PRIMARY RESEARCH PAPER

Salinity regulation of zooplanktonic abundance and vertical distribution in two saline meromictic lakes in south central British Columbia

T. G. Northcote · K. J. Hall

Abstract Zooplankton species abundance and vertical distribution were followed in two south-central British Columbia saline meromictic lakes during the recent decade of their declining water levels. The lower salinity mixolimnion (0–7 m) of both lakes circulates partially most years down to their primary chemoclines marked by a 10–15 cm layer of purple sulfur bacteria (*Amoebobacter purpureus*) heavily grazed upon mainly by late copepodite stages and adults of *Diaptomus connexus*, possibly by some rotifers, but apparently not by cladocerans. Vertical distribution profiles, over an 8-year period, are presented mainly for the rotifer *Brachionus plicatilis*, two cladocerans *Ceriodaphnia lacustris*, and *Daphnia pulicaria*, as well as copepodite and adult *D. connexus* during normal periods of unimeromixis and a period of weak bimeromixis caused by shallow upper low salinity layers coming from drainage basin inputs.

Introduction

Incomplete vertical circulation of some saline lakes results in them being termed meromictic—partly mixing—and has been recognized since the mid-1930s (Findenegg, 1935; Hutchinson, 1937), with their causes and characteristics reviewed by Wetzel (2001). Mahoney Lake in the southern Okanagan Basin of British Columbia was found to be highly saline as well as meromictic in 1961 and its unusual limnological features reported periodically thereafter in a series of publications only partially covered here (Northcote & Halsey, 1969; Northcote & Hall, 1983, 1990, 2000, 2006; Hall & Northcote, 1990, 2002; Chapman et al., 1991; Lowe et al., 1997; Overmann et al., 1999a, b). Over this several decade period, there has been no complete coverage of macrozooplankton species diversity, abundance, and vertical distribution in Mahoney Lake. We do so here over the most recent decade, make comparisons to nearby meromictic Blue Lake and include information on a recent period of bimeromixis in both lakes. The term bimeromixis was first defined by Northcote & Hall (2000) and occurs when a shallow upper layer of

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fresh water restricts mixing in the mixolimnion. Thus, there are two areas of density stratification in the vertical profile of the lake.

This investigation took place when lake levels were decreasing and we wanted to determine how the zooplankton in these two meromictic lakes, of different salinities, would respond during the period of drier climatic conditions.

These two lakes are in protected ecological reserves; therefore, experimental manipulation was not possible.

Methods

Lake water level at Mahoney Lake was determined from a metal pin set in concrete above its southern shoreline at an elevation determined by a registered survey company and measured thereafter by our use of a survey line and level. A metal pin was established at a known elevation near the base of a tree above the Blue Lake shoreline, and the survey line and level were used to determine water levels on each sampling occasion.

Precipitation data were taken for Penticton, BC (Climate ID 1126150, elevation 344.1 m Environment Canada, 2009). The meteorological station at Penticton is located in the main Okanagan valley at lower elevation (344 m) than Mahoney (elevation 472 m) and Blue (elevation 838 m) lakes. Mahoney Lake is 20 km south of Penticton, and Blue Lake is 28 km south of Mahoney Lake.

Vertical temperature and conductivity measurements were measured with a YSI-TC meter (Model 33). Field conductivity was adjusted to specific conductivity at 25°C as previously reported (Hall & Northcote, 1986). Dissolved oxygen measurements were made with a YSI Model 57 or Model 56 meter which was calibrated by the air saturation method before each measurement series.

Lake water samples from selected depths were obtained by a suction pump connected to a 9-m length of 2.4 cm dia. tygon hose with four horizontal sucking hoses (17 cm long) and an iron weight attached to the lower end to keep the main hose tube vertical. The pump was powered by a 12-V battery and had a maximum capacity of $30 \, l \, min^{-1}$. The volume sucked was calibrated periodically.

Samples for nitrate/nitrite and phosphate determination were preserved in the field immediately in 20 ml test tubes with two drops of $0.1 \, g \, 100 \, ml^{-1}$ phenylmercuric acetate in 20% acetone. Water samples in nalgene bottles were transported to the laboratory in coolers and stored at 5°C in a cold room. Samples were filtered through GF/C glass fiber filters (1.2 μm). Water density was measured with an Anton Paar Density Meter (Model DMA 5000) after the water temperature was adjusted to 20.0°C. Water samples for cation and anion analysis were diluted with distilled water to the appropriate range for determination. The cations (Na^{+1}, K^{+1}, Mg^{+2}, and Ca^{+2}) were determined by inductively coupled plasma-atomic emission spectroscopy (ICP-AES) using a Varian Vista-Pro CCD Simultaneous ICP-OES instrument. Sulfate was determined by the barium sulfate turbidity technique using a Turner Spectrophotometer (Model 690) at 420 nm (APHA et al., 1995). Chloride, nitrate, and phosphate were determined using the Quickchem 800 Autoanalyzer. The mercuric thiocyanate flow injection technique was used to measure Cl^{-1} (4500-Cl^{-1} G), the cadmium reduction technique 4500-NO_3^{-1} was used for nitrate–nitrogen, and method 4500-P G was used for phosphate–phosphorus. The bicarbonate and carbonate were determined by alkalinity titration using a pH meter (APHA et al., 1995). Dissolved organic carbon (DOC) was determined on a Shimadzu Total Carbon Analyzer (Model 500) by determining the difference between the total carbon and inorganic carbon channels of the instrument (detection limit $1 \, mg \, l^{-1}$).

A series of vertical samples between 0 and 7.5 m were collected during 2001 and 2003 for primary production and chlorophyll a determination. Primary production was determined by the in situ incubation of ^{14}C–HCO_3^{-1} as reported by Hall & Northcote (1990). Samples were filtered through 47 mm (0.45 μm) cellulose nitrate filters and extracted in the dark with 90% acetone and quantitated for chlorophyll by fluorometry (Hall & Northcote, 2002). Vertical integration of these data was used to determine $g \, C \, m^{-2} \, h^{-1}$ and $mg \, chl \, a \, m^{-2}$ in the photic zone.

Zooplankton samples were collected from selected depths depending on the stratification profile by pumping into a 12-cm diameter Wisconsin-type plankton net fitted with a 100-μm mesh bucket, for

2 min, and the sample preserved with formalin. On a few occasions, a zooplankton net was pulled vertically by towing through specific depth columns and counts adjusted to numbers per depth column sampled. Zooplankton subsamples were taken by a 1-ml subsampler from well-stirred plankton jars with total volume set at a specific level, 100 ml, and then transferred to a 1-ml grided counting cell for species identification and counting usually at $50\times$ magnification with a binocular microscope. In all cases, at least triplicate counts were made for samples at each depth, and in some cases, 4 to 6 replicate counts were made when the counts were more variable.

Zooplankton numbers in depth zone interval samples were integrated over the water column down to the permanent chemocline at 7–7.5 m to determine the number per meter square (no. m^{-2}). Summary statistics were determined for 25 sampling dates (2001–2008) on both lakes between spring and early autumn (for dates see Table 3). A computer statistical package was used to determine the summary statistics, and the differences between zooplankton abundance were observed in the two lakes using the Mann–Whitney U test, since the data were not normally distributed.

Results

Precipitation, water levels, and lake salinity

Total precipitation was relatively low during the first part (2000–2003) of this investigation when compared to the 28-year mean (345 mm) for annual precipitation (Fig. 1a). Two high years of precipitation (>400 mm) occurred in 2004 and 2006. Precipitation decreases southward in the main Okanagan Valley, but increases with elevation; therefore, annual precipitation at these two lakes should not be greatly different from that at the Penticton meteorological station. A 3-year running mean for the precipitation was also plotted (Helsel & Hirsch, 1991) to indicate what the lakes might experience, given the slow flux of groundwater and response to precipitation in the watersheds. Since year 2000, surface water levels in Mahoney and Blue lakes have fallen about 2 m, with minor variations (Fig. 1b). During the 2005–2007 wetter period, the rate of water

loss decreased in both lakes with a half meter increase in Blue Lake when the precipitation running mean was above average. Over this 9-year study period, salinity in the mixolimnion during midsummer in Mahoney Lake increased by 18 g l^{-1} (10–28 g l^{-1}), but in Blue Lake (Fig. 1c) the salinity remained between 5 and 10 g l^{-1} with no large change even though its water level decreases (Fig. 1b).

A weak period of bimeromixis was established in 2006–2007, especially in Blue Lake during this period of higher average precipitation, when a lens of fresher surface water stratifies the mixolimnion causing higher mid-mixolimnion temperatures (Fig. 2c). This level of secondary stratification was much less than had been observed at Mahoney Lake during the 1983–1984 and 1995–1998 periods (Northcote & Hall, 2000) when there were larger increases in the water levels of Mahoney Lake (Northcote & Hall, 2006, Fig. 2). During periods of lower precipitation, bimeromictic conditions did not develop on either Mahoney or Blue Lakes (Fig. 2a, b).

Water quality characteristics of meromictic lakes

Density differences of 0.02–0.03 g cm^{-3} between the mixolimnion and the monimolimnion (Table 1) are sufficient to maintain the meromictic conditions of these two shallow ($Z_{max} = 13$ m) saline lakes and provide the anoxic environment at the permanent chemocline (7–7.5 m) for the establishment of a dense plate of purple sulfur bacteria (Northcote & Hall, 1983, p. 187, Fig. 4). The mixolimnion of Mahoney Lake has 2–3 times higher salinity than occurs in Blue Lake. Mahoney is mainly a sodium sulfate lake, while magnesium is the dominant cation in Blue Lake (Table 1). The spring nitrate–N levels in the mixolimnion in 2007 of both meromictic lakes were relatively low (<0.02 mg l^{-1} N) compared to the phosphate–P (0.03–0.06 mg l^{-1} P; Table 1) and the relative requirements for optimum phytoplankton growth (Wetzel, 2001).

Primary production and chlorophyll *a*

Primary production and chlorophyll *a* were much higher in Blue Lake than in Mahoney during the springs of 2001 and 2003 (Table 2). The primary
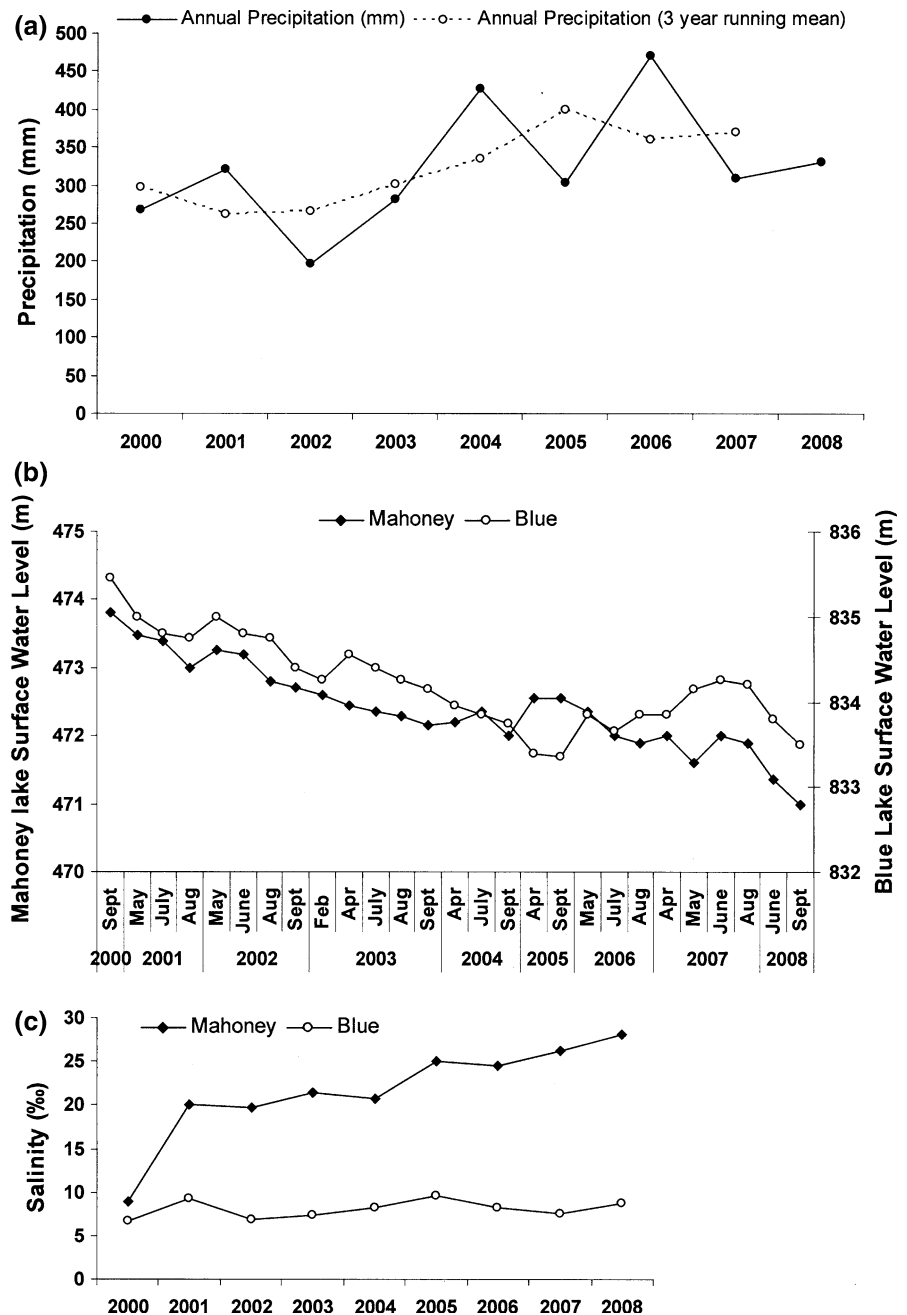
production and phytoplankton biomass in Mahoney
Lake increased during the summer months, but did
not usually reach the levels measured in Blue Lake.
Overall higher phytoplankton biomass in Blue Lake
for these 2 years results in the lower Secchi disk
transparency (mean = 4.5 m, $n = 8$) compared to
Mahoney Lake (mean = 6.5 m, $n = 8$).

Zooplankton in meromictic lakes

The rotifer *Brachionus plicatilis* and the copepod
Diaptomus connexus were the dominant zooplankton
found in Mahoney and Blue Lakes (Table 3). The
cladocerans *Ceriodaphnia lacustris* and *Daph-
nia pulicaria* occurred in Blue Lake but were absent
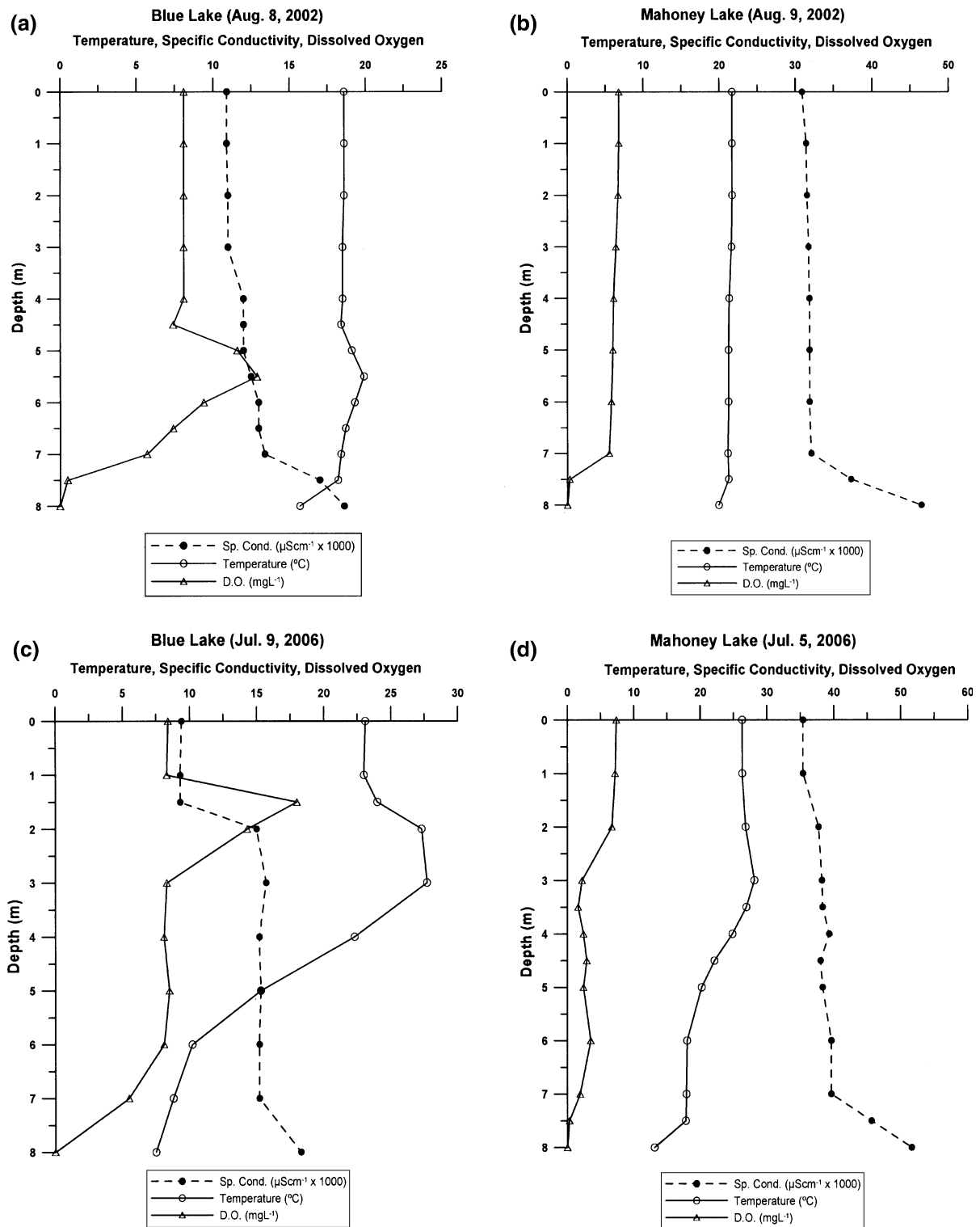
Fig. 2 Vertical temperature (°C), specific conductivity (μS cm^{-1} @ 25°C), and dissolved oxygen (mg l^{-1}) profiles in the mixolimnions of Mahoney and Blue lakes during summer periods of unimeromixis (August 2002) and a weak period of bimeromixis (July 2006)

Table 1 Spring water quality characteristics of two South Okanagan Meromictic Lakes

Characteristic	Blue Lake		Mahoney Lake	
	2 m	8.5 m	2 m	8.5 m
Density	1.0127	1.0359	1.0334	1.0627
Salinity	6.6	14.5	17.1	27.9
Specific conductivity	11,600	24,600	28,000	45,600
Dissolved oxygen	9.4	0.0	5.5	0.0
Temperature	12.6	11.1	17.2	12.2
pH	8.56	7.44	8.75	7.44
Calcium	53	67	47	108
Magnesium	2,110	5,531	2,568	5,315
Potassium	719	1,543	945	1,645
Sodium	1,065	2,501	7,775	13,688
Chloride	176	556	1,311	2,315
Sulfate	12,980	23,510	25,500	40,240
Bicarbonate	824	7057	806	8,601
Carbonate	57	0	264	0
Dissolved organic carbon	23	68	55	73
Phosphate–P	0.029	–	0.061	–
Nitrate–N	0.017	–	0.019	–

All values in mg l^{-1} except density (g cm^{-3}), salinity (g l^{-1}), specific conductivity (μS cm^{-1} @ 25°C), temperature (°C), and pH (pH units). Lakes sampled in May 20–21, 2003. Nutrient data (phosphate and nitrate) in May 10–11, 2007; – not measured

Table 2 Phytoplankton production and biomass in South Okanagan Meromictic Lakes

Date	Primary production		Chlorophyll a	
	Blue L.	Mahoney L.	Blue L.	Mahoney L.
2001				
May 18–19	37.89	5.08	25.07	1.58
Jul. 11–12	47.48	25.71	25.36	2.85
Aug. 29–30	27.08	30.14	2.82	5.12
Oct. 13–14	19.11	13.64	3.18	5.86
2003				
May 20–21	30.83	4.36	18.76	0.63
Jun. 21–22	24.81	8.36	1.56	1.21
Jul. 17–18	74.45	14.4	2.03	1.08
Aug. 21–22	92.88	35.41	8.49	4.02

Primary production in mg C m^{-2} h^{-1}, chlorophyll a in mg Chl a m^{-2}. Values calculated to give areal values in the photic zone from 0 to 7 m

from Mahoney Lake except for one occasion (June 2002) when *Daphnia pulicara* was present. The rotifer *Polyarthra* spp. occurred in both lakes, but

enumeration was incomplete due to clumping problems. Earlier investigations on Mahoney Lake had identified *C. lacustris* and *Keratella* spp. (Northcote & Halsey, 1969) and the predatory rotifer *Asplanchna* spp. (Northcote & Hall, 1983), when salinity levels were lower, but were not found in the 2000–2008 sampling periods.

Determination of the coefficient of variation (CV) on the triplicate counts of zooplankton had relatively low values of 21–24% for the *D. connexus* copepodites where the numbers of individuals were high, but for the cladocerns the CV could be >100% when only a few individuals (<5) were found in samples counted.

A statistical analysis, using the Mann–Whitney *U* test, to compare the differences between the zooplankton populations in the two lakes over the 8-year sampling period (2001–2008) demonstrated that Blue Lake had significantly lower numbers of the rotifer *B. plicatilis* than Mahoney ($P < 0.05$), but significantly higher numbers of *D. connexus* adults ($P < 0.05$) as well as two cladocerns *C. lacustris* ($P < 0.05$) and *D. pulicaria* ($P < 0.05$).

Between 2 (2005/08) and 4 (2001/03/07), vertical series of zooplankton samples were counted and integrated over the mixolimnetic depth during the spring and summer seasons in Mahoney and Blue Lakes over a 8-year period (Table 3). In Mahoney, the abundance of *B. plicatilis* was often highest in the spring while this rotifer did not often reach peak numbers until summer in Blue Lake.

With three stage groupings of the copepod, *D. connexus* (nauplii, copepodites—five instars and adults), the seasonal dynamics become a little more evident. The highest abundance of nauplii occurred mainly in the spring in both lakes (Table 3). The copepodites usually reached peak abundance in the summer. However, an exception to this was the highest abundance of copepodites in Blue Lake during the spring (mid-May) which occurred when the phytoplankton showed high activity and biomass (Table 2). This was likely due to a spring diatom bloom providing a food source in the cooler spring water (Wetzel, 2001). The peak abundance of adult copepods did not show any consistent seasonal pattern in either lake during the 2001–2008 study period.

The cladocern, *C. lacustris*, in Blue Lake was at lowest abundance in spring (April and May) with peak numbers in July and August. The numbers of

Table 3 Zooplankton abundance in two South Okanagan Saline Meromictic Lakes

Lake and date	Brachionus plicatilis	Diaptomus connexus			Ceriodaphnia lacustris	Daphnia pulicaria
		Nauplii	Copepodites	Adults		
Blue Lake						
May 18/2001	650	241,575	238,925	31,800	15,300	32,075
Jul. 11/2001	59,125	20,350	140,025	16,875	604,275	13,500
Aug. 29/01	24,500	31,500	193,450	46,550	203,750	17,500
Oct. 13/2001	6050	2,600	138,850	61,100	207,500	2,550
May 11/2002	3425	157,000	27,750	34,500	0	10,500
Jun. 20/02	2800	41,300	373,800	51,800	170,800	79,020
Aug. 8/2002	10,050	25,050	112,750	18,950	223,050	6,050
May 20/2003	167,500	188,150	541,600	104,900	56,750	300
Jun. 21/2003	16,450	24,450	513,900	52,750	203,750	6,750
Jul. 17/03	4,700	15,100	311,130	31,450	298,100	6,000
Aug. 21/2003	16,250	12,450	323,450	38,650	151,050	0
Apr. 27/04	27,200	297,980	77,210	83,370	7,700	0
Jul. 5/2004	87,700	6,050	430,600	10,750	974,400	0
Sept. 24/2004	38,200	3,300	83,650	98,200	118,000	0
Apr. 25/2005	16,900	359,450	39,000	179,400	0	11,700
Sept. 17/2005	19,650	8,100	188,850	48,150	103,500	0
May 5/06	38,500	67,200	55,300	93,100	0	0
Jul. 5/2006	2,405,450	7,350	455,800	72,800	106,800	0
Aug. 29/2006	402,600	4,050	257,750	53,300	78,600	3,150
April 12/07	7,400	0	45,700	34,200	500	0
May 10/2007	0	122,800	111,300	57,150	21,350	0
Jun. 28/2007	387,600	6,000	274,500	27,500	57,500	200
Aug. 15/2007	0	200	161,800	19,300	83,000	0
Jun. 8/2008	49,000	46,200	116,200	39,200	121,100	0
Sept. 4/2008	10,557	25,550	100,426	26,536	42,010	0
Mahoney Lake						
May 19/2001	652,000	181,150	185,500	131,350	0	0
Jul. 12/2001	16,050	47,710	236,000	13,890	0	0
Aug. 30/2001	58,890	37,680	209,000	29,400	0	0
Oct. 14/2001	31,575	6,950	84,200	103,400	0	0
May 12/2002	637,000	220,825	92,325	207,500	0	0
Jun. 20/2002	244,550	82,400	326,075	120,500	0	600
Aug. 9/2002	144,500	20,342	192,500	46,800	0	0
May 21/2003	1,213,200	54,500	222,670	37,650	0	0
Jun. 22/2003	371,800	11,000	232,760	20,140	0	0
Jul. 18/2003	125,750	34,400	253,700	41,300	0	0
Aug. 22/2003	831,100	50,750	157,100	27,850	0	0
Apr. 27/2004	293,640	1,900	10,700	2,500	0	0
Jul. 6/2004	65,180	9,400	105,350	11,350	0	0
Sept. 26/2004	81,050	11,250	93,050	39,400	0	0
Apr. 25/2005	245,210	69,300	30,800	30,800	0	0
Sept. 17/2005	82,680	4,650	188,670	31,335	0	0

Table 3 continued

Lake and date	Brachionus plicatilis	Diaptomus connexus			Ceriodaphnia lacustris	Daphnia pulicaria
		Nauplii	Copepodites	Adults		
May 6/2006	2,555,000	177,100	63,000	277,200	0	0
Jul. 5/2006	1,136,950	16,350	198,500	25,350	0	0
Aug. 29/2006	31,500	22,800	114,000	11,550	0	0
April 13/2007	144,100	40,200	2500	0	0	0
May 11/2007	75,500	18,800	6550	3150	0	0
Jun. 29/2007	27,050	32,530	86,240	12,700	0	0
Aug. 15/2007	1,666,000	32,000	103,600	13,880	0	0
Jun. 12/2008	91,000	9310	4620	0	0	0
Sept. 4/2008	205,882	58	44,794	10,123	0	0

All values in numbers m^{-2} in mixolimnetic waters 0–7 m in depth

D. pulicaria decreased from several thousand (6,000–80,000 m^{-2}) during the first 2 years of monitoring (2001–2002) and almost disappeared from the lake in 2007–2008. These data were too fragmented to observe any seasonal trends in *Daphnia*.

Mahoney and Blue Lakes zooplankton vertical distribution 2001–2007

Brachionus plicatilis

This rotifer on a series of sampling dates showed marked vertical changes in its abundance with depths covered down to 7 m or greater (Fig. 3). For 10 sampling dates at Blue Lake and 13 at Mahoney Lake, its abundance greatly increased at the lowermost sampling depth (7 m or greater) which closely approached the purple sulfur bacterial plate. Overall, its abundance in the upper water layers of both lakes, especially at their surface, was very low and in some cases entirely absent. This same abundance pattern held for several other sampling periods not included in Fig. 3. A few other species of rotifers were evident in the samples, but they either were clumped together (*Polyarthra* sp.) making counts very difficult or occurred only rarely (*Hexarthra* sp., *Notholca* sp.).

Cladocerans

Two species of cladocerans, *C. lacustris*, and *D. puli-caria* (sensu lato) occurred in our recent sampling

period (Fig. 4), but only in Blue Lake consistently from 2001 to 2007. On April 25, 2005, *D. pulicaria* was rare in Blue (1.8 l^{-1} in a 73.5-l vertical net tow from 6.5 m to the surface), absent in pump sampling at 0, 2, 4, and 6 m on September 17, 2005, rare (1.1 l^{-1}) in a 73.5-l vertical net tow from 6.5 m to the surface on July 9, 2006, only one individual in 58.6 l of pump sampling at 2 m on August 29, 2006, and absent in all 2007 sampling except for a single specimen in 58 l of pump sampling at 2 m on June 28. In sharp contrast to *Brachionus*, both cladocerans usually were most abundant at depths between about 2 and 4 m with low numbers near the surface (0–1 m) and below 4 m. When present *Daphnia* were at much lower abundance than *Ceriodaphnia* and virtually disappeared in the 2004–2007 sampling periods.

Copepods

(a) Copepodite stages I–V (Diaptomus connexus) Pump sampling series for Blue and Mahoney Lakes (Fig. 5) were available for 3 months (May–October) in 2001, one in 2002 (August), four in 2003 (May, June, July, and August), three in 2004 (April, July,

Fig. 3 Depth-abundance profiles for the rotifer *Brachionus* ▶ *plicatilis* in Blue (*triangles*) and Mahoney (*circles*) lakes, 2001–2007, on dates that both were sampled by suction pumping are shown, where two sampling days are given, the first is for Blue, the second for Mahoney; where two months are given the *open symbols* and *dashed* connecting lines are for the earlier sampling month
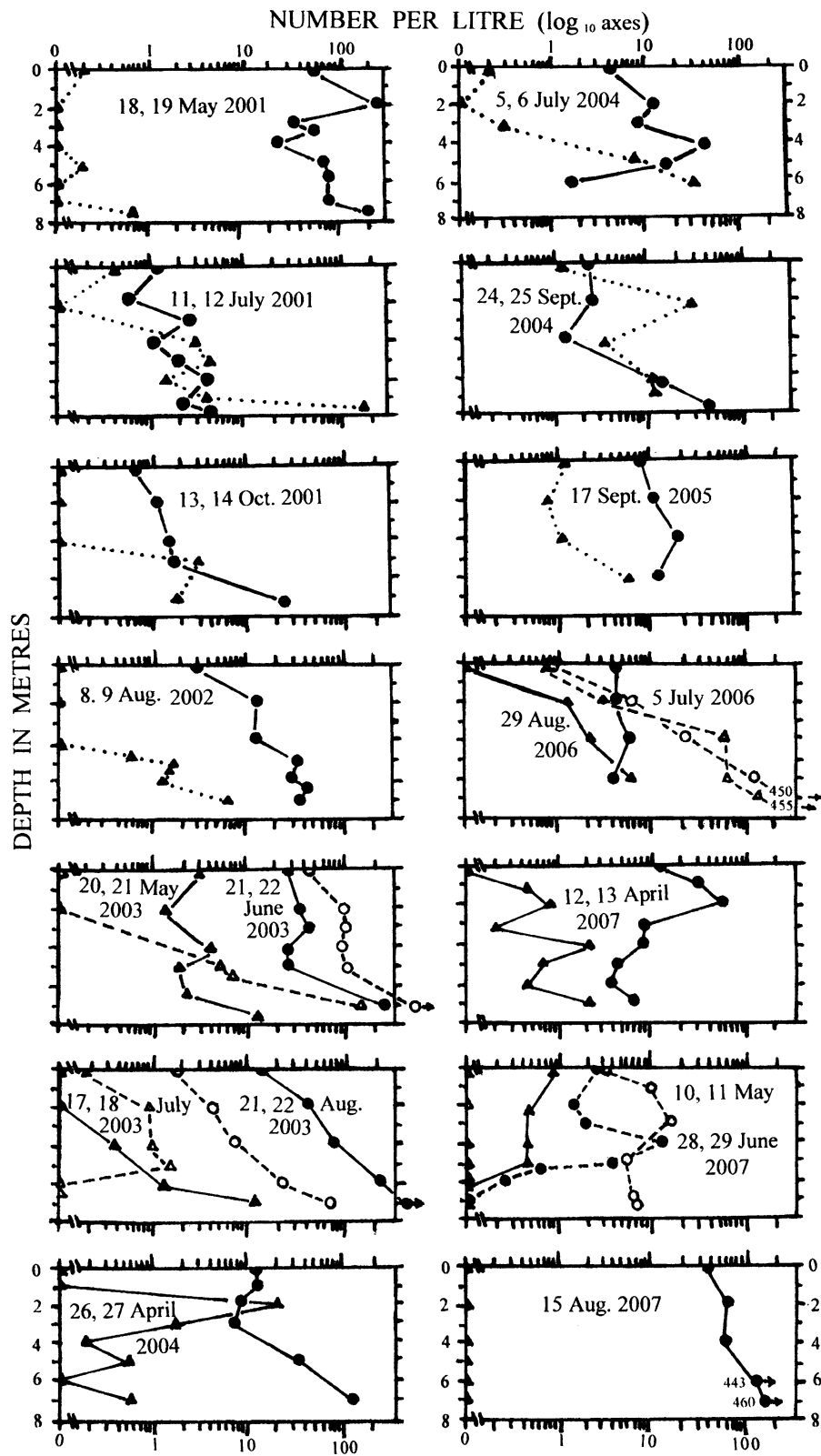
and September), one in 2005 (September), two in 2006 (July and August), and four in 2007 (April, May, June, and August). For both early spring series (April 2004, 2007), copepodite stages in Mahoney Lake only were present in the near-surface waters (0–2 m in 2004 and 0 m in 2007), whereas in Blue Lake they were moderately abundant throughout the water column sampled, even increasing with depth down to 7 m in April 2004 (Fig. 5). Except for May 2007 when copepodites in Mahoney Lake were low in abundance (1–10 l^{-1}), numbers in both lakes and their vertical distributions usually were not greatly different.

(b) Adult Diaptomus connexus (copepodite stage VI) Again for the adults in Mahoney Lake for both April sampling dates (April 27, 2004; April 13, 2007) and even May 2007, there were either very few only in the upper 2 m or none at all (Fig. 6). Thereafter throughout summer and autumn, adult abundance in both lakes increased greatly with depth, often reaching numbers between 10 and 100 close to the depth of the purple sulfur bacterial plate in the 6–7 m level (Fig. 6), a pattern that extended into autumn (October 13, 2001, mid to late September 2004, 2005).

Discussion

A summary of the ionic composition of saline lakes by Hammer (1986, Table 5.1) supports Wetzel's (2001) observation that most saline lakes are dominated by the cation sodium. An exception is the saline lakes of Saskatchewan where magnesium is the dominant cation (Hammer, 1986). However, it is unusual to find nearby saline lakes with different water chemistry which is evident in these two Okanagan region lakes where the concentration of magnesium in Blue Lake is twice the level of sodium, but sodium is the dominant cation in Mahoney Lake.

These differences can be related to their watershed geology. The highly fractured lavas of the Marron Formation with several alkali members on the west side of Mahoney Lake contribute to its higher sodium and salinities (Northcote & Hall, 1983). The Paleozoic rocks of the Kobau group formation in part of the Blue Lake watershed contain green metamorphic minerals such as chlorite which is rich in magnesium

Fig. 4 Depth-abundance profiles for two species of cladocerans, Ceriodaphnia lacustris (solid triangles) and Daphnia pulicaria (open triangles) in Blue Lake, 2001–2007, on dates sampled by suction pumping

and iron (Zhang, 2004; Mathews & Monger, 2005). Nearby Spotted Lake at a lower elevation in Richter pass has such high levels of Epsom salt (magnesium sulfate) that proposals have been made to mine it (Mathews & Monger, 2005).

Previous water quality measurements (Northcote & Hall, 1983) in Mahoney Lake have shown low spring concentrations of nitrogen (<0.01–0.06 mg l^{-1} NO_3–N) and phosphorus (<0.01–0.05 mg l^{-1} PO_4–P). Nutrients limit the phytoplankton production in Mahoney Lake since pre-incubation with P or N + P stimulated primary production between 3 and 4 times that in unfertilized samples. The extensive varving of carbonates in the sediment core of Mahoney Lake (Hall & Northcote, 2000) demonstrate that carbonates precipitate out of the water column and probably remove phosphorus from the photic zone as has been demonstrated in other hard water lakes (Murphy et al., 1983).

The increase in the phytoplankton primary production in Mahoney Lake during the summer can probably be attributed to the nutrient release from the decomposing clumps of purple sulfur bacteria which have been observed in the mixolimnion as lower lake levels allow wind mixing down to the chemocline and these bacteria become more buoyant as gas vacuoles increase (Overmann et al., 1994). The overall higher levels of chlorophyll and primary production in Blue Lake than that found in Mahoney cannot be explained by nutrient concentrations. More detailed research on nutrient and phytoplankton dynamics will be necessary to explain these results.

Limnological studies and texts in dealing with meromictic lakes have focused heavily on their special physical–chemical characteristics, but far less on their zooplankton communities and dynamics. An early exception was that of Ruttner (1952) on the zooplankton of the tropical Sunda lakes as well as in Krottensee (Salzburg) where the abundance of Cyclops reached its vertical maximum at about 20 m depth just above the disappearance of oxygen at 22 m (Ruttner, 1963). Hall Lake, a soft-water meromictic lake near Seattle, Washington, USA,

NUMBER PER LITRE (log$_{10}$ axes)
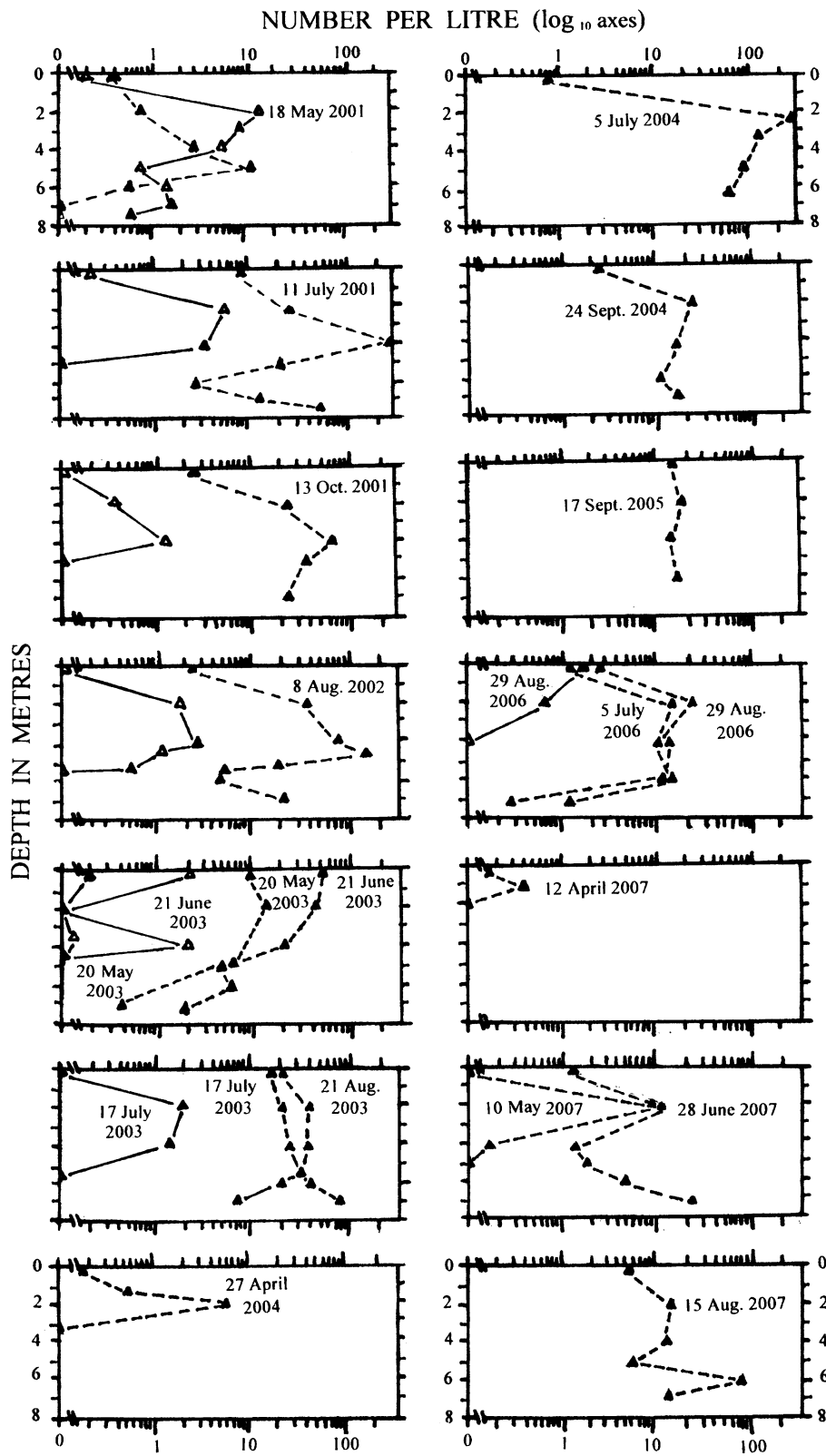
Fig. 5 Depth-abundance profiles for *Diaptomus connexus* copepodites I–V in Blue (*open triangles*) and Mahoney (*solid circles*) lakes, 2001–2007
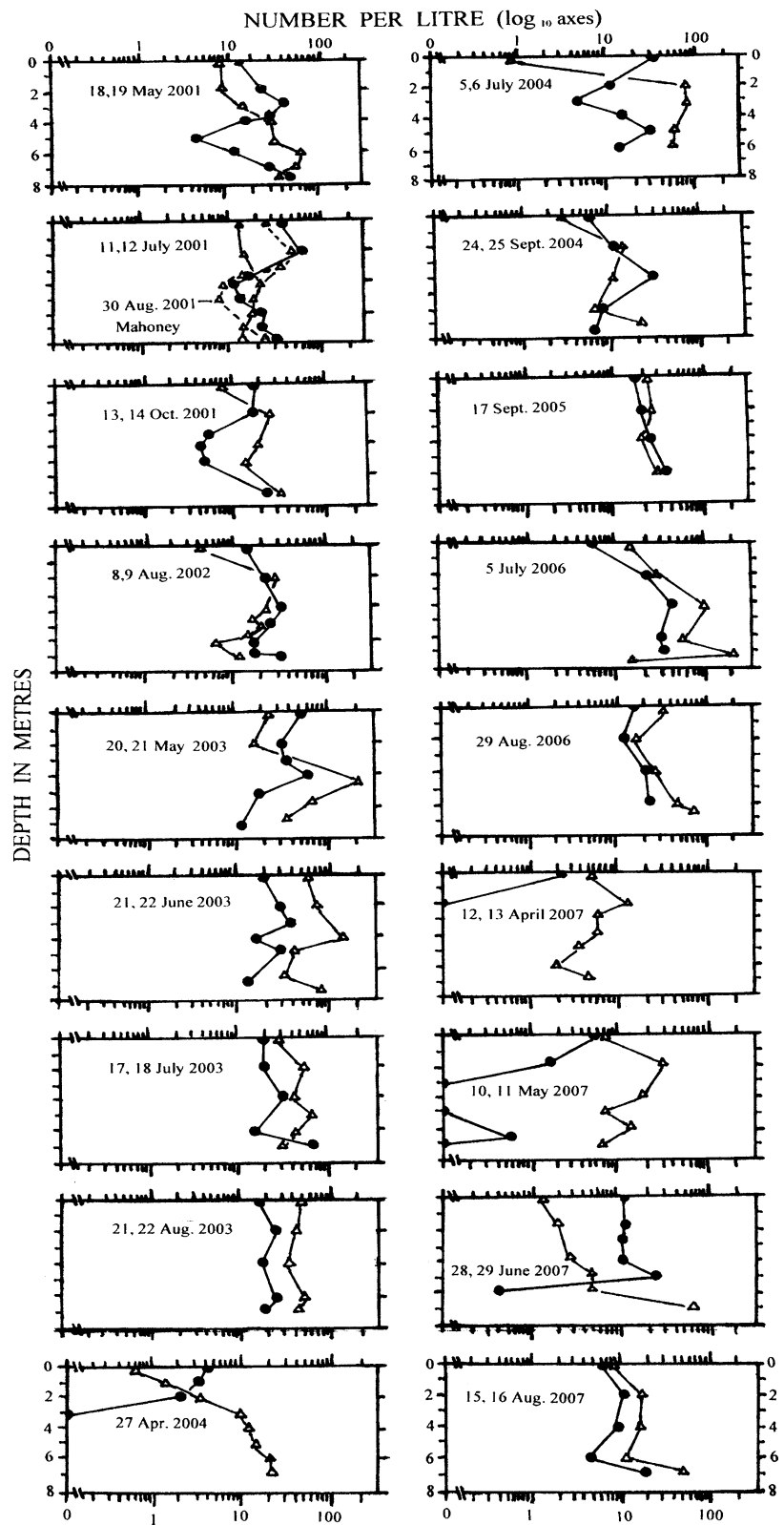
Fig. 6 Depth-abundance profiles for *Diaptomus connexus* adults in Blue (*open triangles*) and Mahoney (*solid circles*) lakes, 2001–2007
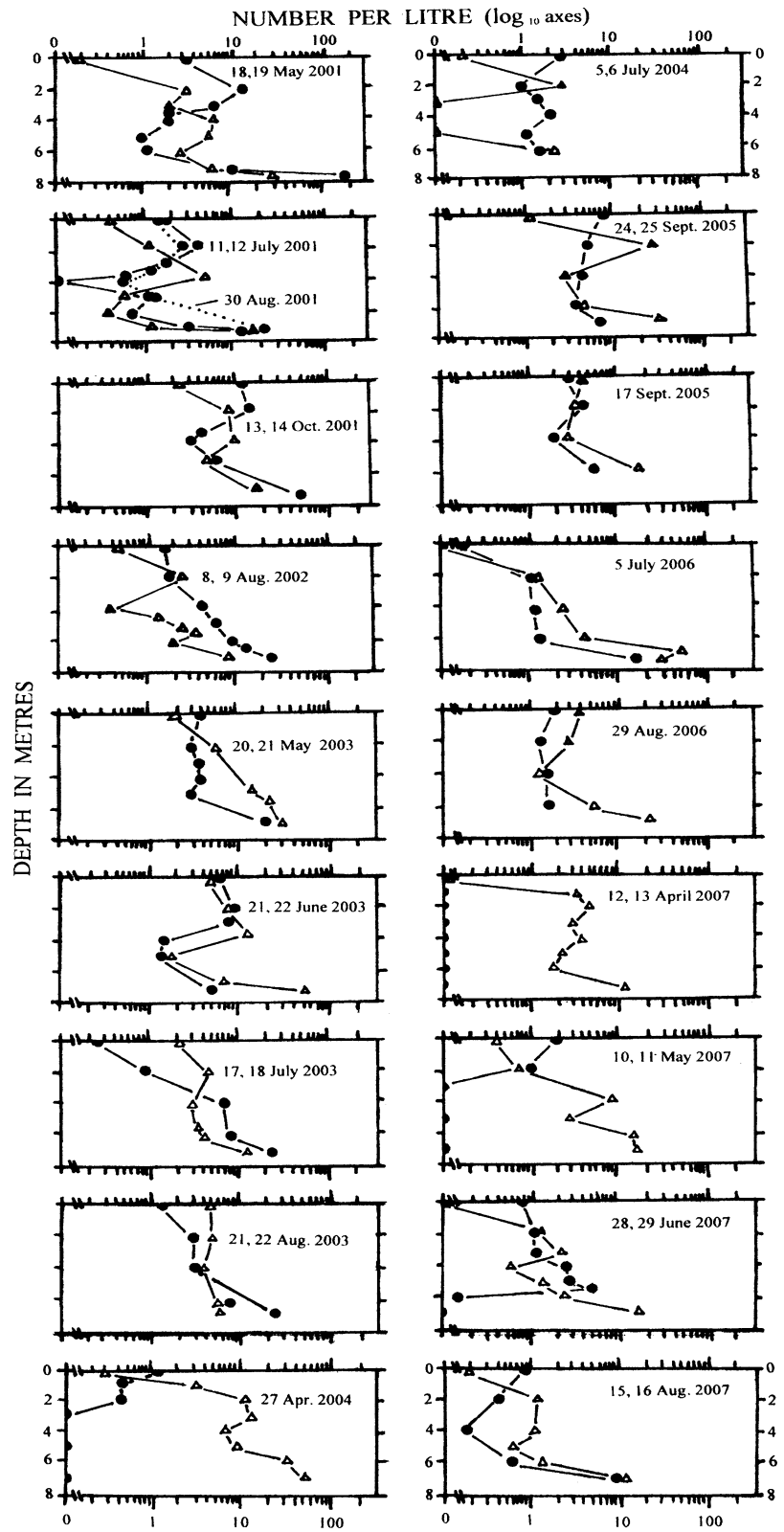
develops large zooplankton populations that include a *Daphnia* maximum of 198 l^{-1}, as well as a planktonic *Chaoborus* larvae population (3 l^{-1} max.) which descend to its lower mixolimnial level during the day (Edmondson, 1963). Bayly & Williams (1973) note that zooplankton in meromictic lakes may feed more on bacteria than on phytoplankton and refer briefly to colored sulfur bacteria being present in some meromictic lakes where they may be the dominant form of bacterial plankton. In our two BC meromictic lakes Mahoney and Blue, there certainly is a rich purple sulfur bacterial layer (PSB—*Amoebobacter purpureus*) at the main chemocline which at times of heavy wind action can be brought in clumps even up to surface levels. Moss (1988) refers to several meromictic lakes throughout the world, some of which only mix completely every several hundred years.

Herein, we show that the abundance of one species of rotifer (*B. plicatilis*) greatly increases at the maximum zooplankton sampling depth (usually about 7 m) in both Mahoney and Blue lakes. Although we have little positive evidence for the use of these abundant purple sulfur bacteria as a food supply for this rotifer, its vertical distribution maximum often within a few centimeters or less from the upper level of the PSB plate is suggestive of such use. In meromictic Lake Shunet, Russia, Khakassia, Tolomeev & Degermendzhy (2005) also found that *B. plicatilis* reached its maximum density (1175 l^{-1}) in August at 5–5.2 m, just above the chemocline which contained abundant purple bacteria.

The vertical distribution of the two cladocerans (*C. lacustris* and *D. pulicaria*), mainly in Blue lake in moderate numbers only between 2 and 4 m, do not make use of PSB as a significant food source because of their absence at that depth. *C. lacustris* was found (46,000 l^{-1}) at 2 m in 1966 in Mahoney Lake, where the mixolimnion dissolved solids were between 9 and 10 g l^{-1}, but the more recent lower lake levels and increases in the dissolved solids (17–24 g l^{-1}) have eliminated this cladocern from this saline meromicitc lake. Saline lake studies of zooplankton distribution in interior British Columbia found that the cladocerns were more abundant in the lower salinity (<5 g l^{-1}) lakes (Hammer & Forró, 1992). In toxicity tests, Shuytema et al. (1997) reported a mean lethal concentration (LC50) of 6.6 g l^{-1} salinity for *Daphnia magna* and Bailey et al. (2004) found that only

10% of diapausing eggs of *Daphnia longiremis* hatched at a salinity of 8 g l^{-1}. However, Weider & Herbert (1987) reported that *Daphnia pulex* clones from highly saline ponds had greater survival, thereby demonstrating that some physiological adaptation is possible.

The presence of moderate to high numbers of the late copepodite stages and adults of *D. connexus* close to the PSB plate or at times in it, along with C^{14} labeled PSB experimental feeding studies and microphotographs using infrared epifluorescence to show the PSB in the guts of adult *D. connexus* (Overmann et al., 1999a), clearly demonstrate such use as a major food supply for adults and late copepodites of this copepod. Overmann et al. (1999a) were able to demonstrate with stable carbon isotope analysis of such copepods and the isolated pigments from *A. purpureus* that these purple sulfur bacteria could represent 75–85% of their diet. The significantly higher abundance of adult *D. connexus* in Blue Lake compared to Mahoney Lake could be related to the importance of the mixolimnetic phytoplankton in the quality of their diet, since Blue Lake had higher levels of algal biomass. Overmann et al. (1999b) reported that the efficiency of carbon transfer from phytoplankton to zooplankton (*D. connexus*) was much higher than from chemotrophic bacteria. It is unlikely that the higher salinity of Mahoney Lake was affecting survival of this copepod since in their saline lake study, Hammer & Forró (1992) found that *D. connexus* preferred the more saline lakes (35–45 g l^{-1}).

The weak period of bimeromixis that occurred during the period of higher rainfall did not have any noticeable effects on the vertical distribution of the zooplankton in these two meromictic lakes. However, when strong bimeromixis is set up in lakes like Mahoney, this micro-stratification can cause oxygen depletion such as occurred in the springs of 1982–1983 (Northcote & Hall, 1990), where the numbers of rotifers and copepods were reduced to zero in this narrow anoxic zone, and the populations of zooplankton became separated at the surface and mid-depth levels until later mixing destroyed the low oxygen barrier. Another strong period of bimeromixis occurred in Mahoney Lake between 1998 and 2000 and caused oxygen supersaturation (as high as 300%) at this microstratification boundary (2–3 m depth) as a result of phytoplankton accumulation at this density boundary (Hall & Northcote, 2002).This provided a

major food source for the zooplankton, and copepod numbers were high here as well as at the purple sulfur bacteria plate at the permanent chemocline (Northcote & Hall, unpublished data). Detailed zooplankton pump sampling at half meter intervals is often necessary to follow the vertical zooplankton dynamics during such periods of bimeromixis.

The term bimeromixis was first used by Northcote & Hall (2000) and again by Hall & Northcote (2002), but this term and its counterpart unimeromixis have not yet been widely used in meromictic limnological terminology. Such conditions may have been mentioned briefly in other saline lakes but the terms are useful to emphasize the obviously important effects on vertical dynamics of zooplankton populations and oxygen stratification conditions produced by microbial decomposition processes or phytoplankton production processes in these micro-stratified layers.

Richardson (2008) reviews the negative impacts of climate change on zooplankton in the marine environment. These effects are mainly related to how temperature influences the water column stability and nutrient enrichment which exerts bottom-up effects on the zooplankton community. Short-term studies (Schallenberg et al., 2003) on an increase in salinity in coastal Lake Waihola in New Zealand due to climate induced salinity intrusion resulted in negative perturbations in zooplankton community structure and abundance. Also, their literature review (Table 2) summarizes how the taxonomic abundance decreased due to salinity increase.

Inland saline meromicitc lakes, usually found in enclosed watersheds, are excellent environments to study climate change impacts on zooplankton since high evaporation rates in these lakes due to higher temperatures can gradually influence lake levels and water salinities over time which could affect zooplankton abundance and diversity. Previous studies on zooplankton salinity tolerance have mainly been done in controlled laboratory studies (Shuytema et al., 1997; Bailey et al., 2004) or by comparing zooplankton presence or absence in lakes of different salinities (Hammer & Forró, 1992), which can have different morphologies and water chemistry. Our long-term (8 years) investigation in the same lakes as the water levels decreased help support literature observations that the cladocerns, such as *D. pulicaria*, disappear first as salinity increases and the rotifers,

such as *B. plicatilis*, appear to be the most tolerant to salinity change.

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