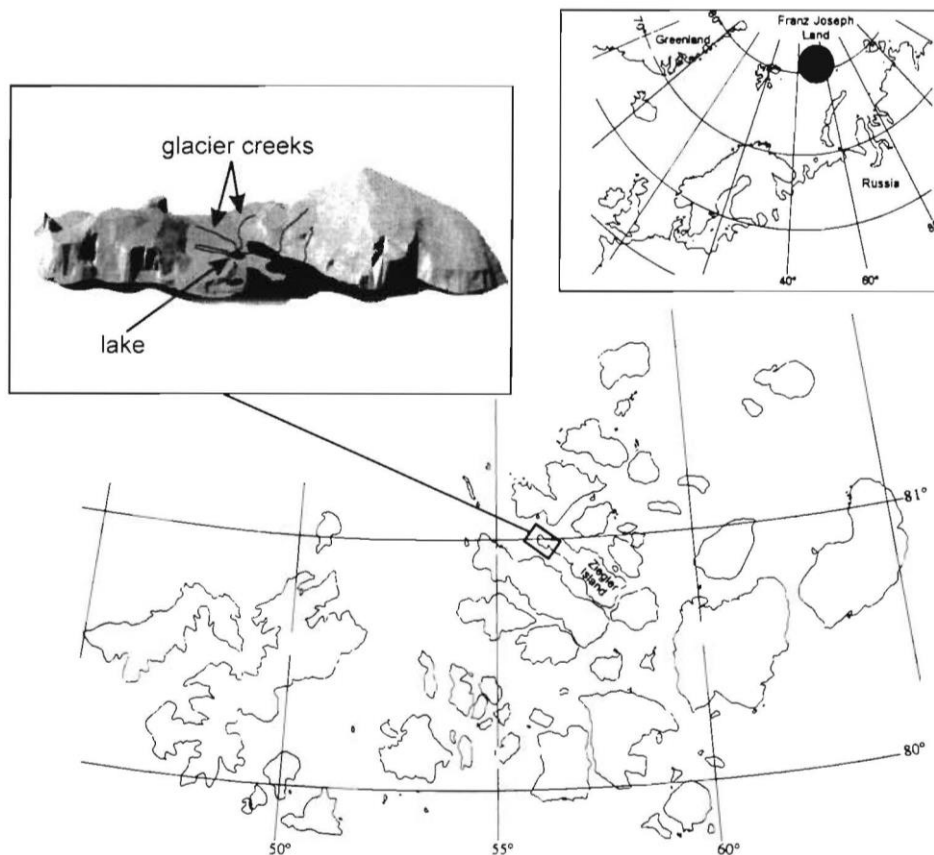


Fig. 1 Location of the study site on Ziegler Island, Franz Joseph Land

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 homogeneously 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 (Kalfß & 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:

$$\text{net PP}_{\text{tot}} = P_{\text{part}} + \text{net } P_{\text{er}} \text{ (apparent in filtrate)}$$

$$\text{gross PP}_{\text{tot}} = P_{\text{part}} + \text{gross } P_{\text{er}}$$

$$\text{gross } P_{\text{er}} = \text{net } P_{\text{er}} + \text{BCD}$$

$$\text{BCD} = \text{BP (thymidine incorporation)} + \text{respiration} \\ \text{(assuming a growth efficiency of 50 \%)}$$

$$\text{gross \% } P_{\text{er}} = (\text{gross } P_{\text{er}} / \text{gross PP}_{\text{tot}}) \times 100$$

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)

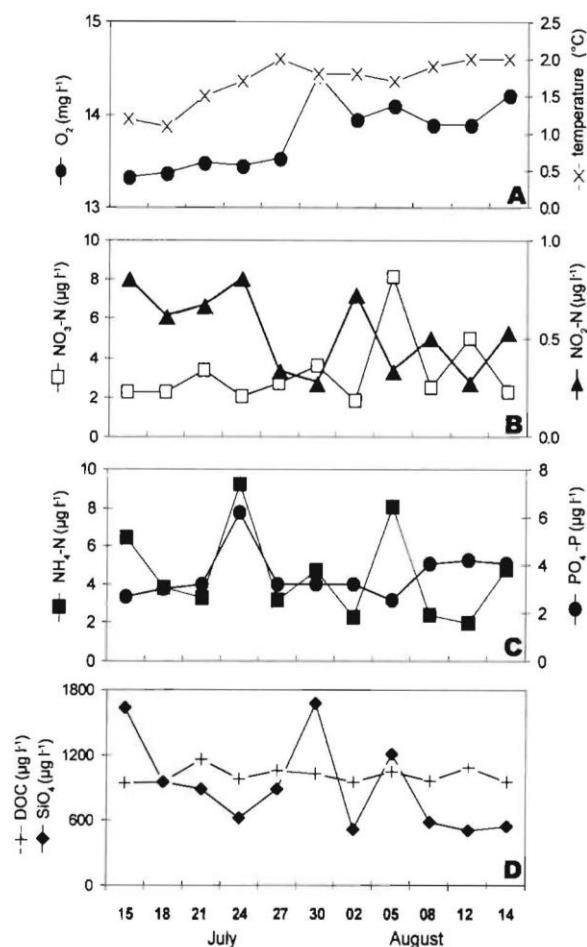


Fig. 2. Chemical and physical parameters of lake water during the investigation period. (A) Oxygen concentration, temperature. (B) $\text{NO}_3\text{-N}$, $\text{NO}_2\text{-N}$. (C) $\text{NH}_4\text{-N}$, $\text{PO}_4\text{-P}$. (D) DOC, silicate

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 $600 \mu\text{E m}^{-2} \text{ s}^{-1}$, 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 $41.5 \mu\text{g C l}^{-1} \text{ d}^{-1}$ (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}) $\times$ 100; % BCD of gross P_{er} = (BCD/gross P_{er}) $\times$ 100; % BCD of gross PP_{tot} = (BCD/gross PP_{tot}) $\times$ 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}
			($\mu\text{g C l}^{-1} \text{d}^{-1}$)						(%)	(%)
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
($\pm$ 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 $\mu\text{g C l}^{-1} \text{d}^{-1}$ (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 15 500 $\mu\text{g l}^{-1}$ (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 $\mu\text{g l}^{-1}$ in glacier-fed lakes and 700 $\mu\text{g l}^{-1}$ 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. Kalf 1967, Miller et al. 1986), which is

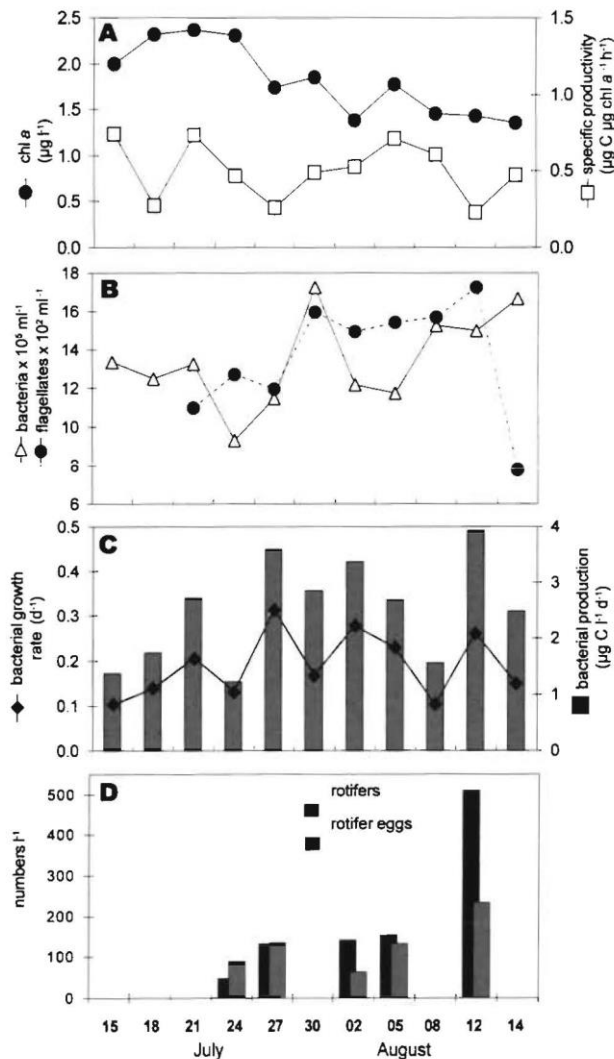


Fig. 3. (A) Chlorophyll *a* concentration and specific productivity (net PP_{tot} /biomass) of phytoplankton. (B) Bacterioplankton and flagellate numbers. (C) Bacterial production (thymidine incorporation) and bacterial growth rate. (D) Number of rotifers and rotifer eggs

supported by the nutrient input during the snow-melting period (Whalen & Cornwell 1985). Nutrient availability 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 $22 \mu\text{g C l}^{-1} \text{ d}^{-1}$ and mean phytoplankton biomass

was $1.8 \mu\text{g l}^{-1}$ 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 $240 \mu\text{g C l}^{-1} \text{ d}^{-1}$ (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 $0.5 \text{ mg C (mg chl a)}^{-1} \text{ h}^{-1}$ (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 $0.22 \text{ mg C (mg chl a)}^{-1} \text{ h}^{-1}$ (Kalff & Welch 1974), and for Antarctic lakes, 0.023 to $0.137 \text{ mg C (mg chl a)}^{-1} \text{ h}^{-1}$ has been reported (Vincent 1981, Parker et al. 1982). However, a specific productivity of as high as $6.3 \text{ mg C (mg chl a)}^{-1} \text{ h}^{-1}$ 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 $0.6 \text{ mg C (mg chl a)}^{-1} \text{ h}^{-1}$, 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 $80 \times 10^5 \text{ ml}^{-1}$ 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 $< 4^\circ\text{C}$ (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.

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4 Effect of solar radiation on photosynthetic extracellular carbon release and its microbial utilization in alpine and Arctic lakes



Gossenköllesee, Tyrol (M. Panzenböck)

Effect of solar radiation on photosynthetic extracellular carbon release and its microbial utilization in alpine and Arctic lakes

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ABSTRACT: The effect of solar radiation (photosynthetically active radiation and ultraviolet radiation [UVR]) on the photosynthetic extracellular release (PER) of phytoplankton and its utilization by bacterioplankton were studied in an alpine lake (Gossenköllesee, Austria) over a seasonal cycle. For comparison, 2 Arctic lakes on the Taymir Peninsula (Siberia) were investigated as well. The contribution of PER to primary production (% net PER) ranged between 0 and 95 % (mean 32 %) in Gossenköllesee (May 1999 to July 2000) following a seasonal trend that was inversely related to phytoplankton biomass. PER was released only under light conditions and was positively related to the intensity of solar radiation. During the ice-covered period, the % net PER increased, while total primary production (P_{tot}) decreased with experimentally increasing irradiance, indicating radiation-induced stress with dark-adapted phytoplankton. During the ice-free period, the increase of % net PER with increasing irradiance was independent of photoinhibition. The fraction of PER not immediately incorporated by bacteria (~60 % of total PER) may be an important contribution to the generally low pool of dissolved organic carbon (DOC) in Gossenköllesee. At the Arctic site, net PER amounted to 21 % of P_{tot} in an ice-free lake and 51 % in the ice-covered Lake Nyagamy. In all lakes, the amount of PER was sufficient to meet the bacterial carbon demand. The UVR-induced inhibition of primary production in the investigated lakes was inversely related to the DOC concentration of the water column, with the lowest effect in the ice-free Arctic lake (3.5 % reduction of P_{tot}) and the highest impact in the alpine lake (56 % reduction of P_{tot} , 61 % reduction of PER); the percentage of net PER was apparently not controlled by UVR. This suggests that the investigated alpine lake is more sensitive to changes in UVR than the Arctic lakes are.

KEY WORDS: Primary production · PAR · UVR · Exudates · Carbon flux

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INTRODUCTION

Planktonic algae release substantial amounts of photosynthesized carbon. While at least some part of this photosynthetic extracellular release (PER) is caused by cell death due to autolysis (Wetzel et al. 1972, Berman & Wynne 2005), viral lysis (Brussaard 2004), or grazing (Lambert 1978), there is also evidence of carbon exudation by actively growing algae (Blaauboer et al. 1982, Baines & Pace 1991). The reasons why intact cells exude photosynthetically fixed carbon are still uncertain. According to Bjørnson (1988), PER occurs due to passive diffusion, a mecha-

nism related to algal cell size and concentration differences between inside and outside the cell. It has also been suggested, however, that PER is an overflow reaction, i.e. algal carbon fixation exceeds synthesis of new cell material during periods of sufficient irradiance under nutrient-depleted conditions (Fogg et al. 1965, Berman-Frank & Dubinsky 1999). Furthermore, PER is thought to create bacteria- and nutrient-enriched microzones around algal cells (Azam & Cho 1987), which can act as a protection shield against viral infection (Berman-Frank & Dubinsky 1999). Specific compounds released by phytoplankton also cause allelopathy (von Elert & Jüttner 1997) or build up the

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mucopolysaccharide matrix of colony-forming species (Hellebust 1974). There is evidence that the amount of PER of phytoplankton depends on the species composition (Blaauboer et al. 1982, Lancelot 1983), cell size (Biddanda & Benner 1997), nutrient status (Lancelot 1983, Obernosterer & Herndl 1995), productivity of the system (Cole et al. 1982, Baines & Pace 1991), temperature (Watanabe 1980), and solar radiation (e.g. Mague et al. 1980, Watanabe 1980).

However, solar radiation as a governing factor of PER still remains poorly understood. For instance, Berman (1976) and Coveney (1982) found the highest PER contribution to total primary production (% PER) in light-limited zones, whereas according to Fogg et al. (1965), % PER increases with irradiance, suggesting that photoinhibition stimulates PER. Elevated PER, measured as the percentage of total primary production (P_{tot}), has been found under both extremely high and low irradiances (Mague et al. 1980, Watanabe 1980, Lee & Rhee 1999). In other studies, however, no such relationship between % PER and irradiance was found (Lancelot 1983, Girollo & Vieira 1999).

Since PER can be responsible for a substantial part of the total flux of dissolved organic carbon (DOC) through bacterioplankton (e.g. Cole et al. 1982), the amount of PER released by phytoplankton determines bacterioplankton production in lakes with little macrophyte biomass and reduced input of allochthonous DOC, such as in alpine (Sommaruga et al. 1999) and many Arctic lakes (Laurion et al. 1997, Ellis-Evans et al. 2001). Therefore, factors like radiation (photosynthetically active radiation [PAR] and ultraviolet radiation [UVR]) controlling primary production and extracellular release of photosynthesized carbon may influence bacterial utilization of PER and consequently the whole food web (Rae & Vincent 1998) and should gain attention especially with respect to global change. For Arctic and alpine regions, drastic impacts of global warming are predicted (Beniston et al. 1997), leading, for instance, to an earlier melting of the ice cover (Livingstone 1997), and consequently to a prolonged exposure to radiation. Furthermore, lakes of elevated latitudes and altitudes are mostly affected by increasing UVR (Blumthaler et al. 1992, Vincent & Pienitz 1996). The role of UVR on PER has only recently received attention (Pausz & Herndl 1999, Carrillo et al. 2002).

Within the water column, PER contributes to the DOC pool, which, in turn, determines the transmission of solar radiation in aquatic ecosystems (e.g. Scully & Lean 1994, Laurion et al. 2000). Compared to light attenuation of allochthonous DOC, the attenuation of PER is low because it contains much less highly absorbing chromophoric dissolved organic matter (CDOM; McKnight et al. 1994). However, the attenua-

tion by PER could be relevant in low DOC lakes (Sommaruga & Augustin 2006). Recently, DOC low in aromatic compounds was found to increase its light absorbing capacity during exposure to solar radiation (Reche et al. 2001, Reitner et al. 2002).

The present study was carried out to investigate the influence of PAR and UVR on planktonic primary production, on PER production, and on the utilization of PER by bacterioplankton in an alpine lake and 2 Arctic lakes. Carbon fluxes through phyto- and bacterioplankton as influenced by irradiance (PAR, UVR) were estimated over a period of 15 mo both *in situ* and under laboratory conditions in the Alps and during summer in the Arctic.

MATERIALS AND METHODS

Study sites. Gossenköllesee (GKS) is a small lake (area: 0.017 km², maximum depth: 9.9 m) located above the timber line (2417 m above sea level) in the Central Alps, Austria (47°13'N, 11°01'E), and is ice covered for about 8 to 9 mo (see Sommaruga & Augustin 2006 for details). Sampling was performed on 8 occasions between May 1999 and July 2000. The 2 Arctic lakes are situated on the Taymir Peninsula (Siberia, Russia) and were sampled in July 2000. The unnamed lake (LI, 70°17.4'N, 88°30.7'E) has an approximate area of 0.025 km², a maximum depth of 6 m, and was ice-free during the investigation period. It is located at the forest-tundra zone with southern shrubby tundra and larch forest. Lake Nyagamy (NYA, 72°42'N, 88°20'E) was still covered with 1 to 1.9 m of ice during sampling, but this lake usually loses its ice cover during summer (T. Walasova pers. comm.). NYA is a large lake (48 km²) of unknown depth, surrounded by typical tundra with mesic graminoid herbaceous vegetation.

Samples were collected with a 1.5 l Ruttner bottle, either from a boat or from the ice. Samples in GKS were collected from 3, 5, and 7 m depth at the deepest part of the lake. In LI and NYA, sampling depths were 3 and 2.5 m, respectively.

Experimental design. To estimate *in situ* primary production in GKS, samples of 3, 5, and 7 m (in triplicate and 1 dark control bottle) were incubated in 100 ml glass bottles at the depth of collection for 5 h.

To test whether PER is a light-dependent process, time courses of primary production were performed 3 times in GKS (0.5 to 10 h incubation) and once in each of the Arctic lakes (6 to 24 h incubation). Samples of 3 m depth were exposed in glass bottles continuously to surface radiation or 3 h (GKS) or 6 h (LI, NYA) to surface radiation and subsequently to the dark, respectively. Primary production fractionated as de-

scribed below was estimated at several time intervals (duplicate samples each). These experiments also provide information on the distribution of phyto- and bacterioplankton within the size classes used for particulate primary production.

For the radiation experiments with PAR performed 8 times in GKS, duplicate samples in glass bottles (sampling depth: 3 m) were incubated at the lake surface in a tray for 6 h. There, each bottle was covered by different layers of wire netting to reduce incoming irradiance to 30, 5, 2.5, and 1% of surface irradiance. Two additional samples were exposed to full sunlight (100% of surface irradiance).

In July 2000, additional primary production measurements were performed in the presence of UVR to test the effects of UVR on photosynthesis and PER. Triplicate samples in quartz (UVR) or glass bottles (PAR) were incubated to full sunlight for 3, 6, and 10 h in GKS. The same experiments with incubations of 6, 18, and 24 h were performed in the Arctic lakes.

Primary production, PER, and phytoplankton biomass. Primary production was measured using the ^{14}C -method (Parsons et al. 1984). Samples were incubated with 1 μCi ^{14}C -sodium bicarbonate (specific activity 55 mCi mmol^{-1} , American Radiolabeled Chemicals) in either 100 ml glass bottles for the experiments with PAR (*in situ* measurements, radiation experiments) or in 100 ml quartz bottles for experiments with UVR (July 2000). In each experiment, 2 dark control bottles were included.

After incubation, 5 ml subsamples were transferred into scintillation vials to estimate P_{tot} . Furthermore, P_{tot} was divided into 3 fractions: a particulate fraction comprising carbon fixed by phytoplankton, a particulate fraction comprising PER incorporated by bacterioplankton ($P_{\text{part 1}}$, $P_{\text{part 2}}$), and the dissolved fraction (PER; Table 1). These fractions were determined by serial filtration (pressure <100 mbar) as mostly applied for primary production fractionation (e.g. Carrillo et al.

2002, Descy et al. 2002). There, 95 ml of the sample were filtered through 1.2 μm ($P_{\text{part 1}}$) and 0.2 μm ($P_{\text{part 2}}$) polycarbonate filters (Millipore Isopore RTTP and GTTP filters). Initially, parallel filtration was also performed. Two different samples were filtered onto 1.2 and 0.2 μm pore size polycarbonate filters, respectively, and the $P_{\text{part 2}}$ was calculated as the difference. The results of these 2 methods did not significantly differ; therefore, serial filtration was used for all experiments. Before September 1999, primary production was only partitioned into particulate carbon (>0.2 μm) and PER (<0.2 μm). Filters were rinsed with GF/F filtered lake water and placed into scintillation vials for radioassays. Before rinsing, 5 ml of the filtrate representing PER were transferred to separate scintillation vials. To the scintillation vials, 100 μl 1 N HCl was added and the vials were left open for 24 h to remove inorganic carbon (Lignell 1992). Before the analysis, 5 ml of scintillation cocktail (Canberra Packard, Ultima Gold) were added to the filters and 10 ml to the liquid samples. Radioactivity was measured in a liquid scintillation counter (Canberra Packard, TriCarb 2000) after 10 h. Quenching was corrected by the external standard ratio. For calculation, the disintegration per min (DPM) values of the dark samples were subtracted from the solar radiation-exposed samples. To calculate primary production, the formula given by Wetzel (1995) was used. Total dissolved inorganic carbon (DIC) was calculated from the alkalinity and pH measurements.

PER was also calculated by subtracting the particulate fractions from P_{tot} (Table 1), since the calculated and the estimated values for PER were in good agreement as tested during the initial period of the investigation.

Chlorophyll (chl *a*) was determined from 1 l samples of each sampling depth (3, 5, 7 m) filtered on 47 mm Whatman GF/F filters. The filters were kept frozen until analysis. Chl *a* was extracted with ethanol (4°C, 24 h). The extract was GF/F filtered and measured fluorometrically (Strickland & Parsons 1972) with a Shimadzu RF 1501 spectrofluorometer. Chl *a* extracted from spinach (Sigma) was used as standard. For the Arctic lakes, chl *a* was extracted with dimethyl sulfoxide (DMSO), and the GF/F filtered extract was measured with a field spectrophotometer (Spectronic mini 20, Bausch & Lomb).

At several dates, parallel samples for chl *a* were filtered through 1.2 μm polycarbonate filters, and the values were compared to the results obtained by the GF/F filters to examine the amount of picophytoplankton passing through the 1.2 μm filter.

Bacterial production and bacterial abundance. Measurements of bacterial production via leucine- (Simon & Azam 1989) and thymidine-incorporation

Table 1. Estimations of the different fractions of primary production

Fraction	Definition
P_{tot}	Total net primary production estimated in the whole liquid sample
$P_{\text{part 1}}$	Particulate primary production, estimated on 1.2 μm filters
$P_{\text{part 2}}$	Particulate primary production <1.2 μm , estimated on 0.2 μm filters
net PER	Calculated PER by subtracting $P_{\text{part 1}}$ and $P_{\text{part 2}}$ from P_{tot}
% net PER	Contribution of net PER to P_{tot}

(Fuhrman & Azam 1980) were performed at the same dates and temperatures as primary production to examine whether $P_{\text{part } 2}$ represents bacteria incorporating PER during the incubation. Triplicate subsamples (10 ml) and 2 formalin-killed blanks were incubated with [^3H]-thymidine (specific activity $84.7 \text{ Ci mmol}^{-1}$, final concentration 10 nmol l^{-1}) or [^3H]-leucine (specific activity 120 Ci mmol^{-1} , final concentration 20 nmol l^{-1}) in the dark at *in situ* temperature for 4 h. Bacteria were filtered onto cellulose nitrate filters (Millipore HA, $0.45 \mu\text{m}$ pore size) and treated with 10 ml ice-cold 5% trichloroacetic acid (Sigma Chemicals) for 10 min. The filters were transferred into scintillation vials, dissolved in 1 ml ethylacetate, supplemented with 5 ml scintillation cocktail, and then radioassayed (see above). Bacterial carbon production was calculated using a conversion factor of $1.1 \times 10^{18} \text{ cells mol}^{-1}$ of thymidine incorporated (Riemann et al. 1987) assuming a cell carbon content of 20 fg cell^{-1} (Bratbak & Dundas 1984) and using a conversion factor of $3100 \text{ g C mol}^{-1}$ of leucine incorporated (Simon & Azam 1989).

Bacterial abundance was estimated by epifluorescence microscopy (Hobbie et al. 1977) on DAPI-stained cells filtered on black polycarbonate filters ($0.2 \mu\text{m}$ pore size). Furthermore, to check how many bacterial cells were retained by the $1.2 \mu\text{m}$ pore size filters, bacterial numbers were also counted in the filtrate of the samples.

Lake water chemistry and solar radiation. Data on surface irradiances at the sampling dates (July 1999 to July 2000) and on DOC and radiation attenuation in GKS in July 2000 were provided by R. Sommaruga. Arctic lake samples for DOC measurements were filtered through pre-combusted GF/F filters into combusted glass vials, acidified with 2 N HCl to pH 2, and

analyzed with a Shimadzu TOC-5000. Surface radiation (PAR) was measured with a Skye quantum sensor. Underwater PAR measurements using a Li-Cor UWQ sensor were made only in NYA. Specific conductivity and pH were measured with electrodes (WTW LF 196 and WTW pH 91).

RESULTS

Algal biomass and *in situ* primary production in GKS

Throughout the water column, chl *a* concentrations ranged from 0.6 ± 0.03 to $3.9 \pm 1.0 \mu\text{g l}^{-1}$ in GKS and varied both with depth and season. During summer, a deep chl *a* maximum was formed ($4.6 \mu\text{g l}^{-1}$ in 7 m), while under ice-cover, the chl *a* maximum was at 3 m depth ($4.9 \mu\text{g l}^{-1}$). Chl *a* was uniformly distributed throughout the water column in May ($0.6 \pm 0.03 \mu\text{g l}^{-1}$) and October ($2.4 \pm 0.2 \mu\text{g l}^{-1}$). At the 3 m depth sampled for the solar radiation experiments, chl *a* concentration increased constantly from $0.6 \mu\text{g l}^{-1}$ in May 1999 to $4.9 \mu\text{g l}^{-1}$ in February 2000 and was low again in May 2000 ($0.7 \mu\text{g l}^{-1}$).

Primary production showed a high seasonal variability in GKS. Under ice cover, *in situ* P_{tot} (normalized to chl *a*) was very low (Fig. 1), ranging between 0.04 ± 0.02 (February 2000) and $0.05 \pm 0.01 \mu\text{g C} (\mu\text{g chl } a)^{-1} \text{ h}^{-1}$ (May 1999). During the open-water period, P_{tot} increased to a maximum of $0.91 \pm 0.02 \mu\text{g C} (\mu\text{g chl } a)^{-1} \text{ h}^{-1}$ in October 1999. In contrast, the contribution of net PER (% net PER) to P_{tot} was highest in May 1999 ($76.9 \pm 3.9\%$) and decreased continuously to $18.2 \pm 2.9\%$ in October 1999 (Fig. 1). The lowest % net PER was estimated in February 2000 ($7.0 \pm 6.5\%$).

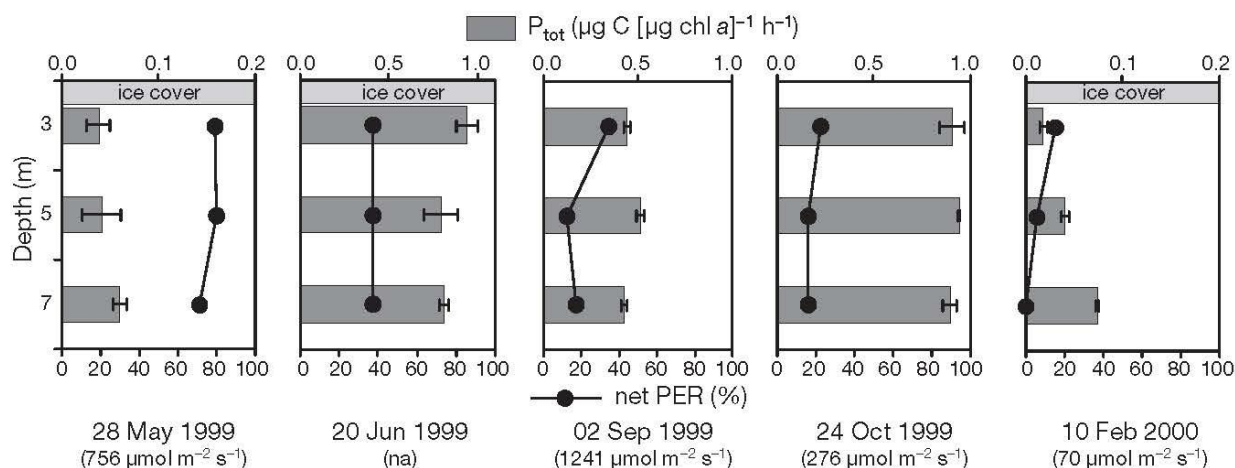


Fig. 1. Seasonal dynamics of *in situ* total primary production (P_{tot} normalized to chl *a*) and the % net photosynthetic extracellular release (PER) at 3, 5, and 7 m in Gossenköllesee (GKS). Note the different scales for P_{tot} in May and February. Mean surface irradiance at each sampling date is given in parentheses. Bars indicate mean $\pm$ SD ($n = 3$), na: data not available

Time course of PER and separation efficiency of phyto- vs. bacterioplankton

The results from the time-course experiment done in October 1999 in GKS suggested that release of photosynthesized carbon was a light-dependent process (Fig. 2). The amount of carbon labeled after 3 h of light exposure further increased in the light but decreased in the dark in both the $P_{part\ 1}$ and the PER fraction. $P_{part\ 2}$, however, slightly increased in the light as well as in the dark (Fig. 2). These results indicate that at least in October, $P_{part\ 2}$ was dominated by heterotrophic bacterioplankton that incorporated PER during the incubation. For the other time-course experiments performed in GKS and the Arctic lakes, the amount of labeled carbon within the $P_{part\ 1}$ and PER fractions always increased during light exposure but decreased or remained stable in the dark. $P_{part\ 2}$, however, showed no clear pattern except that it was always lower in the dark than in the light during the continuous light treatments (results not shown).

Additionally, on several sampling dates, chl *a* and bacterial numbers were estimated in the filtrate following filtration through 1.2 μm pore size filter and compared to the chl *a* concentration and bacterial abundance in unfiltered samples. The size-fractionated chl *a* data showed that, on average, $19.9 \pm 14.5\%$ of the phytoplankton passed the 1.2 μm filter with the lowest amount recorded in May 1999 (5.7%) and the highest in July 2000 (40.2%). From the bacterial cells that varied between 0.3 and $7.7 \times 10^5\ \text{ml}^{-1}$ in GKS, on average $13 \pm 11\%$ were retained by the 1.2 μm filter. Similarly to the size-fractionated chl *a* measurements, the greatest differences (26% retention) occurred in July 2000; however, no differences between the bacterial abundance in the whole sample and the filtrate were observed in May and July 1999.

To examine the contribution of bacterial incorporated PER in $P_{part\ 2}$, this fraction was compared to the bacterial production rates estimated by leucine- and thymidine-incorporation (BP_{Leu} and BP_{TdR}). $P_{part\ 2}$ mirrored BP_{Leu} and BP_{TdR} estimated in GKS and in the Arctic lakes (Fig. 3), although $P_{part\ 2}$ represented commonly higher values. The differences between $P_{part\ 2}$ and the bacterial production estimates, however, were in the same order of magnitude as between BP_{Leu} and BP_{TdR} (Fig. 3). The results obtained with all 3 methods were highly correlated with each other (Spearman rank correlation, $P_{part\ 2}$ and BP_{Leu} : $r = 0.854$, $p < 0.01$; $P_{part\ 2}$ and BP_{TdR} : $r = 0.927$, $p < 0.001$; BP_{Leu} and BP_{TdR} : $r = 0.976$, $p < 0.001$) and highly agreed (Kendall W-test, $p < 0.01$, $n = 8$).

PAR effects in GKS

Depending on their light adaptation, phytoplankton were differently affected by higher than ambient PAR levels (Fig. 4). During the ice-covered season in GKS, the highest primary production was measured at 1 and

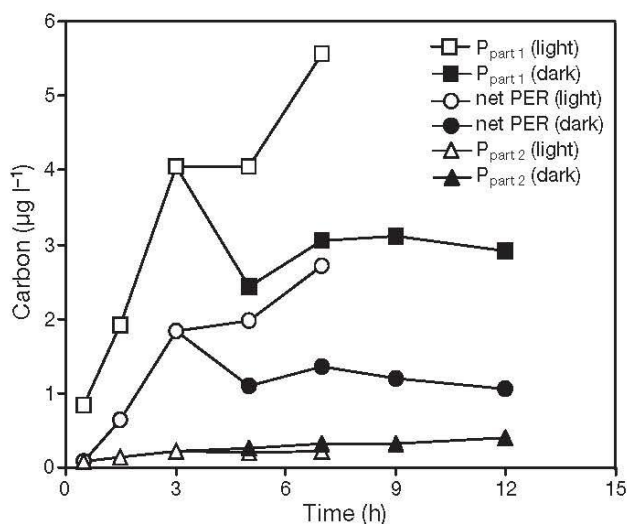


Fig. 2. Time course experiment in GKS performed in October 1999 (samples from 7 m depth). Amount of labeled carbon in the particulate fractions $P_{part\ 1}$ ($>1.2\ \mu\text{m}$) and $P_{part\ 2}$ (0.2 to $1.2\ \mu\text{m}$) and the dissolved fraction (net PER, $<0.2\ \mu\text{m}$) after continuous incubation in the light or in the dark after 3 h of light exposure

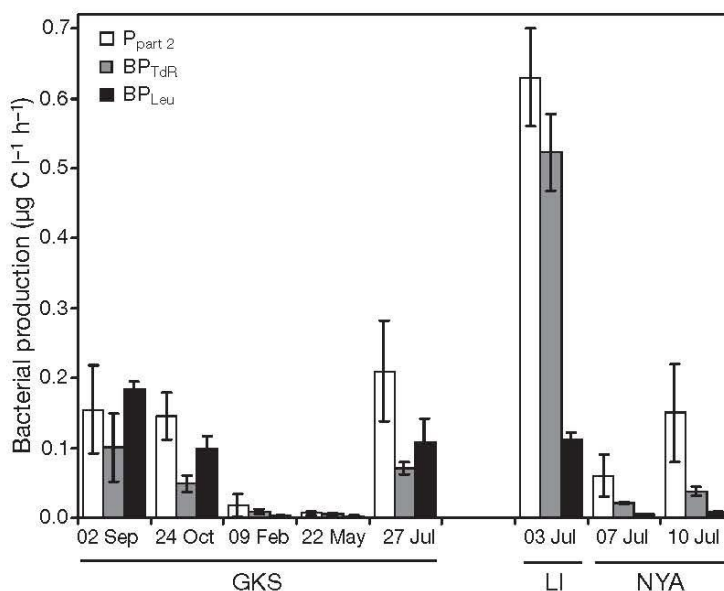


Fig. 3. Comparison of $P_{part\ 2}$ with bacterial production estimated by thymidine (BP_{TdR}) and leucine (BP_{Leu}) incorporation on 5 sampling dates in GKS and in July 2000 in LI and NYA. Bars indicate mean $\pm$ SD ($n = 3$ to 5)

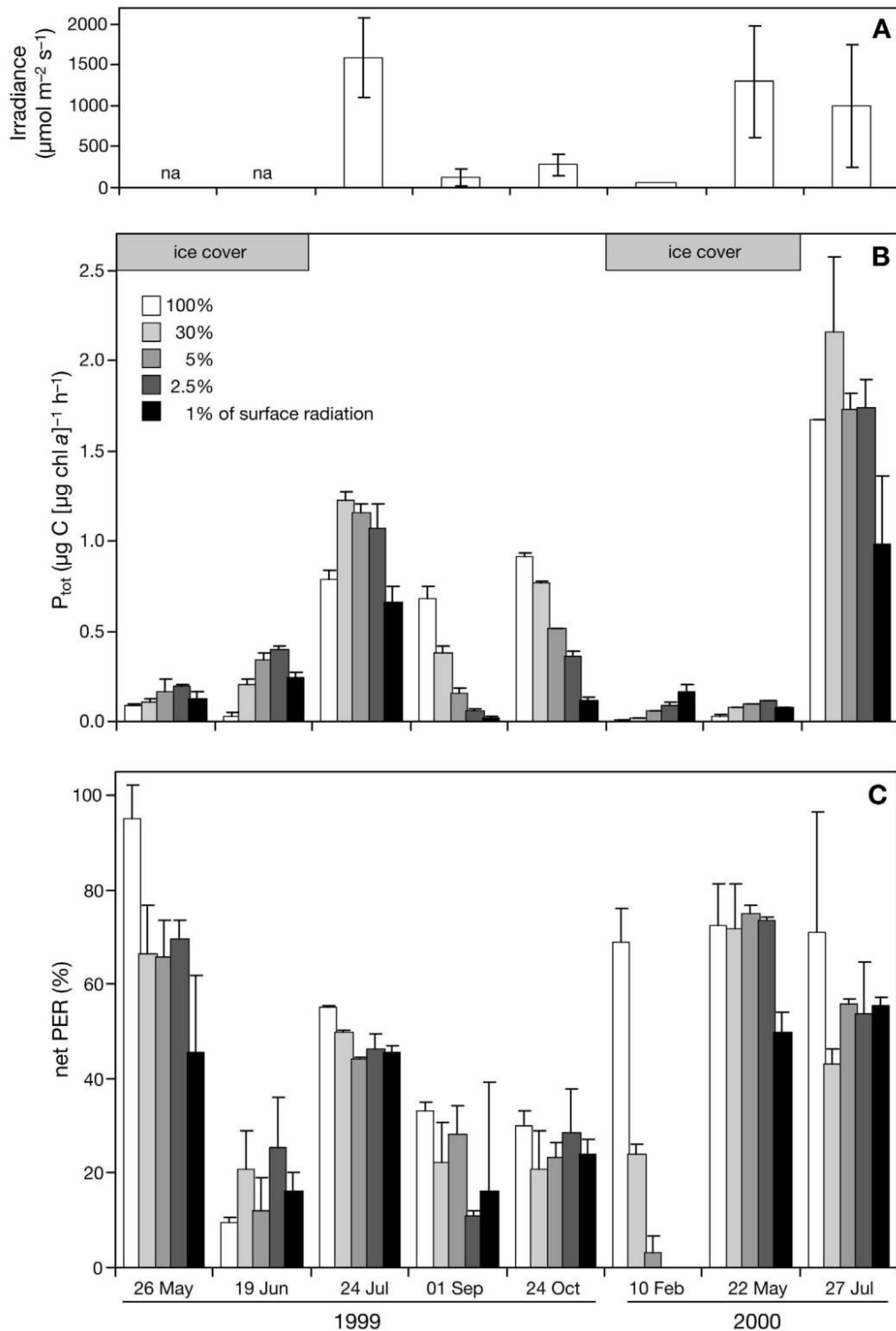


Fig. 4. Annual variability of total primary production (P_{tot}) and the percentage of PER (% net PER) in GKS (samples from 3 m depth) exposed to 100, 30, 5, 2.5, and 1% of surface irradiance. (A) Mean surface irradiance on the sampling dates. (B) P_{tot} normalized to chl *a*; (C) % net PER at the different irradiances. Bars indicate mean $\pm$ SD (A: $n = 29$ to 42 ; B,C: $n = 2$); na: data not available

2.5 % of the surface radiation level, whereas after ice-out with increasing photoacclimatization of phytoplankton, maximum P_{tot} occurred at 30 to 100 % of surface radiation (Fig. 4B). Photoinhibition was observed only in July 1999 and 2000 when ambient solar radiation was very high (Fig. 4A, 1584 and 998 $\mu\text{mol m}^{-2} \text{s}^{-1}$, respectively). The % net PER, however, was almost always highest at the 100 % irradiance level and generally lower at the low light levels (Fig. 4C). The seasonal fluctuation of % net PER showed the same pattern as the % net PER estimated *in situ*. Average % net PER obtained during the radiation experiments decreased from May 1999 ($69 \pm 18\%$) throughout the summer and autumn (with exceptionally low values in June 1999), was lowest in February ($18 \pm 26\%$), and peaked again in May 2000 ($69 \pm 10\%$; Fig. 4C). However, those maximum values of % net PER in May refer to only $0.04 \pm 0.02 \mu\text{g l}^{-1} \text{h}^{-1}$ in terms of absolute amount of PER. On average, 15 times higher rates of PER were observed during the ice-free season, with a maximum in July 2000 ($1.5 \pm 0.3 \mu\text{g l}^{-1} \text{h}^{-1}$).

$P_{\text{part 1}}$ ranged between 0.012 ± 0.01 and $1.04 \pm 0.4 \mu\text{g l}^{-1} \text{h}^{-1}$, and $P_{\text{part 2}}$ ranged between 0.007 ± 0.002 and $0.21 \pm 0.06 \mu\text{g l}^{-1} \text{h}^{-1}$ during the radiation experiments.

Pooling all data of GKS, the fractions of the primary production measurements (i.e. P_{tot} , $P_{\text{part 1}}$, $P_{\text{part 2}}$, net PER, P_{tot} per chl *a*) were highly significantly correlated (Table 2). Furthermore, a significant inverse relationship between % net PER and chl *a* was found (Table 2).

Solar radiation only partially explained the variations in primary production rates in GKS. Net PER production, % net PER, and P_{tot} per chl *a* correlated with irradiance throughout the annual cycle, while the other fractions including P_{tot} did not (Table 2). However, seasonally separated data showed different patterns. During the ice-covered period, the % net PER increased while P_{tot} markedly decreased with increasing irradiance (Fig. 5A). When GKS was ice-free, both P_{tot} and % net PER were positively related to irradiance (Fig. 5B).

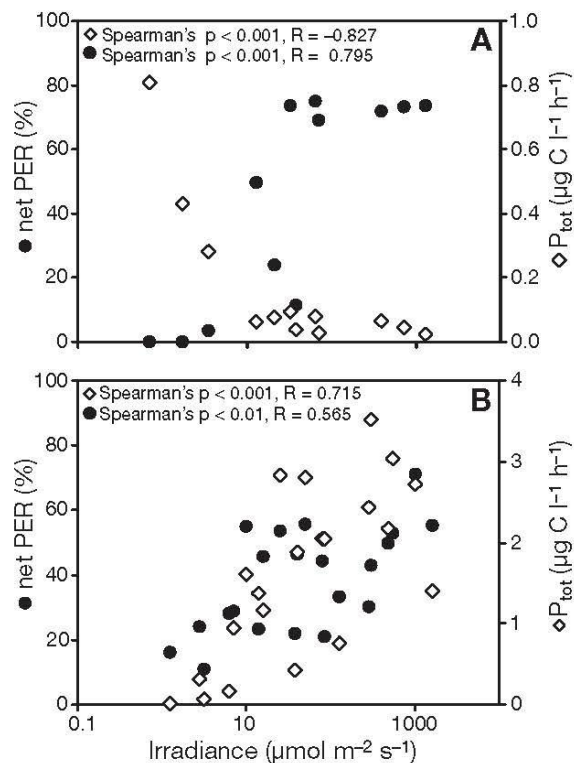


Fig. 5. P_{tot} and % net PER against irradiance. (A) Under ice cover ($n = 12$). (B) During the open-water period ($n = 21$). Note scales on y-axes differ for P_{tot} . Significance levels of the relationships are given in the upper left-hand corner

Cross system comparison and UVR effects

An overview of the physical, chemical, and biological parameters of the investigated alpine and Arctic lakes in July 2000 is presented in Table 3. Unfortunately, UVR data for the Arctic were not available. PAR, however, was comparable among study sites at the time of the radiation experiments (Table 3). The

Table 2. Spearman correlation matrix (r) for all data collected between 1999 and 2000 in Gossenköllesee (GKS). PAR: photosynthetically active radiation; see Table 1 for definition of primary production fractions; Chl *a*: chlorophyll *a*; P_{tot} per chl *a*: P_{tot} normalized to chl *a*. n is given in parentheses. * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$

	PAR	P_{tot}	$P_{\text{part 1}}$	$P_{\text{part 2}}$	Net PER	% net PER	Chl <i>a</i>	P_{tot} per chl <i>a</i>
PAR	–							
P_{tot}	0.347 (32)	–						
$P_{\text{part 1}}$	0.161 (33)	0.956*** (51)	–					
$P_{\text{part 2}}$	0.091 (28)	0.923*** (36)	0.891*** (37)	–				
Net PER	0.556*** (32)	0.862*** (60)	0.731*** (51)	0.789*** (36)	–			
% net PER	0.618*** (32)	–0.099 (60)	–0.193 (51)	0.053 (36)	0.336** (60)	–		
Chl <i>a</i>	–0.281 (33)	0.354** (60)	0.474*** (52)	0.094 (37)	0.052 (60)	–0.601*** (60)	–	
P_{tot} per chl <i>a</i>	0.441* (31)	0.937*** (59)	0.847*** (50)	0.899*** (35)	0.927*** (59)	0.091 (59)	0.044 (26)	–

chl *a* concentrations in the investigated lakes were similar, while primary production normalized to chl *a* was highest in LI and comparable in NYA and GKS. The concentration of DOC as well as the attenuation coefficients (k_d) decreased from LI to NYA and GKS (Table 3). The UVR experiments in GKS and the Arctic lakes were conducted at different time intervals to test whether the duration of exposure influences photosynthesis. In all lakes and radiation treatments (PAR, PAR+UVR), primary production rates declined with increasing time of exposure to solar radiation, with the greatest impact observed in LI (35 % reduction of the 24 h estimates compared to the 6 h estimates). The impact of incubation time, however, did not differ between the different light treatments. Primary production (P_{tot}) did not vary significantly between the PAR and the PAR+UVR treatments in LI but was significantly inhibited by UVR in GKS and NYA (Fig. 6A). Similar results could be observed concerning P_{part1} (Fig. 6B). In NYA and GKS, net PER contributed about half of the P_{tot} , while in LI, primary production was dominated by the particulate fractions (Fig. 6). In all lakes, the % net PER did not greatly vary among the radiation treatments (Fig. 6D). The absolute amount of PER and P_{part2} , however, were significantly reduced in the presence of UVR in GKS (Fig. 6C,E).

DISCUSSION

Phytoplankton and PER

Commonly, primary production is measured taking only the particulate production into account. However, not considering the dissolved primary production (i.e. net PER) might lead to gross underestimations of total primary production (Fogg et al. 1965, Chrost & Faust 1983, Marañón et al. 2004); in GKS, for instance, P_{tot} would be underestimated by $32 \pm 25\%$. Although it has been intensively studied, PER by algae is still poorly understood (Bertilsson & Jones 2003). During this study, active release of carbon occurred only in the light, increasing the amount of PER during light incubation (Fig. 2). In the dark, however, the amount of labeled PER slightly decreased, indicating that phytoplankton stop exudation when exposed to the dark. The fact that PER was primarily performed by healthy, photosynthetically active phytoplankton cells is also supported

Table 3. Cross system comparison among GKS and 2 Arctic lakes (LI: unnamed lake; NYA: Lake Nyagamyia) in July 2000. Physical (temperature, pH, specific conductivity, PAR, UVR, attenuation coefficient k_d), chemical (DOC), and biological (bacterial abundance [BA], primary production per chl *a*, chl *a*) parameters at the sampling dates are presented. na: not available

	LI (03 July 2000)	NYA (10 July 2000)	GKS (27 July 2000)
Temperature (°C)	8.1 ± 0.2	1.7 ± 0.2	9.1 ± 1.2
pH	6.8	6.6	6.9
Specific conductivity ($\mu S\ cm^{-1}$)	33.5	44.0	34.4
PAR ($\mu mol\ m^{-2}\ s^{-1}$)	708 (670–1000)	831 (210–1890)	663 (11–2417)
UVA ($W\ m^{-2}$)	na	na	7.38 (0.17–25.5)
UVB ($W\ m^{-2}$)	na	na	2.47 (0.03–8.6)
k_{dPAR} (m^{-1})	1.3 ^a	0.5	0.04 ^a
k_{d380} (m^{-1})	6.6 ^a	2.4 ^a	0.13
k_{d320} (m^{-1})	15.4 ^a	5.8 ^a	0.25
DOC ($mg\ l^{-1}$)	5.9	2.5	0.5
Primary production ($\mu g\ C\ [\mu g\ chl\ a]^{-1}\ h^{-1}$)	3.3 ± 0.8	1.7 ± 0.4	1.9 ± 0.2
BA ($\times 10^5\ cells\ ml^{-1}$)	14.7	9.0	4.3
Chl <i>a</i> ($\mu g\ l^{-1}$)	1.4 ± 0.7	0.6 ± 0.4	1.5 ± 0.3

^aCalculated as power function of [DOC] (Morris et al. 1995)

by the significant relation of PER to P_{tot} (Table 2). Similar results have been reported in other studies (Blaauboer et al. 1982, Lancelot 1983, Marañón et al. 2004). However, there are few continuous measurements of PER concentrations under dark conditions (Tilzer & Horne 1979, Mague et al. 1980). The fact that the production of PER was light-dependent suggests that passive diffusion (Bjørnsen 1988), viral lysis (Brussaard 2004), and 'sloppy feeding' by grazers (Lambert 1978) are only of minor importance for PER at the investigated study sites, since these processes most likely would continue in the dark.

Variability of PER in GKS

Net PER was highly variable as determined *in situ* (0 to 80 % of *in situ* P_{tot}) and in the experiments with different radiation regimes (0 to 95 % of P_{tot}). The % net PER obtained in GKS is at the upper end of values reported for oligotrophic lakes (e.g. Nalewajko & Schindler 1976, Tilzer & Horne 1979, Cole et al. 1982) but similar to values estimated in oligotrophic mountain lakes (Reche et al. 1996, Camarero et al. 1999) and in Antarctic and Arctic lakes (Parker et al. 1977, Panzenböck et al. 2000).

In GKS, a clear seasonal trend in the % net PER was detected both *in situ* and for the radiation experiments, with the highest contribution to total production in spring, followed by a decrease during the ice-free sea-

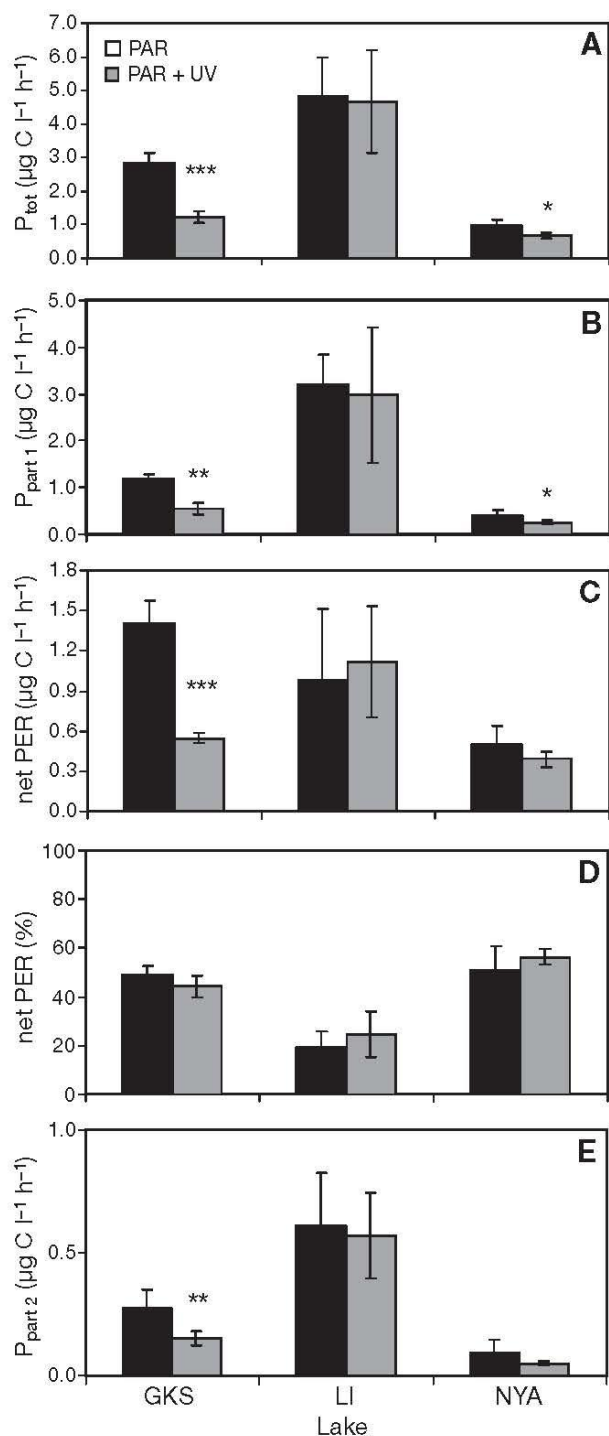


Fig. 6. Fractions of primary production under PAR and PAR + UVR treatments in the 3 lakes (GKS, LI, NYA) in July 2000. (A) Total primary production (P_{tot}); (B) particulate primary production $>1.2 \mu m$ (P_{part1}); (C) net PER; (D) contribution of net PER to P_{tot} (% net PER); (E) particulate primary production 0.2 to $1.2 \mu m$ (P_{part2}). Bars indicate mean $\pm$ SD ($n = 6$ to 9). Significant differences among the light treatments are indicated (t -test): * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$

son and the lowest % net PER recorded in winter (Figs. 1 & 4). In line with several studies (Baines & Pace 1991, Biddanda & Benner 1997, Carrillo et al. 2002), this seasonal pattern shows that % net PER is uncoupled from primary production; the pattern of absolute PER, however, resembles that of P_{tot} throughout the year (Table 2). Moreover, there was a negative correlation between % net PER and chl *a* concentration (Table 2) that has also been noted by other investigators (Berman 1976, Nalewajko & Schindler 1976, Watanabe 1980, Descy et al. 2002) and implies that on a seasonal scale, senescence and autolysis of phytoplankton cells may lead to a generally larger proportion of PER (Wetzel et al. 1972, Descy et al. 2002, Berman & Wynne 2005). Moreover, since phytoplankton influence the light attenuation in the water column (Morris et al. 1995, Laurion et al. 2000), low phytoplankton densities may intensify the effects of environmental stress caused, for instance, by high solar radiation. The seasonal pattern of the % net PER might also be explained by inorganic nutrient availability with nutrient depletion increasing the contribution of PER to P_{tot} (Fogg 1983, Obernosterer & Herndl 1995, Pausz & Herndl 1999).

During this investigation, irradiance was identified as a key factor influencing the PER of phytoplankton in GKS (Table 2). Several studies already reported a higher percentage of PER at elevated irradiances (Fogg et al. 1965, Mague et al. 1980, Fogg 1983) but also at low light levels (Berman 1976, Watanabe 1980, Coveney 1982, Rai 1984). This enhanced PER was often associated with photorespiration producing substantial amounts of glycolate (Fogg et al. 1965, Watanabe 1980). However, conclusions drawn from the % PER can be misleading, because a constant rate of PER at primary production limited by suboptimal irradiances also results in an increased percentage of PER (Mague et al. 1980, Blaauboer et al. 1982, Lee & Rhee 1999, Marañón et al. 2004). This seems not to be the case in GKS, because enhanced percentage of PER at low light limitation was not observed (Fig. 5). Moreover, both the % net PER and the absolute amount of PER significantly correlated with solar radiation intensities (Table 2), supporting the notion that irradiance influences the partitioning of primary production into the particulate and dissolved fraction. Some authors, however, observed no effect of radiation upon PER (Tilzer & Horne 1979, Blaauboer et al. 1982, Lancelot 1983). This lack of consistency in the findings mentioned above represents a major challenge to arrive at a general conclusion regarding the impact of solar radiation on phytoplankton exudation.

In GKS, the extent of this impact depended on the status of algal photoacclimatization. The most pronounced effect of radiation was observed when phytoplankton were dark-adapted (Fig. 5A). For example, in

February, the trend of the % net PER was inverse to that of P_{tot} in the radiation experiments (Fig. 4), and a similar pattern was observed *in situ*, when P_{tot} increased while % net PER decreased with depth (Fig. 1). Here, enhanced carbon release seems to be a consequence of severe light stress as indicated by photo-inhibition and is not due to an overflow of photosynthesized carbon as argued by Fogg (1983). When phytoplankton were acclimated to higher light levels, both P_{tot} and the net % PER increased with increasing irradiance (Fig. 5B), indicating that even when photosynthesis is not light-limited, cells release a large portion of their carbon. This may then be considered an imbalance between photosynthesis and algal growth due to nutrient deficiency (Fogg et al. 1965, Berman-Frank & Dubinsky 1999). Furthermore, phytoplankton may also benefit from these released substances. Azam & Cho (1987) suggested that exudates create microzones around the algae, promoting bacterial growth and consequently nutrient remineralization. The released carbon, at least that part not metabolized by bacteria, also contributes to the DOC pool known to be a source of light attenuation in the water column (Scully & Lean 1994, Morris et al. 1995). Although the absorption of algal-derived DOC is generally low compared to DOC of terrestrial origin (McKnight et al. 1994, Laurion et al. 2000), this DOC could possibly be important in waters with low allochthonous input such as GKS due to the poor vegetation and soil development of the alpine catchments (Sommaruga et al. 1999). Moreover, in-lake processes and solar radiation increase the DOC-specific absorption (Reche et al. 2001). Indeed, a strong correlation between DOC and phytoplankton biomass in GKS indicates phytoplankton as an important carbon source (Sommaruga & Augustin 2006). Although the maximum % net PER occurred under ice in GKS (Fig. 2), the quantity of PER released during the ice-free period was about 15 times higher than during the ice-covered period. The calculation of the contribution of PER to the lake DOC using the mean net PER ($4.5 \mu\text{g d}^{-1}$ assuming a 10 h day length) results in a DOC input of 0.13 mg mo^{-1} . This amount is noticeable compared to 0.41 mg l^{-1} DOC concentration in the lake water in July 2000 and may explain the increase of the DOC concentration between June and August 2000 reported by Sommaruga & Augustin (2006). However, it remains to be shown whether the attenuation of light by PER is of benefit to the algae.

PER as bacterial carbon supply in GKS

PER is a readily available carbon and energy source for bacterioplankton (Cole et al. 1982, Coveney 1982). Therefore, the actually measured amount of PER re-

presents the net PER, i.e. the fraction of PER not incorporated by bacterioplankton during the incubation. In general, bacterial production is estimated by converting the incorporation rate of thymidine or leucine into carbon production, which was also done during this study. The bacterial utilization of PER, however, can also be measured directly by serial filtration with the inherent difficulty of efficiently separating phyto- and bacterioplankton. While in some lakes picophytoplankton are scarce and unimportant in the 0.2 to $1 \mu\text{m}$ size class (Camarero et al. 1999, Carrillo et al. 2002), in some studies the results were corrected depending on the overlap of the size classes (i.e. Reche et al. 1996). The separation of phyto- and bacterioplankton by serial filtration is especially difficult in GKS, where filamentous bacteria can exceed $>1.2 \mu\text{m}$ (Wille et al. 1999), and picophytoplankton passing the $1.2 \mu\text{m}$ filter are sometimes very abundant. $P_{\text{part 1}}$ can be assumed to contain large bacterial cells and $P_{\text{part 2}}$ to contain small algae. The greatest overlap of the size classes ($P_{\text{part 1}}$, $P_{\text{part 2}}$) was observed in July as indicated by the high chl *a* concentration in the $<1.2 \mu\text{m}$ filtrate and the high bacterial numbers retained by the $1.2 \mu\text{m}$ filter. In October, $P_{\text{part 2}}$ appeared to primarily comprise heterotrophic bacteria, since this fraction increased independent of light conditions, in contrast to $P_{\text{part 1}}$, which increased only in the light during the time course (Fig. 2). In comparison to the results obtained by the conventionally used methods, $P_{\text{part 2}}$ was generally slightly higher than BP_{TdR} and BP_{Leu} , which may be related to the appearance of picophytoplankton in this fraction. Interestingly, in lakes with scarce picophytoplankton, the BP estimates obtained by PER incorporation were also up to 1 order of magnitude higher than those by leucine or thymidine incorporation, respectively (Camarero et al. 1999, Carrillo et al. 2002). In the present study, the results based on these 3 methods were significantly correlated and were in the same order of magnitude, indicating that the contribution of bacteria retained by the $1.2 \mu\text{m}$ filter roughly equals the phytoplankton biomass passing through this pore size.

Furthermore, the agreement of $P_{\text{part 2}}$, BP_{TdR} , and BP_{Leu} implies that PER meets the bacterial carbon demand (BCD) in GKS. A similar conclusion was reached by Reche et al. (1996) for another high-mountain lake and by Panzenböck et al. (2000) for a high Arctic lake. In most studies, however, the amount of PER was insufficient to meet the BCD (Chrzanowski & Hubbard 1982, Cole et al. 1982, Sondergaard et al. 1985, Baines & Pace 1991, Descy et al. 2002). Assuming that $P_{\text{part 2}}$ represents bacterially incorporated PER, then 12 to 80% (mean 37%) of the carbon released during the incubation ($\text{net PER} + P_{\text{part 2}}$) and 6 to 16% (mean 10%) of P_{tot} was incorporated into bacterial biomass. As-

suming a bacterial growth efficiency of 20% (Smith & Prairie 2004), 10 to 95% (mean 58%) of the gross PER is channeled through bacteria, corresponding to 25 to 48% (mean 34%) of gross P_{tot} . Calculating these carbon pathways by BP_{TdR} , 2 to 35% (mean 9%) of P_{tot} was incorporated into bacterial biomass. Assuming a bacterial growth efficiency of 20%, 10 to 73% of gross P_{tot} (mean 28%) is channeled through bacteria (based on BP_{TdR}). These carbon flux estimates are within the range reported in the literature (Cole et al. 1982, Chrost & Faust 1983, Sondergaard et al. 1985, Camarero et al. 1999).

This also implies, however, that frequently a substantial portion of the PER is not immediately incorporated into bacteria in GKS (on average 63% of total PER) due to other growth-limiting factors such as low temperatures or UVR (Sommaruga et al. 1997). This carbon remaining in the water column may influence the quantity and quality of the lake DOC (see above).

Cross system comparison

The values of the biological parameters observed in LI and NYA are typical for Arctic lakes, whereas the primary production rates in LI range among the highest values reported for lakes of similar latitude (Markager et al. 1999, Hobbie et al. 2000, Panzenböck et al. 2000, Ellis-Evans et al. 2001, Laybourn-Parry & Marshall 2003), even using only the particulate primary production for comparison, since in most of these studies PER was not included in the primary production measurements. In the present study, carbon fixation (P_{tot}) would be underestimated by 21% in LI and by 51% in NYA if only the particulate fractions were considered. Thus, similar to the proportions in GKS in summer, net PER comprised about half of the P_{tot} in NYA (Fig. 6D). In LI, the % net PER was much lower, likely due to the higher number of bacteria effectively incorporating PER during the incubation (Fig. 6E). Assuming that $P_{\text{part 2}}$ primarily comprises bacterial fixed PER, about 37 and 15% of totally released PER or about 13 and 9% of P_{tot} in LI and NYA, respectively, were incorporated by bacteria. Similarly, BP_{TdR} accounted for 34 and 7% of total PER and for 11 and 4% of P_{tot} in LI and NYA, respectively. Taking the amount of respired PER into account, the carbon flux to bacteria was about 42 and 33% of gross P_{tot} calculated by $P_{\text{part 2}}$ and about 38 and 16% based on BP_{TdR} in LI and NYA, respectively.

These values also stress the importance of including already metabolized PER into primary production measurements; they are comparable to the carbon flux estimates in GKS (see above) and show that BCD can

be met by PER in the investigated Arctic lakes, again indicating the importance of PER for the bacterioplankton carbon and energy demand.

UVR effects and ecosystem implications

UVR contributes substantially to photoinhibition (Helbling et al. 1992, Milot-Roy & Vincent 1994). UVR inhibition is likely greater in cold waters, since enzymatically controlled repair mechanisms in cells are temperature-dependent in contrast to the photochemical damage by UVR (Milot-Roy & Vincent 1994, Doyle et al. 2005). In the present study, primary production was substantially reduced in the presence of UVR in GKS (56% reduction of P_{tot}), followed by NYA (30% reduction of P_{tot} ; Fig. 6A). The extent of the UVR-mediated inhibition is inversely related to the DOC concentration in the investigated lakes (Table 3). In fact, DOC concentration was found to be the main predictor of UVR attenuation in lakes (Scully & Lean 1994, Morris et al. 1995), whereas the proportion of the CDOM was determined to be primarily responsible for the UVR-absorbing property (Laurion et al. 1997, 2000). Autochthonous sources provide DOC of lower aromaticity than terrestrial-derived DOC (Laurion et al. 2000, Reche et al. 2001, Sommaruga & Augustin 2006), which may explain the high impact of UVR in GKS (Fig. 6). In contrast, in LI, where UVR exhibited no significant impact on primary production (Fig. 6), the DOC concentration was very high compared to other Arctic lakes (Laurion et al. 1997, Panzenböck et al. 2000, Ellis-Evans et al. 2001). Moreover, this DOC is likely to be dominated by CDOM derived from the terrestrial surroundings with thawing permafrost soil and forest tundra vegetation as indicated by the yellow color of the lake water.

Considering the UVR impact on primary production, it is reasonable to assume that the carbon flux to bacteria via PER is also affected. In GKS, net PER is highly reduced in the presence of UVR (61% reduction), although % net PER did not differ among the PAR and PAR+UVR treatments (Fig. 6C,D). This agrees with Pausz & Herndl (1999), but contrasts to the findings of Carrillo et al. (2002), who reported a higher amount and a higher percentage of PER under elevated UVR conditions. The UVR-mediated reduction of $P_{\text{part 2}}$ averaged 45% in GKS and 48% in NYA (Fig. 6E). Assuming $P_{\text{part 2}}$ primarily comprises bacteria, this could be the result of direct UVR-induced inhibition of bacterioplankton (Herndl et al. 1993, Sommaruga et al. 1997) or due to indirect effects, as there is a lower amount of PER available for bacteria that can become less bioavailable upon exposure to solar radiation (Pausz & Herndl 1999, Obernosterer et al. 2001). This

reduced carbon flux to the microbial loop with likely cascading effects to higher trophic levels (Rae & Vincent 1998) might be especially important in the investigated lakes, since Arctic and alpine regions are thought to experience increased UV-B radiation (Blumthaler et al. 1992, Vincent & Pienitz 1996). However, since global warming is believed to increase inputs of allochthonous DOC and consequently radiation attenuation in high altitude and latitude lakes (Sommaruga et al. 1999, Pienitz & Vincent 2000), this process may compensate the negative impact of UVR to a certain extent. Therefore, a description of future scenarios under the impact of global change remains difficult.

Since underwater light measurements were not possible in LI and in the UVR-wavelengths in NYA, the attenuations coefficients (k_d) presented in Table 3 were partly estimated from the DOC measurements applying the equation of Morris et al. (1995). The calculated k_{dPAR} (0.50) for NYA corresponded to the measured k_{dPAR} (0.54) obtained in NYA. Moreover, the DOC concentrations in the Arctic lakes were well above 2 mg l⁻¹, a range for which this equation seems to provide realistic K_d values (Laurion et al. 1997, Sommaruga et al. 1999). Comparing the investigated lakes, UVR and PAR penetration was greatest in GKS among the most transparent lakes reported in the literature (e.g. Morris et al. 1995, Laurion et al. 2000). The depth at which UV-B₃₂₀ radiation, for instance, was attenuated to the 1% level of incident intensity ($z_{1\%}$) was 18.3 m in GKS on 27 July 2000, which means that all of the phyto- and bacterioplankton present in the water column were exposed to high UVR on this date. In contrast, the k_d values for the Arctic lakes (Table 3) were at the upper end of ranges reported for Arctic lakes (Laurion et al. 1997, Markager et al. 1999, Ellis-Evans et al. 2001), but well within the values reported for subarctic and temperate lakes (Scully & Lean 1994, Laurion et al. 1997). Thus, the $z_{1\%}$ of UV-B₃₂₀ ranged between 0.3 m in LI and 0.8 m NYA on the sampling date, indicating that in both Arctic lakes, UV-B is completely attenuated within the upper 1 m of the water column.

In conclusion, the phytoplankton in GKS were found to increase the contribution of net PER when exposed to higher irradiances, whereas enhanced PER seemed to be (1) a consequence of severe light stress of dark adapted algae and (2) a mechanism uncoupled from photoinhibition during the ice-free seasons, possibly improving the conditions for photosynthesis and algal growth. The greatly varying % net PER (*in situ* 0 to 80% of P_{tot}) was inversely related to chl *a*. On average, more than half of the released carbon was not used by bacteria and may be an important contribution to the DOC in the water column in GKS. In the Arctic lakes,

% net PER ranged between 21 and 51 % in July. In all lakes, PER seems to fulfill the BCD. While % net PER was not affected by UVR, primary production and PER were suppressed by UVR dependent on the DOC concentration in the investigated lakes, with the greatest effect observed in GKS (56% reduction of P_{tot} , 61% reduction of PER). Thus, DOC-poor high altitude lakes appear more sensitive to UVR radiation and its predicted changes than high-DOC Arctic lakes.

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5 Seasonally varying effects of temperature on bacterial production and growth characteristics in alpine and Arctic lakes



Lake Nyagamia, Taymir Peninsula, Siberia (M. Panzenböck)



Meandering river, Taymir Peninsula, Siberia (M. Panzenböck)

Abstract

Temperature and resources in lakes of cold regions are likely to increase due to ongoing global warming, but at the present the interaction of these two factors in influencing the microbial metabolism is controversially discussed. To examine their relative importance in regulating bacterial production, the effect of experimentally modified temperatures (0-30°) on ^3H -leucine incorporation (Leu_{inc}) as a proxy for protein production and ^3H -thymidine incorporation (TdR_{inc}) as a proxy for cell production was estimated during a complete annual cycle in an alpine lake. While Leu_{inc} responded more strongly and constantly to temperature stimulation up to 25°C indicating continuous temperature limitation of bacterial protein production, TdR_{inc} increased with temperature only during the ice-free season with significantly higher primary production. This lack of thermal response during the ice-covered season suggests resource limitation of cell reproduction then. At 30°C both incorporation rates declined; TdR_{inc} even frequently levelled off between 15 and 25°C but was relatively higher at low temperatures and its optimum temperature correlated with ambient water temperature. This indicates bacterial adaptation to the prevailing cold conditions enabling reproduction to maintain population size. With rising temperatures, however, bacterial protein production increasingly exceeded cell production. The threshold for bacteria to switch from primarily cell to biomass production was at ~24°C during ice-coverage but at ~7°C during the ice free period likely supported by higher resource levels. Thus, higher temperatures as well as improved resource availability enhanced protein synthesis to the disadvantage of cell production. At each incubation temperature, Leu_{inc} and TdR_{inc} were higher during the ice-free period than during ice-coverage indicating improved resource conditions to compensate negative temperature effects to a certain extent. The stimulating effect of substrate was highly pronounced at temperatures > 5°C while in the temperature range between 1 and 4°C temperature exerted the most pronounced effect on bacteria ($Q_{10} = \text{av } 7.6$). Accordingly, the relative importance of temperature and substrate in controlling bacterial growth changed with increasing temperature. Similar responses of bacterial production and investment strategies to temperature were observed in two Arctic lakes investigated during summer highlighting that the observed growth pattern in relation to temperature and resources is a general strategy of bacterioplankton of low temperature lentic systems and strengthening the argument that bacterially mediated biogeochemical cycles in high altitude and high latitude lakes are particularly susceptible to thermal forcing due to global change.

Introduction

Bacteria are a crucial component of aquatic ecosystems as remineralizers but also transformers of dissolved organic carbon (DOC) into bacterial biomass. Since bacteria are effectively grazed by protozoans (Sherr and Sherr 1994), they represent an important link to higher trophic levels (Azam et al. 1983). Thus, environmental factors that affect bacterial growth may influence the whole food web (Rae and Vincent 1998). This could be especially relevant in intensely environmentally controlled ecosystems like high latitude and high mountain lakes. The response of their biocoenoses to climate warming will largely depend on how microbial processes are affected by changes in temperature and nutrient fluxes and how microbes are able to react in terms of adaptation (Wallenstein und Hall 2012).

Besides nutrient availability, temperature is considered as strongly influencing bacterial production (Shiah and Ducklow 1994a, Adams et al. 2010), growth rate (Nedwell and Rutter 1994), growth efficiency (Apple et al. 2006, Hall and Cotner 2007, Berggren et al. 2010, Kritzberg et al. 2010), metabolism (Tibbles 1996, Longnecker et al. 2006, Hoppe et al. 2006), nutrient use efficiency (Hall et al. 2009), the community composition (Adams et al. 2010), cell size of bacteria (Wiebe et al. 1992) and the proportion of actively respiring bacteria (Rae and Vincent 1998). Over a broad range of aquatic systems, bacterial production (BP) was found positively related to temperature across a large range (e.g. White et al. 1991, Shiah and Ducklow 1994a, Adams et al. 2010, Berggren et al. 2010). Often, the observed impact of temperature on bacterial growth was greatest in the lower temperature range (Pomeroy and Wiebe 2001, Middleboe and Lundsgaard 2003, Apple et al. 2006, Sand-Jensen et al. 2007, Kirchman et al. 2009, Adams et al. 2010) or was detected only in the temperature range below 12°C (Hoch and Kirchman 1993, Tulongen 1993, Shiah and Ducklow 1994b). This suggests that bacteria in cold waters may be especially sensitive even to small increases of temperature (Wiebe et al. 1992) and that bacterially mediated processes in cold water lakes e.g. in high altitude and high latitudes are likely greatly affected by temperature enhancement (Rouse et al. 1997, Kritzberg et al. 2010) as especially anticipated for these regions under the light of global warming (Vincent and Pienitz 1996, Beniston et al. 1997, Overpeck et al. 1997, Allen et al. 2014).

Various effects on bacterial metabolism such as reduced enzyme activity (Feller and Gerday 2003) or impaired protein synthesis and ribosome activity (Araki 1991, Farewell and Neidhart 1998) can be attributed to low temperatures. Furthermore, temperature seems to affect bacterial growth characteristics such as influencing the bacterial investment into protein versus cell production as estimated by leucine (Leu_{inc}) and thymidine (TdR_{inc}) incorporation,

respectively. Differences in the incorporation of these tracers are often explained as indicative for unbalanced bacterial growth (e.g. Chin-Leo and Kirchman 1988, Franco-Vidal and Morán 2011), however, resource availability and temperature were also detected to have an impact on bacterial growth characteristics (Longnecker et al. 2006, Petit et al. 1999). At present, contradictory results concerning this impact are reported. While some studies showed enhanced leucine:thymidine incorporation ratios ($\text{Leu}_{\text{inc}}:\text{TdR}_{\text{inc}}$) at low temperatures (Shiah and Ducklow 1997, Petit et al. 1999) indicating bacteria favor protein production over cell reproduction at low temperatures, $\text{Leu}_{\text{inc}}:\text{TdR}_{\text{inc}}$ increasing with temperatures has been reported by others (Tibbles 1996, Ranneklev and Baath 2001, Hoppe et al. 2006, Longnecker et al. 2006) demonstrating controversially the predominance of cell reproduction at low temperatures.

Moreover, there is evidence for a complex interaction of temperature and substrate in controlling bacterial growth (Wiebe et al. 1992, Pomeroy and Wiebe 2001, Vrede 2005). For instance, in order to stay active at low temperatures psychrophilic enzymes decrease their structural stability, resulting in the probably unwanted side-effect of lowered substrate affinity (Feller and Gerday 2003). Likewise, low temperatures lead to structural changes of cell membranes (Russell et al. 1990, Chintalapati et al. 2004) resulting in reduced resource affinity and uptake by bacteria (Nedwell 1999). Thus, the capability of bacteria to thermally adapt such as modulating the fatty acid composition in membranes facilitated by phosphorous availability seems to be important for successful resource competition (Hall et al. 2010). It was previously observed that at high resource levels bacteria can overcome growth constraints due to low temperatures (Pomeroy et al. 1991, Wiebe et al. 1993, Adams et al. 2015) or at least compensate temperature limitation to some extent (Felip et al. 1996, Vrede 2005). Controversely, other authors reported that only at higher temperatures bacteria were stimulated by resource enhancement (Shiah and Ducklow 1994a, Autio 1998, Gurung and Urabe 1999, Carlsson and Caron 2001, Kritzberg et al. 2010). Recently, Adams et al. (2015) found that the speed of bacterial response to elevated nutrients levels increased with rising temperatures and that BP responded faster to elevated temperatures than to nutrient enhancement. Thus, substrate availability determines the responsiveness of bacteria to low temperatures (Nedwell 1999, Pomeroy and Wiebe 2001, Vrede 2005, Kritzberg et al. 2010), however, the relative importance of temperature and resources in controlling bacterial growth might differ between various temperature ranges (Wiebe et al. 1993, Kirchman et al. 2005, Vrede 2005) and between nutrient levels (Adams et al. 2015) thus changing seasonally (Shiah and Ducklow, 1994b, Adams et al. 2010, Calvo-Díaz et al. 2014). Therefore, to get an idea of how increasing temperatures affect bacteria under the light of global warming it is necessary

to take in the role of resource supply, too (Kritzberg et al. 2010). Various further effects of elevated temperatures such as increased melting process in the catchments (Hauer et al. 1997, Rouse et al. 1997, Sommaruga et al. 1999) increasing the input of allochthonous material to lakes (Hobbie et al. 1999, Prowse et al. 2006) or reduced snow- and ice-coverage prolonging the growing season (Stone et al. 2002, Prowse et al. 2011), thus, increasing the productivity of the systems (Michelutti et al. 2005, Vincent et al. 2009) suggest that temperature enhancement will be accompanied by an increase of resources.

The aim of this study was to provide information on the effects of temperature increase over a large range on bacterial production and metabolism and to detect possible interactions with resource supply, for instance co-limitation or stimulation of bacteria, to highlight possible impacts of global warming on the microbial community of cold water lakes like alpine and Arctic ones. Of prime importance was (1) to identify the relative importance of temperature and resource supply in stimulating bacterial production, (2) to analyze the influence of temperature and resource supply on bacterial growth characteristics (cell versus protein production) and (3) to verify the sensitivity of bacteria to even small temperature increases in dependence of the temperature range. To address these questions, temperature manipulation experiments were performed with the bacterial communities of an alpine lake in multiple seasons. At temperatures between 0° and 30°C, BP was measured by incorporation of TdR_{inc} as a proxy for cell production (Chin-Leo and Kirchman 1988, Tibbles 1996) and Leu_{inc} as a proxy for protein production (Servais 1995). Contrasting to studies on temperature effects dealing with bacterial isolates (Christian and Wiebe 1974, Nedwell and Rutter 1994, Wiebe et al. 1993) and/or experimentally altered nutrient conditions (Felip et al. 1996, Kirchman and Rich 1997, Autio 1998, Carlsson and Caron 2001), the temperature experiments in this study were performed with natural bacterioplankton communities at seasonal varying ambient substrate concentrations. Since in the investigated alpine lake autochthonous carbon sources predominate (Sommaruga and Augustin 2006, Panzenböck 2007), resource supply was estimated by measuring phytoplankton biomass, primary production and exudates. To test the breadth of applicability of the results I also investigated microbial activity and growth characteristics in two Arctic lakes during a field trip to Siberia in summer.

Materials und Methods

Study sites

The study was carried out between April 1999 and July 2000 at the Gossenköllesee (GKS, 2417 m a.s.l, Central Alps, Austria, 47°13'N, 11°01'E). This high mountain lake covers an area of 0.017 km² and has a maximum depth of 9.9 m. It is ice-covered for about 8-9 months. Maximum summer temperatures in the epilimnion of this dimictic lake range between 11.3°C (Eppacher, 1968) and 15.4°C (Pernthaler et al. 1998). Additional experiments were done with the bacterioplankton of two Arctic lakes at the Taymir Peninsula (Siberia, Russia) in July 2000. One small, unnamed lake LI (70°17.4' N, 88° 30.7' E, area: 0.025 km², maximum depth: 6 m) was ice-free during the investigation, whereas Lake Nyagamia (NYA, 72°42' N, 82°26' E) was still covered by a 1-1.9 m ice sheet in July but regularly becomes ice-free at the end of summer (Walasova, T., pers. comm.). NYA has an area of about 48 km², the maximum depth is unknown. Lake water was collected with a 1.5 L Ruttner bottle at 3, 5, and 7 m depth in the GKS and at 3 m depth in the Arctic lakes, either by boat or through a hole in the ice, and subsequently processed in a lakeside laboratory. During sampling, *in situ* water temperature was measured.

Bacterial abundance, bacterial production and temperature manipulation experiments

From all sampled depths, water samples for estimating bacterial abundance (10 ml) were preserved with formalin (5% final concentration). For counting, the samples were stained with DAPI (4', 6-diamidino-2-phenylindole) for 6 min (Porter and Feig 1980) and filtered onto black 0.2 µm polycarbonate filters (Millipore GTBP, 25 mm diameter). Cells on the prepared samples were counted using a Nikon epifluorescence microscope (Hobbie et al. 1977).

Bacterial production was measured in parallel as tritiated leucine incorporation (Leu_{inc}) (Simon and Azam 1989) and tritiated thymidine incorporation (TdR_{inc}) (Fuhrman and Azam 1980). For GKS, samples collected at 3 m depth were incubated in water baths at different temperatures including the *in situ* temperature. The incubation temperatures ranged between 1 - 4°C (April and May 1999), 1 - 8°C (June 1999), 1 - 25°C (from July 1999 to Aug 1999) and 0 - 30°C (from Oct 1999 to July 2000). In LI, BP was measured only at the *in situ* temperature (8°C) and in NYA at 0°C, 1.5°C and 4°C using ice, lake water (3 m depth) and surficial pool water for incubations in the field. All the incubations were performed in the dark by covering the samples with aluminum foil. Triplicate 10 ml samples and two formalin-killed controls were incubated with either [³H]-thymidine (specific activity 84.7 Ci/mmol⁻¹, final conc. 10

nM) or [^3H]-leucine (specific activity 120 Ci/mmol $^{-1}$, final conc. 20 nM) for 4 h. Preliminary experiments in GKS showed that these concentrations maximized incorporation of both substrates. Samples were not preadjusted to the incubation temperatures because of the small sample volume. Incubations were terminated by filtering the samples onto cellulose nitrate filters (Millipore HA, 0.45 μm pore size) and rinsing 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 pending analysis. Then, filters were dissolved in 1 ml ethylacetate and 5 mL of scintillation cocktail (Canberra Packard, Ultima Gold LLT) were added. Radioactivity was determined with a liquid scintillation counter (Canberra Packard, Tricarb 2000). The disintegrations per minute (DPMs) of the blanks were subtracted from the DPMs of the samples. Bacterial carbon production estimated by Leu_{inc} (BP_{Leu}) was calculated by applying a conversion factor of 3100 g carbon mol $^{-1}$ Leu_{inc} assuming a twofold isotope dilution (Simon and Azam 1989). Bacterial carbon production estimated by TdR_{inc} (BP_{TdR}) was calculated assuming a conversion factor of 1.1×10^{18} cells mol $^{-1}$ TdR_{inc} (Riemann et al. 1987) and a carbon content of 20 fg cell $^{-1}$ (Loferer-Krößbacher et al. 1998). To describe the response of bacteria to a 10°C change of temperature, Q_{10} values were computed as $Q_{10} = (K_1/K_2)^{10/(t_1-t_2)}$, where K_1 and K_2 are tracer incorporation rates at the high (t_1) and the low temperature (t_2).

Primary production, chlorophyll-a and DOC determinations

In GKS and both Arctic lakes, triplicate samples (100 ml) and one dark control were incubated *in situ* at 3 m depth with 1 $\mu\text{Ci mL}^{-1}$ [^{14}C] - sodium bicarbonate (specific activity 55 mCi mmol $^{-1}$, ARC Inc.) for 5 – 6 h. After incubation, unfiltered 5mL-subsamples were filled into scintillation vials for determination of total primary production (P_{tot}). The remaining 95 mL of the sample were gently (suction pressure < 100 mbar) filtered through 1.2 μm and 0.2 μm pore size polycarbonate filters (Millipore GTTP filters, 25 mm diameter) in order to determine particulate primary production. Subsequently, these filters were placed into scintillation vials as well. To filters as well as liquid samples I then added 100 μL of concentrated HCl to remove inorganic [^{14}C], and 5 and 10 mL of scintillation cocktail (Canberra Packard, Ultima Gold LLT), respectively. Samples were radioassayed as described above. The calculation of primary production followed the method of Wetzel (1995). Photosynthetic extracellular release (PER) was calculated by subtracting the particulate fractions from P_{tot} (see Panzenböck 2007 for details).

For chlorophyll-a (chl-a) determination, 1-1.5 L of water sampled at 3 m depth was filtered onto Whatman GF/F (47 mm diameter) filters, which were extracted overnight with 90%

ethanol at 4°C. Extracts were measured fluorometrically using chlorophyll *a* from spinach (Sigma) as standard. In the Arctic lakes, the samples were extracted with DMSO (dimethyl sulfoxide) and measured in a field spectrophotometer (Bausch and Lomb, Spectronic mini 20); chl-*a* estimations followed Parsons et al. (1984). The two methods were in good agreement as tested with samples of GKS.

Arctic lake samples for DOC measurements were filtered through precombusted Whatman GF/F filters into acid-washed and precombusted glass vials, acidified with 2N HCl to pH < 2 and analyzed with a Shimadzu TOC-5000.

Results

Seasonal variability of physical and biological parameters in Gossenköllesee

GKS is thermally stratified during the ice-covered and the ice-free period. During the investigation, thermal mixing occurred in June and October (Fig. 1A). At a depth of 3 m, which was sampled for the incubation experiments, temperature did not exceed 2.6°C on the sampling dates during periods of ice-coverage and varied between 5.3 and 10.4°C on the sampling dates during the ice-free period (Fig. 1A). Bacterial abundance varied little seasonally and between the depth layers ($0.3 - 5.0 \times 10^5$ cells ml⁻¹) with the exception of August 1999, when bacterial abundance was notably higher at 7 m (Fig. 1B). *In situ* bacterial production at 3 m depth ranged between $0.05 - 5.98 \mu\text{g C L}^{-1} \text{ d}^{-1}$ with generally higher BP_{TdR} estimates compared to BP_{Leu} except in September 1999 and July 2000 (Fig. 1C). Excluding the extremely high BP estimates of September, BP_{TdR} and BP_{Leu} correlated significantly with *in-situ* water temperature (BP_{TdR}: Pearson $r^2 = 0.540$, $p < 0.05$, $n = 8$; BP_{Leu}: Pearson $r^2 = 0.835$, $p < 0.001$, $n = 8$) while bacterial numbers did not (Pearson $r^2 = 0.050$, $p > 0.05$, $n = 9$). The ratio between BP_{Leu} and BP_{TdR} (BP_{Leu} : BP_{TdR}) ranged from 0.18 (April 1999) to 1.96 (July 2000) and was positively correlated with *in-situ* water temperature (Pearson $r^2 = 0.843$, $p < 0.001$, $n = 9$). P_{tot} and PER varied over one order of magnitude between the ice-covered period and the ice-free period (Fig. 1D). Significantly higher values during the ice-free period than during ice-coverage were estimated for P_{tot} (t-test: $df = 7$, $t = 3.40$, $p < 0.05$) and PER (t-test: $df = 7$, $t = 2.51$, $p < 0.05$). Chl-*a* concentrations ranging between 0.6 and 4.9 $\mu\text{g L}^{-1}$, however, were not significantly different among the seasons (t-test: $df = 7$, $t = 0.44$, $p > 0.05$).

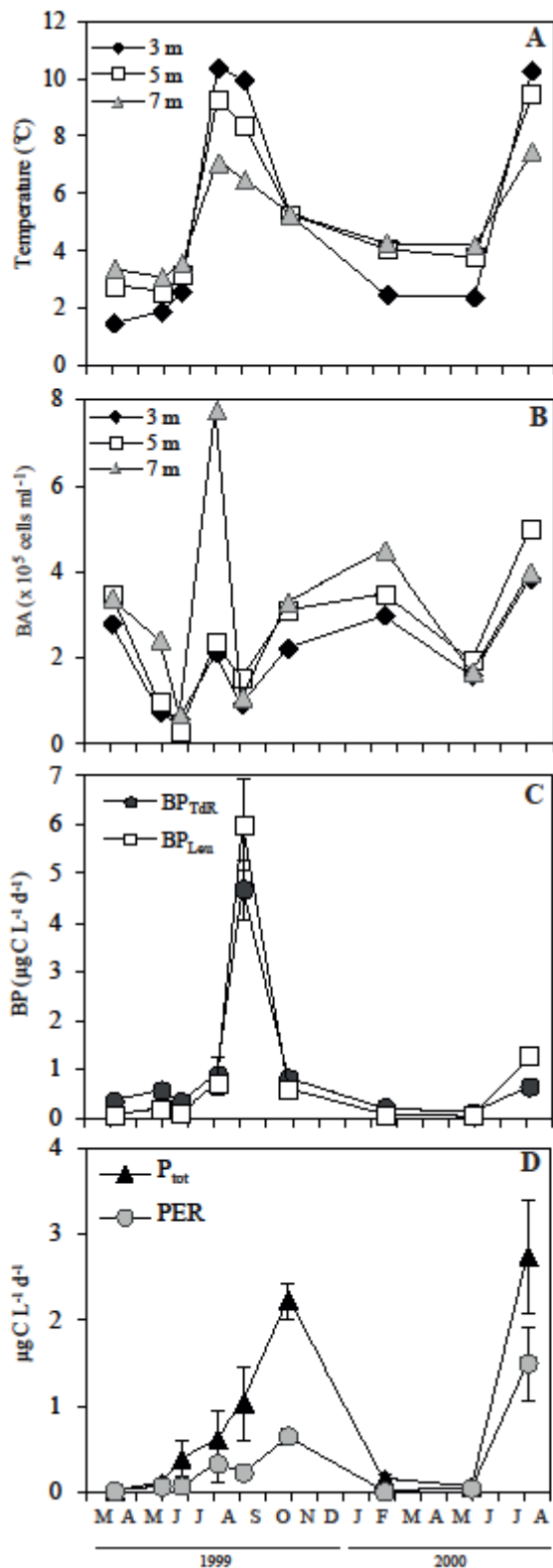


Fig. 1. Seasonal variation of physical and microbial parameters in the Gossenköllesee. A) water temperature and B) bacterial abundance in three depth layers; C) *in situ* bacterial production: BP_{TdR} and BP_{Leu} and D) total primary production (P_{tot}) and photosynthetic extracellular release (PER) at 3 m depth. Mean $\pm$ SD. Error bars are smaller than the associated symbol when not visible.

Temperature manipulation experiments in Gossenköllesee

All Leu_{inc} and TdR_{inc} rates estimated during the temperature manipulation experiments were significantly correlated (Pearson $r^2 = 0.80$, $p < 0.001$, $n = 175$) although their responses to temperature showed different patterns. In all experiments except one, Leu_{inc} increased with temperature up to 25°C , while TdR_{inc} responded to increasing temperatures only during the ice-free period (Fig. 2). Then, however, both Leu_{inc} and TdR_{inc} declined beyond 25°C (Fig. 2A, C and D) whereas in the experiments without thermal response the 30°C values were indifferent from the values at lower temperatures (Fig. 2A and B).

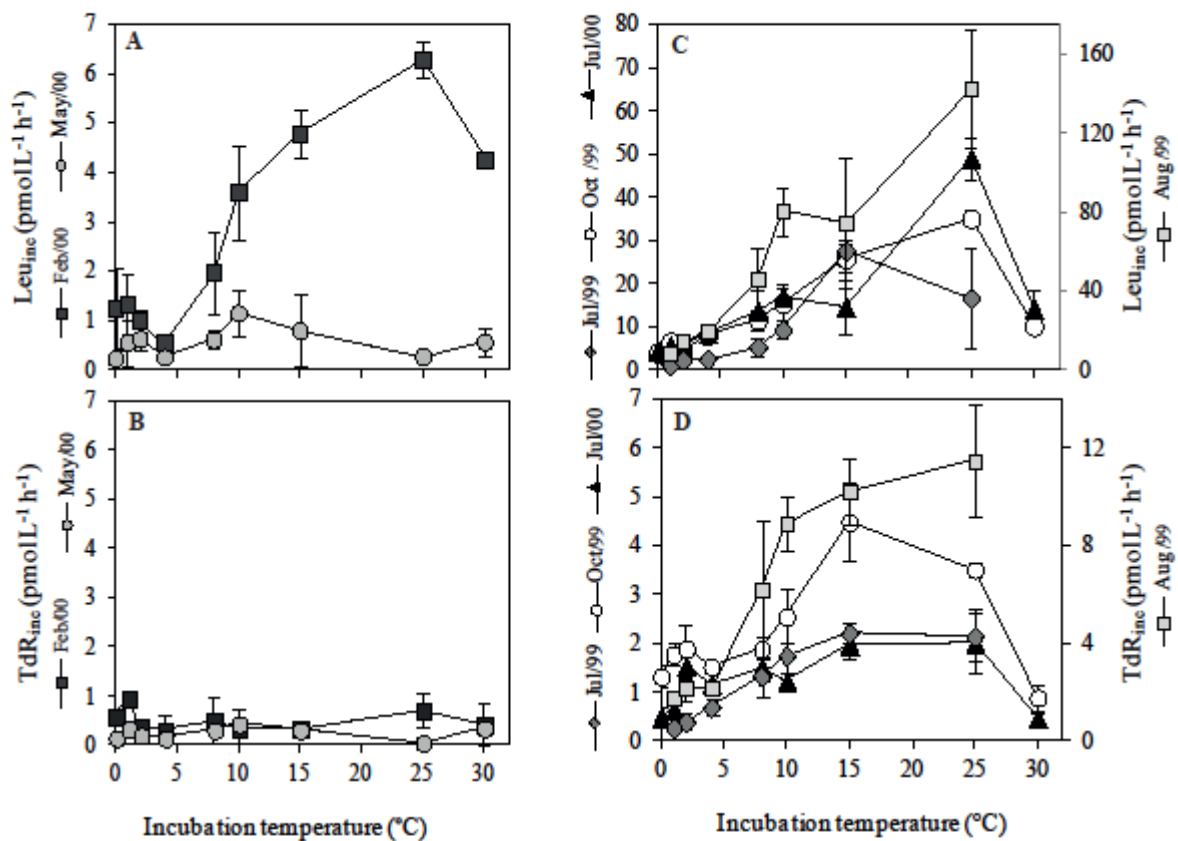


Fig. 2. Tracer incorporation as a function of incubation temperature in GKS. A) Leu_{inc} and B) TdR_{inc} at the sampling dates during ice-coverage; C) Leu_{inc} and D) TdR_{inc} at the sampling dates during the ice-free period. Mean $\pm$ SD ($n = 3$). Error bars are smaller than the associated symbol when not visible. Note that y-scales differ between the graphs and for the tracer incorporation at the sampling dates during the ice-free period.

A linear regression analysis of Leu_{inc} and TdR_{inc} versus temperature excluding the 30°C estimates was done for each experiment and for the seasonally pooled data. While Leu_{inc} correlated significantly with temperature independent of the season, TdR_{inc} correlated with temperature only during the ice-free season (Table 1). Moreover, Leu_{inc} showed significantly higher slopes (normalized to absolute incorporation rates) with increasing temperature (paired

t-test: $df = 8$, $t = 2.34$, $p < 0.05$). In the lower temperature range, however, TdR_{inc} predominated as indicated by the significantly higher y-intercepts of the regression on temperature compared to Leu_{inc} , also normalized to absolute incorporation rates (paired t-test: $df = 8$, $t = -5.03$, $p = 0.001$). The Q_{10} was calculated for four sequential temperature ranges (1–4°C, 4–10°C, 10–15°C, 15–25°C) using the tracer incorporation rates estimated during the ice-free period which positively correlated with temperature (see Table 1) and were presumably unaffected by substrate limitation. The Q_{10} for both, Leu_{inc} and TdR_{inc} decreased from the lower to the upper temperature range (Table 2). Over the whole temperature range, Q_{10} for Leu_{inc} was slightly higher than for TdR_{inc} . The Q_{10} of 1 for TdR_{inc} between 15 and 25°C shows that TdR_{inc} already levelled off at these temperatures while Leu_{inc} declined only at 30°C (Fig. 2C and D).

Table 1. Linear regression statistics of bacterial incorporation of leucine (Leu_{inc}) and thymidine (TdR_{inc}) versus temperature for each experiment and for the seasonally pooled data. ns: not significant.

Month/year	Temperature range (°C)	n	Leu_{inc} (pmoles L ⁻¹ h ⁻¹)				TdR_{inc} (pmoles L ⁻¹ h ⁻¹)			
			Slope	y-intercept	r	p	Slope	y-intercept	r	p
Apr/1999	1 – 4	10	0.619	- 0.232	0.92	< 0.001	0.107	0.498	0.51	ns
May/1999	1 – 8	9	1.10	7.034	0.92	< 0.001	- 0.016	1.70	0.36	ns
June/1999	1 – 8	11	0.213	0.766	0.889	< 0.001	0.031	0.57	0.399	ns
July/1999	1 – 25	19	0.855	1.413	0.671	< 0.01	0.081	0.559	0.791	< 0.001
Aug/1999	1 – 25	23	5.522	3.780	0.919	< 0.001	0.452	1.994	0.859	< 0.001
Oct/1999	0 – 25	26	1.301	3.126	0.971	< 0.001	0.105	1.484	0.768	< 0.001
Feb/2000	0 – 25	23	0.232	0.685	0.918	< 0.001	0.001	0.507	0.028	ns
May/2000	0 – 25	24	0.008	0.522	0.132	ns	- 0.001	0.287	0.054	ns
Jul/2000	0 – 25	26	1.601	1.812	0.911	< 0.001	0.053	0.912	0.712	< 0.001
Ice-free period	0 – 25	95	2.305	2.86	0.59	< 0.001	0.170	1.288	0.46	< 0.001
Ice-covered period	0 – 25	79	0.099	2.12	0.54	< 0.001	- 0.012	0.697	0.17	ns

Table 2. Q_{10} of Leu_{inc} and TdR_{inc} during the ice-free period calculated for four distinct temperature ranges. All regressions used to calculate the Q_{10} ($n=4$) were significant at $p < 0.01$.

Ice-free period		
Temperature range	Leu_{inc} $Q_{10} \pm SD$	TdR_{inc} $Q_{10} \pm SD$
1 – 4 °C	7.8 ± 5.6	7.4 ± 8.1
4 – 10 °C	6.1 ± 3.8	4.6 ± 4.1
10 – 15 °C	3.2 ± 3.8	2.3 ± 0.6
15 – 25 °C	1.75 ± 1.2	1.0 ± 0.1

The temperature at which Leu_{inc} and TdR_{inc} peaked for the temperature manipulation experiments was compared to the ambient water temperature at the sampling depth (T_{amb}) (Fig. 3). At four out of six experiments, this supposed optimum temperature (T_{opt}) for Leu_{inc} was at 25°C and not related to T_{amb} (Pearson $r^2 = 0.067$, $p > 0.05$, $n = 6$). In contrast, T_{opt} for TdR_{inc} significantly covaried with T_{amb} (Pearson $r^2 = 0.729$, $p < 0.05$, $n = 6$) (Fig. 3).

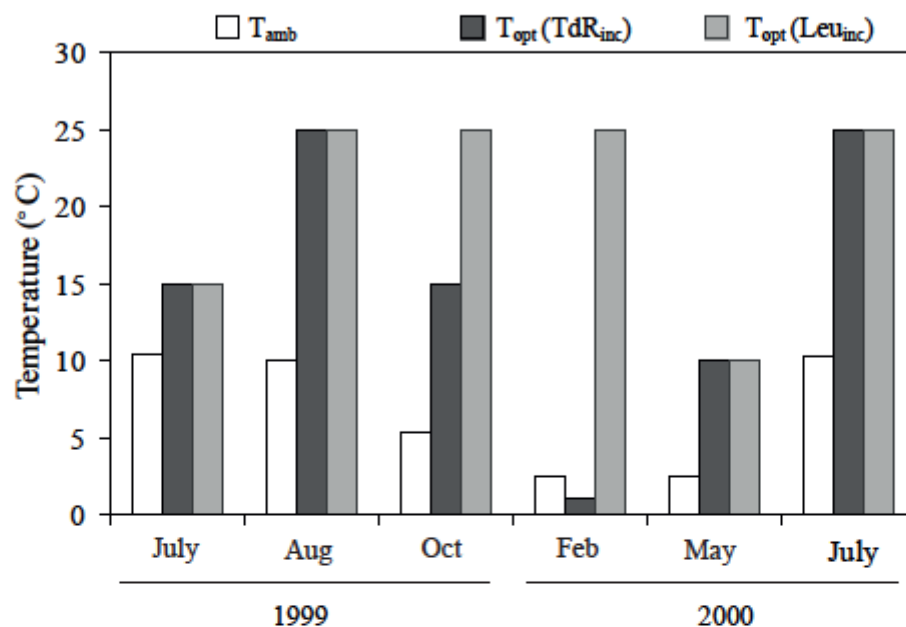


Fig. 3. Annual variation of the optimum temperatures (T_{opt}) for Leu_{inc} and TdR_{inc} and the ambient water temperature (T_{amb}) at 3 m depth in GKS.

For a closer examination of the seasonal effects, the estimates of the temperature-specific tracer incorporation (TI) were averaged across the ice-free and the ice-covered period, respectively, and translated into a ratio of the means ($TI_{ice-free} : TI_{ice-covered}$). At each incubation temperature, mean TI obtained during the ice-free period were higher than during the period of ice-coverage as indicated by ratios > 1 (Fig. 4). Overall, the ratios were significantly higher for Leu_{inc} compared to TdR_{inc} (paired t-test: $df = 8$, $t = 5.09$, $p < 0.001$). $TI_{ice-free} : TI_{ice-covered}$ increased significantly with temperature up to 25°C for both Leu_{inc} (Pearson $r^2 = 0.976$, $p < 0.001$, $n = 8$) and TdR_{inc} (Pearson $r^2 = 0.896$, $p < 0.01$, $n = 8$) and declined again at the upper thermal growth limit of 30°C (Fig. 4).

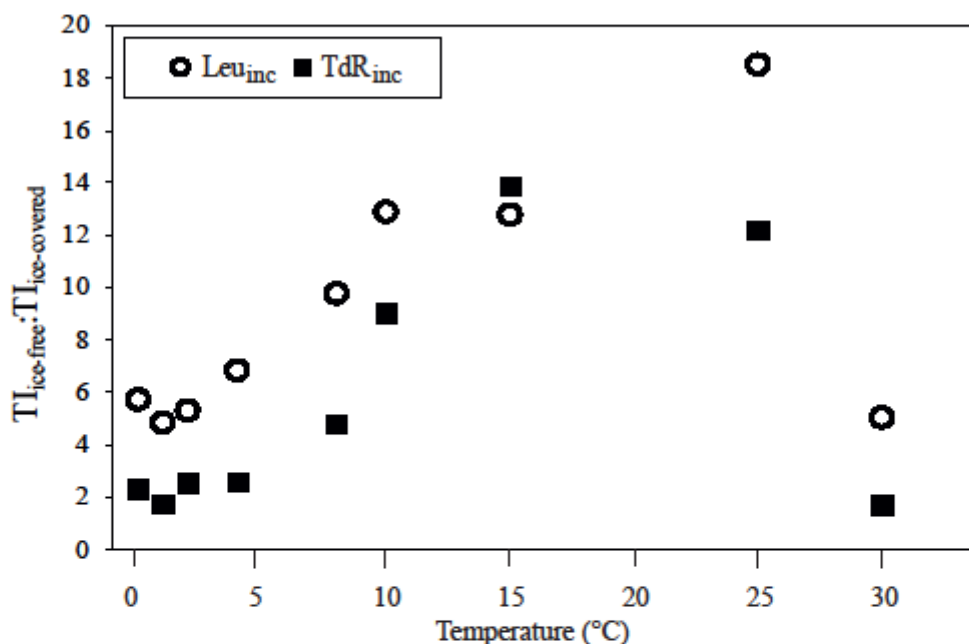


Fig. 4. Ratio of mean Leu_{inc} and TdR_{inc} , respectively, during the ice free period to mean Leu_{inc} and TdR_{inc} during the ice-covered period ($TI_{ice-free} : TI_{ice-covered}$) at each incubation temperature.

The molar $Leu_{inc} : TdR_{inc}$ ratios ranged between 0.33 and 29.7 in the temperature experiments and between 2.4 and 13.9 at *in situ* temperature in GKS. For the following appraisal, the molar incorporation rates were converted into bacterial production and the ratios of BP_{Leu} to BP_{TdR} calculated for each incubation temperature and each experiment. Throughout the seasons, $BP_{Leu} : BP_{TdR}$ increased significantly with temperature indicating that rising temperatures stimulated BP_{Leu} relatively more than BP_{TdR} while BP_{TdR} exceeded BP_{Leu} in the lower temperature range (Fig. 5A and B). The seasonally pooled data showed a steeper temperature dependent slope and significantly higher $BP_{Leu} : BP_{TdR}$ ratios during the ice-free period (t-test: $df = 60$, $t = -4.1$, $p < 0.001$). During ice-coverage, only 13 % of the ratios (estimated between 10 and 30°) were > 1 indicating the predominance of BP_{TdR} then (Fig. 5A) while during the ice-free period, 53 % of the values (also in the lower temperature range)

were > 1 (Fig. 5B). These results with predominating BP_{TdR} at low water temperatures (Fig. 1C) were likely not caused by the conversion into carbon units, since the used theoretical conversion factors are at the lower end for thymidine and at the upper end for leucine compared to empirically derived conversion factors (e.g. Rivkin et al. 1996, Autio 1998, Calvo-Díaz and Moran 2009). Thus, the different responses of BP_{Leu} and BP_{TdR} to temperature manipulation would be even more pronounced if other CFs were used.

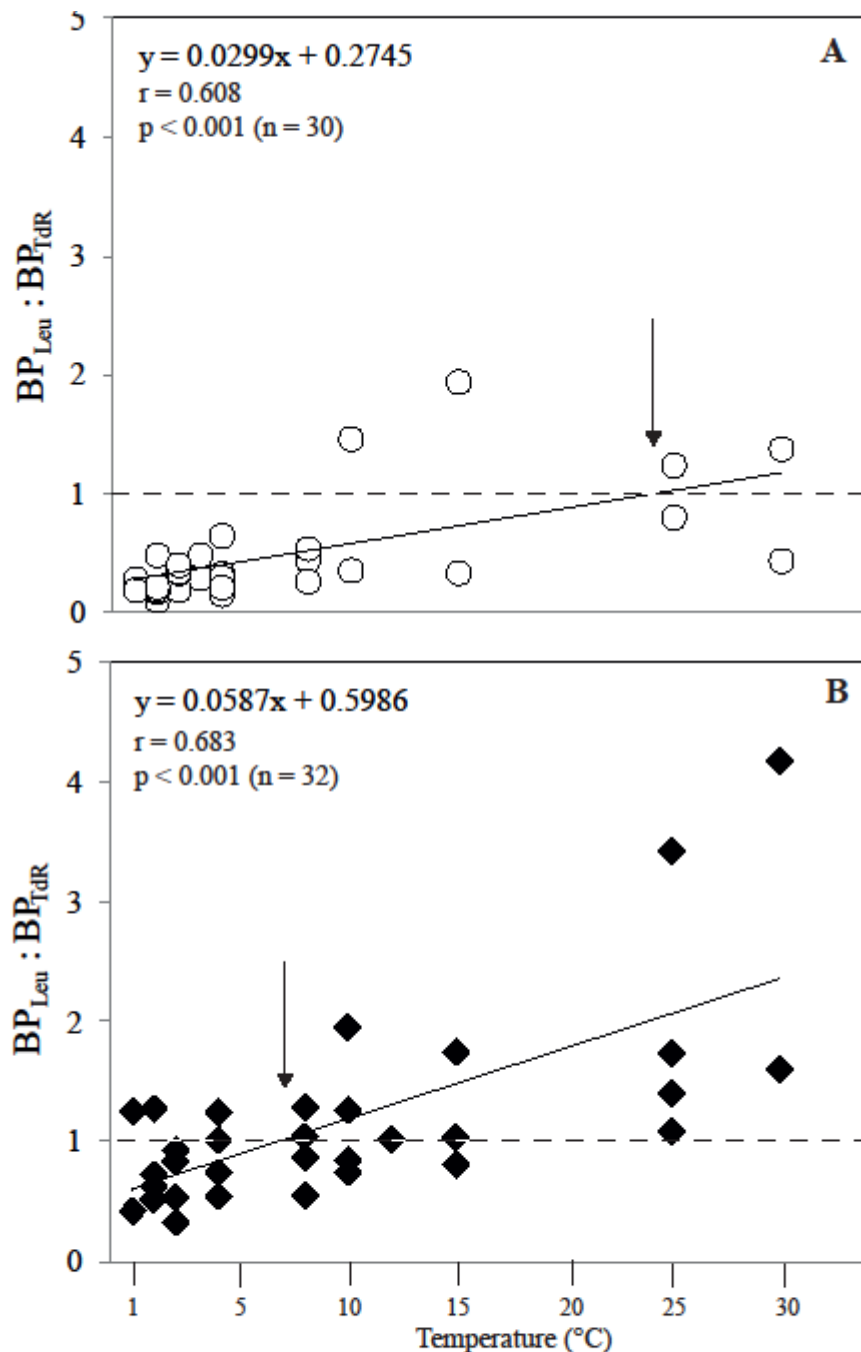


Fig. 5. Ratio of BP_{Leu} to BP_{TdR} versus incubation temperature during A) the ice-covered period and B) the ice-free period in GKS. The dashed line marks the agreement of BP_{TdR} and BP_{Leu} . Arrows mark the temperature at which bacteria switch averagely from cell to protein production.

Physical and biological parameters in the Arctic lakes including temperature effects on BP

The water temperature of LI was comparable to summer temperatures in GKS while in NYA temperature was similar to GKS during winter (Table 3). In LI, primary production (both P_{tot} and PER), bacterial abundance and BP_{TdR} were even higher than in GKS during the ice-free period. In NYA, primary and bacterial production corresponded to the values of GKS estimated during the ice-covered season; bacterial abundance was in the upper range of the values observed in GKS (compare Table 3 and Fig. 1). The bacterial tracer incorporation resulted in a ratio $\text{Leu}_{\text{inc}} : \text{TdR}_{\text{inc}}$ of 0.75 for LI and 1.4 for NYA at *in situ* temperatures (Table 3). The results of the temperature manipulation experiments performed with the bacterial assemblage of NYA showed that both TdR_{inc} and Leu_{inc} increased significantly between 0°C and 4°C (TdR_{inc} : $y = 0.05x + 0.802$, Pearson $r^2 = 0.386$, $p < 0.05$, $n = 12$; Leu_{inc} : $y = 0.01x + 1.10$, Pearson $r^2 = 0.381$, $p < 0.01$, $n = 12$). In both Arctic lakes the calculated BP_{TdR} predominated over BP_{Leu} (Table 3), the $BP_{\text{Leu}} : BP_{\text{TdR}}$ ratios were in the same range as in GKS during ice-coverage and also slightly increased with temperature even within the small temperature range investigated in NYA ($y = 0.01x + 0.1774$, Pearson $r^2 = 0.972$, $p < 0.05$, $n = 3$). The Q_{10} calculated between 0 and 4°C was 1.9 for TdR_{inc} and 3.5 for Leu_{inc} .

Table 3. Summary of biological parameters in the Arctic lakes (unnamed lake: LI, Lake Nyagamia: NYA) in July 2000. T: temperature. P_{tot} : total primary production. PER: photosynthetic extracellular release. Chl-*a*: chlorophyll-*a*. BA: bacterial abundance. Leu_{inc} : molar rate of microbially incorporated leucine; TdR_{inc} : molar rate of microbially incorporated thymidine. BP_{Leu} : bacterial production calculated via leucine incorporation. BP_{TdR} : bacterial production calculated via thymidine incorporation. DOC: dissolved organic carbon. Mean $\pm$ SD.

Parameter	L I	NYA
T (°C)	8.1 $\pm$ 0.2	1.7 $\pm$ 0.15
P_{tot} ($\mu\text{g C L}^{-1} \text{ d}^{-1}$)	148.1 $\pm$ 16	27.4 $\pm$ 1.07
PER ($\mu\text{g C L}^{-1} \text{ d}^{-1}$)	38.2 $\pm$ 13.4	11.0 $\pm$ 2.2
Chl- <i>a</i> ($\mu\text{g L}^{-1}$)	1.45 $\pm$ 0.7	0.58 $\pm$ 0.44
BA ($10^5 \text{ cells mL}^{-1}$)	14.7	8.9 $\pm$ 0.4
Leu_{inc} ($\text{pmol L}^{-1} \text{ h}^{-1}$)	36.0 $\pm$ 3.4	1.4 $\pm$ 0.16
TdR_{inc} ($\text{pmol L}^{-1} \text{ h}^{-1}$)	47.6 $\pm$ 5.1	1.0 $\pm$ 0.12
BP_{Leu} ($\mu\text{g L}^{-1} \text{ d}^{-1}$)	2.6 $\pm$ 0.24	0.19 $\pm$ 0.004
BP_{TdR} ($\mu\text{g L}^{-1} \text{ d}^{-1}$)	12.5 $\pm$ 1.44	0.96 $\pm$ 0.38
DOC (mg L^{-1})	5.9	2.5

Diskussion

Seasonally varying effects of temperature on bacterial production and bacterial growth characteristics in Gossenköllesee

In the investigated alpine lake, bacterial responses to temperature manipulation depended on the temperature range and were different concerning Leu_{inc} and TdR_{inc} . Many of the observed effects, however, cannot solely be attributed to temperature because they varied among the seasons and were thus likely modulated by resource availability.

The greatest impact of temperature on both, Leu_{inc} and TdR_{inc} was found in the lowest temperature range. The responsiveness of bacteria to temperature, however, declined with increasing temperature (Table 2). The same trend was reported by an abundance of studies (Pomeroy and Wiebe 2001, Middleboe and Lundsgaard 2003, Apple et al. 2006, Sand-Jensen et al. 2007, Kirchman et al. 2009, Adams et al. 2010). Even within the small temperature range (0–4°C) investigated in the Arctic lake, NYA, increasing temperature stimulated bacterial growth. This reveals – in line with previous findings (Christian and Wiebe 1974, Wiebe et al. 1992, Rivkin et al. 1996, Panzenböck et al. 2000) – that especially in the lower temperature range bacteria are highly responsive to temperature change and supports the assumption that the microbial community of cold-water lakes might be especially sensitive to global warming (Vincent and Pienitz 1996). At moderate temperatures (10–15°C), however, the estimated Q_{10} is comparable to values generally found in the literature, i.e. ranging between 2.1 and 3.9 (White et al. 1991, Hinder et al. 1999). That Leu_{inc} and TdR_{inc} estimated during the ice free period peaked at 15–25°C but declined again at 30°C (Fig. 2C and D) identifies the summer bacterioplankton community as for the most part psychrotolerant (Morita 1975). However, dividing bacteria into psychrophil and psychrotolerant categories based on their optimum growth temperature using a single method should be taken with caution (Feller and Gerday 2003). During the present study, too, the temperatures for maximum Leu_{inc} and TdR_{inc} often differed. While Leu_{inc} mostly peaked at 25°C irrespective of T_{amb} , the optimum temperature for TdR_{inc} mirrored the annual variation of *in situ* water temperature (Fig. 3). Similarly, Simon and Wünsch (1998) found higher temperature optima for Leu_{inc} than for TdR_{inc} at several dates and depths in Lake Constance. Moreover, in GKS there was no constant trend towards a temperature preference especially during the ice-covered period (Fig. 2A and B), indicating that different bacterioplankton populations were present simultaneously contributing to the bulk bacterial production. Adams et al. (2010) also reported two distinct temperature optima for bacterial growth in Arctic freshwaters demonstrating the presence of psychrophil and psychrotolerant bacterial communities. The

fact that the observed T_{opt} for bacterial production – especially concerning Leu_{inc} - was generally well above T_{amb} (Fig. 3) shows that bacteria grow optimally at temperatures that are rarely reached in GKS (Fig. 1A). Temperature limitation of microbial growth as often the case in several environments (Wallenstein and Hall 2012) seems to be even more pronounced in cold waters (Felip et al. 1996, Takacs and Priscu 1998).

While in many studies the thermal stimulation of bacterial growth was restricted to the temperature range below 12°C (Wikner and Hagström 1991, Hoch and Kirchman 1993, Tulonen 1993), in GKS bacterial production regularly increased up to about 25°C when there was a positive relationship with temperature as it was the case for Leu_{inc} that constantly (with one exception) responded to temperature. This is similar to the findings of Bergggren et al. (2010) and Adams et al. (2010) who observed a positive thermal response of BP estimated by Leu_{inc} over a broad temperature range. TdR_{inc} , however, was stimulated by increasing temperature only during the ice-free period (Fig. 2). Comparable, Kirschner and Velimirov (1999) and Franco-Vidal and Moran (2011) found TdR_{inc} weaker correlated with temperature than Leu_{inc} .

Several more striking differences between the responses of TdR_{inc} and Leu_{inc} to temperature enhancement could be observed, although all Leu_{inc} and TdR_{inc} rates derived from the temperature experiments in GKS correlated. One explanation for these differences may be the thermally altered uptake capacity of the tracers. For instance, nitrate and ammonium are taken up by different transport mechanisms through the cell membrane differently affected by temperature (Reay et al. 1999). More likely, the uptake of both leucine and thymidine is similarly impaired by low temperature as reported for thymidine and glucose uptake (Kirchman and Rich 1997). The variation in tracer incorporation might also be due to the use of thymidine not only for DNA production but also as N- or C-source during nutrient-depleted periods (Riemann et al. 1982, Kirschner and Velimirov 1999) or due to different phylogenetic bacterial groups differing in their ability to take up leucine and thymidine (Perez et al. 2010). For instance, varying abundances of cyanobacteria are reported to incorporate leucine but not thymidine (Hietanen et al. 2002, Petit et al. 1999, Hoppe et al. 2006). However, this may be responsible for seasonal fluctuations of Leu_{inc} compared to TdR_{inc} , but not for the differences of TdR_{inc} and Leu_{inc} during the short-term temperature manipulation experiments presented here since those were performed on samples with the same nutrient status and the same bacterial community, respective. Elsewhere, differences in Leu_{inc} and TdR_{inc} resulting in different corresponding BP estimates were explained as unbalanced growth (e.g. Chin-Leo and Kirchman 1988, Franco-Vidal and Morán 2011). Given that leucine is used for protein

synthesis, hence biomass production (Servais 1995) and thymidine primarily for DNA, hence cell production (Chin-Leo and Kirchman 1988, Tibbles 1996), the different patterns of Leu_{inc} and TdR_{inc} observed during this study can likely be attributed to temperature effects as suggested earlier (Petit et al. 1999).

In general, temperature enhancement had a greater impact on bacterial protein production as evident from the overall temperature responses, significantly steeper slopes of the regression on temperature and higher Q_{10} values of Leu_{inc} compared to TdR_{inc} (Table 1 and 2). Previous studies already reported that Leu_{inc} responds faster to increasing temperatures (Kirchman 1990, Felip et al. 1996, Tibbles 1996) and shows generally higher Q_{10} values than TdR_{inc} (Díaz- Raviña et al. 1994, Kirchman et al. 2005). Contrasting, rising temperatures stimulated TdR_{inc} to a less extent and only during the ice-free season (Fig. 2). In the lower temperature range, however, cell production predominated as indicated by the higher y-intercepts of the regression of TdR_{inc} on temperature compared to Leu_{inc} (Table 1). Supported by the finding that T_{opt} for TdR_{inc} mirrored the ambient water temperature, this implies that bacteria are thermally adapted insofar as at low temperatures they invest primarily into cell production with the purpose to maintain the population at unfavourable conditions. For instance, Georlette et al. (2003) reported on psychrophilic DNA ligases that are highly active at low temperatures. Since cold-adapted enzymes are known as highly thermolabile (Georlette et al. 2003) this may also explain why TdR_{inc} generally levelled off at 15–25°C as evidenced by the Q_{10} of 1 in contrast to Leu_{inc} with a Q_{10} of 1.75 within this temperature range (Fig. 2, Table 2).

With rising temperatures, however, bacterial investment strategies changed. In GKS, higher temperatures favoured bacterial protein production over cell production as indicated by the considerable increase of the $BP_{Leu} : BP_{TdR}$ ratios with temperature (Fig. 5). This is consistent with previous findings (Díaz- Raviña et al. 1994, Tibbles 1996, Rannekleiv and Baath 2001, Hoppe et al. 2006, Longnecker et al. 2006) and supported by the finding that bacterial cell volumes increase with temperature (White et al. 1991, Autio 1998). Contrasting, others showed that the $Leu_{inc}:TdR_{inc}$ ratio declines with temperature assuming that at unfavourable temperature conditions bacteria accumulate protein instead of investing into cell production (Reitner et al. 1997, Petit et al. 1999, Garneau et al. 2009). Also, Shiah and Ducklow (1997) found no consistent trend of the $Leu_{inc}:TdR_{inc}$ ratio in relation to temperature representing opposite patterns during summer and the other seasons and among different temperature ranges, respectively. No seasonal pattern of the $Leu_{inc}:TdR_{inc}$ ratios, however, maximum values in summer or at low temperatures were found by Franco-Vidal and Moran (2011). Simon and Wünsch (1998) even reported different metabolic pathways of bacteria among

various depth layers of a lake. This lack of consistency in the findings may refer to other factors, for instance resources interacting with temperature in influencing bacterial growth characteristics.

In GKS, rising temperatures exerted a more pronounced effect on bacterial growth characteristics during the ice-free period as indicated by the significantly higher $BP_{Leu} : BP_{TdR}$ ratios and steeper slopes of the $BP_{Leu} : BP_{TdR}$ regression on temperature compared to the ice-covered period (Fig. 5). This suggests that the threshold to switch from predominating cell to protein production depends on seasonally varying parameters such as resource supply as well. In GKS with very low DOC concentration ($\sim 0.3\text{--}0.5 \text{ mg L}^{-1}$; Sommaruga and Psenner 1997), PER appears to be the most important carbon source for bacteria (Sommaruga and Augustin 2006, Panzenböck 2007). During this investigation, the amount of PER was on average 17 times higher during summer than during ice-coverage (Fig. 1D). Then, a shift towards preferential protein production at about 7°C could be observed (Fig. 5B), while during the ice-covered period protein production increased to the cost of cell production at average 24°C (Fig. 5A), a temperature not reached *in situ*. The $BP_{Leu} : BP_{TdR}$ ratios estimated at *in situ* temperature correlated significantly with the amount of PER throughout the annual cycle (Pearson $r^2 = 0.619$, $p < 0.05$, $n = 8$) supporting the view that PER influences bacterial investment strategies. With respect to the environmental conditions in GKS, these results explain why bacteria increasingly invest into protein production only during the short summer season with improved substrate and temperature conditions ($10\text{--}15^{\circ}\text{C}$ in the epilimnion) while cell production predominates for the rest of the year (Fig. 1C).

That substrate availability in concert with temperature affects bacterial growth characteristic has been recently suggested by others (Longnecker et al. 2006). Bacteria seem to delay cell division to take advantage of resources and increase in size in the presence of nutrients (Shiomi and Margolin 2007, Adams et al. 2015) as supported by the occurrence of large filamentous forms in nutrient enriched treatments (Adams et al. 2015). In GKS, long filamentous bacteria regularly develop during summer with maximum in early autumn and decrease in number during the ice-covered period (Pernthaler et al. 1998, Wille et al. 1999) supporting the findings that bacteria accelerate biomass production to the disadvantage of cell production not only at higher temperatures but also during periods with improved substrate supply. In contrast to the findings presented here, others found an inverse relationship between the $Leu_{inc} : TdR_{inc}$ ratio and chl-*a* as a proxy for bacterial substrate (Hoppe et al. 2006).

That the response of bacterial metabolism to increasing temperature cannot be interpreted without considering the effect of resources is evident by comparing the seasonally pooled and averaged tracer incorporation rates at each incubation temperature (Fig. 4). At all incubation temperatures, the TI rates were significantly higher during the ice-free season. Additionally, these differences increased with temperature up to the key temperature of 25°C (Fig. 4). This may again be attributed to the higher resource level during the ice-free period strengthening the positive effect of temperature elevation (Autio 1998, Gurung and Urabe 1999). However, contrasting views of less prominent temperature dependency of bacterial growth with increased resource levels also exist (Felip et al. 1996). In this study, even in the temperature range $< 4^{\circ}\text{C}$ Leu_{inc} and TdR_{inc} rates were higher during the ice-free period than during ice-coverage implying resources to moderate the restrictive influence of low temperature on bacterial growth. Several authors have previously demonstrated that at low temperatures bacteria require higher resource levels for growth (Pomeroy et al. 1991, Wiebe et al. 1992, 1993). This is attributed to the fact that the reduced affinity for substrates, which is induced by structural changes of the bacterial cell membrane due to low temperatures, can be overcome by higher substrate concentrations (Russell et al. 1990, Nedwell 1999). Likewise, substrate enhancement may compensate the lowered substrate affinity of cold-active enzymes (Feller and Gerday 2003).

Temperature and resources are difficult to distinguish as controlling factors for bacterial growth since limiting substrate concentrations at low temperatures are different to those at high temperatures (Nedwell 1999). Nevertheless, as an approach to identify the relative importance of temperature and resources in controlling bacterial growth - at least during the ice-free period - the effects likely caused by resources only ($\text{TI}_{\text{ice-free}} : \text{TI}_{\text{ice-covered}}$) were compared with the effects solely attributed to temperature (Q_{10}). Opposite to Wiebe et al. (1992) who postulated the effect of resources on bacterial biomass production to be even greater at lower temperatures, the results of this study reveal that in the lower temperature range (1–4°C) the impact of temperature predominates as indicated by the Q_{10} of averagely 7.6 (Table 2) compared to an average $\text{TI}_{\text{ice-free}} : \text{TI}_{\text{ice-covered}}$ ratio of 4 within this temperature range (Fig. 4). Resource availability, however, becomes the overriding factor in stimulating bacterial growth at approximately 5°C and higher. Moreover, the $\text{TI}_{\text{ice-free}} : \text{TI}_{\text{ice-covered}}$ ratios increasing with temperature clearly demonstrate the impact of resources to be greater at higher, not lower temperatures which is in line with other studies (Kirchman and Rich 1997, Autio 1998, Kirchman et al. 2005). In the temperature range between 15° and 25°C, for instance, the improved resource conditions during summer resulted in averagely 14 times higher bacterial production compared to the ice-covered period (Fig. 4) while the Q_{10}

referring to the effect of a 10°C temperature increase ranged only between 1 and 1.75 (Table 2). In other systems, nutrient amendment stimulated bacterial growth only at higher temperatures (Shiah and Ducklow 1994a, Felip et al. 1996, Autio 1998, Carlsson and Caron 2001). However, at colder temperatures bacteria were found to respond more slowly to nutrient addition than at higher temperature explaining why there may be no response during short-term addition experiments (Kirchman and Rich 1997). Other authors observed bacteria as stimulated by either temperature increases or resource additions (Kirchman et al. 1993, Wiebe et al. 1993), however, in the lower temperature range, temperature appears to be the most important factor (Pomeroy et al. 1991, Vrede 2005) which is consistent with the results of this study. Thus, the relative importance of these two factors may also change seasonally (Shiah and Ducklow 1994b) resulting for instance in a shift from temperature to resource limitation during warmer periods as observed elsewhere (Gurung and Urabe 1999, Apple et al. 2006, Vrede 2005).

In GKS, this shift could not be observed. Constraints due to low temperatures in the ice-covered period were only true for bacterial protein production that positively responded to temperature enhancement also at that time in contrast to cell production (Table 1). The lack of thermal stimulation of TdR_{inc} during ice-coverage, however, rather indicates limitation of resources necessary to produce new cell compounds for increasing reproduction and population growth.

Moreover, resource limitation during the ice-free period could not be observed since both, Leu_{inc} and TdR_{inc} increased continuously with incubation temperatures up to 25° during the ice-free period (Fig. 2C and D). The decline at 30°C is most likely caused by the upper physiological growth limit of the bacteria at this temperature and not due to resource limitation that would rather flatten the curve of Leu_{inc} and TdR_{inc} . Supported by the finding that on average 60 % of the PER available in the water column is not incorporated by bacterioplankton (Panzenböck 2007) this indicates that the amount of PER available during summer fulfils the bacterial substrate demand even at the experimentally modified upper temperatures that are normally not reached in that lake.

Bacterial production and growth characteristics in the Arctic lakes

The bacterial numbers of the investigated Arctic lakes are well within the ranges reported for Arctic freshwaters (Hobbie et al. 2000, Panzenböck et al. 2000, Ellis-Evans et al. 2001, Laybourn-Parry and Marshall 2003) and Antarctic lakes (Takacs and Priscu 1998) but generally higher than those reported for alpine lakes (Reche et al. 1996, Carrillo et al. 2002,

this study). Concerning bacterial production rates, however, the values obtained for NYA are close to the estimates from other high latitude lakes while BP in LI is at the upper end of values reported in the literature (Panzenböck et al. 2000, Ellis-Evans et al. 2001, Laybourn-Parry et al. 2004). Especially in NYA, bacterial growth may be limited by low temperatures as indicated by the low BP in relation to the relatively high DOC concentration (Table 3) and by the thermal stimulation of bacterial growth. For some Arctic lakes, Adams and colleagues (2010) also argued that bacteria were carbon limited early in the season but temperature limited later on. The high responsiveness of bacteria to the small temperature increase (0–4°) used for the experiments points out the sensitivity of cold water microbes to rising water temperatures as proposed due to global warming.

Briefly, the environmental conditions in LI during the investigation resembled more or less the summer conditions in GKS, while in NYA – still ice-covered during sampling – the situation was comparable to GKS during the ice-covered period. In both Arctic lakes, bacterial cell production exceeded protein production similar to the observations in GKS at comparable temperatures (Table 2). Moreover, the significant increase of the $BP_{Leu}:BP_{TdR}$ ratio with temperature also indicates similar investment strategies of bacteria in dependence on temperature as detected in GKS. That the responsiveness of Leu_{inc} to temperature enhancement is greater than that of TdR_{inc} (higher Q_{10}) mirrors the results of the temperature manipulation experiment in GKS.

Conclusion

In alpine and Arctic lakes temperature has a great impact on bacterial production, whereas Leu_{inc} as indicative for protein production and TdR_{inc} as indicative for cell production of bacteria respond differently to temperature changes. These responses are further modulated by resource availability and vary between different temperature ranges. Since there is no effect of temperature enhancement on TdR_{inc} during the ice covered season this indicates substrate limitation of bacterial cell production at this period. In general, however, cell production appears better adapted to the prevailing low temperatures, thus dominating in the lower temperature regime, while bacteria increasingly invest into biomass production as soon as temperature rises and resource conditions improve. Over the whole incubation temperature range, the Leu_{inc} and TdR_{inc} rates were significantly higher during the ice-free period indicating resources to compensate temperature limitation. This stimulating effect of enhanced resource availability was highly pronounced at higher temperatures while below 5°C temperature predominated in controlling bacterial production. With respect to the

environmental conditions in GKS, bacterioplankton growth seems to be primarily limited by the low ambient water temperatures with resource depletion exacerbating this constraint during the ice-covered period. The results obtained in the Arctic lakes show similar responses of bacterial production and growth characteristic to temperature as observed in the GKS strengthening the argument that bacterially mediated biogeochemical cycles in high altitude and high latitude lakes are particularly sensitive to temperature changes due to global change. Concrete conclusions, however, will need more comparative studies between these ecosystems.

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6 Summary

Arctic and alpine lakes are harsh environments with numerous identical properties such as low temperatures, a short growing season, highly variable irradiances and low nutrient concentrations. These conditions result in a more or less simple food web allowing easier tracking of, for instance, carbon flux between the trophic levels.

The first part of this thesis represents the investigation of the pelagic food web structure and primary and secondary production in a high Arctic, permanently ice-covered lake on Franz Joseph Land sampled during a summer expedition. The very simple food web of the investigated lake was dominated by phyto- and bacterioplankton; rotifers represented the highest trophic level. While phytoplankton biomass and primary production decreased, the contribution of photosynthetical extracellular release (PER) to total primary production was relatively high (up to 96%) and increased like bacterial production (BP) during summer. Although water temperature increased only within a narrow range during the investigation, enhanced temperatures positively affected BP. The mean carbon demand of the bacterioplankton accounted for one third of PER indicating PER as sufficient carbon supply. These findings suggest that bacterioplankton were not limited by substrate but rather by low temperature in this investigated high Arctic lake.

There is growing evidence that the biogeochemistry and biocoenoses of alpine and Arctic lakes will alter due to ongoing environmental changes since especially high altitudes and high latitudes are predicted to be greatly affected by climate change. Increasing our knowledge on the factors controlling the carbon cycle within the microbial food web will be important for a better understanding of the response of cold water lakes to global warming. Hence, the second and third part of this thesis focuses on the influence of varying radiation and temperature conditions on phyto- and bacterioplankton production in Arctic and alpine lakes. The data were primarily estimated under experimentally altered settings. The research for these parts was conducted in two lakes on the Taymir peninsula (Siberia) studied during summer and an alpine lake in the Stubai Alps (Tyrol, Austria) monitored over a period of one year which allowed a closer investigation of temperature and light adaptation processes of the microbial community and of the relative importance of temperature and substrate as seasonal varying factors in limiting bacterial growth. In the alpine lake, % PER decreased from spring to winter independent of total primary production and was inversely related to algal biomass. Moreover, % PER was greatly influenced by irradiance. Phytoplankton present in the lakes under ice-coverage were highly susceptible to higher than ambient irradiance and released up to 95% of photosynthetically produced carbon while total primary production decreased with

experimentally increasing irradiance. This indicates PER as a result of photoinhibition with dark-adapted phytoplankton. During the ice-free period when phytoplankton were photo-acclimatized, % PER and total primary production increased with rising irradiances. This can be considered as imbalance of photosynthesis and algal growth possibly due to nutrient deficiency that results in carbon overflow. In all lakes, the amount of PER was capable to fulfil the bacterial carbon demand and represented an important contribution to the in-lake pool of dissolved organic carbon (DOC), especially in the alpine low-DOC lake. Since primary production was suppressed by UV-radiation, the amount of PER as well as the bacterial incorporated proportion were reduced. The extent of this impact was inversely related to the DOC concentration of the lakes indicating the alpine lake as more sensitive to UVR than the Arctic lakes.

Observed effects of temperature on bacterioplankton depended on the temperature range and resource availability and led to different growth characteristics of bacteria. Especially in the lower temperature range bacterial production greatly responded to increasing temperatures while in the upper temperature range resource availability prevailed in controlling bacterial growth. Over the whole investigated temperature range (0–30°C), enhanced resource availability released bacteria from temperature limitation. Bacterial adaptation to ambient environmental conditions resulted in predominating cell production at lower temperature while at higher temperatures supported by improved resource availability bacteria favoured protein production over cell production. Similar patterns of bacterial production and growth characteristics influenced by temperature and substrate supply were observed in two Arctic lakes. Taken together, the results of this study demonstrate that temperature and resources as highly interacting factors influence not only bacterial production but also bacterial investment strategies and ongoing global warming can be expected to alter the microbial growth in alpine and Arctic lakes.

Zusammenfassung

Niedrige Wassertemperaturen, kurze Vegetationsperioden, stark schwankende Strahlungsverhältnisse und geringe Nährstoffkonzentrationen charakterisieren sowohl arktische als auch alpine Seen. Diese extreme Kombination an Umweltfaktoren führt zu meist sehr einfachen Nahrungsnetzen, was die Untersuchung von Stoffflüssen im Ökosystem wie z.B. jenem von Kohlenstoff vereinfacht.

Im ersten Teil dieser Dissertation wurde das pelagische Nahrungsnetz sowie die Primär- und Sekundärproduktion eines arktischen, permanent eisbedeckten Sees auf Franz Joseph Land während einer Sommerexpedition untersucht. Phyto- und Bakterienplankton dominierten das äußerst einfach strukturierte Nahrungsnetz dieses arktischen Sees mit Rotatorien als höchste trophische Ebene. Der Anteil an photosynthetisch produziertem, extrazellulärem Kohlenstoff (% PER) war mit bis zu 96 % der gesamten Primärproduktion sehr hoch und stieg ebenso wie die bakterielle Produktion während des Sommers an, wohingegen die gesamte Primärproduktion und die Algenbiomasse (Chlorophyll a) sanken. Trotz des geringen Anstiegs der Wassertemperatur während des Untersuchungszeitraumes konnte ein stimulierender Effekt auf die bakterielle Produktion beobachtet werden. Im Durchschnitt reichte ein Drittel des gemessenen PER um den bakteriellen Kohlenstoffbedarf zu decken. Diese Ergebnisse deuten darauf hin, dass die niedrigen Temperaturen und nicht die Substratverfügbarkeit limitierend für das mikrobielle Wachstum in diesem arktischen See ist. Immer mehr Studien prognostizieren, dass sich die Biogeochemie und Biozönosen alpiner und arktischer Seen maßgeblich verändern werden, da insbesondere für Polar- und Hochgebirgsregionen beträchtliche Auswirkungen des globalen Klimawandels erwartet werden. Den Kohlenstoffkreislauf innerhalb des mikrobiellen Nahrungsnetzes unter dem Einfluss sich ändernder Umweltfaktoren detaillierter zu verstehen, kann dazu dienen Konsequenzen des globalen Klimawandels auf aquatische Ökosysteme besser abschätzen zu können. Diesbezüglich wurde im zweiten und dritten Teil dieser Dissertation die Auswirkung unterschiedlicher Strahlungs- und Temperaturbedingungen auf die Produktionsraten von Phyto- und Bakterioplankton in arktischen und alpinen Seen untersucht. Diese Arbeiten beruhen weitgehend auf experimentellen Ansätzen. Die Untersuchungen wurden einerseits in zwei Seen auf der Taymir Halbinsel (Sibirien) während einer Sommerexpedition, andererseits in einem alpinen See in den Stubai Alpen (Tirol, Austria) durchgeführt. Bei letzterem erfolgte ein ganzjähriges Monitoring, um einen Einblick in die Adaptation der mikrobiellen Gemeinschaft an Strahlung und Temperatur zu erhalten sowie die relative Bedeutung von Temperatur und Substratverfügbarkeit als limitierende Faktoren für das mikrobielle

Wachstum in Abhängigkeit von der Jahreszeit zu erfassen. Im alpinen See nahm % PER von Frühling bis Winter unabhängig von der Primärproduktion und umgekehrt proportional zur Algenbiomasse ab, wobei ein starker Einfluss der Strahlungsintensität beobachtet werden konnte. Unter Eisbedeckung gab das Phytoplankton bis zu 95% des photosynthetisch produzierten Kohlenstoffs ab, wenn es höheren als den aktuell unter Wasser vorherrschenden Strahlungsintensitäten ausgesetzt war. Währenddessen sank die gesamte Primärproduktion mit zunehmender Lichtintensität. Dies weist darauf hin, dass dunkel adaptierte Algen einen hohen Anteil an PER als Folge von Photoinhibition abgeben. Zunehmende Lichtadaptation der Algen während der eisfreien Periode führten dazu, dass mit steigender Lichtintensität im Rahmen der Strahlungsexperimente sowohl Primärproduktion als auch % PER anstiegen. Dies kann als Ungleichgewicht zwischen Photosynthese und Algenwachstum, vermutlich aufgrund von Nährstoffmangel, und damit als Abgabe von überschüssigem Kohlenstoff in Form von PER interpretiert werden. PER reichte in allen untersuchten Seen aus, um den bakteriellen Kohlenstoffbedarf zu decken und überdies wesentlich zum Pool an DOC (dissolved organic carbon) der Gewässer beizutragen. UVR-Exposition hemmte nicht nur die Primärproduktion, sondern verringerte in Folge auch die Menge an PER und dessen bakterielle Aufnahme. Dieser Effekt war umgekehrt proportional zum DOC-Gehalt des Gewässers und identifiziert den alpinen See als sensibler gegenüber UV-Strahlung aus als die arktischen, DOC-reicheren Seen.

Beobachtete Auswirkungen von Temperatur auf bakterielles Wachstum waren abhängig vom Temperaturbereich als auch von der Substratverfügbarkeit und führten zu verschiedenen Wachstumsstrategien. Eine Temperaturerhöhung wirkte sich besonders im unteren Temperaturbereich drastisch auf die bakterielle Sekundärproduktion (BP) aus, während bei höheren Temperaturen die Substratverfügbarkeit als stimulierender Faktor dominierte. Bei allen Inkubationstemperaturen (0–30°C) war eine Kompensation limitierender Temperatureffekte durch eine höhere Substratkonzentration zu beobachten. Bakterielle Adaptation an die vorherrschenden Umweltbedingungen zeigte sich insofern, als dass die bakterielle Reproduktion (Zellvermehrung) im unteren Temperaturbereich dominierte, während sowohl bei höheren Temperaturen als auch besserer Substratverfügbarkeit Bakterien zunehmend in Biomasse investierten. Ähnliche Muster betreffend die bakterielle Produktion und Wachstumsstrategie in Abhängigkeit von Temperatur und Substrat konnten auch in den arktischen Seen beobachtet werden. Dies zeigt, dass Temperatur und Substrat als interagierende Faktoren die Produktion wie auch die Investmentstrategie der Bakterien beeinflussen und dass durch die Klimaerwärmung Folgen für das bakterielle Wachstum in alpinen und arktischen Gewässern zu erwarten sind.

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