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Salt Ecosystems Section

A comparison of zooplankton communities in saline lakewater with variable anion composition

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Abstract

Although salinity and aquatic biodiversity are inversely related in lake water, the relationship between types of salts and zooplankton communities is poorly understood. In this study, zooplankton species were related to environmental variables from 12 lakes: three saline lakes with water where the dominant anions were SO_4 and CO_3, four saline lakes with Cl-dominated water, and five dilute, subsaline (0.5–3 gl^{-1} total dissolved solids) lakes of variable anion composition. Although this study comprised only 12 lakes, distinct differences in zooplankton communities were observed among the two groups of chemically defined saline lakes. Canonical correspondence analysis identified total alkalinity, sulphate, chloride, calcium, sodium, potassium, and total phosphorus as all contributing to the first two ordination axes ($\lambda_1 = 0.97$ and $\lambda_2 = 0.62$, $P < 0.05$). The rotifer *Brachionus plicatilis* and the harpactacoid copepod *Cletocamptus* sp. prevailed lakes with Cl-dominated water. In contrast, the calanoid copepods *Leptodiaptomus sicilis* and *Diaptomus nevadensis* were dominant in the SO_4/CO_3-dominated lake water with elevated potassium (79–128 mg l^{-1}) and total phosphorus concentrations (1322-2915 $\mu g\ l^{-1}$). The contrasting zooplankton species distribution among these two saline lake types is likely explained by variable selective pressure on zooplankton and their predators from differing physiological tolerances to salt stress and specific ions. While inland saline lakes with Cl as the dominant anion are relatively rare in Canada and SO_4/CO_3 are the common features, our study provided an opportunity to compare zooplankton communities across the two groups of lakes.

Introduction

Saline lakes comprise a small proportion of the total volume of inland water in Canada, but are of scientific interest because they are systems with naturally low biodiversity (Hammer, 1986). Brine composition can be variable among saline lake water and is related to geologic setting and lake position in the drainage basin relative to local and regional groundwater flow (Last, 1992). Most Canadian lakes that contain water with elevated salinities are located in the prairies and aspen parklands of the western provinces of Saskatchewan and Alberta, and in the dry interior of the Province of British Columbia. Sulphate or bicarbonate/carbonate are usually the lead anions and the predominant cations can vary in these inland waters (Last, 1992). With the exception of similarities shared with Siberian saline systems, sulphate-rich saline waters in North American are considered to have rare water chemistry globally. In contrast, sodium chloride is the most common form of salt in saline lakes globally and is most frequently encountered in Australia and South Africa (Hammer, 1986). North American lakes containing water with high concentrations of sodium chloride tend to be found in arid regions of the western United States (Blinn, 1993). There are isolated examples of sodium chloride-dominated lake water in Canada (Hammer, 1993), and several of these are located on the predominantly freshwater boreal plain (Camsell, 1917).

The diversity of aquatic species decline as osmotic tolerances are exceeded with increasing salinity (e.g., Hammer, 1993). In addition to salt concentration, other factors such as habitat permanence, predation, and ion composition can alter the structure of aquatic communities in saline lakes (Williams, 1998; Herbst, 2001). However, the role of salt ion composition relative to salt concentration in determining zooplankton communities is not understood (e.g., Hammer, 1986; Bos et al., 1996; Williams, 1998). Past studies have indicated distinct anion preferences within the ostracod genus *Limnocythere* among carbonate, sulphate, and chloride-dominated waters (Forester, 1986). Bos et al. (1996) identified calcium and magnesium as key determinant cations for the relative abundance of *Artemia franciscana*, *Moina hutchinsoni*, *Daphnia pulex*, *Ceriodaphnia laticaudata*, *Simocephalus* spp., and calanoid copepods among carbonate/bicarbonate and sulphate-dominated waters in the interior of British Columbia. Little work has addressed contrasts in zooplankton community composition among chloride- and sulphate-dominated saline lakes. Our study sought to test the hypothesis that differences in zooplankton communities among chloride- and sulphate-dominated saline lake water were largely a result of contrasting ion dominance rather than overall salinity. We classified the study lakes according to salinity categories described by Hammer (1986): subsaline (0.5–3 g l^{-1} total dissolved solids (TDS), hyposaline (3–20 g l^{-1} TDS), mesosaline (20–50 g l^{-1} TDS), and hypersaline ($>$50 g l^{-1} TDS). Much of the emphasis was placed on subsaline and saline ($>$3 g l^{-1} TDS) lakes containing water dominated by sodium chloride as these lakes have received little scientific attention in Canada. Differences in ion composition of lake water were related to the relative abundance of both crustaceans and rotifers to understand biogeographic patterns of saline habitat utilization in zooplankton.

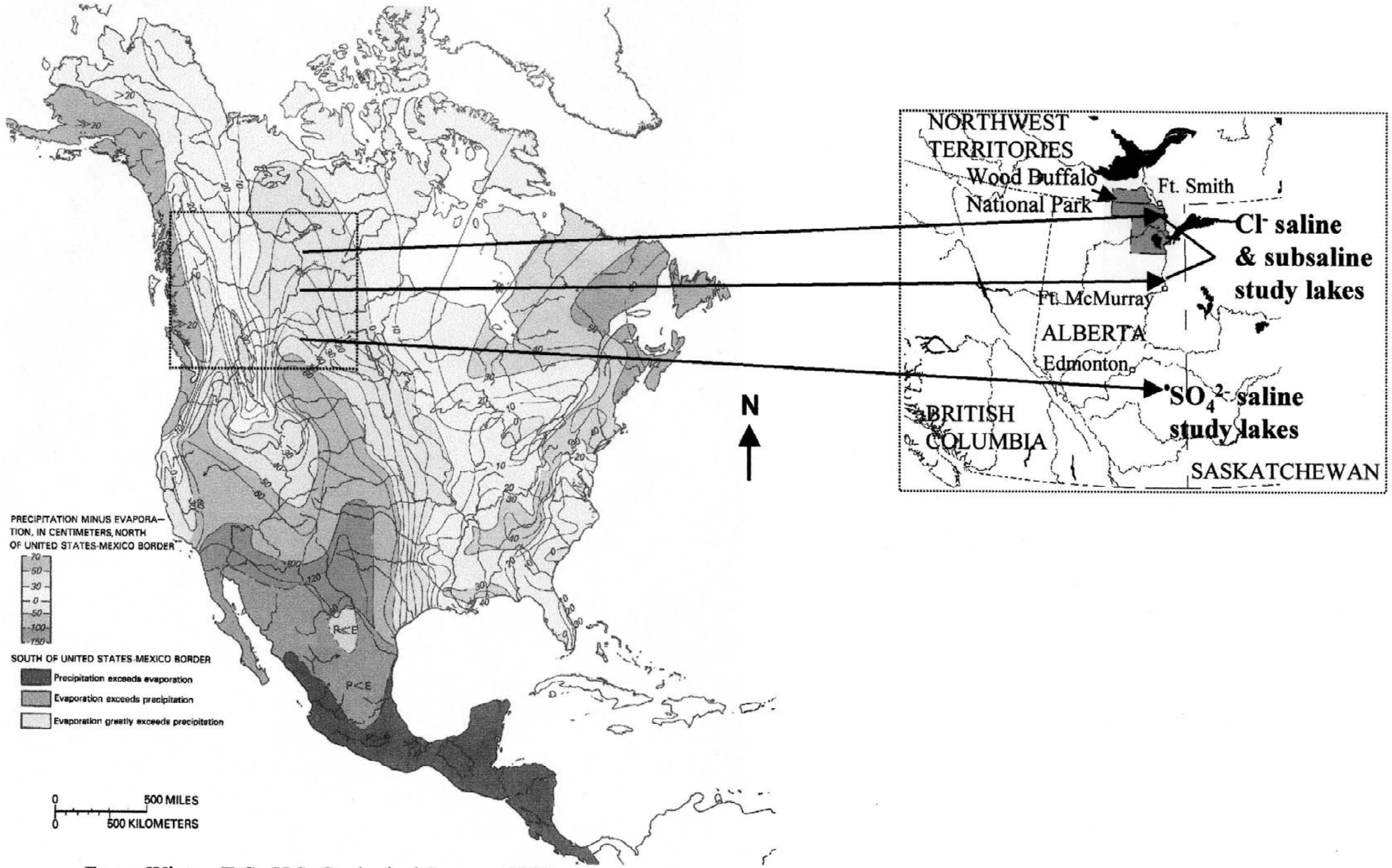
Materials and methods

Description of study lakes

Our study was conducted primarily on four saline lakes with water dominated by chloride anions, two saline lakes with sulphate-dominated waters, one saline lake with carbonate anion dominance, and six subsaline lakes with varying anion chemistry (chloride or sulphate dominance) (Fig. 1). Data collected on the lakes with sulphate-dominated water were augmented with information from Bierhuizen & Prepas (1985), Campbell & Prepas (1986), and Evans & Prepas (1996). At the end of abbreviations for the study lakes, -SO_4 identifies the sulphate-dominated saline lakes, –CO_3 refers to the carbonate-dominated lake, –Cl indicates the chloride-dominated saline lakes, and – D represents the more dilute subsaline lakes.

The study lakes are found in a 800 km band stretching from the northern tip of the Province of Alberta to southeast of the city of Edmonton. Eight of the study lakes (Grosbeak Lake (GB-Cl), HC-Cl, Salt Pan Lake (SP-Cl), GL-D, GW-D, BP-D, FP-D, and WR-D) are found on the boreal plain in Wood Buffalo National Park (Park) where boreal mixed-wood forest is interdispersed with wetlands, prairies, and salt flats (Moser et al., 1998). Also on the boreal plain is Saline Lake (SL-Cl), which is located 330 km south of the Park sites near the city of Fort McMurray. In contrast, the three saline study lakes in central Alberta (Olivia Lake (OL-CO_3), Peninsula Lake (PN-SO_4), and Fluevog Lake (FL-SO_4)) are located 150 km southeast of the city of Edmonton in aspen prairie-parkland, and are surrounded by farmland (Campbell & Prepas, 1986).

The bedrock geology of the Park study lakes (predominantly chloride-dominated waters) is characterized by Middle Devonian limestone ($CaCO_3$), gypsum ($CaSO_4 \cdot 2H_2O$), and dolostone ($CaMg(CO_3)_2$) shale, covered with a thin layer of glacial, glacial-lacustrine, lacustrine and aeolian deposits (Moser et al., 1998). Surface waters are influenced to varying degrees by deep, groundwater springs that discharge sodium chloride salt (Camsell, 1917) from along the dissolution edge of the Cold Lake Formation of marine evaporitic halite (NaCl) (Mejer Drees, 1986). SL-Cl is located near the boundary where limestone, gypsum and dolomite deposits meet Lower Cretaceous sandstone and minor shale (Government & University of Alberta, 1969). The discharge of sodium chloride springs into SL-Cl is periodically diluted when the nearby (0.2 km) Athabasca River floods (M. MacKinnon, Syncrude Canada Ltd., pers. comm.). In contrast, the sulphate/carbonate-dominated waters of the study lakes in central Alberta have a bedrock geology comprised of Upper Cretaceous deposits of sandstone, shale, coal and bentonite (Government & University of Alberta, 1969). Dominant SO_4-based minerals in the prairies and aspen parklands include



From: Winter, T.C., U.S. Geological Survey. 1989.

Figure 1. The location of study lakes in Wood Buffalo National Park and Alberta, Canada in relation to the distribution of the difference between precipitation and open water evaporation in North America.

gypsum, mirabilite ($Na_2SO_4 \cdot 10H_20$) and thenardite (Na_2SO_4), and common $CO_3{}^{2-}$-based minerals are aragonite ($CaCO_3$), calcite ($CaCO_3$), and dolomite ($CaMg(CO_3)_2$. Feldspars containing K^+ are also abundant.

All of the study lakes are found in regions in which lake evaporation exceeds precipitation (Fig. 1). The difference between precipitation and open water evaporation ranges from negative 15 cm for the nine lakes in northern Alberta to negative 35 cm for the three lakes located in central Alberta (Winter, 1989). With the exception of GB-Cl and SP-Cl that have surface outflows but not inflows, all of the saline and subsaline study lakes in the Park have inflowing and outflowing streams. In contrast, the lakes with $SO_4{}^{2-}/CO_3{}^-$-dominated water in central Alberta do not have any permanent hydrographic connections.

Field collection and laboratory analysis

During the summer of 1999, the Park lakes were sampled monthly from June to September and SL-Cl was sampled once in June and August. The three study lakes in central Alberta (OL-CO_3, PN-SO_4, FL-SO_4) were sampled once in June 1999. All sampling was conducted at the point of maximum lake depth. Lake surface area was determined from 1:50 000 topographic maps with a Bioquant HPI digitizer with System IV image analysis software. BP-D was too small to be found on a map, and since this pond was approximately circular, surface area was estimated based on measurements of length and width. Water transparency was estimated with a Secchi disk. Temperature and conductivity of surface lake water were measured in the field with a YSI 30 conductivity meter and pH was measured with a hand-held Fisher pH/temperature meter 119 Model 3D. In September, vertical profiles of temperature and conductivity were measured at the deepest location in saline and subsaline lakes in the Park.

Water samples were collected from a depth of 0.5 m below the lake surface in acid-washed and pre-rinsed polyethylene bottles, and then refridgerated from 1 to 10 d before being shipped on ice for filtration and analysis by the limnology laboratory at the University of Alberta. Samples for nitrite and nitrate analyses were collected in July from lakes in the Park, and in August from SL-Cl; samples were frozen < 2 h of collection and analyzed within 5 d. For chlorophyll *a* (chl *a*) analysis, water was filtered through Gelman GF/C (0.7 μm pore) filters, and the filters were wrapped in foil and frozen on desiccant beads in light resistant containers until analysis.

Water samples were analyzed for total dissolved solids (TDS), total phosphorus (TP), total nitrogen (TN), nitrite ($NO_2{}^-$) and nitrate ($NO_3{}^-$), major cations (Na^{2+}, Ca^{2+}, K^+, Mg^{2+}, Mn^{3+}, and Fe^{2+}), major anions (Cl^- and $SO_4{}^{2-}$), alkalinity, dissolved organic carbon (DOC), turbidity and colour. TDS was determined according to Stainton et al. (1977). TP was measured with the potassium persulfate digestion procedures of Menzel & Corwin (1965), as modified by Prepas & Rigler (1982). TN, $NO_2{}^-$, and $NO_3{}^-$ were analyzed with a Technicon autoanalyzer (Stainton et al., 1977), with modifications based on U.S. EPA Method 353.2. As a result of logistical constraints, $NO_2{}^-$, and $NO_3{}^-$ were not measured for lakes with $SO_4{}^{2-}/CO_3{}^-$-dominated water in central Alberta (OL-CO_3, PN-SO_4, FL-SO_4). Cations were measured with a Perkin Elmer 3300 Atomic Absorption Spectrometer (Stainton et al., 1977) and anion concentrations were determined with a Dionex 2000i/SP Ion Chromatograph (Pfaff, 1993). Alkalinity was analyzed with a Mettler DL21 Titrator (Greenberg et al., 1992). Turbidity was measured with a Hach Turbidimeter Model 2100A and colour was measured at 440 nm with a Milton Roy 1001 spectrometer (Cuthbert & del Giorgio, 1992). Chl *a* was measured by Ostrofsky's ethanol extraction technique (Bergmann & Peters, 1980).

Zooplankton were sampled with a conical 20-cm diameter, 50-cm long, 64-μm mesh size Nitex tow net from near the bottom to the surface of each lake during daylight. While three vertical tows per sample were taken in lakes with maximum depths ≥ 1 m, horizontal drift tows were taken in lakes with maximum depths < 1 m and distances were estimated based on shoreline measurements. Zooplankton were preserved in a chilled 4% buffered formalin-sucrose solution. Taxonomic identifications and counting were conducted on 5–10 ml subsamples with a counting wheel on a dissecting microscope at 50$\times$ and 100$\times$ magnifications. Zooplankton were identified according to the following taxonomic keys: rotifers (Edmondson, 1959; Chengalath et al., 1971; Stemberger, 1979), adult copepods (Smith & Fernando, 1978), and cladocerans (Brooks, 1957; Edmondson, 1959; Devey & Devey, 1971; Brandlova et al., 1972). Densities of zooplankton were expressed in number of individuals/l based on an assumed net filtration efficiency of 100%. Nauplii and other unidentifiable juveniles (mostly copepods) were excluded from statistical analyses. Nelson & Paetz (1992) was employed to identify fish that were caught with minnow traps and then released.

Statistical analysis

Multivariate analyses were performed with CANOCO 4.0 (ter Braak & Šmilauer, 1998) to investigate species-environment relations among the study lakes. Comparisons were drawn to determine key determinants of zooplankton community structure among the subsaline study lakes ($n = 18$), among the Cl^--dominated saline lakes ($n = 13$) with different salt concentrations, and among all of the saline study lakes dominated by Cl^- or SO_4^{2-} ($n = 25$ samples collected in 1984 and 1999). Relationships among species abundance and environmental variables ($n = 35$) among the 1999 samples were evaluated with Spearman Rank Correlations in Sigmastat 2.0 for Windows (SPSS Inc. 1997) to collapse the data set to meet sample size restrictions imposed by multivariate analyses. Detrended correspondence analysis (DCA) was employed to determine whether unimodal (canonical correspondence analysis) or linear (redundancy analysis) models of species response to environmental variables best fit the data. Canonical correspondence analysis (CCA) and redundancy analysis (RDA) are ordination techniques that are employed to infer how environmental variables collectively influence community composition, in which the ordination axes are constained to be a linear combination of environmental variables. Where CCA was applied to the data, we employed downweighting of rare species.

The minimum number of measured environmental variables that could account for the major directions of variance in the species data was determined by forward-selected CCA or RDA with 999 iterations in Monte Carlo permutation tests at $P < 0.05$. Environmental variables that were identified as significant by forward selection but that were strongly correlated with other variables in the minimum set ($P < 0.001$), such that variance inflation factors >20, were excluded to avoid collinearity. Time of sampling in Julian days was a covariate for time-series restricted permutations in all multivariate analyses.

Subtle differences in species distribution among the 13–170 times more dilute subsaline lakes could not be resolved by the ordination axes when subsaline lakes were analyzed with saline lakes, and thus they were analyzed separately. Crustaceans and rotifers were analyzed together in ordinations of saline lakes. These taxa were were analyzed separately in ordinations for subsaline lakes because the number of subsaline crustacean and rotifer species combined in a CCA would have exceeded the difference between number of samples and number of environmental variables (ter Braak & Šmilauer, 1998).

Results

Water chemistry

All of the lakes had small surface areas (≤150 ha) and were shallow (<3.4 m mean depth) (Table 1). With the exception of hypersaline OL-CO_3 (∼100 g l^{-1} TDS), the study lakes ranged from subsaline (0.5–1 g l^{-1} TDS) to hyposaline (7–14 g l^{-1} TDS) to mesosaline (37–40 g l^{-1} TDS) (Table 2). Over the summer, lakewater salinity fluctuated at all sites. The greatest salinity variation occurred in FP-D, which was hyposaline in mid-June (4900 μS/cm) but became subsaline by the end of the month (789 μS/cm) after a major storm (86 mm precipitation over 2 d, Wood Buffalo National Park 1999 data from Benchmark Creek weather station). Although FP-D remained subsaline for most of the summer, the bottom stratum of water overlying the sediments was hyposaline by September (8100 μS/cm). With the exception of chemical stratification observed in FP-D and HC-Cl (maximum conductivity of 56 000 μS/cm on the bottom), all other study lakes in northern Alberta remained isothermal throughout the summer. The three study lakes containing SO_4^{2-}/CO_3^{2-}-dominated water in central Alberta were isothermal in June of 1999, but the water column of OL-CO_3 was inversely chemically stratified by midsummer in other years (Campbell & Prepas, 1986). Water chemistry from 1983 to 1992 (Bierhuizen & Prepas, 1985; Evans & Prepas, 1996) used to augment our data for the saline study lakes located in central Alberta are summarized in Table 3.

Ion composition varied among the study lakes (Table 2). With the exception of one subsaline lake with water dominated by SO_4^{2-} (GL-D), the four other subsaline lakes in the Park had water dominated by Cl^-. The four saline study lakes in northern Alberta with water dominated by Cl^- (4–17 g l^{-1} Cl^-) also had relatively high concentrations of SO_4^{2-} (0.3–2 g l^{-1}). In contrast, the three SO_4^{2-}/CO_3^--dominated lakes in central Alberta had comparatively low Cl^- concentrations (2–21 times lower than SO_4^{2-} and 12–37 times lower than HCO_3^-/CO_3^{2-} anions). Lakes

Table 1. The location and morphometry of study lakes. At the end of the lake designations, -SO_4 and –CO_3 refer to the SO_4^{2-} and CO_3^{2-}-dominated saline waters in central Alberta, respectively. Cl^--dominated saline waters and subsaline waters found in the northern part of the province are represented by –Cl and –D, respectively

Saline lakes	Location	Surface area (ha)	Maximum depth (m)	Mean depth (m)
OL-CO_3	53° 05′N, 111° 36′W	52	1.7	1.3
PN-SO_4	52° 52′N, 111° 29′W	139	3.1	2.1
FL-SO_4	52° 50′N, 111° 19′W	32	2.1	1.4
GB-Cl	59° 25′N, 111° 30′W	38	0.5	0.3
HC-Cl	59° 31′N, 111° 27′W	4.4	0.5	0.3
SP-Cl	59° 48′N, 112° 01′W	32	0.7	0.3
SL-Cl	57° 04′N, 111° 31′W	150	1	0.5
Subsaline lakes				
GL-D	60° 00′N, 112° 37′W	15	11	3.4
GW-D	59° 31′N, 111° 27′W	1.7	2.2	1.0
BP-D	59° 31′N, 111° 27′W	0.78	2.4	0.8
FP-D	59° 31′N, 111° 27′W	3.3	1.7	0.8
WR-D	59° 31′N, 111° 27′W	4.1	2.5	1.3

with water dominated by SO_4^{2-}/CO_3^{2-} anions were 28–68 times more alkaline than the lakes with water dominated by Cl^-. With the exception of GL-D where Ca^{2+} prevailed, Na^+ was the most abundant cation in study lake water, and was followed in abundance by Ca^{2+} in Cl^--dominated waters and by K^+ in SO_4^{2-}/CO_3^{2-}-dominated waters.

Concentrations of nutrients also varied between Cl^-- and SO_4^{2-}/CO_3^{2-}-dominated lake water (Table 2). The Cl^--dominated lake water in northern Alberta had TP and TN concentrations that corresponded with mesotrophic levels of productivity for fresh water (Wetzel, 1983). These lakes had TN:TP ratios that ranged from 12 to 57. The exception among the study lakes located in northern Alberta was oligotrophic and SO_4^{2-}-dominated GL-D. In contrast, saline lakes in central Alberta had hyper-eutrophic concentrations of TP ($>1322\ \mu g\ l^{-1}$ TP) and TN:TP ranged from 0.02 to 0.05. With the exception of the more productive FP-D and HC-Cl, chl *a* concentrations in the saline and subsaline study lakes in this study were indicative of mesotrophy (Table 2).

Biota

Potential differences in exposure to predation exist among the study lakes. With the exception of HC-Cl and FP-D, nine-spined stickleback (*Pungitius pungitius*) and corixids were detected in all of the study lakes in the Park. In contrast, the lakes in central Alberta that have water dominated by SO_4^{2-}/CO_3^{2-} are fishless (Campbell & Prepas, 1986).

Table 2. Average measurements of TDS (mg l^{-1}), conductivity (μS/cm), major nutrient (μg l^{-1}) and ion (mg l^{-1}) concentrations for the study lakes over summer of 1999. pH, DOC (mg l^{-1}), turbidity (NTU), colour (mg l^{-1} Pt), chl *a* (μg l^{-1}), and Secchi depth (m) are also presented. SO_4^{2-}-dominated saline waters in central Alberta (-SO_4) were measured in only June. N.D. indicates where no data was available and B represents 'bottom' for Secchi depths

Saline Lakes Salinity Category	OL-CO_3 Hyper-Saline	PN-SO_4 Hypo-Saline	FL-SO_4 Hypo-Saline	GB-Cl Meso-Saline	HC-Cl Meso-Saline	SP-Cl Hypo-Saline	SL-Cl Hypo-Saline
TDS	96 228	14 277	8028	26 318	25 605	12 676	7282
Conductivity	73 336	16 441	10 230	40 217	36 805	18 926	12 144
TP	25 530	2915	1322	18	64	29	85
TN	862	47	62	741	848	1673	1473
NO_2+NO_3	N.D.	N.D.	N.D.	2	39	2	10
Na^+	37 048	4898	2857	9520	8205	3726	2491
Ca^{2+}	0.6	4.0	2.8	457	679	806	146
K^+	607	128	79	7	25	4	7
Mg^{2+}	46	95	58	36	236	48	64
Fe^{2+}	2.0	0.2	1.2	0.13	0.15	0.06	0.15
Mn^{3+}	0.10	0.02	0.03	0.04	0.06	0.04	0.10
Cl^-	856	280	171	16 765	13 485	5672	3832
$SO4^{2-}$	3 387	7 544	3 590	1209	1412	2219	340
$CaCO_3$	45 232	3264	3778	59	106	54	137
HCO_3^-	9377	2666	3024	72	129	66	167
CO_3^{2-}	22 508	646	778	0	0	0	0
pH	10.2	9.6	9.3	8.4	8.8	8.2	8.3
DOC	290	72	75	14	17	29	20
Turbidity	3.0	10.0	27.0	1.4	3.4	3.3	2.0
Colour	67	35	97	11	68	17	34
Chl *a*	2.0	4.9	2.7	3.2	12.8	6.0	2.6
Secchi Depth	0.6	0.55	0.30	B	B	B	B
Subsaline Lakes	GL-D	GW-D	BP-D	FP-D	WR-D		
TDS	1090	982	608	840	556		
Conductivity	1267	1805	862	1222	824		
TP	15	65	39	124	32		
TN	620	1150	1047	1520	908		
NO_2+NO_3	47	38	26	33	19		
Na^+	31	225	68	127	74		
Ca^{2+}	193	77	50	71	39		
K^+	3.0	8.0	4.9	3.6	6.0		
Mg^{2+}	47	43	42	39	32		
Fe^{2+}	0.003	0.3	0.02	0.4	0.1		
Mn^{3+}	0.007	0.2	0.007	0.05	0.005		
Cl^-	29	465	133	247	178		
$SO4^{2-}$	649	16	90	45	0.6		
CaCO3	83	130	170	203	134		
$HCO3^-$	101	157	1047	239	161		
$CO3^{2-}$	0	0.7	3.3	4.0	0.8		
pH	8	7.8	8.6	7.9	7.8		
DOC	10	27	24	39	22		
Turbidity	0.7	2.2	0.9	6.6	3.2		
Colour	10	94	78	206	92		
Chl *a*	4.0	4.1	6.9	25.3	3.6		
Secchi Depth	3.5	1.7	1.4	0.7	1.2		

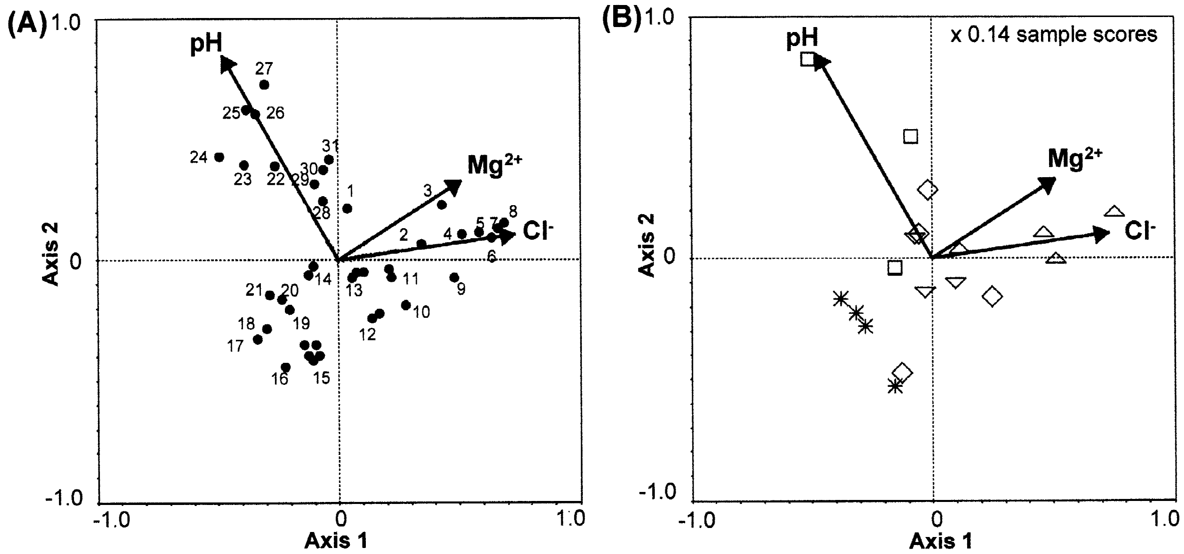


Figure 2. Ordination biplots of (A) species and environmental variables, and (B) sites and environmental variables from partial RDA of rotifer species in the subsaline study lakes. In (A), species ordination positions are represented by numbers: *Testudinella patina*, 2. *Colurella obtusa*, 3. *Lecane luna*, 4. *Monostyla quadridentus*, 5. *Notommata* sp., 6. *Notholca acuminata*, 7. *Keratella quadrata* and *Trichotria tetractis*. *Lepadella patella*, 9. *Lophocharis salpina*, 10. *Anuraeopsis fissa*, 11. *Asplanchna brightwelli* and *Ascomorpha ecaudis*, 12. *M. closterocerca* and *M. lunaris*, *Asplanchna priodonta*, *Collotheca pelagica*, *Encentrum* sp., *K. valga*, *K. hiemalis*, and *Trichocerca multicrinis*, 14. *K. ticinensis* and *Trichotria pocillum*, 15. *Brachionus plicatilis*, *Filinia longiseta*, *Hexarthra* sp., 16. *K. testudo* and *Pompholyx* sp., 17. *Lepadella acuminata*, 18. *K. cochlearis*, 19. *Gastropus stylifer*, *Trichocerca lophoessa*, 20. *Vanoyella globosa*, 21. *T. rattus*, 22. *Ascomorpha ovalis*, 23. *Mytilina ventralis* var. *brevispina*, 24. *Platyias platyias*, 25. *Polyarthra vulgaris*, 26. *Lecane ohioensis*, 27. *B. quadridentatus*, 28. *Synchaeta* sp., 29. *Polyarthra dolichoptera*, 30. *K. serrulata*, 31. *Colurella uncinata*, *T. longiseta*, 32. *Monostyla bulla.* In (B), the symbols represent samples from each of the lakes: squares = BP-D, diamonds = FP-D, upward triangles = GW-D, upside-down triangles = GL-D, and stars = WR-D.

Species-environment relations

Subsaline lakes

Environmental gradients between subsaline lakes were less extreme than between saline lakes, and consequently, species-environment relationships were less clearly defined for rotifers and crustaceans than in the saline lakes. The minimum set of environmental variables that described the greatest variation in rotifer species distribution in the subsaline lakes was determined by forward-selected redundancy analysis (RDA), and included Cl^-, Mg^{2+}, and pH. Na^+ was also identified as a significant variable but was positively correlated with Cl^- ($r = 0.99$), and therefore was not included in the analysis. Axis one ($\lambda_1 = 0.25$) and axis two ($\lambda_2 = 0.11$) explained 26% and 12%, respectively, of the variation in species data. Axis one was most strongly influenced by Cl^- (inter-set correlation = 0.74) and Mg^{2+} (inter-set correlation = 0.51), and axis two was determined primarily by pH (inter-set correlation = 0.84) (Fig. 2).

Rotifer species that ordinated to the right of the origin (0, 0) along the Cl^- and Mg^{2+} vectors were strongly correlated with these elements (Table 4 for species densities; Fig. 2). Species such as *Colurella obtusa*, *Monostyla quadridentus*, *Notommata* sp., *Notholca acuminata*, *Keratella quadrata*, *Trichotria tetractis* and *Lepadella patella* were strongly associated with Cl^-. *Lecane luna* was the only species that was closely affiliated with elevated Mg^{2+} concentrations, but pH influenced many species. Rotifers such as *Lecane ohioensis*, *Brachionus quadridentatus*, *Synchaeta* sp., *Mytilina ventralis* var. *brevispina*, *Polyarthra vulgaris* were most strongly correlated with elevated pH, and reached peak densities at a pH of 9.2 in BP-D. Although trends were detected for rotifers, ordination axes did not explain any variation in crustacean species distribution in the subsaline lakes.

Salt lakes with chloride-dominated water

Environmental variables that described variation in species data among lakes containing water dominated by Cl^- anions were determined by forward-selected RDA and included: Cl^-, Na^+, conductivity, and TDS. Since the latter three variables were strongly correlated with Cl^- ($r = 0.94$, 0.92, and 0.91, respectively), they were excluded from the analysis. Only axis 1 was

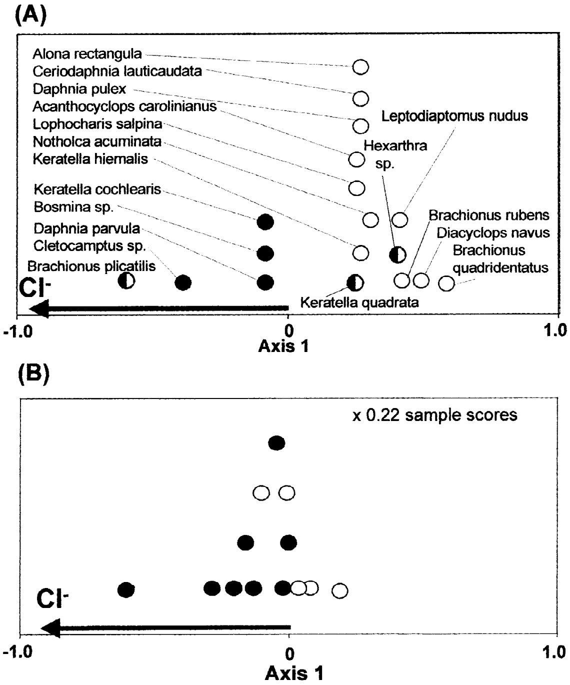


Figure 3. Ordination biplots of (A) species and environmental variables, and (B) sites and environmental variables from partial RDA of rotifer and crustacean zooplankton species within the saline lakes with Cl^--dominated water. In (B), the filled symbols represent samples from the mesosaline lakes and empty symbols represent the hyposaline lakes. In (A), filled symbols indicate species found only in the mesosaline lakes, empty symbols are species found only in the hyposaline lakes, and black-and-white symbols are species that appeared in both mesosaline and hyposaline study lakes.

significant for the RDA (λ_1 = 0.28, 29% of variance explained in species data). Cl^- was the sole environmental influence in the analysis and had an inter-set correlation of −0.70 to axis one (Fig. 3).

Species found to the left of the origin were more strongly correlated with Cl^- than species located to the right of the origin (Tables 4 and 5 for species densities; Fig. 3A). The halophilic rotifer *Brachionus plicatilis* occurred across the entire range of conductivity measured for saline lake water dominated by Cl^- (10–52 mS/cm), but was most abundant in mesosaline waters. The harpacticoid copepod *Cletocamptus* sp. was found in some samples of only the mesosaline lakes (HC-Cl and GB-Cl) at amounts ranging from to 5 to 16 g l^{-1} Cl^-. *Daphnia parvula*, *Keratella cochlearis* and *Bosmina* sp. were present in low densities (25 individuals/ml) on one occasion in mesosaline HC-Cl. In contrast, species found to the right of the origin were most abundant in the hyposaline NaCl lakes (SP-Cl and SL-Cl). Many of these species were found in SL-Cl, the least saline of the salt lakes (Table 4). The highest density of any one species was *Hexarthra* sp. (752 individuals/l), which occurred in the August sample of hyposaline SP-Cl (6 g l^{-1} Cl^-). Mesosaline (10–21 g l^{-1} Cl^-) and hyposaline (3–6 g l^{-1} Cl^-) lake samples are shown in Figure 3B. Although contrasts in zooplankton communities did occur at different salt concentrations, the most abundant taxa were present across the salinity range studied.

Salt lakes with chloride- versus *sulphate/carbonate-dominated water*

The set of environmental variables that described the greatest variation in the species data from our study was determined by forward-selected canonical correspondence analysis (CCA). This set was comprised of total alkalinity (HCO_3 +CO_3), $SO_4{}^{2-}$, Cl^-, Ca^{2+}, surface area, Na^+, K^+, conductivity, and TP. Within the set of variables identified by forward selection, strong correlations ($P > 0.001$) that raised variance inflation factors >20 occurred between Cl^- and Na^+ (r = 0.97), Cl^- and conductivity (r = 0.97), total alkalinity and K^+ (r = 0.91), and between total alkalinity and TP (r = 0.93). Consequently, Na^+, conductivity, K^+ and TP were removed from the analysis to minimize the number of environmental factors tested. CCA with the minimum set of five variables yielded two significant axes (λ_1 = 0.97 and λ_2 = 0.62) (Fig. 4). Axis one was most strongly influenced by total alkalinity (inter-set correlation = 0.99), $SO_4{}^{2-}$ (inter-set correlation = 0.79), and surface area (inter-set correlation = 0.66). This axis explained 35% of the species variance. Axis two was most strongly defined by Cl^- (inter-set correlation = 0.79) along with Ca^{2+} (inter-set correlation = -0.57), and explained 22% of species variance.

Contrasting trends were observed in the water chemistry of OL-CO_3 in 1983/84 and 1999. OL-SO_3 samples from 1983/84 ordinated beside the $SO_4{}^{2-}$ vector when included in the CCA, and reflected the high concentrations of $SO_4{}^{2-}$ anions (29 g l^{-1}) that year (Table 3). In June 1999, however, $CO_3{}^{2-}$ was the dominant anion and Cl^- concentrations were elevated (Table 2). OL-CO_3 was the only lake studied that contained water with hypersaline concentrations of salt, and differences among the other less saline lakes were difficult to discern when samples from OL-CO_3 were active in defining ordination axes. Consequently, OL-CO_3 was excluded from the CCA. *Artemia franciscana* was the predominant crustacean and rotifers were rare in hypersaline OL-CO_3 (Tables 4 and 5).

Table 3. Salinity categories (total dissolved solids (TDS), Hammer 1986a), and summer measurements of conductivity (μS/cm), total phosphorus (μg l^{-1}), ions (mg l^{-1}), total alkalinity (mg l^{-1}), pH, and chlorophyll *a* (μg l^{-1}) for the saline study lakes located in central Alberta. Values are averaged for June, July and August from 1983 to 1992 for PN-SO_4 and FL-SO_4 (Evans & Prepas, 1996) and from 1983 to 1984 for OL-SO_4 (Bierhuizen & Prepas, 1985)

Salinity Category	OL-CO_3 Hypersaline $>$50 g l^{-1} TDS	PN-SO_4 Hyposaline 3 to 20 g l^{-1} TDS	FL-SO_4 Hyposaline 3 to 20 g l^{-1} TDS
Conductivity	53 532	14 547	11 196
Total Phosphorus	14 232	3410	2116
Na^+	23 241	3601	2783
Ca^{2+}	433	113	74
K^+	19	14	14
Mg^{2+}	108	96	55
Cl^-	521	181	155
$SO_4{}^{2-}$	29 422	4693	2905
Total Alkalinity	24 329	2815	2944
pH	9.9	9.3	9.3
Chlorophyll *a*	5.0	6.7	3.9

The CCA ordination diagram of taxa positions in Cl^--dominated and $SO_4{}^{2-}/CO_3{}^{2-}$-dominated saline lake water, excluding OL-CO_3, indicates striking differences in zooplankton communities between these two lake types (Fig. 4A). *Leptodiaptomus sicilis* and *Diaptomus nevadensis* ordinated along the first axis and were strongly associated with alkaline conditions (2.8–3.0 g l^{-1} $HCO_3{}^-+CO_3{}^{2-}$) and high concentrations of $SO_4{}^{2-}$ (2.5–7.5 g l^{-1}). *Daphnia similis* showed similar trends as *L. sicilis* and *D. nevadensis* in 1984. *Brachionus urceolaris* was an outlier that was treated as a supplementary species and therefore, did not influence the definition of the ordination axes. *B. urceolaris* was found only in June, 1999 in PN-SO_4 and FL-SO_4, and the plotting of its position in the ordination diagram after the analysis indicated an affiliation with high concentrations of $SO_4{}^{2-}$ (3.4–7.5 g l^{-1}).

Cl^- and Ca^{2+} accounted for variation in species distribution in the second axis (Fig. 4A). Harpacticoid copepod *Cletocamptus* sp. and rotifer *Brachionus plicatilis* ordinated beside the Cl^- vector and were strongly associated with sodium chloride (NaCl) salts. Also located along the second axis was *Hexarthra* sp., which was found in lakes with elevated concentrations of Cl^- (0.5–20 g l^{-1}) and Ca^{2+}(0.01–1 g l^{-1}) (Table 4). *Lophocharis salpina* was a rare species that appeared once in hyposaline SP-Cl, and *Daphnia parvula* and *Brachionus quadridentatus* were present in low numbers in some of the Cl^-- and Ca^{2+}-rich waters. Although *Keratella quadrata* did appear in both the $SO_4{}^{2-}/CO_3{}^{2-}$- and Cl^--dominated lakes, it was more abundant in lake water dominated by Cl^- (Table 4). The number of species that could be included in the CCA was restricted by the number of study lakes and the frequency of sampling ($n = 25$ samples), as well as by the number of environmental variables tested (5) (ter Braak & Šmilauer, 1998). Species that were positively correlated with *Daphnia parvula*, *K. quadrata*, and *Brachionus quadridentatus* that appeared in low densities in Cl^--dominated saline lake water were not included in the analysis and are listed in Table 6. These less abundant species would have ordinated near their correlated counterparts in the CCA had they been included in the analysis and would not have changed the outcome of the ordination plots.

Discussion

Water chemistry

Large differences in $SO_4{}^{2-}$ concentrations (0.6–649 mg l^{-1}) observed among subsaline lakes were likely related to gypsum ($CaSO_4{\cdot}H_20$) in the bedrock underlying the lakes (Moser et al., 1998). GL-D was unique from all other study lakes because it was the

Table 4. Peak density observed for rotifer species (# individuals/l lake water) in each category of lakewater salinity over the summer of 1999. Dominant anions for each lake category are indicated in brackets

Species	Hyper-Saline CO_3	Hypo-Saline SO_4	Meso-Saline Cl	Hypo-Saline Cl	Sub-Saline SO_4 or Cl
Ascomorpha ecaudis	0	0	0	0	89
Ascomorpha ovalis	0	0	0	0	113
Anuraeopsis fissa	0	0	0	0	26
Asplanchna brightwelli	0	0	0	0	15
Asplanchna priodonta	0	0	0	0	428
Brachionus plicatilis	0	0	869	202	2712*
Brachionus quadridentatus	0	0	0	1	18
Brachionus rubens	0	0	0	0.4	0
Brachionus urceolaris	0	26	0	0	0
Collotheca mutabilis	0	0	0	0	171
Collotheca pelagica	0	0	0	0	2
Colurella obtusa	0	0	0	0	6
Colurella uncinata	0	0	0	0	7
Encentrum sp.	0	0	0	0	1
Filinia longiseta	0	0	0	0	2383
Gastropus stylifer	0	0	0	0	113
Hexarthra sp.	2	0	0.2	752	3
Keratella cochlearis	0	0.3	0	0	1441
Keratella hiemalis	0	0	0	1	122
Keratella quadrata	0	0.1	3	19	6733
Keratella serrulata	0	0	0	0	29
Keratella testudo	0	0.1	0	0	3372
Keratella ticinensis	0	0	0	0	1
Keratella valga	0	0	0	0	1
Lecane luna	0	0	0	0	13
Lecane ohioensis	0	0	0	0	6
Lepadella acuminata	0	0	0	0	9
Lepadella patella	0	0	0	0	13
Lophocharis salpina	0	0	0	2	3
Monostyla bulla	0	0	0	0	239
Monostyla closterocerca	0	0	0	0	13
Monostyla lunaris	0	0	0	0	13
Monostyla quadridentus	0	0	0	0	6
Mytilina ventralis var *brevispina*	0	0	0	0	53
Notholca acuminata	0	0	0	5	26
Notommata sp.	0	0	0	0	51
Platyias patulus	0	0	0	0	29
Polyarthra dolichoptera	0	0	0	0	13
Polyarthra vulgaris	0	0.4	0	0	3130
Pompholyx sp.	0	0	0	0	733
Synchaeta sp.	0	0	0	0	3975
Testudinella patina	0	0	0	0	12
Trichocerca longiseta	0	0	0	0	8
Trichocerca lophoessa	0	0	0	0	3
Trichocerca multicrinis	0	0	0	0	167
Trichocerca rattus	0	0	0	0	5
Trichotria pocillum	0	0	0	0	9
Trichotria tetractis	0	0	0	0	6
Vanoyella globosa	0	0	0	0	3

Table 5. Peak density observed for crustacean species (# individuals/l lake water) in each category of lake-water salinity over the summer of 1999. Dominant anions for each lake category are indicated in brackets

Species	Hyper-Saline CO_3	Hypo-Saline SO_4	Meso-Saline Cl	Hypo-Saline Cl	Sub-Saline Cl or SO_4
Anostracans					
Artemia franciscana	30	0	0	0	0
Calanoid Copepods					
Agalodiaptomus leptopus	0	0	0	0	68
Diaptomus arcticus	0	0	0	0	13
Diaptomus nevadensis	0	0.4	0	0	0
Leptodiaptomus nudus	0	0	0	18	0
Leptodiaptomus sicilis	0	6	0	0	0.2
Cyclopoid Copepods					
Acanthocyclops carolinianus	0	0	0	0.8	0
Acanthocyclops robustus	0	0	0	0	15
Acanthocyclops venustoide	0	0	0	0	97
Acanthocyclops vernalis	0	0	0	0	5
Diacyclops navus	0	0	0	0.5	3
Harpacticoid Copepods					
Cletocamptus sp.	0	0	61	0.8	0
Cladocerans					
Alona circumfimbriata	0	0	0	0	6
Alona costata	0	0	0	0	3
Alona guttata	0	0	0	0	5
Alona rectangula	0	0	0	0.2	2
Bosmina sp.	0	0	0	0	28
Ceriodaphnia laticaudata	0	0	0	0	76
Ceriodaphnia pulchella	0	0	0	4	0
Chydorus brevilabris	0	0	0	0	96
Chydorus piger	0	0	0	0	19
Chydorus sphaericus	0	0	0	0	19
Daphnia parvula	0	0	0	0	38
Daphnia pulicaria/pulex	0	0	0	6	262
Daphnia rosea	0	0	0	0	29
Daphnia schoedleri	0	0	0	0	32
Polyphemus pediculus	0	0	0	0	6

deepest and the only oligotrophic lake studied, as well as being the only subsaline lake that was dominated by $SO_4{}^{2-}$ anions. Although phosphorus released from lake sediments can be greater at higher $SO_4{}^{2-}$ concentrations (Caraco et al., 1989), TP concentrations were low (15 μg l^{-1}). In this lake, phosphorus was likely precipitated as calcium phosphate ($CaPO_4$) (Wetzel, 1983) since Ca^{2+} is in abundance in the limestone bedrock. FP-D also differed from other study lakes because it shared chemical characteristics with both the subsaline and the Cl^--dominated saline lake water. Although FP-D had surface waters that remained subsaline for most of the sampling period, the water column of this lake was inversely stratified by the end of the summer when the bottom stratum was saline. The dilute salts present in the subsaline study lakes contrasted with the concentrated conditions found in the saline lakes.

The Cl^--dominated saline study lakes in northern Alberta are not representative of lake water in this predominantly freshwater boreal region (Pienitz et al., 1997; Moser et al., 1998; Rühland & Smol, 1998).

Table 6. List of zooplankton species present in saline lakes containing Cl^--dominated waters that were positively correlated with *Brachionus quadridentatus*, *Keratella quadrata*, and *Daphnia parvula*. Species listed below were not included in the CCA of all saline study lakes because of the restricted number of species that could be included in the analysis. Species densities are given in Tables 4 and 5

Zooplankton Species in CCA	Correlated Zooplankton Taxa	*r*
Brachionus quadridentatus	*Brachionus rubens*	0.60
	Keratella hiemalis	0.50
	Notholca acuminata	0.55
	Leptodiaptomus nudus	0.80
	Acanthocyclops carolinianus	0.55
	Diacyclops navus	0.80
	Daphnia pulicaria/pulex	0.50
Keratella quadrata	*Keratella hiemalis*	0.43
	Keratella testudo	0.44
	Notholca acuminata	0.42
	Polyarthra vulgaris	0.44
	Daphnia pulicaria/pulex	0.43
Daphnia parvula	*Bosmina* sp.	1.0

The salinity of the study lakes in northern Alberta is a result of groundwater discharging high concentrations of NaCl salt (Camsell, 1917). Other isolated examples of saline lakes derived from NaCl springs are found in the Saskatchewan River delta (Hammer, 1993) and on the interior plateau of British Columbia (e.g., Bos et al., 1996). The chloride-dominated waters that we studied had relatively low total alkalinities ($<$305 mg l^{-1}), and the reduced ratio of sulphate to chloride at higher salinities may have been a result of $CaSO_4 \cdot H_20$ precipitation (Evans & Prepas, 1996). However, SO_4^{2-} was elevated in SP-Cl relative to the other lakes with Cl^--dominated water and this may be related to spatial variation in the amount of gypsum in bedrock underlying the lakes. Similar to GL-D, the relatively low TP concentrations in all of the saline lakes with Cl^--dominated water (18–85 μg l^{-1}) likely resulted from precipitation of phosphorus as $CaPO_4$ (Wetzel, 1983). Although TN was high in these lakes (741–1673 μg l^{-1}), amounts of biologically available NO_2^- and NO_3^- were low (2–39 μg l^{-1}); nitrogen deficiencies are reportedly common among freshwater lakes in the Park (Moser et al., 1998). However, nitrogen fixation in benthic algal mats, such as those found in GB-Cl and SP-Cl, may contribute to TN in saline lakes (e.g., Jellison et al., 1993). The presence of halite deposits in combination with local and regional groundwater flow regimes were likely dominant forces in determining NaCl salinity of surface water (Camsell, 1917; Toth, 1999).

In contrast to Cl^--dominated saline lake water that is infrequently encountered in Canada, the three study lakes sampled in central Alberta are similar to many of the saline lakes on the northern Great Plains of North America (e.g. Bierhuizen & Prepas, 1985; Last, 1992; Blinn, 1993). The high concentrations of SO_4^{2-} and HCO_3^-/CO_3^{2-} in these lakes ($>$3 g l^{-1}) have been attributed to weathering of Cretaceous black shale bedrock in combination with evaporative processes (e.g., Blinn, 1993). Many saline lakes in central Alberta have concentrations $>$1 mg l^{-1} TP as a result of evaporative concentration (Campbell & Prepas, 1986) and phosphorus release from bottom sediments at high SO_4^{2-}concentrations (Caraco et al., 1989). Unlike the SO_4^{2-}/CO_3^{2-}-dominated lake water that we studied, low phosphorus availability has been reported for Saskatchewan lakes and appears to be influenced by the interaction of high DOC, pH and ionic composition (Waiser & Robarts, 1995). Climate, topographic position within the drainage system, and groundwater flow regimes govern salt concentration and ionic composition of lake water on the northern Great Plains (Last, 1992).

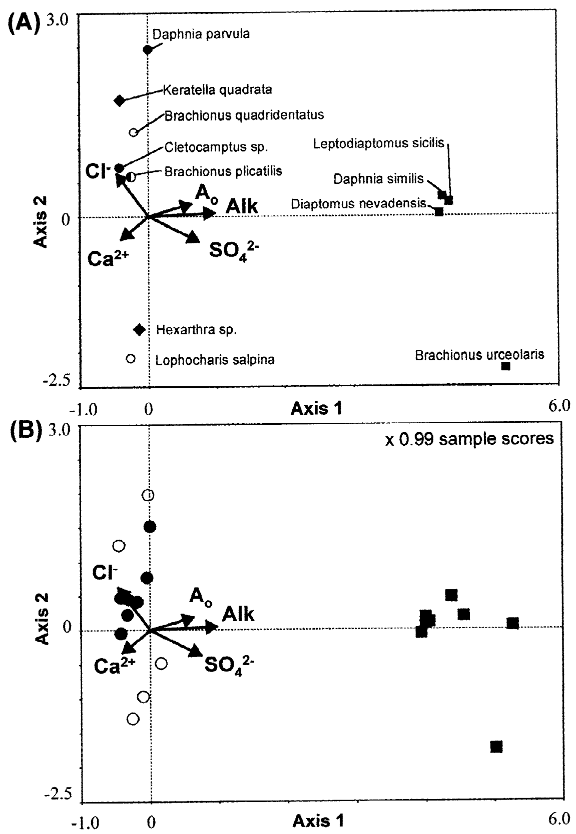


Figure 4. Ordination biplots of (A) species and environmental variables, and (B) sites and environmental variables from partial CCA of rotifer and crustacean zooplankton found in Cl^--dominated (circles) and $SO_4{}^{2-}/CO_3{}^{2-}$-domina ted (squares) saline lake water. Of the Cl^--dominated waters in (A), species found at hyposaline concentrations are represented by empty symbols, species found at mesosaline concentrations are solid circles, and species found at both meso- and hyposaline concentrations are black-and-white circles. Species found only in the $SO_4{}^{2-}/CO_3{}^{2-}$-domina ted lake water are indicated by solid squares in (A). Zooplankton species that appeared in both lakewater ion types are indicated by solid diamonds. Abbreviations: A_O= surface area and Alk = total alkalinity ($HCO_3{}^- + CO_3{}^{2-}$).

Species-environment relations

Among the subsaline and saline NaCl lakes, we discerned distinct patterns in zooplankton community composition along a gradient of salt concentration stress. Most of these lakes were characterized by the presence of nine-spined stickleback fish and corixid predators, and had similar nutrient concentrations (mesotrophic). Almost all rotifer and crustacean species were most abundant in the more dilute subsaline lakes. Rotifer species *Lophocharis salpina*, *Keratella quadrata*, and *Notholca acuminata* demonstrated tolerance to low to intermediate concentrations of Cl^- (133–5672 mg l^{-1} Cl^-). These species were associated with Cl^- in the ordination biplot for the subsaline lakes and also appeared in low densities in the hyposaline Cl^--dominated waters. In contrast to ordination of the NaCl saline lakes, the rotifer genus *Hexarthra* was not associated with the Cl^- vector in the biplot for the subsaline lakes and was likely a different species from what was observed in the saline lakes. The hypo- and meso-saline NaCl lake water of northern Alberta were characterized by an abundance of *Brachionus plicatilis*, and species of *Hexarthra* and *Cletocamptus* that were most likely *H. fennica* (Levander) and *C. albuquerquensis* (Herrick) (Hammer, 1993). The halophile rotifer *Brachionus plicatilis* demonstrated a broad salinity tolerance of intermediate to high concentrations of NaCl (840–26 318 mg l^{-1} TDS). It should be noted that the abundance of *B. plicatilis* in FP-D shown in Table 4 reflects the low precipitation conditions during the spring of 1999 when the entire water column was hyposaline. The persistence of this species in otherwise subsaline FP-D likely reflects the presence of hyposaline water near the bottom of this chemically stratified lake. Although *B. plicatilis* is a species complex consisting of sibling species with different salinity tolerances, Derry et al. (2003) demonstrated that the *B. plicatilis* specimens collected across the salinity gradient of NaCl lakes in northern Alberta were the same species with a broad tolerance to NaCl salt concentration.

Contrasting zooplankton communities in hyposaline lakes were distinct among Ca^{2+}-rich waters dominated by Cl^- anions and alkaline, hypereutrophic $SO_4{}^{2-}/CO_3{}^{2-}$-dominated waters. The most abundant zooplankton in the hyposaline study lakes with $SO_4{}^{2-}/CO_3{}^{2-}$-dominated water consisted of the calanoid copepods *Leptodiaptomus sicilis* and *Diaptomus nevadensis,* and the cladoceran *Daphnia similis*. These large crustacean zooplankton have also been reported in other $SO_4{}^{2-}$-dominated saline waters in North America (e.g. Hammer, 1993; Evans et al., 1995; Leland & Berkas, 1998). Bos et al. (1996) reported that among 111 lakes dominated by $SO_4{}^{2-}$ and $CO_3{}^{2-}/HCO_3{}^{2-}$ in the interior of British Columbia, halophilic calanoid copepods were also associated with lower Mg^{2+} and Ca^{2+} concentrations in lake water. The only rotifer species noted in high abundance in the $SO_4{}^{2-}/CO_3{}^{2-}$ saline lakes in this study was *Brachionus urceolaris*, which has also been recorded in hyposaline $SO_4{}^{2-}$-dominated waters of Devils Lake, North Dakota (Leland & Berkas, 1998). There is no record of *L. sicilis*, *D. nevadensis*, and *D. similis* in Cl^--dominated waters in North America (e.g., Wurtsbaugh & Berry, 1990). Hammer (1993) indicated that *L. sicilis*, *D. nevadensis*, and *D. similis* belonged to entirely different lake categories from *B. plicatilis* and *A. franciscana* based on salinity gradient, pH, Secchi depth, and mean depth. However, Hammer (1993) sampled across lakes with variable ion composition and the role of different ions on zooplankton communities was unclear. Further, differences in predation regimes among lakes were not addressed.

The substantial differences in zooplankton communities observed among lakes with contrasting ion composition are confounded by covariation in nutrient concentration and predation pressure, as well as by the small sample size ($n = 4$ hyposaline lakes). Further, lake surface area, mean depth, and the presence of associated streams were variable among the study lakes and likely affected the composition of zooplankton species. Deeper, larger lakes tend to be characterized by greater zooplankton species richness and abundance than smaller, shallower lakes were there is higher predation pressure by fish and invertebrates (Keller & Conlin, 1994). With the exception of deepest GL-D, the saline lakes with SO_4^{2-}/CO_3^{2-}-dominated water had the largest surface areas and the deepest mean depths (Table 1), but an absence of inflowing or outflowing streams likely restricted opportunities for fish to enter these lakes (Campbell & Prepas, 1986). In contrast, the saline lakes containing Cl^--dominated water were smaller and shallower (Table 1), but had surface connections to other rivers and lakes. Nine-spined stickleback fish were abundant in these shallow but well connected systems. Predation of zooplankton by both nine-spined stickleback (Nelson & Paetz, 1992) and corixids (Tones & Hammer, 1975) was likely strong in the saline lakes containing Cl^--dominated water compared to the lakes with isolated basins containing water dominated by SO_4^{2-}/CO_3^{2-}.

An alternative explanation to restricted hydrographic connections for contrasting zooplankton communities among these saline lakes are gradients of salinity stress, specific ion tolerance, and environmental stability. Herbst (2001) argued that physiological adaptation to extreme physico-chemical conditions provided an avenue of escape from intense predation and competition in more diverse communities of moderate environments. Our findings support Herbst's (2001) model of how physiology of ion tolerance interacts with zooplankton distribution and biography. In our study, large crustacean zooplankton occurred only in lakes with SO_4^{2-}/CO_3^{-}-dominated water, which also lacked fish predators. Large calanoid copepods and cladocerans were absent from the lakes with Cl^--dominated waters that had high densities of predatory corixids and nine-spined stickleback fish. Salt concentration in hypersaline OL-CO_3 and solute composition in the SO_4^{2-}dominated saline lakes, in combination with restricted hydrographic connections, likely acted as a barrier for planktonic predators. Wurtsbaugh & Berry (1990) presented an example of how reduced salinity (50 g l^{-1} compared to 250 g l^{-1} TDS in the mixolimnion) of hypersaline NaCl-dominated Great Salt Lake allowed the penetration of the predatory corixid, *Trichocorixa verticalis*, that depleted *Artemia franciscana* populations from 1985 to 1987. Similar to the lakes with Cl^--dominated water from our study, *B. plicatilis* was the most abundant zooplankter under mesosaline conditions in Great Salt Lake during that time. SO_4^{2-}-dominated waters have been found to be more stressful for osmoregulation in fish larvae than Cl^--dominated waters (Koel & Peterka, 1995), and these differences in ion strength may also reflect variation in selective pressure on zooplankton that inhabit salt lakes.

In conclusion, large crustacean zooplankton such as *Artemia franciscana* may have adapted to osmoregulate in hypersaline waters and species such as *Leptodiaptomus sicilis*, *Diaptomus nevadensis,* and *Daphnia similis* may have evolved tolerance to SO_4^{2-}-dominated salinity to escape predation pressure present in less extreme environments. Selective physiological tests of ion tolerance in different species would provide useful ecological insight to biogeographic patterns of habitat utilization in zooplankton.

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