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Bacterioplankton Dynamics in the McMurdo Dry Valley Lakes, Antarctica: Production and Biomass Loss over Four Seasons

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Abstract

Research of the microbial ecology of McMurdo Dry Valley lakes has concentrated primarily on phototrophs; relatively little is known about the heterotrophic bacterioplankton. Bacteria represent a substantial proportion of water column biomass in these lakes, comprising 30 to 60% of total microplankton biomass. Bacterial production and cell numbers were measured 3 to 5 times, within four Antarctic seasons (October to January), in Lakes Fryxell, Hoare, and Bonney. The winter–spring transition (September to October) was included during one year. Lake Fryxell was the most productive, but variable, lake, followed by Lakes Bonney and Hoare. Bacterial production ranged from 0 to 0.009 μg C ml^{-1} d^{-1}; bacterial populations ranged from 3.2×10^4 to 4.4×10^7 cells ml^{-1}. Bacterial production was always greatest just below the ice cover at the beginning of the season. A second maximum developed just above the chemocline of all the lakes, as the season progressed. Total bacterioplankton biomass in the lakes decreased as much as 88% between successive sampling dates in the summer, as evidenced by areal integration of bacterial populations; the largest decreases in biomass typically occurred in mid-December. A forward difference model of bacterial loss in the trophogenic zone and the entire water column of these lakes showed that loss rates in the summer reached 6.3×10^{14} cells m^{-2} d^{-1} and 4.16×10^{12} cells m^{-2} d^{-1}, respectively. These results imply that bacteria may be a source of carbon to higher trophic levels in these lakes, through grazing.

Introduction

The lakes of the Taylor Valley, Antarctica offer a unique opportunity to study microbial ecology in an extreme environment. These lakes, located at approximately 77° S 168° E in the McMurdo Dry Valleys, are characterized by permanent 3 to 5 m thick ice covers and strong vertical conductivity, nutrient, and oxygen gradients. The ice covers, physical and chemical gradients, and low stream input create distinct layers in which the plankton live [1]. Eukaryotic phototrophs, heterotrophic flagellates, and bacteria dominate the plankton community; macrozooplankton and fish are not present. The physically stable water column [42] and lack of a complex food web provide a relatively simple system to examine microbial processes in a pristine environment, with little anthropogenic influence.

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Rapid growth rates of heterotrophic bacteria in other aquatic systems show that production of bacterial biomass represents an important link among detritus, dissolved organic matter (DOM), and higher trophic levels [9]. Bacteria are also important in scavenging and transforming DOM, degrading substrates that might otherwise accumulate, and producing new biomass that is passed up the food web [14]. A revised concept of pelagic food web structure [32] has been instrumental in determining that bacteria may be a source of organic carbon to higher trophic levels, through grazing by microheterotrophic ciliates and flagellates [2, 7, 29, 38].

The microbial ecology of the Taylor Valley lakes has been studied since 1961 [10, 31, 39, 11, 26, 33]. Much of this work has concentrated on photoautrophs; relatively little is known about the bacterioplankton. Bacteria comprise a significant proportion (33 to 60%) of summer total microplankton biomass in Lakes Fryxell, Hoare, and Bonney [Takacs and Priscu, unpublished data], and are a significant portion of particulate organic carbon in these lakes. Historically, grazing in these lakes has either been ignored or believed absent. Though no experimental data showing phagotrophy in these lakes has been reported, several genera of phytoplankton and protozoans present in Taylor Valley lakes graze bacteria in other systems [23, 27].

The perennially ice-covered lakes of the McMurdo Dry Valleys, Antarctica, have been used extensively as analogues for the study of exobiology, because they pose one of the most extreme environments on our planet that harbors life. Despite the importance of these lakes as an ''end-member'' in the spectrum of environments on earth, there are no focused reports of the bacterioplankton that exist within them. Previous studies were conducted during a period when colony-forming units was still the standard bacterial enumeration method [20] or concentrated on a particular bacterial adaptation or process within usually just one of these lakes [28, 48, 49]. The objectives of our study were to define the spatial and seasonal distribution of bacterial biomass and production in three major lakes in the McMurdo Dry Valleys, and to numerically model bacterial losses.

Materials and Methods

Study Site

The McMurdo Dry Valleys is a 4800 km^2 area of Antarctica's southern Victoria Land that has been ice-free for approxiimately the last 4 million years. Studies were conducted on Lakes Fryxell, Hoare, and the east and west lobes of Lake Bonney. The lakes, which lie in the Taylor Valley, are remnants of Lake Washburn, a larger lake which existed 10,000 to 24,000 years ago [21, 6]. Lake Fryxell, at the easternmost edge of the valley, has a surface area of 7 km^2, and a maximum depth of 18 m. Lake Hoare has a surface area of 3 km^2 and a maximum depth of 30 m. Lake Bonney is situated at the head of the valley, with a surface area of approximately 4 km^2 and a maximum depth of 40 m. Lake Bonney has two basins (lobes), connected by a narrow (~20 m wide), shallow (12 m) channel [1, 42, 43]. While these lakes vary in degree of chemical stratification, all contain nutrient-rich deep water overlaid by a relatively nutrient-poor epilimnion. The permanent ice covers of these lakes prevent wind-driven mixing. This, coupled with low advective stream input, allows vertical gradients to develop and persist. Lake Bonney is the most strongly stratified of the lakes, followed by Lakes Fryxell and Hoare. Detailed descriptions of these lakes may be found in Green and Friedmann [12] and Priscu [34].

Sampling Procedure

Sampling holes were made in the ice over the deepest portion of the lake. Each lake was sampled 3–5 times during the austral spring and summer (October to January) of 1993–1997, or every 20 to 30 days. Each lake was sampled every 10 days during the winter to spring transition (September to October) of 1995. This period marks the transition from complete darkness to continuous sunlight. Samples were collected at selected depths using a Niskin bottle with Teflon-coated components. All sampling depths were measured from the piezometric water level (water level within the sampling hole). The sampling bottle was gently inverted several times before decanting to eliminate possible gradients within the Niskin bottle. Acid-washed, polyethylene bottles were rinsed 3× with sample water. Lake water was then collected in the bottles, and stored at 1 to 5°C until it was processed in a lakeside laboratory.

Bacterial Cell Counts

Bacterial samples (10 ml) were preserved with formalin (5% final concentration) at 4°C until counted. Sample vials were vortexed before cells were stained with acridine orange [0.01% (w/v) final concentration] for 2 min. They were then filtered onto black 0.2 μm polycarbonate filters. Non-autofluorescing rods and cocci were counted by epifluorescent microscopy [13] at 1,000× magnification. At least 200 cells were counted on each prepared filtered. Acridine orange-stained cells were more stable than DAPI-stained cells, in the wide range of salinity (0 to 120 ppt [43]) found in these lakes. All samples were counted 6 mo after collection, with the exception of the 1993–1994 samples, which were counted 16 mo after collection. We adjusted bacterial cell count data by fitting an exponential decay equation to cell counts of Lake Bonney samples mounted between 0 and 365 days after collection [45]. Cell count decay rates were determined for samples collected from the spectrum of salinities found in these lakes.

Heterotrophic Bacterial Activity

Bacterial activity was measured on 10 ml of lake water incubated in the dark, for 20 h, with 20 nM [methyl-^{3}H] thymidine (0.0148 MBq

ml^{-1}), at 1 to 4°C. Three replicates and two kills (formalin at 5% final concentration) were incubated for each sample analyzed. Incubation was ended by adding 10 ml cold 10% trichloroacetic acid (TCA). Samples were stored 1 to 4 weeks before filtering. This storage interval may be a source of minor variability in thymidine uptake rates (TdR). Wicks and Robarts [50] found that 91% and 74% of [^{3}H]DNA was recovered in NaOH treated samples, after being stored at 4°C for 2 and 50 days, respectively. Storage of samples at a low pH, such as when treated with TCA, would allow metals to cleave DNA or form DNA dimers, but should not interfere with the recovery of the extract any more than NaOH would. Samples were filtered onto 0.45 μm polycarbonate filters, and filter towers were rinsed 3 times with 2 ml cold 5% TCA. Radioactivity on the filters was assayed by standard scintillation spectroscopy. Thymidine uptake rates are linear for up to 20 h, using this protocol (Priscu, unpublished data). Thymidine uptake rates (corrected for formalin kills) from laboratory incubations were converted to *in situ* temperature rates using an energy of activation of 12,600 kcal mol^{-1}. This energy of activation was determined from temperature experiments on the east lobe of Lake Bonney. Thymidine uptake was converted to bacterial production based on the published value of 2×10^{18} cells mol^{-1} thymidine. We empirically estimated a thymidine conversion factor (TCF) for each of these lakes by the method of Kirchman and Ducklow [19]. A TCF of 2.57×10^{19} cell mol^{-1} thymidine was computed by the integration method, and 4.75×10^{18} cells mol^{-1} thymidine by the modified derivative method. These results are based upon limited data during one month (December) only. They probably overestimate the TCF for these lakes. Therefore, the published value, based upon 97 marine studies was used; it is commonly derived in fresh water, as well [3]. A value of 11 fg C cell^{-1} was used to calculate bacterial carbon, and was empirically determined, by Kepner et al. [18], from the biovolume of 400 cells. Carbon production was divided by cell counts to determine specific activity (mg C cell^{-1} d^{-1}). One way analysis of variance was used to determine if water column-integrated bacterial production varied among years. Data were normally distributed. Differences between years were determined using Tukey's Test.

Bacterial Cell Loss Rates

During the interval between successive samplings, bacterial cell loss rate (cells m^{-2} d^{-1}) was computed over the trophogenic zone (9 m in Lake Fryxell, 14 m in Lake Hoare, 13 m in Lake Bonney), and over the entire water column of the lakes, using the general relationship:

$$\text{Loss rate} = BP - dB/dt,$$

where BP is the average bacterial production over the time step (cells m^{-2} day^{-1}), B is cell density in cells m^{-2}, and t is the number of days over the time step [16]. The trophogenic zone was defined as the water column above the chemocline in each lake. Loss rates were computed separately here, because this is where a majority of bacterial grazing is believed to occur [15; Roberts and Laybourn-Parry, personal communication]. Loss rates throughout the entire water column were also computed to exclude vertical transport as a means of cell loss. The bacterial cell sedimentation rate was determined to be <0.9% of the loss rate, and negligible in this model, by computing flux of cells to the sediment, according to the relationship:

$$J_{\text{cells}} = V_s \cdot [\text{cells}],$$

where J_{cells} is flux of bacterial cells to the sediment, V_s is sedimentation velocity, and [cells] is cell density just above the sediment. Loss rates were not determined for intervals between sampling seasons, because little is known about the winter period. Loss rate is positive in this model; biomass gains are negative. BP was determined as

$$BP = 0.5(BP_t + BP_{t+1}),$$

where BP_{t+1} and BP_t are the cell production rates on successive sampling days, integrated over the trophogenic zone and the entire water column of each lake. dB/dt was determined by

$$dB/dt = (B_{t+1} - B_t)/t,$$

where B_t and B_{t+1} are the integrated cell counts over the trophogenic zone and entire water column on successive samplings (excluding winter). Turnover rate (d^{-1}) for each interval was estimated by dividing the loss rate by the average B for the corresponding interval. A theoretical grazing rate was calculated by dividing trophogenic zone and water column cell loss by the depth (m) of the trophogenic zone or of the entire lake, to estimate average cell loss rates (cells m^{-3}d^{-1}).

Results

Seasonal and Annual Variations in Bacterial Production and Biomass

The influence of sample storage time on bacterial cell counts was consistent throughout the water column of the east and west lobe of Lake Bonney (which covers the salinity range of all the Taylor Valley lakes). A time course experiment (0 to 365 days) of sample storage produced results that fit an exponential decay function ($r = 0.548$; $n = 60$; $p < 0.01$) of the form:

$$N_t = N_0 e^{-0.0037t},$$

where N_t is the number of cells counted at time t, time t is the time elapsed in days, and N_0 is the number of cells in the sample at time zero. All bacterial cell counts were corrected for storage time using this relationship.

Bacterial production, distribution, and cell specific activity in Lakes Fryxell, Hoare, and Bonney are summarized in Figs. 1 through 4. Production, cell numbers, and specific

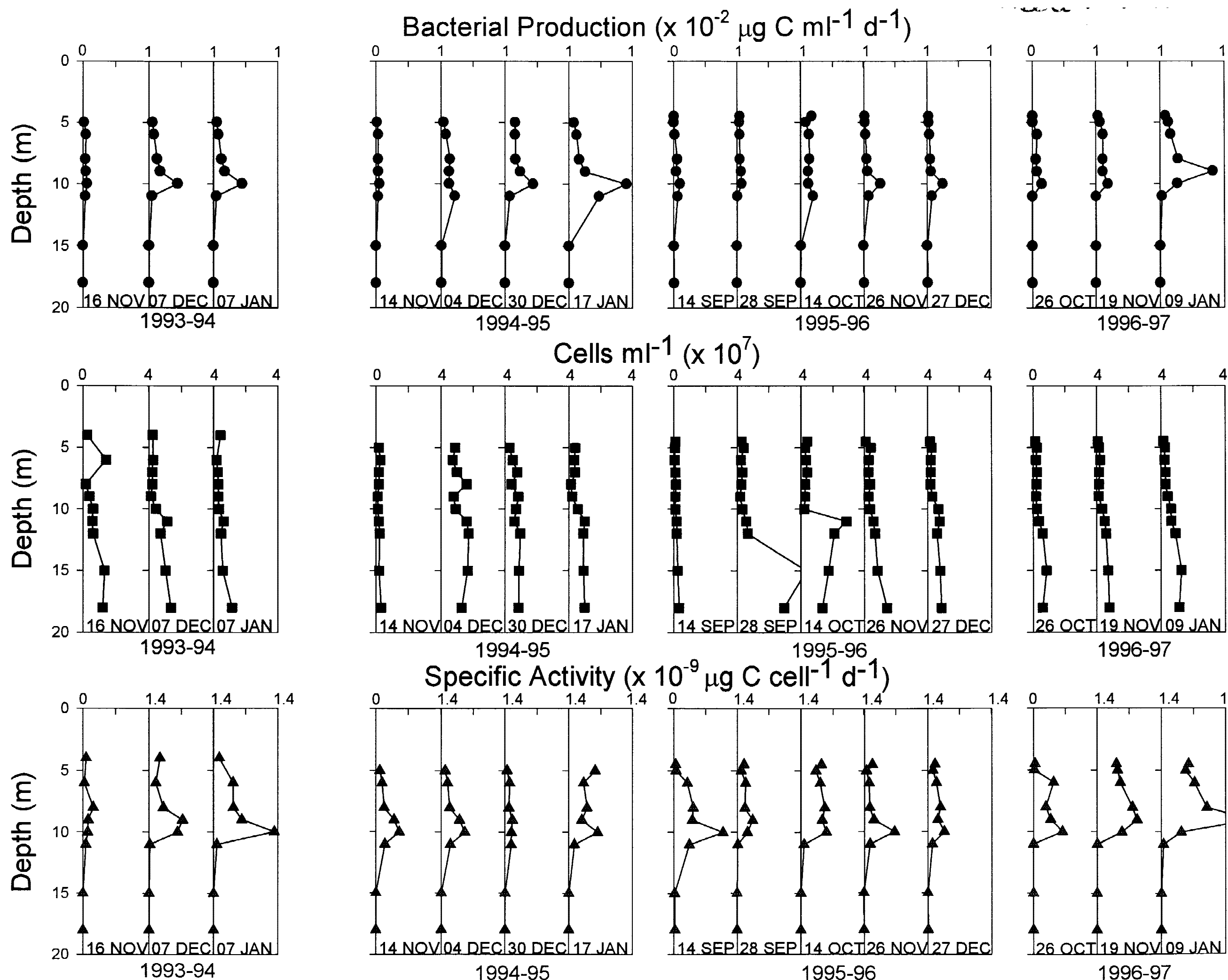

Fig. 1. Lake Fryxell bacterial production ($\times 10^{-2}$ μg C ml^{-1} d^{-1}), cell numbers ($\times 10^{7}$ cells ml^{-1}), and specific activity ($\times 10^{-9}$ μg C cell^{-1} d^{-1}) during the 1993–1997 sampling seasons.

activity showed the same trends in all three lakes, but differed in magnitude. Production was greatest just below the ice cover, with a smaller, less-pronounced peak at or near the chemocline (9 m in Lake Fryxell, 14 m in Lake Hoare, 13 m in Lake Bonney) at the beginning of each season. Both maxima increased as the season progressed. The deeper peak became more pronounced by December to January. Bacterial distributions followed production profiles from November to December. Exceptions were a third peak that formed in Lake Fryxell at 15 m, and high cell numbers in the east lobe of Lake Bonney between 20 and 30 m; both of these maxima were below the trophogenic zone. Biomass typically decreased by up to 88% in mid-December. Following this decrease in cell numbers, biomass began to increase again, often decreasing by January (see Fig. 6). Specific activity was greatest just below the ice cover and at the chemocline, and remained relatively unchanged throughout the season each year.

Areally-integrated bacterial production was greatest in Lake Fryxell, followed by the west lobe of Lake Bonney, Lake Hoare, and the east lobe of Lake Bonney (Fig. 5). One way analysis of variance of areally integrated bacterial production (mg C m^{-2} d^{-1}) showed no significant differences, except in the east lobe of Lake Bonney between the 1994–1995 and 1995–1996 sampling seasons ($p < 0.048$, $n = 16$). Fryxell production was higher in 1994–1995, while production in Lake Hoare remained relatively unchanged. East lobe and west lobe production showed similar trends, though west lobe production was higher. Lake Fryxell was the most productive lake, based on total lake volume, followed by the east

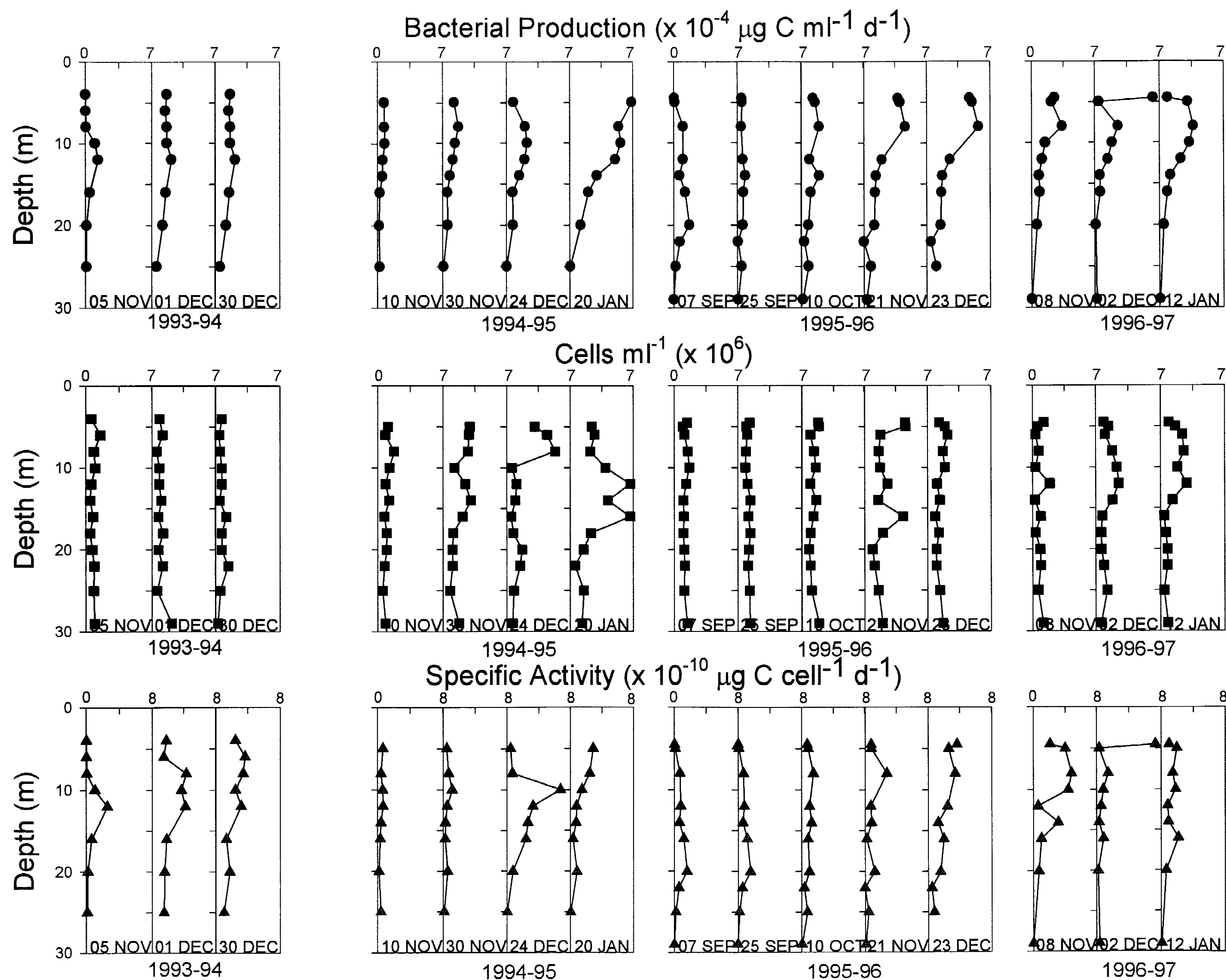

Fig. 2. Lake Hoare bacterial production ($\times 10^{-4}$ µg C ml^{-1} d^{-1}), cell numbers ($\times 10^{6}$ cells ml^{-1}), and specific activity ($\times 10^{-10}$ µg C cell^{-1} d^{-1}) during the 1993–1997 sampling seasons.

lobe of Lake Bonney, Lake Hoare, and the west lobe of Lake Bonney (Table 2). Lake Bonney is more productive than Lake Hoare when the east and west lobes are considered together. Lake Fryxell had the greatest cell densities and the largest seasonal variations, followed by the west lobe of Bonney, the east lobe of Bonney, and Lake Hoare (Fig. 6). Specific activity was greatest in the west lobe of Lake Bonney, followed by Lake Fryxell, the east lobe of Lake Bonney, and Lake Hoare.

Bacterial Gains and Losses

Bacterial cell loss rates and turnover rates in the trophogenic zone, and throughout the entire water column of Lakes Fryxell, Hoare and Bonney, are summarized in Table 3. Lake Fryxell's trophogenic zone showed the greatest biomass loss; loss rates computed in Lakes Bonney and Hoare were lower, and varied within the same range. The higher loss rate computed in Fryxell may be due to the increased stream input this lake received, especially in the 1993–1994 season, compared to other years [5; McKnight, unpublished data]. The relatively fresh stream input has been observed to mix with the upper 2 m of lake water (Welch and Lyons, unpublished data). This would result in cell dilution. Generally, water column loss rates were highest in Fryxell, followed by Lake Bonney's east and west lobes, and Lake Hoare. Loss rates increased mid-season, decreased, and then rose again in January, 1996. Loss rates and turnover rates varied the most, and were greatest, in Lake Fryxell.

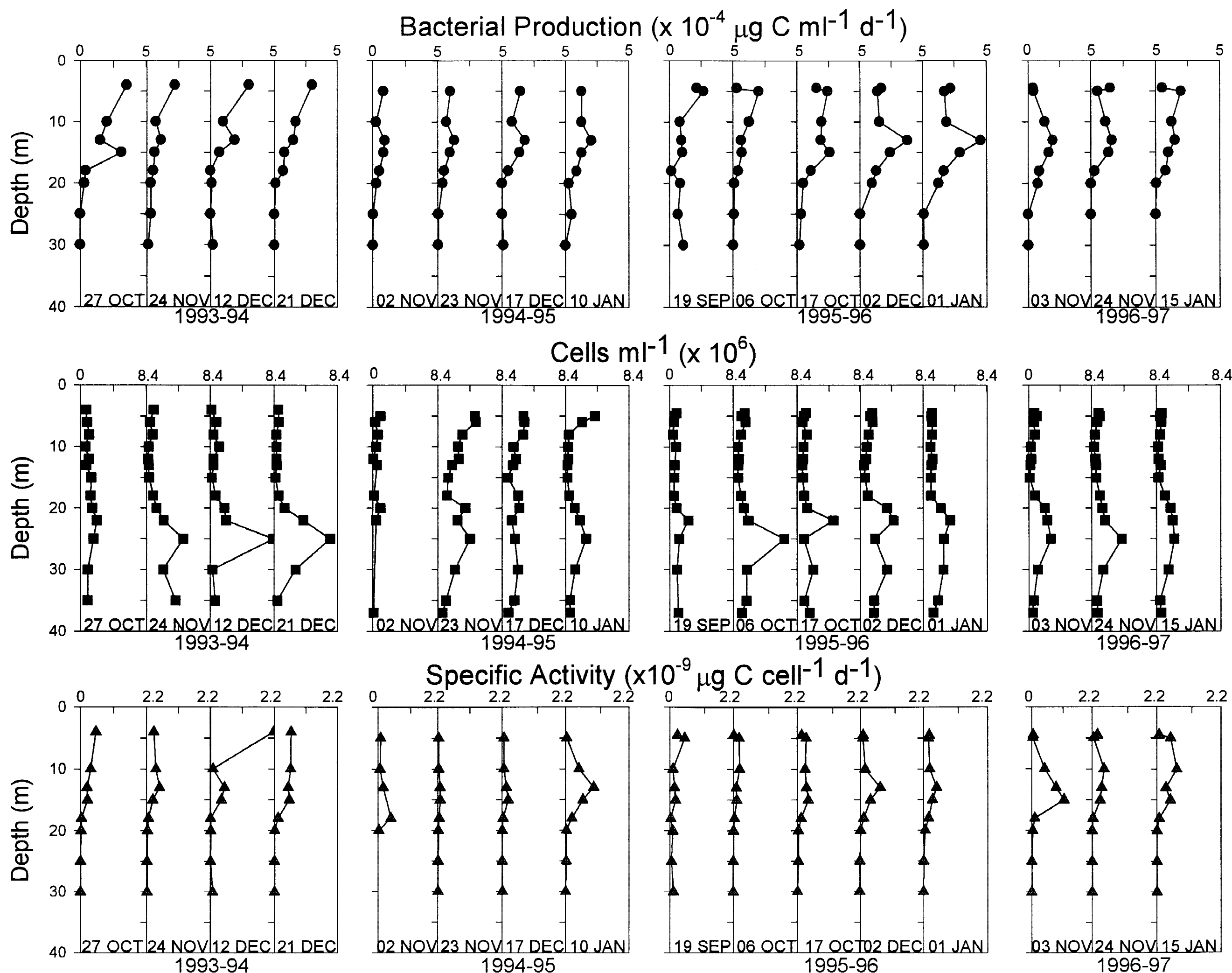

Fig. 3. East lobe, Lake Bonney bacterial production ($\times 10^{-4}$ μg C ml^{-1} d^{-1}), cell numbers ($\times 10^6$ cells ml^{-1}), and specific activity ($\times 10^{-9}$ μg C $cell^{-1}$ d^{-1}) during the 1993–1997 sampling seasons.

Theoretical grazing rates calculated from trophogenic zone loss rates ranged from 1.0×10^9 to 4.8×10^{13} cells m^{-3} d^{-1}. Lake Fryxell had the greatest trophogenic cell loss, followed by Lake Hoare and Bonney's east lobe and west lobe. Grazing rates calculated from water column loss rates ranged from 5.0×10^8 to 3.2×10^{11} cells m^{-3} d^{-1}. They were greatest in Lake Fryxell, followed by the east and west lobes of Lake Bonney and Lake Hoare.

Discussion

Summer bacterial production in the lakes of the McMurdo Dry Valleys is comparable to that in other high latitude lakes in winter. Bacterial numbers are comparable to more productive systems (Table 1). These lakes present a paradox in that bacterial populations are relatively high, yet bacterial production is comparatively low. The following explanations are offered to interpret this paradox: first, low temperature and salinity restrict bacterial production; second, cells accumulate and persist due to the low ambient temperature and long water column turnover time of these lakes; third, though bacterial production is low for most of the year, low grazing rates and viral infection maintain bacterial populations near 10^6 cells ml^{-1}.

The magnitude of bacterial production and cell numbers differs among the three lakes studied, whereas seasonal and annual trends are similar. The increase in bacterial production throughout the sampling season corresponds with an increase in primary production [24; Priscu, unpublished

Fig. 4. West lobe, Lake Bonney bacterial production ($\times 10^{-4}$ μg C ml^{-1} d^{-1}), cell numbers ($\times 10^{6}$ cells ml^{-1}), and specific activity ($\times 10^{-9}$ μg C cell^{-1} d^{-1}) during the 1993–1997 sampling seasons.

data], indicating a close coupling between these two trophic levels. This is most likely due to the release of dissolved organic carbon by phytoplankton, estimated to be between 5 and 23% of primary productivity in these lakes [37]. Interlake differences may be attributed to the distinct nutrient and primary productivity profiles of each lake [33]. Lake Fryxell's trophogenic zone is nutrient rich, compared to the other lakes, and this lake is the most productive (primary and secondary) on a volumetric basis. Lake Hoare, the least productive lake, has the lowest nutrient levels and primary productivity. Phytoplankton are primarily phosphorus deficient in these lakes [33], but repeated bacterial nutrient bioassay experiments have shown little stimulation by inorganic nitrogen, phosphorus, or glucose [46]. Laboratory studies, however, have revealed that the bacterial populations of

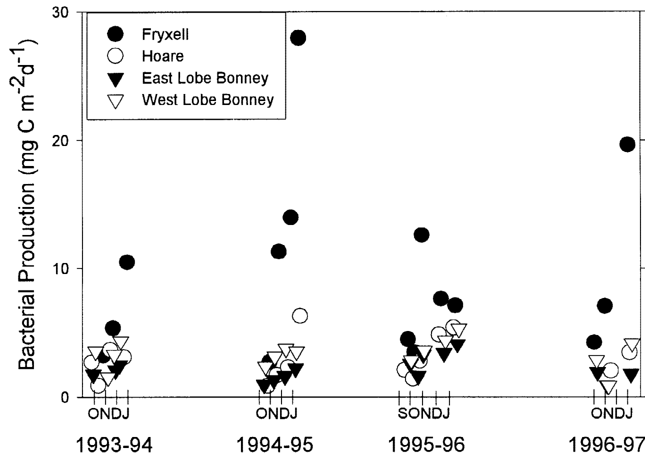

Fig. 5. Water column integrated bacterial production (mg C m^{-2} d^{-1}) in Lakes Fryxell, Hoare, and Bonney during 1993–1997.

these lakes are growing well below their optimum temperature and above their optimum salinity. Ward and Priscu [49] estimated optimal salt concentrations and temperatures for growth of three denitrifiers isolated from Lake Bonney. They found that, under *in situ* conditions, the bacteria were growing at only 42% of their maximum rate. Experiments conducted on unidentified isolates from all three lakes have shown that optimum salt concentration for growth was 0.5% and temperature optima ranged from 12 to 20°C [Takacs and Priscu, unpublished data]. These results show that the low temperature (−5 to 7°C) and high conductivity below the chemocline (0.11 to 14 S m^{-1}) of the lakes [44] are two factors limiting growth of bacteria *in situ.* Presumably, the difference in magnitude of bacterial activity among the lakes is due to the magnitude of primary productivity.

Though bacterial populations are relatively high, with respect to productivity, the percentage of live cells is known only in Lake Bonney. Respiring cells, measured by the tetrazolium salt reduction method, were estimated to be 10 to 35% of total cell counts in the east lobe, and 45 to 73% in the west lobe [41]. A significant fraction of bacterial cells are most likely not respiring in these lakes. Specific activity, therefore, is underestimated. Dead cells may persist, at depth, for extended periods, due to slow decomposition and sinking rates at the low temperatures (−5 to 7°C), and high salinities of these lakes (0 to 120 ppt). Additionally, water column mixing times in these lakes exceed 20,000 years, owing to diffusion coefficients at the molecular level [43].

Marked decreases in bacterial biomass in the midst of the growing season, particularly in Lake Fryxell, imply that bacterial biomass is being ingested by grazers or infected by viruses or parasites. Phototrophic nanoflagellates (PNAN), heterographic nanoflagellates (HNAN), ciliates, and rotifers capable of bacterivory have been detected in these lakes [23]. Populations of PNAN, HNAN, and ciliates are associated with bacterial peaks [15]. Roberts and Laybourn-Parry recently initiated studies to determine ingestion rates in Lakes Hoare and Fryxell. Preliminary results show that phototrophic cryptophytes, present at concentrations up to 6,000 cells ml^{-1} in Lake Fryxell and 1,600 cells ml^{-1} in Lake Hoare, have been observed to ingest bacteria at a rate of 0.6 to 2.2 bacteria $cryptophyte^{-1}$ h^{-1} (Roberts and Laybourn-Parry, unpublished data). Based on these preliminary results, grazing by cryptophytes, alone, may range from 8.6×10^{11} to 31.7×10^{11} cells m^3 d^{-1} in Lake Fryxell. This agrees with our theoretical grazing rates. Grazing by HNAN may be as high

Table 1. Cross system comparison of bacterial production and cell numbers[a]

Aquatic system	nM thymidine 1^{-1} d^{-1}	Cells ml^{-1} ($\times 10^6$)	Reference
Lake Søbygard, Denmark			17
Winter	0.12–0.36	3–8	
Summer	7.2–10.8	15–30	
Hartbeespooort Dam, South Africa			36
Surface	0.024–6.0	2.45–32.20	
Bottom	0–0.64	4–8	
Amazon River System			4
Mainstem	0.11–0.36	0.9–1.26	
Tributaries	0.08–0.63	0.46–2.59	
Upton Lake, NY	~0.06–0.6	4–6	30
Lake Fryxell, Antarctica	**0–0.453**	**0.53–43.6**	**Present study**
	NR	**1–8**	**40**
Ross Sea Polynya	~0.03–0.56	1–4	8
McMurdo Sound, Antarctica	0.00006–0.26	0.06–1	9
West lobe, Bonney, Antarctica	**0–0.05**	**0.1–8.23**	**Present study**
Bottom	**NR**	**0.3**	**47**
Lake Hoare, Antarctica	**0–0.03**	**0.26–6.68**	**Present study**
	NR	**0.1–4**	**28**
East lobe, Bonney, Antarctica	**0–0.02**	**0.032–8.18**	**Present study**
	NR	**0–0.7**	**20**
Bottom	**NR**	**0.1**	**47**
Caribbean Sea	0–0.0144	0.1–0.6	35
Gulf Stream	0.0024–0.0132	0.09–0.9	35
Sargasso Sea	0.0036–0.011	0.15–0.55	35

[a] Aquatic systems are listed in order of decreasing productivity; NR, not reported

Table 2. Average (min-max) bacterial production in Lake Fryxell, Hoare, and Bonney (integrated volumetrically) listed in order of decreasing productivity

Lake	Volume ($m^3 \times 10^5$)	Average bacterial production ($\times 10^5$ mg C d^{-1})
Fryxell	53.56	41.2 (11.1–115.1)
Bonney, East lobe	51.67	3.43 (1.34–6.42)
Hoare	24.34	2.83 (0.89–6.66)
Bonney, West lobe	27.82	2.71 (0.70–4.34)

as 6.5×10^{10} cells m^3 d^{-1} in Lake Fryxell, based on preliminary results. HNAN abundance ranges from 0 to 694 ml^{-1} [Roberts and Laybourn-Parry, unpublished data]. Grazing rates by ciliates in these lakes are not available. Ciliates and HNAN remove up to 9.7% of bacterial production in Crooked Lake, Antarctica, but ciliates were not an important component of the plankton community in Lake Bonney [22, 15]. Removal of bacterial water column biomass averaged 3% d^{-1} (range = 0.01 to 7% d^{-1}), excluding a single rate of 15% d^{-1} on 24 October 1993, in the east lobe of Bonney. Rotifer feeding experiments have thus far been inconclusive [Shultz, Kepner, and Wharton, unpublished data]. Rotifers, however, are not believed to be significant in bacterioplankton losses, because they are primarily confined to the littoral zone of these lakes [15].

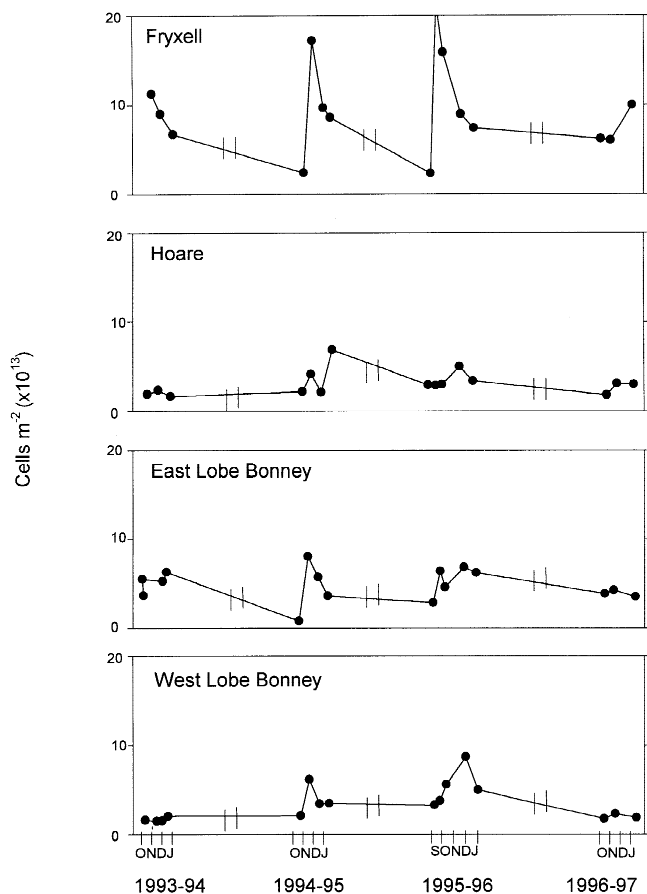

Fig. 6. Water column integrated bacterial populations ($\times 10^{13}$ cells ml^{-1}) in Lakes Fryxell, Hoare, and Bonney during 1993–1997. Hash marks denote winter periods when data was not collected.

Another possibility for the cause of bacterial cell loss may be viruses. Planktonic, extracellular, icosahedral viruses have been observed in Lakes Bonney and Hoare by transmission electron microscopy. Production potential by viruses in Lake Hoare was as much as 58% higher than that measured in coastal seawater mesocosms by the same method [18]. Though bacterial cells infected by viruses have yet to be observed, bacteria have been observed by TEM to be surrounded by them. Additionally, water column virus-like particle (VLP) profiles enumerated by epifluorescent microscopy were found to be significantly correlated with bacterial numbers. VLP profiles were found to increase throughout the season. A mid-summer peak was observed in December [18]. Virally-mediated mortality may be a factor regulating bacterial biomass, and may play a role in the regeneration of nutrients and organic carbon. Additional sources of bacterial loss may be Myxobacteria, *Bdellovibrio* spp., or other parasitic bacteria, but these have not been specifically investigated.

Table 3. Average bacterial cell loss rates and turnover time (min-max) in the trophogenic zone and throughout the entire water column of Taylor Valley Lakes Fryxell, Hoare, and Bonney

Lake	Bacterial cell loss rate ($\times 10^{11}$ cells m^{-2} d^{-1})	Turnover rate (d^{-1})
Fryxell		
TZ[a]	2775 (3.19–6271)	18.3 (0.05–37.9)
WC[b]	22 (8.84–41.6)	0.02 (0.001–0.03)
Hoare		
TZ	2.47 (0.24–5.19)	0.02 (0.001–0.03)
WC	4.59 (0.52–10.3)	0.01 (0.002–0.03)
Bonney East lobe		
TZ	2.49 (0.52–7.10)	0.03 (0.006–0.09)
WC	16.7 (2.4–64.8)	0.03 (0.004–0.14)
Bonney West lobe		
TZ	2.73 (0.78–4.26)	0.03 (0.01–0.05)
WC	6.33 (0.17–17.7)	0.02 (0.009–0.03)

[a] TZ, trophogenic zone
[b] WC, entire water column

Our study is the first to rigorously sample bacterioplankton in Lake Fryxell, Hoare, and Bonney during the winter–spring transition (September–October). Though chlorophyll-*a* and primary productivity during this period were low to undetectable, [24; Priscu, unpublished data], bacterial populations were active and cell numbers were high in September (especially just below the ice cover). These results show that bacterial populations remain active and are not grazed to extinction during the winter. The limited sampling season, due to logistical constraints, has left the autumn and winter period largely unstudied. Phytoplankton data do exist from two winters, for Lake Fryxell, where automated sampling devices were used to collect preserved samples [27]. Though biomass decreased through winter, algal abundance was greatest in April. Populations of two cryptophytes (*Cryptomonas* and *Rhodomonas*) increased during winter. Mixotrophy, as a means of survival, has been proposed for these populations [23]. No longer can the ‘‘long, dark winter’’ be considered insignificant; winter microbial dynamics must be studied in the future, to gain a more complete understanding of these lakes.

The results presented here represent the initial stages of a long-term monitoring program in the McMurdo Dry Valleys, Antarctica. Lake Fryxell is the most dynamic of these lakes, with respect to integrated bacterial production, cell numbers, and loss rates, followed by west lobe Lake Bonney, east lobe Lake Bonney, and Lake Hoare. Changes in physical, chemical, and biological profiles, over time, may be an indication of local or global climate change, or increased anthropogenic impact in the area. One-way analysis of variance did not show an increase in bacterial production during this study, but four years may not be a sufficient period in which to detect ‘‘long-term’’ changes. Increased intra-annual sampling and a longer data set would provide more insight into potential changes in the populations. Changes in bacterial production and biomass are significant in the carbon budgets of these lakes, and may ultimately prove important to the overall food web.

Acknowledgments

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