

Climate control of the spring clear-water phase through the transfer of energy and mass to lakes

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Abstract

We analyzed decade-long time series of water transparency, algal abundance, zooplankton density, heat income, hydrology, and climate from six polymictic lakes of the northern Great Plains to determine how energy and mass transfers interact to regulate lake structure during the spring clear-water phase (CWP). Timing (date of occurrence) and intensity (Secchi transparency) of CWP were highly variable among lakes (mean lake-pair synchrony, $S = 0.072$, $p = 0.53$); however, CWP occurred in all lakes when water overlying the sediments reached $16.1^{\circ}\text{C} \pm 3.7^{\circ}\text{C}$ and *Daphnia* cleared the water column of diatoms. At a decadal resolution, timing and intensity of CWP were correlated strongly and positively ($r^2 > 0.90$, $p < 0.05$) with the net heat income (θ) and lake volume, but not with other independent lake, catchment, or climate features. Instead, at an annual resolution, the strength of correlations between CWP characteristics and heat income ($r_{\text{CWP-}\theta}$) was itself correlated inversely with the winter index of the North Atlantic Oscillation ($r < -0.55$, $p < 0.05$) and with precipitation during February–April ($r < -0.675$, $p < 0.05$). We conclude that the transfer of energy interacts with lake volume to regulate differences in timing and intensity of CWP among lakes, whereas the transfer of mass overrides energetic regulation to introduce temporal variation in CWP characteristics among years.

Climate variability can affect lake ecosystems by altering the influx of energy (E) (solar irradiance, atmospheric heat, wind friction) and mass (m) (precipitation, suspended particles, dissolved substances), as well as by modifying the temporal and spatial characteristics of individual fluxes (Pham et al. 2008). In general, E transfer is relatively uniform over broad geographic areas (Whitfield et al. 2002), occurs directly through the lake surface, and has rapid effects on lake characteristics (e.g., temperature, stratification) (Covich et al. 1997). In contrast, m transfer associated with precipitation is more spatially variable (Quiring and Papakyriakou 2005), often occurs indirectly via the catchment (Kratz et al. 1987), and can be modified by regional geology, soils, vegetation, and land use (Blenckner 2005). Consequently, inputs of E appear to synchronize seasonal variability in physical (ice melt, thermal stratification) and chemical (salinity, ionic composition) properties of lakes (Magnuson et al. 1990), whereas inputs of m reduce temporal coherence among sites (Pham et al. 2008, 2009). However, despite these generalities, relatively little is known of the conditions under which E or m transfers predominate, or of how the different pathways may interact to regulate lake structure.

At present, climatic variability within the northern Great Plains of North America originates from the interaction of three major air masses (Pacific, Arctic, Gulf of Mexico) (Bryson and Hare 1974) and variability in three global atmosphere–oceanic systems; the El Niño–Southern Oscillation (ENSO) (Trenberth and Hurrell 1994), North Atlantic Oscillation (NAO) (Hurrell 1995), and the Pacific Decadal Oscillation (PDO) (Mantua et al. 1997). In general, variation in winter NAO conditions (NAO_w) is correlated positively with cyclone activity over the Prairies

during winter and spring (Wang et al. 2006), whereas ENSO and PDO interact and can produce unusually warm dry winters in this region during years in which both systems exhibit positive indices (Mantua et al. 1997; McCabe et al. 2004). As a consequence of the Earth's orbit, most E transfer to lakes occurs during summer. In contrast, over 70% of annual precipitation in the Canadian Prairies falls as rain, but because of intense summer evapotranspiration (Ferguson et al. 2007) nearly 80% of water runoff to lakes is derived from the melting of winter snowpacks during spring (Steppuhn 1981; Akinremi et al. 1999). In addition, many lakes are strongly influenced by groundwater that is itself derived mainly from winter precipitation (van der Kamp and Maathuis 1991; Pham et al. 2009). Therefore, although irradiance and thermal regimes strongly influence biotic and physicochemical properties of prairie lakes during summer (Covich et al. 1997), these systems are sustained by winter precipitation (Pham et al. 2009). Unfortunately, little is known of how differences in the seasonality of E and m flux may influence ecosystem processes in lakes of the northern Great Plains.

Empirical evidence suggests that the effects of climate fluctuations on lake processes are most pronounced during spring. For example, variation in the NAO system is correlated strongly to the timing of ice melt (Weyhenmeyer et al. 1999), spring phytoplankton bloom (Blenckner et al. 2007), and the clear-water phase (CWP) in Europe (Straile 2000), although there remains uncertainty concerning the relative importance of E and m influx (Malmaeus et al. 2006), as well as their individual components (e.g., light vs. temperature) (Sommer and Lengfellner 2008). Similarly, variation in ENSO and PDO systems influences plankton phenology in lakes of western North America, including onset of stratification, intensity of spring algal bloom, and timing of the CWP (Winder and Schindler 2004). Although evidence from both continents suggests that warmer

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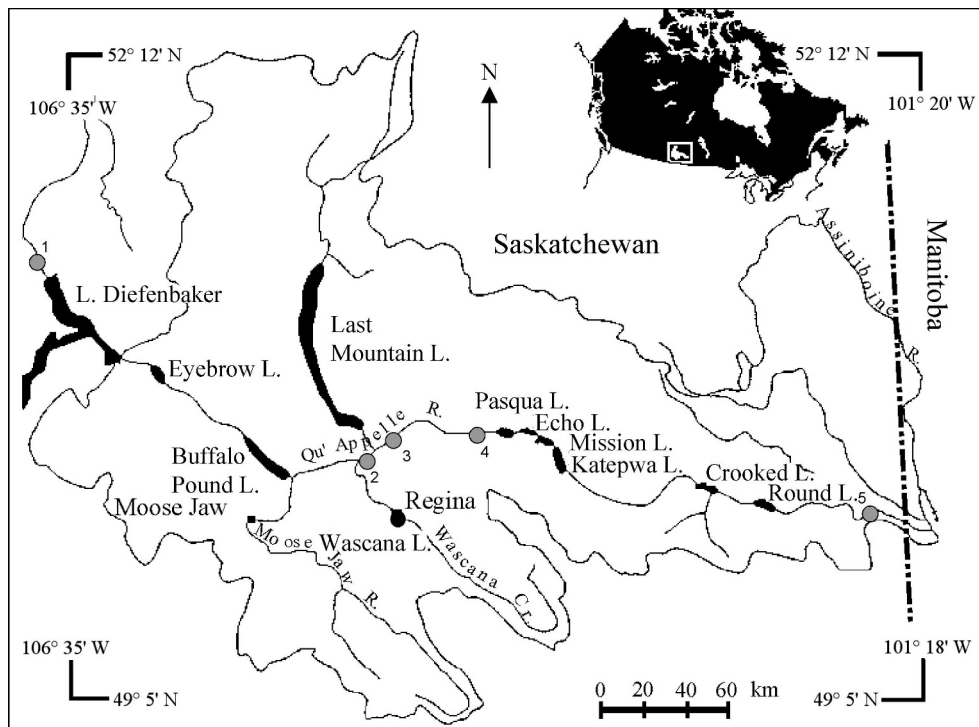


Fig. 1. Map showing the location of the lakes and river discharge sampling stations within the Qu'Appelle River catchment (Saskatchewan, Canada), including weirs at South Saskatchewan River (1), Lumsden (2), Craven (3), Loon (4), and Welby (5). Study lakes include Diefenbaker, Buffalo Pound, Last Mountain, Wascana, Katepwa, and Crooked.

conditions advance the phenology of algae and zooplankton (Adrian et al. 1999; Berger et al. 2007), differences in sensitivity of algae and invertebrates to temperature change—combined with observations that *m* flux (snow melt, precipitation, nutrient influx) and solar irradiance (Sommer and Lengfellner 2008) also vary in spring—act to obscure the precise mechanisms by which climate variability is transmitted to lakes.

Here we use decade-long time series of limnological conditions, primary and secondary producers, heat income, hydrology, and meteorological conditions from six polymictic lakes of the northern Great Plains to quantify how *E* and *m* transfer interact to regulate lake structure during the spring CWP. We focus on the CWP as a model system because the sequence of community change is predictable and well documented (Sommer et al. 1986), the CWP is ubiquitous in our study lakes (Dröscher et al. 2008), and because the CWP is known to be influenced by variations in both energy (atmospheric temperature, light) and mass influx (hydrology, dissolved nutrients) (Blenckner et al. 2007). Our findings demonstrate that spatial variation in the timing and intensity of CWP events is regulated by the interaction between *E* accumulation and lake volume, whereas variation in CWP among years arises because of the influx of water during spring, a mechanism that overrides the effects of *E* transfer.

Methods

Study site—The Qu'Appelle Valley river basin encompasses 52,000 km² in southern Saskatchewan, Canada

(Fig. 1). The regional climate is subhumid continental and is characterized by short warm summers (mean 19°C in July), cold winters (mean −16°C in January), and an average of 105 frost-free days (Leavitt et al. 2006). The drainage basin extends ~400 km from its western headwaters near Lake Diefenbaker to the confluence with the Assiniboine River in Manitoba. Reservoirs were created by impoundment of the South Saskatchewan River (Lake Diefenbaker), Wascana Creek (Wascana Lake), and the outflow of Buffalo Pound Lake. Under natural conditions, the Qu'Appelle River originates near Eyebrow Lake and flows eastward through Buffalo Pound Lake, a central chain of four basins (Pasqua, Echo, Mission, and Katepwa lakes), and two downstream lakes (Crooked and Round lakes). Water from Last Mountain Lake and Wascana Lake flows into the Qu'Appelle River via Last Mountain Creek and Wascana Creek, respectively. In addition, water is transferred into the catchment from Lake Diefenbaker (Leavitt et al. 2006). River flow is monitored in the catchment at five locations, including the headwater on the South Saskatchewan River, three sites in the central reaches of the Qu'Appelle River, and one downstream site (Fig. 1).

The six study lakes vary in mean depth from 2 to 33 m, but all exhibit low relative depths of 0.09–0.51% (Wetzel 2001) and, with the exception of occasionally dimictic Katepwa Lake, are polymictic in all years (Table 1). Because of the shallow nature of all basins, all lakes have elevated indices of climatic exposure (area:mean depth), ranging from 0.250×10^6 to 28.683×10^6 m (Magnuson et al. 1990). In general, nutrient status and algal production

Table 1. Morphometric, chemical, and biological features of the study lakes in the Qu'Appelle Valley catchment, Saskatchewan, Canada. Pearson correlation coefficients (r) are presented for correlations between timing (DOY) and intensity (Secchi depth) of the clear-water phase and various lake parameters. Significance levels include $p < 0.05$ (*) and $p < 0.01$ (**); $n = 6$ for all correlations.

	Diefenbaker	Buffalo Pound	Last Mountain	Wascana	Katepwa	Crooked	r_{timing}	$r_{\text{intensity}}$
Latitude ($^{\circ}$ N)	51.117	50.65	50.083	50.45	50.7	50.6	0.49	0.56
Longitude ($^{\circ}$ W)	106.63	105.5	105.23	104.609	103.65	102.73	0.56	0.44
Elevation (m)	552	509.3	490.1	570.6	478.2	451.7	0.13	0.07
Area (km ²)	500.0	29.1	226.6	0.5	16.2	15.0	0.96**	0.87**
Mean depth (m)	33.0	3.0	7.9	2.0	14.3	8.1	0.93**	0.97**
Max. depth (m)	62.0	5.5	30.8	3.0	23.2	16.5	1.00**	0.98**
Relative depth (%)	0.25	0.09	0.18	0.38	0.51	0.38	-0.15	0.06
Volume (10 ⁶ m ³)	9400.00	87.50	1807.20	0.68	233.20	120.90	0.94**	0.88**
Climatic exposure index (10 ⁶ m)	15.152	9.700	28.684	0.250	1.133	1.852	0.54	0.39
Water residence (yr)	1.3	0.7	12.6	0.05	1.34	0.5	0.26	0.16
Gross drainage (km ²)	0	3356	23,336	2681	48,587	53,161	-0.16	-0.02
Effective drainage (km ²)	0	1282	2902	1248	12,208	13,788	-0.22	-0.07
Conductivity (μ S cm ⁻¹)	420.8	473.6	1777.2	885.6	1088.0	1169.2	-0.12	-0.12
TDP† (μ g L ⁻¹)	22.5	30.0	50.3	351.6	163.0	124.2	-0.60	-0.51
TDN (μ g L ⁻¹)	333.2	492.2	957.3	1381.2	958.7	861.0	-0.62	-0.56
Integrated Chl <i>a</i> (μ g L ⁻¹)	5.4	27.5	12.7	32.1	25.1	27.1	-0.96**	-0.92**
N:P	33.5	21.0	32.9	5.6	7.7	11.5	0.76*	0.60

† TDP, total dissolved P; TDN, total dissolved N.

increase from west to east, with hypereutrophic N-limited lakes predominating in the downstream reaches.

Sampling and laboratory analysis—Diefenbaker, Buffalo Pound, Last Mountain, Katepwa, and Crooked lakes were sampled biweekly through the ice-free season from early May until early September during 1995–2005, whereas Wascana Lake was sampled similarly during 1996–2005. Zooplankton were collected using a 20-cm-diameter, 243- μ m mesh conical net towed to the surface from maximum depth and were preserved with an ethanol–sucrose solution. Adult crustacean and copepod zooplankton were enumerated to species, as were juvenile copepods, whereas rotifers and protozoa were not evaluated. Water transparency was recorded using a 20-cm-diameter Secchi disk. Algae from prescreened (243- μ m mesh) surface water samples were filtered onto prewashed GF/C glass fiber filters and were frozen (-10° C) until analysis for chlorophyll *a* (Chl *a*)

(μ g L⁻¹) by standard trichromatic methods (Leavitt et al. 2006). Depth profiles of temperature ($^{\circ}$ C), oxygen (mg O₂ L⁻¹), conductivity (μ S cm⁻¹), and salinity (g total dissolved solids L⁻¹) were recorded at 1-m intervals using YSI model 85, 33SN, and 51B probes.

CWP identification—Secchi depth, Chl *a* concentration, and zooplankton densities were measured biweekly during the ice-free season and were used to define the CWP in each lake following Dröscher et al. (2008). Briefly, CWP was defined as the first substantial increase in Secchi depth following ice-out that coincided with both low concentrations of Chl *a* and elevated densities of total zooplankton. The timing of the CWP was identified as the calendar day of the year (DOY) corresponding to the date of the greatest water transparency, whereas the intensity of the CWP was defined as the maximum observed Secchi depth. As detailed in Dröscher et al. (2008), CWP in these polymictic lakes

appears to be driven mainly by the selective grazing of large *Daphnia* (*Daphnia pulicaria* and *Daphnia galeata-mendota*) on diatom populations, rather than by changes in stratification or dissolved nutrient content. In this paper, we briefly review these earlier analyses to better define the respective roles of E and *m* transfer in regulating the timing and intensity of CWP development.

Heat income—Changes in the E content of lakes during the ice-free season were estimated as summer heat income (θ_s), the amount of E necessary to raise the water temperature from 4°C to the maximum summer temperature (modified from Hutchinson 1957 and Wetzel 2001). Here $\theta_s = \Sigma H_z \times A_z^{-1}$ in units of J cm⁻² yr⁻¹, where H_z = summer heat content of the water stratum at depth *z* (J) and A_z = the area of the water stratum at depth *z* (cm²) on the basis of digital morphometric maps. In turn, $H_z = M_z \times t_z \times s$, where M_z = the mass of the water stratum at depth *z* (g), t_z = the temperature difference between the maximum observed summer temperature and 4°C of the water stratum at depth *z* (°C), and *s* = the specific heat of water (4.184 J g⁻¹ °C⁻¹). Similarly, heat income at the time of the CWP maximum (θ_{CWP}) was calculated for each lake and year by replacing t_z with the temperature difference between the temperature observed at CWP and 4°C of the water stratum at depth *z* (°C). In both cases, water temperatures for depths greater than 3 m in Buffalo Pound, 6 m in Crooked, and 15 m in Diefenbaker, Katepwa, and Last Mountain lakes were extrapolated by linear regression from the base of the temperature profile in each year. These extrapolations had little effect on whole-lake heat budgets because temperature changed relatively little with depth and because deep waters accounted for a low proportion of total lake volume. Because many aspects of plankton phenology are correlated with water temperature (Blenckner et al. 2007), but water temperature in individual lakes depends on basin morphology and hydrology, local climatic regime, and other regional factors (Straskraba 1985; Schindler et al. 1990), we hypothesized that the timing and intensity of the CWP would be correlated positively to the net accumulation of E in individual lakes and that CWP characteristics should be affected strongly by climatic mechanisms that alter net E influx.

Climate data—Variations in regional climate were estimated for the Qu'Appelle drainage basin during 1995–2005 using a combination of direct measurement of meteorological variability and general indices of large-scale ocean–atmospheric linkages known previously to influence climate in the northern Great Plains (Bonsal et al. 2001). Mean annual and seasonal air temperature and precipitation were obtained from Environment Canada for several climate stations within the Qu'Appelle catchment (http://www.climate.weatheroffice.ec.gc.ca/climateData/canada_e.html), whereas river discharge at several locations (Fig. 1) was estimated from continuous hydrometric monitoring of regional rivers since 1970 and was obtained from Environment Canada (http://www.wsc.ec.gc.ca/hydat/H2O/index_e.cfm?cname=main_e.cfm). These latter data and digital

morphometric maps were used to estimate water residence times of all lakes. Total hours of bright sunlight received each month from 1970 to 2005 and monthly air temperature were also obtained from Environment Canada for a series of eight climate stations representing the entire extent of the Qu'Appelle catchment. This index measures solar irradiance on the basis of the oxidation of a standard substance (paper) using a Campbell–Stokes recorder, and includes the effects of day length, longitudinal position, and cloud cover.

Dates of ice cover melt for Buffalo Pound Lake (1976–2006) were obtained from the Buffalo Pound Lake Water Filtration Plant (B. Boots, Superintendent pers. comm.), whereas those from Echo Lake (1977–2006) were obtained from the Echo Lake Fish Culture Station (J. Banks, Manager pers. comm.). Because this fish hatchery is located only 18 km upstream of Katepwa Lake (Fig. 1), and because direct observation suggests that ice melting occurs within 2 d on both lakes, we used the more reliable ice-off dates from Echo Lake for both sites. Direct observations of ice-off dates for the southern portion of Last Mountain Lake (1964–2006) were obtained from local resident Ruth Marvin (Buena Vista, Saskatchewan), whereas those for Lake Diefenbaker (1968–1999) and Wascana Lake (1940–1989) were obtained from the Canadian Lake-Ice Database (Lenormand et al. 2002) and the Canadian Cryospheric Information Network (<http://www.ccin.ca/>). Ice-off dates in Buffalo Pound Lake were also used to predict infrequent ice-melt dates missing from time series of Diefenbaker, Wascana, and Katepwa lakes. Ice-off dates for Crooked Lake were approximated from a multiple regression model developed using observations from other lakes. The model ($r^2 = 0.754$, $p < 0.001$, $n = 58$, SE = 3.8 d) was based on log-transformed lake mean depth (std. coeff. = 0.576), average March air temperature (−0.510), March precipitation (−0.419), and log₁₀-transformed upstream winter flow (0.215).

The Southern Oscillation Index (SOI), a measure of the intensity of the ENSO climate system, was obtained from the Climate Prediction Center, Maryland (<http://www.cpc.noea.gov/data/indices/soi>), whereas PDO indices were obtained from the Joint Institute for the Study of the Atmosphere and Oceans, University of Washington, Washington (<http://jisao.washington.edu/pdo/PDO.latest>). Finally, the NAO_w (December–March) was obtained from the National Center for Atmospheric Research, Boulder, Colorado (<http://www.cgd.ucar.edu/cas/jhurrell/indices.html>).

Statistical analyses—Simple Pearson correlations (*r*) and unreplicated least-squares linear regressions were used to quantify the relationships between the timing and intensity of CWP, lake features, and climatic conditions. In contrast, one-way ANOVA and Scheffé's post hoc tests were used to determine if water temperature differed among lakes at the time of CWP and on other dates. Finally, simple Pearson correlations were used to determine how the strength of the correlation between CWP characteristics and heat income (or lake volume) varied as a function of measured meteorological conditions or climatic indices. In most

cases, variables were normally distributed, exhibited little temporal autocorrelation, and did not require transformation before analysis. Instead, lake volume and heat content required \log_{10} transformation before statistical analysis.

Temporal synchrony (S) of CWP among lakes was estimated as mean Pearson correlation coefficient for time series of DOY of CWP vs. year of observation for all possible lake-pair combinations (Pham et al. 2008). Mean lake-pair synchrony takes a value of 1.0 when CWP timing covaries perfectly among sites and 0.0 when events lack temporal coherence among lakes. Similar analyses of synchrony were performed for time series of DOY of ice melt, mean monthly temperature (April–August), and total hours of bright sunlight received per month (April–August), the main factors regulating E influx to individual lakes. In the case of ice-melt synchrony, estimates were based only on direct observations of individual lakes and did not include missing data inferred by regression models (see above).

Results

CWP characteristics—The CWP was identified in all lakes in most years, although CWP occurrence was less frequent in mesotrophic Lake Diefenbaker than in the more eutrophic downstream lakes. As the CWP developed, Secchi disk transparency increased an average of 0.5 m (Buffalo Pound) to 1.8 m (Katepwa), whereas Chl a concentration decreased by $1.5 \mu\text{g L}^{-1}$ (Crooked) to $22.6 \mu\text{g L}^{-1}$ (Wascana), relative to spring conditions. In all lakes except Buffalo Pound, the total zooplankton abundance was highest at the time of the CWP and increased by 2.8 individuals L^{-1} (Buffalo Pound) to 73.1 individuals L^{-1} (Wascana), whereas the total *Daphnia* abundance (sum of *D. galeata-mendota*, *D. pulicaria*, *D. retrocurva*, *D. magna*) increased by 3 individuals L^{-1} (Last Mountain) to 27.9 individuals L^{-1} (Buffalo Pound).

Spatial and temporal variability of CWP—The timing of the CWP was highly variable between years and lakes (Fig. 2). For example, the mean date of occurrence of CWP during 1995–2005 varied from DOY 160 in Wascana Lake to DOY 212 in Lake Diefenbaker, although differences in timing were not correlated with longitudinal position of the lake in the catchment ($r^2 = 0.311$, $p = 0.250$). Not surprisingly, timing of CWP was asynchronous among lakes ($S = 0.072$, $p = 0.53$), even though dates of ice melt ($S = 0.895$, $p = 0.006$), mean monthly temperatures between April and August ($S = 0.884$ – 0.970 , $p < 0.005$), and hours of bright sunlight received per month ($S = 0.732$ – 0.840 , $p < 0.005$) varied coherently over the entire Qu'Appelle catchment. Instead, lakes differed substantially in the degree of interannual variability in timing of CWP, with the highest variability observed in Buffalo Pound Lake and the lowest in Crooked Lake (Fig. 2). Interestingly, both standard deviation (SD) and coefficient of variance (CV) of the timing of CWP were correlated significantly with mean total zooplankton abundance ($r > 0.77$, $p < 0.05$) and mean total *Daphnia* abundance ($r > 0.86$, $p < 0.05$), but not with any chemical, physical, or morphometric characteris-

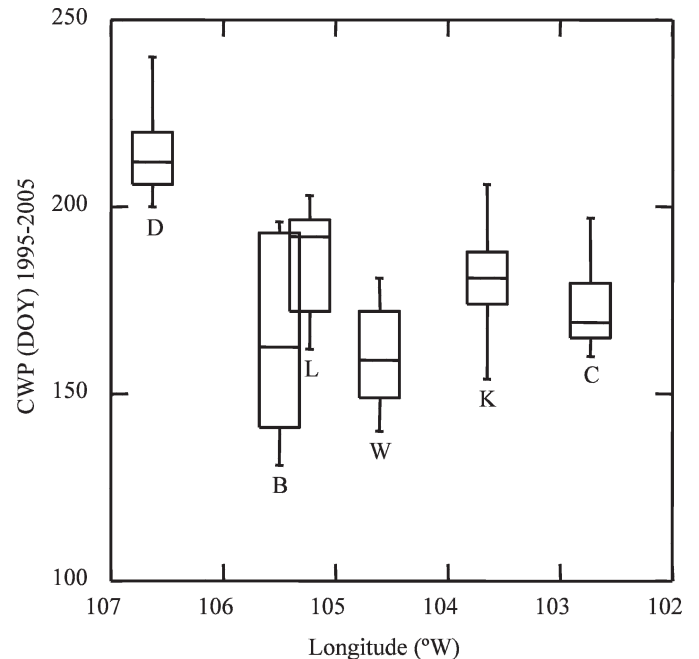


Fig. 2. Calendar day of the year (DOY) of the occurrence of the spring clear-water phase between 1995 and 2005 in the six studied lakes positioned along a longitudinal gradient from west (headwater) to east (downstream), including Diefenbaker (D), Buffalo Pound (B), Last Mountain (L), Wascana (W), Katepwa (K), and Crooked (C) lakes. Boxes represent the interquartile range, the middle line represents the median value for each lake, and $n = 8$ – 11 for each box.

tic of the lakes ($r = -0.50$ to 0.28 , $p > 0.05$ for SD; $r = -0.60$ to 0.49 , $p > 0.05$ for CV), nor with mean total copepod abundance ($r < 0.45$, $p > 0.05$).

Thermal characteristics of CWP—CWP occurred at a similar water temperature in all Qu'Appelle lakes despite significant differences in the rate of lake warming (Fig. 3). As expected, the depth-weighted mean water temperatures of shallow lakes (Wascana, Buffalo Pound) were substantially greater at a given DOY than those of larger lakes (Diefenbaker, Katepwa). These among-lake differences were usually significant on any given date when analyzed using ANOVA with a Scheffé's post hoc test at $p < 0.05$ (analysis not shown). In contrast, the CWP occurred at $16.1^\circ\text{C} \pm 3.7^\circ\text{C}$ (mean \pm SD), with no significant differences among lakes (ANOVA, Scheffé post hoc test, $p > 0.05$), when calculated using water temperatures equivalent to mean depth (polymictic lakes) or mean temperature of epilimnetic zone (stratified Katepwa Lake). Interestingly, CWP occurred at significantly and substantially cooler temperatures in Katepwa Lake ($9.8^\circ\text{C} \pm 3.4^\circ\text{C}$) if calculations were based on mean lake depth at that site.

Correlates of CWP development—Timing and intensity of the CWP were highly correlated with lake morphometry and heat content, but not with most chemical or physical properties of lakes (Table 1, Fig. 4). Linear regression analysis of untransformed data revealed that over 85% of

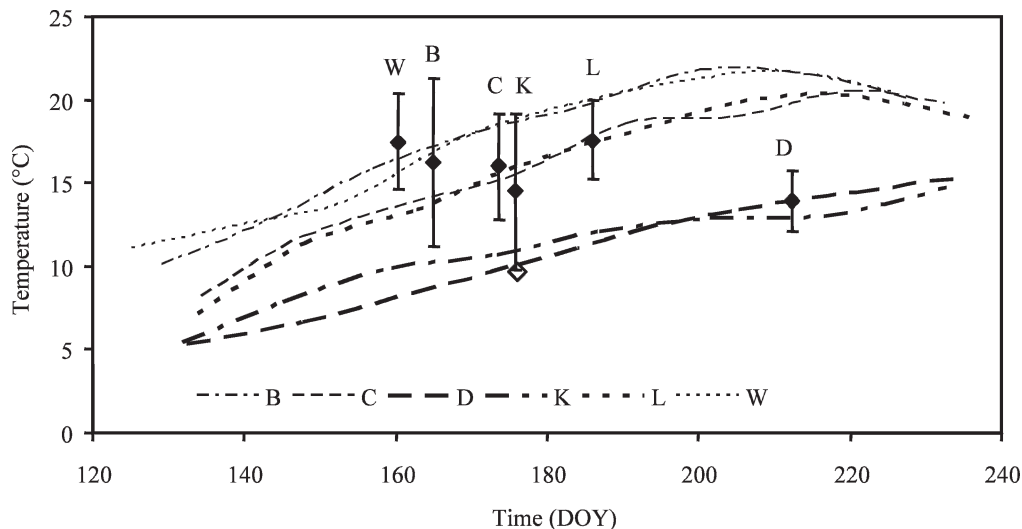


Fig. 3. Relationship between depth-weighted mean water temperature ($^{\circ}\text{C}$) and sampling date (mean DOY, $n = 10\text{--}11$) during 1995–2005 for lakes of the Qu'Appelle Valley, Saskatchewan, Canada. Study lakes include Wascana (W), Buffalo Pound (B), Crooked (C), Katopwa (K), Last Mountain (L), and Diefenbaker (D), in order of increasing basin volume. Solid diamonds and error bars represent depth-weighted mean ($\pm\text{SD}$) water temperature recorded during the CWP event each year and are based on entire lake volumes. For Katopwa Lake alone, the solid diamond represents depth-weighted mean temperature during CWP on the basis of epilimnetic depth, whereas the open diamond represents mean temperature on the basis of the entire lake volume.

variance in timing of CWP among lakes could be predicted by differences in lake volume ($r^2 = 0.876$, $p = 0.006$) (Fig. 4a) or heat income at CWP (θ_{CWP}) ($r^2 = 0.982$, $p = 0.0001$) (Fig. 4c), whereas more than 75% of variation in maximum Secchi depth during CWP was predictable by differences in lake volume ($r^2 = 0.776$, $p = 0.020$) (Fig. 4b) and θ_{CWP} ($r^2 = 0.901$, $p = 0.004$) (Fig. 4d). Regressions were equally strong if total summer heat income (θ_{S}) was used to predict timing ($r^2 = 0.940$, $p = 0.001$) or intensity ($r^2 = 0.911$, $p = 0.003$) of CWP events. In contrast, correlations of CWP characteristics and regional meteorology or climate indices (NAO, PDO, ENSO) were nonsignificant for all lakes analyzed either together or on a site-by-site basis (analyses not shown). Finally, the timing of CWP was inversely correlated with mean annual N:P ratio and depth-integrated Chl *a* concentrations (Table 1), although both predictors were correlated with lake area and maximum depth ($r_{\text{Chl}} = -0.92$ and -0.95 ; $r_{\text{N:P}} = 0.71$ and 0.84 , respectively).

Influence of climate on CWP development—The strength of correlation between CWP and heat income (or lake volume) varied substantially from year to year and in concert with changes in precipitation and, secondarily, river discharge. For example, Pearson correlation coefficients relating the CWP timing to θ_{CWP} in any given year ($r_{\text{timing-}\theta}$) ranged from -0.393 to 0.981 , whereas those for maximum Secchi depth and θ_{CWP} ($r_{\text{Secchi-}\theta}$) varied from -0.260 to 0.908 . In addition, the magnitude of $r_{\text{timing-}\theta}$ was itself correlated negatively with NAO_w ($r = -0.564$ to -0.624 , $p < 0.05$), mid-reach Qu'Appelle River discharge during winter ($r = -0.394$ to -0.561 ,

$p = 0.05\text{--}0.10$), and precipitation during February–April ($r = -0.675$ to -0.781 , $p < 0.05$) (Table 2). In most instances, these same environmental features were also correlated with the strength of correlation between CWP characteristics and lake volume ($r_{\text{Secchi-volume}}$, $r_{\text{timing-volume}}$) (Table 2). In contrast, the strength of the correlations between CWP characteristics and heat income (or lake volume) was not significantly correlated with variation in annual or seasonal air temperature, headwater or downstream river flow, or SOI and PDO climatic indices (all $p > 0.1$). Taken together, these analyses suggest that increases in winter or spring precipitation reduce the regulatory effect of E influx on the timing and intensity of CWP events.

Analysis of meteorological data suggests that regional climate variability during late winter and spring was most strongly associated with variation in the NAO system, and that the magnitude of NAO effect varied by lake size. For example, mean water temperature during spring (first 6 weeks of sampling) was up to 3.5°C greater during years with an elevated NAO_w than during those with low indices, particularly in large lakes. In addition, the date of ice melt was correlated negatively with NAO_w index (annual r varied -0.487 to -0.829), reflecting the significantly greater mean air temperatures during February–April ($r_{\text{temp-NAO}_w} = 0.637$, $p < 0.05$) and increased precipitation during the March–May runoff period ($r_{\text{ppite-NAO}_w} = 0.752$, $p < 0.01$) during years with elevated NAO_w . In contrast, timing of ice melt and spring precipitation were uncorrelated to both ENSO and PDO indices, although the PDO index was correlated weakly with air temperatures in early spring ($r = -0.570$, $p < 0.1$).

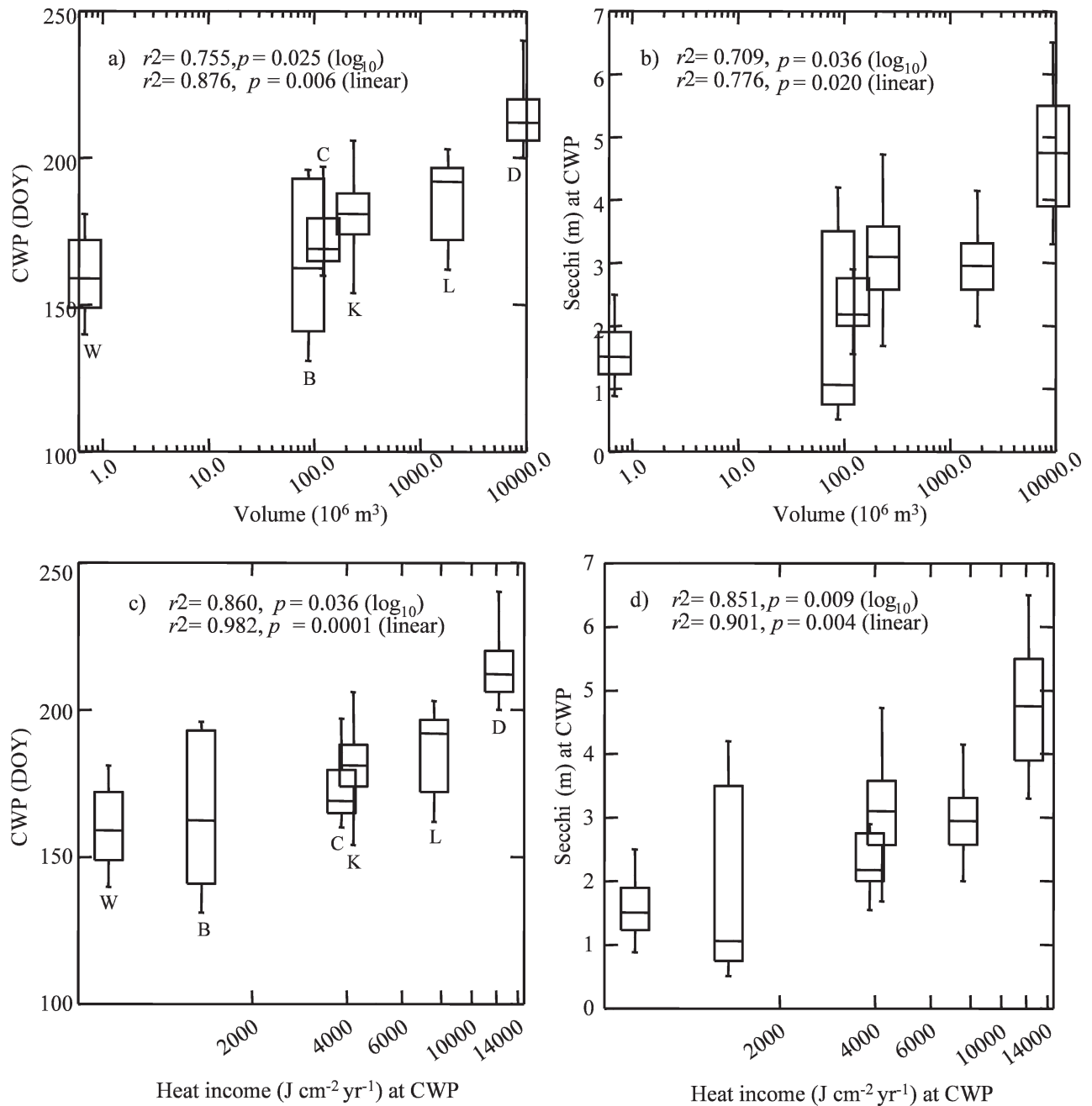


Fig. 4. Relationship between (a, c) timing and (b, d) intensity of CWP events (1995–2005) and (a, b) lake volume and (c, d) the heat income at CWP for the six study lakes. Boxes as in Fig. 2. Figures are plotted on a \log_{10} -transformed axis. Regression statistics are reported for both untransformed (linear) and \log_{10} -transformed data using mean values for each lake. Study lake abbreviations as in Fig. 3.

Discussion

Analysis of decade-long time series of limnological conditions, plankton abundance, heat income, hydrology, and climate from six prairie lakes revealed that the timing and intensity of CWP was regulated by a combination of E transfer from the sun and atmosphere (Fig. 4) and m transfer from precipitation (Table 2). In all lakes, CWP peaked when the water temperature of the mixed layer reached about 16°C (Fig. 3) and *Daphnia* spp. reduced

diatom densities, often to an annual minimum (Dröscher et al. 2008). At a decadal resolution, timing and intensity of CWP was correlated strongly and positively ($r^2 > 0.90$, $p < 0.05$) with net heat income (θ_{CWP} or θ_{S}) and lake volume (Table 1, Fig. 3), but not with other independent lake, catchment, or climate features (Table 1). Instead, at an annual resolution, the strength of correlations between CWP characteristics and heat income ($r_{\text{Secchi-}\theta}$, $r_{\text{timing-}\theta}$) was itself correlated inversely with the NAO_w and associated spring precipitation (Table 2). Furthermore, the magnitude

Table 2. Pearson correlation coefficients (r) for regressions of regional environmental variability (left column) vs. the strength of correlations between clear-water phase characteristics (DOY timing, Secchi depth) and lake volume ($r_{\text{timing-volume}}$, $r_{\text{Secchi-volume}}$) or heat income ($r_{\text{timing-}\theta}$, $r_{\text{Secchi-}\theta}$). Environmental variables include mean (1995–2005) winter (W) and summer (S) discharge of the South Saskatchewan River or the Qu'Appelle River at Lumsden, Craven, Loon, and Welby measuring stations (see site 1–5 in Fig. 1, respectively), indices of atmosphere–ocean linkage (PDO, SOI, NAO_w), mean annual and seasonal precipitation (mm), and mean annual and seasonal air temperature (°C). Correlations are significant at $p < 0.05$ (*), $p < 0.02$ (**), and $p < 0.01$ (***); $n = 10$ for all correlations.

	$r_{\text{timing-volume}}$	$r_{\text{Secchi-volume}}$	$r_{\text{timing-}\theta}$	$r_{\text{Secchi-}\theta}$
South SK River (W) ($\text{m}^3 \text{s}^{-1}$)	0.042	−0.016	0.095	−0.063
South SK River (S) ($\text{m}^3 \text{s}^{-1}$)	−0.219	−0.272	−0.378	−0.394
Lumsden (W) ($\text{m}^3 \text{s}^{-1}$)	−0.380	−0.465	−0.394	−0.561*
Lumsden (S) ($\text{m}^3 \text{s}^{-1}$)	0.532	0.371	0.471	0.403
Craven (W) ($\text{m}^3 \text{s}^{-1}$)	−0.367	−0.459	−0.082	−0.414
Craven (S) ($\text{m}^3 \text{s}^{-1}$)	0.576*	0.475	0.416	0.505
Loon (W) ($\text{m}^3 \text{s}^{-1}$)	−0.357	−0.513	−0.097	−0.499
Loon (S) ($\text{m}^3 \text{s}^{-1}$)	0.527	0.418	0.358	0.442
Welby (W) ($\text{m}^3 \text{s}^{-1}$)	−0.199	−0.249	−0.021	−0.292
Welby (S) ($\text{m}^3 \text{s}^{-1}$)	0.024	−0.074	−0.201	−0.103
PDO (annual mean)	−0.124	−0.086	−0.203	−0.144
SOI (October)	0.079	0.218	0.204	0.432
SOI (annual mean)	0.001	−0.010	0.050	−0.007
NAO _w (December–March)	−0.727***	−0.793***	−0.546*	−0.624*
Precipitation (annual mean) (mm)	−0.049	−0.601*	0.344	−0.622*
Precipitation (February–April) (mm)	−0.573**	−0.623*	−0.781***	−0.675**
Precipitation (March–May) (mm)	−0.592**	−0.758**	−0.478	−0.609*
Precipitation (April–June) (mm)	−0.299	−0.524	−0.133	−0.475
Air temp. (annual mean) (°C)	−0.071	−0.299	0.009	0.203
Air temp. (February–April) (°C)	−0.198	−0.361	0.112	−0.152
Air temp. (March–May) (°C)	−0.182	−0.311	0.012	−0.207
Air temp. (April–June) (°C)	−0.169	−0.325	−0.267	−0.384

(SD) of interannual variation in timing of CWP was correlated positively ($r = 0.86$, $p < 0.05$) with annual mean density of *Daphnia*. Taken together, these patterns suggest a hierarchical mechanism of control in which the transfer of E regulates differences in the timing and intensity of CWP among lakes, whereas the transfer of *m* alters CWP characteristics among years, both by reducing the effects of heat income and by altering the intensity of grazing by herbivores.

Mechanism of CWP development—Spring CWP is a characteristic event in the plankton phenology of many temperate lakes that arises because of complex interactions between light, temperature, nutrients, and biotic interactions of plankton and their consumers (Sommer et al. 1986). In principle, CWP can initiate because of expansion of herbivore populations (Lampert et al. 1986), depletion of essential pools of dissolved nutrients (Huppert et al. 2002), reduction of water-column turbulence and algal suspension following thermal stratification (Berger et al. 2007), or suppression of low light-adapted algae by increasing irradiance (Romo and Miracle 1995). Similarly, the CWP might terminate because of starvation of zooplankton (Shei et al. 1988), development of inedible algal populations (Webster and Peters 1978), or intensification of zooplanktivory by fish (Leucke et al. 1990). However, in contrast to those findings, CWP development in the polymictic lakes of the Qu'Appelle Valley appears to be regulated mainly by selective grazing of *Daphnia* on diatom populations rather

than by thermal stratification, loss of low-light-adapted algae, seasonal changes in nutrient concentrations, or grazing by other herbivores (Dröscher et al. 2008). Therefore, given this observation, as well as the strong relationships between heat income, lake temperature, and CWP occurrence (Figs. 3, 4), we conclude that CWP is initiated in these lakes when E transfer heats mixed-layer water sufficiently to allow *Daphnia* populations to expand sufficiently to control growth of spring algae (Straile 2000).

Temperature can influence the development of *Daphnia* populations through complementary mechanisms that affect both pelagic and sedimentary habitats. For example, temperature regulates development of planktonic populations of *Daphnia* by altering the age at first reproduction, somatic growth rates, and rates of embryo development (Goss and Bunting 1983). In fact, recent experimental evidence suggests that these water-column processes can lead to coherent occurrence of the CWP when water reaches $\sim 16^\circ\text{C}$ (H. Feuchtmayr unpubl.). Similarly, increased water temperature can initiate hatching of diapausing eggs in lake sediments during spring (Vandekerckhove et al. 2005), although the critical hatching temperature also varies with geographic location, thermal history, and light regime (Schwartz and Hebert 1987). *Daphnia* ephippia are abundant in sediments of Qu'Appelle lakes, whereas occasional winter sampling suggests that *Daphnia* do not overwinter as adults (Wyn et al. 2007). Thus, although mean depth varies by 10-fold among Qu'Appelle lakes (Table 1), the polymictic nature of these sites ensures that

the temperature of water overlying sediments is similar throughout individual basins, a condition that favors synchronous hatching of ephippia at a common threshold temperature. Consistent with this mechanism, occasionally stratified Katepwa Lake only conformed to the thermal threshold identified here ($16.1^{\circ}\text{C} \pm 3.7^{\circ}\text{C}$) when calculations of mean temperature were based on depth of the mixing zone rather than mean depth of the basin.

Regulation of spatial variation of CWP—One of the main findings of this study is that timing of CWP events varied directly with lake volume ($r^2 > 0.776$, $p < 0.02$) and heat content ($r^2 > 0.901$, $p < 0.004$) (Fig. 4), but not with lake position in the catchment ($r^2 = 0.311$, $p = 0.250$), despite strong landscape gradients in lake chemistry, trophic status, and algal metabolism (Patoine et al. 2006). As a consequence, timing of the CWP was asynchronous among lakes ($S = 0.072$, $p = 0.53$), despite their proximity within a region of similar soils, geology, land use, and climate (Leavitt et al. 2006). We infer that differences in CWP timing among lakes arise from the large ($\sim 10^4$) variation in lake volume (Table 1) and consequent time required to heat lake water to a critical temperature of $16.1^{\circ}\text{C} \pm 3.7^{\circ}\text{C}$ (see above), rather than from differences in the rate of E influx to individual basins. Consistent with this hypothesis, all main controls of E influx to lakes varied coherently over the Qu'Appelle catchment, including the date of ice melt ($S = 0.895$, $p = 0.006$), mean monthly air temperature ($S = 0.884$ – 0.970 , $p < 0.005$), and total hours of bright sunlight per month ($S = 0.732$ – 0.840 , $p < 0.005$).

Strong correlations between CWP characteristics and lake morphometry (Fig. 4, Table 1) are consistent with monitoring and models that show that differences in lake morphometry influence variations in thermal properties (Robertson and Ragotzkie 1990), heat uptake (Loranger and Brakke 1988), spring warming (Straskraba 1985), and timing of CWP (Straile and Adrian 2000). These morphometric controls may be particularly pronounced in polymictic Qu'Appelle lakes where the absence of thermal stratification allows water to heat relatively uniformly in each basin. In contrast, the presence of thermal stratification may favor more coherent variation in CWP events among other lakes (Blenckner et al. 2007) because epilimnion thickness usually varies less than lake depth within a given lake region (Fee et al. 1996). Specifically, synchrony of CWP events may be more common in stratified lakes because areal E influx does not vary substantially over the lake surface; therefore the rate of warming will depend mainly on the thickness of the epilimnion. However, because stratification can also affect the importance of the sedimentary seed bank to population dynamics of plankton (Vandekerckhove et al. 2005), further research will be required to quantify the interaction between E flux, lake stratification, and plankton phenology (Blenckner et al. 2007).

Although the intensity of the CWP (maximum Secchi) varied among lakes because of differences in heat income (Fig. 4), several lines of evidence suggest that this pattern reflects the combined effects of morphometric controls of transparency and herbivory by *Daphnia*. On one hand,

prior analysis has demonstrated that *Daphnia* increase water clarity during CWP by selective herbivory on diatoms, the predominant algal taxon in spring (Dröscher et al. 2008). Similarly, variation in mean *Daphnia* density was a significant predictor ($r = 0.85$, $p < 0.05$) of variation (SD) in the timing of CWP events (see below). In contrast, a posteriori analysis revealed that correlations between lake volume and mean Secchi depth were as strong before or after CWP ($r^2 > 0.75$, $p < 0.05$) as those performed during CWP (Fig. 4), a finding consistent with the positive relationship between lake size and water-column transparency observed in boreal lakes (Fee et al. 1996). Taken together, these findings suggest that although the absolute transparency achieved during CWP increases with lake size, variations in E influx may provide a secondary control of the rate of *Daphnia* population expansion and the intensity of CWP events.

Regulation of temporal variation in CWP—Although E accumulation regulated spatial variability of CWP, *m* transfer reduced the effect of heat income and induced temporal variability in CWP characteristics both at the catchment scale and within individual lakes. For example, the strength of correlations between heat income and CWP features ($r_{\text{Secchi}-\theta}$, $r_{\text{timing}-\theta}$) declined linearly with both late winter (February–April) and spring precipitation (March–May), and, to a lesser extent, with measured river discharge at mid-catchment (Lumsden) stations (Table 2). Similarly, although the mean temperature during CWP ($\sim 16^{\circ}\text{C}$) did not differ between lakes (ANOVA Scheffé's test $p > 0.05$), there was considerable variability in this temperature among years (Fig. 3) at individual sites (SD up to 5°C). Such site-specific interannual variation was uncorrelated with among-year differences in lake volumes (all lake levels are regulated), heat content, or E transfer from sun or atmosphere (e.g., DOY of ice melt, mean monthly air temperature, mean hours of bright sunlight), suggesting that interannual variation in CWP events did not arise from differences among years in E transfer to lakes. Instead, our findings are consistent with mass-balance studies of other prairie lakes that demonstrate that *m* transfer associated with precipitation (e.g., water, dissolved substances) both reduces the spatial coherence of lake chemistry and increases the temporal variability of lake hydrology (Pham et al. 2009).

In principle, *m* transfer could override the effects of E transfer on CWP through several complementary mechanisms. First, increased nutrient influx during spring runoff events may stimulate spring growth of diatoms and favor increased density of *Daphnia* that alter timing of CWP among years. Consistent with this mechanism, research on European lakes reveals that effects of regional climate on the intensity of spring algal blooms and CWP characteristics are altered by changes in phosphorus influx (Malmmaeus et al. 2006; Blenckner et al. 2007). Second, because winter snowfall accounts for 80% of annual surface runoff in the northern Great Plains (Akinremi et al. 1999), changes in winter and spring precipitation may have had an unusually great effect on the heat budget of Qu'Appelle lakes by delaying the net accumulation of heat in years with

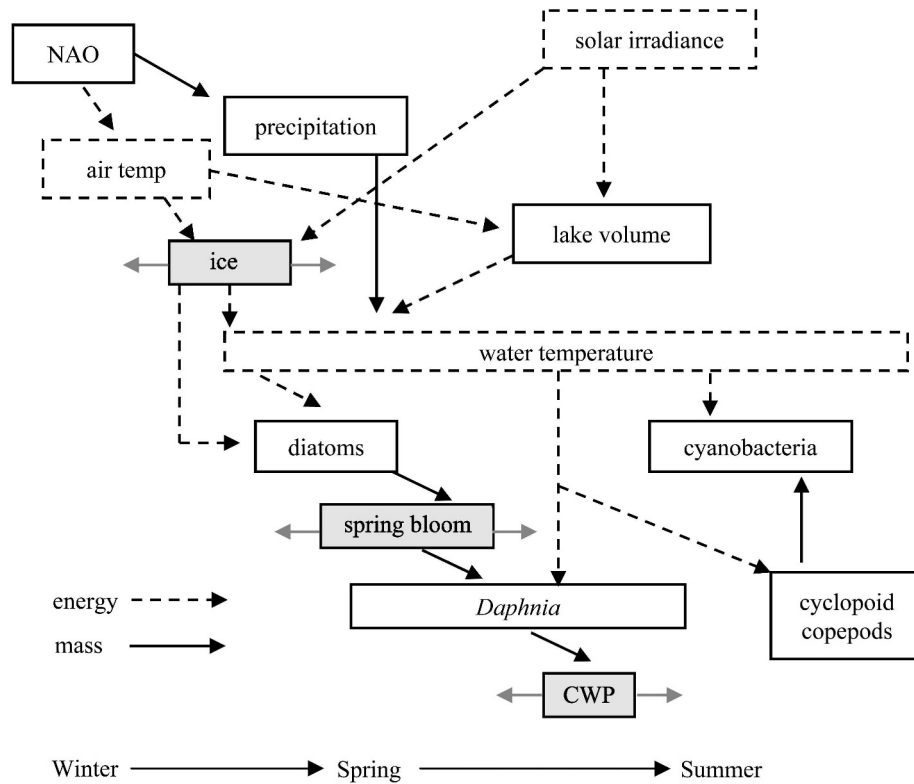


Fig. 5. Pathways of energy (E) and mass (m) flow that influence development of the clear-water phase (CWP) in productive lakes, modified from Blenckner et al. (2007). Solid arrows and boxes indicate predominantly m transfer, dashed arrows and open boxes indicate mainly E transfer, and gray boxes and gray arrows indicate system components for which timing is known to be highly variable. Findings herein demonstrate that E and m transfer affect the timing of CWP through unique pathways that interact to determine the thermal properties of lakes in spring, and consequently the timing and intensity of the CWP. In particular, energetic pathways appear to be overridden by paths that transfer m , at least for processes that influence CWP events.

elevated influx of cold meltwater. Similarly, energetic control of CWP features may be diminished during years with higher precipitation or runoff because of hydraulic washout of plankton (Denke and Nixdorf 1999), an observation that is supported both by the high variability in water residence times among lakes (Table 1) and by the observed 10-fold variation in the volume of river discharge among years in the Qu'Appelle catchment (Patoine et al. 2006). Finally, we note that mean concentrations of dissolved organic matter (DOM) are very high in these lakes (5.9–17.7 mg C L⁻¹), particularly during spring (Leavitt et al. 2006), and speculate that variation in DOM influx may alter absorbance of solar E and heating of water among lakes and years. At present, we have no rationale to favor any specific explanation; therefore we are continuing research to better understand the mechanisms that regulate interactions between transfer of E and m as controls of ecosystem properties.

Role of climate in regulating CWP—Despite the clear relationship between heat income, lake temperature, and CWP development (Figs. 3, 4), neither large-scale climatic processes (NAO_w, PDO, ENSO) nor local meteorology had a significant direct correlation with CWP characteristics, in contrast to findings from western North America (Winder

and Schindler 2004) and Europe (Straile 2000; Straile and Adrian 2000). Instead, our analysis demonstrates that variation in the NAO climate system affected CWP indirectly by increasing spring temperatures ($r_{\text{temp-NAO}_w} = 0.637$, $p < 0.05$) and precipitation ($r_{\text{ppte-NAO}_w} = 0.752$, $p < 0.01$), and by advancing the date of ice melt (i.e., start of heat accumulation) in years with an elevated NAO_w index ($r_{\text{icemelt-NAO}_w} = -0.892$, $p < 0.01$). The lack of direct correlation between NAO_w and CWP features is particularly interesting given that elevated NAO_w indices are correlated directly with earlier ice melt, warmer winters, and higher precipitation in the United Kingdom (George et al. 2004), Scandinavia (Weyhenmeyer et al. 1999), and central Europe (Blenckner et al. 2007). We speculate that these continental differences in NAO effect on CWP events may arise because of differences in water-column circulation within polymictic prairie lakes and the predominantly stratified systems studied in Europe (*see above*). Consistent with this view, Gerten and Adrian (2001) showed that the influence of the NAO on water temperatures differs as a function of thermal and mixing regimes, with a significant NAO effect lasting only into spring for polymictic systems, whereas NAO signals persist until the following winter in deep or stratified lakes because of their greater heat-storage capacity.

In conclusion, comparison of whole-lake heat budgets, seasonal plankton variability, and decade-long changes in lake and meteorological conditions revealed that the transfer of E interacts with lake morphology to directly regulate the timing and intensity of the CWP through herbivory by *Daphnia* in these polymictic lakes (Fig. 5). Variability in major climate systems (NAO) appears to alter the role of both E and herbivores by changing those meteorological conditions that regulate *m* transfer to lakes during spring. However, unlike previous studies, our analysis also suggests that E and *m* transfer act through different pathways, with the transfer of *m* overriding energetic effects, at least under the range of conditions represented by the present study. This paramount effect of *m* transfer on lake processes has also been noted for closed basin saline lakes on the northern Great Plains (Pham et al. 2008, 2009), and suggests that forecasts of the effects of future global change on lake ecosystems must explicitly quantify the unique pathways by which E and *m* transfer regulate lake structure. In particular, because human activity mainly alters *m* flux to lakes rather than E transfer, we predict that anthropogenic disturbances may override the effects of climate warming in many future scenarios.

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