CO₂ concentrations in perennially ice-covered lakes of Taylor Valley, Antarctica

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Abstract. Lakes in Taylor Valley, southern Victoria Land, Antarctica, are unusual in that they are perennially covered by a 3-5 m thick ice layer. Previous work on gas concentrations in these lakes has shown that the surface waters are supersaturated with respect to O2, N2O, as well as the noble gases. Our data show that the dissolved CO_2 ($CO_{2(aq)}$) concentrations, calculated from pH and ΣCO_2 , can be highly undersaturated at shallow depths of the lakes. CO_2 partial pressure values (p CO_2) are as low as $10^{-4.3}$ atm and $10^{-4.2}$ atm in the east and west lobes of Lake Bonney, respectively, and $10^{-3.8}$ atm in Lake Hoare. $CO_{2(a0)}$ depletion occurred only in the uppermost part of the water column, in association with elevated primary productivity (PPR). The upward diffusion of $CO_{2(aq)}$ from the aphotic zone, and the annual input of CO₂ via glacial meltwater can not replenish the amount of CO_{2(aq)} annually lost to primary productivity in the uppermost meters of the water column. Calcification is a limited source of CO_{2(aq)}, since the lakes are undersaturated with respect to calcite through portions of the austral summer. Preliminary respiration rates have been used to obtain an annual inorganic carbon balance. Further down in the water column, at the sites of the deepwater maximum in primary production (PPRmax), which in Lakes Bonney and Fryxell is associated with nutrient gradients, CO_{2(aq)} is not undersaturated. A large upward flux from CO_2 -supersaturated aphotic waters provides a surplus of $CO_{2(aq)}$ at the PPR_{max}. Lake Fryxell, unlike the other lakes, is supersaturated with $CO_{2(aq)}$ throughout the entire water column.

Introduction

 CO_2 is an essential requirement for primary production. Although inorganic carbon is the most abundant nutrient in most aquatic systems (Quay et al. 1986), low dissolved CO_2 ($CO_{2(aq)}$) concentrations can be a limiting factor for primary production in certain situations (Riebesell et al. 1993; Schidlowski

et al. 1994; Gleitz et al. 1995). Previous work has demonstrated that the majority of lakes on Earth, particularly those in the northern polar regions (Kling et al. 1992), are a sink for terrestrially fixed CO_2 , resulting in $CO_{2(aq)}$ supersaturation with respect to the atmosphere. Consequently, these lakes are thought to be a source of CO_2 to the atmosphere (Cole et al. 1994). Even during times of rapid CO_2 uptake via photosynthesis, and the removal of carbon into biomass/sediments, diffusional CO_2 input from the atmosphere can replenish the supply of $CO_{2(aq)}$ in most lacustrine environments, thereby minimizing the role of $CO_{2(aq)}$ as a limiting nutrient (Schindler et al. 1997).

The lakes of the McMurdo Dry Valleys in southern Victoria Land, Antarctica (76°30′-78°30′ S, 160-164° E, Figure 1) are unique on this planet in that they maintain a thick (3 to 6 m), permanent ice cover overlying a liquid water column (McKay et al. 1985). The ecology of these permanently icecovered Antarctic lakes is greatly influenced by the presence of their ice covers, which restrict or eliminate completely the exchange of gases such as CO₂ between the lake waters and the atmosphere (Wharton et al. 1993; Priscu 1997). In addition, the lakes are fed by glacier melt water streams in landscapes where little or no terrestrial organic matter enters the lake ecosystem. Although much research has been done in the past decade to discern the role of ice-cover on gas dynamics in these lakes, little attention has been paid to $CO_{2(aq)}$. For example, the restriction of atmosphere-lake exchange results in an increase in dissolved O₂, N₂O and Ar above saturated conditions (Wharton et al. 1987; Craig et al. 1992; Priscu et al. 1996; Priscu 1997; Hood et al. 1998). Conversely, dissolved He and Ne are greatly undersaturated with respect to the atmosphere (Hood et al. 1998). The ice cover could lead to elevated CO_{2(aq)} levels by preventing CO₂ produced via respiration of organic matter from evading into the atmosphere, or it could cause undersaturation of $CO_{2(aq)}$ if the biological uptake is greater than its replenishment.

These lakes have been studied since the International Geophysical Year (1957–1958), but it has only been recently that carbon dynamics within the lakes have been well enough understood so that budgets can be constructed (Priscu et al. 1999). To describe the biogeochemistry of the lakes, an understanding of the $CO_{2(aq)}$ balance in these systems is essential. Photosynthesis and respiration, advective fluxes from streams, diffusion of $CO_{2(aq)}$ from deeper waters, and calcification can all alter the $CO_{2(aq)}$ balance in these lakes. Because the uptake of $CO_{2(aq)}$ is the main source of carbon for primary producers, this paper focuses on the distribution of $CO_{2(aq)}$ in the trophic zone of these lakes, and quantifies the processes that control its distribution. Concentrations of $CO_{2(aq)}$ will be given as the partial pressure of CO_2 in water (pCO₂), a common practice that is best suited to describe the wide range in concentrations encountered in these lakes.

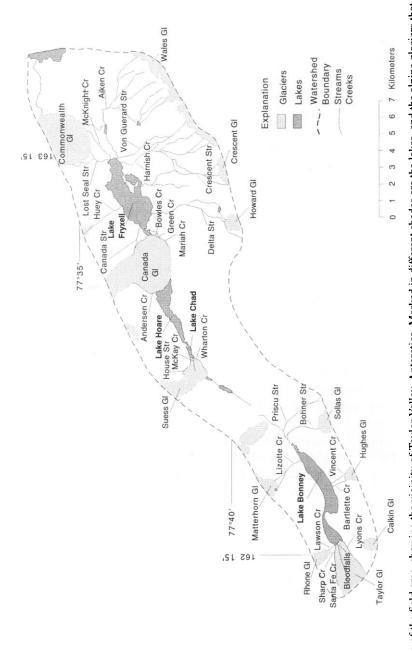


Figure 1. Map of the field area, showing the vicinity of Taylor Valley, Antarctica. Marked in different shades are the lakes, and the alpine glaciers that feed the lakes in the Austral summer.

Site description

The McMurdo Dry Valleys region is the largest ice-free area in Antarctica. Taylor Valley is one of the valleys in the McMurdo region of southern Victorialand (\sim 78° S latitude). Taylor Valley has an average temperature of -20 °C and a mean precipitation rate of $< 10 \text{ cm yr}^{-1}$ (Clow at al. 1988). The lakes in Taylor Valley vary in size from 1 to 7 km², and occupy hydrologically closed basins. The water balance is maintained by inflow of glacial meltwater over a 6–12 week period during the austral summer, and the ablation of ~ 0.4 m of ice per year. Evaporation of water and uninhibited gas exchange with the atmosphere can only occur through the moats that can form at the shore of the lakes during about ten weeks of the summer. These moats cover only about 3% of the lake area (Wharton et al. 1986). The role of the moats in gas exchange with the atmosphere is difficult to estimate since the relationship of moat water chemistry and the chemistry of the lake water is not established (Priscu et al. 1996). In general, the Taylor Valley lakes share common features such as chemical stratification and, hence, a high water column stability (Matsubaya et al. 1979; Green et al. 1988; Spigel & Priscu 1996, 1998), and biological communities consisting solely of microorganisms (Vincent 1988; Priscu et al. 1999).

The three largest lakes in Taylor Valley are Lake Fryxell, Lake Hoare and Lake Bonney (Figure 1). Lake Bonney has two lobes separated by a 12 m deep sill that allows exchange of the surface waters, but separates the more dense, saline deep waters (Lawrence & Hendy 1989; Spigel & Priscu 1998). The geochemistry of these lakes is very different, ranging from the hypersaline deep waters of Lake Bonney, to the entirely fresh water of Lake Hoare, and the brackish waters of Lake Fryxell (Green et al. 1988; Lyons et al. 1998a). Many of the chemical differences between the lakes, and especially the existence and composition of the monimolimnions of Lakes Bonney and Fryxell, were caused by past climatic variations that greatly affected the hydrologic balances of the lakes (Matsubaya et al. 1979; Lyons et al. 1998b). Since 1993 the McMurdo Dry Valleys region in general, and Taylor Valley, in particular, has been designated a Long Term Ecological Research (LTER) site, and the lakes have been monitored on a routine basis. More information on the MCM-LTER can be found at http://huey.colorado.edu/LTER.

Materials and methods

Water samples were collected three to four times during the austral summer (November through January) with 5-L Niskin bottles that were lowered through holes in the ice cover at the locations of greatest lake depth. pH

was measured with a Beckman portable pH-meter with silver/silver chloride glass electrodes in sub-samples immediately after sampling (accuracy = ± 0.05 pH units). Temperature was measured with a Sea-Bird CTD probe lowered down the same holes in the ice. Samples were stabilized with chloroform, and dissolved inorganic carbon (DIC) measured in the field with a MSA Lira infrared carbon analyzer (standard deviation of measurements = $\pm 3\%$). Major cations and anions were determined on filtered aliquots at McMurdo Station, Antarctica, by ion chromatography, using a Dionex DX-300 chromatographic system. The ionic balance of this data set, using all the major element data including HCO_3^- calculated from the DIC, and expressed as difference between total cations and total anions, had an error between 1.4% and 3.0%. A detailed description of the chromatography techniques can be found in Welch et al. (1996). A detailed description of the pH and DIC methods can be found at the McMurdo LTER website http://huey.colorado.edu/LTER/lakedata.html.

Chemical, pH and temperature data from the 1994-1995 austral summer were used to calculate the CO_{2(aq)} and CaCO₃ saturation indices under the ambient conditions with the chemical equilibrium models PHREEQE and PHROPITZ (Parkhurst et al. 1980; Plummer et al. 1988). These models calculate pCO₂ at *in-situ* temperatures and pH values. The accuracy of the models is mainly controlled by the errors in the pH and DIC measurements. Changes of 0.05 pH units cause an average error of $\pm 3.3\%$ in pCO₂, and a 3% error in the DIC measurements produces a $\pm 1.3\%$ error in pCO₂. The total error depends on pH and DIC in a non-linear manner, and decreases with increasing pH and increases with increasing DIC concentration. Using data from this study, the errors in pCO₂ are larger than 5% only in the low-pH, high-DIC deep waters of Lake Bonney (maximum error has been calculated to be 10% at 20 m in the west lobe and 8% at 22 m in the east lobe). In the waters above 9 m, high pH and low DIC concentrations reduce the average pCO₂ errors caused by pH and DIC measurements to ± 1.4 and 0.5%, respectively.

To verify the model and calculated $CO_{2(aq)}$ concentrations, several water samples were taken during the 1996/1997 austral summer to measure the $CO_{2(aq)}$ concentration directly via headspace analysis (Kling et al. 1992; Cole et al. 1994). Samples were taken in 250 mL flint glass bottles, with 5 mL of headspace, and stabilized with 0.2 mL concentrated HgCl₂ solution. Following several days of equilibration, a sample from the headspace was extracted through a Teflon septum, and the $CO_{2(aq)}$ concentration was measured with a HP 5890 Series II gas chromatograph. The average error of the $CO_{2(aq)}$ measurements was 8.4%. The amount of atmospheric CO_2 trapped in the headspace during sampling was subtracted in our calculations,

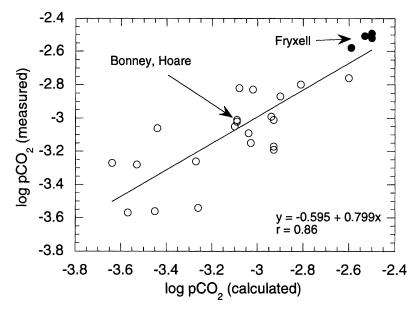


Figure 2. 1996 pCO₂ values modeled with PHREEQE, compared to pCO₂ values obtained from gas-chromatographic headspace measurement (only exponents shown). Open symbols are corrected for calcite precipitation before CO₂ measurement, solid symbols mark the uncorrected Lake Fryxell measurements. See text for further explanation of the calculations. The line represents a least square fit through the data.

assuming a pCO₂ of $10^{-3.47}$ atm (340 ppmv) in the air (the calculations of pCO₂ from the CO_{2(aq)} measurements using Henry's law followed Hope et al. 1995). Due to logistical problems (i.e. the transport of the samples from Taylor Valley to McMurdo Station, ~80 km away), the samples warmed to 21 °C before the CO₂ concentration in the equilibrated headspace could be measured. A white precipitate, assumed to be CaCO₃, was observed in a number of the bottles containing water from Lake Bonney. The precipitation was presumably caused by the temperature increase. For these samples, the pCO₂ of the water was calculated to be in equilibrium with calcite at 21 °C. In Lake Fryxell, the calcite precipitation is probably inhibited by high DOC and PO₄³⁻ concentrations (Neumann et al. 1998b), and it was not initiated by increasing temperatures. Calculations in Lake Fryxell, based on non-equilibrium with CaCO₃, coincide with values calculated from pH and DIC. All these data show that the calculated values are close to the direct measurements of CO_{2(aq)} in our study lakes (Figure 2). Studies on other lakes also show that calculated pCO₂ values using equilibrium thermodynamic calculations generally are in good agreement with measured values (Quay et al. 1986; Berman-Frank et al. 1994; Cole et al. 1994).

Results

Table 1 shows the pH and DIC values that were used to calculate the partial pressures of dissolved CO_2 . The high concentrations of DIC in some of the monimolimnions are caused by lake level variations over time, and have nothing to do with modern processes (Lyons et al.1998b). In brief, Lake Hoare is proposed to be less than 1200 yrs old (Lyons et al.1998b). Lakes Bonney and Fryxell have undergone a series of evaporitic drawdowns and refillings as the climate has changed during the Holocene (Matsubaya et al. 1979; Lyons et al. 1998b). These drawdowns have helped concentrate DIC in the bottoms of these lakes. The last fresh water influx, over the past \sim 1200 yrs, placed a low-salinity water column on top of the saline brine. The saline and the fresh layers of the water column are separated by sharp gradients. Constituents with elevated concentrations in the monimolimnions such as nutrients, DIC, and the major elements move upward via diffusion (Priscu 1995; Lyons et al. 1998a, b).

Both lobes of Lake Bonney and Lake Hoare had pCO₂ values below atmospheric equilibrium values at various times during the 1994–1995 austral summer (Figure 3). In the west lobe of Lake Bonney, the water just below the ice cover had a pCO₂ as low as $10^{-4.2}$ atm early in the summer, which, in the next three months, increased by one order of magnitude ($10^{-3.2}$ atm). This increase was most predominant in the water just below the ice cover, but could be observed to a depth of 10 m ($10^{-3.3}$ to $10^{-2.7}$ atm). Below the chemocline at 13 m, values were well above atmospheric values, and increased rapidly to 10^{0.1} atm at 20 m, below which PHRQPITZ is not capable of computing carbon dioxide pressures (due to high total dissolved solids, $> 100 \text{ g L}^{-1}$). The water in the east lobe of Lake Bonney had similar temporal shifts in the uppermost 13 m ($10^{-4.3}$ to $10^{-3.4}$ atm). Below this depth, however, pCO₂ increased, reaching $10^{-0.3}$ atm at 22 m, and then decreased to $10^{-1.8}$ atm at the bottom of the lake. In contrast to the fluctuations in Lake Bonney, pCO₂ in Lake Hoare was relatively stable over the season, varying from $10^{-3.8}$ atm to $10^{-3.6}$ atm in the water just below the ice cover. Values increased to $10^{-2.1}$ atm between 8 m and 16 m depth, and changed little below that depth.

Lake Fryxell is the only lake in Taylor Valley having pCO₂ values above atmospheric pressure throughout the entire water column through the entire austral summer. Water just below the ice cover had a pCO₂ of $10^{-2.4}$ atm at the beginning of the austral summer, and later increased to $10^{-2.0}$ atm. The pCO₂ was constant throughout the top 4 m, and increased below the chemocline (9 m).

Table 1. pH and DIC values in three Taylor Valley lakes at the beginning and the end of the 1994/1995 Austral summer

		Bonn	Bonney-West			Bonr	Bonney-East			H	Hoare			Fr	Fryxell	
	Depth pH	hd	DIC	pCO ₂	Depth	hd	DIC	pCO ₂	Depth	Hd	DIC	pCO ₂	Depth	Hd	DIC	pCO ₂
	E		mg C/I		E		mg C/I		ш		mg C/I		E		mg C/I	
Nov.	5	8.8	13.2	4.17	2	9.1	16.5	4.33	S	8.8	26.1	-3.79	5	7.6	47.8	-2.43
1994	9	8.8	13.0	4.17	9	8.9	15.8	4.14	9	8.8	25.9	-3.84	9	7.7	63.2	-2.34
	∞	8.6	15.7	-3.86	∞	8.9	17.3	4.18	∞	8.8	28.2	-3.77	7	7.7	73.3	-2.33
	10	8.1	22.4	-3.28	10	8.4	24.3	-3.49	10	9.8	34.5	-3.55	∞	7.9	102.5	-2.33
	12	7.2	52.7	-2.04	12	7.3	53.7	-2.09	12	8.3	46.6	-3.06	6	7.8	179.2	-2.04
	13	9.9	118.3	-1.25	13	6.9	78.8	-1.62	14	7.8	53.3	-2.53	10	7.7	236.2	-1.80
	14	6.1	546.7	-0.30	15	6.7	122.3	-1.30	16	7.5	64.3	-2.21	11	9.7	347.0	-1.54
	15	0.9	635.0	-0.17	18	6.7	145.9	-1.18	18	7.5	70.4	-2.11	12	9.7	429.6	-1.45
	17	5.9	639.5	-0.15	20	6.3	213.5	99.0-	20	7.4	71.0	-2.08	15	7.5	587.4	-1.31
	20	5.8	639.5	-0.11	22	0.9	227.3	-0.41	22	7.5	71.5	-2.10	18	7.5	703.8	-1.22
	22	5.7	756.9	-0.01	25	6.2	151.3	-0.65	25	7.4	73.0	-2.02				
	25	5.7	761.5	0.02	30	6.7	57.9	-1.56	26.5	7.4	74.0	-2.02				
	30	5.6	793.5		35	6.7	35.4	-1.80								
	35	5.6	876.1		37	6.7	36.9	-1.83								
	38	5.6	833.2													

Table 1. Continued

		Bon	Bonney-West		į Į	Bonn	Bonney-East			Ŧ	Hoare			F	Fryxell	
	Depth	Hd	DIC	pCO ₂	Depth	Hd	DIC	pCO ₂	Depth	Hd	DIC	pCO ₂	Depth	Hd	DIC	pCO ₂
	Ħ		mg C/I		ш		mg C/I		ш		mg C/l		ш		mg C/I	
Jan.	5	7.7	10.8	-3.16	5	7.9	8.7	-3.46	5	8.5	21.2	-3.57	5	7.0	31.3	-2.05
1995	9	8.1	13.7	-3.47	9	8.5	10.1	4.00	9	9.8	24.0	-3.65	9	7.3	54.8	-2.05
	∞	8.1	20.8	-3.28	∞	8.5	15.0	-3.84	∞	9.8	26.8	-3.61	7	7.4	72.1	-2.07
	10	7.8	34.1	-2.74	10	8.4	19.7	-3.61	10	8.4	34.0	-3.34	∞	7.5	84.7	-2.09
	12	7.3	62.5	-2.06	12	7.3	44.2	-2.18	12	8.0	44.9	-2.83	6	9.7	151.7	-1.89
	13	6.5	203.6	-0.97	13	6.7	93.7	-1.44	14	7.5	59.5	-2.23	10	7.5	229.5	-1.61
	14	6.0	800.3	-0.08	15	9.9	126.0	-1.23	16	7.3	64.2	-1.98	11	7.3	306.0	-1.38
	15	5.9	829.9	-0.03	18	6.5	162.2	-1.02	18	7.2	71.5	-1.90	12	7.4	381.2	-1.32
	17	5.9	871.2	0.01	20	6.2	225.7	-0.58	20	7.1	72.4	-1.82	15	7.3	652.0	-1.04
	20	5.8	948.3	0.08	22	0.9	240.3	-0.32	22	7.1	72.1	-1.78	18	7.2	739.9	-0.93
	22	5.7	1193.6		25	6.1	141.6	-0.61	25	7.1	74.0	-1.77				
	25	5.6	1365.2		30	9.9	62.7	-1.39	29	7.0	8.68	-1.64				
	30	5.5	1333.5		35	6.7	55.4	-1.51								
	35	5.5	1419.8		37	9.9	41.3	-1.68								
	38	5.5	1513.6													

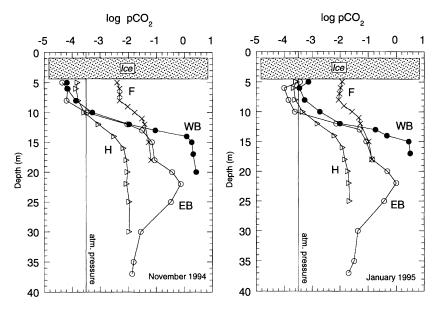


Figure 3. pCO₂ versus depth for the three lakes at the beginning and end of the Antarctic summer season (November and January). Only exponents are shown. WB = Lake Bonney, west lobe; EB = Lake Bonney, east lobe; H = Lake Hoare and F = Lake Fryxell. The atmospheric pressure of CO₂ ($10^{-3.5}$ atm) is marked with a vertical line. Except for Lake Hoare, water below the chemoclines is highly supersaturated with CO₂, and shows no seasonal change.

Discussion

The low concentrations of $CO_{2(aq)}$ in the upper waters of Lakes Bonney and Hoare are in stark contrast to dissolved O_2 , N_2 , Ar and N_2O concentrations which are highly supersaturated as a result of exsolvation during the freezing of water onto the bottom of the ice cover (Wharton et al. 1987; Priscu et al. 1996, 1997; Hood et al. 1998). $CO_{2(aq)}$ will also exsolve when the water freezes, and should therefore be supersaturated in the uppermost part of the water column too. However, the observed undersaturation of $CO_{2(aq)}$ is caused by the same perennial ice layer that has led to the supersaturation of other gases. $CO_{2(aq)}$ is lost from the upper water via incorporation through primary biologic production and subsequent sedimentation of particulate organic carbon (Neumann 1999; Priscu et al. 1999). Unlike in temperate lakes, and just opposite to its behaviour with respect to O_2 , O_2 , Ar and O_2 0 where it prevents the escape to the atmosphere, the ice cover also acts as a barrier to O_2 infusion from the atmosphere.

The various processes that are involved in the CO₂ production and consumption within the lakes are depicted in Figure 4. The undersaturation

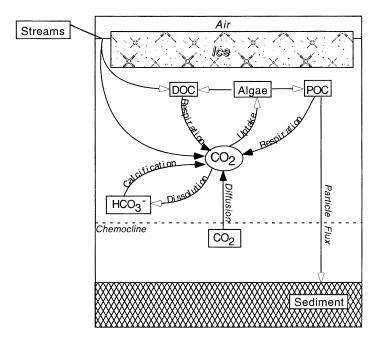


Figure 4. Conceptional model of processes involved in the carbon cycles in the dry valley lakes with chemoclines. Solid arrows denote CO_2 sources. Diffusion across the chemocline is driven by high CO_2 concentrations in the monimolimnion that are not the result of ongoing respiration, but remnants of previous lake level lowstands. The unbalanced 'calcification' and 'dissolution' stand for the reaction $Ca^{2+} + 2 \ HCO_3^- \leftrightarrow CaCO_3 + CO_2 + H_2O$. Note the lack of CO_2 recharge from the atmosphere.

of $CO_{2(aq)}$ observed in the Taylor Valley lakes occurs in other perennially ice-covered Antarctic lakes. For example, Anderson et al. (1998) have also observed $CO_{2(aq)}$ undersaturated water in Lake Joyce (in Pearse Valley, 77°43′ S, 161°37′ E) and Lake Miers (in Miers Valley, 78°06′ S, 164° E). Doran et al. (in press) have reported that White Smoke Lake, Bunger Hills, East Antarctica, demonstrates a similar situation.

A comparison of the amount of dissolved CO_2 in the water with the annual demands for biological CO_2 uptake is shown in Figure 5. In the uppermost waters of the east and west lobe of Lake Bonney the uptake of CO_2 , over the duration of a year, is more than 250% and 180% of the dissolved CO_2 , respectively. In Lake Hoare biological uptake utilizes between 70 and 90% of the $CO_{2(aq)}$, while in Lake Fryxell the uptake consumes only up to 12% of the CO_2 in the lake water. This corresponds to lower p CO_2 in the east and west lobe of Lake Bonney, followed by higher values in Lake Hoare (Figure 3). This high utilization rate could be especially important to primary production in these lakes if the $CO_{2(aq)}$ removal and potential replenishment

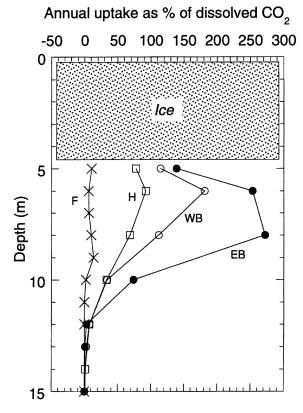


Figure 5. Annual uptake of CO₂ expressed as percent of CO₂ dissolved in water (CO_{2aq}). Values of 250% in the west lobe of Lake Bonney mean that, statistically, every CO₂ molecule is recycled two and a half times each year, while the 10% in Lake Fryxell suggest that every molecule is used for primary production only every tenth year. Symbols as in Figure 3.

occur at different times and rates. For example, respiration could gradually recharge the water over the whole year, while PPR is limited to the summer (i.e., no sunlight in winter). $CO_{2(aq)}$ produced *in situ* during the winter can become a source for PPR in the summer. Some $CO_{2(aq)}$ must be replenished in the winter, since the pCO_2 values at the beginning of the growth season have been similar in several years of measurement (on average, the pCO_2 values varied by ± 0.06 log units; Neumann 1999). In these lakes, CO_2 can be replenished from four potential sources (Figure 4): (1) from $CO_{2(aq)}$ -rich meltwater streams that flow for only a few weeks in the austral summer season and advect water just under the ice cover; (2) from the respiration of organic matter in the aerobic zone; (3) from diffusive input from the lower, $CO_{2(aq)}$ -rich zones of the lakes; and (4) from calcification $(Ca^{2+} + 2 HCO_3^- \leftrightarrow CaCO_3 + CO_{2(aq)} + H_2O$; Note that this process simultaneously leads to an increase

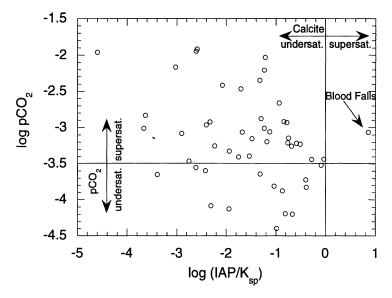


Figure 6. Calcite saturation indices for stream water are plotted against the partial pressure of CO₂. With only one exception (Blood Falls, a highly saline glacier discharge at the west lobe of Lake Bonney), all streams are undersaturated with respect to calcite. Also, most of the streams are supersaturated with respect to CO₂, some of them by more than an order of magnitude.

of biologically available $CO_{2(aq)}$ and to a decrease in DIC). Another potential source of CO_2 is exsolution when water freezes to the bottom of the ice cover, the main source for the supersaturations of O_2 , N_2 , Ar and N_2O .

Glacial meltwater

Glacial meltwater provides $CO_{2(aq)}$ to the surface waters of all the lakes, as a majority of the streams recharging the lakes are $CO_{2(aq)}$ -supersaturated with respect to the atmosphere (Figure 6). Because of its lower density, stream water flowing into the lake is confined to the ice-liquid water interface (McKnight & Andrews 1993; Spigel & Priscu 1998). We have assumed that the stream input mixes with the uppermost meter of lake water. This input of $CO_{2(aq)}$ occurs in the late austral summer, as low-DIC water from streams can be observed in the $CO_{2(aq)}$ versus depth profiles for all the lakes (Figure 3). We calculated the annual influx of $CO_{2(aq)}$ to the lakes from stream alkalinity and pH data, using the computer code PHREEQE and the steam discharges (McKnight et al. 1998, Table 2). The amount of $CO_{2(aq)}$ that entered the uppermost meter of the lakes during the 1994/1995 austral summer was 1 mmol m⁻² $CO_{2(aq)}$ in Lake Hoare, 3 mmol m⁻² $CO_{2(aq)}$ in Lake Fryxell, and 34 and 5 mmol m⁻² $CO_{2(aq)}$ in the west and east lobe of Lake Bonney,

respectively. Only in the west lobe of Lake Bonney does the annual influx of $CO_{2(aq)}$ from streams support the primary production in the uppermost meter of water (Neumann 1999). This supply of $CO_{2(aq)}$ -rich water comes during the later part of the growing season, while phytoplankton production starts much earlier, in October/November (Vincent & Vincent 1981; Sharp & Priscu 1992). This temporal gap between demand and supply helps account for the undersaturated conditions at the beginning of the growing season as light levels increase.

Respiration

Preliminary bacterial respiration rates were obtained by using estimates of electron transport system (ETS) activity converted to respiration assuming that 0.61 moles of O_2 are consumed per unit of ETS activity (Priscu et al. 1999). Oxygen consumption was converted to CO_2 production assuming a 1:1 ratio. The estimated amount of CO_2 released by respiration is shown in Table 2. CO_2 respiration by phytoplankton and bacteria exceeds the uptake of CO_2 in most cases (Priscu et al. 1999, Lyons et al. 2000), yet, as will be shown later, contributes little to the overall CO_2 balance.

In-situ remineralization of particulate organic carbon (POC) partially explains rising $CO_{2(aq)}$ levels through the summer. Yet, there is evidence that a large portion of the phytoplankton biomass produced in the surface waters is lost from this region as it sinks toward deeper parts of the lakes before it gets remineralized (Wharton et al. 1989).

No respiration rates or POC decomposition rates have been measured during the austral fall and winter (between February and October), nor has the organic flux to the sediment been accurately quantified in the lakes (Priscu et al. 1999). Although these missing data leave uncertainties in the assessment of the role of respiration on the carbon budget in these lakes, we show below that these data may not be needed in order to constrain the $CO_{2(aq)}$ budgets of these lakes.

Diffusion

Because of their density-induced stabilities, and permanent ice covers that eliminate wind-driven mixing, vertical transport in the lakes is dominated by molecular diffusion (Spigel & Priscu 1996, 1998). Recent work also indicates that density-driven mixing can occur, at least sporadically, in Lakes Fryxell and Hoare (Miller & Aiken 1996, Hood et al. 1998, Tyler et al. 1998). This density-driven circulation takes place as the edges of the lake ice, when they thaw in the summer and form 'moats' up to 10 m wide. When the moat begins to freeze at the end of the austral summer, salts are excluded from the ice and

Table 2. CO_2 concentrations, sources, and sinks. WB = west lobe of Lake Bonney, EB = east lobe of Lake Bonney, H = Lake Hoare, F = Lake Fryxell. All rates are given for one year, and for a vertical profile segment of 1 m length. The diffusion is given through a plane of 1 m² yr⁻¹.

	Depth m	Area m ²	PPR $mol m^{-2}$	CO_{2aq} mol m ⁻²	Diffusion $mol m^{-2}$	Stream mol m ⁻²	Resp. mol m ⁻²	Balance $molm^{-2}$	PPR/ Resp	Uptake as $\%$ of CO _{2aq}
WB	5	1,004,976	0.027	0.024	-0.0001	0.034	0.032	0.039	8.0	115.0
	9	1,004,976	0.024	0.013	0.005					182.0
	∞	897,409	0.026	0.024	0.051					112.0
	10	790,946	0.027	0.079	0.593		0.037	0.603	0.7	34.0
	13	610,887	0.160	4.929	7.359		0.071	7.270	2.2	3.0
	15	561,552	0.050	37.010	1.478		0.033	1.461	1.5	0.1
EB	5	3,037,673	0.023	0.017	-0.0014	0.005	0.022	0.003	1.0	139.0
	9	3,037,673	0.021	0.008	-0.00013					253.0
	∞	2,875,404	0.021	0.008	0.002					272.0
	10	2,717,680	0.016	0.022	0.089		0.025	960.0	9.0	74.0
	13	2,447,838	0.018	1.696	0.255		0.029	0.266	9.0	1.0
	7	2 332 853	0.019	3 188	0.070		0.018	7200	-	90

Table 2. Continued

	Depth	Area m ²	PPR $mol m^{-2}$	CO_{2aq} mol m ⁻²	Diffusion mol m ⁻²	Stream mol m ⁻²	Resp. mol m ⁻²	Balance molm ⁻²	PPR/ Resp	Uptake as % of CO _{2aq}
Н	5	1,471,798	0.013	0.016	-0.00066	0.001	0.027	0.015	0.5	78.0
	9	1,471,798	0.011	0.012	0.00002					93.0
	∞	1,339,927	0.011	0.017	0.00237		0.028	0.019	0.4	0.69
	12	1,070,634	0.007	0.084	0.03871		0.024	0.056	0.3	8.0
	16	807,719	0.004	0.618	0.02266		0.014	0.033	0.3	9.0
	20	555,119	0.002	0.904	-0.00575		0.012	0.005	0.1	0.2
Į,	5	2,930,082	0.056	0.518	0.017	0.003	0.053	0.017	1.1	11.0
	9	2,930,082	0.039	0.615	0.002		0.081	0.044	0.5	6.0
	7	2,410,044	0.042	0.620	0.004					7.0
	∞	2,104,570	0.072	0.689	0.101		0.080	0.108	6.0	10.0
	6	1,831,355	0.150	1.081	0.317		0.100	0.268	1.5	14.0
	10	1,587,426	0.044	2.152	0.520		0.163	0.638	0.3	2.0
	11	1,369,842	900.0	3.671	0.177		0.193	0.364	0.3	0.2

increase the density of the water. Miller and Aiken (1996) suggest that in Lake Fryxell this process could add $\sim 1\%$ of the present volume to a depth of 18 m annually. However, they did not see any evidence for recharge into the depths between 5 and 18 m, and, according to Hood et al. (1998), density-driven circulation is weak compared to diffusive processes within the lake column. Hence, we have assumed that this density driven caballing does not greatly affect the $CO_{2(aq)}$ budgets of the lakes.

Because the waters below the chemoclines of Lakes Bonney and Fryxell have a large $CO_{2(aq)}$ pool, with pCO_2 values well above equilibrium with the atmosphere (Figure 3), they are potential sources of $CO_{2(aq)}$ to the photic zones. We have computed the upward flux of $CO_{2(aq)}$ across the chemocline using the Fickian equation F = D ($\partial C/\partial z$), where F = flux (mol cm⁻² s⁻¹), D = temperature-dependent diffusion coefficient for $CO_{2(aq)}$ (1.085×10^{-4} cm² s⁻¹), C = concentration of $CO_{2(aq)}$ (mol cm⁻³), and z = distance between two points of known $CO_{2(aq)}$ concentration (cm).

The results of the diffusion calculations show that at the top of the chemoclines (sites of PPR_{max}), upward diffusion of CO_{2(aq)} from deeper waters is the most important source of $CO_{2(aq)}$ to the euphotic zone (Table 2). For example, the upward diffusion is 7.36 mol m⁻² yr⁻¹ CO_{2(a0)} across the 13 m plane in the west lobe of Lake Bonney, compared to an uptake from primary production of $0.16 \text{ mol m}^{-2} \text{ yr}^{-1}$ for the 12 to 13 m depth interval. In the east lobe, between 11 and 12 m, the diffusion across the 12 m plane provides 0.4 mol m^{-2} yr⁻¹ CO_{2(aq)}, while the uptake from primary production is only 0.06 mol m^{-2} yr⁻¹ CO_{2(aq)}. In Lake Fryxell, between 8 and 9 m, the annual upward diffusion of 0.32 mol m⁻² yr⁻¹ $CO_{2(aq)}$ at the chemocline (9 m) exceeds the uptake of 0.15 mol m⁻² yr⁻¹ $CO_{2(aq)}$. In Lake Hoare, both the $CO_{2(aq)}$ concentrations and the PPR_{max} are relatively low compared to the other lakes. However, below 12 m depth, the diffusive flux (0.02-0.04 mol m⁻² yr⁻¹) is larger than the uptake rate (0.003-0.007 mol m⁻² yr⁻¹ at various 1 mdepth intervals). In Lake Bonney and Lake Fryxell, large quantities of CO2 diffuse upward into the region of PPR_{max}, and photosynthetic uptake does not utilize all of this CO_2 . Our calculations imply that the $CO_{2(aq)}$ concentration could be increasing above the chemocline, and that the chemocline is moving upward over time, an observation that agrees with other work (Matsubaya et al. 1979; Lawrence & Hendy 1985). The work of Doran et al. (1999) using ¹⁴C measurements demonstrated that much of the DIC in these lakes is not recent. Although the antiquity of the DIC may be due, in part, to direct input of glacier melt without reequilibration with the atmosphere, this process of carbon recycling brought about by the diffusive flux from the depth, and lack of atmospheric change due to the permanent ice covers, also adds to the 'older' ages of the DIC in these lakes.

Unlike at the chemoclines (9–13 m depth), diffusion from below is contributing little $CO_{2(aq)}$ to the surface waters of the lakes (4–6 m depth, directly below the ice cover). In these uppermost layers of the west and east lobes of Lake Bonney and of Lake Hoare, the net diffusive flux of CO_2 is downward (–0.1, –1 and –1 mmol m⁻² yr⁻¹ $CO_{2(aq)}$, respectively). The flux from the streams exceeds the upward $CO_{2(aq)}$ diffusion into the surface water in Lake Bonney and in Lake Hoare, but is smaller than the diffusive flux in Lake Fryxell. In the west lobe of Lake Bonney, the $CO_{2(aq)}$ flux from streams also exceeds the photosynthetic carbon uptake, while in the other lakes the uptake is as much as 15 times higher than the stream influx of $CO_{2(aq)}$. This large $CO_{2(aq)}$ stream flux into the west lobe of Lake Bonney probably reflects the high input from streams draining Blood Falls, a hypersaline discharge at the snout of Taylor Glacier (Figure 1; Nezat 1998).

Calcification

The precipitation of CaCO₃ (calcification) in the water column also can produce CO_{2(aq)} (McConnaughey et al. 1994). The potential impact of calcification on pCO₂ variation can be evaluated by determining calcite saturation indices (SI = log (IAP/ K_{sp}); IAP = ion activity product, K_{sp} = solubility product) for the lakes. Saturation indices for these lakes have recently been presented by Lyons et al. (1998b) and Neumann (1999). In Lake Bonney, at the beginning of the austral summer, calcification is a potential source of $CO_{2(aq)}$ to the surface waters, while, towards the end of the austral summer, this source becomes unlikely as the SI values decrease and the waters become undersaturated with respect to CaCO₃. In Lake Hoare, calcification can contribute CO_{2(aq)} during the entire growing season. Conversely, Lake Fryxell was undersaturated with respect to calcite at 5 m (just below the ice) at the beginning of the summer, and became undersaturated to a depth of 8 m by the end of the season. Calcite undersaturation in the photosynthetically active zone eliminates calcification as a source of $CO_{2(aq)}$. Because no massive precipitation events such as lake whitings have been reported for any of the lakes, we have assumed that calcification plays only a small role as a $CO_{2(a\alpha)}$ source to these waters. However, calcification is occurring in the benthic algal mats of these lakes, in which abundant calcite crystals have been recorded (Wharton et al. 1983). Whether this process is a contributor to benthic mat primary production via increased $CO_{2(aq)}$ availability is not known.

CO_{2(aq)} mass balance

To understand better CO_2 dynamics in these lakes, a $CO_{2(aq)}$ mass balance for the mixolimnions of the three lakes have been calculated (Figure 7).

1994/95 CO₂ balance (mol m⁻³)

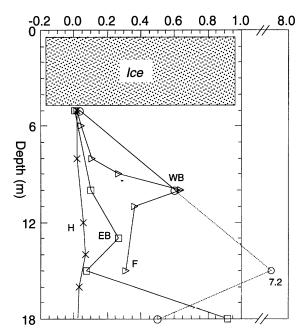


Figure 7. Annual balance for CO_2 in the three Taylor Valley lakes. The CO_2 concentration in the water underlying the ice remains basically unchanged, while just above the chemoclines the CO_2 concentrations should increase over time.

This is achieved by comparing the $CO_{2(aq)}$ sinks (primary productivity) with the sources (respiration, stream input, and diffusion), all normalized for a one-year interval. For this calculation, we assume that photosynthesis is active half a year (the austral summer), while respiration and diffusion occur continuously. The stream input is used s described above.

In the upper parts of all the lakes, this annual $CO_{2(aq)}$ balance is very close to zero. In the uppermost meter of the east lobe of Lake Bonney and of Lake Fryxell, the balance is slightly negative (-0.008 and -0.01 mol m⁻² yr⁻¹), while in Lake Hoare the balance is +0.01 mol m⁻² yr⁻¹, and in the west lobe of Lake Bonney it is +0.023 mol m⁻² yr⁻¹. Given the uncertainties of the data used in these calculations, we conclude that the upper depths of the lakes are essentially in balance with respect to $CO_{2(aq)}$ production and consumption over an annual period. This is the case, regardless of the varying absolute amounts of DIC, $CO_{2(aq)}$, or PPR, in these lakes. However, as shown above, the $CO_{2(aq)}$ concentration is not static. Times of low pCO₂ will be especially significant, when the ratio between PPR uptake and the pool of available $CO_{2(aq)}$ is large, as for Lake Bonney. In this case, the $CO_{2(aq)}$ can not 'buffer'

an increased demand from PPR, resulting in pCO_2 values below atmospheric equilibrium. Only the input via stream water later in the summer, and a rather constant recharge by diffusion and respiration balances the $CO_{2(aq)}$ budget through the year. At the chemoclines, the sources of $CO_{2(aq)}$ are clearly higher than the sinks in Lakes Bonney and Fryxell, and, to a lesser degree, in Lake Hoare. The $CO_{2(aq)}$ surplus is caused by the high rate of diffusion from the lower, supersaturated water column.

An important aspect of our results is the potential for CO_{2(aq)} to limit primary productivity. In these Antarctic lakes, it has been shown that light and nutrients, especially inorganic P, can limit phytoplankton growth (Lizotte & Priscu 1992; Priscu 1995). No experiments have yet addressed whether or not CO_{2(aq)} could also limit primary production, especially in the upper portions of Lake Bonney and Lake Hoare. Even if the $CO_{2(aq)}$ concentrations are not low enough to limit growth, they may decrease the fractionation of ¹²C/¹³C during CO₂ uptake by phytoplankton (Fogel et al. 1992). This is of special concern because the CO_{2(aq)} undersaturation changes seasonally in some of the lakes, possibly causing changes in the isotopic signature of both organic matter and CaCO₃ produced in the photic zone (Doran et al. 1998, 2000; Neumann 1999; Neumann et al. 1998a). These effects of CO₂ limitation have been described in White Smoke Lake, Bunger Hills, Antarctica (Doran et al. 2000), and Bird et al. (1991) used them to explain the δ^{13} C values for the sedimentary organic matter in both Highway and Organic Lakes in the Vestfold Hills, Antarctica. This transient fractionation also adds an additional variable to the interpretation of the sedimentary δ^{13} C record, which is already complicated due to very different δ^{13} C signatures at different depths of the lakes (Neumann et al. 1995).

Conclusion

The fluxes of $CO_{2(aq)}$ in the Taylor Valley lakes can be summarized as follows: $CO_{2(aq)}$ from deep, highly supersaturated water diffuses upward across the chemocline into the mixolimnion, providing $CO_{2(aq)}$ that is necessary to support planktonic photosynthesis at the deep photosynthetic maximum. The diffusive contribution of deep-water $CO_{2(aq)}$ to planktonic photosynthesis immediately beneath the ice is negligible. The advective input of $CO_{2(aq)}$ via streams is significant, but, except for the west lobe of Lake Bonney, does not provide adequate $CO_{2(aq)}$ to support the measured primary production rates observed there. $CO_{2(aq)}$ production via respiration in the lakes is less than the uptake of CO_2 via primary production, except for Lake Hoare. In the surface waters of Lake Bonney, $CO_{2(aq)}$ supply via calcification could be significant in the beginning of the photosynthetic season, and, in Lake Hoare,

it can provide additional $CO_{2(aq)}$ throughout the entire season. When these processes are combined, the CO_2 dynamics (uptake vs. input) are balanced in the surface waters of these lakes.

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