

A Whole-Lake Experiment to Determine the Effects of Winter Droughts on Shallow Lakes

Suzanne McGowan,¹ Peter R. Leavitt, and Roland I. Hall²

¹Department of Biology, University of Regina, Regina, Saskatchewan S4S 0A2, Canada

ABSTRACT

Lake-level fluctuations are common in the North American Great Plains region, where large-scale climate systems (El Niño, the Pacific Decadal Oscillation) and periodic droughts cause substantial hydrologic variability in both summer and winter. To date, most such research has focused on the effects of summer droughts on prairie lake ecosystems; therefore, we studied the impact of water-level decline during winter on ecosystem structure and function. Specifically, we hypothesized that lower lake levels during winter would increase anoxia, freezing and scouring of benthos, fish kills, herbivory by zooplankton, and nutrient release from sediments. In addition, we tested the hypothesis that winter droughts may initiate a switch between alternative stable states (turbid, clear). Physical, chemical, and biological variables were monitored from 1996 to 2001 in both Wascana Lake, which experienced a 50% decline in lake level, and Buffalo Pound Lake, where water levels were constant. A combination of before-after-control-impact (BACI) and multivariate analyses showed that drawdown resulted in elevated NH₄-N concentrations following reinunda-

tion; otherwise there were few detectable effects on lake water chemistry (PO₄-P, NO₃-N, total dissolved nitrogen, total dissolved carbon) or pelagic food web structure (phytoplankton, zooplankton), and the experimental lake remained in a macrophyte-rich state. There was, however, a 2.5-fold increase in macrophyte abundance and a shift from a community dominated by *Ceratophyllum demersum* before drawdown to one composed of *Potamogeton pectinatus* after manipulation. Overall, the lack of substantial dewatering effects suggests that lakes of the northern Great Plains may be resilient to severe winter conditions, possibly because of the recruitment of fish from regional metapopulations during summer. Further, our results indicate that lower water levels during winter likely promote the buffer mechanisms that reinforce a macrophyte-rich, clear-water state in shallow prairie lakes.

Key words: alternative stable states; Before-after-control impact (BACI) analysis; droughts; lake drawdown; macrophytes; phytoplankton pigments; prairie lakes; shallow lakes; whole-ecosystem experiment; zooplankton.

INTRODUCTION

Lakes of the northern Great Plains have been subject to extreme changes in surface and groundwater

hydrology for at least 2,000 years (Laird and others 2003). The effects of hydrologic variability on ecosystem structure are dependent on the magnitude, frequency, and seasonality of lake-level fluctuation. In shallow prairie lakes, evapotranspiration during summer can cause some small wetlands to dehydrate completely (Winter and Rosenberry 1998). Depending on the precise changes in sediment chemistry, structure, and organic matter sources (for example, macrophytes) (Watts 2000),

Received 15 October 2003; accepted 10 May 2004; published online 9 September 2005.

Present address: ¹School of Geography, University of Nottingham, Nottingham NG7 ZRD, UK.

²Department of Biology, University of Waterloo, Waterloo, Ontario N2L 3GL, Canada.

*Corresponding author; e-mail: suzanne.mcgowan@nottingham.ac.uk

water-level recessions can favor the oxidation and mineralization of organic phosphates (De Groot and Van Wijck 1993), thereby increasing the release of sedimentary phosphorus (P) on reflooding (James and others 2001). Similarly, sediment desiccation can alter nitrogen (N) cycling by increasing aerobic nitrification and nitrate buildup in sediments (Kadlec 1962) or by mineralizing sedimentary organic-N and intensifying denitrification in underlying anoxic sediments (De Groot and Van Wijck 1993). Further, sediment density may increase due to exposure (James and others 2001), and suspended material precipitated during re- inundation (McLachlan 1974) may modify aquatic plant (Gafny and Gasith 1999) and benthic invertebrate (Verschuren and others 2000) communities in littoral habitats. The diversity and abundance of emergent macrophytes and zoobenthos may also be reduced by complete exposure of the sediment (Kadlec 1962) or by frequent, large water-level fluctuations (Hunt and Jones 1972), although submerged aquatic macrophyte biomass may benefit from declines in lake depth (Coops and Hopper 2002).

Little is known of the whole-ecosystem effects of lake-level decline during winter. In general, variation in snow pack depth regulates ice thickness and lake insulation in the northern Great Plains (Fang and others 1999). Thus, because strong ElNiño–Southern Oscillation events reduce winter precipitation in this region (Shabbar and others 1997), and because global warming is expressed mainly in winter (IPCC 2001), prairie lakes may be particularly susceptible to changes in winter hydrology and lake level. For example, lower lake levels during the winter should expose littoral sediments to temperatures below -20°C , increase the extent of ice scouring, and reduce the unfrozen volume, possibly leading to anoxia under the ice (Fang and others 1999; Meding and Jackson 2001) and fish kills (Gaboury and Patalas 1984). These physical and chemical changes are likely to modify sediment–water interactions and cause changes in nutrient release during the following spring, but few studies have tested this hypothesis. Further, because the freezing of sediments will cause the death of invertebrates and some macrophytes, changes in these communities should be evident in the growth season following lake-level decline, both because of selection for taxa with better overwintering strategies and because of increased reliance on upstream recolonization (Paterson and Fernando 1969; Cooke and others 1986). Finally, because previous research and theory suggests that lake-level fluctuation can

initiate switches between clear, macrophyte-rich and turbid, algal-dominated states (Blindow and others 1993; Scheffer and others 1993), and because many of the stabilizing mechanisms are impacted by dewatering (see above), we hypothesized that changes in winter lake level would be an important control of the structure and function of shallow lakes.

Our aims were to use lake-level drawdown to intervention mimic the effects of winter droughts on shallow prairie lakes and to assess the impacts of dewatering on ecosystem function during the following growth season. We used a (before-after-control-impact BACI) design (Stewart-Oaten and Murdoch 1986) to compare experimental and reference lakes before, during, and after the experimental drawdown. We hypothesized that declines in winter lake level would (a) increase nutrient release by modifying chemical (mineralization and mobilization) and physical (freezing and scouring) processes in the sediment, (b) reduce zooplanktivory through increased fish mortality, and (c) select for freeze-tolerant taxa with effective overwintering strategies. Further, we hypothesized that such changes in lake ecosystem structure would favor clear waters, abundant macrophytes, and low algal biomass and therefore reinforce the buffers of the macrophyte-dominated state (Scheffer and others 1993).

METHODS

Study Sites

The study lakes are located in the subhumid region of the northern Great Plains in Saskatchewan (Figure 1), where annual mean precipitation is 320 mm, annual evaporation exceeds precipitation by approximately twofold, and most precipitation occurs as rain during May–July. Air temperatures fluctuate widely through the year from a minimum in January (-15.8°C) to a maximum of (19.0°C) in July (Environment Canada climate normals 1971–2000).

Our experimental system, Wascana Lake, is a small, shallow, macrophyte-rich lake situated in urban parkland in the city of Regina (Table 1 and Figure 2a). The lake was created in the 1930s by the impounding and deepening of Wascana Creek, a permanent stream that flows into the Qu'Appelle Valley drainage system. We used a reference lake to detect regional changes that may have affected the interpretation of the experiment (used in this context, the term “reference” does not denote a pristine baseline lake). The reference

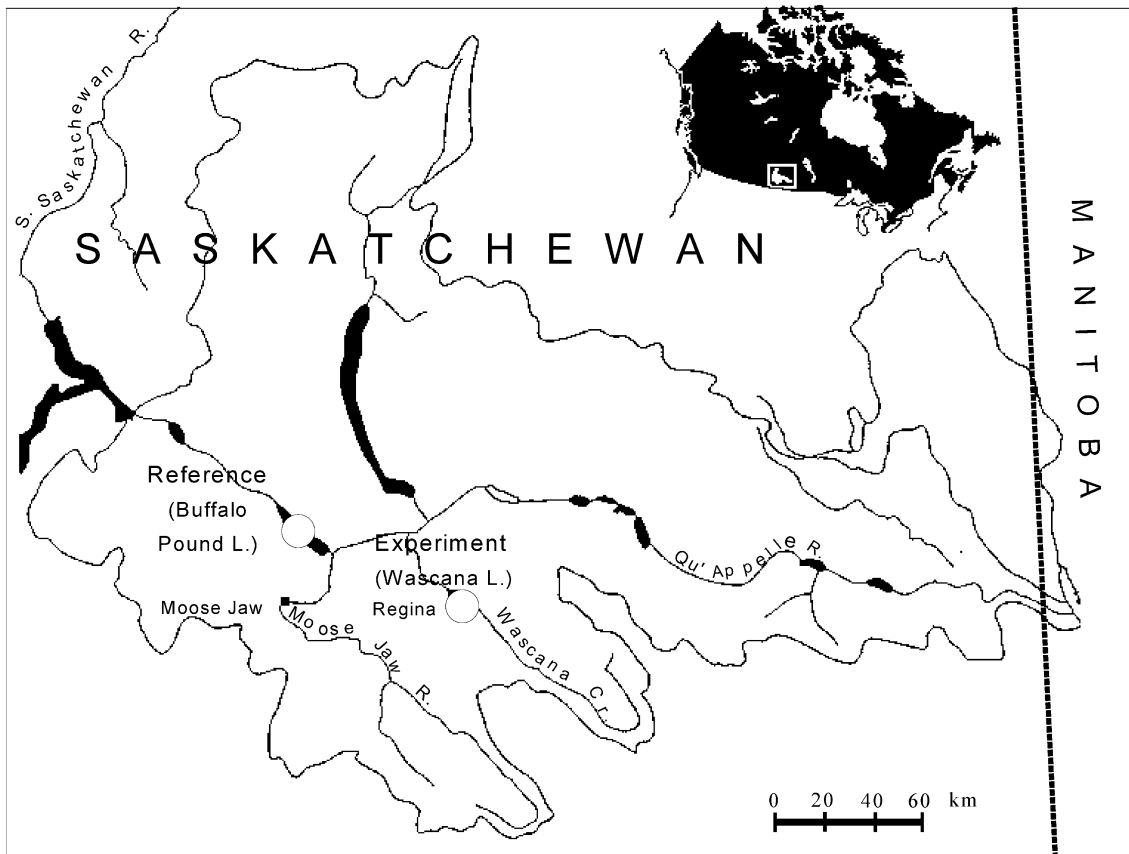


Figure 1. Map of the Qu'Appelle River drainage, Saskatchewan, Canada, showing the location of the study sites (open circles).

system, Buffalo Pound Lake, is a shallow natural water body that is also regulated to supply water to the cities of Regina and Moose Jaw, Saskatchewan. Buffalo Pound receives surface flow from Lake Diefenbaker, a reservoir located west on the South Saskatchewan River (Figure 1). Water diversion was initiated in 1967 and reduced natural fluctuations in lake level (Hall and others 1999a). Both Wascana and Buffalo Pound Lake have large macrophyte beds in shallow (less than 2 m) waters and are characterized by regular blooms of planktonic cyanobacteria during summer (Hall and others 1999b). Deepwater anoxia is common in both lakes during winter and late summer, although neither site normally freezes throughout the water column.

Experimental Manipulation

The drawdown was part of a permitted manipulation of an urban reservoir conducted by the City of Regina. In October 1997 (an El Niño year) and 1998, water levels were reduced in Wascana Lake

by approximately 1 m, resulting in an approximately 50% decline in maximum lake depth (Figure 2). Although most shallow upstream reaches were completely dry (Figure 2b), downstream areas of the lake remained submerged (Figure 2c); however, depth was reduced such that the entire water column froze in both years. Water drawdown was maintained until snowmelt in March–April, when natural runoff restored lake levels. Summer and annual water levels in Buffalo Pound Lake remained constant (± 20 cm) due to control structures.

Lakes were sampled biweekly during the growing season (May–September) over a 6-year period (1996–2001). Integrated water samples (0–2 m) were taken from the deepest point of each lake with a van Dorn sampler and were analyzed for $\text{PO}_4\text{-P}$, $\text{NH}_4\text{-N}$, $\text{NO}_3\text{-N}$, total dissolved N (TDIN), and total organic carbon (TOC) by standard procedures (for example, see Strickland and Parsons 1984) at the Water Chemistry Laboratory, Trent University, Ontario, Canada. Total chlorophyll (Chl) (sum of Chl *a*, *b*, *c*₁, and *c*₂) was quantified by standard spectrophotometric procedures (Jeffrey

Table 1. Physical and chemical features of the study sites

	Wascana Lake (Experiment)	Buffalo Pound Lake (Reference)
Area (ha)	194	2910
Maximum depth (m)	3	5.5
Mean depth (m)	1.5	3
Annual mean PO ₄ -P (µg L ⁻¹)	420	70
(SD)	(530)	(310)
Annual mean TDIN (µg L ⁻¹)	170	70
(SD)	(320)	(110)

TDIN, total dissolved nitrogen

and Humphrey 1975). Quantitative estimates of zooplankton density were made by vertical tows of a 243-µm mesh plankton net, preservation of animals in sugar-saturated 95% ethanol, and enumeration on a Wilde dissecting microscope (× 40–400 magnification) with reference to Pennack (1978) and Thorp and Covich (1991). Changes in the phytoplankton communities were estimated using high-performance liquid chromatographic (HPLC) analysis of diagnostic Chl and carotenoids following concentration of phytoplankton onto 0.45-µm glass-fiber filters and extraction of pigments using our standard protocols (reviewed in Leavitt and Hodgson 2001).

Due to logistic constraints, macrophyte biomass was estimated in Wascana Lake only for each of 3 seasons, including one pre-drawdown (1997) and 2 drawdown years (1998, 1999). Paired quadrats (0.25 m²) were sampled monthly every 5 m along eight transects arranged at regular intervals perpendicular to the lakeshore (5–25 m in length). All aboveground biomass of aquatic macrophytes was removed, sorted to species level, and dried at 60°C for approximately 72 h to estimate dry mass m⁻². Mean standing crops were calculated among transects to estimate dry biomass at each of four depth intervals (less than 0.5 m, 0.5–0.7 m, 0.7–1.0 m, 1–1.25 m).

Statistical Analyses

A combination of before-after-control-impact (BACI) analysis (Stewart-Oaten and Murdoch 1986) and multivariate analyses were used in the analysis of drawdown data. Our BACI analysis used three treatments instead of the more con-



Figure 2. Aerial view of Wascana Lake before (A) and during (B, C) experimental drawdown. Dewatering reduced lake levels approximately 1 m (50% of Z_{\max}) in the deepest portion of the basin (C).

ventional two (Zimmer and others 2001) and included years before (1996, 1997), during (1998, 1999), and after (2000, 2001) drawdown to test for both the immediate and longer-term effects of winter dewatering on Wascana Lake. Ideally, reference and experimental lakes should be sampled simultaneously, but because this was not possible, we paired the sampling occasions that were closest in time from each lake. Usually,

sampling occurred within about 3 days of the other (median, 3 days). One-way analysis of variance (ANOVA) with Tukey's multiple comparison was used to assess how lakes differed ($P < 0.05$) among the 3 treatment periods for variables where BACI analysis was deemed appropriate. Prior to BACI analysis, time series were smoothed using a three-point running mean to better estimate true population means (Stewart-Oaten and Murdoch 1986), whereas $\log_{10}(x + 1)$ transformations were used to normalize variance and reduce problems of non-additivity.

Application of BACI analysis requires that the difference between experimental and reference lakes is constant in the pretreatment period, both on a seasonal and interannual basis (Stewart-Oaten and Murdoch 1986). We tested for the presence of seasonal departures by regressing $\log_{10}(x + 1)$ -transformed interlake differences against calendar day of the year (Table 2). Regression slopes that deviated significantly from zero ($P < 0.05$) were assumed to be inappropriate for BACI analysis. Similarly, transformed interlake differences were regressed against sample order during the entire premanipulation period to identify the presence of long-term deviation between lakes. Third, we used regression analysis to test how interlake difference varied as a function of average abundance of the variable in both lakes; slopes that deviated significantly ($P < 0.05$) from zero were assumed to have problems with non-additivity and deemed inappropriate for BACI analysis. Finally, variables were screened for significant positive first-order autocorrelation ($P < 0.05$) in the 3 treatment periods using a Durban-Watson test and an autocorrelation function test to assess whether significant ($P < 0.05$) autocorrelation existed. Variables that did not pass all of these selection criteria were considered unsuitable for BACI analysis (Table 2).

Because BACI analysis was inappropriate for some variables, we used principal components analyses (PCA) of chemical, algal, and invertebrate time series to identify the presence of coherent shifts among lakes caused by regional factors. In this analysis, unique changes in the experimental lake were assumed to have arisen because of the manipulation. Principal components analysis was performed on $\log_{10}(x + 1)$ -transformed variables using CANOCO for Windows v. 4.02 (Microcomputer Power, Ithaca, NY).

Coherence analysis was used to assess the degree of synchrony of biotic variables between lakes (Rusak and others 1999). Prior to analysis, variables were screened for significant autocorrelation

using the methods described above. If significant ($P < 0.05$) autocorrelation existed, variables were transformed by first-difference and \log_{10} conversions as necessary. Following removal of autocorrelations, time series synchrony was estimated using Pearson Correlation Coefficients with lag equal to zero. All computations were performed using SYSTAT v. 10.0.

RESULTS

Chemical Responses

Analysis of nutrient concentrations (PO_4 , NH_4 , NO_3 , TDIN, and TOC) (Figure 3) demonstrated that inter- and intraannual variability was high in both lakes and that marked seasonal trends were also present. Overall, nutrient status was higher in the experimental system than in the reference lake. Seasonal variability in secchi depth was greater in the experimental lake than the reference lake. However, experimental manipulation did not result in significant changes in seasonal trends or nutrient concentrations in Wascana Lake either during (1998, 1999) or after (2000–01) drawdown periods.

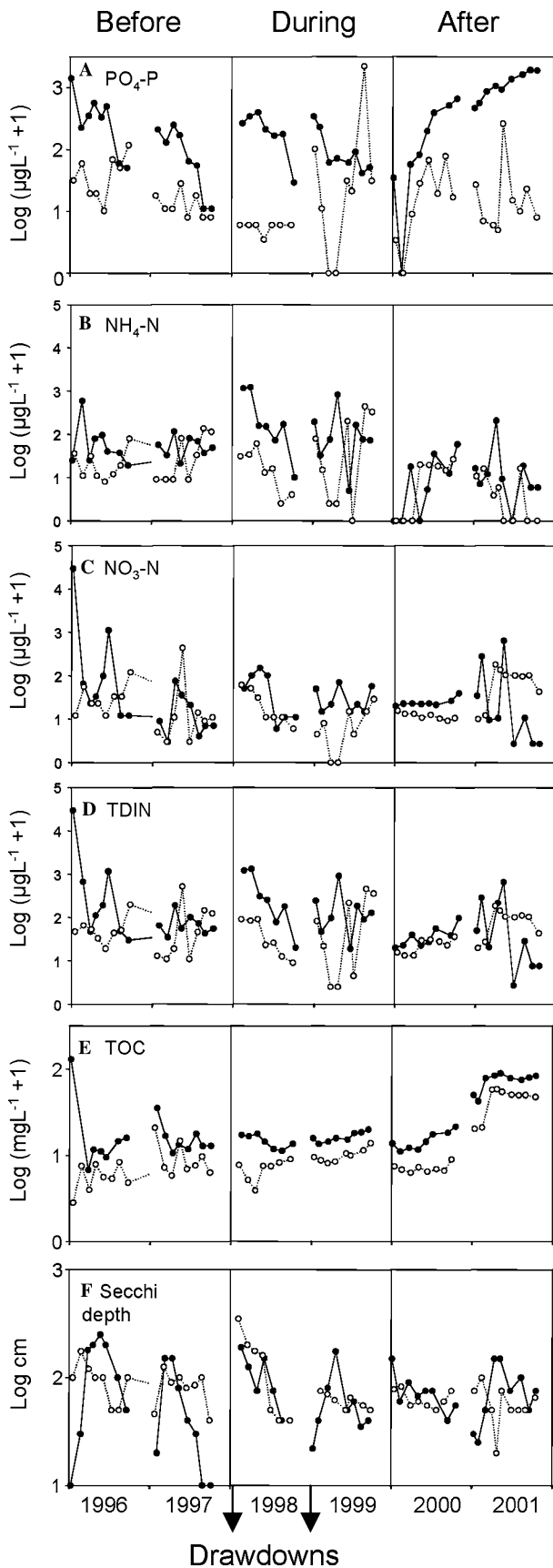
Concentrations of PO_4 in Wascana Lake exceeded those in the reference lake by at least an order of magnitude on most sampling dates (Figure 3a). In general, PO_4 concentrations declined throughout the summer both before (1996–97) and during treatment years (1998–99), then increased through the summer thereafter (annual mean, around $1,200 \mu\text{g L}^{-1}$ in 2001). No strong seasonal trends in PO_4 were recorded for Buffalo Pound Lake. In both lakes, ammonium was the predominant form of N (Figure 3 b, c, and d) during the ice-free period. Although trends in ammonium- and nitrate-N were evident in individual years, there were few consistent seasonal patterns among years. Similarly, TOC concentrations showed few seasonal trends, but tended to be approximately twice as high in the experimental lake as in the reference one (Figure 3e).

Secchi depths were more variable in the experimental lake than in the reference system (Figure 3f). Transparency was usually low during May, reflecting diatom blooms (see below) and elevated loading of suspended mineral material during snowmelt. In most years, water clarity in Wascana Lake increased markedly in early summer (June–July) and declined thereafter because of increased phytoplankton abundance. In most years, water clarity was elevated initially in Buffalo Pound Lake and then declined toward the end of the season.

Table 2. Test criteria to screen variables for suitability for before-after-Control-Impact (BACI) analysis

Variable	(c) Trends			(d) Nonadditivity		(e) Autocorrelation	
	(a) Transformation	(b) Normality	Seasonal	Before	Before	Before	After
			r ² (slope)	r ² (slope)	r ² (slope)	Durban-Watson statistic	
PO ₄ -P	Log (x + 1)	Y	0.493 (-0.129) ^b	0.350 (-0.054) ^a	0.342 (0.769) ^a	1.358	1.831
NH₄-N	Log (x + 1)	Y	0.076 (-0.038)	0.100 (-0.020)	0.132 (-0.705)	2.679	2.942
NO ₃ -N	Log (x + 1)	Y	0.245 (-0.192)	0.415 (-0.124) ^b	0.748 (1.635) ^b	1.983	1.873
TDIN	Log (x + 1)	Y	0.322 (-0.173) ^a	0.496 (-0.107) ^b	0.675 (1.617) ^b	1.957	2.650
TOC	Log (x + 1)	Y	0.234 (-0.077)	0.343 (-0.046) ^a	0.445 (2.399) ^b	1.467	1.248 ^a
Secchi depth	Log x	Y	0.010 (0.018)	0.046 (-0.019)	0.765 (1.825) ^b	0.648 ^a	1.283
Total Chl	Log (x + 1)	Y	0.205 (0.053)	0.024 (0.009)	0.341 (0.572) ^a	1.465	1.469
Copepods	Log (x + 1)	Y	0.041 (-0.028)	0.005 (-0.005)	0.015 (-0.094)	1.446	1.367
Large <i>Daphnia</i>	Log (x + 1)	Y	0.068 (-0.042)	0.033 (-0.014)	0.320 (0.834) ^a	1.313	2.290
Small cladocerans	Log (x + 1)	Y	0.540 (-0.174) ^b	0.590 (-0.090) ^b	0.694 (-1.233) ^b	1.433	2.053
Fucoxanthin	Log (x + 1)	Y	0.001 (0.003)	0.104 (-0.029)	0.001 (-0.243)	1.170	1.745
Alloxanthin	Log (x + 1)	Y	0.034 (-0.014)	0.000 (0.000)	0.013 (-0.274)	1.963	1.438
Chl <i>b</i>	Log (x + 1)	Y	0.056 (-0.016)	0.001 (-0.001)	0.444 (1.203) ^b	0.658 ^a	1.020
Echinonone	Log (x + 1)	n	0.318 (0.027) ^a	0.321 (0.022) ^a	0.562 (0.639) ^b	1.400	1.733
β-carotene	Log (x + 1)	Y	0.139 (0.048)	0.319 (0.036) ^a	0.772 (1.086) ^b	0.561 ^a	0.927

P, phosphorus; *N*, nitrogen; TDIN, total dissolved nitrogen; TOC, total organic carbon; Chl, chlorophyll
 After-transformation (a) variables (the difference between smoothed experimental and control variables) were tested for normality of distributions (b) using frequency histograms, significant seasonal and overall trends (c) in the before treatment period, significant nonadditivity (d) in the before-treatment period, and autocorrelation (e) in the before-, during-, and after-treatment periods using linear regression to determine the Durban-Watson statistic and also by using the autocorrelation function (ACF) function with 95% confidence intervals.
 Significant tests are reported at the P < 0.05 (^a) and P < 0.01 (^b) levels.
 Variables that satisfied all the screening criteria are shown in boldface type



Biological Responses

Phytoplankton (as total Chl) and zooplankton showed distinct seasonality in both lakes through the sampling period (Figure 4). The spring clear-water phase (around mid-May to mid-June) was typified by low total Chl concentrations (Figure 4a) and high abundance of large *Daphnia* spp. (Figure 4c), including *D. magna*, *D. pulicaria*, and *D. galeata* var. *mendota*. Elevated densities of copepods (*Leptodiaptomus* and *Diacyclops* spp.) were recorded also during the clear-water phase (Figure 4b), although these populations also continued to increase, in contrast to large *Daphnia* spp. In most years, densities of small cladocerans (Figure 4d) began to increase sharply in June and maintained higher abundances toward late summer. After the spring clear-water phase, phytoplankton abundance increased regularly to a maximum in late August or September.

Average plankton community composition differed among lakes, based on analysis of 6-year means. For example, although average concentrations of total Chl ($37 \mu\text{g L}^{-1}$) and densities of copepods ($35\text{--}50 \text{ ind. L}^{-1}$) were similar between lakes, mean densities of large *Daphnia* spp. were substantially greater in Wascana Lake (8 ind. L^{-1}) than in Buffalo Pound Lake (1 ind. L^{-1}), whereas small Cladocera were less common in the experimental lake (6 ind. L^{-1}) than at the reference site (77 ind. L^{-1}). In both lakes, phytoplankton abundance increased from early to late summer, except during 2000–01. Coherence analysis of detrended time series revealed a high degree of synchrony between lakes in terms of Chl concentrations ($r = 0.491$; $P < 0.0001$) and copepod densities ($r = 0.482$; $P = 0.001$), but not abundances of large ($r = 0.175$; $P = 0.239$) or small ($r = 0.001$; $P = 0.994$) Cladocera.

In general, intra-annual variability of algae was greater during the 1996–1999 period than during 2000–01, excluding chlorophytes and cyanobacteria in Buffalo Pound Lake (Figure 5). In both lakes and most years, the abundance of chlorophytes (Figure 5c) and cyanobacteria (Figure 5d) were the highest in late summer. In contrast, siliceous algae (Figure 5a) were abundant in spring and late summer, whereas cryptophytes (Figure 5b) had variable

Figure 3. Changes in lake chemistry May–September 1996–2001 in Wascana Lake (experiment; closed symbols) and Buffalo Pound Lake (reference; open symbols). Parameters include orthophosphate-P (A), ammonium-N (B), nitrate-N (C), total dissolved nitrogen-N (D), organic carbon (E), and secchi depth (F).

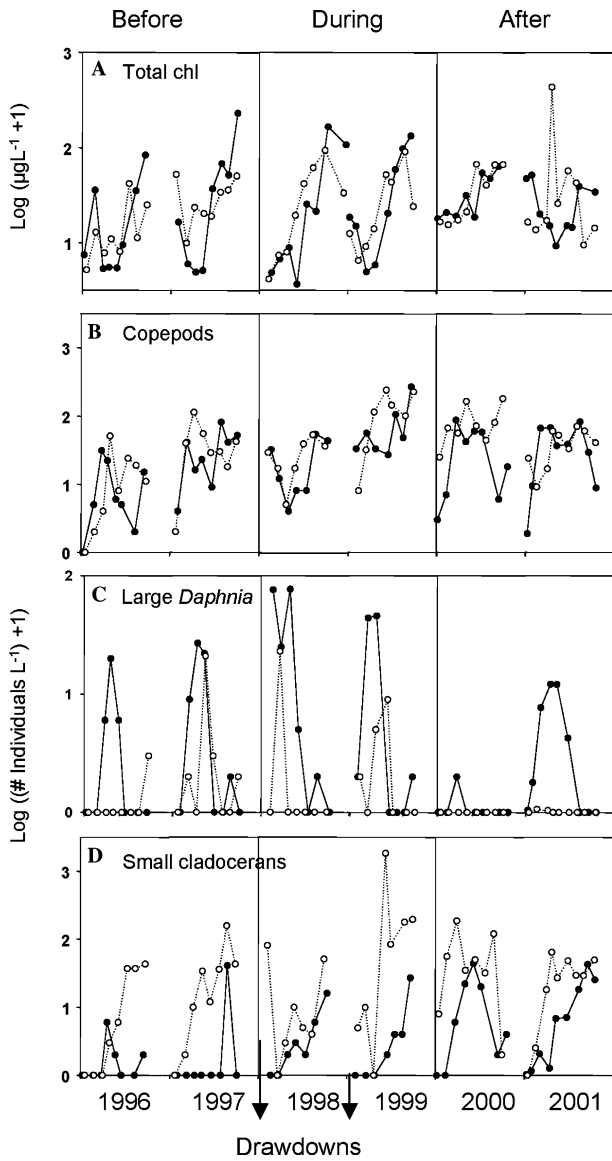


Figure 4. Changes in abundance of **A** total phytoplankton (as total Chl) **B**, copepods (*Leptodiatomus* + *Diacyclops* spp) **C**, large *Daphnia* (*D. pulex* + *D. magna*) and **D** small cladocerans (*D. galeata* var. *mendota*, *D. retrocurvata*, *Bosmina* spp., *Diaphanosoma* spp., *Ceriodaphnia* spp. and *Chydorus* spp.) in the experimental (closed symbols) and reference (open symbols) systems.

seasonal patterns. Concentrations of ubiquitous β-carotene (Figure 5e) were correlated strongly with those of pigments from cyanophytes ($r > 0.836$, $P = 0.0001$), reflecting the predominance of this algal group (Graham 1997). Coherence analysis revealed synchronous changes between lakes in cyanobacteria (echinenone $r = 0.635$; $P = 0.0001$) and total algae (β-carotene $r = 0.288$; $P = 0.047$) but not chlorophytes (chl b $r = 0.243$; $P = 0.100$), siliceous algae (fucoxanthin

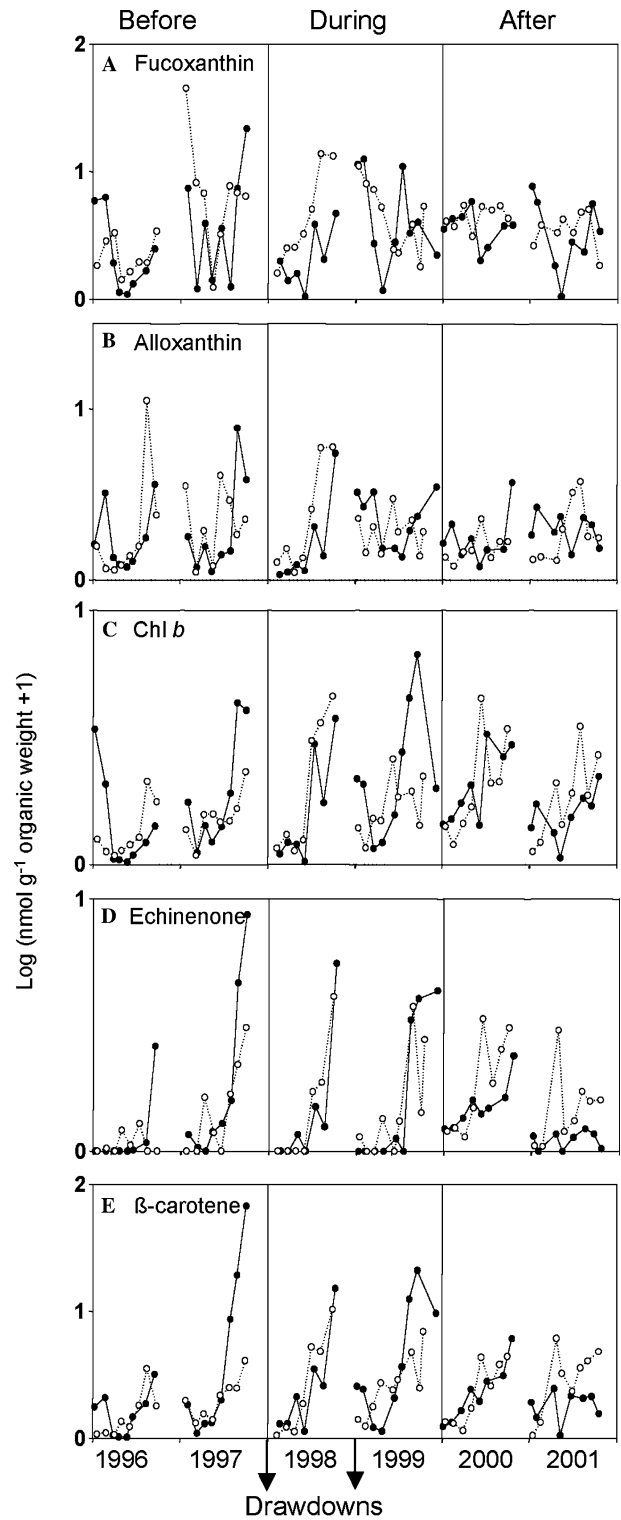


Figure 5. Changes in abundance of phytoplankton pigments from **A** siliceous algae (fucoxanthin), **B** cryptophytes (alloxanthin), **C** chlorophytes (Chl b), **D** total cyanobacteria (echinenone), and **E** total algae (β-carotene) between 1996 and 2001 (May–September) in the experimental (closed symbols) and reference (open symbols) systems.

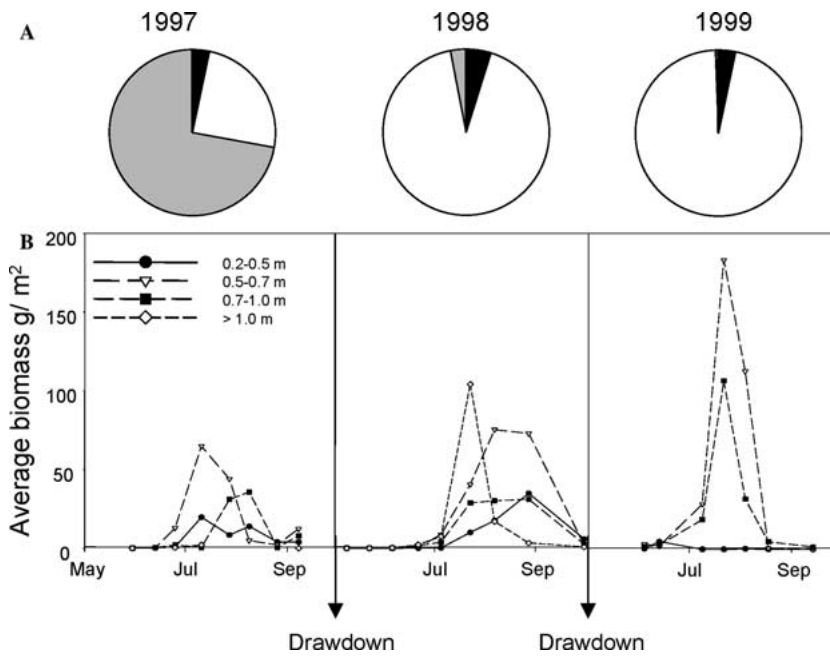


Figure 6. Changes in (A) % composition of aquatic macrophytes *Ceratophyllum demersum* (gray), *Potamogeton pectinatus* (white), and *Potamogeton richardsonii* (black) and (B) macrophyte density (dry biomass in g/m²) at four depth intervals in Wascana Lake between 1997 and 1999 (May–September).

Table 3. Before-After-Control-Impact (BACI) Analysis using one-way Analysis of Variance of the Difference between Smoothed Experimental and Reference Variables in the Before-, During-, and After-drawdown Periods

	Mean difference \pm SD			F ratio	P Value
	Before	During	After		
NH ₄ -N	0.368 \pm 0.327	0.733 ^a \pm 0.508	0.245 \pm 0.411	5.740	0.006
Copepods	-0.089 \pm 0.333	-0.176 \pm 0.265	-0.330 \pm 0.352	1.901	0.161
Fucoxanthin	-0.132 \pm 0.279	-0.140 \pm 0.243	-0.067 \pm 0.182	0.439	0.647
Alloxanthin	-0.049 \pm 0.184	-0.020 \pm 0.155	0.035 \pm 0.140	1.127	0.333

^aTreatment periods that were significantly different ($P > 0.01$) using Tukey's least significant difference test

$r = 0.217$; $P = 0.139$) or cryptophytes (alloxanthin $r = 0.106$; $P = 0.473$).

Macrophyte community composition changed markedly after the drawdown treatment, from a community composed mainly of *Ceratophyllum demersum* to one dominated by *Potamogeton pectinatus* after 1998 (Figure 6a). Qualitative observations suggested that the postdrawdown community was retained in Wascana Lake until at least 2001 (P. R. Leavitt, unpublished data), and quantitative surveys revealed that *Ceratophyllum demersum* was reestablished by 2003 (P.R. Leavitt unpublished data). Macrophyte density increased more than twofold between 1997 and 1999, reflecting increased growth at depths greater than 0.5 m and loss of plants in water less than 0.5 m (Figure 6b). Overall, macrophyte growth began in mid-June, reached a maximum density in August, and died back by mid-September.

BACI Analysis

BACI analysis showed that dewatering of Wascana Lake caused an increase in ammonium-N concentrations ($P < 0.006$), but had no impact on diatom (fucoxanthin), cryptophyte (alloxanthin), or copepod abundance (Table 3). When the remaining variables (Table 2) were also analyzed by BACI, the results suggested that no chemical, physical (Figure 3) or biological (Figures 4 and 5) variable was significantly altered ($P < 0.05$) during or after experimental drawdown. Although pre-analysis tests show that such analyses must be regarded with caution, the results nevertheless suggest that any effects of the drawdown were probably subtle at best. Negative results of BACI analysis, combined with the high synchrony of many planktonic parameters, suggested that although winter conditions did not have a significant impact on lake

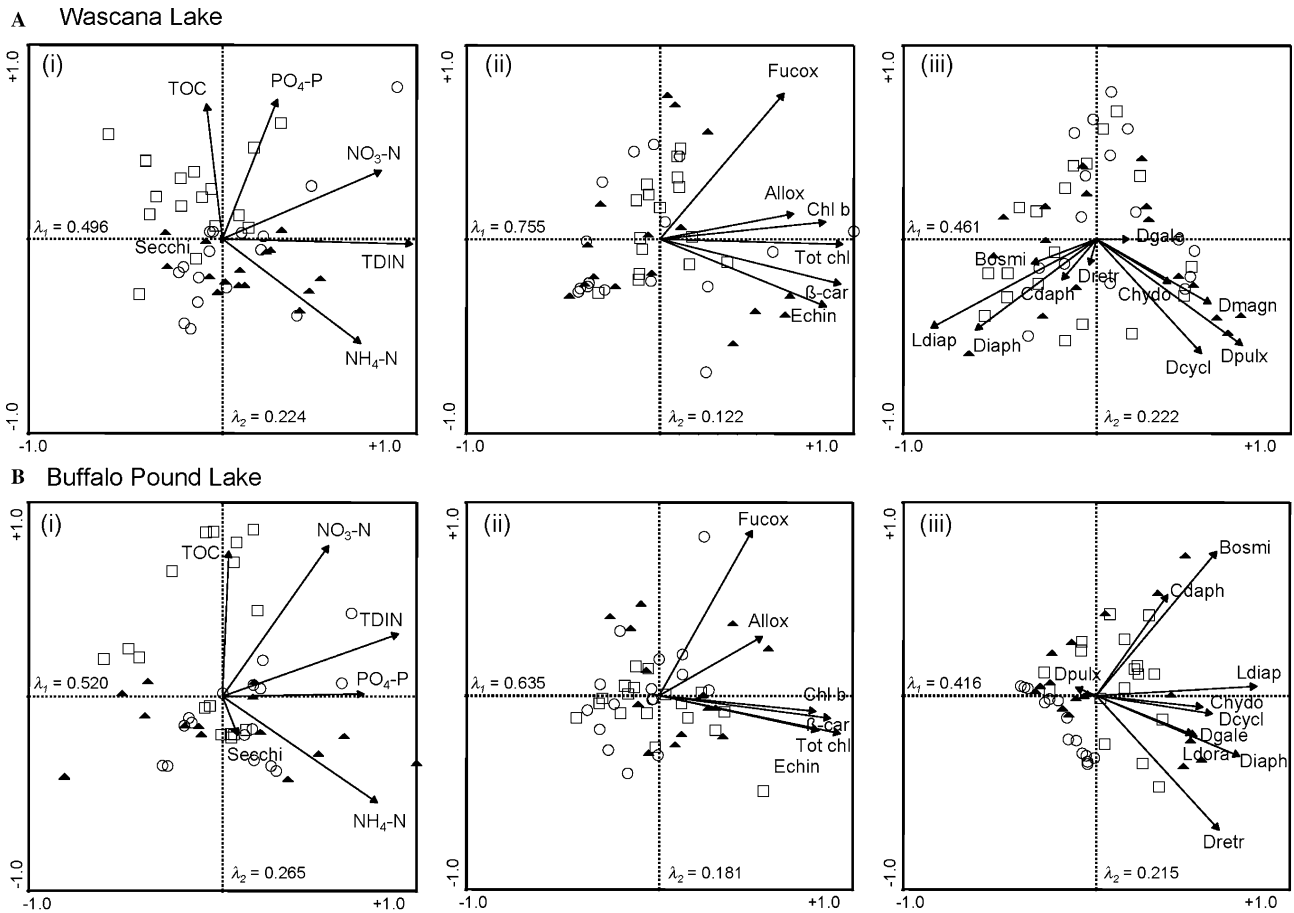


Figure 7. Principal components analyses of water chemistry (i), phytoplankton pigments fucoxanthin (Fucox), alloxanthin (Allox), chlorophyll *b* (Chl *b*), echinenone (Echin), β -carotene (β -car), and total chlorophyll (Tot chl) (ii), and zooplankton taxa *Bosmina* spp. (Bosmi), *Ceriodaphnia* spp. (Cdaph), *Chydorus* spp. (Chydo), *Diaphanosoma* spp. (Diaph), *Diacyclops* spp. (Dcycl), *Daphnia galeata* var. *mendota* (Dgale), *D. magna* (Dmagn), *D. pulex* (Dpplx), *D. retrocurvata* (Dretr), *Leptodiptomus* spp. (Ldiap), *Leptodora* spp. (Ldora) (iii) from **A** Wascana Lake and **B** Buffalo Pound Lake. Samples are separated into years before (open circles), during (black triangles), and after (open squares) treatment.

structure, variations in summer climate may influence temporal patterns in lake chemistry and biology.

Multivariate Analysis

Principal components analyses also suggested that the drawdown had minimal effects on the chemical and biological structure of Wascana Lake. Water chemistry and phytoplankton communities in Wascana Lake (Figure 7a) remained within the pretreatment (1996, 1997) range of variability during drawdown years (1998, 1999) and exhibited ordination patterns similar to those of the reference lake (Figure 7b). Together, these results demonstrate that the drawdown years were not anomalous and that the experimental results are unlikely to have been obscured by regional interannual

forcing. During the drawdown years, zooplankton assemblages in Wascana Lake (Figure 7a-iii) diverged slightly from those prior to manipulation, mostly as a result of elevated abundances of *Daphnia pulex* and *D. magna* (see Figure 4c) during spring. However, zooplankton abundance also increased in the reference lake after the drawdown (1998–2001) (Figure 7b-iii), suggesting that factors other than the experimental treatment might be responsible for changes in the invertebrate community of Wascana Lake.

DISCUSSION

The results of the experiment indicate that a 50% reduction (approximately 1 m) in winter lake depth had little effect on lake chemistry or food-web

structure during subsequent summer seasons. Further, although drawdown resulted in elevated ammonium concentrations in the water column, a substantial shift in aquatic macrophyte community composition, and elevated macrophyte biomass in deeper areas, these changes did not affect the densities of zooplankton, algal abundance, and community composition, nor other major chemical or physical parameters ($\text{PO}_4\text{-P}$, $\text{NO}_3\text{-N}$, TOC, secchi depth). Overall, there was little evidence that dramatic changes in winter dewatering initiated changes in the state of Wascana Lake (compare Blindow and others 1993).

The pattern of elevated ammonium concentrations after dewatering is consistent with predictions from summer drawdown studies in north temperate lakes (James and others 2001). However, unlike these studies we did not detect increases in sedimentary P release (De Groot and van Wijk 1993; James and others 2001). The exposure and oxidation of previously anaerobic sediments is thought to promote nitrate accumulation via nitrification (De Groot and van Wijk 1993; Crumpton and Goldsborough 1998) such that desiccation and reinundation leads to elevated sedimentary ammonium release (James and others 2001). In addition, desiccation of the sediment often increases redox potential but reduces sorption properties such that P is usually released as the sediments become reinundated (Watts 2000; James and others 2001). In contrast, our drawdown treatment had no obvious effect on P concentrations, possibly because P concentrations are naturally high in Wascana Lake and may limit the diffusion of P released from sediments. Alternatively, enhanced P release may occur only after summer drawdown. Further experimentation is required to distinguish among hypotheses. Regardless, our analysis suggests that although reduced lake depths during north temperate winters may slightly increase $\text{NH}_4\text{-N}$ release, disruptions of biogeochemical cycling are short-lived (1 year) and comparatively minor (for example, they exert no effect on $\text{NO}_3\text{-N}$, TDIN, or $\text{PO}_4\text{-P}$).

This experiment showed that drawdown had no significant effect on food-web structure, despite several lines of argument predicting that lake-depth decline would have a strong impact on biotic interactions. First, the reduction in lake volume should have increased under-ice anoxia (Meding and Jackson 2001), significantly reduced the availability and quality of habitat for overwintering fish, and resulted in increased fish kills during winter (Fang and others 1999). For example, in Wascana Lake, dewatering enabled the lake to

freeze throughout the water column during drawdown years. Second, exposure to temperatures below -20°C and desiccation of the littoral zone should eliminate overwintering structures of macrophytes, benthic invertebrates, zooplankton, and algae. Finally, we had expected that drawdown might alter the texture and chemical composition of the sediment substrate and thereby affect the growth of macrophytes and benthic organisms. Instead, algal, plant, and invertebrate populations appeared resilient to winter dewatering. This is consistent with the analyses of Hall and others (1999b) and Quinlan and others (2002), who showed that algal and invertebrate structure varied little in lakes of this region in response to winter conditions.

Analysis of invertebrate composition and size structure suggested that there was little net effect on fish survival after winter drawdown. We expected that fish kills due to freezing or anoxia would release large cladocerans from zooplanktivory, leading to lower phytoplankton biomass and more transparent water (Carpenter and others 1987) until fish were able to recolonize the lake. Although Wascana Lake had greater abundances of large *Daphnia* spp. during spring following the two drawdowns, the abundances were not substantially different from other years in the time series, nor was there evidence of a reduction in phytoplankton standing crops relative to nondrawdown years (Figure 4a). Instead, fish were observed in the shallow waters of Wascana Lake by July of the drawdown years, suggesting either that survival of fish was equally poor during nondrawdown years or that upstream recruitment of young-of-the-year fish (brook sticklebacks and fathead minnows) (Fisheries and Oceans Canada, unpublished data) was sufficient to constrain invertebrate populations in each year.

Changes in lake depth also had no direct impact on phytoplankton communities (Figure 5), despite the observation that abundant and diverse phytoplankton communities can form under ice in prairie lakes (Phillips and Fawley 2002) when winds reduce snow cover and increase light penetration (Meding and Jackson 2001). Similarly, ice duration is known to influence the timing and composition of phytoplankton during spring in continental European lakes subject to large-scale changes in winter climate (for example, see Adrian and others 1999). However, our experiment demonstrated that phytoplankton communities in Wascana Lake were resistant to perturbations arising from reduced water depths during winter, possibly because the lake has an extensive ice cover (ice thickness of

at least 1 m) during winter, unlike maritime-influenced European lakes. Instead, seasonal patterns of cyanobacterial and total algal abundance were well developed and coherent, suggesting that variation in spring and summer climate is a substantial control on population development (compare Baines and others 2000).

The freezing and desiccation of sediments did not strongly influence zooplankton abundance, composition or development during the growth season. Zooplankton may overwinter as water-column populations or as resting eggs or immature stages in the sediment. We had expected that conditions associated with water-level lowering would promote overwintering by resting eggs (Hairston 1996) and favor the emergence of Cladocera over copepods (compare Arnott and Yan 2002). Instead, we found no strong evidence of community change or of unexpected increases in water column colonization of populations during spring. The absence of zooplankton community shifts may reflect the observation that the emergence of resting eggs is more dependent on spring than winter conditions (Caceres 1998) and suggests that hydrologic variability during winter will not greatly alter total herbivory in such shallow lakes.

There were substantial changes in macrophyte community composition and up to an approximately 2.5-fold increase in macrophyte biomass after drawdown. Although we lacked a reference ecosystem to verify this interpretation, our results agree with those of drawdowns of prairie marshes (van der Valk and Davis 1978), where *Potamogeton pectinatus* increased to predominance after drawdown. Seed bank recruitment is of greater importance for macrophyte survival in shallow than in deep waters (Abernethy and Willby 1999), so the ability of *P. pectinatus* to propagate large numbers of seeds (van Wijk 1989) may facilitate overwintering survival under variable lake-level conditions. Similarly, water-depth declines during both growth and winter seasons are known to promote the growth of aquatic plants in other lakes due to increased light receipt on benthic surfaces (Blindow and others 1993; Coops and Hosper 2002; Wagner and Falter 2002). However, given that substantial interannual variability in macrophyte biomass can be driven by temperatures during the early growth season (Rooney and Kalff 2000) and the powerful 1997 El Niño increase in winter and spring temperatures (Environment Canada climate normals), we suggest that changes in total macrophyte biomass be interpreted with caution.

Our analyses showed that differences between the experimental and reference lakes (Table 2) may

have reduced our ability to statistically evaluate the drawdown effects of some variables using a BACI design. Although the reference lake had lower nutrient concentrations and relative abundances of large *Daphnia* spp. than the experimental system, such differences do not invalidate the BACI design (Stewart-Oaten and Murdoch 1986). Rather, BACI analysis of some variables was inappropriate because the differences between experimental and reference lakes changed seasonally, interannually, or as a function of the magnitude of a variable (Table 2) in the absence of manipulation (that is, the lakes behaved differently). A priori selection of an appropriate reference lake is difficult because apparently similar lakes can differ substantially in variability (for example, see Rusak and others 2001). Further, ideal reference lakes are rare because of the scarcity of undisturbed sites in this intensively agricultural region. Despite these limitations, BACI analysis was deemed appropriate for at least four key variables representing water chemistry (NH_4), phytoplankton (siliceous algae and cryptophytes), and zooplankton (copepods).

Lack of lake response to winter drawdown suggests that shallow prairie lakes may be resilient to winter climatic variability resulting in lake-level decline. We had expected that strong benthic-pelagic links in shallow lakes (Schindler and Scheuerell 2002) would make these lakes particularly susceptible to the effects of winter lake-level lowering, and that the resulting change in food-web structure would have effects that persisted until later in the year. Instead, the absence of substantial changes in biotic composition suggests that even a reduction of about 50% in lake level (approximately 1 m) is well within the natural range of hydrological fluctuations (see also Fritz and others 2000) and that more extensive climatic variability may be required to alter lake structure. We hypothesize that part of this resilience may arise from the recruitment of fish and other biota to Wascana Lake via the inflow creek. In this scenario, large impacts of winter droughts may only be evident if autumn and winter conditions are severe enough to eliminate regional metapopulations, as has been suggested by Zimmer and others (2001). In addition, the independence of growth-season community dynamics from winter community structure leads us to speculate that the overwintering survival strategy of dormancy could lead to a decoupling of winter and summer lake communities.

Our analysis contrasts with evidence from other lakes showing that winter temperatures and ice duration are good predictors of food-web structure

during the ice-free season. For example, in deep European lakes, variation in winter and spring temperatures driven by the North Atlantic Oscillation influence spring and summer plankton dynamics by regulating stratification processes (George and Taylor 1995) and the development of vernal zooplankton populations (Straile and Adrian 2000). Variation in winter temperature also impacts shallow polymictic lakes in Europe, although the effects (Scheffer and others 2001) tend to be detectable only early in the year (Adrian and others 1999; Gerten and Adrian 2001). Although this aspect was not specifically tested by our study, we suggest that in our continental climates, where temperature extremes are more pronounced, the rapid increase in temperature between winter and spring combines with the low thermal capacity of shallow lakes to eliminate the residual effects of winter temperature, so that lake communities respond more directly to conditions during the ice-free season (for example, see Adrian and others 1999). Consistent with this view, we note that the high temporal coherence of late-summer phytoplankton (for example, cyanobacteria; Figure 5d) is consistent with the presence of regional climate controls of primary production during summer.

In the context of the alternative stable states model (Scheffer and others 1993), Wascana Lake appears to have been in a macrophyte-rich, clear-water state throughout the study period (1996–2001). Abundant populations of large *Daphnia* spp. in most years (50–75 ind. L⁻¹) likely reduced Chl concentrations during the spring and summer, thereby promoting the establishment of aquatic macrophytes as a consequence of greater light penetration. Although our experiment yielded few significant results, trends in our data during the drawdown years (for example, elevated macrophyte biomass, deeper colonization in the lake, elevated abundance of *Daphnia* spp.) all suggest that a decline in lake depth during winter may strengthen the buffer mechanisms that stabilize the macrophyte-dominated state in shallow prairie lakes.

The broader implications of our study are that severe water shortages during El Niño events will not result in dramatic short-term changes in the biogeochemistry or food-web structure of shallow prairie lakes. Instead, these sites are likely to continue to exist in a macrophyte-rich, clear-water state, with a pronounced spring clear-water phase, even at high nutrient concentrations (Table 1). In fact, winter conditions in this continental region likely promote the buffer mechanisms that maintain the macrophyte-dominated state, including winter fish kills (Fang and others 1999) and selec-

tion for disturbance-tolerant macrophyte species. This effect is likely to be enhanced in isolated lakes with no fish recruitment because of an absence of transfer among regional metapopulations. Conversely, periods of higher water depths may favor a switch to the turbid state (Jackson 2003); however, this hypothesis has yet to be tested. Although it is often difficult to determine the cause of a switch between alternative stable states, in some European lakes, the intensity and long history of cultural disturbances has been implicated (Stansfield and others 1989). It is still a matter of debate whether climate has the potential to determine lake ecosystem state (Scheffer and others, 2001, 2003; Jeppesen and others 2003; McKee and others 2003; van Donk and others 2003), but Canadian prairie lakes with a short history of cultural disturbance and extreme climatic influences may prove to be model sites in which to test this hypothesis.

ACKNOWLEDGMENTS

Funding for this project was provided by Wascana Centre Authority, Saskwater Corp, and an NSERC Canada operating grant to P.R.L. We are indebted to past and present members of the University of Regina Limnology Laboratory for their input, including Mark Graham and Nicole Knezacek (HPLC pigment analyses); Jeff Hovdebo, Curtis Brock, Mark Zurowski, John Sweetman, and Brent Smith (drawdown experiment and lake monitoring); and Brian Gordon, Shannon Smith, Rebecca-Jane Schuler, Jerret Romanow, and Chris Teichreb (lake monitoring). We thank Fisheries and Oceans, Canada, for providing information on the fish communities in Wascana Creek and the two anonymous reviewers for their useful comments on the manuscript.

REFERENCES

- Abernethy VJ, Willby NJ. 1999. Changes along a disturbance gradient in the density and composition of propagule banks in floodplain aquatic habitats. *Plant Ecol* 140:177–90.
- Adrian R, Walz N, Hintze T, Hoeg S, Rusche R. 1999. Effects of ice duration on plankton succession during spring in a shallow polymictic lake. *Freshwater Biol* 41:621–32.
- Arnott SE, Yan ND. 2002. The influence of drought and re-acidification on zooplankton emergence from resting stages. *Ecol Applic* 12:138–53.
- Baines SB, Webster KE, Kratz TK, Carpenter SR, Magnuson JJ. 2000. Synchronous behaviour of temperature, calcium and chlorophyll in lakes of northern Wisconsin. *Ecology* 81:815–25.
- Blindow I, Andersson G, Hargeby A, Johanssen S. 1993. Long-term pattern of alternative stable states in two shallow eutrophic lakes. *Freshwat Biol* 30:159–67.

- Caceres CE. 1998. Interspecific variation in the abundance, production, and emergence of *Daphnia* diapausing eggs. *Ecology* 79:1699–710.
- Carpenter SR, Kitchell JF, Hodgson JR, Cochran PA, Elser JJ, Elser MM, Lodge DM, Kretzmer D. 1987. Regulation of lake primary productivity by food web structure. *Ecology* 68:1863–76.
- Cooke GD, Welch EB, Peterson SA, Newroth PR, editors. 1986. Restoration and management of lakes and reservoirs. Boca Raton (FL): Lewis.
- Coops H, Hoser SH. 2002. Water-level management as a tool for the restoration of shallow lakes in the Netherlands. *Lake Reserv Manage* 18:293–298.
- Crumpton WG, Goldsborough LG. 1998. Nitrogen transformation and fate in prairie wetlands. *Great Plains Res* 8:57–72.
- De Groot CJ, Van Wijck C. 1993. The impact of desiccation of a freshwater marsh (Garcines Nord, Camargue, France) on sediment–water–vegetation interactions. *Hydrobiologia* 252: 83–94.
- Fang X, Stefan HG, Alam SR. 1999. Simulation and validation of fish thermal DO habitat in north-central US lakes under different climate scenarios. *Ecol Model* 118:167–91.
- Fritz SC, Ito E, Yu Z, Laird KR, Engstrom DR. 2000. Hydrologic variation in the Northern Great Plains during the last two millennia. *Quat Res* 53:175–84.
- Gaboury MN, Patalas JW. 1984. Influence of water level drawdown on the fish populations of Cross Lake, Manitoba. *Can J Fish Aquat Sci* 41:118–25.
- Gafny S, Gasith A. 1999. Spatially and temporally sporadic appearance of macrophytes in the littoral zone of Lake Kinneret, Israel: taking advantage of a window of opportunity. *Aquat Bot* 62:249–67.
- George DG, Taylor AH. 1995. UK Lake plankton and the Gulf Stream. *Nature* 378:139 .
- Gerten D, Adrian R. 2001. Differences in the persistency of the North Atlantic Oscillation signal among lakes. *Limnol Oceanogr* 46:448–55.
- Graham MD. 1997. Omnivory and selective feeding by zooplankton along a lake production gradient: complementary ¹⁵N isotope and gut pigment analysis. [thesis]: Biology Department, University of Regina Canada.
- Hairton NG, Jr. 1996. Zooplankton egg banks as biotic reservoirs in changing environments. *Limnol Oceanogr* 41:1087–92.
- Hall RI, Leavitt PR, Dixit AS, Quinlan R, Smol JP. 1999a. Limnological succession in reservoirs: a paleolimnological comparison of two methods of reservoir formation. *Can J Fish Aquat Sci* 56:1109–21.
- Hall RI, Leavitt PR, Quinlan R, Dixit AS, Smol JP. 1999b. Effects of agriculture, urbanization and climate on water quality in the northern Great Plains. *Limnol Oceanogr* 44:739–56.
- Hunt PC, Jones JW. 1972. The effect of water level fluctuations on a littoral fauna. *J Fish Biol* 4:385–94.
- [IPCC] Intergovernmental Panel on Climate Change. 2001. Climate change 2001: synthesis report. A contribution of Working Groups I, II and III to the Third Assessment Report of the Intergovernmental Panel on Climate Change. Cambridge (UK): Cambridge University Press.
- Jackson LJ. 2003. Macrophyte-dominated and turbid states of shallow lakes: evidence from Alberta lakes. *Ecosystems* 6:213–23.
- James WF, Barko JW, Eakin HL, Helsel DR. 2001. Changes in sediment characteristics following drawdown of Big Muskego Lake, Wisconsin. *Arch Hydrobiol* 151:459–74.
- Jeffrey SW, Humphrey GF. 1975. Spectrophotometric equations for determining chlorophylls a, b, c₁ and c₂ in higher plants, algae and natural phytoplankton. *Biochemi Physiol Plan* 167:191–4.
- Jeppesen E, Søndergaard M, Jensen JP. 2003. Climatic warming and regime shifts in food webs: some comments. *Limnol Oceanogr* 48:1346–9.
- Kadlec JA. 1962. Effects of a drawdown on a waterfowl impoundment. *Ecology* 43:267–81.
- Laird KR, Cumming BF, Wunsam S, Rusak J, Oglesby RJ, Fritz SC, Leavitt PR. 2003. Lake sediments record large-scale shifts in moisture regimes across the northern prairies of North America during the past two millennia. *Proc Nat Acad of Sci USA* 100:2438–88.
- Leavitt PR, Hodgson DA. 2001. Sedimentary pigments. In: Smol JP, Birks HJB, Last WM, eds. Tracking environmental changes using lake sediments. Dordrecht: The Netherlands: Kluwer. p 295–325.
- McKee D, Atkinson D, Collings SE, Eaton JW, Gill AB, Harvey I, Hatton K, others . 2003. Response of freshwater microcosm communities to nutrients, fish, and elevated temperature during winter and summer. *Limnol and Oceanogr* 48:707–22.
- McLachlan AJ. 1974. Recovery of the mud substrate and its associated fauna following a dry phase in a tropical lake. *Limnol and Oceanogr* 19:74–83.
- Meding ME, Jackson LJ. 2001. Biological implications of empirical models of winter oxygen depletion. *Can J of Fish Aquat Sci* 58:1727–36.
- Paterson CG, Fernando CH. 1969. The effect of winter drainage on reservoir benthic fauna. *Can J Zool* 47:589–95.
- Pennack RW. 1978. Freshwater invertebrates of the United States New York: Wiley.
- Phillips KA, Fawley MW. 2002. Winter phytoplankton community structure in three shallow temperate lakes during ice cover. *Hydrobiologia* 470:97–113.
- Quinlan R, Leavitt PR, Dixit AS, Hall RI, Smol JP. 2002. Landscape effects of climate, agriculture, and urbanization on benthic invertebrate communities of Canadian prairie lakes. *Limnol Oceanogr* 47:378–91.
- Rooney N, Kalff J. 2000. Inter-annual variation in submerged macrophyte community biomass and distribution: the influence of temperature and lake morphometry. *Aqua Bot* 68:321–35.
- Rusak JA, Yan ND, Somers KM, McQueen DJ. 1999. The temporal coherence of zooplankton population abundances in neighboring north-temperate lakes. *Am Nat* 153:46–58.
- Rusak JA, Yan ND, Somers KM, McQueen DJ, Ramcharan CW. 2001. Differences in the variability of crustacean zooplankton communities between manipulated and reference lakes. *Arch Hydrobiol* 56:171–86.
- Scheffer M, Hoser SH, Meijer ML, Moss B, Jeppesen E. 1993. Alternative equilibria in shallow lakes. *Trends Ecol Evol* 8:275–9.
- Scheffer M, Straile D, van Nes EH, Hoser H. 2001. Climatic warming causes regime shifts in lake food webs. *Limnol Oceanogr* 46:1780–3.
- Scheffer M, Straile D, van Nes EH, Hoser H. 2003. Climatic effects on regime shifts in lakes: a reply. *Limnol and Oceanogr* 48:1353–6.

- Schindler DE, Scheuerell MD. 2002. Habitat coupling in lake ecosystems. *Oikos* 98:177–89.
- Shabbar A, Bonsal B, Khandekar M. 1997. Canadian precipitation patterns associated with the Southern Oscillation. *J Clim* 10:3016–3027.
- Stansfield J, Moss B, Irvine K. 1989. The loss of submerged plants with eutrophication. III. Potential role of organochlorine pesticides: a palaeoecological study. *Freshwater Biol* 22:109–32.
- Stewart-Oaten A, Murdoch WW. 1986. Environmental impact assessment: “pseudoreplication in time?” *Ecology* 67:929–40.
- Straile D, Adrian R. 2000. The North Atlantic Oscillation and plankton dynamics in two European lakes: two variations on a general theme. *Global Change Biol* 6:663–70.
- Strickland JDH, Parsons TR. 1984. A practical handbook of seawater analysis. 3rd ed. Bulletin of the Fisheries Research Board of Canada.
- Thorp JH, Covich AP. 1991. Ecology and classification of North American freshwater invertebrates San Diego (CA): Academic Press.
- van der Valk AG, Davis CB. 1978. The role of seed banks in the vegetation dynamics of prairie glacial marshes. *Ecology* 59:322–35.
- van Donk E, Santamaria L, Mooij WM. 2003. Climate warming causes regime shifts in food webs: a reassessment. *Limnol and Oceanogr* 48:1350–3.
- van Wijk RJ. 1989. Ecological studies on *Potamogeton pectinatus* L. III. Reproductive strategies and germination ecology. *Aquat Bot* 33:271–99.
- Verschuren D, Tibby J, Sabbe K, Roberts N. 2000. Effects of depth, salinity, and substrate on the invertebrate community of a fluctuating tropical lake. *Ecology* 81:164–82.
- Wagner T, Falter CM. 2002. Response of an aquatic macrophyte community to fluctuating water levels in an oligotrophic lake. *Lake Reserv Manage* 18:52–65.
- Watts CJ. 2000. Seasonal phosphorus release from exposed, re-inundated littoral sediments of two Australian reservoirs. *Hydrobiologia* 431:27–39.
- Winter TC, Rosenberry DO. 1998. Hydrology of prairie pothole wetlands during drought and deluge: a 17-year study of the Cottonwood lake wetland complex in North Dakota in the perspective of longer term measured and proxy hydrological records. *Clim Change* 40:189–209.
- Zimmer KD, Hanson MA, Butler MG. 2001. Effects of fathead minnow colonization and removal on a prairie wetland ecosystem. *Ecosystems* 4:346–57.