

Bacterial dissolved organic carbon demand in McMurdo Dry Valley lakes, Antarctica

Abstract—The proximal substrate source of planktonic bacteria is dissolved organic carbon (DOC), and the combined sources of DOC (bulk, phytoplankton production, and advected) set an upper limit on how much C is available for bacterial respiration (BR). We compared measurements of bacterial production (BP) and estimates of BR to measurements of what we assumed to be the major DOC inputs for three permanently ice-covered lakes in Antarctica: Lakes Fryxell, Hoare, and Bonney. These measured inputs, which included phytoplankton extracellular release (ECR), stream input, and upward diffusion of DOC across the chemocline, sediments, and benthic microbial mats, were three to eight times smaller than planktonic BR, suggesting that a major source of bacterial C was unaccounted for. Despite overestimating DOC and doubling bacterial growth efficiency (BGE), BR in the lakes was 1.25–2 times greater than our estimate of DOC supply. We hypothesize that a major source of organic C for planktonic bacteria in these lakes comes from drawdown of bulk DOC and/or decomposition of particulate material.

Dissolved organic carbon (DOC) represents the proximal substrate of heterotrophic planktonic bacteria production, and the sum of DOC inputs (bulk, phytoplankton production, and advected) restricts how much C is available for bacterial respiration (BR). The classical view holds that phytoplankton production sustains planktonic communities; however, depending on the temporal and spatial scales used to analyze the ecosystem, respiration often exceeds production in many oligotrophic waters (Coveney and Wetzel 1995; del Giorgio et al. 1997; Carignan et al. 2000). Determining the balance of production and respiration is fundamental to understanding C flow in aquatic ecosystems.

The Taylor Valley Lakes (Lakes Fryxell, Hoare, and Bonney) of the McMurdo Dry Valleys, Antarctica, provide a unique system in which to study bacterioplankton DOC demand because phytoplankton production is limited to approximately 5 months each year, whereas bacterial activity occurs throughout the year (Takacs and Priscu 1998; Priscu et al. 1999). Additionally, the lakes are virtually closed systems owing to the permanent 4- to 5-m ice cover, lack of outflow, and relatively low inflow. Although $\approx 20\%$ of the DOC pool in Lakes Fryxell and Hoare is comprised of low-molecular-weight fulvic acid that is microbial in origin (McKnight et al. 1991, 1993), the remainder of the bulk DOC pool of these lakes is relatively high-molecular-weight DOC that is presumably recalcitrant. Phytoplankton extracellular release (ECR) and upward diffusion from the nutrient-rich hypolimnia (Howes et al. 1992; Priscu 1995) are believed to be the two dominant mechanisms that supply new DOC to the trophogenic zone of the lakes.

To test this assumption, we constructed partial C budgets for Lakes Fryxell, Hoare, and Bonney to compare measurements of DOC supplied from primary production, stream input, and diffusion to bacterial production (BP). DOC demand and supply relationships were further explored by in-

cluding estimates of BR to determine the role of unaccounted-for sources of DOC in the regulation of bacterial productivity during the Austral summer. The results of our budgets are discussed with respect to the annual light:dark cycle in Taylor Valley Lakes.

Site description—Our study concentrated on Lakes Fryxell, Hoare, and the east and west lobes of Lake Bonney, which lie in the Taylor Valley ($\sim 77^{\circ}37'S$, $\sim 163^{\circ}00'E$). While these lakes have varying degrees of chemical stratification, generally all contain nutrient-rich deep water covered by a relatively nutrient-poor trophogenic zone (Priscu 1995; Spigel and Priscu 1998). The trophogenic zone is defined as the layer where oxygenic photosynthesis is measurable: to 18 m in Lake Hoare and the east lobe of Lake Bonney, to 17 m in the west lobe of Lake Bonney, and to 9 m in Lake Fryxell. The permanent ice cover of these lakes prevents wind-driven mixing, which, coupled with low advective stream input, allows vertical chemical and biological gradients to develop and persist (vertical mixing is at the molecular level throughout the water column; Spigel and Priscu 1998). DOC in these lakes increases with depth, and in the highly stratified Lakes Fryxell and Bonney, the gradients are extreme (Fig. 1). DOC concentrations range from 0.16 mg L^{-1} in the surface waters of the lakes to 34 mg L^{-1} in the bottom waters. Temporal changes in trophogenic zone and water-column DOC concentrations (volume weighted and depth integrated) were most variable in Lake Bonney's east lobe and Lake Fryxell during the Austral summers of 1993–1997, whereas DOC concentrations in the west lobe of Lake Bonney and Lake Hoare were less variable (Fig. 2). Although DOC varied over the season, a clear temporal trend was not apparent. Phytoplankton and bacterioplankton production (Fig. 3) are greatest just below the ice cover (5 m) in the spring, but production peaks at the chemocline become more pronounced than the 5-m peaks as the summer progresses (Priscu 1995; Lizotte et al. 1996; Takacs and Priscu 1998). Detailed descriptions of the lakes and streams may be found in Green and Friedmann (1993) and Priscu (1998).

Partial DOC budgets—Budgets based on the presumed major DOC inputs (phytoplankton ECR, stream input, and diffusion) were calculated for each sampling season (October–January, except for the 1995–1996 season, which was September–January) in the trophogenic zone and water column of each of the lakes. Lake Bonney has two basins (east and west lobes), connected by a narrow ($\sim 20 \text{ m}$ wide), shallow (12 m) sill (Spigel and Priscu 1998) that prevents mixing of waters between the two lobes below 12 m. Therefore, separate budgets were constructed for the east and west lobes of Lake Bonney because of the lack of deep-water interchange between the two lobes. Samples were collected at least once a month during the Austral summer over the deepest portion of the lakes at 2–3-m intervals throughout the

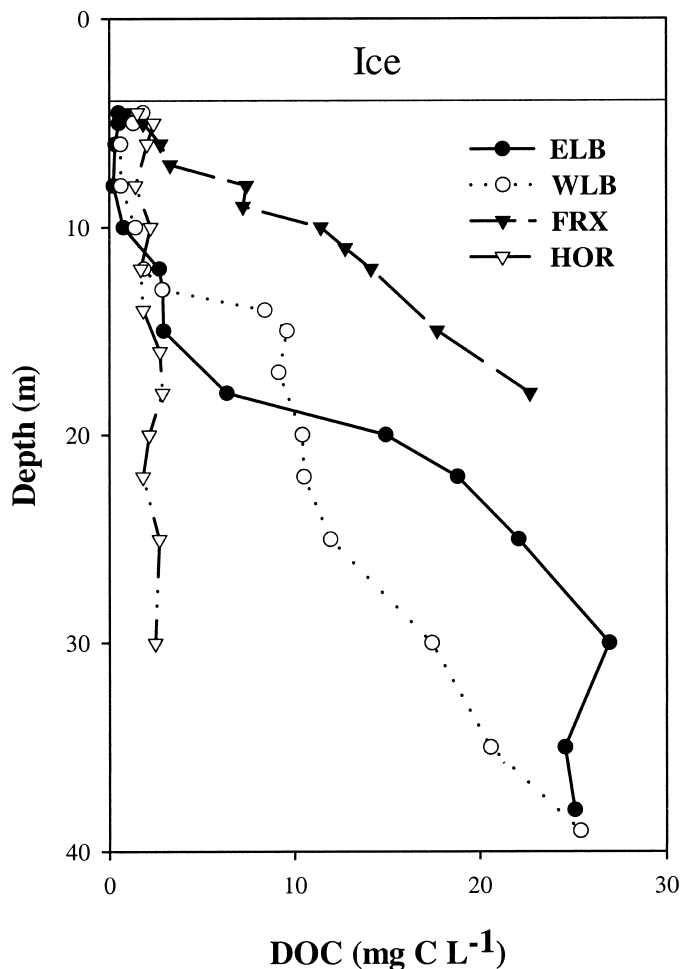


Fig. 1. DOC profiles in Lakes Fryxell (FRX), Hoare (HOR), east lobe Bonney (ELB), and west lobe Bonney (WLB) during early December 1995.

water column; all depths are reported from the water level within the sampling hole. Biological and chemical profiles do not significantly differ horizontally in Lake Bonney (Priscu unpubl.). Stream flow is highly variable in the valley on both a daily and annual basis (Conovitz et al. 1998). Discharge was computed for streams with continuous flow recorders as the sum of mean daily flows at the site recorded. Estimates for nongauged streams were computed by comparing periodic discharge measurements at nonrecording sites to discharge simultaneously occurring at neighboring gauged streams, and computing a ratio of discharges at the respective streams (Conovitz et al. 1998).

Seasonal BP (kg C) was estimated as the sum of volume-weighted, depth-integrated BP during each sampling season. Bacterioplankton productivity was assayed by ^3H -thymidine incorporation (20 nM final concentration; Takacs 1999) on whole lake water in the dark at 1–4°C as described previously (Takacs and Priscu 1998). The thymidine incorporation to cell production conversion factor determined for these lakes during peak bacterial growth (Takacs and Priscu 1998) is approximately two times greater than commonly used published values (Ducklow and Carlson 1992). Because we

did not want to overestimate BP in our budget, we used the more conservative value of 2.0×10^{18} cells (mole thymidine) $^{-1}$, which is the average of 97 studies (Ducklow and Carlson 1992). A C conversion factor of 11 fg C cell $^{-1}$ was applied, which was determined from bacterial biovolume measurements in these lakes (Kepner et al. 1998; Takacs and Priscu 1998).

DOC supply (kg C) to the trophogenic zone of the lakes was calculated as the sum of phytoplankton ECR, stream input, and diffusion (upward DOC flux across the chemocline into the trophogenic zone and DOC flux from sediment pore waters and microbial mats during the sampling period). We used these three sources of DOC because although they do not comprise total DOC supply, they were expected to be the major contributors of DOC to the trophogenic zones of the lakes. Thus, DOC supply is incomplete. Potential DOC inputs, including sources that we did not quantify, are shown in Fig. 4. ECR was estimated from particulate primary production using the upper end of the range (3–25% of volume-weighted primary production) reported by Sharp (1993). Primary production was determined by measuring light-mediated uptake of ^{14}C -bicarbonate into particulate matter during 24-h in situ incubations (Lizotte et al. 1996).

Stream DOC load (kg C) to the lakes was computed during each season by multiplying the average DOC concentration of each stream by its respective discharge during the sampling season. Taylor Valley stream nutrients are derived from the microbial mats that inhabit the streambeds (Vincent et al. 1993; Aiken et al. 1996). Stream DOC is highest during the beginning of the summer when streams first begin to flow (Aiken et al. 1996); therefore, stream DOC load has been overestimated in this budget.

DOC diffused upward across the 18-m plane (9 m in Lake Fryxell) into the trophogenic zone during each sampling season (kg C) was computed according to the following equation:

$$\text{DOC}_{\text{diffused}} = \left(D \frac{\partial C}{\partial z} \right) A \cdot t \quad (1)$$

where D is the vertical diffusion coefficient ($\text{m}^2 \text{d}^{-1}$) estimated for the lakes, $\partial C / \partial z$ is an average DOC gradient ($\text{kg C m}^{-3} \text{m}^{-1}$) across the bottom of the trophogenic zone of each lake, A is the area (m^2) of the lake at the bottom of the trophogenic zone, and t is the length of the sampling season (in days). The vertical diffusion coefficient is assumed to be near $1.8 \times 10^{-4} \text{m}^2 \text{d}^{-1}$ in these lakes (Spigel and Priscu 1998); however, this diffusion coefficient would overestimate DOC flux because of the molecular mass of the labile DOC in these lakes (463–468 Daltons; Aiken et al. 1991). We estimated a vertical diffusion coefficient of $1.6 \times 10^{-5} \text{m}^2 \text{d}^{-1}$ for DOC based on the Wilke–Chang correlation (Bird et al. 1960), which accounts for the molecular mass of the solute. Our diffusion coefficient is similar to the one used to predict chlorofluorocarbon (CFC) concentration profiles in Lakes Fryxell and Hoare ($4.93 \times 10^{-5} \text{m}^2 \text{d}^{-1}$; Tyler et al. 1998) if the molecular mass of CCl_3F (137 Daltons) is taken into account. Lake Fryxell sediment pore-water DOC is of a different composition than deep-water DOC and is a significant source of DOC to Lake Fryxell and presumably the other lakes (Aiken et al. 1991; McKnight et al. 1993). DOC

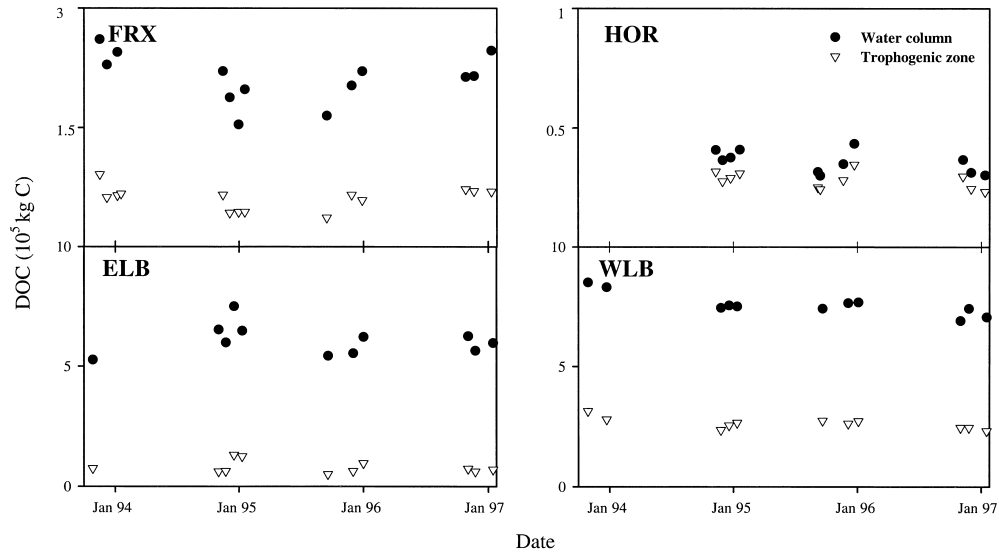


Fig. 2. Volume-weighted DOC integrated throughout the trophogenic zone and the entire water column of Taylor Valley Lakes Fryxell (FRX), Hoare (HOR), and the east (ELB) and west lobe of Lake Bonney (WLB) during the Austral summers of 1993–1997. Note the different axes scales for the lakes and that DOC was not measured during the 1993–1994 sampling season in Lake Hoare.

flux from sediment pore water was calculated as in Eq. 1, but tortuosity and bioturbation were ignored because little is known about the composition of the sediments of these lakes, and their benthic fauna are primarily microbial. The diffusion coefficient ($1.6 \times 10^{-5} \text{ m}^2 \text{ d}^{-1}$) that we used for DOC is on the same order of magnitude applied in other pore waters (Jones and Bowser 1978). We estimated the DOC gradient at the bottom of the lakes from a second-order polynomial function fitted to DOC concentration plotted against depth (z) from the sediment ($r^2 = 0.82\text{--}0.99$). The

first derivative of this function was evaluated at $z = 0$ to estimate the DOC gradient at the bottom of each lake. An additional source of DOC is from the microbial mats that inhabit the littoral and photic zones of Lakes Fryxell and Hoare and, to a lesser extent, of Lake Bonney (Hawes and Schwarz 1999). Dissolved organic nitrogen (DON) gradients within Lake Hoare benthic mats (Hawes et al. 1999) were used to estimate a mat DOC supply rate of $3.6 \text{ mg m}^{-2} \text{ d}^{-1}$ by assuming a DOC:DON flux ratio of 1:10 (by moles) for the mats (Hawes pers. comm.). Microbial mats were as-

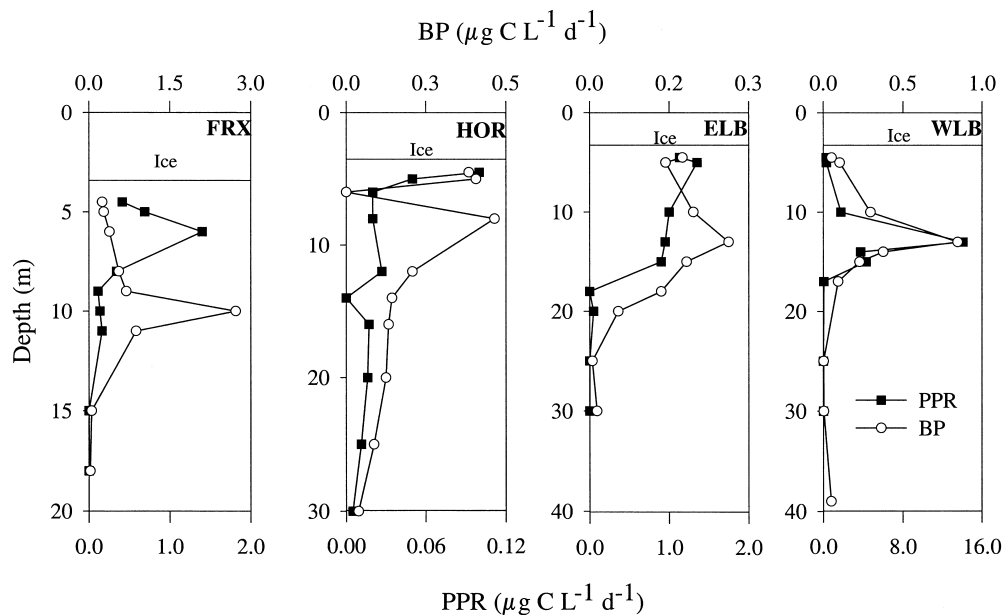


Fig. 3. Primary productivity (PPR) and BP rate in Lakes Fryxell (FRX), Hoare (HOR), east lobe Bonney (ELB), and west lobe Bonney (WLB) during early December 1995. Note the different axes scales for the lakes.

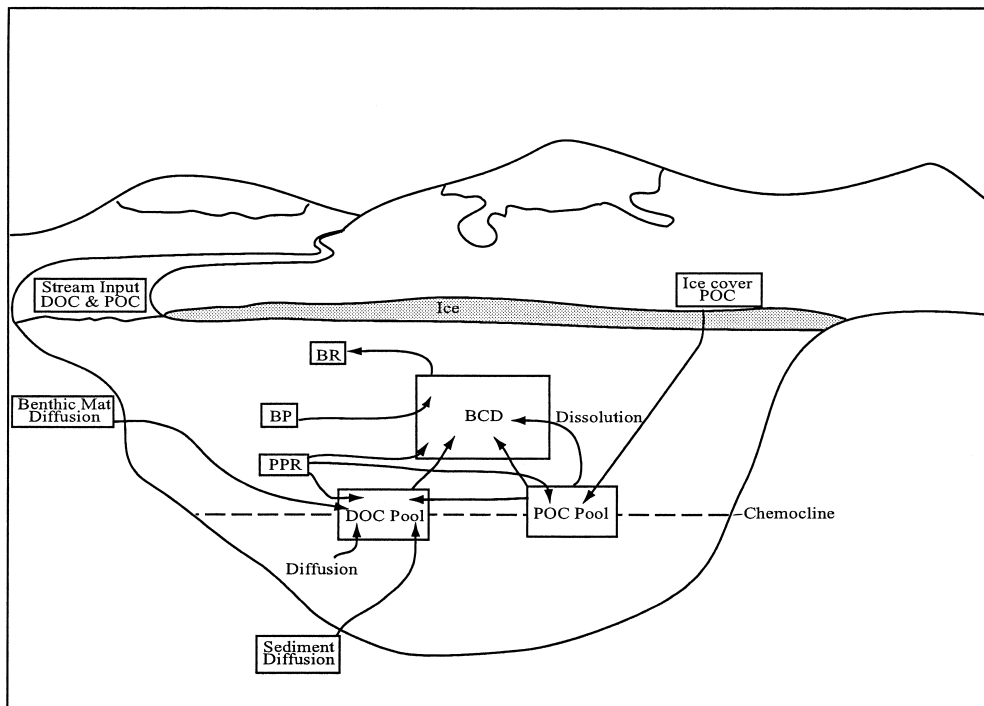


Fig. 4. Summer DOC supply and bacterial carbon demand (BCD) of Taylor Valley Lakes. In this study, we measured ECR from phytoplankton primary productivity (PPR), stream DOC, and diffusion, which were believed to be the major DOC sources to the lakes. Other DOC sources, such as stream POC and its subsequent dissolution, were estimated. DOC and POC from cell lysis and predation are unknown, and POC sedimented through cracks in the ice cover is a potentially large but undetermined source of carbon to the lakes. BR was estimated from BP.

sumed to inhabit the entire area of the photic zone benthos in the budgets. DOC supply to the entire water column of the lakes was calculated similar to the trophogenic zone, except DOC flux from the hypolimnion was omitted.

In general, BP was two to three times greater than DOC supply measured (ECR, stream input, and diffusion) in Lakes Fryxell and Hoare, whereas DOC supply was approximately 1.6 times greater than BP in Lake Bonney. Water column BP and DOC supply relationships were similar to trophogenic zone (data not shown). Phytoplankton ECR provided the majority of DOC supplied to the trophogenic zone of the lakes relative to stream input and diffusion.

Because BP represents the transfer of organic C from the dissolved pool to bacteria, BP is not a true loss from the system; rather, BP represents a temporary conversion of DOC to bacterial cells. We used our measurements of BP to estimate BR, which is a loss of organic C. In general, BR varies with BP and the trophic status of an ecosystem and can be described by the following relationship (del Giorgio and Cole 1998):

$$BR = 3.7 \times BP^{0.41} \quad (2)$$

Bacterial growth efficiency (BGE) in Taylor Valley Lakes determined from Eq. 2 averaged 0.22, 0.09, 0.08, and 0.11 in Lakes Fryxell, Hoare, and the east and west lobes of Lake Bonney, respectively. Because of the relatively low BGEs that result by applying Eq. 2 to Taylor Valley Lake BP data, BR further imbalances supply and demand relationships in

Lakes Fryxell and Hoare and results in BR exceeding measured supply in Lake Bonney.

In addition to the DOC sources that we measured, other potential inputs were estimated. An important but relatively unexplored C source to the lakes is stream particulate organic carbon (POC), which was measured during a 1-week period in 1997 and was on the same order of magnitude as stream DOC (Welch et al. pers. comm.). Dissolution of POC supplied from stream input, combined with the bulk POC pool of the lakes, is potentially a large source of DOC. Although dissolution has not been measured directly in the lakes, bacterial decomposition of ^{14}C -labeled phytoplankton was measured in Lake Bonney (Prisco 1992) and was greatest ($0.08\% \text{ d}^{-1}$) just below the ice cover. If this decomposition rate is applied to water-column and stream POC during the sampling season, the relative difference between supply and demand is decreased, but the general outcome of the budgets is unchanged. Data from 1995 to 1996, the season that we sampled most frequently, are shown in Table 1. BR was three to eight times greater than estimated DOC supply. Even if BGE is doubled, BR is still greater than the DOC sources that we have estimated. Our DOC budgets clearly indicate that summer BP is not balanced by DOC supplied from ECR, streams, diffusion, and POC in Lakes Fryxell, Hoare, and Bonney, despite underestimating BP and overestimating DOC supply. Consequently, BP in Taylor Valley Lakes must be dependent on a relatively large, unaccounted-for source of DOC during the Austral summer.

Table 1. Partial DOC budget for the photic zone of Taylor Valley Lakes during the 1995–1996 sampling season. ECR, streams, and diffusion were hypothesized to be the major sources of DOC to the lakes; other relatively unexplored sources such as POC dissolution are potentially important in DOC supply. East and west lobes of Lake Bonney, ELB and WLB.

kg DOC source (sink)	Fryxell	Hoare	ELB	WLB
ECR	304	24	668	365
Streams	154	15	136	94
Diffusion	97	27	29	12
POC dissolution	803	201	449	185
Input	1,358	267	1,282	656
BP	1,109	205	561	277
Outputs				
BR	4,615	2,334	5,915	1,966
BR _{2×BGE}	1,753	1,065	2,677	845
Net (deficit)	(3,257)	(2,067)	(4,633)	(1,310)
Net (deficit) _{2×BGE}	(395)	(798)	(1,395)	(189)

ECR, streams, diffusion, and BP were measured in the lakes. BR was calculated from BP (del Giorgio and Cole 1998), and dissolution of stream and lake POC was estimated assuming a dissolution rate of 0.08% d⁻¹ (Priscu 1992). Stream POC was measured by K. Welch, W. B. Lyons, and C. Nezat (pers. comm.). BR_{2×BGE} represents bacterial respiration when BGE is doubled.

C demand and supply imbalances in other lakes have been reconciled by recognizing the importance of reassimilation of bacterial biomass by other consumers, including bacteria (Strayer 1988). However, because of the low BGE estimated for the lakes and presumably low nonrespiratory losses (*L*) (the lakes have no outflow and sinking rates are low; Priscu 1992; Takacs and Priscu 1998), BP cannot sustain as much reassimilation as other systems where BGE is higher. For example, the amount of C that remains in an ecosystem after *n* cycles of assimilation is $I(BGE)^n$, where *n* can be determined as:

$$n = \frac{\log\left(\frac{L}{I}\right)}{\log G} \quad (3)$$

and *I* represents total organic C input (allochthonous and autochthonous, including contemporaneous secondary production). When BGE is ≈ 0.01 (Lakes Hoare and Bonney) and *L* is assumed to be between 1 and 10%, *n* ranges from 1 to 1.5 times. However, because BGE is higher in Lake Fryxell, the amount of C available for reassimilation is greater ($n > 3$). Based on BGE, two different scenarios of C supply and demand relationships emerge within Taylor Valley Lakes. Although summer BR is not balanced by contemporaneous DOC supply in Lakes Hoare and Bonney, there is ample organic C from BP alone in Lake Fryxell to balance summer BP. In Lakes Hoare and Bonney, additional sources of DOC are necessary to balance the budgets.

Additional sources of DOC for the bacterioplankton include DOC provided from the lysis of cells by grazers and viruses, the bulk DOC pool, and dissolution of additional POC sources. Although grazing and viruses are important in

Taylor Valley Lakes (Laybourn-Parry et al. 1997; James et al. 1998; Kepner et al. 1998), we are presently unable to estimate the DOC contribution made by these groups of the food web. The low-molecular-weight fraction of DOC in the lakes (20% of the DOC pool) is presumed to be relatively labile and important to BP in these lakes (McKnight et al. 1991, 1993). The turnover time of water-column DOC ranged from 46 to 407 yr, or from 9 to 82 yrs if only 20% of the DOC was assumed to be utilizable. Additionally, the remaining fraction of the DOC pool, which is of a relatively higher molecular mass, is presumed to be less labile, but it would offer an additional source of DOC to the bacteria. A large imbalance between water-column production (1,951 mg m⁻² yr⁻¹) and sinking flux (8,556 mg m⁻² yr⁻¹) in the east lobe of Lake Bonney (Priscu et al. 1999) points to the importance of POC supplied through conduits and cracks in the permanent ice covers. Sediments and organic matter of aeolian origin are effectively trapped in the ice cover, which also harbors microbial consortia that are productive during the summer months when liquid water forms within the ice column (Priscu et al. 1999). Because it is presently unknown how much of this sediment flux is introduced during sediment trap retrieval, the contribution of C through the ice cover is still unclear. Understanding the importance of the ice cover to lake C fluxes will be crucial to determining the trophic status of Taylor Valley Lakes as net autotrophic or heterotrophic systems.

Our budgets are based solely on measurements from the sampling season because, due to logistical constraints, we could not collect data from autumn and winter. Hence, it is not clear whether bacterioplankton DOC demand is balanced by the sources measured here on an annual basis. Autumn is potentially a period of rapid phytoplankton growth because of increased light penetration through the ice cover (Fritsen and Priscu 1999). Based on light-driven primary production models, autumn phytoplankton growth can provide a considerable pulse of DOC to the bacterioplankton (Priscu et al. 1999), which would be important in an annual budget. Based on the bacterial DOC demand and summer DOC supply budgets presented here, there is no significant surplus of DOC supplied to Lakes Hoare and Bonney during the sampling season that would enable bacterioplankton to sustain summer production rates into the winter. Winter bacterioplankton growth must be dependent on decomposition of particulate organic matter, the bulk DOC pool, and DOC released by lysed cells. Year-round data collection will allow the ecological significance of the seasonal uncoupling of phytoplankton and bacterioplankton production in these lakes to be determined.

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