

Climate-induced changes in the dissolved organic carbon budgets of boreal lakes

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Abstract. During 20 years of climatic warming, drought and increased forest fires between 1970 and 1990, DOC concentrations declined by 15–25% in lakes of the Experimental Lakes Area, northwestern Ontario, allowing increased penetration of both UV and photosynthetically-active radiation (PAR), and causing deeper euphotic zones and thermoclines. Decreased input to the lakes of DOC from terrestrial catchments and upstream lakes was the primary reason for the decline, although in-lake removal also increased slightly. Decreased streamflow caused by drought was more important than forest fires in affecting DOC exports from catchments. Experimental acidification of lakes caused even greater losses in DOC, by enhancing rates of in-lake removal. DOC in Lake 302S, acidified to pH 4.5 during the 1980's, declined to less than 10% of preacidification values.

Introduction

The role of DOC in boreal lakes

Dissolved organic carbon (DOC) is the most abundant dissolved substance discharged to most oligotrophic boreal lakes from their catchments. DOC participates in a number of important functions in lakes, including flocculation of chemical substances (Weilenmann et al. 1989), “fuelling” of microbial food chains (Hobbie 1992; Wetzel 1992), attenuating photosynthetically-active radiation (PAR, Schindler 1971; Rasmussen et al. 1989; Engstrom 1987), which restricts the depth of the euphotic zone and stabilizes the depth of the thermocline (Schindler et al. in press), attenuating UV light to protect organisms from harmful wavelengths (Williamson & Zagarese 1994; Scully & Lean 1994), and participating in a number of photochemical reactions that yield reactive chemicals such as peroxides (Lean et al. 1994).

In a recent analysis of PAR extinction in boreal lakes, Fee et al. (1996) attributed all but 6% of average light attenuation in natural lakes of north-western Ontario to DOC. Similarly, Scully and Lean (1994) found that little of the attenuation of UV light was caused by either phytoplankton or suspended particulate matter in lakes of the Precambrian Shield, and that DOC was almost entirely responsible for UV attenuation.

The effects of climatic warming in the Experimental Lakes Area

During the period 1970–1990, average annual temperatures at ELA warmed by 1.6 degrees. Precipitation declined by about 40 %. The decline in precipitation and increased evaporation caused by warmer air temperatures combined to reduce runoff from catchments by about 70%. Indeed, first-order streams that flowed continuously in the ice-free season in the early 1970s were dry for an average of 150 days by the late 1980s (Schindler et al. 1996a). Forest fires burned parts of the ELA watersheds described here in both 1974 and 1980, causing substantial increases in the concentrations and yields of most chemical elements (Schindler et al. 1980a; Bayley et al. 1992a, b), although over 20 years yields of chemical substances from catchments declined, as the result of lower hydrological flows (Schindler et al. 1996a). Many of the physical, chemical and biological changes in lakes, streams and terrestrial catchments during this period of climatic change have been documented elsewhere (Schindler et al. 1980a, 1990, 1992, 1996a, b; Bayley et al. 1992a, b). In addition, a number of whole-lake acidification experiments were conducted during the period (summarized by Schindler et al. 1991).

DOC concentrations declined in both reference and acidified lakes during the period. Declines in DOC at ELA have been accompanied by increases in transparency, deeper thermoclines, decreased cold water refugia, and deeper penetration of ultraviolet light (Schindler et al. 1990, 1992, 1996a, b).

In this paper, we examine changes to the sources and sinks of DOC caused by climatic warming in two reference lakes and sulfuric acid in one experimentally-acidified lake, in order to deduce reasons for the declining concentrations. Because DOC measurements were not made before 1972 and the period of warming ended (at least temporarily) after 1990, we restrict our analysis to 1972–1990.

Description of the lakes and their catchments

This study is focussed on lakes 239 and 240, affected only by natural events, and Lake 302S, which was acidified to pH 4.5. Characteristics of the lakes, catchments and the effects of climate or acidification have been described in many other papers (Brunskill & Schindler 1971; Schindler et al. 1976, 1980,

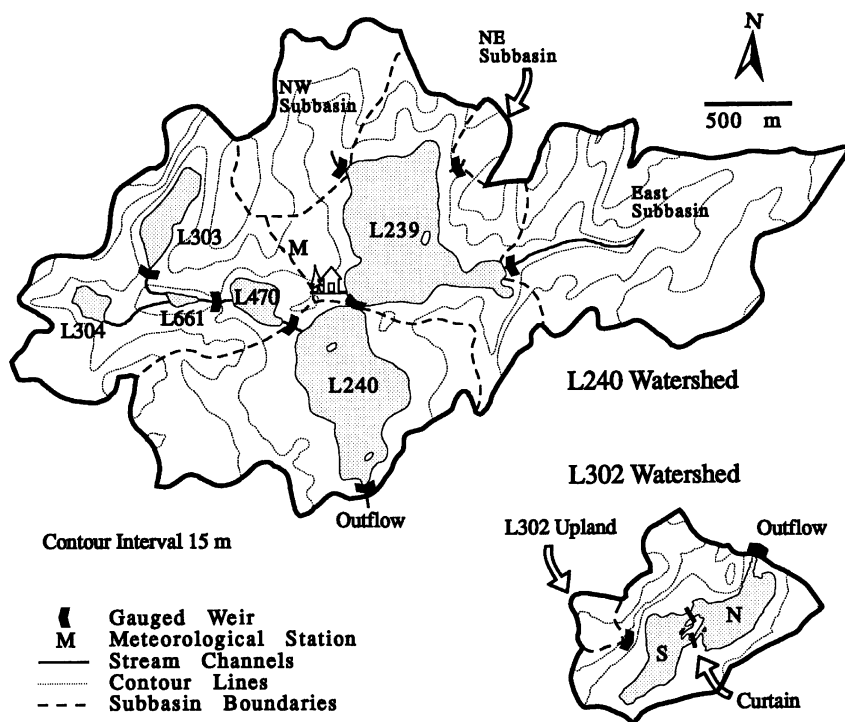


Figure 1. A map of the catchments of lakes 239, 240 and 302, with inflows. Locations where key hydrological, meteorological and chemical measurements were made are indicated.

1991; Bayley et al. 1992a, b; Rudd et al. 1990). Here, only an abbreviated description is given.

Reference lakes 239 and 240, which were affected only by natural variation, have different morphometric and hydrological characteristics. Lake 239 is a headwater lake, which receives all of its water and chemical inputs from first-order streams, direct terrestrial runoff and precipitation. In contrast, most of the water and chemical inputs to Lake 240 come from upstream lakes: either from the outflow of Lake 239 or from a chain of small lakes and wetlands to the west of the lake (Figure 1). There are no first-order streams reaching the lake. As a result of its larger catchment and shallower depth, Lake 240 has a much shorter water renewal time than Lake 239 (Table 1). The water renewal times of all lakes in the area increased 4-fold during the period, due to declining precipitation and increased evaporation and evapotranspiration (Schindler et al. 1996a).

Like Lake 239, Lake 302 is a headwater lake. Following an experiment with hypolimnion injection of nutrients into the north basin of the lake in the early 1970's (Schindler et al. 1980b), Lake 302 was monitored for several

Table 1. Morphometric data for the three study lakes and their catchments.

Lake	239	240	302S
Lake area, ha	54.3	44.2	10.9
Mean depth, m	10.9	6.0	5.1
Direct catchment area, ha*	393.3	162.0	54.3
Area drained by upstream lakes, ha	0	561.1	0
Water renewal times, years	4–26	<1–6	4–12

* Includes area drained by first-order streams.

years to ensure that the lake had fully recovered. For this study, we only use the records from 1981 and after. An acidification experiment was begun in 1982, following separation of the two basins of the lake in 1981 with a heavy vinyl-coated nylon sea curtain. Following separation, the two basins of the lake were treated as separate lakes, with the south basin (L302S) becoming the headwater basin. L302S was acidified from initial pH values of 6.0–6.7 to pH 4.5 over several years, using sulfuric acid. The north basin (L302N) was acidified to pH 5.0 with nitric acid, following which the pH was held constant with hydrochloric acid. Some biological and chemical results of the experiments were reported by Rudd et al. (1990); Schindler et al. (1991) and Kelly et al. (1995).

Methods

Inflowing streams and outflows of the lakes were monitored continuously at several locations (Figure 1) using calibrated v-notch weirs and automatic water level recorders (Beatty & Lyng 1989). Weekly chemical samples were taken whenever streams were flowing, returned to the ELA laboratory and preserved the same day for later analysis.

Lake 239 was sampled for DOC from 1972–1990. Lake 240 was sampled in summers of 1972, 1975–1978 and 1984–1990 and all winters except 1972–4 and 1976–81. Outflows only were sampled in 1973–74 and 1979–83, and these were assumed to be equal to lake concentrations, based on similarities in years when both were measured. Inflow chemical samples were taken weekly throughout the 1970–1990 period, and flow was continuously measured. Lake 302 was sampled for DOC from 1981 through 1990.

In each year, the three lakes were sampled monthly or more frequently during the ice-free season and 2–4 times in winter.

On each sampling date, a broad range of physical, chemical and biological variables, including DOC, were measured at several depths in the water column of each lake.

In the ice-free season, bulk precipitation samples were collected using a Plexiglass collector on an island in either Lake 239 or 240. Large particles were prevented from entering the collector by 1mm nylon mesh. Samples were collected after each precipitation event, filtered and prepared for analysis the same day. In winter, a similar sampler was used at the meteorological site in the Lake 239 basin. The winter sampler emptied through a large slot into a clean plastic bag. After each snowfall, all collected snow was pushed into the bag with a Plexiglass paddle, sealed, and kept frozen until the day of analysis. A summary of precipitation chemistry from 1970–1982 was given by Linsey et al. (1987).

All DOC samples were filtered through precombusted Whatman GF/F filters, acidified, stripped of inorganic carbon, and digested with acid persulfate by autoclaving (1971–75), irradiating with UV (1975–85) or heating to 102°C (1986 and after). The resulting CO₂ was measured by gas chromatography (thermal conductivity detector 1971–75) change in specific conductance after barium stripping (1976–85) or infrared absorbance (1986 and after). Methods changes were extensively intercalibrated in order to ensure that all data were comparable.

Inputs (I), outputs (O) and masses (M) of DOC in the lakes were calculated from hydrological, morphometric and chemical data. Average annual masses for each year were used to calculate year to year differences (ΔM). Catchment areas that drained directly to lakes were assumed to yield the same mass of DOC per unit area as the Northwest Subbasin of Lake 239, which had average morphological characteristics most similar to areas draining directly to lakes. The outflow from L302S to L302N was calculated by partitioning the outflow from the north basin between the two basins, based on catchment and lake surface areas.

The residence time of DOC in the lakes was calculated as M/I . DOC loading is defined as I/A_o , where A_o is the surface area of the lake.

Results

DOC inputs to the reference lakes

Annual average inputs of DOC in precipitation varied about threefold during the 20 year period (Figure 2a), and showed no trend with time. The long-term average concentration was 367 μM .

DOC inputs to Lake 239 from first-order streams declined about 40% during the period (Figure 2b). There was considerable year to year variation, most notably an increase during the wet year 1985, so that the relationship between declining DOC and time was not statistically significant. The declines

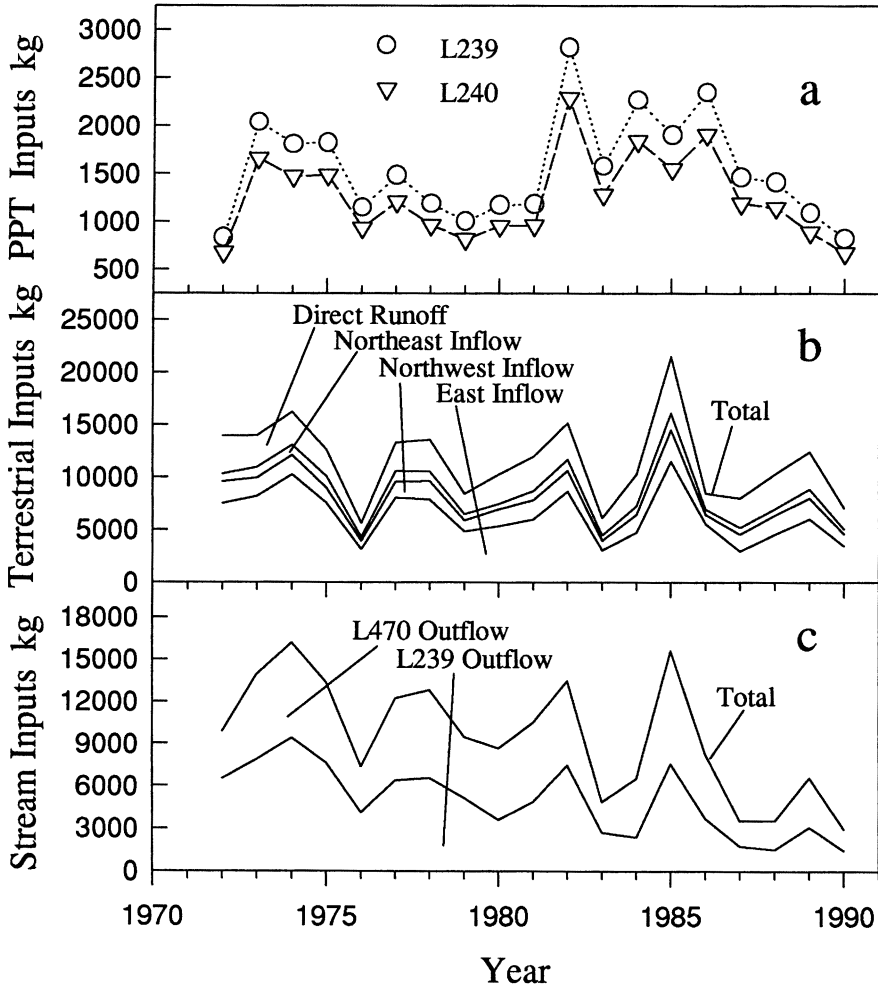


Figure 2. Changes in annual DOC inputs to lakes 239 and 240 from: a. Precipitation to lake surfaces. b. First-order streams and direct drainage to Lake 239. c. Upstream lakes and direct drainage to Lake 240.

were caused by reduced streamflows, and average concentrations of DOC in streams actually increased by 30–80% during the period. DOC concentrations were particularly high during storms following periods of prolonged drought (Schindler et al. 1992; see also papers by Hinton et al. in press).

The decline in DOC inputs to Lake 240 was even more pronounced than declines to Lake 239, because of lower discharge of DOC from upstream lakes (Figure 2c). The trend with time was statistically significant ($p = 0.02$).

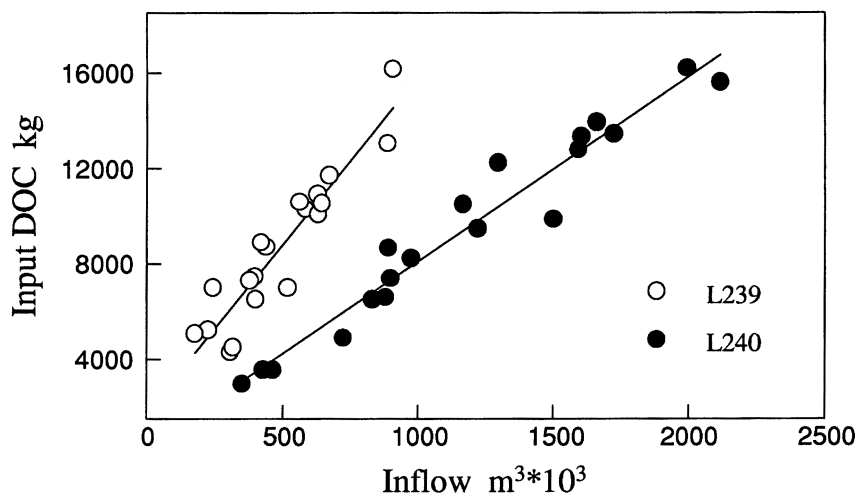


Figure 3. The relationship between annual input of water ($10^3 \text{ m}^3 \text{ a}^{-1}$) and annual input of DOC (kg a^{-1}) to lakes 239 and 240. Both relationships are highly significant ($p \ll 0.001$).

In the case of both lakes, annual inputs of DOC were strongly related to annual water inputs (Figure 3).

DOC Budgets

Reference lakes

Declines in losses of DOC via lake outflow were also observed during the period (Figure 4). Reduced losses of DOC via outflow were due largely to declines in outflow volume, but also in part to lower in-lake concentrations, as described below. The retention of incoming DOC was higher in Lake 239, probably because of the lake's much longer water residence time. Also, most of the DOC reaching Lake 239 was highly colored material from the catchment, which tends to be removed faster than the DOC received by Lake 240 from upstream lakes (Curtis & Schindler 1996). The DOC retention in both lakes 239 and 240 increased during the period (Figure 5), probably because longer water retention allowed more time for in-lake processes that remove DOC to have an effect (Schindler et al. 1992; Dillon & Molot 1996; Curtis & Schindler 1996).

DOC concentrations in the reference lakes decreased 15–25% during the 1980's (Figure 6). The combination of decreasing DOC concentration and higher retention indicates that much of the “retained” DOC was lost either to lake sediments or to the atmosphere. The decline was preceded by a noticeable increase in the concentration of DOC in headwater lakes in the two years following the 1980 fire, which we believe was caused by carbon

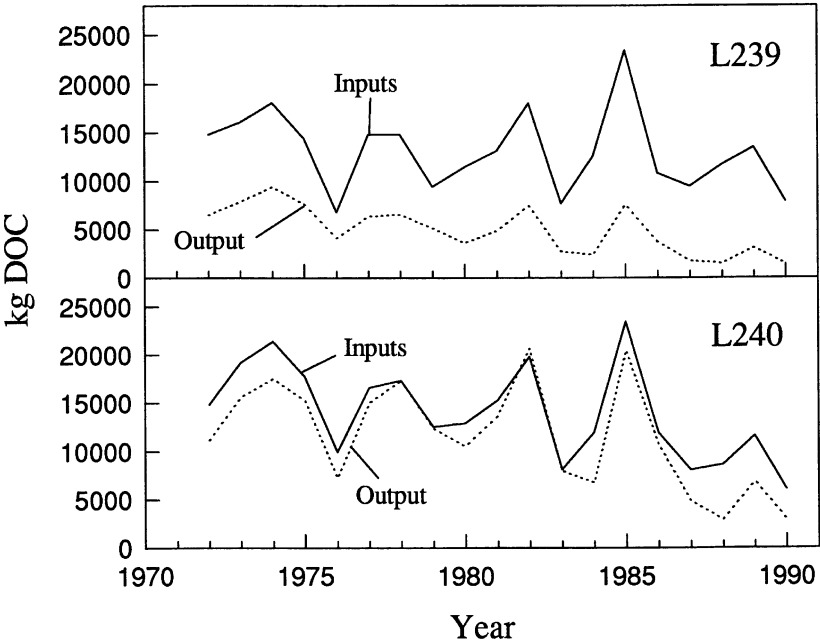


Figure 4. Total DOC inputs and losses via outflow for lakes 239 and 240.

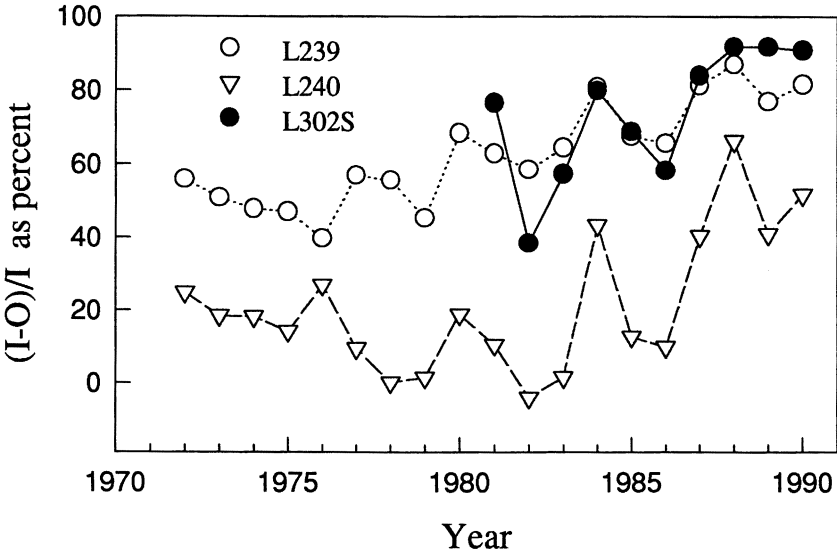


Figure 5. Annual DOC retention ($R = I - O$) as a percent of total DOC input (I) for lakes 239, 240 and 302S.

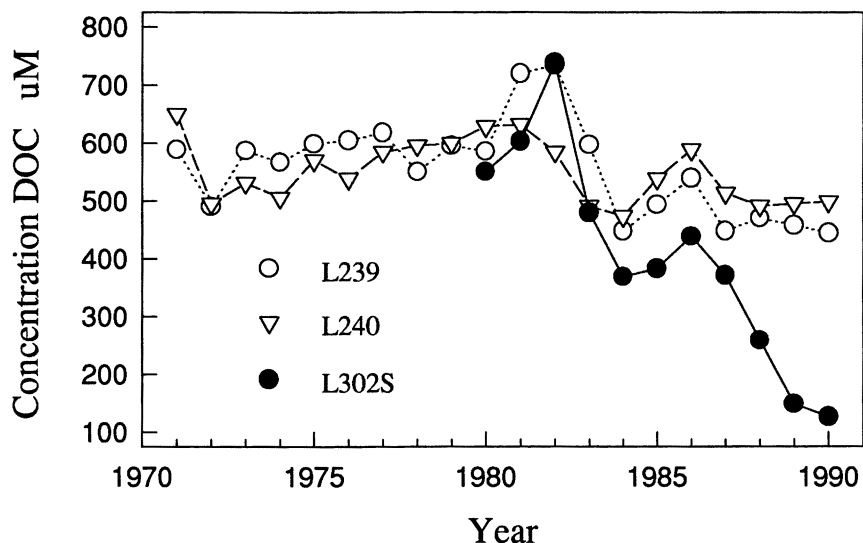


Figure 6. Mean annual DOC concentration over time in lakes 239, 240 and 302S.

blown or washed directly into the lake from the catchment, for on windy days, visibility was reduced by blowing soot, and occasionally it was not possible to see across the lakes. The effect was not noticeable in Lake 240, possibly because of the high proportion of DOC inputs from upstream lakes.

Acidified lakes

Although experimentally-acidified Lake 302S was exposed to the same climatic trends as reference lakes, DOC concentrations declined much more markedly (Figure 6). DOC retention was as high as in Lake 239, despite the two-fold faster water renewal in L302S (Figure 5). Together, these data show that acidification accelerates in situ removal of DOC, as found by Effler et al. (1985) and Dillon and Molot (1996).

Dillon and Molot (1996) calculated “apparent sedimentation velocity” as:

$$v = (R \cdot q_s)(1 - R) \quad (1)$$

where v is in units of m yr^{-1} , R is DOC retention, and q_s is water “loading” in m yr^{-1} . Because it actually represents the rate of all non-outflow losses of DOC and has been shown to follow first-order kinetics (Dillon & Molot 1996), v might more correctly be called a “mass transfer coefficient”, representing losses to both sediments and mineralization. When v is plotted over time for the three ELA lakes, the extreme effects of acidification on in-lake removal processes are very obvious, with v increasing significantly ($p = 0.006$) from 1–2 m yr^{-1} to 6–10 m yr^{-1} as L302S was acidified (Figure 7). There also

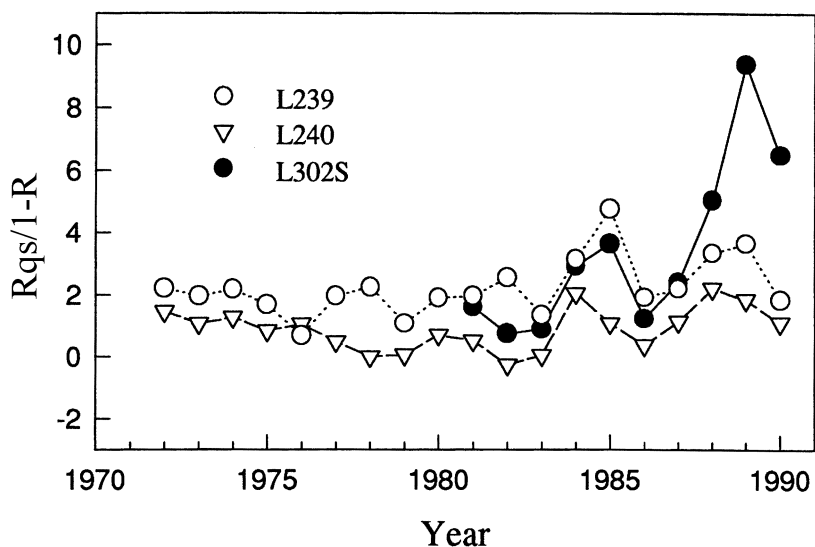


Figure 7. Mass transfer coefficients ($v = R^*q_s / (1 - R)$) for DOC over time calculated after Dillon and Molot (1996). The increases are significant ($p = 0.006$) for L302S, nearly significant ($p = 0.055$) for Lake 239 and not significant for Lake 240.

appears to be a slight increase over time in v in the reference lakes. Values in Lake 239 increased from 2–3 to 3–4 m yr^{-1} , and in Lake 240 from 0–1 to 1–2 m yr^{-1} . Neither value was statistically significant, although Lake 239 was close ($p = 0.055$).

However, equation (1) only accurately represents v when there is little or no year to year change in the mass of DOC in a lake, i.e. it is at steady state. This is not the case for the ELA lakes, particularly L302S during the period of extreme acidification, for changes in mass (ΔM) must be subtracted from R . The result (S), exceeded inputs in some years during the acidification of the lake, due to the large declines in concentration in the lake. Of course, this cannot happen once a new steady-state is reached. In order to illustrate the importance of such a correction, we have calculated (S) and (v) for two three year blocks at the beginning and end of the period of study, when stable concentrations of DOC indicated that lakes were rather close to steady state. These are shown in Table 2. Results confirm the modest increases in rates of DOC loss caused by climatic warming and drought, and the much greater effect of acidification.

Because of the decline in DOC inputs from catchments, precipitation became an increasingly important proportion of DOC inputs during the period. In the early 1970's, atmospheric inputs were typically about 10–12% of the total DOC inputs to Lake 239 and 7–8% of the total inputs to Lake 240.

Table 2. Differences in inputs, retention and sinks for DOC from early to late in the period. Values given are 30 year averages, in $\text{g C m}^{-2} \text{yr}^{-1}$. MTC = Mass Transfer Coefficient.

Lake 239				
	1972–1974 $\text{g C m}^{-2} \text{yr}^{-1}$	%I	1988–1990 $\text{g C m}^{-2} \text{yr}^{-1}$	%I
Total Input (I)	29.04	–	19.72	–
Outflow (O)	14.16	49	3.62	18
Retention (R)	14.87	51	16.10	82
Lost from Lakes (S)	15.80	54	16.20	82
MTC (v)	2.11	–	2.94	–

Lake 240				
	1972–1974 $\text{g C m}^{-2} \text{yr}^{-1}$	%I	1988–1990 $\text{g C m}^{-2} \text{yr}^{-1}$	%I
Total Input (I)	41.93	–	19.87	–
Outflow (O)	33.50	80	9.60	48
Retention (R)	8.43	20	10.27	52
Lost from Lakes (S)	6.37	15	2.42	12
MTC (v)	1.27	–	1.72	–

Lake 302S				
	1972–1974 $\text{g C m}^{-2} \text{yr}^{-1}$	%I	1988–1990 $\text{g C m}^{-2} \text{yr}^{-1}$	%I
Total Input (I)	14.39	–	13.76	–
Outflow (O)	6.38	44	1.16	8
Retention (R)	8.01	56	12.61	92
Lost from Lakes (S)	12.95	64	17.59	128
MTC (v)	1.08	–	6.96	–

However, because the input of DOC from catchments declined while input from precipitation remained relatively constant, by the late 1980s DOC from precipitation increased to 11–14% of total inputs to Lake 239 and 12–13% to Lake 240. Atmospheric DOC is nearly colorless, so that its increasing proportion of total inputs may alone impart small but significant changes to lake transparency.

Discussion

There is considerable interannual variability in DOC concentrations and inputs, with wet years generally having higher DOC inputs and concentrations than adjacent drier years. Nevertheless, the long-term pattern is very clear: both climatic warming and acidification caused declines in DOC inputs and concentrations during the 1970s and 1980s. This is particularly apparent if data for the two more or less steady-state periods are compared, early and late in the period of record (Table 2). In addition to a strong influence of reduced hydrological flows on DOC transport, both warming and acidification caused increased in-lake removal. In the case of acidification, the effect on in-lake processes was very strong, probably reflecting accelerated rates of *in situ* processes (Table 2). For lakes affected only by climate the effect was weaker, probably largely representing longer residence time rather than accelerated processing. In Lake 239, outflow declined from 49 to 18% of inflowing DOC, with all of the difference caused by losses to sedimentation and mineralization. In Lake 240, outflow of DOC declined from 79% of inflow to 48%. In this case, the relatively large interannual changes in ΔM accounted for much of the retention, and the long-term change in sedimentation (S) was only from 12 to 15%. In Lake 302S, outflow of DOC declined from 44% of inflow to 8%. *In situ* losses increased to an average of 128% of inflow in the final three years of the period, when the lake was being held at pH 4.5, illustrating that not only incoming DOC but also concentrations in the lake were being depleted.

In general, strong correlations between water renewal or water “loading” and retention of DOC have been noted in headwater lakes, illustrating that losses are first-order (Dillon & Molot 1996; Curtis & Schindler 1996). This is most easily seen in a plot of $1/R$ vs q_s , which is typically a strong linear relationship, with an average slope of $1/v$. As expected, the relationship for Lake 239 was significant ($p = 0.02$ Figure 8). However, the relationship was not statistically significant for either Lake 240 or L302S. In second-order lakes like Lake 240, where much of the DOC is removed or modified in passing through upstream lakes, DOC retention may be a less predictable function of water residence than when DOC is derived primarily from terrestrial catchments. Similarly, the departure of Lake 302S from first-order losses may indicate that several in-lake processes are simultaneously being modified, in ways that are not uniformly affected by acidification.

The chemical characteristics of DOC change as a function of water renewal time, and lake order. Terrestrially-derived, highly colored DOC fractions have a much shorter residence time in lakes than the general DOC pool (Curtis & Schindler 1996), suggesting that the terrestrial sources would be strongly affected by flushing. In addition, both relative fluorescence and

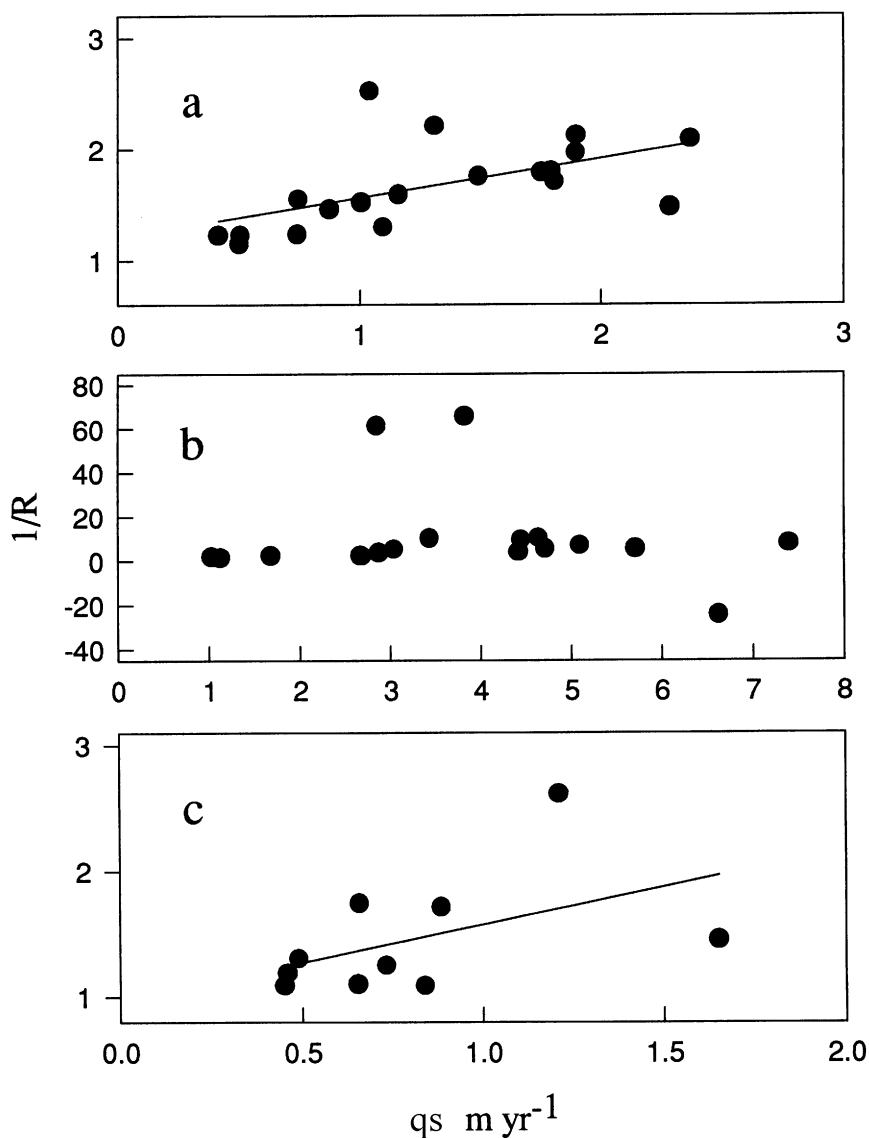


Figure 8. $1/R$ vs q_s for the three ELA lakes. a. Lake 239. $p = 0.02$, indicating that DOC losses are first-order. b. Lake 240. c. Lake 302S. Neither b. nor c. is statistically significant, indicating that first order kinetics may not apply to DOC losses in second-order lakes, or to acidified lakes.

relative absorbance of DOC declined as water residence time increased, probably indicating lower photoreactivity of the remaining DOC (Curtis & Schindler 1996).

In L302S, the strong effect of acidification on in-lake DOC removal probably simply overwhelmed the normally-expected dependence of DOC retention on water renewal. Again, relative fluorescence and absorbance indicate major changes in the properties of remaining DOC.

As Dillon and Molot (1996) found for Blue Chalk and Dickie Lakes, DOC loading to all three lakes was a predictable function of q_s (Figure 9), confirming that streamflow was the major factor causing the declining DOC in lakes during the period.

The residence time for DOC varied considerably between the lakes. As expected from the mass transfer rates (Figure 7), it was longest in Lake 239, and it became particularly short in L302S after the lake was acidified. In all cases, the residence time was shorter for DOC than for water, indicating the importance of in situ removal. For all three lakes, there was a tendency for slightly faster relative removal of DOC with time, indicating an acceleration of in-lake processing as DOC declined and lakes became clearer (Figure 10), indicating an acceleration of in situ removal of DOC, in addition to reduced rates of DOC supply to lakes. These changes, coupled with the decreased ability of older DOC to reduce the penetration of UV radiation, indicate that climatic warming and drought could have important effects on the UV exposure of freshwater organisms (Schindler et al. 1996b).

Other factors modifying DOC inputs

Comparisons of DOC concentrations at other sampling sites in the catchments revealed some interesting modifiers to the general pattern related to climate change, that should be noted by researchers interested in DOC budgets. While the DOC input to Lake 240 from Lake 470, declined steeply, it was affected by several features of the drainage from the chain of small lakes. DOC concentrations declined over time in lakes 304 and 303, headwaters in the drainage. However, concentrations usually nearly doubled as water passed through Lake 661, a small bog lake, then declined again in passing through Lake 470. The DOC concentrations in lakes 661 and 470 were more affected by beaver dams at the outflows, which raised water levels by up to several decimeters in the 1980s, than they were by climatic change. In general, DOC concentrations were higher when wetland areas around the lakes were flooded (S. E. Bayley, unpubl. data).

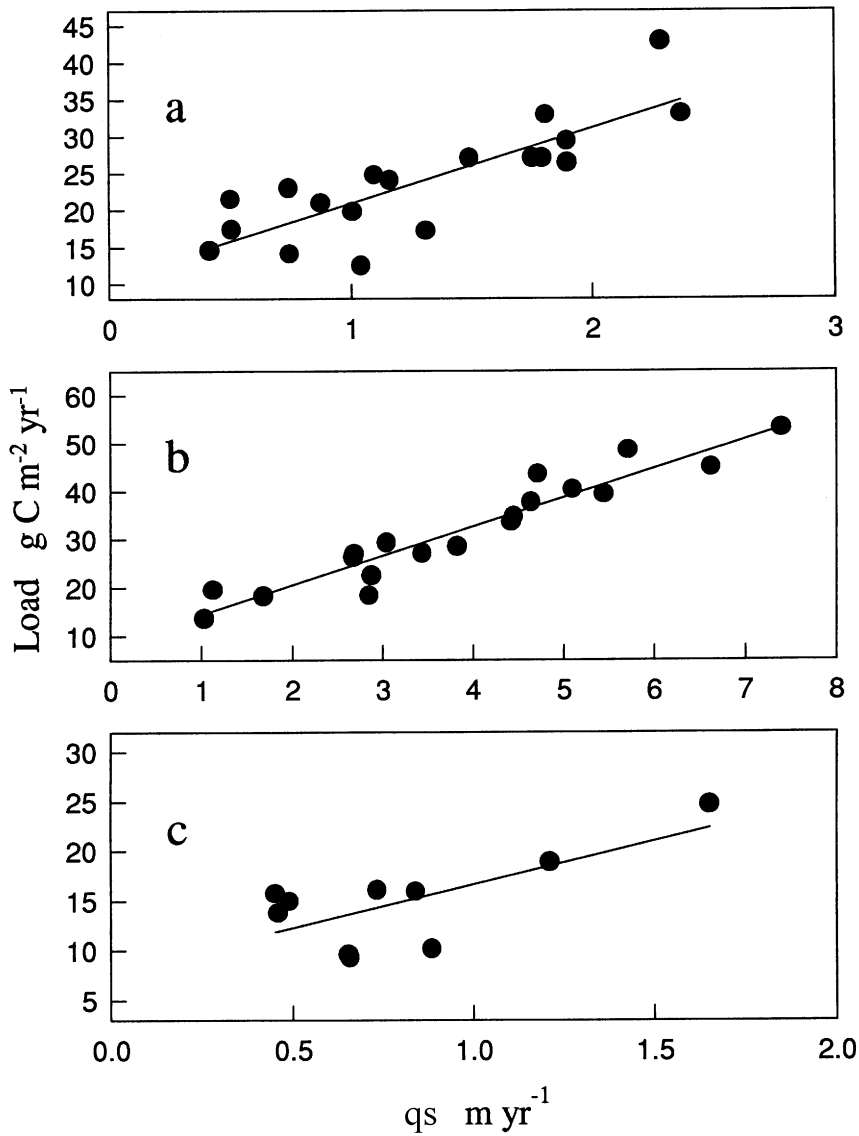


Figure 9. DOC “loading” (I/A_0) vs. q_s for the ELA lakes. The relationships are all highly significant ($p = 0.001-0.02$). a. Lake 239. b. Lake 240. c. Lake 302S.

The effects of drought and forest fire

Results from Lake 239 and 240 show that most of the decline in DOC in natural lakes is caused by reduced inputs from catchments and upstream lakes, resulting from reduced streamflow under warmer, drier climatic conditions

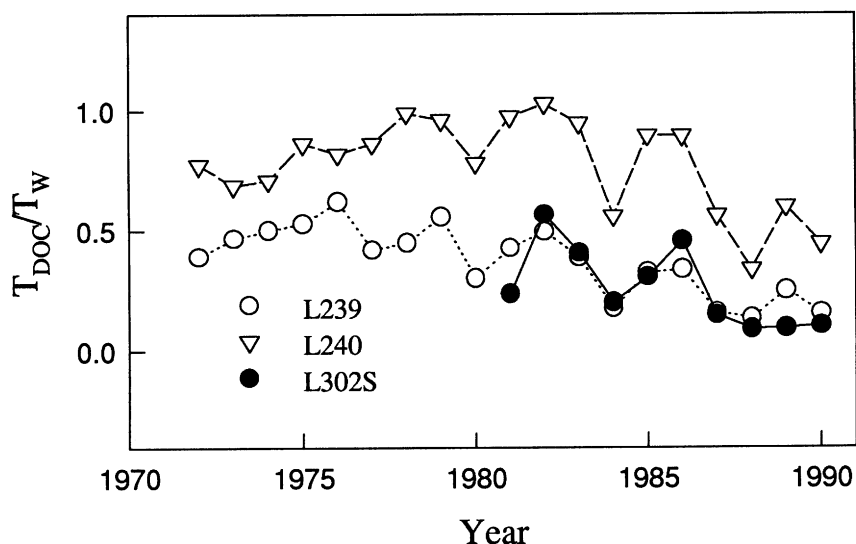


Figure 10. Changes in the ratio of DOC/water retention times for the three lakes, 1970–1990. The declines in the ratio with time are statistically significant in lakes 239 and 302S ($p = 0.001$ and 0.04 , respectively), but just below significant in Lake 240 ($p = 0.07$).

(Schindler et al. 1992, 1996a). The lack of any obvious “step” changes in DOC inputs following the two forest fires in 1974 and 1980 indicates that drought is the factor primarily responsible for the observed decline (Figure 2b), even though organic soils were nearly completely burned in extensive parts of the catchment. The high inputs of DOC in 1985, a single wet year following several years of drought and during the period when soil development was still very slight, also suggests that reduced water flows were much more important influences on DOC export than either fire or the thickness of organic deposits. Indeed, DOC exports from catchments in 1985 were similar to those observed in years with similar precipitation in the early 1970s. The lack of dependence of DOC decline on soil development suggests that much of the DOC exported from catchments must be relatively young, or derived from sources that are not affected by fire. This is confirmed by other studies in this volume (Hinton et al. 1996).

Comparisons with Dorset Lakes

There is a rather remarkable similarity between the behavior of DOC in lakes at Dorset and those at ELA. While the areas are geologically rather similar, there are significant differences in climate, with Dorset being considerably warmer and wetter. Also, catchments in the Dorset area are vegetated largely with hardwoods. Circumneutral Dorset Lakes had values of $2.2\text{--}3.3 \text{ m yr}^{-1}$

for v, i.e. comparable to lakes 239 and 240. Acidified Plastic Lake had a higher coefficient (4.6 m yr^{-1}), which is consistent with our observations on L302S.

It is somewhat surprising that DOC inputs from precipitation were much higher at ELA than at Dorset, Ont. Dillon and Molot (1996) found atmospheric DOC inputs to average $839 \text{ mg C m}^{-2} \text{ yr}^{-1}$ for 1981–1989. Our rates were nearly four-fold higher, $3180 \text{ mg C m}^{-2} \text{ yr}^{-1}$ for the same period. Even the lowest annual input at ELA, $1470 \text{ mg m}^{-2} \text{ yr}^{-1}$ was higher than the Dorset average.

The highest mass transfer coefficients at both Dorset and at ELA were for acidified lakes, indicating that in-lake removal mechanisms are enhanced by acidification. The nature of these mechanisms is under active investigation.

Dillon and Molot (1996) attempted to differentiate sinks for DOC by one more step. By making the assumption that C:P ratios in lake sediments could be used to calculate downward DOC fluxes, they were able to calculate a term for losses via mineralization and loss of the resulting CO_2 to the atmosphere. Their calculations suggest that sedimentation exceeds losses to the atmosphere for most lakes. However, in acidified Plastic Lake, the term for losses to the atmosphere exceeded that for sedimentation, suggesting that enhanced mineralization of DOC may be an important mechanism in the observed DOC decline in acidified lakes. This observation needs validation with other studies.

The combined effects of climatic change and acidification on DOC

In comparison to natural lakes, acidified lakes showed large increases in the rates of in-lake DOC removal. We did not investigate the removal mechanisms, and several seem likely to have been affected. Firstly, acidification is known to enhance the flocculation of DOC with aluminum or iron (Effler et al. 1985; Urban et al. 1988). Secondly, UV light penetration in the lake increased from 30 cm to almost 3 m as the result of DOC declines, probably allowing photochemical processing of DOC to increase in intensity (Schindler et al. 1996b). Finally, the warming of acidified lakes was even greater than reference lakes, due to greater light penetration, which also caused thermocline deepening (Schindler et al. 1996a). As a result of warmer temperatures, microbial utilization of DOC may also increase, although Dillon (pers. comm.) found that microbial DOC consumption was much lower than photolytic degradation of DOC in lakes at Dorset.

Whatever the mechanism, the increased in situ removal of DOC in acidified lakes must have important consequences. DOC concentrations in lakes near Sudbury, Ontario decreased to as low as $30\text{--}40 \mu\text{M}$ (P. J. Dillon, pers. comm.). At such low DOC values, exposure of aquatic organisms to UV light increases

dramatically (Scully & Lean 1994). The decreased biodiversity observed in acidified lakes may be due at least in part to declining DOC concentrations.

Given the many important roles of DOC in aquatic processes, the decreases in rates of supply to lakes under changing climate and the increases in in-lake removal under acidification must be of considerable concern. Although at most locations warming was not as extreme as at ELA, climatic warming was widespread in boreal regions of Canada in the 1970's–1990 (Hengeveld 1991). In addition, many lakes in the eastern boreal region are affected by acid precipitation (Minns et al. 1990, 1992). Approximately 40% of the lakes in Ontario have DOC values less than 330 μM (Neary et al. 1990), low enough that even small decreases in DOC concentrations will cause relatively large increases in the penetration of photosynthetically-active and ultraviolet wavelengths (Schindler et al. 1996b; Scully & Lean 1994). In addition, several percent of eastern Canadian lakes have been acidified to pH values of 5 or less, where increased in-lake DOC removal can be expected. As we have shown elsewhere, a 10% reduction in DOC in a lake which initially has a concentration of 250 μM will increase the UV exposure of freshwater organisms by more than projected decreases in stratospheric ozone (Schindler et al. 1996). In summary, the effects of DOC losses caused by climatic warming and acidification can have important implications for chemical and biological processes in lakes. Identifying the mechanisms that control DOC and how they respond to human-caused perturbations should be regarded as of high priority.

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