

Climate change drives coherent trends in physics and oxygen content in North American lakes

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Abstract Using a 25-year record of monitoring data, we show that recent climate change has affected the thermal properties and oxygen content of seven lakes in south-central Ontario, Canada, and five lakes in north-central Wisconsin, USA. Coherent patterns in autumnal lake warming were driven by increased autumn air temperature in both lake districts. Temperature increases were restricted to the epilimnion and metalimnion of the lakes, resulting in increased thermal stability of the water column. Mixing depths also decreased over the study period. Shallower mixing depths in the Ontario lakes were due to climate-driven increases in lake-water dissolved organic carbon concentrations. Collectively, changes in the thermal regime of the lakes suggest autumn mixing of the water column may be delayed. Metalimnetic oxygen also increased in the Wisconsin lakes, perhaps in response to increased algal production as lake thermal regimes changed. The response of individual lakes to climate change was modified by lake chemistry in the Ontario lake district and by lake chemistry and morphometry in the Wisconsin lake district. Our results demonstrate coherent lake response to climate change and highlight the importance of both regional and local factors in regulating individual lake response to global climate change.

1 Introduction

Climate change is predicted to alter the quality and quantity of the world's freshwater resources (Schindler 2001; IPCC 2013), and is one of the greatest threats to inland lakes (Environment

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Canada 2004; U.S. Global Change Research Program 2009). Current and projected impacts of climate warming include increased lake surface temperature and changes in thermal structure (Schindler et al. 1996), altered transparency and depth of the mixing zone (Fee et al. 1996; Schindler et al. 1997), and prolonged, more extensive, summer anoxia (Blumberg and Di Toro 1990; Fang and Stefan 2009). Such changes in the physical properties and oxygen content of lakes could greatly affect nutrient cycling and food webs (Sahoo et al. 2012), the availability of preferred habitat (De Stasio et al. 1996), and phenology and morphology of freshwater biota (Daufresne et al. 2009; Winder et al. 2009).

The response of individual lakes to future climate change is still uncertain, however, and may be contrary to climate change model predictions (e.g., Tanentzap et al. 2008). Lake response to climate variability is synchronized within regions subject to the same climatic forces (Magnuson et al. 1990), suggesting neighboring lakes will respond similarly to climate change. Conversely, lake-specific characteristics, such as morphometry, hydrology, and exposure to the atmosphere (Magnuson et al. 1990; Webster et al. 2000), as well as localized stressors like acidification and land use (Christensen et al. 2006) can filter regional climate signals and diversify lake response to climate change (Blenckner 2005). The relationship between climatic drivers and lake properties can also differ among regions (Arnott et al. 2003), further confounding attempts to generalize lake response to climate change. Knowledge of lake responses to current climatic forcing (Chen and Folt 1996; Livingstone et al. 2005), and how regional and local factors modify these responses, is needed for accurate prediction of climate change impacts.

In this paper, we describe 25-year (1981–2005) trends in lake thermal properties and dissolved oxygen content for seven lakes in south-central Ontario, Canada, and five lakes in north-central Wisconsin, USA. Annual air temperature for the study regions is predicted to increase by 1.5–7 °C by the year 2100 (IPCC 2013). As climate is an important determinant of physical properties in the study lakes (Magnuson et al. 1990; Arnott et al. 2003), projected climate warming is expected to have pronounced impacts (De Stasio et al. 1996). Lake properties, particularly upper strata water temperature and mixing depth, behave similarly over time in the study lakes, suggesting climate is driving interannual variability (Benson et al. 2000; Arnott et al. 2003). However, Benson et al. (2000) focused on a small number of key thermal properties and restricted their analyses to the summer period in a small number of years. Long-term changes in the thermal regime and oxygen content of the study lakes and the regional and local factors driving these changes have not been previously investigated. For each lake district, our specific objectives were (1) to determine whether the physical environment and oxygen content of the lakes had changed over time, (2) to determine whether temporal trends were synchronous among lakes, (3) to identify the climatic forces driving synchronous trends, and (4) to identify the local factors regulating individual lake response to regional climate change.

2 Methods

2.1 Study lakes

The seven lakes in south-central Ontario are located within a 34 km radius (Fig. 1), and have been sampled by the Ontario Ministry of the Environment, Dorset Environmental Science Centre (DESC) since the mid-1970s. The lakes are on the Precambrian Shield, and are underlain by granitic bedrock overlain by thin (<1 m) glacial till and soil, although deeper deposits occur. The lakes are small headwater lakes with the exception of Red Chalk, which is

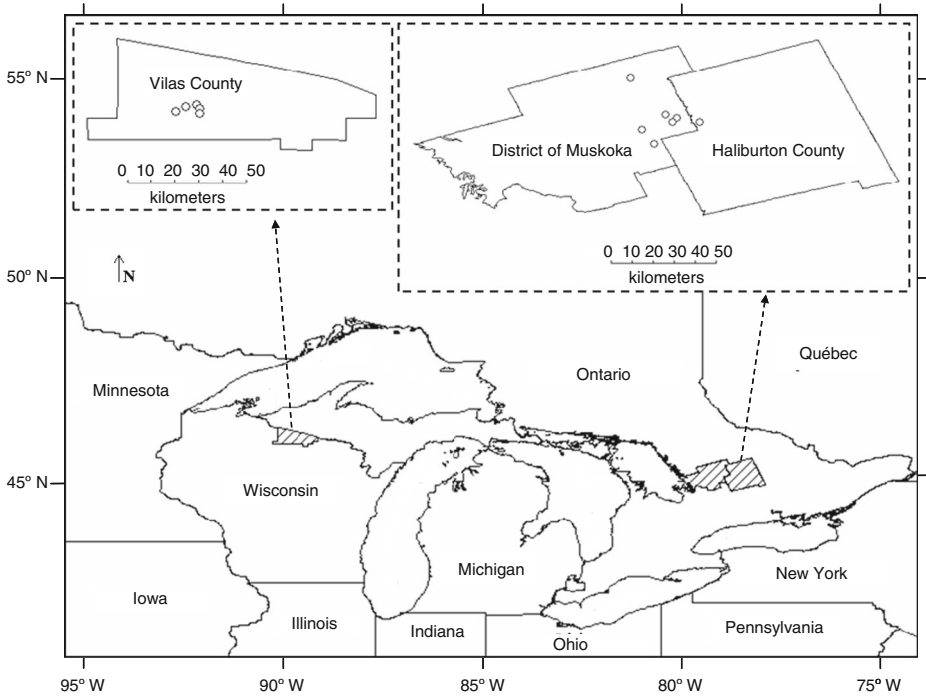


Fig. 1 Location of the seven Dorset, Ontario (DESC) and five Trout Lake Area, Wisconsin (NTL-TLA) study lakes

downstream of Blue Chalk. They are softwater, low productivity lakes (Table 1), and are dimictic, although Dickie exhibits weak stratification.

The five lakes in north-central Wisconsin are within a 10 km radius in the North Temperate Lakes-Trout Lake Area (NTL-TLA; Fig. 1). The NTL-TLA lakes have been monitored by the North Temperate Lakes Long-Term Ecological Research program since 1981 (lter.limnology.wisc.edu) and are described in Magnuson et al. (2006). Like the DESC lakes, the NTL-TLA lakes are located on the Precambrian Shield but glacial deposits are much deeper at 30–50 m. The NTL-TLA lakes are in the same groundwater flow system and are seepage lakes with the exceptions of Allequash and Trout, which are principally drainage lakes with surface inlets and an outlet (Magnuson et al. 1990). The lakes are dimictic with low to moderate ion concentrations (Table 1). Both the NTL-TLA and DESC lakes are within secondary growth forested watersheds with zero to moderate lakeshore development. The study regions are within the north temperate climate zone.

2.2 Data collection

Vertical temperature and dissolved oxygen (DO) profiles were measured at a weekly to monthly interval over the ice-free period from 1981–2005. Profiles were measured at the deepest point of the lakes using YSI DO meters (YSI Inc., Yellow Springs, Ohio, USA) with a temperature probe. Secchi disc depth was also recorded. Temperature and DO were used in conjunction with bathymetric and volumetric data at 1 m (NTL-TLA) and 2 m (DESC) depth intervals to characterize the thermal and DO status of the lakes. Lake parameters are listed in Table 2 and described further in Online Resource 1.

Table 1 Selected characteristics of the Dorset, Ontario (DESC) and Trout Lake Area, Wisconsin (NTL-TLA) study lakes. Lake level and chemistry values shown are means for the year 2005

	Area (ha)	Volume ($\text{m}^3 \times 10^5$)	Mean Depth (m)	Climatic Exposure ^a ($\text{m} \times 10^4$)	Residence Time ^b (yr)	Lake Level (masl)	Lake Level Slope ^c (m yr^{-1})	Conductivity ($\mu\text{S cm}^{-1}$)	pH	DOC (mg L^{-1})	Total Phosphorus ($\mu\text{g L}^{-1}$)	Chlorophyll <i>a</i> ($\mu\text{g L}^{-1}$)
DESC												
Blue Chalk	52.4	44.7	8.5	6.2	4.0	344	NC	26.1	6.7	2.4	6.5	1.8
Chub	34.4	30.4	8.9	3.9	1.9	371	NC	22.0	5.7	5.4	7.4	2.8
Crosson	56.7	52.2	9.2	6.2	1.5	332	NC	20.2	5.7	5.5	10.0	4.3
Dickie	93.6	46.7	5.0	18.7	1.5	355	NC	39.6	6.0	5.5	10.6	4.0
Harp	71.4	95.1	13.3	5.4	2.9	327	NC	36.3	6.2	3.9	5.8	2.7
Plastic	32.1	25.2	7.9	4.1	3.0	376	NC	16.9	5.7	2.7	4.7	1.9
Red Chalk ^d	44.1	73.5	16.7	2.6	2.4	343	NC	24.3	6.3	3.3	6.5	2.0
NTL-TLA												
Allequash ^d	112.4	43.0	3.8	29.3	2.0	494	-0.009	100.7	7.8	4.1	8.9	11.9
Big Muskellunge	396.3	298.8	7.5	52.6	8.0	500	-0.018	51.5	7.4	4.3	5.2	3.4
Crystal	36.7	38.0	10.4	3.5	12.0	501	-0.015	12.2	6.6	2.3	4.6	3.0
Sparkling	64.0	69.5	10.9	5.9	10.0	495	-0.012	96.4	7.5	3.5	4.0	3.4
Trout ^d	1090.9	1630.9	14.9	73.0	5.0	492	-0.003	99.9	7.6	3.1	4.4	3.6

^a Ratio of lake surface area to mean depth (Magnuson et al. 1990)

^b From Arnott et al. (2003), and Hanson et al. (2006)

^c NC indicates no change; only Allequash showed a significant (MK $p < 0.05$) decrease in lake level

^d Excludes east, south, or north basin, respectively

Table 2 Summary results of Regional Kendall analysis of trends in lake thermal characteristics and dissolved oxygen content for the DESC and NTL-TLA lake districts

Lake Property	Abbreviation	Units	DESC			NTL-TLA		
			1981–2005 Mean	z	Rate of Change (yr ⁻¹)	1982–2005 Mean	z	Rate of Change (yr ⁻¹)
Surface temperature	T _{surf}	°C	18.5±0.3	2.7**	0.08±0.03	14.9±0.6	2.9**	0.09±0.01
Epilimnion temperature	T _{epi}	°C	18.2±0.3	2.7**	0.08±0.03	14.8±0.6	2.8**	0.09±0.01
Metalimnion temperature	T _{meta}	°C	12.0±0.8	2.5*	0.05±0.03	11.7±0.8	3.0**	0.05±0.02
Hypolimnion temperature	T _{hylo}	°C	6.6±1.5	1.1	NS	8.0±1.3	1.4	NS
Lake temperature	T _{lake}	°C	13.6±2.8	2.1*	0.04±0.02	13.5±1.0	2.6**	0.07±0.02
Heat content	H	calories cm ⁻²	53265±12765	2.0*	121.7±58.5	52508±19773	2.6**	243.1±54.3
Thermal stability	S	g-cm cm ⁻²	1486±1105	2.0*	8.1±4.6	1854±2025	3.0**	26.8±19.8
Thermocline depth	Z _{thermo}	m	6.5±1.4	-2.4*	-0.02±0.02	11.2±2.7	-2.4**	-0.05±0.03
Metalimnion depth	Z _{meta}	m	6.2±1.6	-2.7**	-0.01±0.02	10.0±2.6	-2.3*	-0.05±0.03
Hypolimnion depth	Z _{hylo}	m	9.5±1.9	-1.8	NS	13.2±3.3	-1.7	NS
10 °C depth	Z _{10°}	m	8.9±2.1	-1.3	NS	11.0±3.6	0.7	NS
Secchi disc depth	Z _{Secchi}	m	5.0±1.6	1.1	NS	4.8±1.9	-0.2	NS
Metalimnion dissolved oxygen	VWMO	mg L ⁻¹	7.1±3.5	-1.4	NS	5.5±2.8	3.0**	0.11±0.04
Hypolimnion dissolved oxygen	VWHO	mg L ⁻¹	3.5±2.2	0.2	NS	2.1±1.6	0.5	NS
Volume at DO ≤4 mg L ⁻¹	V _{DO4}	m ³ ×10 ⁵	5.8±3.5	1.5	NS	43.6±84.4	0.5	NS

Temporal trend z-values significant at $p < 0.05$ (*) and 0.01 (**) are indicated. Rate of change values represent the mean slope (± standard deviation) for lakes within a lake district; NS indicates temporal change was not significant. The 1981/82–2005 mean of the lake properties are also shown for the DESC (September) and NTL-TLA (September–October) lakes; the long-term mean for each lake was calculated and then averaged across lakes

2.3 Temporal trends in lake physics and oxygen content

Temporal trends within each lake district were assessed using Regional Kendall tests executed in Systat 12 (Systat Software Inc., Chicago, Illinois, USA). This nonparametric technique tests for a consistent trend at multiple locations regardless of whether trends at individual locations are significant and does not require trends to be linear nor data to be normally distributed; trends were considered significant at $p < 0.05$ after adjusting for spatial autocorrelation (Hirsch and Slack 1984; Helsel and Frans 2006). Prior to analyses, a monthly mean for each parameter was calculated to standardize sampling frequency across lakes. Global trend tests (van Belle and Hughes 1984) and Holm-Sidak multiple comparison tests indicated the direction of trends was homogeneous among lakes but heterogeneous among months so Regional Kendall tests were performed for each month. Allequash Lake (NTL-TLA) was not included in October trend tests for metalimnetic and hypolimnetic parameters because it tended to destratify by early October.

2.4 Temporal coherence of lake physics and oxygen content

Temporal coherence, a measure of the degree to which different locations within a region behave similarly over time (Magnuson et al. 1990), was assessed for each lake district. Only parameters found to significantly increase or decrease over time were examined. Coherence was measured using r_i , the intraclass correlation coefficient from a two-way (year and lake) analysis of variance (Rusak et al. 2008). Data were unit variance standardized (i.e., z -scored) prior to analysis so that r_i equaled the mean Pearson correlation coefficient for all pairwise lake comparisons. A r_i of one indicates exact synchronous behavior over time. As regional coherence can be reduced by the inclusion of lakes with opposing temporal patterns, synchronous subsets of lakes were identified prior to coherence analysis using Brien's test for correlation matrices (Rusak et al. 2008).

2.5 Regional drivers of lake physics and oxygen content

For each lake district, the climatic factors explaining the greatest amount of interannual variation in lake properties were identified using forward stepwise multiple linear regressions. Explanatory variables were monthly mean air temperature (based on the average of daily values), total precipitation, the North Atlantic Oscillation (NAO) and El Niño-Southern Oscillation (ENSO) indices, and lake-water dissolved organic carbon (DOC). Temperature and precipitation values were from Environment Canada meteorological stations at Muskoka Airport (DESC) and the Wisconsin State Climatology Office (NTL-TLA). NAO and ENSO were from the National Weather Service Climate Prediction Centre (cpc.ncep.noaa.gov). For temperature, precipitation and the NAO, monthly values were averaged and regressions performed using winter (December of the previous year to February of the current year), spring (March–May), summer (June–August), autumn (September–October), ice-covered (November–April), ice-free (May–October), and annual (January–December) values. ENSO represented the sum of monthly values from September–March, a period that encompasses most El Niño events. Z -scored ice-free season mean DOC averaged across all lakes within a district was included since DOC is regulated by climate and affects lake physics (Keller et al. 2006, 2008). DOC sampling regimes and laboratory methodologies are detailed elsewhere (OMOE 1983; Girard et al. 2007; lter.limnology.wisc.edu/protocols.html).

Prior to stepwise regression analyses, the mean z -score for each parameter was calculated to summarize temporal patterns across the lake district. As nearly all parameters were

significantly correlated (Pearson correlation p -values < 0.05), principal components analysis (PCA) was used to reduce the dimensionality of the data. Although climatic and chemical signals can persist in lakes over periods > 1 year (Coats et al. 2006), cross-correlation analyses indicated 1–10 year lag periods did not improve correlations between the principal components (PCs) and explanatory variables. Regression analyses were performed in Systat 12 and retained explanatory variables were significant at $p < 0.05$ after Bonferroni adjustment for multiple significance tests. Model residuals were examined for normality, homoscedasticity and independence, and outliers removed as necessary to meet linear regression requirements. To assess whether the regression results were an artifact of relating nonstationary time series, regression analyses were repeated using data that had been detrended (by removing the linear trend over time) or first-order differenced (Chatfield 2004).

2.6 Local regulators of regional drivers

The importance of lake-specific factors in determining individual lake response to regional drivers was assessed using the multivariate ordination technique redundancy analysis (RDA) executed in CANOCO version 4.02 (Centre for Biometry, Wageningen, The Netherlands). For each lake district, the changes in lake thermal properties and oxygen content over time were included as dependent variables. Predictor variables included the morphometry, hydrology, and 1981–2005 mean for lake level and ice-free season chemistry variables detailed in Table 1. Because lake chemistry changed over the study period (Palmer et al. 2011; Palmer, unpublished data), the change in each chemistry variable was calculated using Sen's estimator of slope and also included as a predictor. Annual mean lake level decreased (Mann-Kendall (MK) trend test p -value = 0.004) in Allequash by 0.2 m (estimated using Sen's slope; Table 1) over the study period. Although not significant (MK p -values ~ 0.1), there was also a tendency towards lower lake levels in Big Muskellunge and Crystal. The change in lake level based on Sen's slope was included as a predictor to account for any effect from decreasing lake levels. For the DESC lakes, the change in lake depth was not included as a predictor because Yao et al. (2009) found that DESC lake levels have not changed over time. Predictors were log-transformed as necessary to meet RDA normality requirements. Detrended correspondence analysis confirmed the dependent-predictor relationships were linear. A forward selection step was included in the RDA to reduce predictor variable collinearity.

3 Results

3.1 Temporal trends in lake physics and oxygen content

Temporal trends largely occurred in the autumn months. In the DESC district, eight physical parameters changed (p -values < 0.05) with all changes occurring in September. In the NTL-TLA district, 19 of the 23 significant trends occurred in September and/or October so trend tests were repeated using the average of the monthly values. Oxygen was not available for the NTL-TLA lakes in September of 1981 so trends were based on 1982–2005. Trends reported are from September (DESC) and the September–October means (NTL-TLA; Table 2). Subsequent analyses were restricted to these autumn periods because 87% of the significant trends in lake physics occurred in the autumn and our objective was to investigate the factors driving long-term changes in the study lakes. An examination of the factors driving interannual variation in parameters that did not significantly increase or decrease over time was beyond the scope of the present study.

Lakes became warmer and more stable with shallower mixing depths (Table 2). In the DESC lakes, T_{surf} and T_{epi} increased by 2 ± 0.7 °C while T_{meta} increased by 1.2 ± 0.7 °C, which resulted in higher T_{lake} , H, and S (respective increases of 0.9 ± 0.5 °C, $6 \pm 3\%$, and $22 \pm 17\%$). T_{hypo} did not change regionally but increased by 1.1 °C in Plastic, which had the deepest euphotic zone relative to lake depth. Z_{meta} and Z_{thermo} became shallower but the maximum decrease was only 1.3 m and decreases were <0.1 m in three lakes. In the NTL-TLA lakes, T_{surf} and T_{epi} similarly increased by 2 ± 0.3 °C while T_{meta} increased by 1.2 ± 0.5 °C. T_{lake} , H, and S also increased (respective increases of 1.6 ± 0.5 °C, $12 \pm 4\%$, and $60 \pm 25\%$) while Z_{meta} and Z_{thermo} decreased by 1.2 ± 0.7 m. Unlike in the DESC lakes, VWMO increased by 2.5 ± 1 mg L⁻¹ in the NTL-TLA lakes.

3.2 Temporal coherence of lake physics and oxygen content

Temporal patterns were generally synchronous among lakes within each district (all r_i values were significant at $p < 0.01$), indicating lakes were responding to a regional driver. Where asynchrony was detected, it was due to 1–2 years and their removal only increased r_i by 0.05 ± 0.03 so lakes were considered coherent. Temporal coherence was highest for T_{surf} and T_{epi} , decreased slightly for whole-lake measures of temperature, H, and S, and was lowest for mixing and metalimnetic parameters (Fig. 2). In the DESC lake district, r_i for T_{surf} , T_{epi} , T_{lake} , H, and S averaged 0.61 ± 0.06 . Coherence of Z_{thermo} was 0.42 while r_i of T_{meta} and Z_{meta} was much lower at 0.18–0.19. Coherence was consistently higher in the NTL-TLA district with r_i of 0.77 ± 0.10 for T_{surf} , T_{epi} , T_{lake} , H, and S and 0.53 ± 0.04 for Z_{thermo} , Z_{meta} , and T_{meta} . Coherence of VWMO was 0.55. Benson et al. (2000) also found that coherence within these lake districts was highest for surface conditions and declined for mixing depth. They argued that higher coherence in the NTL-TLA lakes was due to the smaller size of the study area and greater sampling frequency.

3.3 Regional drivers of lake physics and oxygen content

For both lake districts, ~90% of the variability among lakes was summarized along the first two PCA axes (Online Resource 2). PC1 represented a positive temperature and stability gradient (correlations between parameters and PC1 of 0.81–1.00) while PC2 represented a positive mixing depth gradient (0.73–0.89) for both lake districts. PC2 was also negatively correlated (–0.91) with VWMO for the NTL-TLA lakes. PC1 and PC2 scores were used to summarize lake properties in regression analyses. Reported regression models were significant ($p < 0.05$) and included untransformed data as r^2 values decreased by only 0.04 ± 0.04 when data were detrended and differenced, indicating results were not an artifact of relating nonstationary time series.

Air temperature was the most important predictor of lake temperature, H, and S. In the DESC lake district, September air temperature explained 57% of the temporal variability in regional values of PC1 (Fig. 3a). This relationship was reduced to 34% with the inclusion of the outlier year 1991. September air temperature increased at a rate of 0.1 °C yr⁻¹ for a total increase of 2.4 °C between 1981–2005 (Fig. 3a). In the NTL-TLA lake district, autumn air temperature similarly explained 60% of the variability in PC1 (Fig. 3b). Autumn air temperature increased by 0.04 °C yr⁻¹ for a total increase of 1 °C. For both districts, the air temperature increase was most prominent after the early-1990s. Change in autumn air temperature for the NTL-TLA lake district was driven by a 2 °C increase in September air temperature (rate of 0.09 °C yr⁻¹) as October air temperature did not change over the study

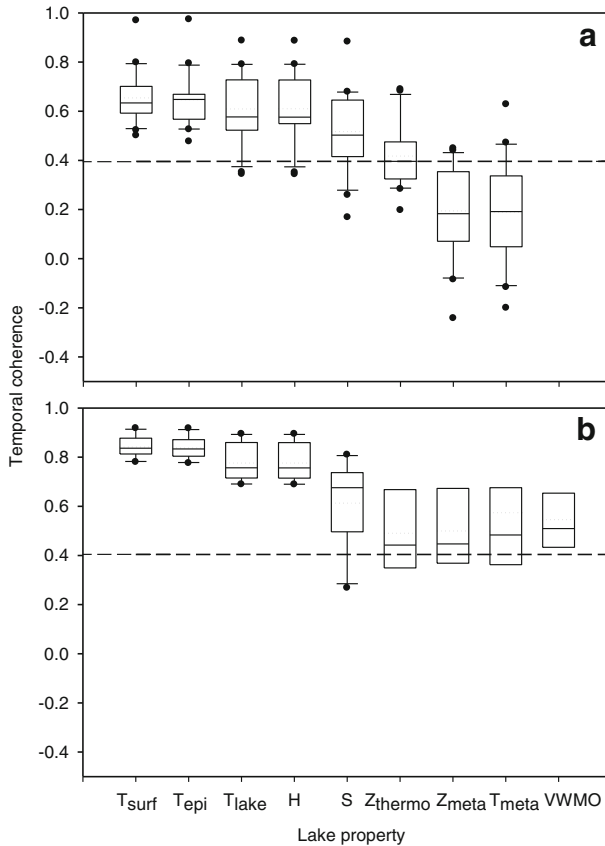


Fig. 2 Box plot diagrams of temporal coherence between lake pairs within the (a) DESC and (b) NTL-TLA lake districts. The dotted lines of the boxes indicate the r_1 values, the solid center lines of the boxes indicate the median coherence values, the boxes indicate the 25th and 75th percentiles, the vertical bars indicate the 10th and 90th percentiles, and the points indicate outliers. The dashed lines indicate the Pearson correlation coefficient values at which positive pair-wise comparisons are significant (two-tailed $p=0.05$). Abbreviations are defined in Table 2

period (MK $p=0.7$). For both lake districts, the mean rates of increase in T_{surf} and T_{epi} (Table 2) were similar to the rate of increase in September air temperature, further illustrating the close association between air and lake temperatures.

The best predictor of mixing depths differed between lake districts. In the DESC district, 57% of the regional variation in PC2 was explained by DOC (Fig. 3c). When the outlier years 1995 and 1996 were included, DOC accounted for 32% of the PC2 variation. The regional trend in DOC was significant (MK $p=0.001$) with DOC increasing by $0.7 \pm 0.4 \text{ mg L}^{-1}$. In the NTL-TLA lake district, mixing depths and VWMO were best predicted by spring air temperature, which accounted for 43% of the variation in PC2 (Fig. 3d). Although spring air temperature did not change monotonically over the study period (MK $p=0.4$), there was a non-significant $2.3 \text{ }^\circ\text{C}$ decrease in May air temperature (MK $p=0.12$) that may have contributed to shallower mixing depths and increased VWMO. However, the lack of significance suggests factors not examined in this study also contributed to the decrease in PC2.

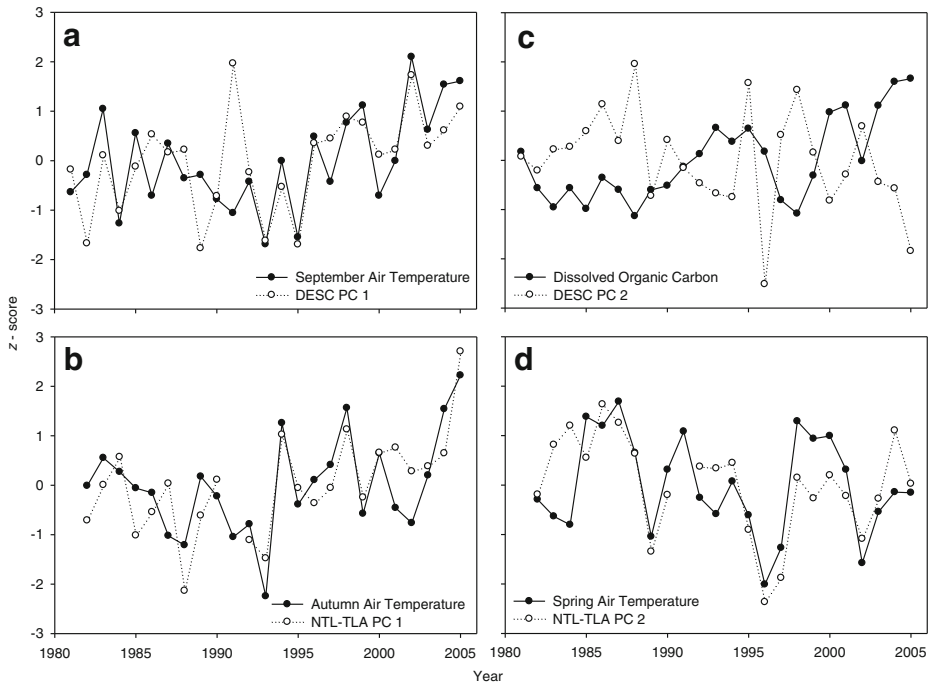


Fig. 3 Regional change in lake properties and stepwise regression selected predictors for the DESC (**a** and **c**) and NTL-TLA (**b** and **d**) lake districts. PC1 trend lines summarize increases in temperature, heat, and stability, while PC2 trend lines summarize decreases in mixing depths (**c** and **d**) as well as increases in metalimnion oxygen (**d**)

3.4 Local regulators of regional drivers

In the DESC lakes, 71.8% of the among-lake variance in lake warming and decreased mixing depths was explained by pH and the temporal change in DOC (ordination $p=0.01$; Online Resource 3). RDA axis 1 represented a gradient in DOC increases and explained a large amount of the variance in T_{surf} and T_{epi} (86%), Z_{thermo} (74%), T_{meta} , S, and Z_{meta} (39–47%). Lakes with greater increases in DOC had greater increases in temperature in the upper strata of the water column and greater reductions in mixing depths. Along RDA axis 2, lakes with lower pH and smaller increases in DOC had greater increases in T_{lake} and H (84 and 96%, respectively).

In the NTL-TLA lakes, 92.4% of the among-lake variance in lake warming, shallower mixing depths, and increased VWMO was explained by mean lake depth and change in chlorophyll-*a* (Online Resource 3). RDA axis 1 was positively correlated with mean depth and explained a large amount of the variance in H (92%), T_{surf} , T_{lake} , S, T_{epi} , and T_{meta} (56–86%), as well as Z_{meta} and Z_{thermo} (46 and 36%, respectively). Shallower lakes had greater temperature increases but smaller increases in H and S. Reductions in mixing depths were also slightly greater in deeper lakes. RDA axis 2 was positively correlated with chlorophyll-*a* and explained 91% of the variance in VWMO and about half of the variance in Z_{thermo} and Z_{meta} (59 and 49%, respectively). Lakes with larger increases in chlorophyll-*a* had greater increases in VWMO and greater reductions in mixing depths. However, RDA results for the NTL-TLA

lakes were only suggestive as the ordination p -value was 0.06 (retained parameters were significant at $p < 0.15$) and correlations were based on only four lakes.

4 Discussion

Twenty-five year (1981/82–2005) trend analyses clearly demonstrate that regional climate change drives coherent responses in the thermal properties and oxygen content of lakes in south-central Ontario and north-central Wisconsin. Warmer autumn lake temperatures and the resultant increases in H and S were driven by increased air temperature in both lake districts. Air temperature, which is primarily determined by large-scale air masses, is coherent across the Great Lakes region (Benson et al. 2000). Not surprisingly then, autumn air temperature increases were similar between the lake districts and caused similar responses. At warmer air temperatures incident atmospheric longwave radiation increases while latent and sensible heat loss decrease, warming surface waters (Livingstone 2003). On average, 80 (DESC) and 100% (NTL-TLA) of the air temperature increases were mirrored in T_{surf} and T_{epi} increases while ~50% of the increases were transmitted to the metalimnion of the lakes. Hypolimnetic temperatures, which are largely determined by spring conditions in dimictic lakes (Hondzo and Stefan 1993), were unaffected by increases in autumn air temperature. Disproportionate warming of the upper strata of the lakes, combined with the nonlinear increase in water density with increasing temperature, resulted in stronger thermal density gradients and greater S. Our results corroborate extensive empirical evidence showing air temperature strongly affects water temperature in North American lakes (e.g., Shuter et al. 1983). Changes in the study lakes were also similar to those reported for other lakes with available long-term thermal data (Schindler et al. 1996; Livingstone 2003).

Unlike lake warming trends, shallower mixing depths were driven by forces acting at the smaller scale of the lake district. In the DESC lakes, shallower mixing depths were best predicted by regional increases in DOC, which has previously been identified as the most important determinant of late summer and early fall mixing depths for <700 ha lakes in Ontario (Pérez-Fuentetaja et al. 1999; Keller et al. 2006). In non-eutrophic lakes like the DESC lakes, DOC controls vertical light attenuation and absorption of solar radiation by surface waters. As DOC increases, vertical light attenuation increases while surface waters heat faster, causing thermal density gradients to develop faster at shallower depths (Fee et al. 1996; Pérez-Fuentetaja et al. 1999; Cahill et al. 2005). Thermal resistance to mixing is also enhanced at higher DOC concentrations (Holloway 1980), which may have delayed wind and density-driven deepening of mixing depths. DOC increases were likely due to changes in air temperature and precipitation (Keller et al. 2008). Although air temperature is coherent between the lake districts (Benson et al. 2000), precipitation is a localized force which may explain why a concurrent increase in DOC did not occur in the NTL-TLA district (Regional Kendall $p=0.8$). In contrast to the current study, Schindler et al. (1997) document deepening thermocline depths due to drought-induced reductions in DOC export that increased light penetration in the Experimental Lakes Area, Ontario. These contrasting results demonstrate the complexity of climate impacts on DOC and lake mixing depths.

Spring air temperature best predicted autumn mixing depths in the NTL-TLA lakes. Surface waters heat faster at warmer air temperatures, resulting in earlier onset of stratification and shallower Z_{thermo} (Blumberg and Di Toro 1990; Cahill et al. 2005). Surprisingly, this relationship was reversed as shallower mixing depths occurred during cool springs. Over the study period, ice breakup occurred six days earlier in the NTL-TLA lakes (Regional Kendall $p=$

0.02). The earlier open water season combined with cooler May air temperature may have kept surface temperatures cool throughout the spring. Thus, when air temperature increased, density differences may have developed quickly, resulting in shallower mixing depths.

Mixing depths are also influenced by wind, which generates currents that deepen autumn mixing depths. Wind was not included in the regression analyses as wind data were not consistently available. However, wind data for a subset of the study years were available from the Woodruff Airport meteorological station located <15 km from the NTL-TLA lakes. These data show that mean fall wind speed (based on daily wind speed averages) decreased by nearly 20% (0.5 m s^{-1}) between 1989–2005 (MK $p=0.01$). If this represents a long-term trend, reduced wind speed may have contributed to shallower mixing depths. Uncertainty as to the mechanisms driving shallower fall mixing depths is not limited to the current study. In Lake Tahoe, USA, decreases in Z_{thermo} between 1970–2002 were not correlated with wind, temperature-induced increases in S , nor decreases in water clarity (Coats et al. 2006).

Collectively, warmer lake temperatures, greater S , and shallower mixing depths suggest delayed autumn mixing. Prolonged stratification in response to autumn lake warming and shallower mixing depths has also been predicted for Lake Mendota in south-central Wisconsin and the Great Lakes (Robertson and Ragotzkie 1990; Trumpickas et al. 2009). Based on models for Lake Mendota, Robertson and Ragotzke (1990) estimated that a 3–6 °C increase in autumn air temperature would delay overturn by 5–10 days. Although overturn dates were not available, the 2–2.5 °C increase in September air temperature coincided with a non-significant (trend test p -values < 0.13) 4–6 day delay in ice-on in the lakes, suggesting overturn may indeed have been delayed.

Warming of lake waters is generally predicted to result in lower DO concentrations (Blumberg and Di Toro 1990; Fang and Stefan 2009). Contrary to expectations, VWMO did not decrease in either lake district and VWMO increased in the NTL-TLA lakes. Cooler spring air temperatures may have contributed to greater VWMO. Oxygen influx to the lakes largely occurs by air-water gas exchange during periods of thermal mixing (Hanson et al. 2006). Under cooler spring conditions the DO saturation point of water is elevated, thus a higher concentration of DO may be retained in the metalimnion as stratification develops following spring mixing. As well, entrainment of DO from the metalimnion into the oxygen depleted hypolimnion may have been reduced as temperature-induced increases in the vertical density gradient would have limited vertical diffusion of DO (Stefan and Fang 1994). Increased algal oxygen production may also have contributed to VWMO increases. As mixing depths decreased, a greater proportion of the metalimnion was within the euphotic zone. Because oxygen production in the metalimnion is limited by light, increased overlap between the metalimnion and euphotic zone, as well as warmer water temperatures, may have enhanced production. There is some support for this hypothesis as autumn chlorophyll- a concentrations increased by $1 \mu\text{g L}^{-1}$ (Regional Kendall $p=0.0008$). As well, the positive relationship between chlorophyll- a and increased VWMO was driven by Crystal Lake, which had the greatest increase in chlorophyll- a over the study period. The same pattern of increasing VWMO did not occur in the DESC lakes where chlorophyll- a decreased (Regional Kendall $p=0.03$).

Lake response to climate change was modified by lake-specific characteristics. Among the DESC lakes, greater increases in DOC limited light penetration causing greater reductions in mixing depths and greater warming of the upper strata of the lakes, presumably through enhanced heat absorption. As heating was restricted to shallower upper strata, stability increases were intensified and whole-lake warming and H increases were smaller. Lower pH was also related to greater increases in T_{lake} and H . This relationship was driven by differences

between Plastic with a pH of 5.7 and the non-acidic Blue Chalk and Red Chalk. As Plastic is shallow (maximum depth 16.3 m) and has a relatively deep euphotic zone (25-year average of 14 m), the entire water column including the hypolimnion warmed in response to increased air temperature. The depth of warming in the other DESC lakes was restricted due to relatively shallow euphotic zones (mean euphotic depth was $35 \pm 14\%$ as deep as maximum lake depth), thus increases in T_{lake} and H were limited. Yan (1983) similarly found that increased light penetration in acidified lakes increased hypolimnetic heating. Lake morphometry was important in the NTL-TLA district where shallower lakes responded more strongly to climatic warming, although deeper lakes with greater water volume had greater total (but proportionally smaller) increases in H and stability.

5 Summary and implications

Climate change is expected to cause large-scale changes to lake environments. To better predict and prepare for these changes, we need to understand how lakes respond to current climatic forcing and identify regional and local factors that modify these responses. Here, we document 25-year trends in lake warming, increased stability, shallower mixing depths, and increased metalimnetic oxygen content for lakes in Ontario and Wisconsin. Trends were synchronous indicating changes were driven by climate. Air temperature was the dominant force driving increased lake temperature and stability in both lake districts while forces driving shallower mixing depths differed between regions. The magnitude of climate-induced change was modified by lake-specific factors. These findings demonstrate the important role both regional and local factors play in determining how a lake will respond to global climate change. Our results are based on statistical analysis of long-term monitoring data and should be further verified across larger temporal and spatial scales. The influence of confounding factors, such as drought and water use, should also be examined. Although it is uncertain whether current climatic forcing is indicative of long-term climate change, current changes in the study lakes are similar to those predicted to occur in the NTL-TLA lakes following a doubling of CO_2 (De Stasio et al. 1996). Our results also provide a real-world reference for lake response to warming autumn air temperatures and increasing DOC. Understanding how lakes will respond to these changes is vital as autumn air temperature for the Great Lakes region is expected to increase by 2.6–6 °C with a doubling of greenhouse gases (Robertson and Ragotzkie 1990; Mortsch and Quinn 1996) and recent changes in DOC are widespread (Monteith et al. 2007). This study details climate-induced changes in lake thermal properties and oxygen content. Trends in ice breakup (Wynne et al. 1998; Futter 2003) and coherent interannual variation in the chemistry and biota of the study lakes have also been linked to climate (Baines et al. 2000; Amott et al. 2003; Rusak et al. 2008). Clearly, continued climate change has the potential to profoundly impact lake environments.

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