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Importance of landscape position and legacy: the evolution of the lakes in Taylor Valley, Antarctica

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SUMMARY

1. The major factor influencing the chemical composition and evolution of the major lakes in Taylor Valley, Antarctica, is their location within the landscape. Present-day microclimatic variation and its manifestation over the past 6000 years have led to the differences observed in these lakes today.
2. Geographical and topographical variables within the Taylor Valley magnify subtle changes in the hydrological balances of these lakes. Even short-term variation of the surface temperatures and albedo greatly impact the run-off into the lakes, leading to positive or negative water balances.
3. The legacy of past climatic changes has had a profound effect on the ecology of the lakes today.

Keywords: Antarctica, chemical composition, evolution, lakes, landscape

Introduction

The limnology of the perennially ice-covered lakes in Taylor Valley of Southern Victoria Land, Antarctica (Fig. 1), has traditionally been evaluated lake-by-lake with little focus on comparative relationships. With the arrival of the McMurdo Dry Valleys (MCM) Long-Term Ecological Research (LTER) site, a more synthetic approach to studying the aquatic ecosystems in these unusual environments has developed (Priscu, 1998). For example, because the major source of water to the lakes in Taylor Valley is from seasonal glacier melt, a detailed knowledge of climatic variation and glacier dynamics was needed to establish a quantitative understanding of the hydrological balances of these lakes.

Over the past 6 years of LTER investigations in Taylor Valley, it has become clear that landscape characteristics, both past and present, greatly influence the variability observed in the lakes (Fig. 2). These variations are great and the three major lakes in Taylor Valley are different in many aspects. The most obvious difference is in their chemistry. Lake Hoare is the freshest of the lakes throughout the water column, Lake Fryxell has a brackish monimolimnion and the monimolimnia of both lobes of Lake Bonney are hypersaline (Fig. 3). In addition, the major ionic ratios of the Taylor Valley lakes, even in their fresh surface waters, are quite different (Lyons *et al*., 1998a). The lakes are different in their nutrient characteristics (Priscu, 1995), as well as their chlorophyll and algal distributions (Lizotte & Priscu, 1998). Primary production rates are also different in the lakes (see below). These lakes are a portion of a suite of various types of lakes which exist throughout the McMurdo region. Since the initiation of the study of these lakes (Angino, Armitage & Tash, 1962; Angino & Armitage, 1963), the reason for these differences has remained unclear. Their proximity and similar climate and basin geology have left Antarctic limnologists at a loss in explaining their extraordinary chemical differences. We believe that the current climatic conditions and

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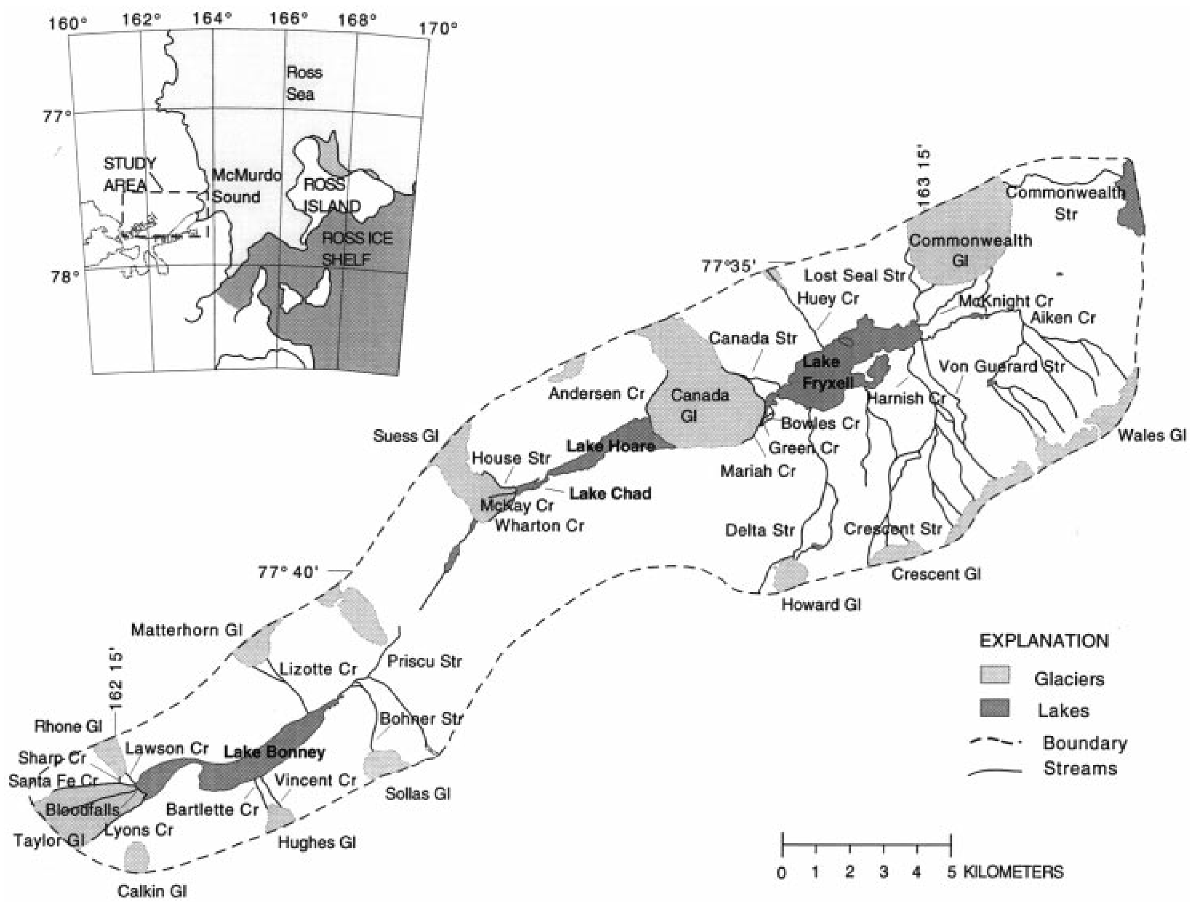

Fig. 1 Location map of Taylor Valley, southern Victoria Land, Antarctica.

their past response to climate has been similar at each location.

Clearly, the position of these three individual lakes within the landscape of Taylor Valley has led to some of the major differences observed in these lakes today. Although not all of the lake variability observed can be explained completely, the degree to which the *individual* lakes interact with their surrounding environment, especially the small variations in climate within the Taylor Valley, are a major key to understanding their present and past development. Although the emphasis of this paper will be on the physical and chemical variations in the lakes within Taylor Valley, there is little doubt that subtle climate differences within the landscape also may account for the biological variations among the lakes. In this paper, we will argue that subtle differences in climate, as dictated by location within Taylor Valley, have a profound effect on the geochemistry and biogeochemistry of these lakes. In addition, subtle climatic effects of the past also greatly direct present-day ecological processes within the lakes.

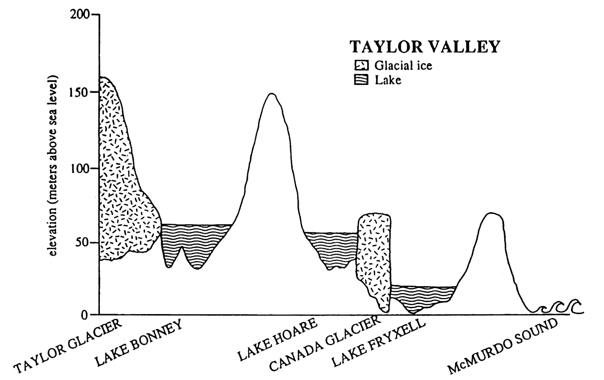

Fig. 2 East–west profile of Taylor Valley showing locations of the lakes (from Spaulding *et al.*, 1997).

Taylor Valley, part of the McMurdo Dry Valleys system, is a polar desert with a mean annual temperature of approximately –20 °C (Clow *et al.*, 1988) and a total annual precipitation of ≤ 10 cm

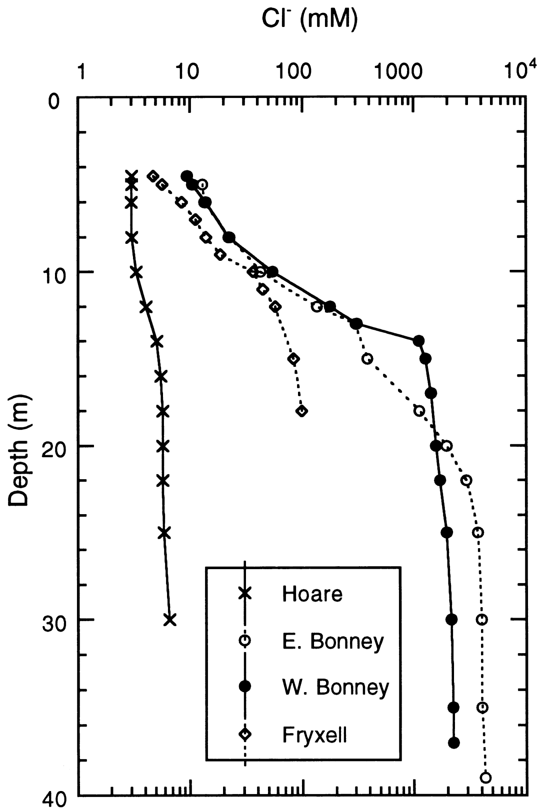

Fig. 3 Chloride versus depth profiles of the Taylor Valley Lakes.

(Keys, 1980). Therefore, the MCM is the coldest and driest of all the current LTER sites, and is among the coldest and driest terrestrial environments on earth.

Taylor Valley is a mosaic of ice-covered lakes, ephemeral streams, soils and surrounding glaciers (Fig. 1). Water flows from the glaciers to the three major lakes in the valley intermittently with flow generally beginning in late November to mid-December and ending in mid-January to late February (Conovitz *et al.*, 1998). Flow is highly variable, both daily and seasonally (Conovitz *et al.*, 1998). Water is lost from the lakes through sublimation of the ice-cover. During the past 20 years, there has been a net gain in water to the lakes as lake levels have been generally rising (Chinn, 1993).

The presence of liquid water remains the primary limiting condition for life in Antarctica (Kennedy, 1993), and therefore, the relationship of energy balance to liquid water availability, ecological function and biological diversity has been a major interest in MCM-LTER research.

The valley's geomorphology has been modified by the movement of glaciers, the inflow of ocean waters, and the waxing and waning of lacustrine environments over the past few million years (Porter & Beget, 1981). Three types of glacier advances are documented:

1 advances of ice from the east as a result of the growth of the West Antarctic Ice Sheet;

2 advances of ice from the west which are thought to be related to thickening of the East Antarctic Ice Sheet (i.e. advance of the Taylor Glacier); and

3 advances of the alpine glaciers within the valley.

Initial research suggested that the Taylor Glacier and the various alpine glaciers advanced during warmer, interglacial times, while the Ross Ice Shelf advances (from the east) were associated with cooler glacial periods (Hendy *et al.*, 1977). More recent work suggests a more complicated pattern of events which are difficult to correlate to known glacial events (Campbell & Claridge, 1987). Because of these glacier movements, the valley floor contains a mosaic of tills of differing age and composition (Péwé, 1960; Stuvier *et al.*, 1981; Burkins *et al.*, 1999). The ages of the morainal materials in the region date to 2.5 million years (Brown *et al.*, 1991).

The eastern portion of Taylor Valley has been in direct contact with the ocean through time with fjord-like conditions until the early Pliocene (Porter & Beget, 1981). The entire valley has been modified by lacustrine sedimentation with a maximum lake high-stand called Glacial Lake Washburn between ≈ 11 000 and 24 000 years ago (Denton *et al.*, 1989). The lake probably existed until ≈ 6000 years ago and it was the precursor to the present-day lakes in the Taylor Valley (Doran, Wharton & Lyons, 1994). Lake levels reached their Holocene lows ≈ 1000 years ago (Matsubaya *et al.*, 1979; Lyons *et al.*, 1998b). The waxing and waning of these lacustrine environments have had a profound effect on the Taylor Valley ecosystem, and the imprints of these changes are just beginning to be understood as important legacies to the present-day ecology (Priscu, 1995; Burkins *et al.*, 1999).

Methods

Detailed outlines of the analytical techniques utilized in this work are presented elsewhere (Priscu, 1995; Welch *et al.*, 1996; Lizotte & Priscu, 1998; Lyons *et al.*, 1998a) and will not be repeated here. We urge the reader to see our web site for details (*http://huey.colorado.edu*).

Table 1 Characteristics of the Taylor Valley Lake District

Characteristic	Lake Fryxell	Lake Hoare	Lake Bonney
Surface area (m^2)	7.1×10^6	1.9×10^6	4.8×10^6
Volume ($\times 10^6$ m^3)	25.2	17.5	64.8
Maximum depth (m)	21	34	40
Depth of oxycline (m)	9.5	28	20
Water temperature (°C)	0 ± 1.0	0 ± 4.0	–2.0 ± 7.0
Conductivity (μmho cm^{-1})	500–8600	400–800	500–156 000

Results

Taylor Valley is 33 km long and contains three major lakes: Lake Bonney, Lake Hoare and Lake Fryxell. Lake Fryxell is closest to the ocean, ≈ 8 km from the coast (Fig. 1). It is also the shallowest lake (Table 1). Lake Hoare is ≈ 15 km west of the ocean and it is 'held' in place by the Canada Glacier (Fig. 1). Without the Canada Glacier in its current location, Lake Hoare would flow east and drain into Lake Fryxell. Lake Bonney begins ≈ 30 km inland. Deep drilling in Taylor Valley has revealed that the last marine incursion in the Miocene did not reach as far westward as the Lake Hoare sub-basin, although it is certain that at least the eastern portion of the Fryxell sub-basin was under marine influence (Porter & Beget, 1981). Lyons *et al*. (1998a) recently referred to Taylor Valley as four distinct 'watersheds', the Fryxell, Hoare and Bonney catchments which drain into their respective closed-basin lakes of the same name, and the Commonwealth catchment at the easternmost portion of Taylor Valley which drains eastward into the Ross Sea.

In Lake Bonney, which has two basins separated by a 13-m-deep sill, the biological characteristics (Table 2; Priscu, 1997; Ward & Priscu, 1997) of the bottom waters of two basins are, in many cases, grossly different, implying very different histories.

The geochemistries of the monimolimnia of the three lakes are very different from each other (Table 2), also implying different developmental histories and/or different sources of solutes. There are even subtle differences in the surface waters among the lakes (Table 2). The enrichment of Ca^{2+}, relative to the other major cations in the bottom of the east lobe of Lake Bonney, is similar to the monimolimnion of Lake Vanda in Wright Valley to the north (Matsubaya *et al*., 1979). Ca^{2+}-enriched waters in saline to hypersaline systems are very rare, and their presence in Lake Bonney implies some unusual climatic and geologic circumstances (Lyons & Mayewski, 1993). As pointed out recently by Lyons *et al*. (1998b), upon sublimation and/or evaporation, the surface waters from Lake Hoare and Lake Bonney would evolve to Na^+-, Mg^{2+}-, SO_4^{2-}- and Cl^--rich waters, while Lake Fryxell would evolve to Na^+-, HCO_3^-- and CO_3^{2-}-rich waters. The reasons for these differences in geochemistry, given the similar climatic regime and geological setting, are unknown.

The lakes have abundant planktonic and benthic microbial populations (Vincent, 1988). No higher forms of life, such as pelagic crustacea, mollusc, insects or fish, have been observed (Doran, Wharton & Lyons, 1994). Microbial mats are primarily composed of cyanobacteria, pennate diatoms and eubacteria (Wharton, Parker & Simmons, 1983). Differences

Table 2 Chemical composition of the Taylor Valley lakes, September 1995

Sample name	Depth (m)	Na (mM)	K (mM)	Mg (mM)	Ca (mM)	Cl (mM)	SO_4 (mM)	DIC (mmol)	pH
Hoare	5	2.47	0.27	0.22	0.75	2.20	0.42	1.72	8.60
	30	7.81	0.77	1.40	2.14	6.30	0.92	8.18	7.10
Fryxell	5	7.90	0.54	0.99	1.35	7.59	0.45	4.68	–
	18	116.9	4.79	13.15	3.76	99.39	1.58	47.70	–
West Bonney	5	10.27	0.36	1.47	1.79	11.87	1.54	0.91	8.33
	38	1789	42.93	402.22	62.05	2299	47.03	78.18	5.51
East Bonney	5	11.70	0.38	1.78	2.05	14.35	1.73	1.41	8.51
	39	2701	66.63	1246	32.46	5100	36.30	3.66	6.72

in biomass (chlorophyll *a*) and net primary production occur between the lakes (Priscu, 1995). Maxima in primary production generally coincide with peaks in biomass.

Climatic variations between the lakes of Taylor Valley

Meteorological stations were installed on all the lakes as part of the LTER core data collection effort in Taylor Valley beginning in 1993 (Doran *et al*., 1995). Each station includes equipment for measuring air temperature and humidity, and wind speed and direction; all measurements are made at 3 m. Other variables were measured, but will not be discussed here. The seasonal climates of the Taylor Valley lakes show many similarities. Summer (December–January) temperatures are close to freezing and winter temperatures dip below –30 °C. Relative humidity varies between 45% in mid-winter (August) and 70% in January. Winds in the valley typically flow east or west, parallel with the axis of the valley, except for near-calm periods when local drainage flow from the valley walls dominates (Clow *et al*., 1988). Average monthly winds are highest in the summer and range from 2.5 to 5.0 m s^{-1}. The lowest winds, typically less than 2 m s^{-1}, occur in autumn (February and March) and/or late winter (August to September). High-velocity winds, known as katabatic or drainage winds, flow off the East Antarctic Ice Sheet and into Taylor Valley over the Taylor Glacier. These winds occur mostly during the winter months (Clow *et al*., 1988). Overall, these characteristics are broadly consistent with the measurements in the adjacent Wright Valley (Keys, 1980) and may be typical for many of the McMurdo Dry Valleys.

Precipitation in the valley is not well known because of the difficulties in measuring snowfall using automatic recorders in a windy desert environment. Snowfall does not seem more frequent in one season or another. Because little snow falls in the valley bottoms (Keys, 1980), a single storm of a few centimetres easily changes summer–winter precipitation differences, given the short time series of observations.

Significant differences in climate exist between the lakes during the 3 years of record from 1994 through 1996 (unpublished data available at *http://huey.colorado.edu/meteordata.html* or P. Doran *et al*., unpublished data). During the winter months (March through September), Lake Fryxell has ≈ 5 °C lower air temperatures on average than Lakes Bonney and Hoare, which are similar. During the summer, Lake Bonney has ≈ 1 °C higher air temperatures on average than the other two lakes, which are similar. The relative humidity at Lake Bonney is consistently lower than Lakes Hoare and Fryxell by an average of ≈ 6.5%. This difference is less pronounced during the winter months (≈ 5% difference) than during the summer months (≈ 8.5% difference). While there are month-to-month variations, there is no overall significant difference between Lakes Fryxell and Hoare with regards to relative humidity. Except in the summer, Lake Bonney is almost always windier than the other two lakes by an average of ≈ 1 m s^{-1}; Lake Hoare is windier in the summer by ≈ 2 m s^{-1} on the average. There is one month on record (August 1994) where Lake Bonney and Lake Hoare have essentially the same mean monthly wind speed, which reflects Lake Fryxell being slightly windier than Lake Hoare in the summer, but Lake Hoare being slightly windier than Lake Fryxell in the winter.

Our observations of snowline in the valleys, those of Keys (1980) and snow accumulation on the alpine glaciers show a precipitation gradient in the valley, with more snowfall near the valley outlet by McMurdo Sound and less snowfall at the head of the valley at the Taylor Glacier (Fountain *et al*., 1998). In one case, snowfall distribution was measured along the axis of the valley immediately after a storm. At Lake Fryxell, the water equivalent snow depth was 1 cm of water, 0.8 cm on Lake Hoare and 0 cm on Lake Bonney. We believe this is partly a result of its closer proximity to the ocean, the major source of moisture to the atmosphere. Because of the albedo differences between snow and glacial ice, differences in snow precipitation are of great importance to the overall water budgets of the lakes. For instance, snow cover, especially in the Fryxell catchment, decreases the amount of meltwater flux into the lake.

The $\delta^{18}O$ in precipitation in the Taylor Valley decreases rapidly from ≈ 29 for the Commonwealth Glacier to 40–41 for the snout of Taylor Glacier (Matsubaya *et al*., 1979; Stuvier *et al*., 1981; Lyons *et al*., 1998b), again indicating a large gradient in atmospheric moisture from the Fryxell catchment to the Bonney catchment. We believe that the overall amount of precipitation in the Taylor Valley is linked to sea ice extent in McMurdo Sound which is, in turn, controlled by large-scale climatic patterns and ocean circulation.

The differences in climate within Taylor Valley are largely related to topographic setting within the valley. One important cause of the climatic differences is the presence of Nussbaum Riegel, an 800-m-high hill in the centre of Taylor Valley. Nussbaum Riegel splits the valley into the Bonney basin and the Hoare and Fryxell basins (Fig. 2). The long-term effect of the Nussbaum Riegel on the valley climate is reflected in the change in glaciers along the valley walls with less snowfall and warmer summer temperatures in the Bonney basin, compared to the Hoare and Fryxell basins (Fountain *et al*., 1998). Another important topographical feature in the valley is Canada Glacier, which blocks much of the narrow valley floor at the east end of Lake Hoare. Clearly, Lake Bonney experiences a more continental climate strongly influenced by katabatic winds, while Lake Fryxell experiences a more marine climate. The climate of Lake Hoare tends to be closer to Lake Fryxell, but depending on the season, shifts towards a Lake Bonney climate.

Clearly, our recent work through the LTER programme has shown that there is spatial variation of climate within the valley. It is small, but measurable, changing from wetter, colder, cloudy conditions near the coast, to warmer, drier conditions at the head of the valley ≈ 33 km inland. The persistence of this gradient dramatically affects snow accumulation and glacier melt, and therefore, the flux and variability of meltwater. This is seen in the variation of meltwater contributions by various streams to Lakes Fryxell and Bonney (Fig. 4). In the Bonney catchment, the percentage of water contributed to the lake among the streams varied little from the 1993–1994 season to the 1994–1995 melt season. In the Fryxell catchment, the variation was quite large, with the Canada Glacier streams contributing ≈ 65% of the total water to the lake in 1994–1995, but only ≈ 30% the previous year. Conversely, smaller contributions from streams originating from the Commonwealth Glacier and the glaciers from the south of the catchment occurred in 1994–1995 compared to 1993–1994. This changing response is caused by the small but important variability in the climatic forcing (i.e. increased snowfall) in the Fryxell catchment described above. The difference in climatic conditions and the degree of variability is a function of position in the landscape of the lakes. The interplay of the influence of the ocean (i.e. source of moisture), the influence of East Antarctic Ice Sheet (i.e. offshore winds) and the topography of the valley (i.e. location of the Nussbaum Riegel and Canada Glacier) dictates the local microclimate, and hence, is driven by the short-term glacier response to climate. Fountain *et al*. (1998) have shown that the distribution of glacier area with altitude can control the response of streamflow to temperature variations. Because Canada Glacier has more area at lower elevation than many of the alpine glaciers in the western portion of the valley, the meltwater flux increases rapidly as the surface temperature increases (Fountain *et al*., 1998). This also supports the notion of the importance of land-

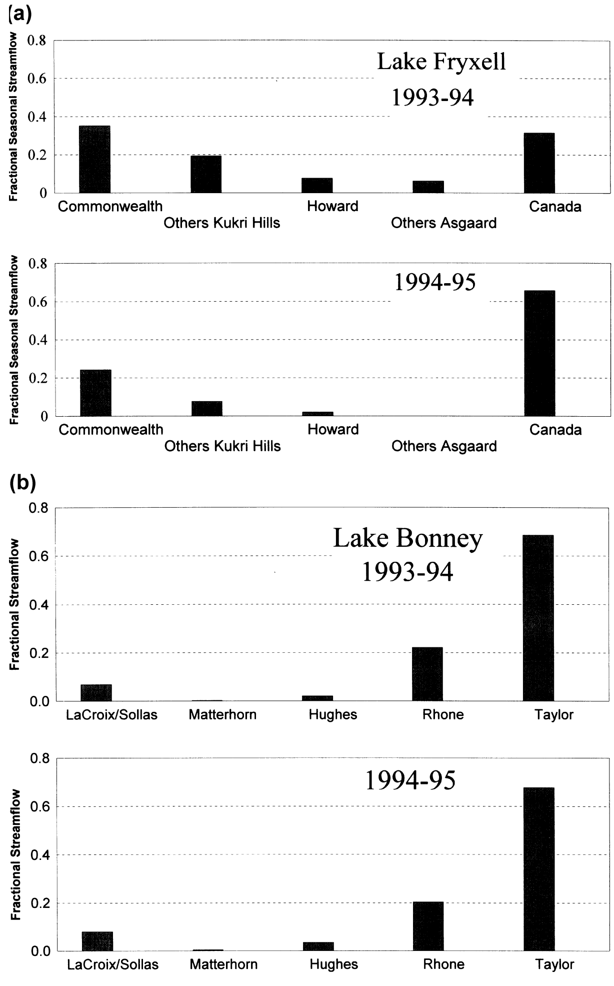

Fig. 4 Seasonal variation in stream input to (a) Lake Fryxell and (b) Lake Bonney from the major glaciers feeding these bodies of water.

scape position (i.e. glaciers to lakes) in the generation and variability of lacustrine hydrologic balances in the Taylor Valley district.

Discussion

Influence of landscape position on climatic legacy of the Taylor Valley lakes

Past climatic conditions have strongly influenced the current ecological conditions in Taylor Valley (Lyons *et al*., 1998b). This is evident in the aquatic environments (Priscu, 1995, 1997) as well as the terrestrial ones (Burkins *et al*., 1999). The concept of legacy implies that carryover or memory is of great significance to the evolution and function of the current lacustrine ecosystems. It is also clear that difference in positions within the Taylor Valley landscape has led to differences in responses of each lake to this legacy. The most direct example is that of the last major 'drawdown' of the lakes which has been interpreted as a cold and/or dry period that ended between 900 and 1200 years ago (Wilson, 1964; Hendy *et al*., 1977; Matsubaya *et al*., 1979; Lyons *et al*., 1998b). It has been argued that the monimolimnia of Lake Bonney, Lake Fryxell and Lake Vanda (in Wright Valley to the north) were produced via evapoconcentration of the lakes during times when surface water input through glacier melt was either greatly reduced or nonexistent. This evaporitic lake hypothesis has been generally accepted for Lake Vanda and the east lobe of Lake Bonney because the $\delta^{18}O$ of the monimolimnic waters have a distinct evaporitic signal (Wilson, 1964; Matsubaya *et al*., 1979). The west lobe of Lake Bonney also is hypersaline, but shows no enrichment of the $\delta^{18}O$. Matsubaya *et al*. (1979) have argued that melt from the Taylor Glacier and saline discharge from a large saline body located under the snout of Taylor Glacier, known as Blood Falls, continued to contribute very saline water to the lake, as it does today (Fig. 5). Because of this continual input of saline water to the west lobe of the lake, no $\delta^{18}O$ evaporitic signal is observed during this cold/dry event. (Essentially, the argument is that the input of melt was faster than the rate of evaporation.)

Lake Hoare and Lake Fryxell also show no evaporitic signal in their monimolimnic waters by either δD or $\delta^{18}O$ measurements (Lyons *et al*., 1998b). However, as shown and discussed above, Lake Fryxell does have a brackish water monimolimnion. Lyons *et al*. (1998b) have argued that Lake Fryxell dried to a playa-like saline lake, only ≈ 0.01% its present size. Modelling indicates that the depth of the playa before the refilling event began was £ 3 cm. This would explain the lack of evaporitic signal in the isotopic profiles, but a higher salt content at depth in the lake today. Because of the very large increase in volume since ≈ 1000 years ago, any isotopic evaporitic signal which was originally present has been 'diluted' out, whereas the salt in the bottom of the playa has redissolved and has been diffusing back into the overlying water (Lyons *et al*., 1998b).

The history of Lake Hoare must have been very different because it has no isotopic signal of the drawdown event nor a salty monimolimnion. There are at least three opinions on the evolutionary history of Lake Hoare including: (1) its complete dry-down during this cold event; (2) its freezing to the bottom; and (3) its disappearance as a result of the retreat of the Canada Glacier (Spaulding *et al*., 1997; Lyons *et al*., 1998b).

Presently, we cannot eliminate any of these possibilities. Currently, Lake Hoare receives ≈ 40% of its meltwater directly from the Canada Glacier, as opposed to stream runoff. This figure has been calculated by the difference in water volume increase in the lake, sublimation loss from the lake ice and the gauged streamflow into the lake. (All streams not flowing directly off glaciers entering the lake are currently gauged.) During the drawdown event, it is possible that water continued to enter Lake Hoare through thermal erosion of the ice because it remained in direct contact with the Canada Glacier (Fig. 1).

Mayewski *et al*. (1995) have analysed an ice core record directly above (≈ 1700 m) Taylor Valley on the

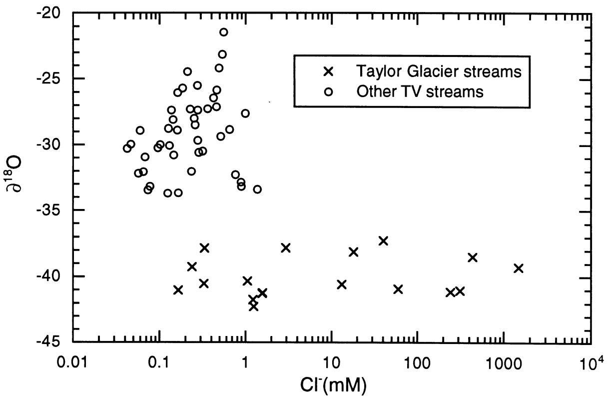

Fig. 5 $\delta^{18}O$ versus Cl^- for Taylor Valley streams.

Newell Glacier and have observed periods of extremely high evaporitic salt loading in the ice. The above authors attributed this increased salt loading to 'drying' events followed by aeolian transport from the surrounding dry valleys. This occurred in the ice core record before the end of the drawdown event (≈ 1500 years ago). These data indicate that the complete loss of Lake Hoare during this time period is feasible. Data from fossil diatom assemblages in the sediments also support this idea. The lack of a shallow water assemblage in the deeper portions of the lake indicates the potential loss of sediments through wind scouring, as discussed above (Spaulding *et al.*, 1997). Bottom water dissolved inorganic carbon (DIC) ages measured by ^{14}C and corrected for the reservoir effect are ≈ 1000–1200 years (Doran *et al.*, 1999). This strongly supports the idea that Lake Hoare dried completely before ≈ 1000 years ago. Borehole measurements on the southern shore of Lake Hoare made in the 1970s indicated that Lake Hoare had probably undergone five different periods of drawdown in its history (McGinnis *et al.*, 1981).

The alpine glaciers, such as the Canada Glacier, are presently at their most advanced location, over the past few million years (Denton *et al.*, 1989). Could the Canada Glacier have advanced by 10–100 m in the past ≈ 1000 years in order to produce Lake Hoare? This would be an advance of ≈ 0.1 m $year^{-1}$. This seems rapid for these glaciers in Taylor Valley which are currently frozen to their base and appear to be close to equilibrium in their mass balance (Chinn, 1980). Currently, data suggest that the alpine glaciers and Taylor Glacier are slowly advancing (Chinn, 1980; A. Fountain, unpublished results). It is unlikely that the Canada Glacier could have moved this rapidly over the past 1000 years.

Spaulding *et al.* (1997) have suggested that Lake Hoare was completely frozen prior to ≈ 1000 years ago. The lake would have been similar to present-day Lake Vida in Victoria Valley to the north, which is deeply frozen today (Calkin & Bull, 1967). This idea cannot be ruled out completely, but there is no compelling evidence to support it strongly. The stable isotope profile from Lake Hoare (Lyons *et al.*, 1998b) offers no insights into this possibility. If freezing did occur, one might expect a brine body to form at depth in the lake, such as is observed in Lake Vida (P. Doran, unpublished data).

No matter what the response of Lake Hoare was to the colder and drier climatic conditions which culminated in Taylor Valley ≈ 1000 years ago, it is clear that each lake responded somewhat differently and the response was indeed related to the position of the lake in the landscape. Perhaps the proximity to glaciers, and hence, water source is the most important factor. Because the west lobe of Bonney, and possibly, Lake Hoare were in direct contact with glacial ice, their sources of water continued and their hydrologic balances were maintained in a manner similar to today. (Glaciers in contact with lakes appear to supply melt directly.) If glacier melt were to be transported via streams to the lake, extensive evaporation would occur during transport or no net input would have occurred at all.

There are important biological ramifications to this climatic legacy. For example, in the lakes that have saline monimolimnia, a major source of nitrogen (N) and phosphorus (P) for phytoplankton growth is from diffusion from the bottom, saline waters (Priscu, 1995). In addition, Priscu (1995) has demonstrated that Lake Hoare and Lake Fryxell are N and P deficient whereas Lake Bonney is solely P deficient using *in situ* nutrient ratio data and nutrient enrichment experiments. The above has shown that the primary reason for this occurrence is not any biochemical or physical processes occurring today, but instead, is the nutrient geochemistry of the diffusing bottom waters. Because the nutrients in the monimolimnia are remnants of the past, the present nutrient dynamics in the photic zones are a legacy of the past climatically induced drawdown. This 'nutrient memory' represents a major influence on the current ecology of the lakes. This is partly a result of the oligotrophic nature of the upper, fresher portions of all the lakes and the low nutrient fluxes into the lakes each year (Green *et al.*, 1989; Priscu, 1995).

Green *et al.* (1989) showed that, given the mean epilimnetic chlorophyll *a* concentration, compared to other lakes, Lake Fryxell should have an N loading from streams between seven and thirty-three times higher than currently measured. This evaluation also strongly supports the idea of a source of nutrients other than stream input in order to maintain the primary production in Lake Fryxell. Calculated N and P fluxes for Lake Fryxell streams, using both Green *et al.* (1989) and our more recent data, range from 0.3

to 30 mmoles m^{-2} year^{-1} for N and 0.3–1 mmoles m^{-2} year^{-1} for P. These values are at the very low end for aquatic environments.

The lakes with the nutrient-rich monimolimnia have higher volumetric primary production (PP) rates measured via ^{14}C uptake (i.e. compare Lake Fryxell to Lake Hoare in Fig. 6). The lakes with chemoclines higher in the euphotic zone generally have higher volumetric primary production rates (i.e. compare Lake Fryxell to the west lobe of Lake Bonney in Fig. 6). Clearly, as outlined above, lake position within the landscape is an indirect cause of these higher rates. The legacy of the monimolimnia and the depths of the lakes are responsible for the nutrient fluxes, and hence, the primary production, and the position in the landscape has dictated which lakes have saline monimolimnia and at what depths these occur.

Respiration versus primary production

Respiration rates (R) and the relationship of R to PP may also be influenced by lake position in the landscape. A comparison of numerous aquatic ecosystems, both terrestrial and marine, has shown that most unproductive systems (PP = 100 μg C L^{-1} day^{-1}) are net heterotrophic systems, i.e. there is more carbon processed by bacteria than fixed by phytoplankton (del Giorgio, Cole & Cimbleris, 1997). The source of this excess carbon for respiration is thought to be from allochthonous sources in most cases (Cole *et al.*, 1994). The Taylor Valley lakes appear to have R > PP (Fig. 5) in all but one case, but the input of allochthonous organic carbon into these lakes is very low (Aiken *et al.*, 1996). Dissolved organic carbon (DOC) values for Taylor Valley streams are low compared to data from temperate and Arctic streams (Aiken *et al.*, 1996) with the

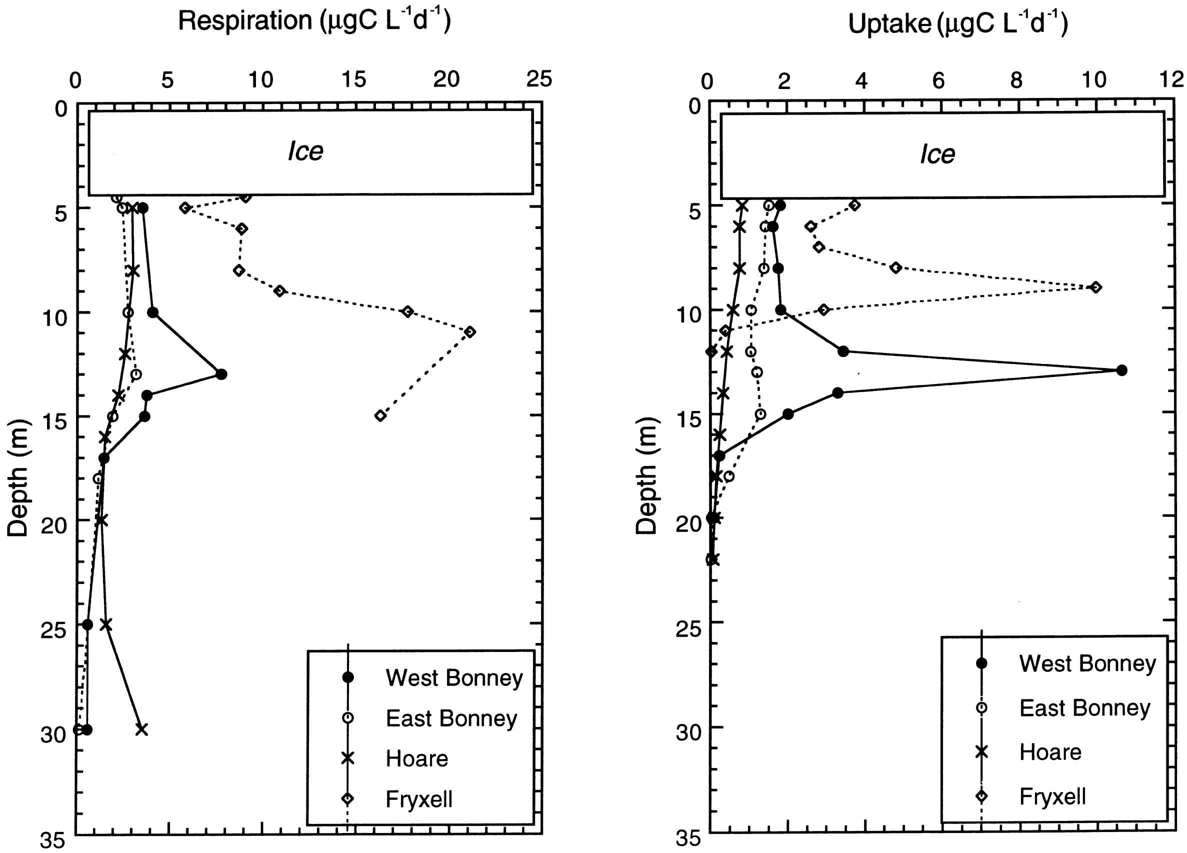

Fig. 6 Primary production rates, measured by ^{14}C uptake and total respiration rates, measured by the ETS technique, for the Taylor Valley lakes.

majority of values 1 mg C L^{-1} or less. The source of this DOC is the leaching of algal and bacterial mats and mosses in the stream channels because no higher plants exist in the catchment and no overland flow into the streams takes place. In addition, not all streams have abundant algal mats in them and their visual abundance is low compared to many of the Lake Fryxell basin streams (Alger *et al.*, 1997). Aiken *et al.* (1996) observed the highest DOC concentrations in the Fryxell basin in streams with abundant biota. These streams are associated with shallow ponds and/or shallow gradients. Values of DOC were as high as 9.5 mg C L^{-1} and values above 1 mg C L^{-1} were common. This indicates that the Fryxell basin has the highest potential flux of allochthonous organic carbon into the lake because of its broad, flat nature. This is partly reflected in the DOC values for the surface waters of the lakes with Lake Fryxell at 3.3 mg C L^{-1} and Lake Hoare at 1.3 mg C L^{-1} at 5.5 m depth (McKnight, Aiken & Smith, 1991).

Therefore, it is possible that the high R-values in Lake Fryxell, compared to the other lakes (Fig. 5), are due, at least in part, to a small but significant flux of allochthonous organic carbon input in the lake and not just its high PP rate. A relationship exists between PP:R and DOC in all the lakes (Fig. 7). Unlike the observations of del Giorgio & Peters (1994) for Quebec lakes, the influence of DOC on planktonic photosynthesis to respiration ratios were not a result of depressing photosynthesis because Lake Fryxell has the highest DOCs and the highest PP (Figs 5 & 6). This may be a result of the fact that the high molecular weight DOC in the Taylor Valley aquatic systems is not primarily

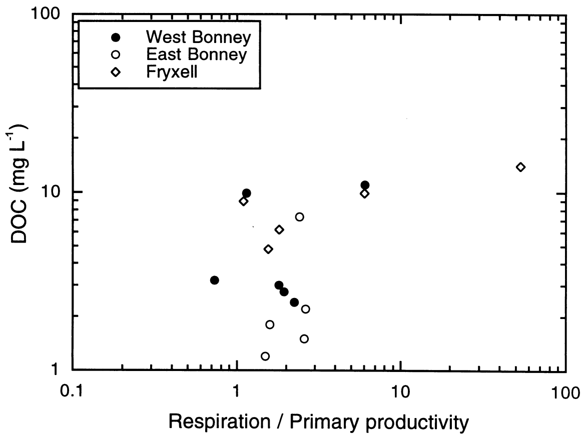

Fig. 7 Dissolved organic carbon (DOC) versus respiration: primary production rate ratio for Lake Fryxell and Lake Bonney.

composed of aromatic moeities as in most terrestrial systems in lower latitudes. It also suggests that, perhaps, some of the DOC is very old, being 'left over' from previous climatic fluctuations as what has been described above for the major elements.

Odum & Prentki (1978) argued that the dominance of heterotrophy or autotrophy in lakes was controlled by autochthonous production of carbon rather than allochthonous influx. Their theory suggests that the importance of external carbon input should become less important as phytoplankton fixation of carbon increases (del Giorgio & Peters, 1994). This may not be the case in Lake Fryxell because the legacy of the nutrient memory drives PP but current allochthonous carbon input increases R. In both cases, the position of Lake Fryxell in the Taylor Valley landscape has produced these processes. In general, these data support the notion of Duarte & Agusti (1998) that unproductive systems support a disproportionately high respiration rate.

As pointed out by Swanson *et al.* (1988), understanding the historical context of landscapes is crucial to understanding ecosystems. The lakes in Taylor Valley, Antarctica are greatly influenced by both present spatial climatic variations and chemical processes which are directly controlled by the position of the lake within the landscape. Because of the nature of this polar desert environment, what would be considered subtle changes or variations in climate in more temperate regions have magnified impacts on the hydrological cycle within Taylor Valley. This is particularly the case in small variations around 0 °C so that the state of water is changed (i.e. solid to liquid). The geographical relationship of the individual lakes within the valley to glaciers, streams and geographic barriers, as well as their proximity to the ocean and the East Antarctic Ice Sheet, controls their hydrological response to climate change. Chemical, physical and biological variations within the lake district are, in strong part, determined by the location of each lake. The current differences in the lakes developed through the individual response of each lake to glacier and stream fluctuation manifested by changes in temperature and precipitation. In turn, the pattern of the landscape, such as distance from the ocean, breadth of the valley floor and proximity to glaciers, has either amplified or muted the climatic effects.

Perhaps in no other aquatic environment but deserts are such small fluctuations in hydrological parameters so critical in controlling ecosystem change. In these polar desert lakes, the lack of vascular plants, crustaceans and vertebrates, minimal input of terrestrial organic carbon, and low species diversity all support the notion that physical factors largely control the biological processes. Although these lakes are buffered from the most severe, short-term climatic fluctuations, loss of stream discharge or ice-cover over long periods of climate change can greatly affect the aquatic ecosystem. From our discussion above, contact with a glacier and the development of a saline monimolimnion might lessen the shock of a changing climate on these lake systems. Conversely, lakes which are fed by long streams rather than direct glacier melt are more susceptible to water deficits during cold or dry conditions. In turn, this leads to lake volume and area loss, and finally, perhaps, to the complete elimination of the lake itself.

Because landforms regulate the movement of both water and energy across a landscape, streams in Taylor Valley provide the only mechanism (other than the wind) to transport allochthonous carbon into the lakes. Increased respiration may be the ecological response in lakes with many streams as opposed to lakes with few.

It is clear from our investigations of the Taylor Valley lakes that these are ecosystems where disturbance (a change in climate) may be short relative to the recovery time and would then be classified as 'unstable' (Turner *et al*., 1993). The Taylor Valley ecosystem today is continually adjusting to the legacy of past climatic changes. That climatic change occurred ≈ 1000 years ago in the lacustrine ecosystem and this event controls contemporaneous phytoplankton growth.

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