



Impact of Episodic Warming Events on the Physical, Chemical and Biological Relationships of Lakes in the McMurdo Dry Valleys, Antarctica

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Abstract. Lakes in the Taylor Valley, Antarctica were investigated to determine the impact of a significant air temperature warming event that occurred during the austral summer of 2001–2002. The warming in the valleys caused an increase in glacial run-off, record stream discharge, an increase in lake levels, and thinning of the permanent ice covers. These changes in the physical environment drove subsequent changes in the biogeochemistry of the lakes. Primary production in West Lake Bonney during the flood was reduced 23% as a consequence of stream induced water column turbidity. Increased nutrient levels within the lakes occurred in the year following the temperature induced high flow year. For example, soluble reactive phosphorus loading to Lake Fryxell was four-fold greater than the long-term average loading rates. These high nutrient levels corresponded to an increase in primary production in the upper water columns of Lakes Bonney and Fryxell. Depth integrated chlorophyll-a values increased 149% in East Lake Bonney, 48% in West Lake Bonney, and showed little change in Lake Fryxell; chlorophyll-a in Lake Hoare decreased 18% compared to long-term averages recorded as part of our ten year monitoring program, presumably from a reduction in under-ice PAR caused by increased sediment loads on the ice cover. Overall the warming event served to “recharge” the ecosystem with liquid water and associated nutrients. Such “floods” may play an important role in the long-term maintenance of liquid water in these dry valley lakes.

Key words: Antarctica, McMurdo Dry Valleys, lakes, stoichiometry, nutrients, climate change, production

1. Introduction

Lakes in the McMurdo Dry Valleys of Antarctica are among the most pristine ecosystems to study lake biogeochemistry (Vincent et al., 1981; Lyons et al., 1998b). The first known observations made on these lakes

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came from Captain Robert Falcon Scott's Discovery Expedition in 1903. From these early records it has been possible to recreate historic lake levels which has revealed the extent to which the water levels in some of these lakes have risen in the past century (Chinn, 1993). After the International Geophysical Year (IGY) of 1957–1958 scientists began to study the lakes in more detail (Angino et al., 1962; Angino and Armitage, 1963; Goldman, 1970). These seminal studies have provided a long-term database from which to compare measurements. Since 1993, the McMurdo Dry Valleys have been the site of a National Science Foundation sponsored Long-Term Ecological Research project (MCM-LTER) that seeks to understand ecosystem level dynamics in the dry valleys (Priscu, 1998).

Examinations of historical records show decadal scale warming events in Lake Vanda (1971) in the Wright Valley (Chinn, 1993), as well as several high flow events (1985, 1990, 2001) over the last twenty years in the Taylor Valley. What is driving the periodicity of these events is unclear; there is no evidence in the Antarctic Oscillation, (Southern Annular Mode) record that correlate with these events (see Welch et al., 2003). Important questions are: Is a large-scale climatic change necessary to initiate these warming events or are regional alterations all that are required; and how sensitive are end-member systems such as the dry valleys to changing climatic drivers that influence hydrological inputs? These lakes are extremely dynamic systems that respond rapidly to what would be considered "subtle" climate variations in more temperate environments (Lyons et al., 2001). Owing to the large amount of ice poised near the melting point during the austral summer, subtle climate changes are amplified to produce a cascade of dramatic ecosystem changes (Doran et al., 2002). In such systems one can begin to test the ideas of ecosystem stability in terms of rates of recovery, trophic interactions, and the role of diversity in these processes.

Climatic factors can act on lakes in ways that affect the ratios of elements in organisms and their energy balance (Redfield, 1958, 1963). These effects may be manifest through increased stream flow and the consequent loading of essential elements to the lakes or through dilution of the extant lake nutrient pool. The stoichiometry of the bulk water, and organisms that live in it, have been shown to be closely related (Redfield, 1958). Hence, a change in bulk nutrient concentrations can influence cellular growth rates, which in turn influences cellular stoichiometry. The balance of these proportions affects production, cycling of nutrients and overall food-web dynamics (Elser et al., 2000). There are a number of hydrologic factors that can alter stoichiometric interactions in the dry valley lakes: the generation of glacial melt-water and potential flushing of cryoconites (cylindrical holes in the ablation zones of glaciers containing a

layer of sediment on the bottom, from “cryo” meaning ice and “conite” meaning dust) on the glaciers; the onset, intensity and duration of stream flow; the opening up of the moat ice surrounding the lakes; and the metabolic activity of organisms.

Here we present data on the physical, chemical and biological responses to a significant warming event that occurred during the austral summer of 2001–2002 in the Taylor Valley, Antarctica. This year will subsequently be referred to as “the year of the flood.”

2. Study Site

The McMurdo Dry Valleys are an ice-free area adjacent to the western edge of McMurdo Sound. Located at 77°45′–77°30′ South latitude and 162°–163°40′ East longitude the Taylor Valley lies in the middle of the McMurdo Dry Valley system and contains three major lake basins (Lakes Fryxell, Hoare and Bonney), created by the advancement and retreat of the glaciers. Lake Fryxell has a maximum depth of 18 m and occupies the eastern portion of the valley, closest to McMurdo Sound (9 km). Lake Hoare is 34 m deep and lies in the next catchment up the valley, 15 km from the Sound. Finally, the Bonney basin abuts the terminal edge of the Taylor Glacier and lies 25 km from McMurdo Sound. The east lobe of Lake Bonney is 38 m deep and the west lobe of Lake Bonney is 39 m deep. Although these three lakes lie in the same valley, they have very different histories, ages, hydrology, and geochemical compositions (Lyons et al., 2000).

The valleys receive less than 5 mm (water equivalents) of precipitation per year and have a mean annual temperature near $-20\text{ }^{\circ}\text{C}$ (Clow et al., 1988; Fountain et al., 1998). Winds are the dominant force controlling air temperature in the valleys (Doran et al., 2002). In the summer of 2001–2002, the year of the flood, the dry valleys experienced average summer temperatures of $-1.8\text{ }^{\circ}\text{C}$, as well as several days with temperatures above $4\text{ }^{\circ}\text{C}$, well above the typical average of $-6\text{ }^{\circ}\text{C}$ experienced during the summer of 2000–2001 (Fountain et al., 2004). During the austral summer light is present 24 h a day, and this period of total sunlight is the time when most of the photoautotrophic primary production occurs in the region (Priscu et al., 1998a). The period of melt and stream flow may last anywhere from 4 to 10 weeks (Conovitz et al., 1998) and provides the primary water input to the lakes; groundwater input to the lakes is thought to be negligible. These streams contribute a source of inorganic solutes and organic matter to the closed basin lakes (Green et al., 1988; Aiken et al., 1996). During the flood, annual stream discharge in the dry valleys was twice the volume of the previous eight seasons combined (<http://huey.colorado.edu/LTER>).

3. Methods

3.1. SAMPLE COLLECTION

Samples were collected on approximately monthly intervals during the austral summers (October–January) from 1993 to present in West Lake Bonney, Lake Fryxell, and Lake Hoare, while samples in East Lake Bonney have been collected routinely since 1989. Water samples were collected with 5L-Niskin bottles through holes drilled in the permanent ice covers of the lakes. Samples were collected from the same sampling depths each year in order to monitor various physical, chemical and biological parameters. Once collected samples were returned to lakeside laboratories in darkened insulated containers and either processed immediately or stabilized for later analyses.

3.2. ANALYTICAL METHODS

Sampling protocols for the dry valley lakes have been previously described (Priscu, 1995; Welch et al., 1996; Takacs and Priscu, 1998). Briefly, major ions, nutrients, and dissolved organic carbon (DOC) were determined with a Dionex ion chromatograph, Lachat nutrient analyzer, and Shimadzu 5000 TOC analyzer, respectively, using standard methods recommended by the manufacturer. Owing to the low levels of soluble reactive phosphorus (SRP) in these systems, samples were analyzed manually using the antimony-molybdate method (Strickland and Parsons, 1972) with a 10 cm pathlength cuvette. Primary production was measured by incorporation of ^{14}C -bicarbonate (Priscu, 1995) over 24 h *in situ* incubations through the photic zones of the lakes. Dissolved inorganic carbon was analyzed by infrared gas analysis of acid-sparged samples. Conductivity, temperature and depth were measured with a Seabird SBE 25 profiler fitted with fine-scale sensors (Spigel and Priscu, 1998).

3.3. STREAM NUTRIENT LOADING

Annual hydraulic loading ($\text{m}^3 \text{ year}^{-1}$) for each lake basin represents the summation of annual discharge for stream gage sites and for sites where stream discharge rates were computed manually. Flow volume, conductivity and temperature were recorded at each stream gage site on 20-minute intervals. Geochemical parameters (i.e., NO_3^- , NH_4^+ , SRP, POC, PON) were determined on a more limited basis (i.e., 3–5 specific time points) at each stream gage. Simple linear regression was used to evaluate the relationships between stream flow characteristics and nutrient concentrations. Ostensibly, stream conductivity may be used as a surrogate for dissolved nutrients and total dissolved solids within the discharge. For instance, following periods of no flow, the initial phase of stream flow should have increased solute

concentrations sequestered from the dry streambed. Thus, conductivity values should reflect the increased solute concentrations. However, there were no significant relationships found between discharge, conductivity, and geochemical parameters. Therefore, we opted for the more simple approach of estimating stream nutrient loadings (g year^{-1}) by multiplying the average annual nutrient concentration (g m^{-3}) by the discharge rate ($\text{m}^3 \text{ year}^{-1}$).

3.4. LAKE LEVEL MEASUREMENTS

Lake level measurements were made annually using known elevational benchmarks: ground-penetrating radar in concert with manual lake soundings were used to map basin morphometry (Spigel and Priscu, 1998). Lake volume was subsequently determined from basin morphometry. Annual ice thickness measurements for each lake were used together with basin morphometry to determine changes in ice layer water equivalent volume (assuming an ice density of 0.91 g mL^{-1}). Annual hydraulic residence times (year) were computed for each lake basin by dividing the whole lake water volume (m^3) by the annual hydraulic loading rate.

3.5. UNDERWATER PHOTOSYNTHETICALLY ACTIVE RADIATION

Underwater photosynthetically active radiation (PAR, 400–700 nm) was monitored on a continual basis in each of the lakes using a Licor 4π spherical quantum sensor (LI-193). The underwater PAR sensors were located 7 m below the ice surface in Lake Fryxell and 10 m below the ice surface in both lobes of Lake Bonney and Lake Hoare. Data were logged with Campbell CR10 or 21X surface units.

4. Results

4.1. PHYSICAL

4.1.1. Changes in Lake Water Levels

Data from 1991 to 2000 show a slow decline in annual lake levels resulting in relatively modest inter-seasonal change (Doran et al., 2002). The volume of the lakes in 1991 were 79×10^6 , 24×10^6 , and $54 \times 10^6 \text{ m}^3$ in Lakes Bonney, Hoare, Fryxell, respectively. Between 1991 and 2001 lake volumes dropped $9,100 \text{ m}^3$ in Lake Bonney, $30,700 \text{ m}^3$ in Lake Hoare and $466,200 \text{ m}^3$ in Lake Fryxell. Changing lake levels occur when stream inflow is not balanced by losses (evaporation and sublimation; the lakes have no surface water or groundwater losses). During the flood year (2001–2002) lake volumes rose $274,500 \text{ m}^3$ in Lake Bonney and $403,300 \text{ m}^3$ in Lake Fryxell. The flood of 2001–2002 increased levels back to pre-1991 values, rapidly reversing

the slow decline (average loss of 0.05 m year^{-1} Fryxell, 0.04 m year^{-1} Bonney and 0.01 m year^{-1} Hoare) in lake levels seen over the previous decade. Ice thickness increased from 1989 until the flood event in conjunction with the slow decrease in lake levels (Doran et al., 2002), causing a related decrease in under-ice PAR. Following the flood event the ice covers on the four lakes decreased (0.25 m in ELB, 0.34 m in WLB, 1.65 m in Hoare and 0.09 m in Fryxell) in response to the warmer temperatures and higher stream flow.

The hydraulic residence times of the lakes declined between 1995 and 2001, the year of the flood (Figure 1). The median residence time (1995–2001) was 77 years in Lake Bonney, 281 years in Lake Hoare and 107 years in Lake Fryxell. The residence time for the photic zone, where most of the freshwater stream flow is constrained, is significantly less (35 years in Lake Bonney, 260 years in Lake Hoare and 58 years in Lake Fryxell) than when the entire water volumes are considered. Whole lake hydraulic residence times in Lake Fryxell declined from the 1995–2001 average of 107 years to 9 years during the flood year, i.e., more than 10% of the total volume of the lake entered during the flood event, highlighting the high stream discharges in this basin. The warmer temperatures during the flood season resulted in increased lake levels and thinner ice covers in all lakes.

4.1.2. Underwater Light Profiles

Underwater PAR values typically begin increasing during the spring and peak in December followed by a gradual decline as the fall wanes and the months of darkness begin (Figure 2) (see also Priscu et al., 1999). However, following the flood event in 2001 the West Lobe of Lake Bonney showed a sharp decline in underwater PAR, dropping off to near zero at 10 m depth. This decline in underwater PAR values is the result of turbidity caused by sediment entering the west lobe from streams coming from the Taylor, Rhone and Calkin Glaciers at the western end of Lake Bonney. Similar patterns were not evident in the other lakes, presumably because the streams are of a lower gradient, and have lower flow, resulting in smaller sediment loads.

4.1.3. Conductivity and Temperature Profiles

Maximum temperatures in the four lakes studied occur well below the ice covers ($5.2 \text{ }^{\circ}\text{C}$ at 17 m in West Lake Bonney, $1.8 \text{ }^{\circ}\text{C}$ at 15 m in East Lake Bonney, $0.3 \text{ }^{\circ}\text{C}$ at 6 m in Lake Hoare, and $2.2 \text{ }^{\circ}\text{C}$ at 15 m in Lake Fryxell), while the lowest temperatures ($-4.4 \text{ }^{\circ}\text{C}$) are found in the bottom waters of East Lake Bonney. The water columns remain stable despite the buoyancy-induced forces caused by temperature because of the density imparted by the saline bottom waters (Spigel and Priscu, 1998). Conductivities in the upper water columns of the lakes are indicative of relatively freshwaters and

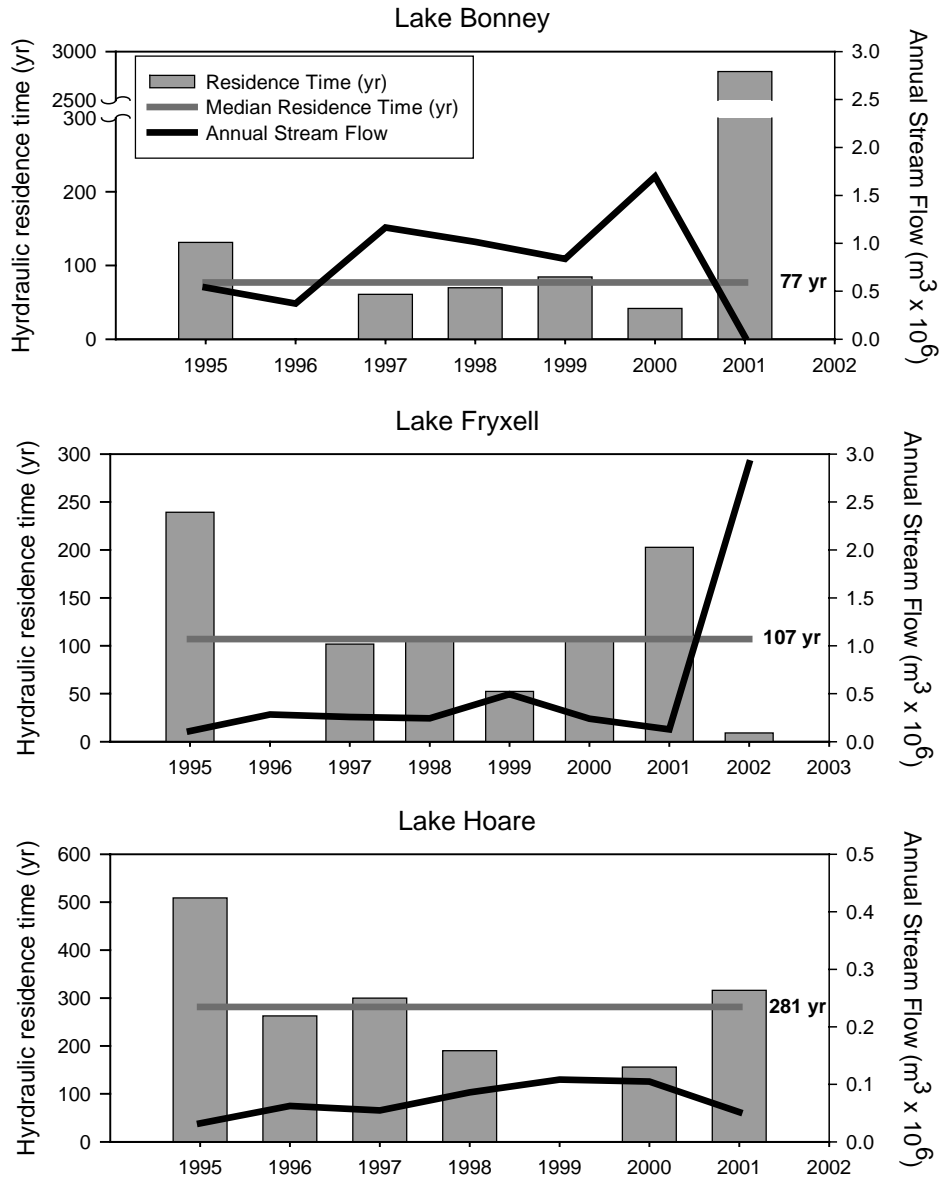


Figure 1. Annual hydraulic residence time (years) was calculated by dividing the lake water volume by the annual hydraulic load.

increase precipitously below the chemocline in both lobes of Lake Bonney to values exceeding seawater (>100 practical salinity units (PSU)). Temperature and conductivity profiles are remarkably stable from year to year, as well as intra-annually in the dry valley lakes (Spigel and Priscu, 1998), although some variation has been observed at Lake Vanda (W. Vincent, personal

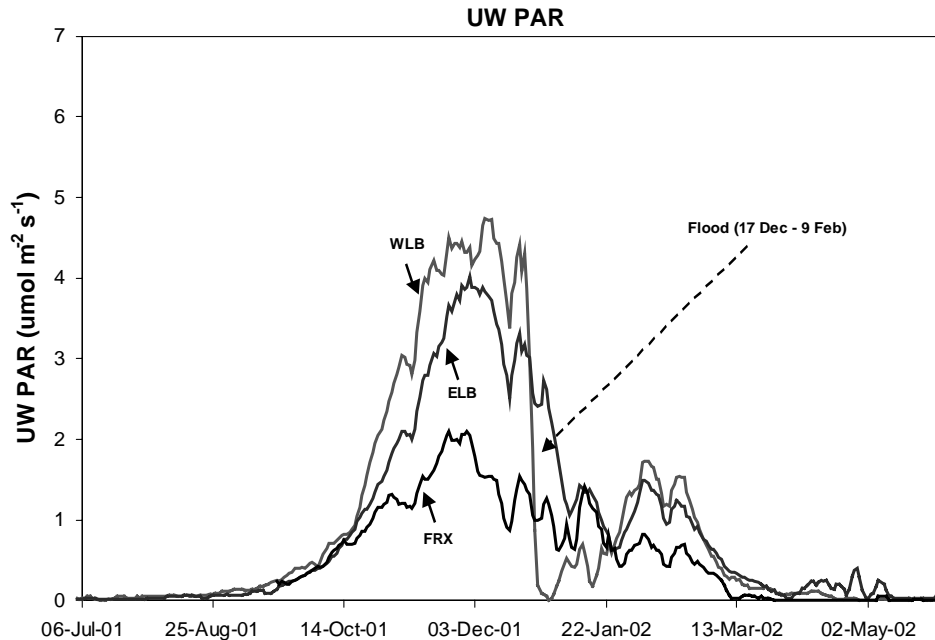


Figure 2. Underwater photosynthetically active radiation (PAR) logged from July 2001 until May 2002. The period of the flood (17 December–9 February 2001) is indicated by the dashed arrow.

communication). Profiles of conductivity and temperature, and changes in temperature with depth are shown from West Lake Bonney before and during the flood, revealing the extreme hydraulic stability typical of the water column (Figure 3a). However, the high stream flow at the end of December 2001 in West Lake Bonney created regions of relatively fine scale temperature and conductivity instability below the ice layer down to the chemocline, indicative of turbulence (Figure 3b). This water column instability has only been observed during the flood period. There was no such change in the temperature and conductivity profiles for East Lake Bonney, Lake Hoare or Lake Fryxell. Unfortunately, our sampling schedule may not have detected flood-induced instabilities in these lakes that may have occurred later in the season.

4.2. GEOCHEMICAL

4.2.1. Long-term and Flood Related Nutrient Profiles

Dissolved inorganic nitrogen (DIN) concentrations are relatively low in the surface waters of the lakes and increase precipitously at the chemocline. The DIN maxima occur between 30 and 35 m in East Lake Bonney, and at 38, 18, and 30 m in West Lake Bonney, Lake Fryxell and Lake Hoare, respectively.

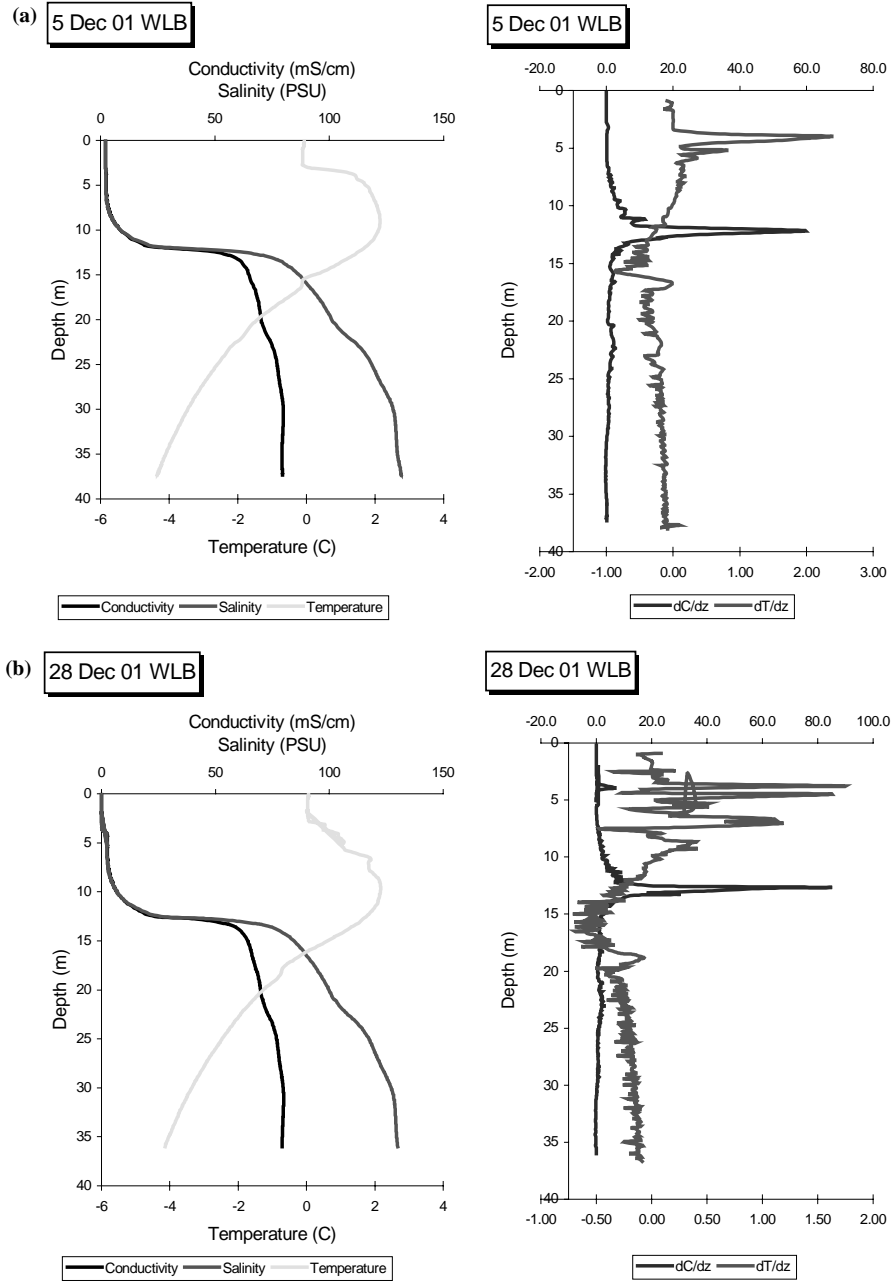


Figure 3. (a) Temperature, conductivity and salinity profiles, and changes in conductivity and temperature with depth through the water column of West Lake Bonney before the flood (5 December 01) and (b) during the flood (28 December 2001), showing inversions in the profiles above the chemocline.

The depth integrated DIN above the photic zone has remained low and relatively constant in both East Lake Bonney and West Lake Bonney from 1993 to the present (Figure 4a), below the photic zone the depth integrated DIN is greater but also remains relatively constant through time.

Changes in the nutrient pools of the lakes occurred following the flood. At 5 m in West Lake Bonney there was 56% less total DIN, NH_4^+ increased but NO_3^- was reduced. At the chemocline there was also 46% less DIN, however this was due to a reduction in NH_4^+ . In East Lake Bonney there was 22% less DIN directly below the ice cover, while at 13 m there was 46% less DIN. In Lake Fryxell the dissolved inorganic nitrogen concentrations are relatively low (DIN $< 1 \mu\text{M}$ above 11 m); however, during our first sampling event in the year following the flood (30 October 2002) NO_3^- levels were greater than $1 \mu\text{M}$.

SRP profiles generally resemble those of nitrogen, being low at the surface, but increasing at, and below the chemocline; although, even in the deep waters of Lake Bonney SRP never exceeds $\sim 1 \mu\text{M}$ (Figure 4b). Values of SRP in East and West Lake Bonney are often near the analytical detection limit of our methods ($0.03 \mu\text{M}$). Because these values are so low, it is difficult to discern minor changes; however, in West Lake Bonney SRP was clearly removed from the upper water column during the flood (Figure 5). SRP concentrations in the upper 5 m of the water column changed from $0.15 \mu\text{M}$ in the early season to below our limits of detection during the flood.

4.2.2. Stream Nutrient Loadings

Stream nutrient loading and upward diffusion of nutrients across the chemocline are the two primary sources of “new” nutrients into the trophogenic zones of Lakes Bonney and Fryxell. The trophogenic zones in Lakes Bonney (east and west lobe) and Fryxell begin directly below the ice layer and extend down to the chemocline positioned at 18, 17, and 10 m, respectively. The incoming relatively low ionic strength stream flow is generally confined to the upper 2 m of the water column in Lake Fryxell and East and West Lake Bonney. West Lake Bonney is different because it receives a portion of its total stream flow from Blood Falls, purportedly an outlet for an entrapped hypersaline marine seep located beneath the Taylor Glacier (Keys, 1979; Mikucki et al., this volume). This denser stream water plunges below the chemocline in West Lake Bonney until it reaches a level of equal density (~ 25 m).

The upward diffusion of nutrients across the chemocline was estimated using Fick’s law as outlined by Priscu (1995):

$$\frac{dC}{dt} = \frac{\delta}{\delta Z} \left(K_Z \frac{\delta C}{\delta Z} \right),$$

where dC/dt is the upward flux of the solute ($\text{mg m}^{-2} \text{d}^{-1}$), K_z the vertical diffusion coefficient for solutes across a boundary ($8.6 \times 10^{-5} \text{ m}^{-2} \text{d}^{-1}$) and Z is the depth (m). The horizontal planes of diffusion were the 14 m layer,

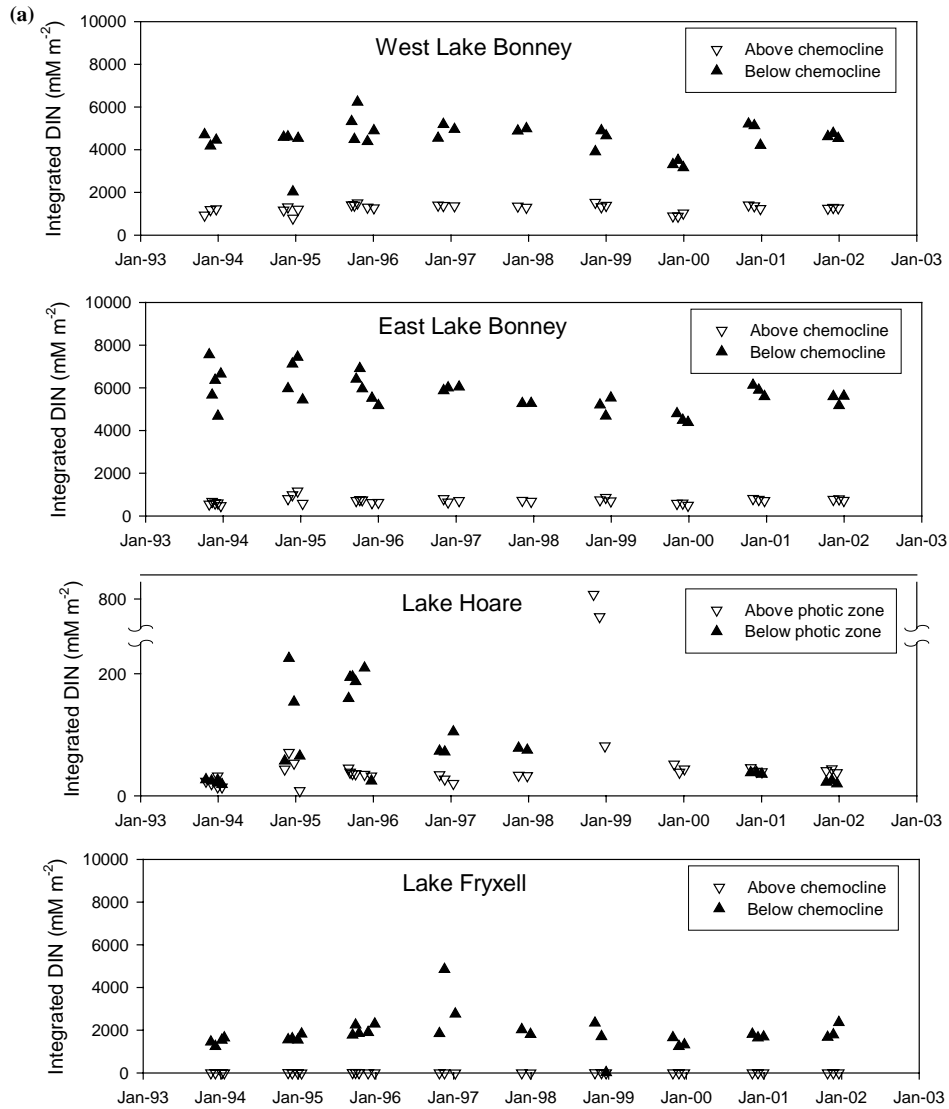


Figure 4. Depth integrated values of (a) dissolved inorganic nitrogen (DIN) and (b) soluble reactive phosphorus (SRP) above the chemocline in West Lake Bonney, East Lake Bonney, Lake Fryxell and above the photic zone in Lake Hoare; below the chemocline in West Lake Bonney, East Lake Bonney, Lake Fryxell and below the photic zone in Lake Hoare. The year designations refer to the end of the austral summer season, for example January 02 refers to the 2001–2001 season beginning in October 2001 and ending in January 2002.

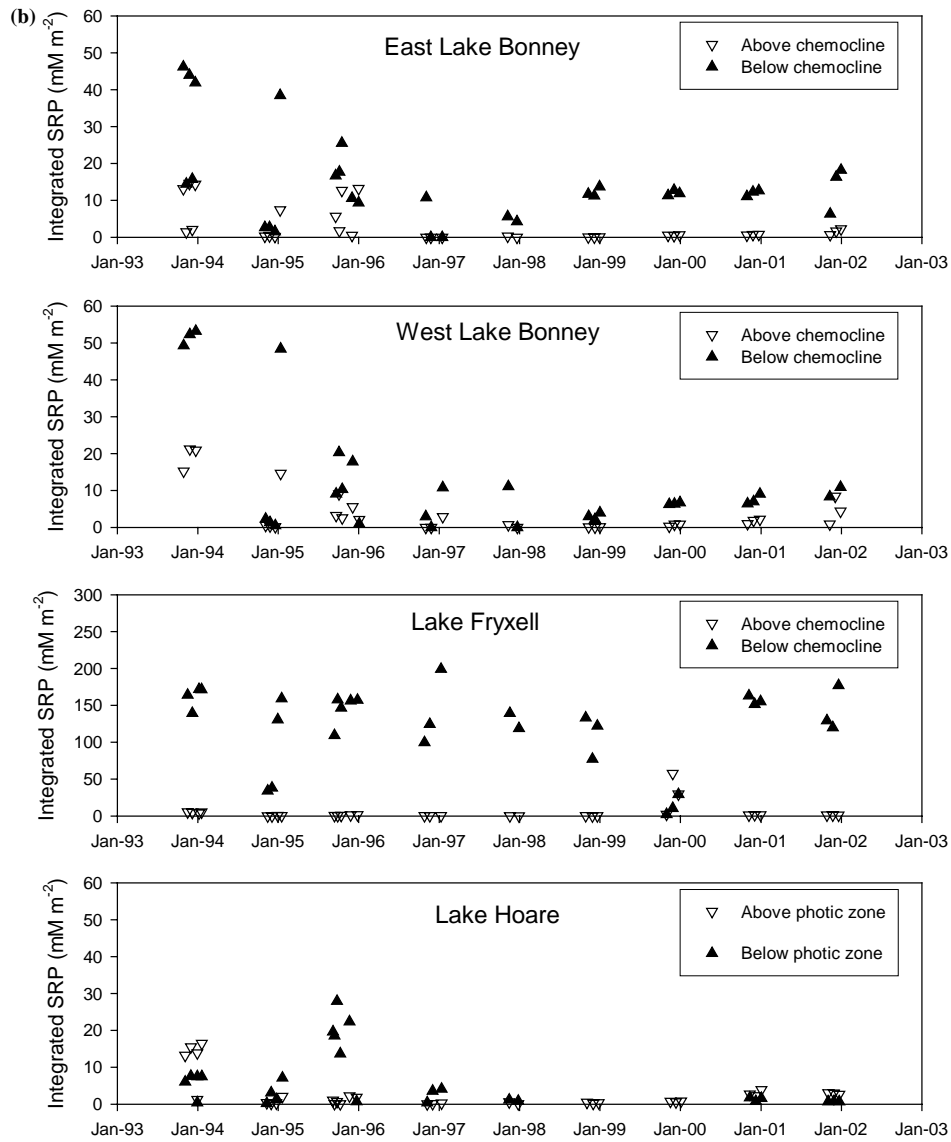


Figure 4. Continued.

West Lake Bonney; 15 m layer, East Lake Bonney; and 10 m layer, Lake Fryxell. Given the known area (m²) of each the chemocline layer, the diffusional mass loading for selected macronutrients could be determined for each season (Figure 6a and b). The long-term average annual dissolved inorganic nitrogen ($\text{DIN} = \text{NH}_4^+ + \text{NO}_2^- + \text{NO}_3^-$) loading via diffusion across the chemocline in East Lake Bonney and Lake Fryxell account for approximately 67 and 63%, respectively, of the total DIN mass entering the

trophogenic zone. Whereas in West Lake Bonney the long-term average annual diffusion load is only 12% of the total DIN load. During the flood year this trend was reversed for Lake Fryxell, when only 16% of the total annual DIN load was attributed to diffusion across the chemocline.

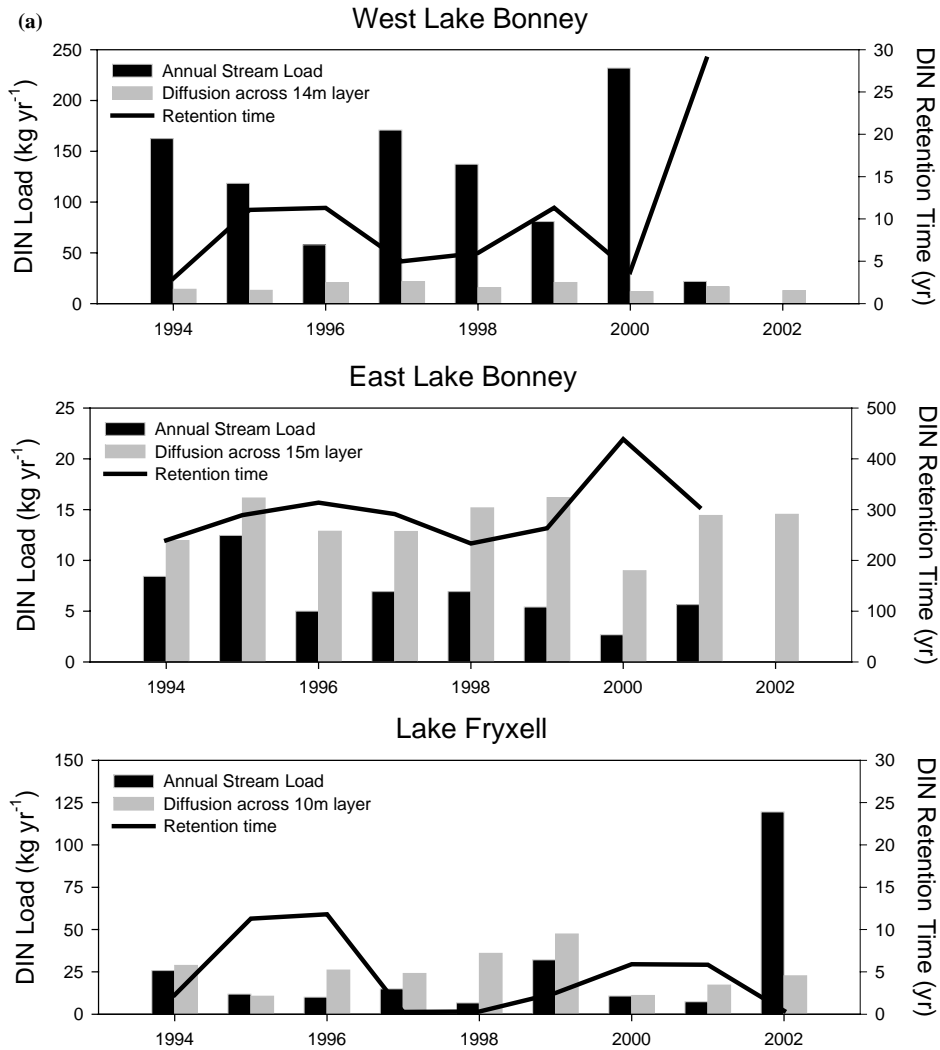


Figure 5. Annual stream loadings of (a) dissolved inorganic nitrogen (DIN) and (b) soluble reactive phosphorus (SRP) above the chemocline in the dark bars, diffusional loading in the light bars, and turnover time indicated by the black lines in West Lake Bonney, East Lake Bonney and Lake Fryxell. The year designations refer to the end of the austral summer season, for example 2002 refers to the 2001–2002 season beginning in October 2001 and ending in January 2002. The break in the line corresponds to the period for which there is no available stream data.

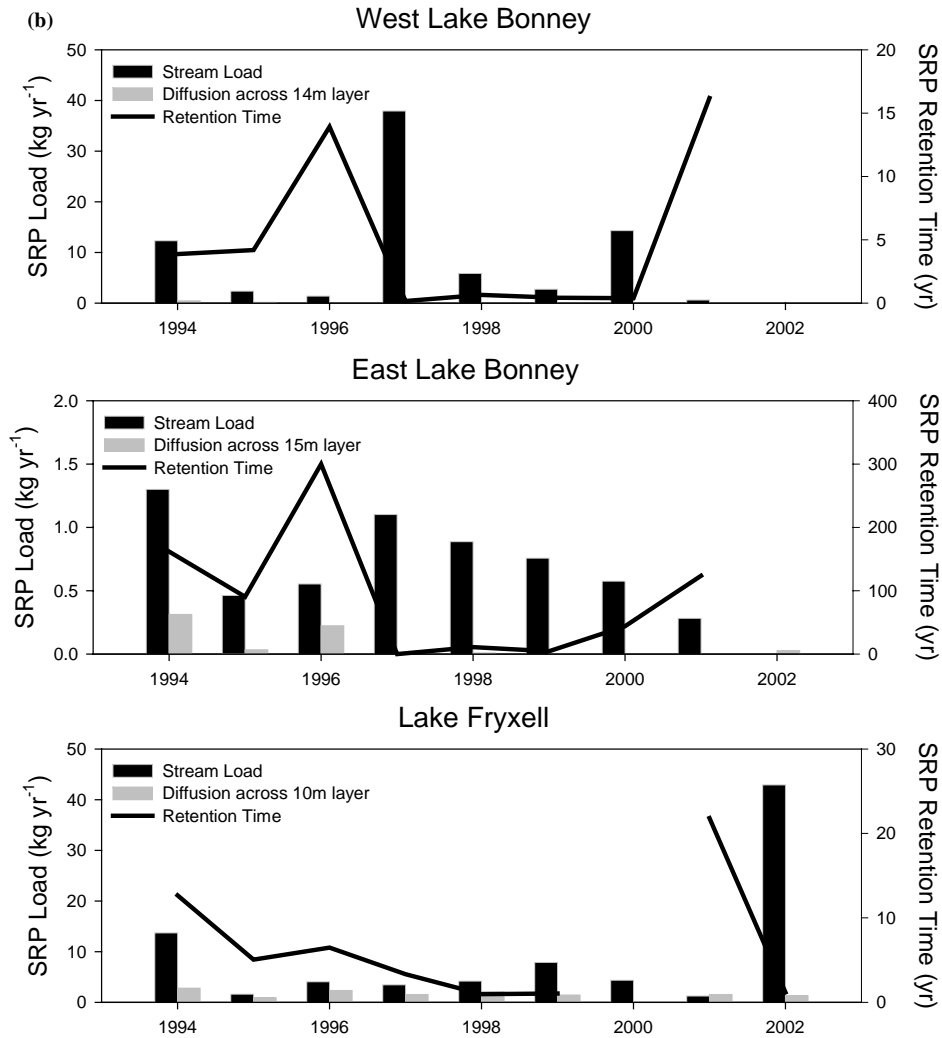


Figure 5. Continued

Unfortunately, high water flows damaged the stream gauging stations so that we could not compute the relative importance of stream and diffusional nutrient loads for East Lake Bonney or West Lake Bonney.

Stream loading is the primary source of “new” soluble reactive phosphorus (SRP) entering the trophogenic zones of East and West Lake Bonney and Lake Fryxell. This is a consequence of the relatively small SRP pools below the chemoclines, which produces low gradients across the diffusional planes and subsequently small upward diffusive fluxes of SRP (Figure 6b). Long-term annual averages of SRP stream loads in East and West Lake Bonney and Lake Fryxell account for 90, 99, and 84%, respectively, of the

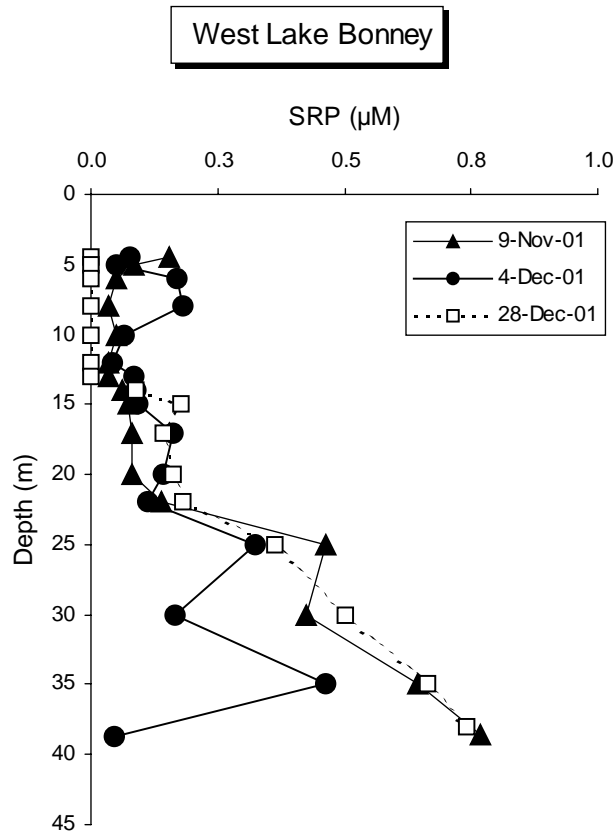


Figure 6. Soluble reactive phosphorus (SRP) in West Lake Bonney, 2001. During the flood, 28 December 2001, SRP was stripped from the upper water column.

total SRP load entering the trophogenic zone. During the flood, the annual stream load entering Lake Fryxell was over four-fold greater than the long-term average stream load.

4.2.3. Stoichiometric Relationships

Elemental stoichiometry is frequently used to examine the availability of nutrients and foodweb dynamics in aquatic systems (Redfield, 1958; Goldman, 1979; Healey and Hendzel, 1980; Priscu and Goldman, 1983; Dodds, 2003). Deviations from the classic Redfield ratio (C:N:P 106:16:1 by mol) generally implies imbalanced growth of the microbial assemblage as a result of either nitrogen or phosphorus deficiency. N:P (DIN:SRP) ratios well above the Redfield ratio are found throughout the water columns in the dry valley lakes (Table I) implying that microbial activity in these systems is phosphorus deficient. The highest depth integrated N:P ratios (> 10,000) occur in the deep

Table I. Long-term N:P (molar) ratios for East Lake Bonney, West Lake Bonney, Lake Hoare, and Lake Fryxell from 1993 to 2001

Depth (m)	ELB N:P	WLB N:P	Hor N:P	FrX N:P
5	632	357	71	18
10	844	386	119	33
13	1275	2650	361 ^a	78 ^c
15	1728	7573	780 ^b	398
20	5790	2330	579	667 ^d
22	385	2516	167	
25	478	1754	184	
30	1115	1228	21	
38	1666	635		

^a13 m corresponds to 12 m in Hor.

^b15 m corresponds to 14 m in Hor.

^c13 m corresponds to 12 m in Frx.

^d20 m corresponds to 18 m in Frx.

waters of both lobes of Lake Bonney (Figure 7). During the flood, N:P ratios in West Lake Bonney increased in the upper water column as a result of the loss of SRP. In November 2002, the year following the flood, N:P ratios were elevated in the upper water column of East Lake Bonney (1050 at 5 m, 1180 at 10 m), but decreased throughout the entire profile of Lake Fryxell (0 at 5 m due to DIN being non-detectable [$< 0.03 \mu\text{M}$], 4.1 at 10 m, 10.3 at 12 m, 10.1 at 15 m and 4.1 at 18 m) and Lake Hoare (4.5 at 5 m, 1.1 at 10 m, 1.8 at 12 m, 0.9 at 14 m, 23.5 at 20 m, and 23.1 at 22 m). The N:P ratios in West Lake Bonney were nearly double the year after the flood, with phosphorus concentrations remaining low until mid-summer. Experimental bioassays and *in situ* stoichiometry all show that the east and west lobes of Lake Bonney are strongly phosphorus deficient (Priscu, 1995; Takacs and Priscu, 1995; Dore and Priscu, 2001) corroborating the stoichiometric ratios.

4.3. BIOLOGICAL

4.3.1. Primary Production

Primary production (PPR) maxima occur just above the chemocline in Lakes Bonney and Fryxell; secondary maxima are often apparent just below the ice cover (Figure 8). Depth integrated production (ELB 4.5–22 m, WLB 4.5–20 m, Hor 5–22 m, Frx 5–12 m) typically increases during the course of the austral summer and then drops as the summer wanes (Figure 9; and Priscu et al., 1999). West Lake Bonney has 56% more depth integrated primary production (mean $24.2 \text{ mg C m}^{-2} \text{ d}^{-1}$, SD = 12.2, n = 33) than East Lake Bonney (mean $10.8 \text{ mg C m}^{-2} \text{ d}^{-1}$, SD 8.6, n = 42), 61% more than Lake

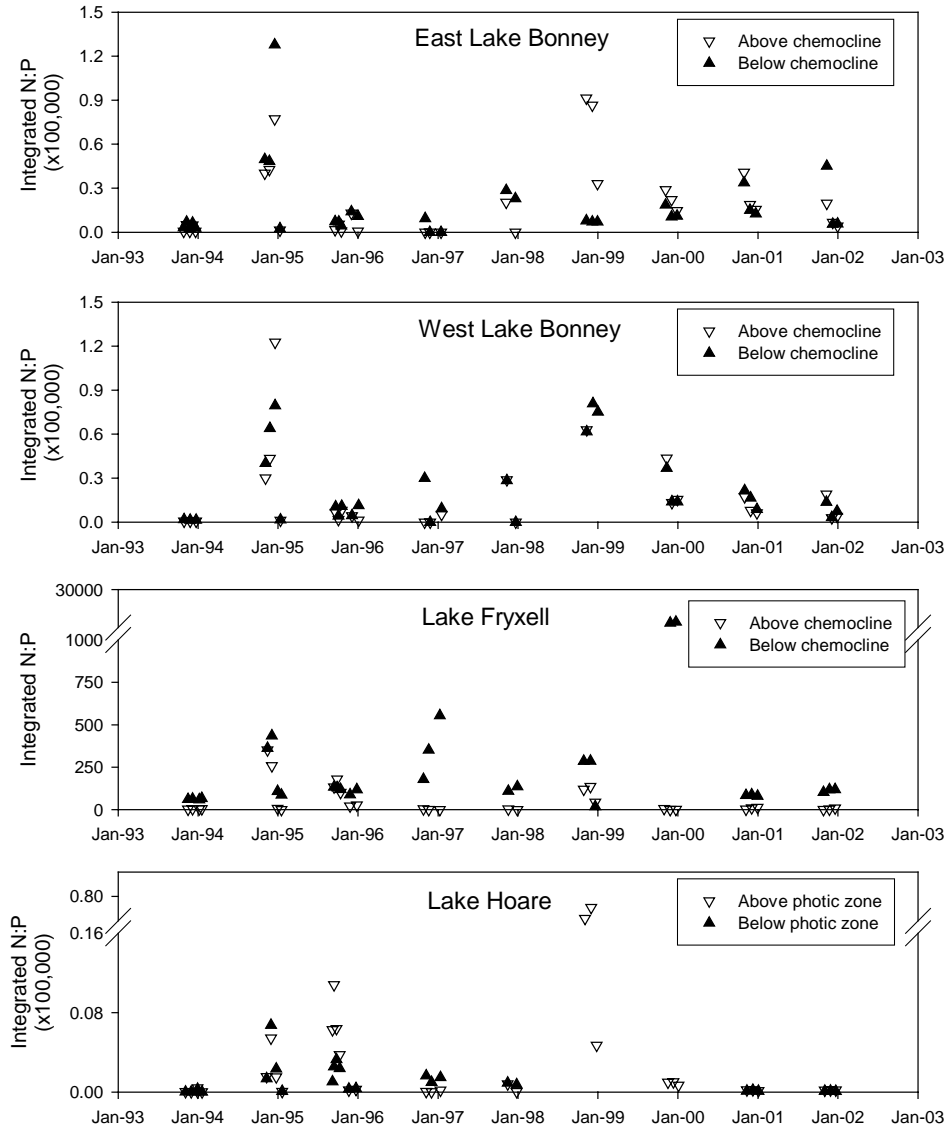


Figure 7. Depth integrated nitrogen to phosphorus ratios (molar) above the chemocline in West Lake Bonney (5–20 m), East Lake Bonney (5–22 m), Lake Fryxell (5–12 m) and above the photic zone in Lake Hoare (5–22 m), below the chemocline in West Lake Bonney (20–40 m), East Lake Bonney (22–38 m), Lake Fryxell (12–18 m) and below the photic zone in Lake Hoare (22–30 m). The year designations refer to the end of the austral summer season, for example January 02 refers to the 2001–2002 season beginning in October 2001 and ending in January 2002.

Fryxell (mean $9.5 \text{ mg C m}^{-2} \text{ d}^{-1}$, $SD = 8.6$, $n = 31$) and 67% more than Lake Hoare (mean $8.0 \text{ mg C m}^{-2} \text{ d}^{-1}$, $SD = 8.7$, $n = 31$). Primary production declined in both lobes of Lake Bonney and in Lake Fryxell from

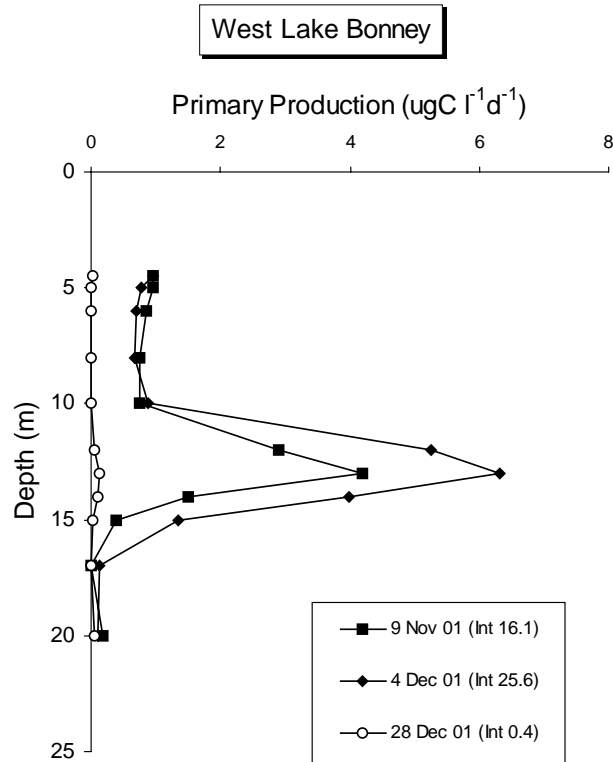


Figure 8. Primary production (PPR) in West Lake Bonney, 2001. Depth integrated values for the sampling periods are given in parentheses.

1993 to 2001, as a result of a thicker ice cover related to cooler air temperatures during this period (Doran et al., 2002). Lake Hoare showed an increase in production over this same period (Figure 9), despite thicker but more transparent ice.

The advent of the flood caused several changes in primary production in the dry valley lakes. Integrated primary production decreased by 23% in West Lake Bonney during the flood in concert with a 95% reduction in PAR at 10 m. Depth integrated primary production in Lake Fryxell during the period of increased stream flows (20 December 2001) was five-fold greater than the two previous sampling periods when stream flows were relatively low. Such a large seasonal increase in primary production is not a trend typical for this lake and can be attributed, in part, to increased loading of nutrients from the streams. During 2002, the year following the flood event, increases in primary production were observed in both lobes of Lake Bonney (Figure 9). Directly beneath Lake Fryxell's ice cover primary production also peaked following the flood year (PPR at 5 m = $15.2 \mu\text{g C l}^{-1} \text{d}^{-1}$), reaching the highest recorded value measured over the previous 10 years (long-term average PPR

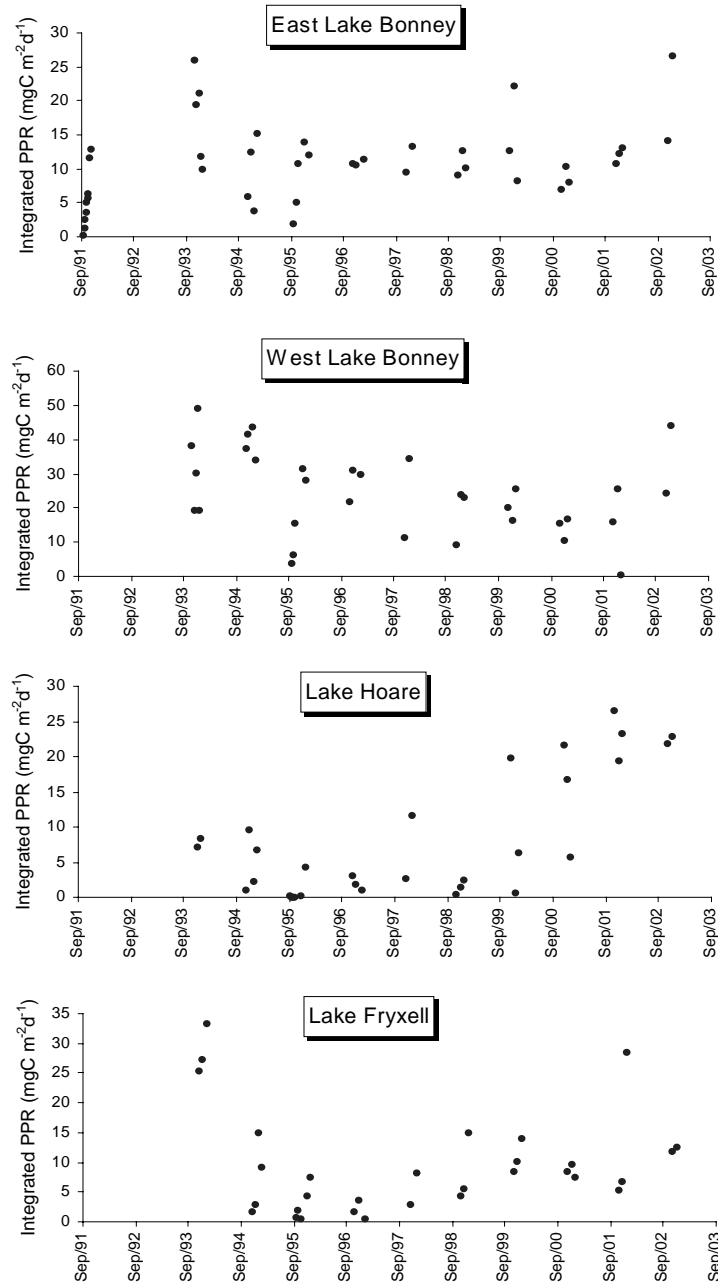


Figure 9. Depth integrated primary production (PPR) in the photic zones of East Lake Bonney (5–22 m), Lake Hoare (5–22 m), West Lake Bonney (5–20 m), and Lake Fryxell (5–12 m). The year designations refer to the end of the austral summer season, for example September 2002 refers to the 2001–2002 season beginning in October 2001 and ending in January 2002.

at 5 m = $2.4 \mu\text{g C l}^{-1} \text{d}^{-1}$). Primary production at 9 m in Lake Fryxell was greatest during our first sampling event in 2002 and then decreased. This pattern is quite different from the usual one of increasing production over the course of the austral summer, implying that advected nutrients from the flood stimulated primary production early in the subsequent year.

4.3.2. Chlorophyll-a

Depth integrated photic zone chlorophyll-a concentrations (an indicator of phytoplankton biomass) decreased from 1991 to 2001 in the east and west lobes of Lake Bonney, but increased over this same period in Lake Fryxell (Figure 10). Long-term seasonal chlorophyll-a averages during the November–December sampling period (1991–2001) were 11.4 mg m^{-2} in East Lake Bonney, 23.0 mg m^{-2} in West Lake Bonney, 37.3 mg m^{-2} in Lake Hoare and 55.0 mg m^{-2} in Lake Fryxell. Following the flood event, integrated chlorophyll-a values increased 149% in East Lake Bonney, 48% in West Lake Bonney, had a minimal change (2%) in Lake Fryxell and decreased 18% in Lake Hoare over the long-term averages, and increased 305, 154, 3 and 7% over the 2001–2002 averages, respectively. The east lobe of Lake Bonney showed a dramatic increase in chlorophyll-a concentrations ($\text{Chl-a} = 7.7 \mu\text{g l}^{-1}$) directly below the ice cover in the year following the flood. This increase was well above the long-term average (mean = 1.76, SD = 1.17, n = 73) and is the highest recorded chlorophyll-a value at 5 m measured in this lake over the past 12 years, implying that the elevated stream flow stimulated phytoplankton in the lakes.

The relationship between chlorophyll-a and particulate carbon (PC) and nitrogen (PN) changed in West Lake Bonney as a consequence of the flood. The cellular carbon to chlorophyll-a ratio represents the nutritional state of phytoplankton biomass, particularly in the presence of non-autotrophic organisms and detrital particles (Goldman, 1979), but is also strongly affected by irradiance. In the photic zone (5–20 m), the slope of PC:Chl decreased from 90.6 ± 24.7 ($r^2 = 0.60$, n = 11) to 68.3 ± 17.2 ($r^2 = 0.64$, n = 11) during the flood, while the y-intercept increased from 94.2 ± 28.5 to 107.7 ± 23.2 . In the deeper waters below the photic zone the relationship between PN and chlorophyll-a also shifted as an apparent result of the flood. Before the flood the PN:Chl slope and y-intercept were 67.4 ± 36.6 ($r^2 = 0.53$, n = 5) and -0.14 ± 2.2 respectively. During the flood the slope increased to 97.5 ± 29.9 ($r^2 = 0.78$, n = 5) and the y-intercept to 0.38 ± 0.99 .

5. Discussion

Disturbances are discrete events in time that disrupt ecosystems and change resource or substrate availability and the physical environment. Because

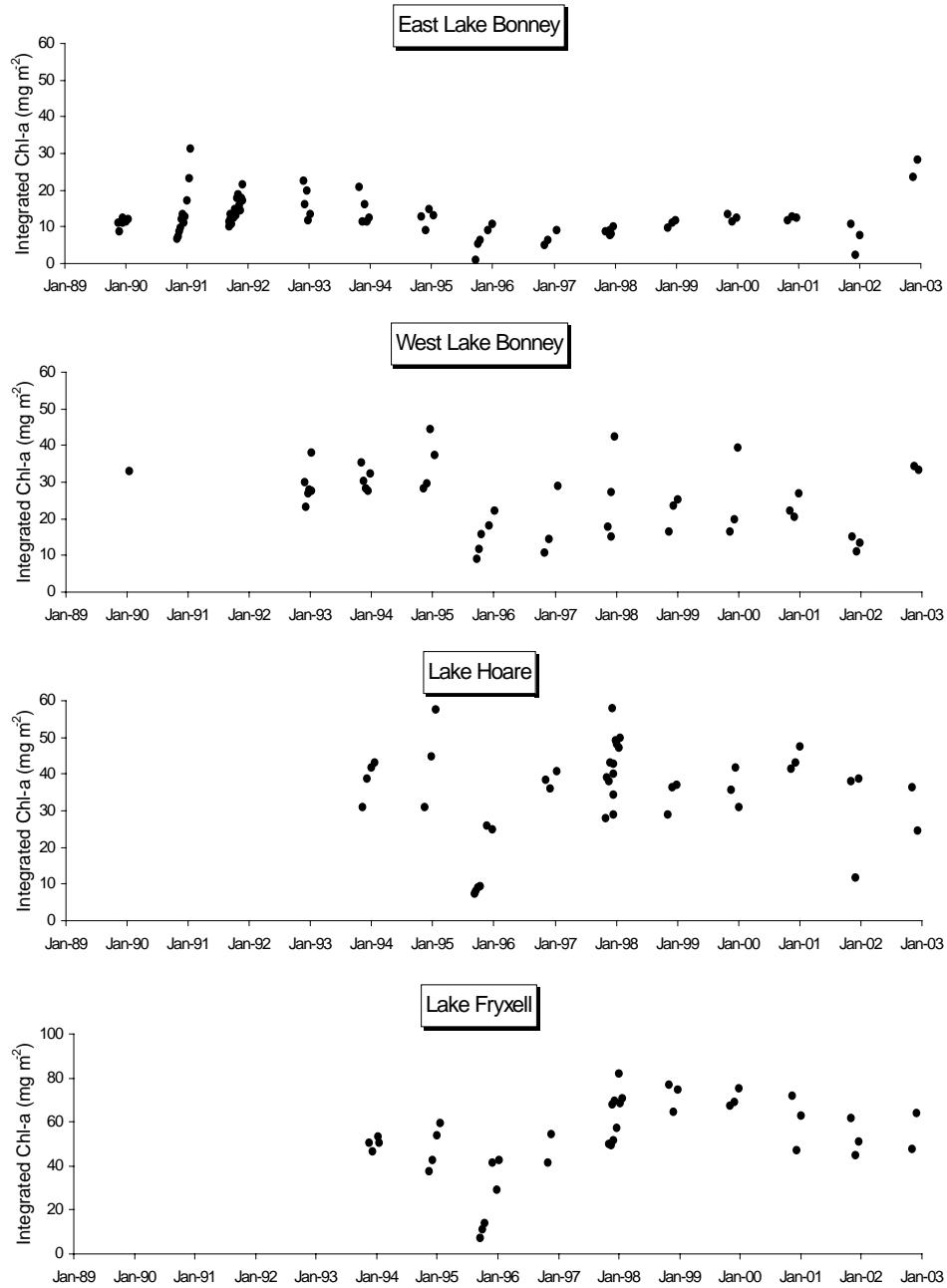


Figure 10. Depth integrated chlorophyll-a (Chl a) in the photic zones of East Lake Bonney (5–22 m), Lake Hoare (5–33 m), West Lake Bonney (5–20 m), and Lake Fryxell (5–12 m). The year designations refer to the end of the austral summer season, for example January 02 refers to the 2001–2002 season beginning in October 2001 and ending in January 2002.

organisms in the dry valleys are poised at the edge of their survival ranges they are highly susceptible to disturbances, particularly when it involves the transformation from solid to liquid water. The presence of liquid water affords a key habitat in the frozen deserts of the McMurdo Dry Valleys and, importantly, acts as a medium to transport nutrients from glaciers, soils and streambeds to the lakes. Clearly, the common currency linking individual components within the dry valley ecosystem is the availability of liquid water. In the summer of 2001–2002 the dry valleys experienced average summer temperatures of $-1.8\text{ }^{\circ}\text{C}$, as well as several days with temperatures above $4\text{ }^{\circ}\text{C}$, well above the typical average of $-6\text{ }^{\circ}\text{C}$ experienced during the summer of 2000–2001 (Fountain et al., 2004). These relatively high temperatures enhanced glacial melting and subsequent stream flow. The increase in stream flow, together with meteorologically induced ablation of the permanent lake ice, thinned the lake ice by up to 1 m in many of the lakes. The elevated stream flow also led to a rapid rise in lake levels. Increased melt on the surface of the glaciers allowed cryoconite holes to lose their structure and flush their contents, thus adding more carbon and nutrients to downstream systems (Fountain et al., 2004). All along this hydrological pathway, beginning at the glaciers and ending in the lakes, alterations in the elemental balance of the starting materials may occur due to biological activity and physical processes (Lyons et al., 2003). Cycles of growth, mineralization and immobilization by biota within cryoconites or in-stream microbial communities as well as physical adhesion processes may incorporate and transform the available pool of nutrients (Tranter et al., 2004 in press). Enrichment versus depletion of the existing nutrient pools in the lakes depends upon the glacial sources of the melt-water, the length of the streams leading to the lake, contact time with in-stream biota (algal and bacterial mats, mosses), freeze-thaw events, and characteristics of the individual watersheds (McKnight et al., 1999; Lyons et al., 2003).

Biogeochemically, a flood may have conflicting effects on a lake (Vinçon-Leite et al., 1998). Nutrient and organic matter loads may increase, thereby stimulating growth of organisms. But high loads of suspended solids may also reduce light transmission and limit algal growth (Reynolds, 1984). These suspended solids can also adsorb nutrients, especially phosphorus, and decrease their availability. Our data shows that individual lakes in the dry valleys exhibited a range of responses to the flood, with some parameters increasing, some decreasing and some showing no change.

5.1. PHYSICAL PARAMETERS

Lake volumes in the dry valley lakes all increased following the flood, reversing a declining trend reported from 1993 to 2000 (Doran et al., 2002). This decline in lake volumes was rapidly ameliorated with a single flood.

According to historical measurements these periods of oscillating lake levels are not uncommon. Chinn measured rising water levels from 1971 to 1993 (Chinn, 1993). Using photographs and measurements from Captain Scott's Discovery Expedition, Chinn further extrapolated a rise of 13.5 m in the level of Lake Bonney from 1903 to the early 1990s. Though the lake level in Lake Bonney clearly increased from 1903 to the early 1990s, our data infer that lake filling occurred episodically. Lake level measurements dating back to the IGY 1957–1958 in nearby Lake Vanda (Wright Valley) show periods when the lake level was static, as well as episodic pulses such as those measured in 1971 (2.35 m rise), and in 1981 (4.64 m rise) that resulted in substantial increases in the lake level (Chinn, 1993). Long-term data (~20 kyears) also imply numerous fluctuations in lake levels accompanying shifts in climate (Doran et al., 1994; Lyons et al., 1998a; Hall and Denton, 2000).

The thickness of the permanent ice covering the lakes in the dry valleys decreased (0.25 m in ELB, 0.34 m in WLB, 1.65 m in Hoare and 0.09 m in Fryxell) following the flood year, also reversing a 10-year trend (Doran et al., 2002). Ice thickness is controlled by meteorological conditions which control surface ablation; snow cover which greatly affects surface albedo, wind deposited sediment, and the sub-ice melting and freezing regime (Adams et al., 1998). Changes in lake ice thickness can have profound effects on the lake biota, as these permanent ice covers control the transfer of gases, sediments and light entering the lakes (Wharton et al., 1993; Adams et al., 1998; Fritsen et al., 1998). Warmer air temperatures would also have changed the availability of liquid water within the permanent ice covers, potentially allowing the in-ice biota a longer period of time to actively metabolize and grow (Priscu et al., 1998b).

5.2. NUTRIENT DYNAMICS

Nutrient dynamics are inextricably related to changes in physical processes, including climatic events, such as the flood of 2001–2002. The flux of nutrients into streams and lakes is dependent upon atmospheric deposition, nutrient pools within glacial ice, the mineral composition of the surrounding rocks and soils, in-stream biological activity and hydrological factors (Allan, 1995). The availability of nutrients in the dry valleys is related to the ages of the tills draping the landscape, with the eastern Taylor Valley (Lakes Fryxell and Hoare basins) having younger soils with more available phosphorus than those in the western (Lake Bonney basin) Taylor Valley (Gudding, 2003). Annual stream discharge in the dry valleys during the flood season was twice the volume of the previous eight seasons combined (<http://huey.colorado.edu/LTER>). Flood induced stream inputs in Lake Fryxell increased the DIN and SRP loads to the lake eight-fold over the long-term average. Typically most of the DIN mass above the chemocline in Lake Fryxell is

supplied via diffusion across this chemocline. However, during the flood a large portion of trophogenic zone nutrients were supplied by stream flow. This increase could have been supplied, in part, as nutrients were flushed from the glacier ice or from cryoconites down into the streams (Howard-Williams et al., 1986; Fountain et al., 2004). Nutrient concentrations were measured in 47 cryoconites from glaciers in the McMurdo Dry Valleys (Tranter et al., 2004); NO_3^- and SRP concentrations were $1.7 (\pm 2.5)$ and $0.08 (\pm 0.09) \mu\text{M}$ respectively, within the cryoconites, thus flushing of the cryoconites may have provided increased nutrients to downstream systems.

Nutrient transformation and release are highly dynamic processes that may operate over very short time scales. Imbalances in short-term supply and demand can result in episodic or chronic nutrient replete or nutrient limited conditions within the lakes. The phytoplankton in Lakes Fryxell, Hoare and Bonney were suggested to be nitrogen limited in the early to mid-1980s (Vincent, 1981; Vincent and Vincent, 1982; Priscu et al., 1989; Sharp, 1993 MS thesis). Detailed long-term nutrient bioassay experiments conducted in the mid-1990s imply that phytoplankton productivity in all of the lakes is phosphorus deficient. P-deficiency is severe in Lake Bonney, and moderate in Lakes Fryxell and Hoare which both show signs of N and P co-limitation (Priscu, 1995; Dore and Priscu, 2001).

Our long-term data set show that East Lake Bonney is similar to Lake Fryxell in that the majority of the DIN loadings are via diffusion instead of stream-flow, conversely in West Lake Bonney annual diffusion across the chemocline typically accounts for only 12% of the DIN loadings with the majority coming from stream inputs, primarily from Blood Falls. We do not have stream flow data from Lake Bonney for 2001–2002, however based on observations in the field it can be assumed that stream flow increased relative to previous years as with the other streams in the Taylor Valley. The short, high gradient streams entering West Lake Bonney are turbid compared with the longer, lower gradient flows entering Lake Fryxell. The strong depletion of SRP measured during the period of high water column turbidity in WLB indicates that the stream particulate matter may have adsorbed SRP from both the stream and lake waters. Phosphorus concentrations in West Lake Bonney during, and following the flood, were low throughout the entire water column (depth integrated SRP on 4 December 2001 = $53.8 \mu\text{M}$, 28 December 2001 = $15.3 \mu\text{M}$, and 15 November 2002 = $3.2 \mu\text{M}$).

Early studies by Redfield (1958) showed that phytoplankton in balanced growth displayed a molar C:N:P stoichiometry of 106:16:1, which was close to the bulk dissolved nutrient pools. The N:P ratios measured in the dissolved and particulate pools in the dry valley lakes, as well as the low Chl-a levels, indicate that the surface waters of these lakes are nutrient limited. Couple this nutrient limitation with the additional stresses of minimal temperatures, low

light levels, and a short growing season and it becomes obvious that phytoplankton in the dry valley lakes are at the edge of their survival. Clearly, the advent of the flood altered nutrient availability to microorganisms. The flood exacerbated the already severe phosphorus limitation in West Lake Bonney and decreased the dissolved inorganic nitrogen pool, hence there were no associated changes in the N:P ratios throughout the water column. Following the flood, the upper waters of East Lake Bonney were depleted in dissolved inorganic nitrogen and SRP, and N:P ratios rose. In Lakes Fryxell and Hoare there was a decline in N:P values throughout the water columns post-flood. These results emphasize the importance of episodic liquid water production to nutrient dynamics and hence microbial metabolism within the lakes of the dry valleys.

5.3. BIOLOGICAL RESPONSE

Changes in physical and geochemical parameters following the flood event had an affect on the biology within the lakes. The optical properties of the ice cover and water column control the amount and wavelengths of light available to phototrophic organisms (Howard-Williams et al., 1998; Fritsen and Priscu, 1999; Lizotte and Priscu, 1992). Increased light attenuation by the ice cover as well as upper water column turbidity probably both occurred from this unusually warm period in the dry valleys. Periods of warmer weather may not only change the optical properties of the ice cover but could also increase the influx of water, nutrients, and particulate matter carried by meltwater to the lakes. All together these physical alterations, coupled with changes in nutrient availability, influenced the amount of primary production possible because phytoplankton in the dry valley lakes have been shown to be both light (Lizotte and Priscu, 1992; Priscu et al., 1999) and nutrient limited (Priscu, 1995; Dore and Priscu, 2001).

Primary production in West Lake Bonney during the flood was greatly reduced throughout the water column; however chlorophyll-a concentrations remained unchanged. Measures of chlorophyll-a are often used as a surrogate for phytoplankton biomass; however these two often do not track because of the plasticity of cellular chlorophyll contents within phytoplankton (Falkowski and Raven, 1997). Ratios of primary production to chlorophyll-a, a measure of photosynthetic efficiency, decreased 98% (depth integrated PPR/Chl-a on 4 December 2001 = 1.54, on 28 December 2001 = 0.02) during the flood in West Lake Bonney. Because of the severe light limitation caused by the large influx of sediments and subsequent decrease in PAR values, phytoplankton in West Lake Bonney may have increased their chlorophyll-a content in order to receive as much light as possible, thereby decreasing their photosynthetic efficiency. We cannot rule out either light limitation or overall lower production efficiency as the main

driver in reducing the primary production levels in West Lake Bonney during the flood.

The C:Chl ratio in phytoplankton has been shown to respond rapidly to shifts in irradiance, nutrient availability and temperature (Falkowski, 1980). Pigment metabolism in phytoplankton is highly dynamic, changes in chlorophyll content per cell are a physiological response of the photosynthetic apparatus to variations in environmental conditions (Fennel and Boss, 2003). In West Lake Bonney flood associated changes were evident based on changes in the relationships between chlorophyll-a and phytoplankton biomass (in units of particulate carbon or nitrogen).

Following the flood, rates of primary production increased in the upper water columns of the lakes along with Chl-a, particularly in East Lake Bonney and West Lake Bonney (data not shown). These increases are in sharp contrast to the overall declines noted over the previous ten years (Doran et al., 2002) and may denote the importance of these episodic warming events in “recharging” the dry valley lakes.

6. Conclusions

The McMurdo Dry Valley lakes are poised near a significant threshold in terms of water dynamics; any small change in climate can lead to major changes in liquid water production, which produces a cascade of ecosystem responses (Doran et al., 2002). The warmer temperatures during the summer of 2001–2002 produced an increase in glacial run-off, record stream discharges, an increase in lake levels and a thinning of the permanent lake ice covers. These changes brought about greater inputs of dissolved and particulate matter, nutrients, and had a clear effect on lake biota. The high variability in lake responses shown in this study reaffirms the unique character of each lake in the McMurdo Dry Valleys, and drives home the need for continued long-term monitoring of these systems. Episodic climate events, such as infrequent floods, may have a long-term influence on the structure and functioning of these ecosystems. In an environment where life is limited by the availability of liquid water, the flood of 2001–2002 was a significant event governing life processes in this extreme polar desert ecosystem.

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References

- Adams E. E., Priscu J. C., Fritsen C. H., Smith S. R. and Brackman S. L. (1998) Permanent ice covers of the McMurdo Dry Valley Lakes, Antarctica: Bubble formation and metamorphism. In *Ecosystem Dynamics in a Polar Desert. The McMurdo Dry Valleys, Antarctica* Ed. J. C. Priscu, American Geophysical Union, Washington D.C. Vol. 72, pp. 281–295.
- Aiken G. R., McKnight D., Harnish R. and Wershaw R. (1996) Geochemistry of aquatic humic substances in the Lake Fryxell Basin, Antarctica. *Biogeochemistry* **34**, 157–188.
- Allan J. D. (1995) *Stream Ecology: Structure and Function of Running Waters*. Chapman and Hall, London, UK.
- Angino E. E., Armitage K. B. and Nash J. C. (1962) Chemical stratification in Lake Fryxell, Antarctica. *Science* **138**, 399–402.
- Angino E. E. and Armitage K. B. (1963) A geochemical study of Lakes Bonney and Vanda, Victoria Land, Antarctica. *J. Geology* **71**, 89–95.
- Chinn T. J. (1993) Physical hydrology of the Dry Valley lakes. In *Physical and Biogeochemical Processes in Antarctic Lakes* (Eds. W. J. Green and E. I. Friedman), Vol. 59, pp. 1–51, Antarctic Research Series.
- Clow G. D., McKay, C. P. Simmons, Jr. G. M. and Wharton R. A. (1988) Climatological observations and predicted sublimation rates at Lake Hoare, Antarctica. *J. Climate* **1**, 715–728.
- Conovitz P. A., McKnight D. M., MacDonald L. H., Fountain A. G. and House H. R. (1998) Hydrologic Processes Influencing Streamflow Variation in Fryxell Basin, Antarctica. In *Ecosystem Dynamics in a Polar Desert. The McMurdo Dry Valleys, Antarctica* (Ed. Priscu, J. C.), Vol. 72, pp. 93–108, American Geophysical Union, Washington, D.C.
- Dodds W. K. (2003) Misuse of inorganic nitrogen and soluble reactive phosphorus concentrations to indicate nutrient status of surface waters. *J. North American Benthological Society* **22**, 171–181.
- Doran P. T., Wharton Jr. R. A. and Lyons W. B. (1994) Paleolimnology of the McMurdo Dry Valleys, Antarctica. *J. Paleolimnology* **10**, 85–114.
- Doran P. T. Priscu J. C., Lyons W. B., Welch J. E., Fountain A. G., McKnight D. M., Moorhead D. L., Virginia R. A., Wall D. H., Clow G. D., Fritsen C. H., McKay C. P. and Parsons A. N. (2002) Antarctic climate cooling and terrestrial ecosystem response. *Nature* **415**, 517–520.
- Dore J. E. and Priscu J. C. (2001) Phytoplankton nutrient deficiency and alkaline phosphatase activity in McMurdo Dry Valley lakes, Antarctica. *Limnology and Oceanography* **46**(6), 1331–1346.
- Elser J. J., Fagan W. F., Denno R. F., Dobberfuhl D. R., Folarin A., Huberty A., Interlandi S., Kilham S. S., McCauley E., Schulz K. L., Stiemann E. H. and Sterner R. W. (2000) Nutritional constraints in terrestrial and freshwater foodwebs. *Nature* **408**, 578–580.
- Falkowski P. G. (1980) Light-shade adaptation in marine phytoplankton. In *Primary Productivity in the Sea*. (Ed. P. G. Falkowski), pp. 99–119 Plenum, New York.
- Falkowski P. G. and J. A. Raven (1997) *Aquatic photosynthesis*. Blackwell Science Publishers, Oxford.
- Fennel K. and Boss E. (2003) Subsurface maxima of phytoplankton and chlorophyll: Steady-state solutions from a simple model. *Limnology and Oceanography* **48**, 1521–1534.

- Fountain A. G., Dana G. L., Lewis K. J., Vaughn B. H. and McKnight D. M. (1998) Glaciers of the McMurdo Dry Valleys, Southern Victoria Land, Antarctica. In *Ecosystem Dynamics in a Polar Desert, The McMurdo Dry Valleys, Antarctica* (Ed. J. C. Priscu), Vol. 72, pp. 65–76, Antarctic Research Series, American Geophysical Union, Washington, D.C.
- Fountain A. G., Lyons W. B., Burkins M. B., Dana G. L., Doran P. T., Lewis K. J., McKnight D. M., Moorhead D. L., Parsons A. N., Priscu J. C., Wall D. H., Wharton Jr. R. A. and Virginia R. A. (1999) Physical controls on the Taylor Valley Ecosystem, Antarctica. *Bio-science* **49**(12), 961–971.
- Fountain A. G., Tranter M., Nysten T. H., Lewis K. J. and Mueller D. (2004) Evolution of Cryoconite Holes and their Contribution to Melt-Water Runoff from Glaciers in the McMurdo Dry Valleys, Antarctica. *J. Glaciology*. in press.
- Fritsen C. H., Adams E. E., McKay C. P., and Priscu J. C. (1998) Permanent Ice Covers of the McMurdo Dry Valleys Lakes, Antarctica: Liquid Water Contents. In *Ecosystem Dynamics in a Polar Desert. The McMurdo Dry Valleys, Antarctica*. (Ed. J. C. Priscu), Vol. 72, pp. 269–280, American Geophysical Union, Washington D.C.
- Fritsen C. H. and Priscu J. C. (1999) Seasonal Changes in the Optical Properties of the Permanent Ice Cover on Lake Bonney, Antarctica: Consequences for Lake Productivity and Phytoplankton Dynamics, *Limnology and Oceanography*. **44**, 447–454.
- Goldman C. R. (1970) Antarctic Freshwater Ecosystems. In *Antarctic Ecology*. Academic Press, New York, pp. 609–627.
- Goldman J. C. (1979) Physiological processes, nutrient availability, and the concept of the relative growth rate in marine phytoplankton ecology. In *Factors in Marine Phytoplankton Ecology*, pp. 179–193.
- Green W. J., Angle M. P. and Chave K. E. (1988) The geochemistry of Antarctic streams and their role in the evolution of four lakes in the McMurdo Dry Valleys. *Geochim. Cosmochim. Acta*. **52**, 1265–1274.
- Gudding J. A. (2003) Phosphorus in Taylor Valley, Antarctica: The Connection between Landscape Age and Nutrient Limitation in Aquatic Ecosystem Components, MSc. Thesis, The Ohio State University, 118 pp.
- Hall B. L. and Denton G. H. (2000) Extent of the Wilson Piedmont Glacier and the Ross Sea ice sheet along the Scott Coast at and since the last glacial maximum. *Geografiska Annaler*. **82B**, 411–432.
- Healey F. P. and Hendzel L. L. (1980) Physiological indicators of nutrient deficiency in lake phytoplankton. *Can. J. Fisheries and Aquatic Science* **37**, 42–453.
- Howard-Williams C., Vincent C. L., Broady P. A. and Vincent W. F. (1986) Antarctic stream ecosystems: variability in environmental properties and algal community structure. *Internationale Revue gesamten de Hydrobiologie* **71**, 511–544.
- Howard-Williams C., Schwarz A. M., Hawes I., Priscu J. C. (1998) Optical Properties of the McMurdo Dry Valley Lakes, Antarctica. In *Ecosystem Dynamics in a Polar Desert. The McMurdo Dry Valleys, Antarctica*. (Ed. J. C. Priscu), Vol. 72, pp. 189–203, American Geophysical Union, Washington, D.C.
- Keys J. R. (1979) The saline discharge at the terminus of the Taylor Glacier. *Antarctic J. US* **14**, 82–85.
- Lizotte M. P. and Priscu J. C. (1992) Spectral irradiance and bio-optical properties in perennially ice-covered lakes of the Dry Valleys (McMurdo Sound, Antarctica), In *Contributions to Antarctic Research III, Antarctic Research Series 57*, (Ed. D. H. Elliott), pp. 1–14, AGU, Washington, D.C.
- Lyons W. B., Tyler S. W., Wharton Jr. R. A., McKnight D. M. and Vaughn B. H. (1998a) A late Holocene desiccation of Lake Hoare and Lake Fryxell, McMurdo Dry Valleys, Antarctica. *Antarctic Science* **10**, 247–256.

- Lyons W. B., Welch K. A., Neumann K., Toxey J. K., McArthur R., Williams C., McKnight D. M. and Moorhead D. (1998b) Geochemical Linkages Among Glaciers, Streams, And Lakes Within the Taylor Valley, Antarctica. In *Ecosystem Dynamics in a Polar Desert. The McMurdo Dry Valleys, Antarctica* (Ed. J. C. Priscu), Vol. 72, pp. 77–92, American Geophysical Union, Washington, D.C.
- Lyons W. B., Fountain A., Doran P., Priscu J. C., Neumann K. and Welch K. A. (2000) Importance of landscape position and legacy: the evolution of the lakes in Taylor Valley, Antarctica. *Freshwater Biology* **43**, 355–367.
- Lyons W.B., Welch K. A., Priscu J. C., Laybourn-Parry J., Moorhead D., McKnight D. M., Doran P. T. and Tranter M. (2001) The McMurdo Dry Valleys Long-Term Ecological Research Program: New Understanding of the Biogeochemistry of the Dry Valley Lakes: A Review. *Polar Geography* **25**(3), 202–217.
- Lyons W. B., Welch K. A., Fountain A. G., Dana G. L., Vaughn B. H. and McKnight D. M. (2003) Surface glaciochemistry of Taylor Valley, southern Victoria Land, Antarctica and its relationship to stream chemistry. *Hydrological Processes* **17**, 115–130.
- McKnight D. Niyogi MD. K., Alger A. S., Bomblies A., Conovitz P. A. and Tate C. M. (1999) Dry valley streams in Antarctica: ecosystems waiting for water. *Bioscience* **49**, 985–995.
- Priscu J. C. and Goldman C. R. (1983) Suspensoid characteristics in sub-alpine Castle Lake, California: I. Chemical composition. *Archives for Hydrobiology* **97**, 373–388.
- Priscu J. C., Vincent W. F. and Howard-Williams C. (1989) Inorganic nitrogen uptake and regeneration in perennially ice-covered Lakes Fryxell and Vanda, Antarctica. *J. Plankton Research* **11**, 335–351.
- Priscu J.C. (1995) Phytoplankton nutrient deficiency in lakes of the MCMurdo Dry Valleys, Antarctica. *Freshwater Biology* **34**, 215–227.
- Priscu J. C. (1998) *Ecosystem Dynamics in a Polar Desert. The McMurdo Dry Valleys, Antarctica* (Ed. J. C. Priscu), Vol. 72, American Geophysical Union, Washington, D.C.
- Priscu J. C., Fritsen C. H., Adams E. A., Giovannoni S. J., Paerl H. W., McKay C. P., Doran P. T., Gordon D. A., Lanoil B. D. and Pinckney J. L. (1998) Perennial Antarctic Lake Ice: An Oasis for Life in a polar desert. *Science* **280**, 2095–2098.
- Priscu J. C., Wolf C. F., Takacs C. D., Fritsen C. H., Laybourn-Parry J., Roberts E. C., Sattler B. and Lyons W. B. (1999) Carbon Transformations in a Perennially Ice-Covered Antarctic Lake. *Bioscience* **49**(12), 997–1008.
- Redfield A. C. (1958) The biological control of chemical factors in the environment. *American Scientist* **46**, 205–221.
- Redfield A. C. (1963) The influence of organisms on the composition of seawater. In *The Sea*, (Ed. M. N. Hill) Vol. 2, pp. 26–77, Wiley, New York.
- Reynolds C. S. (1984) *The Ecology of Freshwater Plankton*. Cambridge University Press, Cambridge.
- Sharp T. R. (1993) Temporal and spatial variation of light, nutrients, and phytoplankton production in Lake Bonney, Antarctica. M.S. Thesis. Montana State University-Bozeman.
- Spigel R. H. and Priscu J. C. (1998) Physical Limnology of the McMurdo Dry Valley Lakes. In *Ecosystem Dynamics in a Polar Desert. The McMurdo Dry Valleys, Antarctica* (Ed. J. C. Priscu), Vol. 72, pp. 153–188, American Geophysical Union, Washington, D.C.
- Strickland J. H. and Parsons T. R. (1972) A practical handbook of seawater analysis, 2nd Edn. *Bull. Fish. Res. Bd Can.* 167.
- Takacs C. D. and Priscu J. C. (1995) Responses of bacterial growth to inorganic and organic nutrient enrichment in the lakes of the Dry Valleys, Antarctica. *Antarctic J. United States* **30**, 303–305.

- Takacs C. D. and Prisco J. C. (1998) Bacterioplankton Dynamics in the McMurdo Dry Valley Lakes, Antarctica: Production and Biomass Loss over Four Seasons. *Microbial Ecology* **36**, 239–250.
- Tranter M., Fountain A., Fritsen C., Lyons B., Prisco J., Statham P., and Welch K. (2004) Extreme hydrochemical conditions in natural microcosms entombed within Antarctic ice. *Hydrological Processes* **18**, 379–387.
- Vincent W. F. (1981) Production strategies in Antarctic inland waters: phytoplankton eco-physiology in a permanently ice-covered lake. *Ecology* **62**, 1215–1224.
- Vincent W. F. and Vincent C. L. (1982) Factors controlling phytoplankton production in Lake Vanda (77S). *Can. J. Fisheries and Aquatic Science*. **39**, 1602–1609.
- Vinçon-Leite B., Bournet P.-E., Gayte X., Fontvieille D. and Tassin B. (1998) Impact of a flood event on the biogeochemical behaviour of a mesotrophic alpine lake: Lake Bourget (Savoy). *Hydrobiologia*. **373/374**, 361–377.
- Welch K. A., Lyons W. B., Graham E., Neumann K., Thomas J. W. and Mikesell D. (1996) The determination of major element chemistry in terrestrial waters of Antarctica using ion chromatography. *J. Chromatography A* **739**, 257–263.
- Welch K. A., Lyons W. B., McKnight D. M., Doran P. T., Fountain A. G., Wall D., Jaros C., Nylen T. and Howard-Williams, C. (2003) Climate and hydrological response in the McMurdo Dry Valleys, Antarctica. In *Climate Variability and Ecosystem Response at Long-Term Ecological Research Sites* (Eds. D. Greenland, D. G. Goodin and R. C. Smith) Oxford University Press, Oxford.
- Wharton Jr. R. A., McKay C. P., Clow G. D., and Anderson D. T. (1993) Perennial ice covers and their influence on Antarctic lake ecosystems, In *Physical and Biogeochemical Processes in Antarctic Lakes, Antarctic Research Series*, (Eds. W. Green and W. Friedmann), Vol. 59, pp. 53–70, AGU, Washington, D.C.