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Interannual variation in the thermal structure of clear and colored lakes

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Abstract

We used end-of-summer temperature profiles to examine the thermal structure of 86 small (<500 ha) lakes in Killarney Park, Ontario, Canada, during one cool (1997) and two extremely warm years (1998 and 1999). The main effect of the warm years, which had unusually high air temperatures during the spring, relative to the cool year was to create warmer surface waters, shallower mixing depths, and stronger metalimnetic thermal gradients in nearly all lakes. Changes in deep water temperatures differed between clear (DOC < 2 mg L^{-1}) and colored (DOC > 4 mg L^{-1}) lakes. During warm years, the volume of cold water (<10°C) was reduced in clear lakes. In colored lakes, deep water temperatures were more stable, and cold water volume actually increased during one warm year. We suggest that clear lakes will be more sensitive than colored lakes to the warming effects of climate change. Because clear lakes exhibit large thermal changes in response to small differences in DOC, they will also be more sensitive to changes in DOC levels associated with altered hydrological inputs, climate change, or acidification.

Examining the annual variation in thermal characteristics of lakes may provide insight into the response of aquatic habitats to global climate change. Particularly valuable as natural experiments are extreme El Nino/Southern Oscillation (ENSO) events, the result of anomalies in oceanic circulation and atmospheric pressure in the tropical Pacific, which have been associated with unusually warm air temperatures in parts of North America (Rasmussen and Wallace 1983). ENSO warming events have been shown to produce strong limnological signals such as earlier ice breakup, warmer epilimnia, and shallower mixing depths (Strub et al. 1985; Anderson et al. 1996; King et al. 1997, 1999*a*). In boreal regions of central Canada, ENSO events often result in droughts (Dillon et al. 1997) that reduce the export of colored dissolved organic carbon (DOC) from lake catchments, thereby altering water clarity and corresponding lake thermal structure (Schindler et al. 1996, Curtis and Schindler 1997). Small lakes, which dominate the Canadian Shield and comprise the majority of lakes in Ontario (estimated 98% < 100 ha; Cox 1978), are especially responsive to such interannual variation in inputs of DOC (Schindler et al. 1990).

Discrepancies in the observed thermal responses of large and small lakes to climatic variability appear to be related to differences in the relative effects of basin morphometry and water clarity. The mixing depths of large lakes (>500 ha) are controlled mainly by fetch or other aspects of wind exposure, whereas the mixing depths of small lakes (<500 ha) can be affected by wind exposure (France 1997) but are controlled largely by water clarity (Mazunder and Taylor 1994; Fee et al. 1996). The observed effects of warmer climate on large lakes have included earlier stratification, shallower thermoclines, higher epilimnetic temperatures, and larger thermal gradients across the thermocline but not changes in hypolimnetic temperatures (King et al. 1997, 1999*a*). Robertson and Ragotzkie (1990) expected the hypolimnetic temperatures of large lakes to change little or to actually increase slightly with climate warming. By contrast, the responses of small lakes to warmer climate and increased water clarity documented by Schindler et al. (1990, 1996) include deeper epilimnions and increased average volume-corrected water temperatures but not increases in maximum epilimnion temperatures. In addition, increased light penetration in small lakes linked to lower DOC levels has been associated with greater thermocline depth, increased hypolimnetic heating, and weaker temperature gradients in the metalimnion (Yan 1983; Bukaveckas and Driscoll 1991; Perez-Fuentetaja 1999).

The small oligotrophic lakes of the La Cloche Mountain Range in Killarney Park, Ontario, are among the clearest waters in North America and represent very sensitive lakes for monitoring the effects of climate change (Gunn et al. 2000). The park contains not only ultraclear lakes, but also a variety of other lakes that differ widely in their optical properties. The opportunity to assess the thermal response of this diverse assemblage of lakes to extremes in annual weather was presented by the occurrence of two exceptionally warm years, including the 1998 ENSO event, subsequent to a cool year in 1997. We used end-of-summer temperature profiles to examine the differences in thermal properties among small lakes (<500 ha surface area) during cool and warm years.

Methods

Study site—Killarney Park is a 48,110-ha wilderness area located about 35–60 km southwest of Sudbury, Ontario. Its watershed contains >600 waterbodies. The La Cloche Mountain Range forms an arc of high, erosion-resistant, orthoquartzite ridges that occupy about half the park. The remainder of the area consists of low-lying lands with thicker soils overlying geological formations more prone to mineral weathering. These spatial differences in topography and surficial and bedrock geology strongly influence the chemi-

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Table 1. Physical and chemical characteristics of the 86 study lakes.

	Minimum	Median	Maximum
Surface area (ha)	1.7	22.6	406.3
pH	4.3	5.6	7.2
DOC (mg L^{-1})	0	3.4	17.4
Volume (10^4 m^3)	2.6	105.3	8,160.7
Mean depth (m)	0.7	5.2	22.0
Maximum depth (m)	2.5	12.0	79.0
Fetch (km)	0.20	0.95	5.88
Elevation (m)	181	223	348
Secchi depth (m)	1.1	5.7	31.0
Latitude (N)	46°01′16″		46°11′31″
Longitude (W)	81°09′29″		81°36′06″

cal makeup of the lakes. Clear waters are a natural feature of the ridge-top lakes, which tend to have few if any wetlands in their catchments (Gunn et al. 2000). By contrast, many waterbodies in the lowlands are located in catchments with wetland sources of DOC and have correspondingly lower clarity. Some of the lakes in the park were also acidified by atmospheric deposition of pollutants (Beamish and Harvey 1972), and the reductions in DOC levels that accompanied acidification further increased the clarity of the lakes. The topography of the area also affects physical mixing of the lakes by locally modifying wind direction and speed, but we were unable to address this issue in the current study.

Based on the results of an extensive survey of Killarney lakes conducted during 1995–1997 (Snucins and Gunn 1998), a set of 86 lakes was chosen for annual monitoring of late-summer thermal structure. The selected lakes are all small (surface area range 1.7–406 ha) and span a wide range in physical and chemical characteristics (Table 1), including many lakes with very low DOC levels and correspondingly high water clarity (up to 31 m Secchi depth).

Data collection and analysis—Temperature profiles were obtained once at the deepest point of each lake during 25 August–1 September 1997, 24 August–31 August 1998, and again during 24 August–1 September 1999. All 86 lakes were sampled in 1997 and 1998. In 1999, we sampled 60 of the lakes, each of which had been thermally stratified in one or both of the first 2 yr. YSI meters were used to measure water temperatures at 1-m intervals from surface to 1 m off bottom. The meters were calibrated with a National Bureau of Standards certified mercury thermometer prior to each year's survey. Surface temperature was defined as the temperature 1 m below the lake surface. Bottom temperature was defined as the temperature at 1 m above the lake sediments. The mixing depth was defined graphically by the intersection of trend lines fitted to the thermal profiles, one through the upper part of the epilimnion and the second through the metalimnion (Wetzel 1975). DOC and pH values were obtained by sampling water through the ice during the winter of 1996 (Snucins and Gunn 1998). Analytical methods followed OMOEE (1996): DOC was determined colorimetrically following UV acid–persulfate digestion and dialysis; pH was measured using a Radiometer Model PHM64 meter. To assess temporal variation in DOC levels, a set of 21 lakes was sampled again during the winter of 1999.

We used stepwise multiple linear regression analysis and stepwise discriminant analysis (SPSS) to identify the factors that accounted for the greatest amount of variation in lake thermal properties both within and between study years. Five descriptors of thermal structure were each used as dependent variables: 10°C depth ($10°C_d$), mixing depth (E_d), surface temperature (S_t), bottom temperature (B_t), and depth interval below the epilimnion over which a 10°C drop in temperature occurs (G_{10}). Independent variables included in the analyses were surface area (AREA), elevation (ELEV), maximum depth (MXDEP), mean depth (MNDEP), volume (VOL), fetch (FETCH), dissolved organic carbon (DOC), and mean air temperature 1 d prior to sampling (TEMP). Variables with nonnormal distributions were log-transformed prior to analysis. We present only regression equations that include the noncorrelated variables (Table 2) that explained the greatest amount of variance.

Results

Mean annual temperature data for Sudbury, collected by Environment Canada since 1956, indicates that 1998 was the warmest year on record, 1999 the second warmest, and 1997 the sixth coldest. June and July temperatures were above normal in all 3 yr of this study, but cooler than average temperatures occurred in May and August 1997 (Table 3). The exceptionally warm air temperatures and greater insolation during April and May 1998 and 1999 (Table 3) suggest that during those years springtime heating of the lakes occurred more rapidly than in 1997. Ice-out dates were earlier in 1998 and 1999 than in 1997, a phenomenon that is typical of El Nino years (Anderson et al. 1996). Although precise ice-out dates are not available for the Killarney lakes, an approximation was obtained from records obtained for Ramsey Lake, a lake about 40 km northeast of Killarney Park. Ice-out in Ramsey Lake, defined as the earliest date the main basin was free of ice, occurred 14 d earlier in 1998 (17 April) than in 1997 (1 May). The ice-out date for the lake in 1999 (16 April) was similar to 1998.

Water clarity and lake depth strongly influenced the thermal structure of the study lakes. Of the 86 lakes in the survey set, thermal stratification was documented in 63 lakes during 1997, 64 lakes during 1998, and 58 lakes in 1999. The remainder of the lakes had either uniformly warm temperatures from surface to bottom or had temperatures that declined with depth but with no apparent stratification. A discriminant analysis, with overall correct classifications of 80.2% (1997 data) and 84.9% (1998 data), revealed that the lakes that failed to stratify tended to be shallow and clear. Most lakes with maximum depth <5 m failed to stratify, regardless of water clarity (Fig. 1). In deeper lakes water clarity influenced stratification. For example, all lakes with maximum depth > 10 m and DOC > 1 mg L^{-1} were stratified, but ultraclear lakes (DOC < 1 mg L^{-1}) stratified only if they had maximum depth greater than 18 m. Even among the lakes that stratified (i.e., had an epilimnion and metalimnion), not all lakes developed hypolimnia with uniformly

Table 2. Spearman correlations for dependent and independent variables used in regression equations. Significant correlations based on Bonferroni-adjusted probabilities are indicated by * $P < 0.05$ and ** $P < 0.01$.

	AREA	MXDEP	MNDEP	VOL	ELEV	DOC	FETCH	TEMP97	TEMP98	TEMP99
MXDEP	0.527**									
MNDEP	0.460**	0.921**								
VOL	0.924**	0.748**	0.730**							
ELEV	−0.443**	−0.045	−0.094	−0.375						
DOC	−0.020	−0.485**	−0.435**	−0.163	−0.304					
FETCH	0.946**	0.480**	0.418**	0.867**	−0.469**	−0.001				
TEMP97	0.057	−0.115	−0.108	0.011	0.093	−0.061	0.025			
TEMP98	−0.174	0.144	0.083	−0.115	0.124	−0.435**	−0.155	0.010		
TEMP99	0.035	0.122	0.228	0.119	−0.351	−0.121	0.021	−0.189	0.172	
$S_{t(1997)}$	0.172	−0.233	−0.194	0.065	−0.273	0.474**	0.168	0.041	−0.310	0.192
$S_{t(1998)}$	−0.040	−0.263	−0.163	−0.084	−0.322	0.114	−0.010	−0.046	0.062	0.376
$S_{t(1999)}$	0.168	−0.129	−0.015	0.142	−0.511**	0.273	0.170	−0.036	0.101	0.757**
$G_{10(1997)}$	0.413	0.487	0.259	0.417*	0.060	−0.643**	0.346	0.264	0.414	−0.207
$G_{10(1998)}$	0.221	0.490*	0.365	0.298	0.069	−0.719**	0.136	0.195	0.477	−0.038
$G_{10(1999)}$	0.237	0.244	0.133	0.204	0.039	−0.467	0.133	0.105	0.251	0.031
$E_{d(1997)}$	0.252	0.623**	0.519**	0.364	0.104	−0.907**	0.198	0.044	0.521**	0.047
$E_{d(1998)}$	0.279	0.679**	0.626**	0.418	0.070	−0.913**	0.220	0.134	0.461**	0.161
$E_{d(1999)}$	0.174	0.619**	0.534**	0.310	0.126	−0.895**	0.119	0.179	0.449	0.073
$10^\circ C_{d(1997)}$	0.317	0.699**	0.613**	0.463	0.079	−0.929**	0.290	0.128	0.466	0.069
$10^\circ C_{d(1998)}$	0.335	0.768**	0.668**	0.491	−0.043	−0.896**	0.290	0.218	0.454	0.160
$10^\circ C_{d(1999)}$	0.420	0.692**	0.506**	0.473	−0.016	−0.858**	0.351	0.289	0.434	0.106
$B_{t(1997)}$	−0.428	−0.711**	−0.647**	−0.543**	0.218	−0.016	−0.379	0.182	0.126	−0.139
$B_{t(1998)}$	−0.473**	−0.646**	−0.614**	−0.574**	0.257	−0.139	−0.430**	0.149	0.165	−0.007
$B_{t(1999)}$	−0.225	−0.438**	−0.380**	−0.281	0.278	−0.298	−0.164	0.119	0.133	−0.054
$S_{t(98–97)}$	−0.200	−0.053	−0.015	−0.171	−0.057	−0.346	−0.165	−0.004	0.353	0.060
$S_{t(99–97)}$	0.082	0.039	0.080	0.097	−0.318	−0.032	0.082	−0.064	0.294	0.780**
$G_{10(98–97)}$	−0.374	−0.186	−0.055	−0.326	−0.061	0.149	−0.326	−0.179	−0.108	0.059
$G_{10(99–97)}$	−0.272	−0.067	0.088	−0.204	−0.262	0.167	−0.274	−0.223	−0.284	0.442
$E_{d(98–97)}$	0.162	0.121	0.158	0.155	−0.136	0.079	0.212	−0.078	−0.219	0.150
$E_{d(99–97)}$	0.222	0.226	0.177	0.205	0.076	−0.106	0.290	0.045	−0.609	−0.232
$10^\circ C_{d(98–97)}$	0.604	0.426	0.289	0.166	0.102	−0.413	0.000	−0.190	0.192	0.014
$10^\circ C_{d(99–97)}$	0.225	0.291	−0.043	0.173	0.239	−0.393	0.140	0.112	0.212	0.012
$B_{t(98–97)}$	−0.318	−0.211	−0.249	−0.345	0.075	−0.392	−0.255	−0.180	0.250	0.132
$B_{t(99–97)}$	0.027	0.050	−0.026	0.048	−0.040	−0.389	0.053	−0.144	0.179	0.038

cold temperatures. Well-defined hypolimnia occurred in 29 lakes in 1997, 35 lakes in 1998, and 34 lakes in 1999.

DOC was a good predictor ($R^2 = 0.66$–0.87) of $10^\circ C_d$ and mixing depth (E_d) (Table 4). DOC also predicted ($R^2 = 0.34$–0.56) the depth interval below the epilimnion, over which a 10°C drop in temperature occurred (G_{10}). The addition of lake size (fetch, volume, area) to the regression equations increased the explained variance only slightly. These relationships indicate the greatest values for $10^\circ C_d$, E_d, and G_{10} occurred in lakes with the lowest DOC levels, and it is in the clearest lakes that these thermal properties will be most affected by small changes in clarity. For example, in lakes with DOC < 2 mg L^{-1}, the range of values for G_{10} (ranges: 4.2–18.5 m in 1997; 3.3–27.5 m in 1998;

Table 3. Mean air temperatures at Sudbury Airport (Environment Canada), with station normals for the period 1956–1980, and hours of bright sunshine during the spring months.

	Mean air temperature (°C)				Hours bright sunshine		
Month	1997	1998	1999	1956–1980	1997	1998	1999
Apr	2.8	6.1	5.3	2.7	227.0	263.6	252.8
May	7.4	14.8	14.1	10.5	199.0	278.9	287.2
Jun	18.6	16.6	18	16			
Jul	19.5	19.1	20.3	18.7			
Aug	16	19.1	17	17.3			
Ice-out* to 1 Sep	15.2	16.4	16.2	—			

* Based on observed ice-out dates (1 May 97, 17 Apr 98, 16 Apr 99) for Ramsey Lake, located 18 km from Sudbury airport.

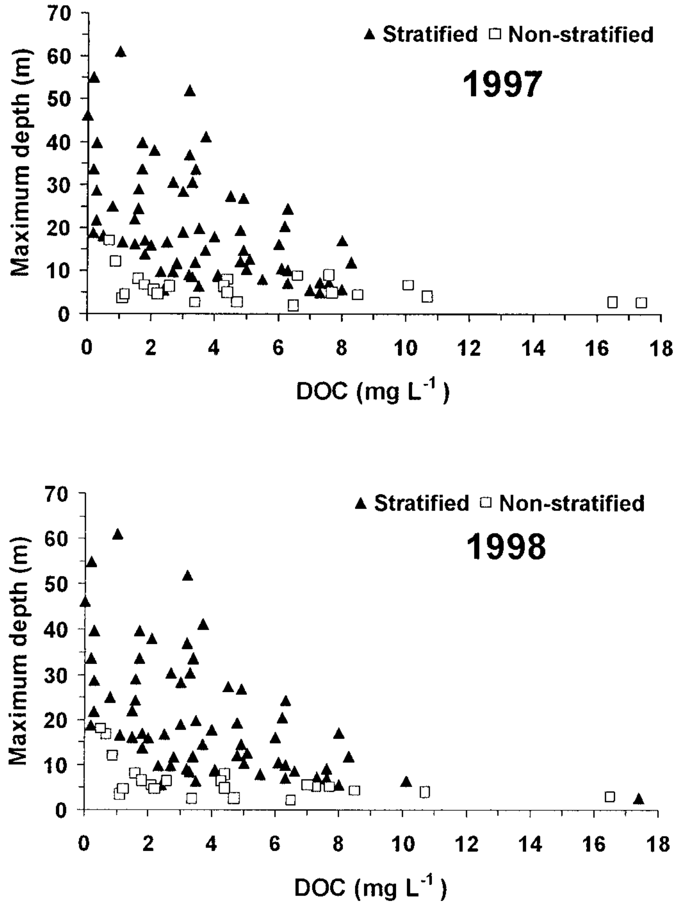

Fig. 1. Maximum depth and DOC of lakes that stratified and lakes that did not stratify in 1997 and 1998.

3.4 to >43.9 m in 1999) was much higher than in lakes with DOC $>$ 2 mg L^{-1} (ranges: 2.4–7.6 m in 1997, 1.5–3.4 m in 1998, 1.4–4.1 m in 1999).

The between-lake variance in surface temperatures was explained in part by DOC, but TEMP was an important factor because the mean daily temperatures during the surveys in 1998 (14.3–21.0°C) and 1999 (10.9–23.0°C) were much more variable than in 1997 (15.7–18.2°C). The regressions for B_t include maximum depth and not DOC, because those two variables were correlated in our set of lakes (Table 2). Nevertheless, in lakes of similar depth, bottom temperature tended to increase with decreasing DOC.

Interannual differences in thermal structure—Many aspects of lake thermal structure differed between the cool and warm years (Table 5). The changes that were most consistent across lakes were an increase in the surface temperature (97–100% of lakes) and a decrease in the depth interval for a 10°C drop in temperature below the epilimnion (94–97% of lakes). In addition, many of the lakes (58–72%) had shallower mixing depth during the warm years.

The variables included in the regression analysis accounted for only small amounts of the between-lake variation in changes to thermal structure during the warm years (Table 6). Exceptions were the relationship of surface temperatures to mean air temperature the day prior to sampling in 1999 (TEMP99) and, in lakes with DOC $<$ 2 mg L^{-1}, the negative relationship of lake depth to B_t. Regression analysis failed to find variables to explain the interannual variation in mixing depth; therefore, a discriminant function was developed to differentiate lakes with large reductions in mixing depth $\geq$ 1 m (N = 17) from lakes with mixing depths that changed (increased or decreased) by less than 1 m (N = 44) between 1997 and 1998 (Fig. 2). With 68.9% overall correct classification accuracy, the discriminant function indicated that reductions in mixing depth $\geq$ 1 m tended to occur in the lakes with greatest clarity and shallowest depths.

For all lakes combined, mean deep water temperatures (B_t, 10°C$_d$) did not differ between 1997 and 1998 and increased significantly in 1999 (Table 5), but interesting patterns emerged when the waterbodies were categorized by DOC (Fig. 3). The mixing depth was reduced during both warm years in the high-DOC lakes, but only during one of those years in the low-DOC lakes. Even more striking were the differences in the deep water temperatures. The overall trend to higher values for B_t and 10°C$_d$ in 1999 but not 1998 (Table 5) held for the low-DOC lakes, but not for the high-DOC lakes (Fig. 3). In the colored lakes, B_t and 10°C$_d$ relative to the cool year were actually lower in 1998 and unchanged in 1999. Thus, colored lakes exhibited less heating of the deep waters during warm years. Such a difference might be expected if clear lakes were much shallower than colored lakes. However, the opposite was true in our data set: the maximum depth averaged 10.3 m in the colored lakes and 24.4 m in the clear lakes.

Most (16 of 19) of the lakes that were unstratified in both 1997 and 1998 exhibited higher bottom temperatures (mean increase 2.1°C) in the warm year, but there was still some evidence of high DOC levels reducing bottom warming even in these unstratified lakes. For example, three of the four most colored (DOC 7.7–16.5 mg L^{-1}) unstratified lakes exhibited lower bottom temperatures (mean decrease 1.7°C) during the warm year. The fourth lake had higher bottom temperature, but that may be because it is much shallower (2.8 m maximum depth) than the lakes that did not experience bottom warming (4.1–5.0 m maximum depth).

In the 21 lakes that were water sampled in both 1996 and 1999, DOC levels decreased in 16 lakes (range -0.1 to -0.5 mg L^{-1}; mean -0.3 mg L^{-1}), increased in two lakes (0.1 and 1.0 mg L^{-1}), were unchanged in one lake, and were only at detectable trace levels in the remaining two lakes. Thus, the majority (16 of 19) of lakes with valid DOC measurements exhibited decreases in DOC between 1996 and 1999.

Discussion

The overall influence of the years with extremely warm spring months was to create narrower and warmer epilimnia and steeper thermal gradients through the metalimnion of stratified lakes. The stronger thermal density gradients at shallower depths probably resulted from rapid surface heating of the lakes during the extremely warm spring periods. In addition, we observed changes in deep water temperatures (B_t, 10°C$_d$), both increases and decreases, that were related

Table 4. Regression equations for thermal properties of Killarney lakes for 1997, 1998, and 1999. All regressions were significant ($P<0.05$). $10°C_d$ = 10°C depth; E_d = mixing depth; G_{10} = distance below the epilimnion for a temperature decrease of 10°C; S_t = temperature 1 m below surface; B_t = temperature 1 m above bottom.

Equation	*P*-value	R^2	*N*
$\log_{10}10°C_{d(1997)} = 1.38 + 0.12\log_{10}\text{FETCH} - 0.68\log_{10}(\text{DOC}+1)$	0.0000	0.91	49
$= 1.40 - 0.69\log_{10}(\text{DOC}+1)$	0.0000	0.86	
$\log_{10}10°C_{d(1998)} = 1.42 + 0.15\log_{10}\text{FETCH} - 0.76\log_{10}(\text{DOC}+1)$	0.0000	0.92	48
$= 1.43 - 0.76\log_{10}(\text{DOC}+1)$	0.0000	0.87	
$\log_{10}10°C_{d(1999)} = 1.40 + 0.17\log_{10}\text{FETCH} - 0.69\log_{10}(\text{DOC}+1)$	0.0000	0.87	41
$= 1.40 - 0.66\log_{10}(\text{DOC}+1)$	0.0000	0.77	
$\log_{10}E_{d(1997)} = 0.96 + 0.08\log_{10}\text{VOL} - 0.63\log_{10}(\text{DOC}+1)$	0.0000	0.73	63
$= 1.16 - 0.66\log_{10}(\text{DOC}+1)$	0.0000	0.66	
$\log_{10}E_{d(1998)} = 0.91 + 0.07\log_{10}\text{VOL} - 0.58\log_{10}(\text{DOC}+1)$	0.0000	0.82	64
$= 1.10 - 0.62\log_{10}(\text{DOC}+1)$	0.0000	0.75	
$\log_{10}E_{d(1999)} = 1.13 + 0.15\log_{10}\text{FETCH} - 0.64\log_{10}(\text{DOC}+1)$	0.0000	0.77	58
$= 1.12 - 0.61\log_{10}(\text{DOC}+1)$	0.0000	0.70	
$G_{10(1997)} = 9.03 + 1.35\log_{10}\text{AREA} - 10.09\log_{10}(\text{DOC}+1)$	0.0000	0.64	36
$= 11.51 - 10.40\log_{10}(\text{DOC}+1)$	0.0000	0.56	
$G_{10(1998)} = 11.80 - 12.33\log_{10}(\text{DOC}+1)$	0.0000	0.52	51
$G_{10(1998)} = 4.95 + 0.63\log_{10}\text{AREA} - 3.90\log_{10}(\text{DOC}+1)$	0.0000	0.43	42
$= 6.00 - 3.94\log_{10}(\text{DOC}+1)$	0.0001	0.34	
$S_{t(1997)} = 19.32 + 1.31\log_{10}(\text{DOC}+1)$	0.0000	0.20	86
$S_{t(1998)} = 29.00 + 0.11\ \text{TEMP98} - 0.34\log_{10}\text{MXDEP} - 3.51\log_{10}\text{ELEV}$	0.0166	0.12	86
$= 30.09 - 0.29\log_{10}\text{MXDEP} - 3.12\log_{10}\text{ELEV}$	0.0426	0.07	
$= 29.77 - 3.12\log_{10}\text{ELEV}$	0.0224	0.06	
$S_{t(1999)} = 16.02 + 2.55\log_{10}(\text{DOC}+1) + 0.27\text{TEMP99}$	0.0000	0.74	60
$= 18.20 + 0.24\text{TEMP99}$	0.0000	0.48	
$B_{t(1997)} = 23.53 - 10.89\log_{10}\text{MXDEP}$	0.0000	0.48	70
$B_{t(1998)} = 24.68 - 12.05\log_{10}\text{MXDEP}$	0.0000	0.41	86
$B_{t(1999)} = 17.96 - 6.88\log_{10}\text{MXDEP}$	0.0042	0.13	60

to water clarity. In clear lakes the volume of cold water decreased during warm years, presumably because of greater solar heating of the hypolimnetic waters. In colored lakes, the volume of cold water was more stable and actually increased during one of the warm years, presumably because the rapid establishment of sharp thermal density gradients in the spring inhibited further mixing of warm surface waters and cooler bottom waters. This contrasts with studies on large waterbodies that suggest warmer air temperatures do not lead to lower deep water temperatures (Robertson and Ragotzkie 1990; King et al. 1997).

Consistent with other studies (Mazunder and Taylor 1994; Fee et al. 1996; Perez-Fuentetaja et al. 1999), our analysis revealed that the thermal structure of small lakes is controlled in large part by water clarity. Clear lakes (DOC < 2 mg L^{-1}) exhibited the greatest warming of deep waters and very large thermal changes (e.g., G_{10}) associated with small differences in DOC, suggesting that it is in these clear-water lakes that DOC reductions from altered hydrological inputs, climate change, or acidification will have their greatest effect. Although lakes with DOC < 2 mg L^{-1} are relatively uncommon, estimated to represent 7% of all Ontario lakes (Neary et al. 1990) and 10.5% of lake trout lakes on the Canadian Shield (J. Gunn unpubl. data), their sensitivity is of particular significance given the emerging evidence that some Ontario lakes have become clearer over the past 30 years (Schindler et al. 1990; Gunn et al. 2000).

The end-of-summer temperature profiles, single DOC measurements, and lake morphometry data explained only some of the variation in lake thermal properties. Schindler (1971) hypothesized that the interannual variability in mixing depths of small lakes in the Experimental Lakes Area (ELA) might be determined by wind and air temperatures in the days immediately after the onset of stratification. Fee et al. (1996), examining a larger ELA data set, identified solar irradiance during the month when lakes stratify as a potential influence on mixing depths. The deepening of thermoclines has also been attributed to increased wind velocities and decreased DOC inputs (Schindler et al. 1990, 1996; France 1997). Thus, it is possible that more of the variation in thermal properties of the Killarney lakes could have been accounted for if additional monitoring data were available.

Interannual variation in DOC levels that occurred during our study, as suggested by the changes between 1996 and 1999 in most of the 21 lakes with repeat sampling, could help explain some of the between-year changes in thermal properties that are strongly influenced by water clarity, such as E_d, $10°C_d$, and B_t. However, variation in DOC cannot account for the changes in S_t and G_{10}. Surface water temperatures are known to be strongly influenced by air temperatures (Shuter et al. 1983). In addition, and during the warm years we observed decreases in G_{10}, which is opposite the response expected if, as suggested by the repeat sampling, DOC levels in most lakes declined between 1996 and 1999. Weather-related variables—for example, the rate and amount

Table 5. Changes in thermal structure of Killarney Park lakes. To facilitate interannual comparison, the means for each descriptor include only lakes with data for all 3 yr. S_t = temperature 1 m below surface; B_t = temperature 1 m above bottom; E_d = mixing depth; G_{10} = distance below the epilimnion for a temperature decrease of 10°C; 10°C_d = 10°C depth. Means with same letters are not significantly different (P>0.05; repeated measures ANOVA).

				No. of lakes that changed relative to 1997		
Parameter	No. of lakes	Year	Mean	Increase	Decrease	No change
S_t (°C)	60	1997	20.09	—	—	—
		1998	22.35	60	0	0
		1999	22.78	58	2	0
B_t (°C)	45	1997	9.18 a	—	—	—
		1998	9.08 a	26	16	3
		1999	10.03	25	16	4
E_d (m)	60*	1997	6.73	—	—	—
		1998	6.24	10	43	7
		1999	6.51	16	35	9
G_{10} (m)	34	1997	4.66	—	—	—
		1998	3.00	1	33	0
		1999	3.34	2	31	1
10°C_d (m)	45†	1997	9.47 a	—	—	—
		1998	9.38 a	20	22	3
		1999	10.13	31	10	4

* Means calculated using only the 56 lakes that had epilimnia less than maximum depth in all 3 yr. The four lakes not included in the means calculations did not stratify in 1997 (N = 2), 1998 (N = 1), or 1999 (N = 2).

† Means calculated using only the 40 lakes with 10°C depth in all 3 yr. The five lakes not included in the means calculations had 10°C depth in 1997 but warmed to temperatures >10°C throughout the water column in 1998 (N = 2) or 1999 (N = 5).

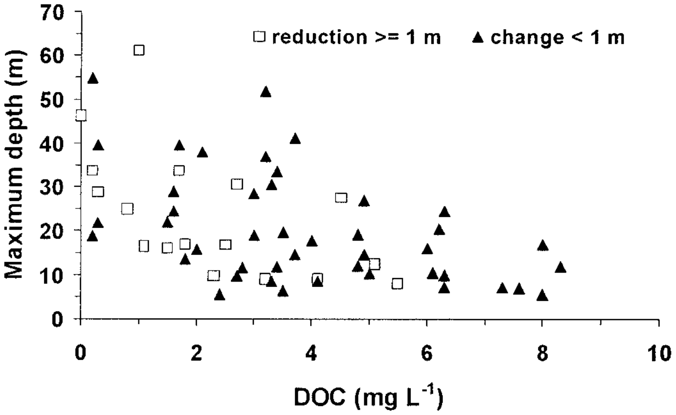

Fig. 2. Maximum depth and DOC of lakes that had mixing depths reduced by ≥1 m and lakes that had mixing depths change (increase or decrease) by <1 m between 1997 and 1998.

of heating—were probably more important than DOC levels in determining the interannual variation in S_t and G_{10}.

The interannual differences in water temperatures and thermal gradients, such as those observed in our study and those that are expected to occur with climate warming, could have profound implications, both positive and negative, for aquatic species. Fish may experience constrictions or expansions of thermal habitat volume, depending on the species' thermal niche, with corresponding decreases or increases in growth rates (Magnuson and Destasio 1996; King et al. 1999*b*). The magnitude and direction of effects will differ not only among species, but also among lakes and years, depending on meteorological conditions; lake morphometry; and DOC levels. Changes in the vertical distributions of fish and zooplankton in response to changing thermal and oxygen conditions could affect predator–prey interactions and zooplankton productivity (DeStasio et al. 1996). In addition, we speculate that changes in metalimnetic thermal density gradients, which tend to strengthen during warm years but

Table 6. Regression equations for differences between years in thermal properties of Killarney lakes. All regressions were significant (P<0.05).

Equation	P-value	R^2	N
All lakes			
$S_{t(1998-1997)} = -1.54 + 0.20(\text{TEMP98})$	0.0000	0.18	86
$S_{t(1999-1997)} = -1.39 + 0.24(\text{TEMP99}) - 0.60\text{Log}_{10}\ \text{MNDEP}$	0.0000	0.64	60
$= -1.67 + 0.22(\text{TEMP99})$	0.0000	0.61	
$B_{t(1998-1997)} = 4.16 - 0.96\ \log_{10}\ \text{VOL} - 2.85\ \log_{10}(\text{DOC}+1)$	0.0000	0.30	70
$B_{t(1999-1997)} = 2.65 - 3.22\ \log_{10}(\text{DOC}+1)$	0.0091	0.15	45
$G_{10(1998-1997)} = -2.01 + 2.94\ \log_{10}(\text{DOC}+1) - 0.96\ \log_{10}\text{AREA}$	0.0034	0.29	36
$G_{10(1999-1997)} = -2.63 + 2.09\ \log_{10}(\text{DOC}+1)$	0.0355	0.14	34
$10°C_{d(1998-1997)} = -2.54 - 3.23\ \log_{10}(\text{DOC}+1) - 0.27\ \log_{10}\text{AREA}$	0.0003	0.32	46
$10°C_{d(1999-1997)} = 3.06 - 3.73\ \log_{10}(\text{DOC}+1)$	0.0010	0.26	40
Lakes with DOC < 2 mg L^{-1}			
$S_{t(1989-1997)} = 3.94 - 1.12\ \log_{10}\text{MXDEP}$	0.0009	0.39	25
$S_{t(1999-1997)} = -0.35 + 0.15(\text{TEMP99})$	0.0010	0.48	19
$B_{t(1998-1997)} = 4.95 - 4.23\ \log_{10}\text{MNDEP}$	0.0000	0.60	21

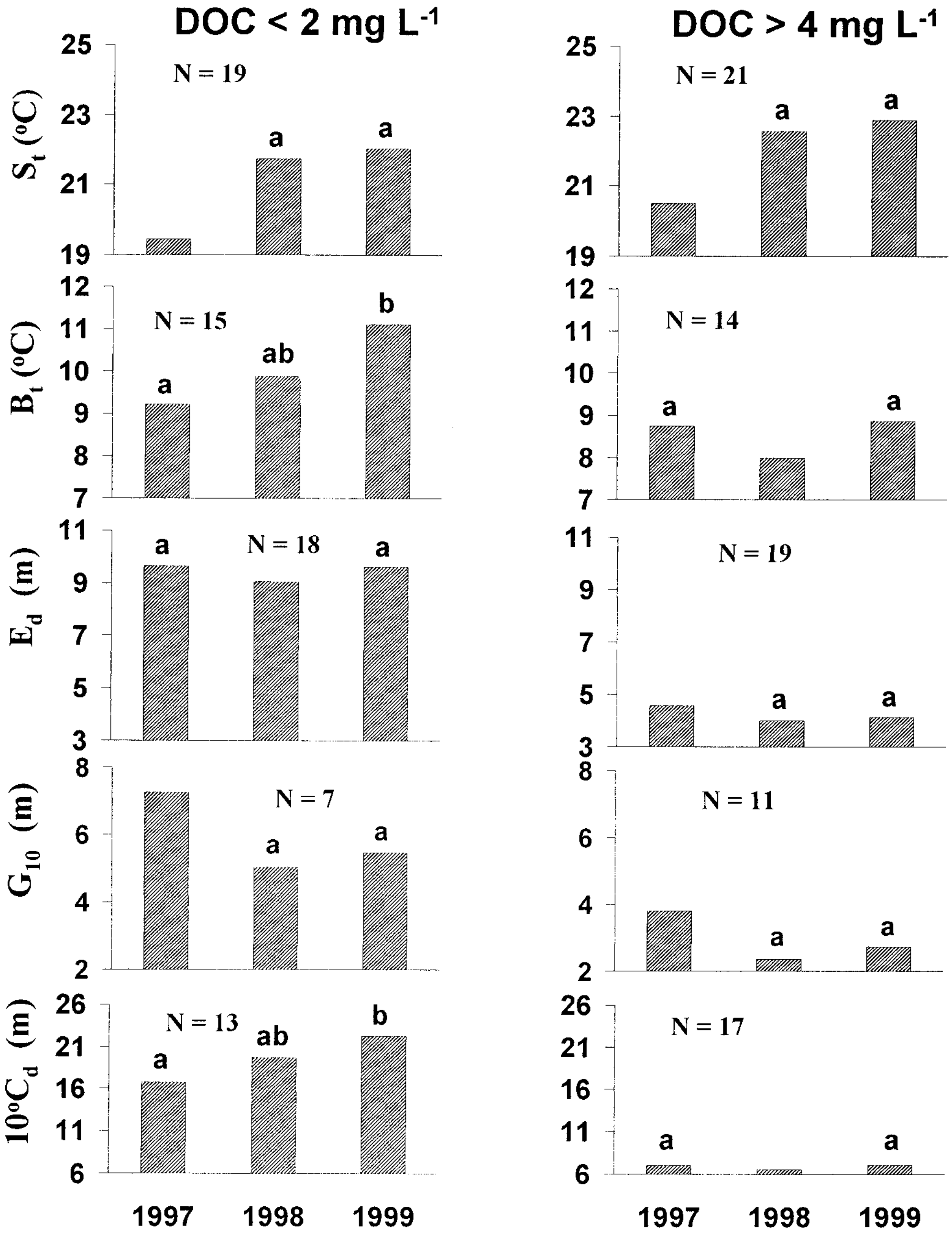

Fig. 3. Changes in thermal structure of low-DOC (<2 mg L^{-1}) and high-DOC (>4 mg L^{-1}) Killarney Park lakes. Only lakes with data for all 3 yr are included. S_t is the temperature 1 m below the surface; B_t is the temperature 1 m above the bottom; E_d is the mixing depth; G_{10} is the distance below the epilimnion for a temperature decrease of 10°C; 10°C_d is the depth at 10°C. Means within each DOC category with the same letters are not significantly different ($P > 0.05$; repeated measures ANOVA). Lakes that experienced heating to >10°C throughout the water column in one or two of the years had the lake's maximum depth assigned as the value for the 10°C depth.

weaken with reductions in DOC levels, could affect the movements of species that exhibit diurnal migrations from hypolimnion to epilimnion (e.g., zooplankton) and might affect the feeding efficiency of zooplankton that take advantage of the accumulation of algae that typically settle at steep density gradients in the metalimnion of oligotrophic lakes (Wetzel 1975).

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