Carbon Transformations in a Perennially Ice-Covered Antarctic Lake

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Autotrophic production of organic carbon and its subsequent heterotrophic transformations drive biogeochemical reactions and influence species abundance and diversity in all ecosystems. The timing and magnitude of organic carbon production is particularly critical in desert ecosystems, where a paucity of liquid water, together with extremes in temperature, limits the period when biological activity can exist. Polar desert systems have additional stresses imposed on them by amplified seasonal patterns in sunlight. The McMurdo Dry Valleys of Antarctica is one of the most extreme deserts on the planet, with precipitation of less than 10 cm·yr^{-1} and an average annual air temperature near –20 °C (range from approximately –55 °C to –5 °C; Clow et al. 1988). These valleys, which are located adjacent to McMurdo Sound (76.5–78.5° S, 160–164.5° E), form the largest ice-free region (approximately 4500 km^2) on the Antarctic continent (Fountain et al. 1999). The McMurdo Dry Valley landscape is a pristine mosaic of perennially ice-covered lakes, intermittent streams, arid soils, barren mountains, and surrounding glaciers (Moorhead et al. 1999, Virginia and Wall 1999). There are no vascular plants or vertebrates, and no established insects; microbes dominate the life forms in the area.

Despite the extremely dry and cold conditions, the perennially ice-covered lakes of the dry valleys provide a habitat in which liquid water and associated life persist throughout the year. Perennial lake ice overlying liquid water occurs nowhere else on Earth but the McMurdo Dry Valleys. McKay et al. (1985) developed a physical model that describes how a relatively thin (3–6 m) ice cover can persist over a liquid water column and concluded that the existence of perennially ice-covered lakes is determined not by average air temperatures but by the generation of glacial meltwater during the brief summer periods, when air temperatures are near or above freezing. This model has also been applied to Mars, where permanently ice-covered lakes are thought to have existed between 3.8 billion and 3.1 billion years ago (McKay 1997). It is this delicate meteorological balance that provides the only annual oasis for aquatic life in the McMurdo Dry Valleys, in what would otherwise appear to be an inhospitable environment. Work on other high-latitude systems (Vincent and Ellis-Evans 1989, Priscu 1998) underscores the importance of lake systems as major refugia for biological activity and

ANTARCTIC LAKES IN THE MCMURDO DRY VALLEYS CONTAIN A COMPLEX FOOD WEB THAT IS DRIVEN BOTH BY ONGOING ORGANIC CARBON PRODUCTION AND CARBON LEFT AS A LEGACY OF PAST EVENTS

stresses the role of extremes in solar radiation and temperature in shaping and regulating these environments.

The early British Antarctic expeditions were the first to describe the lakes in the McMurdo Dry Valley region (e.g., Scott 1905, Taylor 1922). The lakes remained unstudied after these seminal studies until the early 1960s, when the first quantitative measurements were made of their physical, chemical, and biological properties (e.g., Angino and Armitage 1963, Angino et al. 1964, Goldman et al. 1967, Goldman 1970). Results from these latter studies led to the general conclusion that the lakes are relatively simple ecosystems, with food chains and nutrient cycles that are much reduced or nearly absent (Parker and Simmons 1985). Despite the apparent lack of ecological complexity, work that began in the mid-1980s has shown that complex

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food webs and biogeochemical cycles do exist. These polar desert lakes harbor a complex consortium of interacting organisms, albeit microbial ones (e.g., Vincent and Ellis-Evans 1989, Green and Friedmann 1993, Lyons et al. 1997, Priscu 1998).

It is now clear that the presence of liquid water in the McMurdo Dry Valleys produces a cascade of tightly coupled events that ultimately leads to the biological production and cycling of organic carbon and related elements. It is also evident that an integrated knowledge of biological, chemical, and physical factors is required to understand biogeochemical dynamics within this cold desert ecosystem. The paucity of liquid water and the delicate balance between gains and losses of organic carbon make the McMurdo Dry Valleys ecosystem one of the most sensitive indicators of environmental change on the planet. This "polar amplification"—in which certain chemical, physical, and biological properties are exaggerated—make Antarctic lakes ideal experimental systems that offer potential insights into ecosystem structure and function that are not obvious in less extreme systems.

Ecosystem dynamics in the McMurdo Dry Valleys are even more complex in light of the recent recognition that much contemporary biological activity is related to natural legacies of past events. For example, dissolved organic carbon and nutrient salts that accumulate in the deep waters of many dry valley lakes were deposited during the complex evolutionary history of the region (Burkins et al. 1996, Lyons et al. 1998a, 1998b, 1999). The upward diffusion of these constituents supports a large portion of the biological activity within the lakes (Priscu 1995, Takacs and Priscu 1998). Thus, current patterns of biological activity and diversity reflect past distributions of water, nutrients, and organic carbon. The McMurdo Dry Valleys ecosystem must be viewed in the context of this temporal legacy to understand many of the features that are observed today. In this article, we describe the physical, chemical, and biological conditions in Lake Bonney, a prominent lake within the McMurdo Dry Valleys. We then use this framework to discuss microbial transformations of organic carbon within the water column.

Lake Bonney

The McMurdo Dry Valleys contain a number of perennially ice-covered lakes. However, those within the Taylor Valley currently receive the most attention because they are the focus of the McMurdo Dry Valleys Long-Term Ecological Research (LTER) program. The McMurdo LTER program is currently examining long-term relationships between the conditions in Lakes Bonney, Hoare, and Fryxell and temporal variation in other facets of the ecosystem (e.g., meteorology, glacial melt, soils, stream dynamics). Although the lakes are located relatively close to one another, they differ drastically in their physical, chemical, and biological properties (e.g., Priscu 1997, Lyons et al. 1999). In this article, we focus on the east lobe (or basin)

of Lake Bonney, for which the longest continuous set of water column biological measurements is available.

Lake Bonney consists of two distinct basins (east lobe, 3.5 km²; west lobe, 1.3 km²), each approximately 40 m deep and permanently covered with approximately 4 m of ice (Figure 1). The permanent ice cover is important to the biology, chemistry, and physics of the lake for many reasons: wind-induced turbulence is nonexistent, resulting in vertical mixing being controlled by molecular diffusion (Spigel and Priscu 1998); exchange of gases between the liquid water and the atmosphere is highly restricted (Craig et al. 1992, Priscu et al. 1996, Priscu 1997); attenuation of light is high (Priscu 1991, Howard-Williams et al. 1998, Fritsen and Priscu 1999), leading to reduced rates of primary production (e.g., Lizotte and Priscu 1992a, 1992b); and sediment deposition through the water column is modified significantly (Nedell et al. 1987, Squyres et al. 1991). The lake ice also provides a viable habitat for microorganisms during periods of high ice porosity (Fritsen and Priscu 1998, Fritsen et al. 1998, Priscu et al. 1998).

Temperatures in Lake Bonney range from near 0 °C, just beneath the ice cover, to a maximum of 6.1 °C at 14 m and a minimum of −1 °C in the deep saline water at 36 m (Figure 1). Despite the unusual temperature profile, the water column remains highly stable (i.e., it is not mixed by buoyant forces) because of the salt gradient, which forms a distinct chemocline in the water column. Spigel and Priscu (1996, 1998) have shown that the salinity profile is extraordinarily constant from year to year and that the curvature of the profiles is consistent with the effects of diffusion. The temporal stability in salinity, and subsequently density, leads to the high stability of this system and the absence of turbulence in the interior of the basin. Spigel and Priscu (1998) also showed that temperature profiles, although retaining their general shape from year to year, vary more than salinity profiles. The difference between salinity and temperature is to be expected, because temperature responds to the seasonal variation in heat transfer between the lake and the atmosphere. The typical temperature increase during the austral summer (November–January) is approximately 0.09 °C and is confined to the upper 25 m of the water column, below which only approximately 0.11% of the incident solar radiation remains (based on a water column extinction coefficient of 0.15/m and 3% transmission through the ice cover).

Dissolved oxygen from just beneath the ice to 15 m in depth exceeds 1000 µM, which is between 250% and 350% higher than what would occur if the water was saturated with the air above the lake (Figure 1). Oxygen diminishes precipitously below 15 m, reaching a minimum of 17.8 µM at 17 m. Oxygen at depths below 20 m is only about 10% of air saturation values. The small oxygen peak at 35 m has persisted for more than 10 years (John C. Priscu, unpublished data), and we believe it to be a legacy of a past drawdown event that occurred perhaps 1200 years ago (Lyons et al. 1999). Vertical dissolved inorganic nitrogen

Figure 1. Physical and chemical properties under the permanent ice cover of Lake Bonney. (a) Researchers drilling through the 4 m ice cover of Lake Bonney. (b) Vertical water column profiles of dissolved oxygen (O_2) and soluble reactive phosphorus (PO_4^{3-}) superimposed over temperature (°C) contours in the east lobe of Lake Bonney. (c) Vertical water column profiles of ammonium (NH_4^+), nitrite (NO_2^-), and nitrate (NO_3^-) superimposed over salinity (PSU, or practical salinity scale; essentially equivalent to parts per thousand) contours in the east lobe of Lake Bonney. Salinity, temperature, and dissolved oxygen data were collected in 1993; phosphorus and nitrogen data represent averages from 1989 through 1997. PSU.

and phosphorus profiles from 1989 through 1996 are similar to the salinity profiles, with relatively low values above 15 m followed by large increases below 15 m (Figure 1). The average molar ratio of dissolved inorganic nitrogen to soluble reactive phosphorus ranges from 64 to 616 between 5 m and 17 m, reaches a maximum of 1620 at 20 m, and then averages approximately 600 from 21 m to the bottom. These ratios are well above that required for balanced phytoplankton growth, indicating phosphorus limitation, an implication that has been proven experimentally (Priscu 1995, Dore and Priscu 1996).

Measurements of bacterial productivity based on tritiated thymidine incorporation into DNA reveal that bacterial activity is essentially nonexistent below 20 m (Takacs and Priscu 1998, Voytek et al. 1998). The paucity of bacterial activity below 20 m has also been shown by the lack of organic matter decomposition in this region (Priscu 1992). The lack of deepwater bacterial activity, in concert with the high nitrate and low oxygen levels in the deep water, also indicate a complete absence of bulk denitrification (Priscu 1997) below the chemocline. We currently have no simple biochemical explanation for the lack of bacterial activity beneath the chemocline, although toxicity caused by high levels of certain metals seems likely (Ward and Priscu 1997).
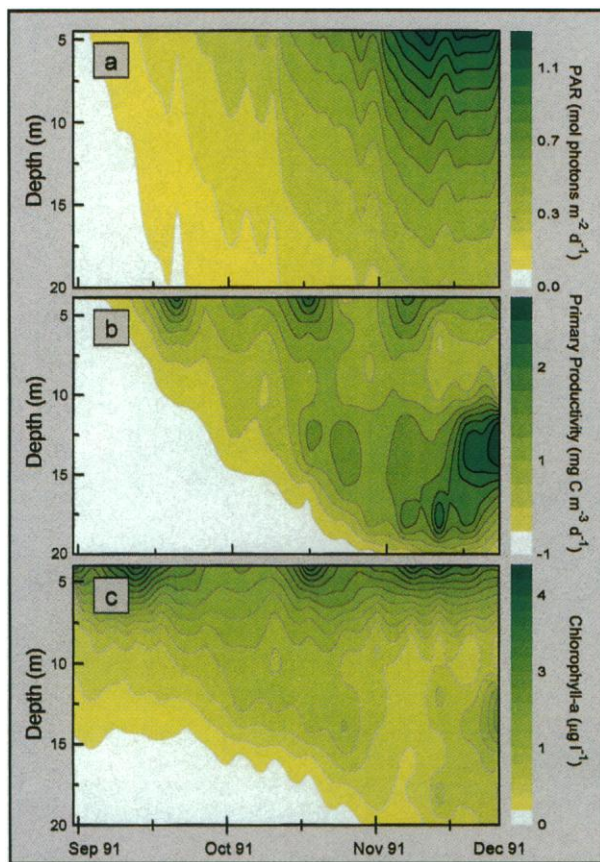
The most complete set of phytoplankton biomass (chlorophyll *a*) and primary productivity data for Lake Bonney was collected from early September 1991 to early December 1991. Photosynthetically available radiation (PAR) in the water column during this period increased from zero to approximately 1.3 mol·m⁻²·d⁻¹ just beneath the ice (Figure 2a). The vertical penetration of PAR also increased through the water column, with photon flux reaching approximately 0.3 mol·m⁻²·d⁻¹ at 20 m in December. Phytoplankton primary productivity and biomass followed the trend in PAR, developing in the surface
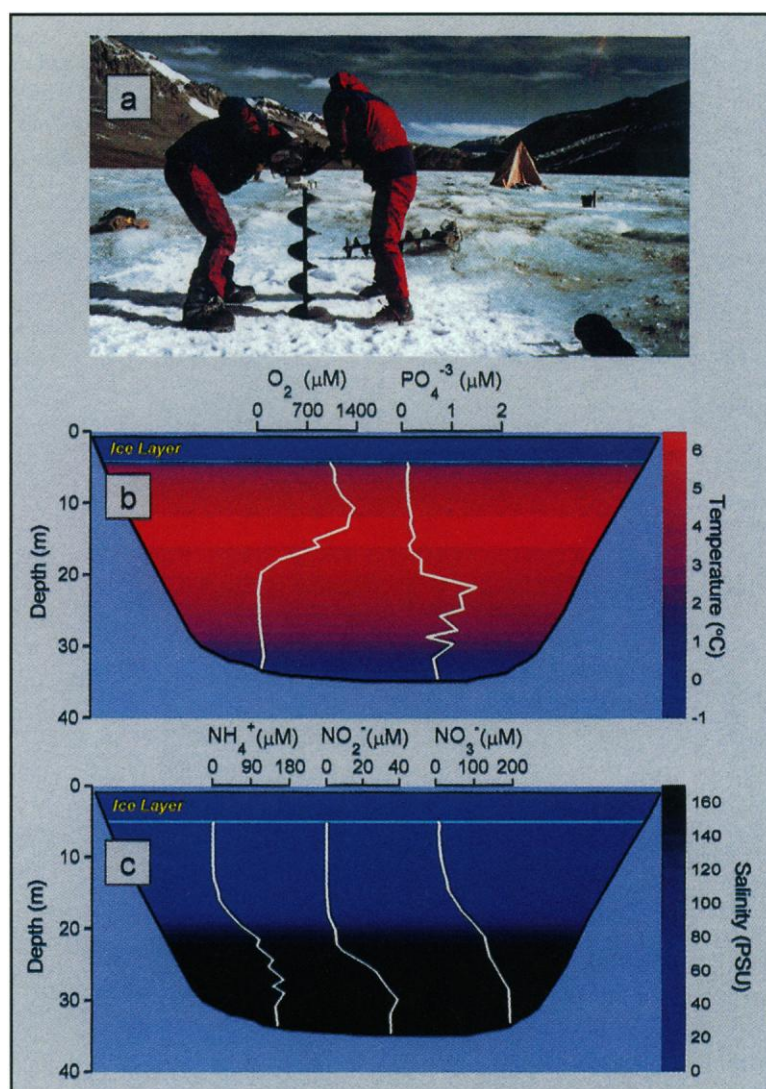
water and proceeding downward to 20 m as the season progressed (Figures 2b and 2c). The bottom of the trophogenic zone, below which there is no phytoplankton productivity, is effectively 20 m in this lake, which corresponds to the depth of 0.5% light penetration and the depth of the primary chemocline (see Figure 1).

Development of maxima in phytoplankton biomass and primary productivity proceeded sequentially from shallower to deeper depths, in a manner that implies a seasonal descent of the threshold irradiance required for net production. Distinct phytoplankton species were responsible for the sequential vertical development of the phytoplankton community. Cryptophyte and chlorophyte algae dominated the assemblage from 4 m to 8 m, chrysophyte algae dominated from 8 m to 16 m, and chrysophyte and chlorophyte algae dominated from 16 m to 20 m (Lizotte et al. 1996, Lizotte and Priscu 1998).

Unlike many pelagic systems, in which spring growth of phytoplankton is triggered by a combination of decreasing mixed-layer depth and increasing incident PAR (e.g., Smetacek and Passow 1990), the initiation of spring phy-
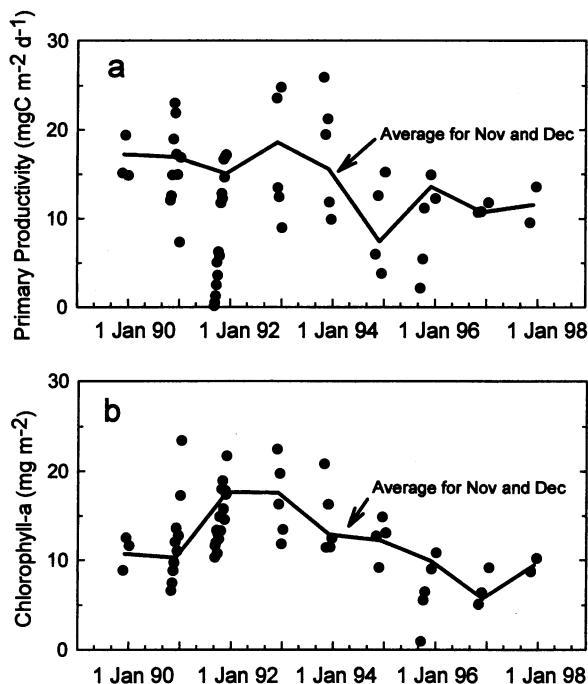
Figure 2. Contour plots of water column properties for the east lobe of Lake Bonney during late winter and summer of 1991. (a) Photosynthetically available radiation (PAR; mol·m^{-2}·d^{-1}). (b) Primary productivity (carbon production in mg·m^{-3}·d^{-1}). (c) Chlorophyll a (μg·L^{-1}).

toplankton growth in the nonturbulent waters of Lake Bonney is solely a function of the seasonal increase in incident PAR. Increases in phytoplankton productivity rates are usually followed by increases in chlorophyll *a*, often with a lag of several weeks. This temporal separation, combined with vertical segregation of phytoplankton

species, shows that deepwater phytoplankton biomass results from in situ production rather than from sinking or vertical migration of cells. Photosynthetic efficiency—the ratio of carbon dioxide fixed per unit photon absorbed by photosynthetic pigments—has been shown to increase with depth, which is indicative of deepwater photoacclimation (Neale and Priscu 1995, 1998, Lizotte et al. 1996, Morgan et al. 1998).

Unfortunately, because of logistic constraints, most of the limnological field measurements made in the McMurdo Dry Valleys end in late summer (January). However, it is clear from the data in Figure 2 and in other reports (e.g., Lizotte et al. 1996, Howard-Williams et al. 1998, Fritsen and Priscu 1999) that primary productivity and phytoplankton biomass are still increasing after this period. Trends in depth-integrated (0–20 m) phytoplankton production and biomass in Lake Bonney from 1989 through 1997 (Figure 3) highlight the importance of obtaining annual data. Measurements made within each field season show that phytoplankton productivity and biomass increase when solar radiation first penetrates the ice cover of the lake, generally reaching their highest levels in January, when field studies typically end. Averages for November and December, a period when data are available for each field season from 1989 through 1997, show that phytoplankton production was relatively constant from late 1989 to January 1994, after which activity decreased approximately 30% and remained low through 1997. The long-term chlorophyll *a* record shows a similar pattern. All of our measurements of primary productivity were made using standard $^{14}CO_2$ uptake methods over a 24-hour incubation (Priscu 1995). Previous work (Priscu et al. 1987, 1988) has shown that cellular lipid, polysaccharide, and protein macromolecules are equilibrium labeled within this time period; hence, our results should reflect rates of net primary productivity (Falkowski and Raven 1997).

These long-term trends in primary productivity and chlorophyll *a* reflect changes in environmental factors,

Figure 3. Temporal trends in water column productivity and chlorophyll a in the east lobe of Lake Bonney from the 1989–1990 through the 1997–1998 field seasons. (a) Primary productivity (carbon production in mg·m^{-2}·d^{-1}). (b) Chlorophyll a (mg·m^{-2}). Data are depth integrated over the trophogenic zone (4.5–20 m) and weighted for lake morphometry. The symbols represent individual measurements; the line represents average values for November and December of each year.

Figure 4. Photosynthetically available radiation (PAR) 10 m beneath the ice surface and corresponding areal primary productivity predicted from PAR using a hyperbolic tangent model. PAR (dotted line) is given in terms of photon flux (mol·m⁻²·d⁻¹), and primary productivity (solid line) is given in terms of carbon production (mol·m⁻²·d⁻¹) predicted from PAR using a hyperbolic tangent model. Numbers in parentheses represent annual areal primary production of organic carbon (in g·m⁻²) followed by total annual carbon production (in kg) over the entire trophogenic zone (4.5–20 m) for the 4 years when annual underwater PAR records were collected. All values are weighted for the volume of the trophogenic zone in the east lobe of Lake Bonney.
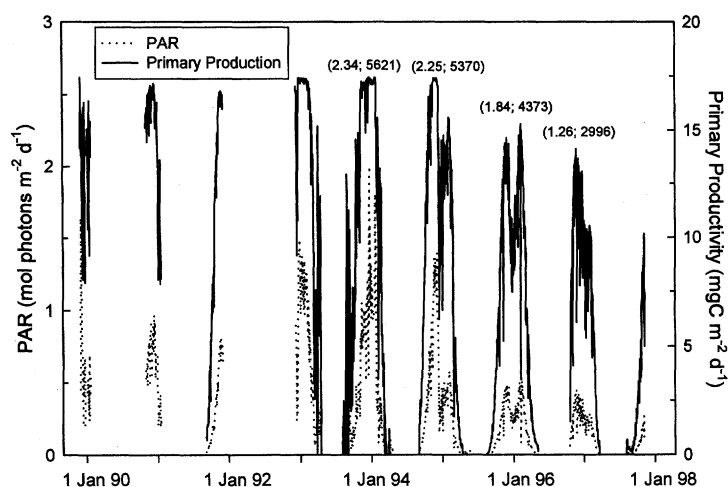
such as irradiance (through cloud cover or changes in ice transparency), ultraviolet radiation, and variation in stream-derived nutrients related to glacial melt over this period. Temperatures were warmer during the late 1980s than in the mid-1990s, resulting in higher ice cover porosity (Fritsen et al. 1998) and stream flow (Conovitz et al. 1998, McKnight et al. 1999), the latter yielding greater nutrient loading to the lake. A recent study (Vincent et al. 1998) has also shown that sufficient ultraviolet radiation penetrates the ice cover of certain dry valley lakes to inhibit algal growth. These facts, together with the region's sensitivity to ozone depletion (Madronich et al. 1995) and climate warming (McBean 1994), emphasize the need to understand phytoplankton and associated organic carbon dynamics in the dry valley lakes if they are to be used to gauge environmental change. The water column of these lakes provides the only persistent annual liquid water habitat and presumably supports the only biological activity throughout the winter in the McMurdo Dry Valleys. Therefore, a thorough understanding of the organic carbon dynamics in these lakes will provide information that will allow a better assessment of the potential effects of climate change.

Phytoplankton production of organic carbon

The first step toward understanding organic carbon dynamics within Lake Bonney is to estimate annual sources and sinks of particulate organic carbon. Because primary production can be measured for only a portion of the phytoplankton growing season, a sta-

tistical (hyperbolic tangent) model (Jassby and Platt 1976, Behrenfeld and Falkowski 1997) was developed to predict productivity from PAR during the portion of the season when primary productivity measurements cannot be made. This model was constructed using available data on depth-integrated primary productivity and daily PAR at 10 m during the 1989–1997 field seasons. The model has the form carbon production, in $mg·m^{-2}·d^{-1}$, is equal to $17.5 \times \tanh ([43.4 \times$ PAR at 10 m, in $mol·m^{-2}·d^{-1}]/17.5)$. Predicted annual photosynthetic carbon fixation (weighted for lake morphometry) during the years when complete underwater PAR records exist was 2.34, 2.25, 1.84, and 1.26 $g·m^{-2}$ for the years centered on 1 January 1994, 1995, 1996, and 1997, respectively (Figure 4). These values translate to annual carbon yields of 5621 kg, 5370 kg, 4373 kg, and 2996 kg, respectively, if the volume of the lake is accounted for.

In accordance with the hyperbolic tangent model, there is a threshold PAR level at which phytoplankton productivity becomes light-independent. The PAR value representing the onset of this threshold is 0.4 $mol·m^{-2}·d^{-1}$.

Figure 5. Net primary production to respiration (P:R) ratios for the trophogenic zone (4.5–20 m; solid bars) and the entire water column (4.5–30 m; gray bars) from 1993 to 1997 in the east lobe of Lake Bonney. Data are presented for both the phytoplankton growing season (1 September–15 April) and for the entire year (annual).
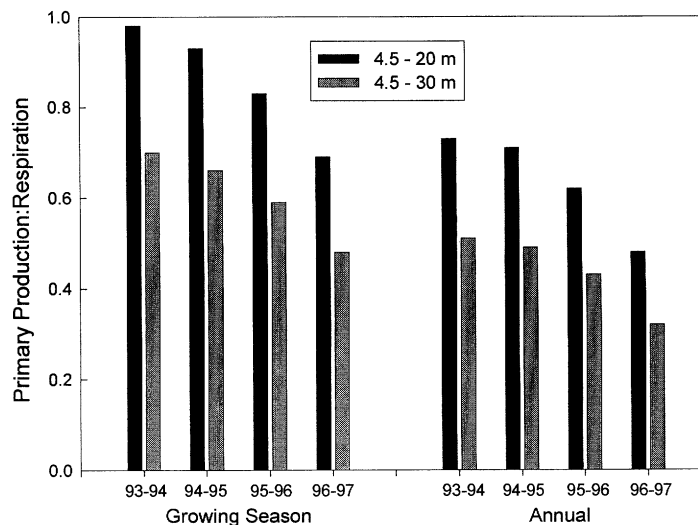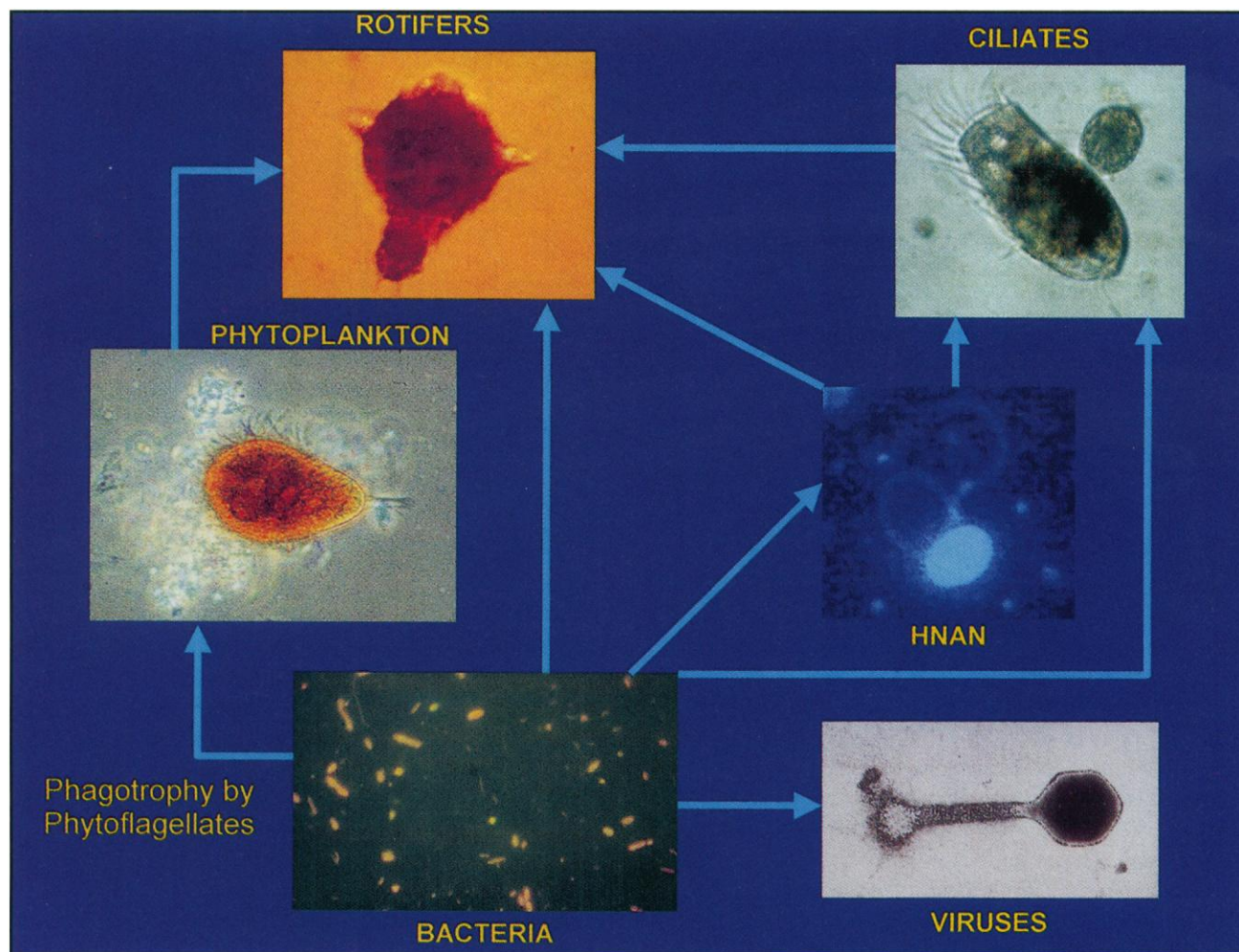
Figure 6. Pictorial representation of the major food web components and their linkages within Lake Bonney. The rotifer is Philodina *sp. (most of the rotifers in the dry valley lakes belong to this genus), the large ciliate is* Euplotes *sp., and the phytoplankter is* Chlamydomonas *sp. Bacteria attached to the surface of* Chlamydomonas *appear as threadlike structures on the upper portion of the cell; flagella are evident on the right apex of the cell. HNAN, heterotrophic nanoflagellates.*

Approximately 60% of the daily PAR values at 10 m (the depth of the underwater PAR sensor) exceed this threshold value, as shown in Figure 4 by the plateau in predicted primary productivity when PAR exceeds 0.4 mol·m⁻²·d⁻¹. PAR reaching 10 m in Lake Bonney after January 1995 was lower than that in previous years, yielding production estimates that are 20–40% lower than those that occurred before 1995. This trend in predicted primary productivity corroborates the long-term pattern in phytoplankton biomass shown in Figure 3.

Respiratory losses

One of the primary losses of carbon fixed by phytoplankton is through respiration—both directly, by the phytoplankton themselves, and indirectly, through the metabolic contributions of myriad heterotrophic organisms, such as bacterioplankton and protozoa. Because the water throughout most of the trophogenic zone of Lake Bonney is supersaturated with oxygen, and relative metabolic rates in this zone are low, it is impossible to accurately measure respiration rates using experimental changes in oxygen concentration. Instead, we have measured activity of the respiratory electron transport system (ETS), which drives oxidative phosphorylation and hence oxygen consumption in all aerobic organisms (Packard 1985). A first-order relationship exists between ETS activity and respiratory capacity in aquatic microorganisms (e.g., Kenner and Ahmed 1975, Christiansen et al. 1980). In Lake Bonney, 44% and 56% of measured ETS activity is from bacterioplankton and phytoplankton, respectively (Takacs 1999). Using these percentages, in concert with published respiration:ETS ratios (Packard 1985), we derived a community respiration:ETS ratio of 0.61 for the water column of Lake Bonney. Individual respiration:ETS ratios for bacteria and phytoplankton were 0.513 and 0.097, respectively. Annual respiration was estimated by scaling to primary productivity (Takacs 1999, John C. Priscu, unpublished data).

Respiration rates in the trophogenic zone (4.5–20 m) from late August to early April are approximately 70% of the total water column respiration. Higher respiratory activity in the trophogenic zone during this period reflects both higher activity per unit volume (Takacs and Priscu 1998, Takacs 1999) and greater lake volume (all data are volume weighted) in this zone relative to that below 20 m. The higher volumetric activity results from respiration directly by phytoplankton and by heterotrophs using dissolved organic compounds excreted by phytoplankton; phytoplankton excretion has been shown to be near 5% of the primary productivity rate (Sharp 1993). On an annual basis, average daily areal respiration in the trophogenic zone is almost 20% lower than the average during the growing season (early September through early April) due to the extended period of winter darkness, when phytoplankton respiration and photosynthetic excretion of dissolved organic carbon are absent from the water column.

The light-mediated temporal uncoupling of respiration and photosynthesis in Lake Bonney leads to questions regarding the trophic nature of the system. The ratio of net primary production to community respiration (P:R) is an important ecosystem variable that allows one to determine if a system is net autotrophic (P:R > 1) or net heterotrophic (P:R < 1). This ratio also has important biogeochemical ramifications, such as indicating whether the system is a net source or sink of carbon dioxide. This ratio also indicates whether there is a surplus of carbon available for higher trophic levels or for sediment deposition. Over the growing seasons from 1993–1994 through 1996–1997, P:R ratios averaged 0.86 and 0.61 for the trophogenic zone and entire water column in Lake Bonney, respectively (Figure 5). However, these values decreased to 0.64 and 0.44 over the annual cycle due to a 4-month period of darkness, when primary productivity does not occur. The computed P:R ratios indicate that Lake Bonney was a net heterotrophic system during the period of study. That is, respiratory carbon losses exceeded new carbon gains via autochthonous primary production.

Bacterial respiration has been shown to exceed net primary production in a number of other oligotrophic aquatic systems in which net primary productivity (i.e., carbon fixation) is below approximately 100 $\mu g \cdot L^{-1} \cdot d^{-1}$ (del Giorgio et al. 1997). Primary productivity in Lake Bonney is usually below 1 $\mu g \cdot L^{-1} \cdot d^{-1}$, categorizing it as extremely oligotrophic. Based on a bacterial growth efficiency of 13% (Takacs 1999), bacterial respiration represents approximately 84% of the community respiration in Lake Bonney and uses more carbon than is fixed by phytoplankton. This large heterotrophic sink of organic carbon raises questions regarding sources of organic carbon required to sustain heterotrophic activity in the system. Potential sources of organic carbon, other than that fixed by phytoplankton, include stream inflow (McKnight et al. 1993), excretion from benthic microbial mats (Hawes and

Schwarz 1999), upward diffusion of dissolved organic carbon across the chemocline, and downward flux of particulate organic matter that is trapped or produced within the permanent ice cover (Squyres et al. 1991, Priscu et al. 1998). If these sources of carbon are added to water column primary production, however, P:R ratios increase by only 5–7% and remain below 1, indicating that this system is still net heterotrophic and a source of carbon dioxide during the study period.

A water-column P:R ratio of less than 1 will eventually lead to a system with low dissolved oxygen and little to no reduced carbon. The supersaturated oxygen levels in the upper trophogenic zone of Lake Bonney result primarily from physical out-gassing of oxygen as oxygen-saturated glacial meltwater enters the lake and freezes (Wharton et al. 1986, Craig et al. 1992). Consequently, it is difficult to relate the concentration of dissolved oxygen in the trophogenic zone to autochthonous metabolism within this zone. It is also important to realize that our data represent a short period (9 years) in the history of the lake. Past (and possibly future) conditions presumably produced (and may again produce) a P:R ratio greater than 1. The P:R ratios in the lake may be in a dynamic equilibrium, oscillating temporally between net phototrophy and net heterotrophy.

Food web and carbon dynamics

Research over the past 40 years has revealed few metazoan plankton and no fish in the water column of the McMurdo Dry Valley lakes, making them unlike any other lakes on Earth (e.g., Parker and Simmons 1985). The lack of higher organisms is generally attributed to the extreme environmental conditions of these lakes, their oligotrophy, and their geographical isolation. Until recently, it was thought that heterotrophic protozoans were also absent from the water column of the lakes in the McMurdo Dry Valleys. However, seminal reports by Laybourn-Parry et al. (1997), James et al. (1998), and Roberts and Laybourn-Parry (1999) have now shown that these lakes contain a complex microbial food web consisting of mixotrophic flagellates, heterotrophic flagellates, bactivorous ciliates, flagellate-feeding ciliates, and rotifers (Figure 6). Interestingly, lakes within the Taylor Valley display a wide range of difference in heterotrophic food web components, particularly among ciliates. For example, ciliate biomass and diversity are much lower in Lake Bonney than in either Lake Hoare or Lake Fryxell. The reasons for the differences are not entirely clear, but they may reflect the overall lower bacterial activity in Lake Bonney (Takacs and Priscu 1998) or its distinct evolutionary history (Lyons et al. 1999).

The general structure of the food web in Lake Bonney reveals well-developed microbial linkages that also exist in other lakes on the Antarctic continent (Laybourn-Parry 1997). The structure depicts the importance of bacteria and protozoa in the transformation of organic carbon
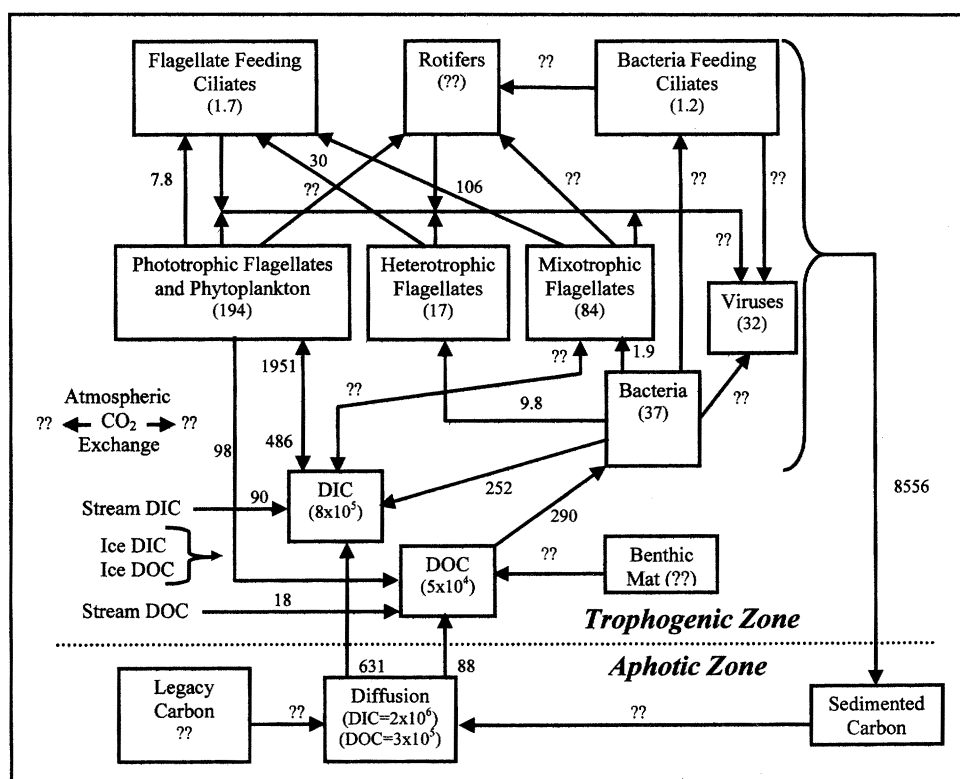
Figure 7. Pelagic food web and associated carbon fluxes in the east lobe of Lake Bonney. Values in the boxes represent the depth-integrated size of respective carbon pools (mg·m^{-2}); values associated with arrows represent depth-integrated carbon fluxes (mg·m^{-2}·yr^{-1}). Question marks indicate pool sizes and fluxes that are unknown. All biological fluxes were determined experimentally during the summer and extrapolated over a year. Diffusive fluxes of dissolved inorganic carbon (DIC) and dissolved organic carbon (DOC) are based on gradients across the 18 m plane (i.e., near the bottom of the trophogenic zone). Sinking fluxes to the aphotic zone were determined with sediment traps suspended at the bottom of the trophogenic zone (20 m).

produced by phytoplankton back into the food web. This pathway was originally alluded to in a seminal paper by Pomeroy (1974) and formalized with the term "microbial loop" by Azam et al. (1983). In most aquatic systems, the microbial plankton form an integral part of a complex food web that also includes invertebrates and vertebrates. Within lakes of the McMurdo Dry Valleys, rotifers and predatory ciliates are the top consumers in the water column. Interestingly, many of the phytoplankton are composed of flagellated species. Presumably, these low–kinetic energy systems select for motility, which allows the phytoplankton to respond to favorable stimuli (Priscu and Neale 1995).

A large amount of data have been collected on various carbon pools and fluxes within the lakes of the McMurdo Dry Valleys. We have used data on the east lobe of Lake Bonney to compile the first model outlining the existing carbon linkages, the magnitudes of carbon flux among pools, and the pool sizes (Figure 7). The model is instructive in several ways. First, it shows where information on important carbon pools and fluxes is lacking; second, it allows us to assess the accuracy of our existing data set from a carbon-balance perspective; and third, it reveals the relative importance of abiotic and biotic carbon sources and sinks in the system.

For example, the model shows the importance of mixotrophy, a "low-light" (or winter) phytoplankton survival strategy, which allows certain phytoplankton species to incorporate particulate organic carbon by ingesting bacteria during periods of low or no light. Of the total carbon incorporated into phytoplankton biomass, 70% is

from photoautotrophy and 30% is from ingestion of bacteria. These results imply that algal growth and standing carbon in Lake Bonney cannot be completely reconciled from a model of primary productivity alone, as is done in many systems (e.g., Falkowski and Raven 1997). Instead, heterotrophic production of both bacterioplankton and phytoplankton must be considered. Phagotrophy has been shown to be an important life-history strategy of phytoplankton existing in the dimly lit deep-chlorophyll layers of certain temperate lakes (Bird and Kalff 1986). In a sense, the entire water column of the dry valley lakes can be considered to be a deep-chlorophyll layer, due to the low light, temperature, and turbulence and to the presence of a distinct nutricline—all features typically found in association with deep-chlorophyll layers (e.g. Priscu and Goldman 1983). Interestingly, certain cryptophytes in temperate lakes do not practice phagotrophy (Gasol et al. 1993, Gervais 1997, 1998), whereas the same species are phagotrophic in Antarctic lakes (Roberts and Laybourn-Parry 1999). Perhaps the long dark period and overall low-light regime in Antarctic lakes impart a greater selection pressure for phagotrophic carbon incorporation.

Interestingly, the sinking flux of organic carbon through the trophogenic zone exceeds the production of new carbon in this region by more than fourfold (the annual carbon production rate is 1951 mg·m^{-2}·yr^{-1}; the sediment trap collection rate for the same period is 8556 mg·m^{-2}·yr^{-1}). The sediment flux includes material settling from the water column and the ice cover. Several studies (e.g., Squyres et al. 1991, Adams et al. 1998, Fritsen et al. 1998) have shown that the permanent ice cover acts as a

physical trap for sediments and associated organic matter of aeolian origin. In addition, organic matter accrues in the ice cover via photosynthetic production during the summer months, when liquid water is present (Priscu et al. 1998). Sediment and associated organic matter are released to the water column from the ice cover via conduits within the ice that allow them to settle rapidly to the bottom of the lake. Hence, sediment-trap collections represent a combination of water-column and ice-cover processes. The large imbalance between sinking flux and production within the trophogenic zone indicates the overwhelming importance of sinking matter originating from the ice cover. The "biological seeding" of the lake from the ice has important ecological ramifications for the lake water column and benthos in terms of the introduction of species, nutrient enrichment, and sediment accumulation and diagenesis.

In addition to the "traditional" components of the food web, recent work has shown that viruses are abundant components of many aquatic ecosystems, where they are involved in gene transfer and microbial mortality (e.g., Suttle 1994, Hennes and Simon 1995, Wilhelm and Suttle 1999). Extracellular viruses, whose density averages approximately $10^7 \cdot mL^{-1}$, have recently been observed in Lakes Hoare and Fryxell (Kepner et al. 1998), and we have identified them in Lake Bonney (Figures 7 and 8). These viruses include not only typical bacteriophages but also viruses that are morphologically similar to double-stranded DNA viruses that are known to infect algae and protozoa. The densities at which viruses occur in the dry valley lakes are within the range of those found in moderately productive temperate aquatic systems. Assuming an average trophogenic zone virus density of $10^7 \cdot mL^{-1}$ and a specific carbon content of 0.2 fg per virus (Kepner et al. 1998), the resulting areal virus density in the east lobe of Lake Bonney is $1.6 \times 10^{14} \cdot m^{-2}$, which equates to a carbon content of 32 $mg \cdot m^{-2}$. This value is approximately 87% of the bacterial carbon estimate (Figure 7), implying an important role for viruses as a carbon sink in this system. Although we are only beginning to examine the importance of viruses in Antarctic lakes, the relatively high virus biomass and the lack of upper trophic levels in Lake Bonney indicate that viral infections (see Figure 8) influence species abundance and community structure to a much greater degree than in temperate systems (Gobler et al. 1997).

The food web components in Lake Bonney show many instances of disequilibrium. Disequilibria are exemplified by the grazing fluxes on mixotrophic and heterotrophic flagellates, both of which exceed the pool sizes of the prey. Clearly, the prey will become extinct under these conditions unless their growth rates balance or exceed the grazing rates. As with all of our biological data, the data shown in the model are based on austral summer collections that have been extrapolated over a year. Hence, what appear to be net gains or losses in the food web may in fact be dif-
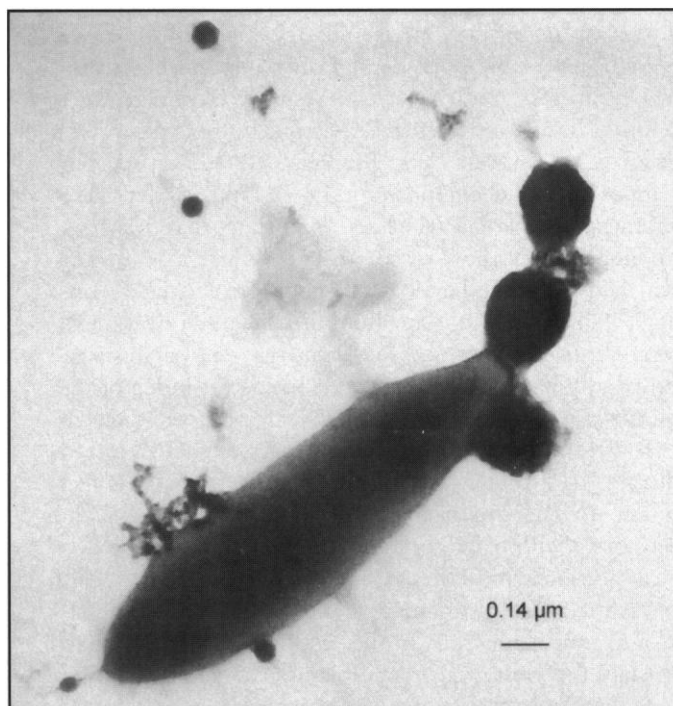

Figure 8. Electron micrograph of a virus-infected bacterium from the water column of Lake Bonney.

ferent if actual data from winter collections and experiments could have been included. The bacterial demand for dissolved organic carbon (290 $mg \cdot m^{-2} \cdot yr^{-1}$) also exceeds its supply from phytoplankton extracellular release and diffusion (187 $mg \cdot m^{-2} \cdot yr^{-1}$), despite a relatively large dissolved organic carbon pool (5×10^4 $mg \cdot m^{-2}$), implying the existence of other sources of dissolved organic carbon to the trophogenic zone.

As mentioned previously, potential candidates for dissolved organic carbon flux to the trophogenic zone are stream flow, lake ice, and excretion from benthic cyanobacterial mats (Moorhead et al. 1997, Priscu et al. 1998, Hawes and Schwarz 1999, Takacs 1999). Stream flow provides less than 0.1% per year to the dissolved organic pool in the trophogenic zone; ice flux has yet to be measured, although particulate organic carbon flux from the ice is thought to be high (Figure 7). There have been few studies of benthic mat activity in Lake Bonney, but benthic mats are localized in the shallow region around the periphery of the lake (Wharton et al. 1983). Such localization presumably makes benthic mats an insignificant source of dissolved organic carbon to the water column of Lake Bonney.

Another interesting feature of the carbon flux in Lake Bonney is the relatively large amounts of dissolved inorganic carbon and dissolved organic carbon that enter the trophogenic zone via upward diffusion across the chemocline. Despite diffusion coefficients near the molecular level (Priscu et al. 1996, Spigel and Priscu 1998), large gradients in dissolved inorganic and dissolved organic carbon

at the bottom of the trophogenic zone maintain a relatively high upward flux (W. Berry Lyons, unpublished data). The deepwater gradients are the result of large deepwater pools of these constituents. The source of these deepwater pools is not entirely clear, although, in addition to contemporaneous decomposition of sinking matter, geochemical and periglacial evidence indicates that they have developed over the past 10,000 years, a period during which hydraulic and biological regimes have varied (Lyons et al. 1998a, 1999). It is apparent that the natural legacy of past events plays a critical role in current ecosystem structure and function in these lakes. Specifically, much of the biological structure and activity that are observed today in the water column are based on processes that occurred during the evolutionary history of these lakes. This fact points to the importance of interpreting the current ecosystem within the context of the natural legacy left by past biogeochemical events.

Clearly, many gaps remain in our model of carbon fluxes and transformations in the east lobe of Lake Bonney. Perhaps the most important omission is the lack of winter data. Most of the data we have presented in this article were collected during the annual 4-month period (October–January) when logistical support make it possible to conduct field research. In lieu of seasonal data, the model we present here uses solar radiation, in concert with experimentally determined photosynthesis–irradiance relationships, to compute annual rates of primary production and, through a secondary relationship with respiration, annual respiration. Community production and respiration provide the basis of any carbon model and must be known accurately for a true representation of the system. The temporal discontinuity in production and respiration in these high-latitude lakes makes them unique in that loss processes are largely uncoupled from production processes.

The role of organic carbon transformations during winter by the microbial food web is particularly important because it allows for efficient recycling of photosynthetically produced organic carbon in what would otherwise appear, by virtue of the paucity of higher trophic levels and the extreme environmental conditions, to be a relatively linear system. Heterotrophic recycling of inorganic nutrients during the winter will also "prime" the water for phytoplankton growth during the ensuing summer, when solar radiation drives photosynthesis; this recycling process has been shown to occur in coastal Antarctic lakes (Laybourn-Parry et al. 1995).

The popular idea that the permanently ice-covered lakes of the McMurdo Dry Valleys are highly simplified assemblages is no longer true. We now know that a highly evolved food web exists in these systems that is driven by both contemporaneously produced organic carbon and carbon left as the legacy of past events. Future research should focus on answering the many questions raised in this article, particularly the role of the microbial food web in overall carbon dynamics. This work must be placed in the context of the uncoupled light–dark cycle and the natural legacy imprinted on the system during the evolution of the lakes to gain a comprehensive understanding of the ecosystem.

References cited

Adams EE, Priscu JC, Fritsen CH, Smith SR, Brackman SL. 1998. Permanent ice covers of the McMurdo Dry Valleys lakes, Antarctica: Bubble formation and metamorphism. Pages 281–295 in Priscu JC, ed. Ecosystem Dynamics in a Polar Desert: The McMurdo Dry Valleys. Antarctic Research Series, Vol. 72. Washington (DC): American Geophysical Union.

Angino EE, Armitage KB. 1963. A geochemical study of Lakes Bonney and Vanda, Victoria Land, Antarctica. Journal of Geology 71: 89–95.

Angino EE, Armitage KB, Tash JC. 1964. Physicochemical limnology of Lake Bonney, Antarctica. Limnology and Oceanography 9: 207–217.

Azam F, Fenchel T, Field JG, Meyer-Reil LA, Thingstad F. 1983. The ecological role of water-column microbes in the sea. Marine Ecology 10: 257–263.

Behrenfeld MJ, Falkowski PG. 1997. A consumer's guide to phytoplankton primary productivity models. Limnology and Oceanography 42: 1479–1491.

Bird DF, Kalff J. 1986. Bacterial grazing by planktonic lake algae. Science 231: 493–495.

Burkins MB, Chamberlain CP, Virginia RA, Freckman DH. 1996. The natural abundance of carbon and nitrogen isotopes in potential sources of organic matter to soils of Taylor Valley, Antarctica. Antarctic Journal of the United States 31: 209–210.

Christiansen JP, Owens TG, Devol AH, Packard T. 1980. Respiration physiological state in marine bacteria. Marine Biology 55: 267–276.

Clow GD, McKay CP, Simmons GM Jr, Wharton RA Jr. 1988. Climatological observations and predicted sublimation rates at Lake Hoare, Antarctica. Journal of Climate 1: 715–728.

Conovitz PA, McKnight DM, MacDonald LH, Fountain AG, House HR. 1998. Hydrologic processes influencing streamflow variation in Fryxell Basin, Antarctica. Pages 93–108 in Priscu JC, ed. Ecosystem Dynamics in a Polar Desert: The McMurdo Dry Valleys, Antarctica. Antarctic Research Series, Vol. 72. Washington (DC): American Geophysical Union.

Craig H, Wharton RA Jr, McKay CP. 1992. Oxygen supersaturation in an

ice-covered Antarctic lake: Biological versus physical contributions. Science 255: 218–221.

del Giorgio PA, Cole JJ, Cimbleris A. 1997. Respiration rates in bacteria exceed phytoplankton production in unproductive aquatic systems. Nature 385: 148–151.

Dore JE, Priscu JC. 1996. Phosphorus deficiency and alkaline phosphatase activities in lakes of Taylor Valley, Antarctica. Antarctic Journal of the United States 31: 206–208.

Falkowski PG, Raven JA. 1997. Aquatic Photosynthesis. Malden (MA): Blackwell Science.

Fountain AG, et al. 1999. Physical controls on the Taylor Valley ecosystem, Antarctica. BioScience 49: 961–971.

Fritsen CH, Priscu JC. 1998. Cyanobacterial assemblages in permanent ice covers on Antarctic lakes: Distribution, growth rate, and temperature response of photosynthesis. Journal of Phycology 34: 587–597.

_____. 1999. Seasonal change in the optical properties of the permanent ice cover on Lake Bonney, Antarctica: Consequences for the lake productivity and phytoplankton dynamics. Limnology and Oceanography 44: 447–454.

Fritsen CH, Adams EE, McKay CP, Priscu JC. 1998. Permanent ice covers of the McMurdo Dry Valleys lakes, Antarctica: Liquid water contents. Pages 269–280 in Priscu JC, ed. Ecosystem Dynamics in a Polar Desert: The McMurdo Dry Valleys. Antarctic Research Series, Vol. 72. Washington (DC): American Geophysical Union.

Gasol JM, García-Cantizano J, Massana R, Guerrero R, Pedrós-Alió C. 1993. Physiological ecology of a metalimnetic *Cryptomonas* population: Relationships to light, sulfide and nutrients. Journal of Plankton Research 15: 255–275.

Gervais F. 1997. Diel vertical migration of *Cryptomonas* and *Chromatium* in the deep chlorophyll maximum of a lake. Journal of Plankton Research 19: 533–550.

_____. 1998. Ecology of cryptophytes coexisting near a freshwater chemocline. Freshwater Biology 39: 61–78.

Gobler CJ, Hutchins DA, Fisher NS, Cosper EM, Sañudo-Wilhelmy S. 1997. Release and bioavailability of C, N, P, Se, and Fe following viral lysis of a marine chrysophyte. Limnology and Oceanography 42: 1492–1504.

Goldman CR. 1970. Antarctic freshwater ecosystems. Pages 609–627 in Holdgate M, ed. Antarctic Ecology. New York: Academic Press.

Goldman CR, Mason DT, Hobbie JE. 1967. Two Antarctic desert lakes. Limnology and Oceanography 12: 295–310.

Green WJ, Friedmann EI, eds. 1993. Physical and Biogeochemical Processes in Antarctic Lakes. Antarctic Research Series, Vol. 59. Washington (DC): American Geophysical Union.

Hawes I, Schwarz AM. 1999. Photosynthesis in an extreme shade environment: Benthic microbial mats from Lake Hoare, a permanently ice-covered Antarctic lake. Journal of Phycology 35: 448–459.

Hennes KP, Simon M. 1995. Significance of bacteriophages for controlling bacterioplankton growth in a mesotrophic lake. Applied and Environmental Microbiology 61: 333–340.

Howard-Williams C, Schwarz AM, Hawes I, Priscu JC. 1998. Optical properties of the McMurdo Dry Valley Lakes, Antarctica. Pages 189–203 in Priscu JC, ed. Ecosystem Dynamics in a Polar Desert: The McMurdo Dry Valleys. Antarctic Research Series, Vol. 72. Washington (DC): American Geophysical Union.

James MR, Hall JA, Laybourn-Parry J. 1998. Protozooplankton and microzooplankton ecology in lakes of the Dry Valleys, southern Victoria Land. Pages 255–268 in Priscu JC, ed. Ecosystem Dynamics in a Polar Desert: The McMurdo Dry Valleys, Antarctica. Antarctic Research Series, Vol. 72. Washington (DC): American Geophysical Union.

Jassby AD, Platt T. 1976. Mathematical formulation of the relationship between photosynthesis and light for phytoplankton. Limnology and Oceanography 21: 540–547.

Kenner RA, Ahmed SI. 1975. Measurements of electron transport activities in marine phytoplankton. Marine Biology 33: 119–127.

Kepner RL, Wharton RA Jr, Suttle CA. 1998. Viruses in Antarctic lakes. Limnology and Oceanography 43: 1754–1761.

Laybourn-Parry J. 1997. The microbial loop in Antarctic lakes. Pages 231–240 in Lyons WB, Howard-Williams C, Hawes I, eds. Ecosystem Processes in Antarctic Ice-Free Landscapes. Rotterdam (The Netherlands): A. A. Balkema.

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

Laybourn-Parry J, James MR, McKnight DM, Priscu JC, Spaulding SA, Shiel R. 1997. The microbial plankton of Lake Fryxell, southern Victoria Land, Antarctica during the summers of 1992 and 1994. Polar Biology 17: 54–61.

Lizotte MP, Priscu JC. 1992a. Photosynthesis–irradiance relationships in phytoplankton from the physically stable water column of a perennially ice-covered lake (Lake Bonney, Antarctica). Journal of Phycology 28: 179–185.

_____. 1992b. Spectral irradiance and bio-optical properties in perennially ice-covered lakes of the Dry Valleys (McMurdo Sound, Antarctica). Pages 1–14 in Elliot DH, ed. Contributions to Antarctic Research III. Antarctic Research Series, Vol. 57. Washington (DC): American Geophysical Union.

_____. 1998. Pigment analysis of the distribution, succession, and fate of phytoplankton in the McMurdo Dry Valley lakes of Antarctica. Pages 229–239 in Priscu JC, ed. Ecosystem Dynamics in a Polar Desert: The McMurdo Dry Valleys, Antarctica. Antarctic Research Series, Vol. 72. Washington (DC): American Geophysical Union.

Lizotte MP, Sharp TR, Priscu JC. 1996. Phytoplankton dynamics in the stratified water column of Lake Bonney, Antarctica. I. Biomass and productivity during the winter–spring transition. Polar Biology 16: 155–162.

Lyons WB, Howard-Williams C, Hawes I. 1997. Ecosystem Processes in Antarctic Ice-Free Landscapes. Rotterdam (The Netherlands): A. A. Balkema.

Lyons WB, Welch KA, Neumann K, Toxey JK, McArthur R, Williams C. 1998a. Geochemical linkages among glaciers, streams, and lakes within the Taylor Valley, Antarctica. Pages 77–92 in Priscu JC, ed. Ecosystem Dynamics in a Polar Desert: The McMurdo Dry Valleys. Antarctic Research Series, Vol. 72. Washington (DC): American Geophysical Union.

Lyons WB, Welch KA, Sharma P. 1998b. Chlorine-36 in the waters of the McMurdo Dry Valley lakes, southern Victoria Land, Antarctica: Revisited. Geochimica et Cosmochimica Acta 62: 185–191.

Lyons WB, Fountain AG, Doran PT, Priscu JC, Neumann K, Welch KA. 1999. Importance of landscape position and legacy: The evolution of the lakes in Taylor Valley, Antarctica. Freshwater Biology 42: 1–13.

Madronich S, McKenzie RL, Caldwell MM, Björn LO. 1995. Changes in ultraviolet radiation reaching the earth's surface. Ambio 24: 143–152.

McBean GA. 1994. Global change models: A physical perspective. Ambio 23: 13–18.

McKay CP. 1997. The search for life on Mars. Origins of Life and Evolution of the Biosphere 27: 263–289.

McKay CP, Clow GD, Wharton RA Jr. 1985. Thickness of ice of perennially frozen lakes. Nature 313: 561–562.

McKnight DM, Aiken GR, Andrews ED, Bowles EC, Harnish RA. 1993. Dissolved organic material in Dry Valley lakes: A comparison of Lake Fryxell, Lake Hoare, and Lake Vanda. Pages 119–133 in Green WJ, Friedmann EI, eds. Physical and Biogeochemical Processes in Antarctic Lakes. Antarctic Research Series, Vol. 59. Washington (DC): American Geophysical Union.

McKnight DM, Niyogi DK, Alger AS, Bomblies A, Conovitz PA, Tate CM. 1999. Dry valley streams in Antarctica: Ecosystems waiting for water. BioScience 49: 985–995.

Moorhead DL, Davis WS, Wharton RA Jr. 1997. Carbon dynamics of aquatic microbial mats in the Antarctic dry valleys: A modeling synthesis. Pages 181–196 in Lyons WB, Howard-Williams C, Hawes I, eds. Ecosystem Processes in Antarctic Ice-Free Landscapes. Rotterdam (The Netherlands): A. A. Balkema.

Moorhead DL, Doran PT, Fountain AG, Lyons WB, McKnight DM, Priscu JC, Virginia RA, Wall DH. 1999. Ecological legacies: Impacts on ecosystems of the McMurdo Dry Valleys. BioScience 49: 1009–1019.

Morgan RM, Ivanov AG, Priscu JC, Maxwell DP, Huner NP. 1998. Structure

and composition of the photochemical apparatus of the Antarctic green alga, *Chlamydomonas subcaudata*. Photosynthesis Research 56: 303–314.

Neale PJ, Priscu JC. 1995. The photosynthetic apparatus of phytoplankton from a perennially ice-covered Antarctic lake: Acclimation to an extreme shade environment. Plant and Cell Physiology 36: 253–263.

_____. 1998. Fluorescence quenching in phytoplankton of the McMurdo Dry Valley lakes (Antarctica): Implications for the structure and function of the photosynthetic apparatus. Pages 241–253 in Priscu JC, ed. Ecosystem Dynamics in a Polar Desert: The McMurdo Dry Valleys, Antarctica. Antarctic Research Series, Vol. 72. Washington (DC): American Geophysical Union.

Nedell SS, Anderson DW, Squyres SW, Love FG. 1987. Sedimentation in ice-covered Lake Hoare, Antarctica. Sedimentology 34: 1093–1106.

Packard TT. 1985. Measurement of electron transport activity in microplankton. Advances in Aquatic Microbiology 3: 207–261.

Parker BC, Simmons GM Jr. 1985. Paucity of nutrient cycling and absence of food chains in the unique lakes of southern Victoria Land. Pages 238–244 in Siegfried WR, Condy RR, Laws RM, eds. Antarctic Nutrient Cycles and Food Webs Berlin: Springer-Verlag.

Pomeroy LR. 1974. The ocean's food web, a changing paradigm. BioScience 24: 499–504.

Priscu JC. 1991. Variation in light attenuation by the permanent ice caps of Lake Bonney during spring and summer. Antarctic Journal of the United States 26: 223–224.

_____. 1992. Particulate organic matter decomposition in the water column of Lake Bonney, Taylor Valley, Antarctica. Antarctic Journal of the United States 27: 260–262.

_____. 1995. Phytoplankton nutrient deficiency in lakes of the McMurdo Dry Valleys, Antarctica. Freshwater Biology 34: 215–227.

_____. 1997. The biogeochemistry of nitrous oxide in permanently ice-covered lakes of the McMurdo Dry Valleys, Antarctica. Global Change Biology 3: 301–315.

_____, ed. 1998. Ecosystem Dynamics in a Polar Desert: The McMurdo Dry Valleys, Antarctica. Antarctic Research Series, Vol. 72. Washington (DC): American Geophysical Union.

Priscu JC, Goldman CR. 1983. Seasonal dynamics of the deep-chlorophyll maximum in Castle Lake, California. Canadian Journal of Fisheries and Aquatic Sciences 40: 208–214.

Priscu JC, Neale PJ. 1995. Phototactic response of phytoplankton forming discrete layers within the water column of Lake Bonney, Antarctica. Antarctic Journal of the United States 30: 301–303.

Priscu JC, Priscu LR, Vincent WF, Howard-Williams C. 1987. Photosynthate distribution by microplankton in permanently ice-covered Antarctic desert lakes. Limnology and Oceanography 32: 260–270.

Priscu JC, Priscu LR, Howard-Williams C, Vincent WF. 1988. Diel patterns of photosynthate biosynthesis by phytoplankton in permanently ice-covered Antarctic lakes under continuous sunlight. Journal of Plankton Research 10: 333–340.

Priscu JC, Downes MT, McKay CP. 1996. Extreme supersaturation of nitrous oxide in a poorly ventilated Antarctic lake. Limnology and Oceanography 41: 1544–1551.

Priscu JC, Fritsen CH, Adams EE, Giovannoni SJ, Paerl HW, McKay CP, Doran PT, Gordon DA, Lanoil BD, Pinckney JL. 1998. Perennial Antarctic lake ice: An oasis for life in a polar desert. Science 280: 2095–2098.

Roberts EC, Laybourn-Parry J. 1999. Mixotrophic cryptophytes and their predators in the dry valley lakes of Antarctica. Freshwater Biology 41: 737–746.

Scott RF. 1905. The Voyage of the Discovery. Vol. 2. London: Smith Elder.

Sharp TR. 1993. Temporal and spatial variation of light, nutrients, and phytoplankton production in Lake Bonney, Antarctica. Master's thesis. Montana State University, Bozeman, MT.

Smetacek V, Passow U. 1990. Spring bloom initiation and Sverdrup's critical-depth model. Limnology and Oceanography 35: 228–234.

Spigel RH, Priscu JC. 1996. Evolution of temperature and salt structure of Lake Bonney, a chemically stratified Antarctic lake. Hydrobiologia 321: 177–190.

_____. 1998. Physical limnology of the McMurdo Dry Valley lakes. Pages 153–187 in Priscu JC, ed. Ecosystem Dynamics in a Polar Desert: The McMurdo Dry Valleys. Antarctic Research Series, Vol. 72. Washington (DC): American Geophysical Union.

Squyres SW, Anderson DW, Nedell SS, Wharton RA Jr. 1991. Lake Hoare, Antarctica: Sedimentation through a thick perennial ice cover. Sedimentology 38: 363–379.

Suttle CA. 1994. The significance of viruses to mortality in aquatic microbial communities. Microbial Ecology 28: 237–243.

Takacs CD. 1999. The factors affecting the distribution and dynamics of bacterioplankton biomass and productivity in Taylor Valley lakes, Antarctica. PhD dissertation. Montana State University, Bozeman, MT.

Takacs CD, Priscu JC. 1998. Bacterioplankton dynamics in the McMurdo Dry Valley Lakes, Antarctica: Production and biomass loss over four seasons. Microbial Ecology 36: 239–250.

Taylor TG. 1922. The physiography of the McMurdo Sound and Granite Harbor region. Pages 5–62 in British Antarctic (Terra Nova) Expedition 1910–1913. London: Harrison.

Vincent WF, Ellis-Evans JC. 1989. High Latitude Limnology. Hydrobiologia. Vol. 49. Dordrecht (The Netherlands): Kluwer Academic.

Vincent WF, Rae R, Laurion I, Howard-Williams C, Priscu JC. 1998. Transparency of Antarctic ice-covered lakes to solar UV radiation. Limnology and Oceanography 43: 618–624.

Virginia RA, Wall DH. 1999. How soils structure communities in the Antarctic dry valleys. BioScience 49: 973–983.

Voytek MA, Ward BB, Priscu JC. 1998. The abundance of ammonium-oxidizing bacteria in Lake Bonney, Antarctica determined by immunofluorescence, PCR, and in situ hybridization. Pages 217–228 in Priscu JC, ed. Ecosystem Dynamics in a Polar Desert: The McMurdo Dry Valleys. Antarctic Research Series, Vol. 72. Washington (DC): American Geophysical Union.

Ward BB, Priscu JC. 1997. Detection and characterization of denitrifying bacteria from a permanently ice-covered Antarctic lake. Hydrobiologia 347: 57–68.

Wharton RA Jr, Parker BC, Simmons GM Jr. 1983. Distribution, species composition and morphology of algal mats in Antarctic dry valley lakes. Phycologia 22: 355–365.

Wharton RA Jr, McKay CP, Parker BC, Simmons GM Jr. 1986. Oxygen budget of a perennially ice-covered Antarctic dry valley lake. Limnology and Oceanography 31: 437–443.

Wilhelm SW, Suttle CA. 1999. Viruses and nutrient cycles in the sea. BioScience 49: 781–788.