

The influence of catchment size on lake trophic status during the hemlock decline and recovery (4800 to 3500 BP) in southern Ontario lakes

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Abstract

We investigated the ecological effects of terrestrial ecosystem change during the hemlock decline and recovery (4,800–3,500 BP) on lake communities (diatoms and chrysophytes). This study specifically assessed the role of catchment area and slope in determining the magnitude of lake eutrophication during the hemlock decline by analyzing sediment cores from five alkaline, holomictic lakes in southeastern Ontario, Canada. The study lakes were similar in most limnological aspects, but differed widely in the relative sizes of their catchments. Diatoms were used to quantitatively infer past lake-water total phosphorus (TP) concentrations.

All five lakes showed shifts in their algal communities during the hemlock decline, but most lakes exhibited only minor changes in trophic status. The magnitude of the limnological response appears to be related to catchment size and slope. Long Lake, Burridge Lake, and Gunter Lake possess the smallest catchments and exhibited the weakest responses to the hemlock decline. The catchment area of Flower Round Lake is considerably larger and steeper than these lakes, and was the only lake to show a marked eutrophication. *Aulacoseira ambigua* bloomed and diatom-inferred TP concentration increased by $14 \mu\text{g l}^{-1}$.

Catchment slope appears to have influenced the type of material exported into the lakes. Lake basins draining catchments with gentle relief received proportionally greater amounts of organic matter, whereas steeper catchments supplied relatively greater proportions of mineral matter. Faster water flow associated with steeper catchment slope may have enhanced mineral erosion.

Following the hemlock decline, nutrient supplies to most of the study lakes were reduced. The period of forest recovery was associated with an $11 \mu\text{g l}^{-1}$ reduction in diatom-inferred lake-water TP concentration in Flower Round Lake, and algal populations decreased. Our results generally support the ecological theory of forest ecosystem development and secondary succession developed from long-term data collected at the Hubbard Brook Experimental Ecosystem.

Introduction

Hemlock (*Tsuga canadensis* (L.) Carr.) populations were decimated in eastern North America approximately 4,800 BP, during an event known

as the hemlock decline (Davis, 1981; Allison *et al.*, 1986). Davis (1981) hypothesized that the decline was caused by the outbreak of a forest pathogen. Several lines of evidence have provided strong support for this hypothesis. First, the hemlock

decline occurred synchronously (Davis, 1981) and rapidly, during a period as short as 10 to 60 years (Davis, 1981; Allison *et al.*, 1986), throughout its entire range in eastern North America. Second, a pollen record from laminated lake sediments demonstrated a strong similarity in the duration and pattern between the decline of hemlock and the recent decimation of *Castanea dentata* (Marsh.) Borkh. populations, also caused by a pathogen (Allison *et al.*, 1986). Third, the pattern of forest succession following the hemlock decline was analogous to historically documented patterns following the chestnut blight (Davis, 1981). In both cases, pollen concentrations of successional species, such as *Betula*, increased initially. This was followed by increases in *Acer* and *Fagus*, taxa that compete with hemlock in mature stands.

Before 4,800 BP, hemlock was the most abundant conifer (Mott & Farley-Gill, 1978), and was a dominant tree in the landscape of southeastern Ontario (Anderson, 1987). The rapid demise of hemlock provides an example of a major natural disturbance to the forest ecosystem, which was followed by stages of terrestrial ecosystem development, including secondary succession (e.g. Bormann & Likens, 1979). It took approximately 2,000 years for hemlock populations to fully recover from this disturbance. During this period, changes in the structure and function of the terrestrial ecosystem probably exerted strong influences on lake-watershed interactions. Ecological theory (Vitousek & Reiners, 1975; Bormann & Likens, 1979) and evidence (Bormann *et al.*, 1974; Likens *et al.*, 1970; Hobbie & Likens, 1973; Hornbeck, 1975; Bormann & Likens, 1979; Gorham *et al.*, 1979) suggest that a catastrophic forest disturbance, such as the hemlock demise, could initially cause a sharp decline in evapotranspiration (due to tree loss), and increase both water and nutrient supplies from the watershed. The increase in water discharge could greatly enhance catchment erosion, and particulate and dissolved matter loadings (Likens, 1984). Furthermore, large quantities of nutrients (e.g. phosphorus and nitrogen) may have been supplied to lakes by processes leading to increased organic

matter decomposition, increased transport of particulate matter, and increased soil nitrification (Hobbie & Likens, 1973; Likens, 1984). As a result, lakes may have become more eutrophic in response to the decline in hemlock.

Ecological models (Vitousek & Reiners, 1975; Bormann & Likens, 1979) and empirical data (Marks & Bormann, 1972; Bormann & Likens, 1979) also suggest that nutrients and water become strongly retained in accumulating plant biomass during initial stages of forest recovery and ecosystem development. As a result, lakes may have experienced sharp declines in nutrient inputs, and aquatic productivity may have become reduced during forest reorganization following the hemlock demise.

Lake basins, because they lie downhill from surrounding terrestrial ecosystems, often archive information of past changes in terrestrial and aquatic ecosystems. The paleolimnological record, therefore, allows for the investigation of changes in terrestrial ecosystem structure and function, lake-watershed interactions, and their influences on aquatic biota over the long time scale at which they occur. A paleolimnological analysis of the biological and chemical changes that occurred during the hemlock decline provides an opportunity to assess ecological theory and validate models developed from empirical studies of much shorter duration.

Several paleolimnological studies have demonstrated the influence of hemlock loss on aquatic ecosystems, but the results have often been contradictory. Aquatic productivity increased during the hemlock decline in Berry Pond (Whitehead *et al.*, 1973) and North Pond (Crisman, 1977), Massachusetts. Increased erosion, a larger input of deciduous leaf litter (from replacement of hemlock by deciduous trees), decomposition of hemlock detritus, and changes in spring and summer runoff were believed responsible for the increased nutrient supply to the lakes. Likens & Davis (1975), however, detected very little change in nutrient inputs or aquatic productivity in Mirror Lake (New Hampshire) at the time of the hemlock decline. The influence of the hemlock decline on the trophic status of alpine lakes in New

Hampshire and Vermont (Ford, 1990), and lakes in New York (Whitehead *et al.*, 1989) was largely masked by processes contributing to natural acidification of the lakes. Boucherle *et al.* (1986) showed that the biotic responses to the hemlock decline were different in each of three lakes in southern Ontario. These lakes drained similar catchment areas, and the magnitude of the aquatic change was largely influenced by lake size, with smaller lakes exhibiting more pronounced eutrophication. Little Round Lake showed the greatest limnological change, but its trophic state was also influenced by periodic changes in meromixis. None of these studies specifically addressed the effects that forest recovery and subsequent ecosystem development have on lake trophic status.

A strong relationship exists between catchment size and phosphorus export (Prairie & Kalff, 1986), and between catchment size and lake trophic status for lakes with equal volumes (Schindler, 1971). For this reason, the magnitude of limnological responses to the hemlock decline may vary along a "catchment size-to-lake volume" gradient. In this study, we specifically investigated the influence of catchment area on

the limnological responses in five alkaline, holomictic southern Ontario lakes during the decline and recovery of hemlock (4,800–3,500 BP). These lakes were selected on the basis of their similarities in most physical aspects (i.e. lake size and morphometry, geology, native vegetation zones). However, they differ widely in the relative sizes of their catchments. We employed a number of paleoindicators (diatom and chrysophyte microfossils, biogenic silica, sediment geochemistry, pollen) to establish relationships between changes in the terrestrial watersheds and limnological communities. This is the first time diatoms have been used to quantitatively infer long-term trends in lake-water total phosphorus (TP) concentration.

Site descriptions

The five study lakes all occupy small, relatively deep basins with simple morphometry. Selected limnological and geographical information are presented in Table 1. The five basins have similar lake surface areas and volumes, but differ up to 68-fold in the relative sizes of their catchments

Table 1. Selected morphometric, geographic and physical characteristics of the five study lakes. "Relative catchment size" and "Relative catchment/lake volume" refer to values relative to the smallest lake. Data are compiled from the Ministry of the Environment's Southeastern Ontario Lake Database (unpublished data, Kingston District Office).

Lake name	Long	Burridge	Gunter	Flower Round	Singleton*
Latitude	44° 48' N	44° 40' N	44° 54' N	45° 10' N	44° 31' N
Longitude	76° 15' W	76° 34' W	77° 32' W	76° 41' W	76° 07' W
Elevation (m a.s.l)	129	152	335	195	91
Surface area (km ²)	0.91	0.93	0.74	1.01	0.97
Maximum depth (m)	19.8	16.2	18.3	12.8	13.4
Mean depth (m)	5.0	4.5	3.5	6.0	5.6
Volume ($\times 10^6$ m ³)	4.25	5.90	12.63	5.95	4.28
Shoreline (km)	7.9	6.9	5.5	5.3	5.8
Flushing rate (yr ⁻¹)	2.5	0.3	2.9	3.5	23
Catchment area (km ²)	4.1	5.1	18.4	55.2	277
Relative catchment area	1.0	1.2	4.5	13.5	67.6
Relative catchment/lake volume	1.1	1.0	1.7	10.8	75.2
Surface area/catchment ratio (%)	22	18	4	1.8	0.3
Highest elevation in catchment above lake (m)	30	15	91	137	61
Lake-water pH	7.6	7.8	8.1	7.9	8.2

* Singleton L. drains a very complex catchment; values for the catchment area are a theoretical estimate of the actual size.

(Table 1). The lakes are situated within a 100-km radius north of Kingston (Ontario), and all lie within the mixed deciduous forest zone of the Ottawa Valley-Lake Ontario region (Anderson, 1987). All lakes drain similar metamorphosed Precambrian (Grenville) bedrock belonging to the Central Metasedimentary Belt (Baer *et al.*, 1977), overlain by carbonate-rich glacial tills (Kettles & Shilts, 1987).

Burrige L. and Long L. are headwater lakes, and possess the smallest catchment areas (Table 1). In contrast, Gunter L., Flower Round L. and Singleton L. all have other lakes lying upstream within their catchments. Most of the study lakes drain areas of low topographic relief. Long L. and Flower Round L. are the only exceptions, having relatively steep catchments. Flower Round L. occupies the steepest basin, with hills rising up to 137 m within its catchment (Table 1). Calculation of Singleton L.'s catchment area from topographic maps estimates that it drains a relatively huge area (277 km²), including the Rideau Canal system. However, the drainage pattern is very complex, and extensive northeastern portions of the catchment have very low relief and are poorly drained. As a result, significant portions of the calculated catchment area probably contribute little or no water to Singleton L. Based on available data, an accurate estimate of the 'true' or effective catchment area cannot be calculated for Singleton L.

Materials and methods

Sediment cores were taken from central, deep water areas in each of the lakes, using a 3.8-cm diameter modified Livingstone piston corer (Livingstone, 1955; Vallentyne, 1955). All coring was performed through the lake ice during the winters of 1988, 1989 and 1990.

The cores were extruded horizontally in the lab and sectioned into 1-cm intervals. Pollen preparation followed standard techniques (Faegri & Iversen, 1975), but without the use of hydrofluoric acid. For each sample a minimum of 400 pollen grains was identified and enumerated at 400× magnification using either Olympus BH-2

or Leitz Dialux microscopes with bright field optics. Pollen taxonomy followed Kapp (1969), McAndrews *et al.* (1973), and McAndrews & King (1976).

Sediment chronology was estimated from correlations of bulk radiocarbon dates (from the literature) and visually determined pollen zone boundaries, based primarily on syntheses by Terasmae (1981) and Anderson (1987) from nearby lake cores. A single chronology was used for all five lakes. In this region of southeastern Ontario, the hemlock decline and recovery occurred at about 4,800 and 3,500 BP, respectively.

Sediment organic and mineral matter contents were determined by weight loss during 1 hour ignition at 550 °C, and residual weight after 1 hour ignition at 1000 °C, respectively (Dean, 1974). Sediment geochemical analyses were performed on dried (90 °C for 24 hours) and milled bulk lake sediments. Geochemical elements were extracted in multi-acid reagent (HF/HNO₃/HClO₄) and measured by inductively-coupled plasma (ICP) spectrometry at X-Ray Assay Laboratories (Toronto, Ontario). Geochemical data were expressed as concentrations and as ratios relative to Ti. Elements such as Ti, K, Na, and Mg are mainly derived from mineral erosion (Mackereth, 1966; Engstrom & Wright, 1984). Other elements, e.g. Ca, P, Mn, Fe, Cu, and Zn, while often common in mineral phases, may also be supplied from organic phases. Ratios of these two groups of elements, e.g. Fe:Ti, provide a proxy for soil development, because humus-rich soils enhance the supply of organic-bound elements and inhibit mineral erosion. Titanium ratios are useful for interpreting bulk sediment geochemistry because they correct for the proportion of P, Mn, Fe, Cu, and Zn in mineral lattices by standardizing to Ti, which occurs almost entirely in clastic phases (Whitehead *et al.*, 1989).

Diatom valves, and chrysophycean scales and cysts were prepared using the same standard digestive technique (Battarbee, 1973; Smol, 1983). Microfossils were counted from each sample along transects under oil immersion using an Olympus BHS microscope equipped with bright field optics (1000× magnification, N.A. = 1.40).

A minimum of 500 diatom valves were identified and enumerated from each sample. Diatom taxonomy followed Hustedt (1930), Patrick & Reimer (1966, 1975), Koppen (1975), Germain (1981), Håkansson & Stoermer (1984a, b), Stoermer & Håkansson (1984), Camburn *et al.* (1986), and Krammer & Lange-Bertalot (1986–1991). Planktonic diatoms included all centric taxa, and members of the following pennate genera: *Asterionella*, *Diatoma*, *Meridion*, *Synedra* and *Tabellaria*, and *Fragilaria crotonensis* Kitton. Chrysophyte scales and cysts were enumerated in all samples, but were not identified according to their morphotypes. Siliceous microfossil abundance was also estimated from sediment biogenic silica concentrations, following Conley (1988).

Lake-water total phosphorus concentrations (TP) were inferred from diatom percent abundance data using a weighted averaging regression and calibration model (WACALIB v. 2.1; Line & Birks, 1990) developed from diatoms in British Columbia lakes (Hall & Smol, 1992). While weighted averaging paleolimnological inference procedures always produce results, there are no simple criteria for evaluating their reliability (Birks *et al.*, 1990). We assessed inference reliability using two criteria, as detailed below, which closely follow criteria established by Birks *et al.* (1990).

1. Lack-of-fit to total phosphorus concentration

Diatom assemblages that exhibit a close relationship to TP concentration are likely to provide reliable TP inferences. The residual distance of modern samples to the TP axis in a constrained canonical correspondence analysis (CCA) of the calibration lake-set provides a measure to assess 'lack-of-fit' to TP (Hall & Smol, 1992). Samples with high residual distance from the TP axis exhibit 'poor fit' to TP (Birks *et al.*, 1990). Fossil samples, when made "passive", can also be positioned on this TP axis by means of transition formulae (Ter Braak, 1988). In this way, fossil diatom assemblages were positioned passively in a canonical correspondence analysis (CCA) of the B.C. calibration lake set in which axis 1 was constrained to TP. Fossil diatom assemblages

with a residual distance to CCA axis 1 greater than or equal to the residual distance of the extreme 5% of the calibration set samples were considered to have a 'very poor fit' to TP. Those with values greater than or equal to the extreme 10% were considered to have a 'poor fit' (Birks *et al.*, 1990). CCA ordinations were performed using the computer program CANOCO v. 3.10 (Ter Braak, 1988, 1990).

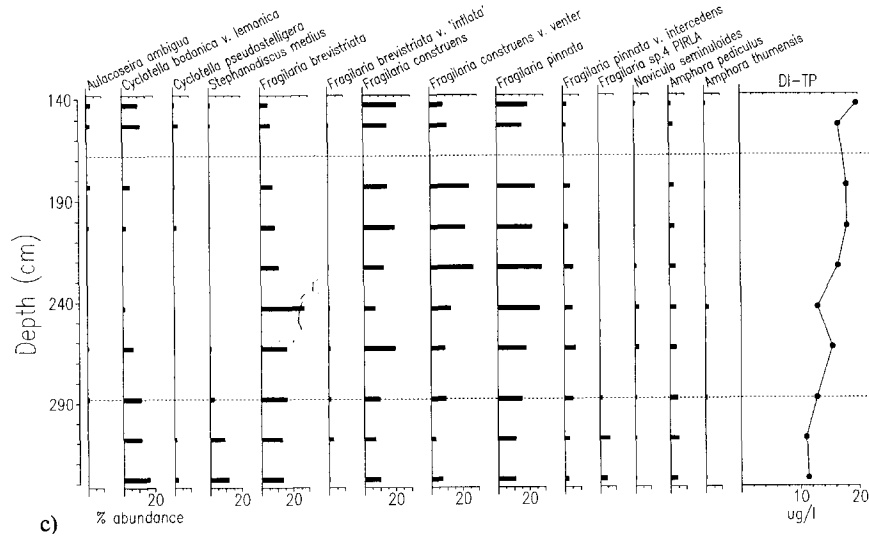
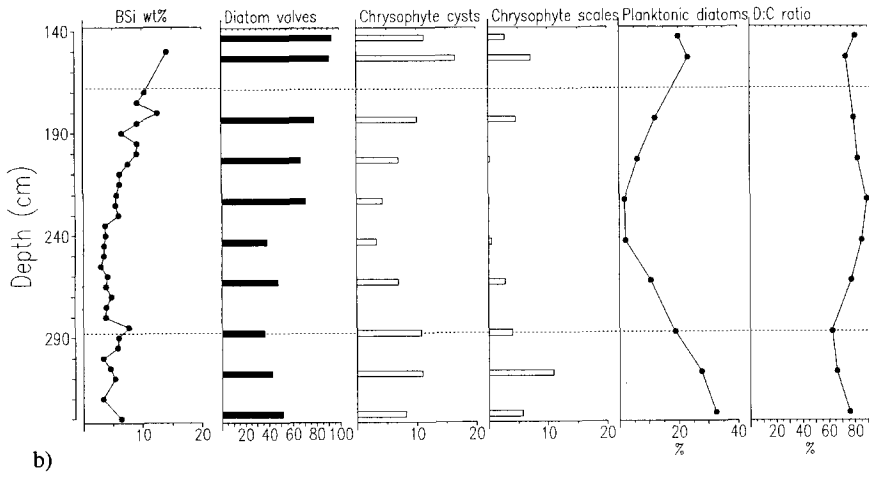
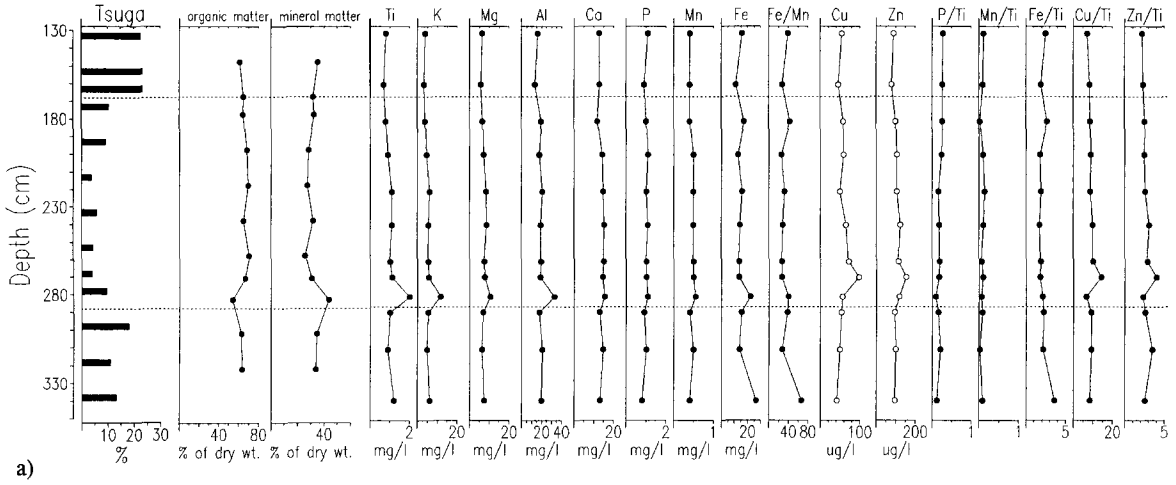
2. Modern analogue measures

Diatom-inferred TP values are likely to be more reliable if fossil samples have close modern analogues within the calibration lake-set (Birks *et al.*, 1990). We used a method of analogue matching to identify fossil diatom assemblages with poor analogy to modern assemblages in the calibration lake-set. A squared χ^2 dissimilarity index (Prentice, 1980) was used to compare every fossil sample with all calibration samples, and the following criterion was established from the observed distributions of squared χ^2 distances between all the modern calibration samples, with Monte Carlo permutation tests: Fossil samples with a minimum squared χ^2 greater than the extreme 5% of the squared χ^2 distribution for comparisons between all the modern calibration samples were considered to have no 'good' modern analogue. Analogue matching was computed by Professor John Birks (University of Bergen, Norway) using the computer program ANALOG version 1.6 (Line & Birks, unpublished program).

Bootstrapping provides perhaps the best method for estimating errors associated with individual inferences from fossil samples (e.g. Birks *et al.*, 1990). However, a computer program for this intensive re-sampling procedure was not yet available for a data-set such as ours at the time of writing and is not discussed further.

Results and discussion

Full postglacial trajectories were investigated for all five study lakes (Hall, 1993). However, only data from the period of hemlock decline and recovery (4800–3500 BP) are presented here.



Three lines of evidence suggest our diatom-inferred TP concentrations may be reliable. First, the 131 diatom taxa included in the TP inference model (Hall & Smol, 1992) included more than 80% of the total diatom sum in each of the fossil samples, indicating a good correspondence between modern and fossil assemblages. Second, all sediment diatom samples exhibited a 'good fit' to TP in a constrained CCA of the B.C. calibration set, except for one sample at 478 cm in the Gunter L. core which had a 'poor fit'. Third, most fossil diatom assemblages had 'good' modern analogues within the calibration lake-set. Only one sample from Gunter L. (552 cm), and three samples from Burrige L. (236, 256, and 290 cm) lacked a 'good' modern analogue.

The following discussion of lake trajectories is presented in order of smallest to largest relative catchment area.

Long Lake

The decline and recovery of hemlock occurred between 288 and 168 cm (Fig. 1a). *Betula* pollen increased initially, and later shade-intolerant hardwoods (*Quercus*, *Fagus*, *Ulmus*), and *Pinus* expanded (data not shown, all details in Hall, 1993).

Sediment mineral content increased by 10% across the boundary, but subsequently declined to values similar to the pre-decline condition (30%) (Fig. 1a). Concentrations of most geochemical elements increased during the hemlock decline (Fig. 1a), especially elements derived mainly from bedrock erosion (e.g. Ti, K, Mg, Al). Initially Cu and Ca (which have a large component associated or bound to organic matter) decreased relative to Ti, indicating that clastic erosional input may have briefly exceeded or-

ganic matter supply to Long L. sediments. However, 10 cm above the hemlock decline (271 cm), ratios of Cu and Zn to Ti doubled. This may indicate increased organic matter decomposition and supply from the catchment at the time of hemlock minimum abundance. Sediment mineral matter, organic matter, and geochemical concentrations generally stabilized above 260 cm (Fig. 1a).

Changes in the algal community during the hemlock decline occurred gradually, rather than suddenly (Fig. 1b,c). Planktonic diatoms decreased, scaled chrysophytes were virtually eliminated, and chrysophyte cysts declined to low levels (Fig. 1b). Diatoms increased relative to chrysophyte cysts, indicating a possible shift towards more productive conditions (Smol, 1985). However, sediment diatom concentrations showed very little change (Fig. 1b). Between 250 and 200 cm, chrysophyte microfossil concentrations and planktonic diatom abundances attained the lowest values of the entire Holocene (Hall, 1993).

The diatom assemblage also displayed slow, consistent taxonomic changes. *Cyclotella bodanica* var. *lemanica* (O. Müll. ex Schröter) Bachmann, the dominant planktonic diatom prior to the hemlock decline, decreased steadily to very low percent abundance (Fig. 1c). Benthic *Fragilaria* taxa (*F. brevistriata* Grun., *F. construens* (Ehrenb.) Grun., *F. construens* var. *venter* (Ehrenb.) Grun., *F. pinnata* Ehrenb.) increased during most of the period of hemlock decline and recovery. The diatom assemblage inferred a $4 \mu\text{g l}^{-1}$ increase in lake-water TP concentration during the hemlock decline (Fig. 1c). When compared to the mean Holocene variability between stratigraphic levels of $2 \mu\text{g l}^{-1}$, this represented a moderate increase in nutrient concentration,

Fig. 1. Stratigraphic profiles from the Long L. sediment core, including: (a) hemlock (*Tsuga*) pollen percent abundance, mineral and organic matter content, and concentrations and ratios of selected geochemical elements; (b) concentrations of biogenic silica, and diatom (solid bars) and chrysophyte (open bars) microfossils ($\times 10^7 \text{ g}^{-1}$ dry sediment wt.), the percent abundance of planktonic diatoms, and the ratio of diatom frustules to chrysophyte cysts (D:C) expressed as a percent (see Smol, 1985); (c) percent abundances of the most common diatom taxa, and diatom-inferred total phosphorus concentration (DI-TP). Standard error of the TP inference model is $3 \mu\text{g l}^{-1}$. Dotted lines indicate the lower (4,800 BP) and upper (3,500 BP) boundaries of the hemlock decline and recovery, respectively.

and may indicate increased nutrient supply from the catchment. The diatom-inferred TP concentration subsequently declined (15 to 13 $\mu\text{g l}^{-1}$) between 260 and 240 cm, and may indicate a period of nutrient retention during forest regeneration and biomass accumulation. Above 240 cm, diatom-inferred TP concentration, as well as diatom, chrysophyte, and biogenic silica concentrations increased, thereby indicating a shift towards increased aquatic productivity during the hemlock expansion (Fig. 1b,c).

Burridge Lake

The decline and recovery of hemlock occurred between 300 and 205 cm (Fig. 2a). Hemlock pollen declined more gradually than in the other study lakes (Fig. 2a). The sediment core consisted of laminated gyttja during most of the Holocene period (Hall, 1993). However, laminations disappeared during the interval 280 to 186 cm, shortly after the hemlock decline.

Burridge L. sediments recorded no discernable increase in catchment erosion or nutrient supply as hemlock declined (Fig. 2a). The hemlock decline was associated with marked limnological changes (Fig. 2b,c), but evidence concerning changes in lake trophic status is contradictory. Siliceous algal microfossil data indicate a possible increase in aquatic productivity during the initial decline in hemlock. For example, biogenic silica concentration increased slightly, concentrations of diatom valves and chrysophyte cysts doubled and chrysophyte scales increased 4-fold (Fig. 2b). However, taxonomic changes in the diatom assemblage during the hemlock decline appear to be largely unrelated to changes in aquatic productivity, and inferred only a small change in lake-water TP concentration (Fig. 2c). Diatom-inferred TP declined by 2 $\mu\text{g l}^{-1}$ during the hemlock decline (300 to 320 cm). However, diatom-inferred TP concentration only varied on average by 2 $\mu\text{g l}^{-1}$ between stratigraphic levels during the Holocene in Burridge Lake (Hall, 1993), indicating that the change in TP concentration was relatively small.

Changes in algal communities during the hemlock decline were relatively short-lived. Microfossil concentrations rapidly returned to pre-disturbance values between 280 and 250 cm in the core. The decline in microfossil concentrations above 280 cm coincided with a brief, steep reduction in planktonic algal communities (Fig. 2b,c). As hemlock populations recovered to pre-decline values (above 210 cm), algal microfossil concentrations, biogenic silica, and planktonic diatoms increased. Diatoms inferred a consistent lake-water TP concentration (ca. 10 $\mu\text{g l}^{-1}$) during the period of low hemlock pollen (290–240 cm) (Fig. 2c). A small decrease in diatom-inferred TP concentration (2 $\mu\text{g l}^{-1}$) occurred as hemlock recovered.

Gunter Lake

The hemlock decline and recovery occurred between 610 and 474 cm (Fig. 3a). Hemlock declined very sharply between 614 and 605 cm (Fig. 3a).

Sediment organic matter increased strikingly in response to the hemlock decline, and mineral matter correspondingly declined (Fig. 3a). Soil profiles may have become severely disturbed during the hemlock decline, resulting in large-scale organic decomposition and export of catchment soil from the landscape. During the remainder of the hemlock decline and recovery, above 577 cm, sediment composition and geochemistry did not change.

Algal microfossil and biogenic silica data indicated no clear trends in lake trophic status change during the hemlock decline (Fig. 3b). Planktonic diatoms increased as hemlock declined (Fig. 3b). However, this increase was mainly due to an increase in *C. stelligera* (Cleve & Grun.) Van Heurck, a diatom which generally indicates oligotrophic conditions (Stoermer & Yang, 1968; Christie, 1993) (Fig. 3c). *C. stelligera*, the relative abundance of planktonic diatoms, and total algal microfossil concentrations subsequently decreased at 550 cm. A number of epiphytic diatoms increased at this time, including *Achnanthes*

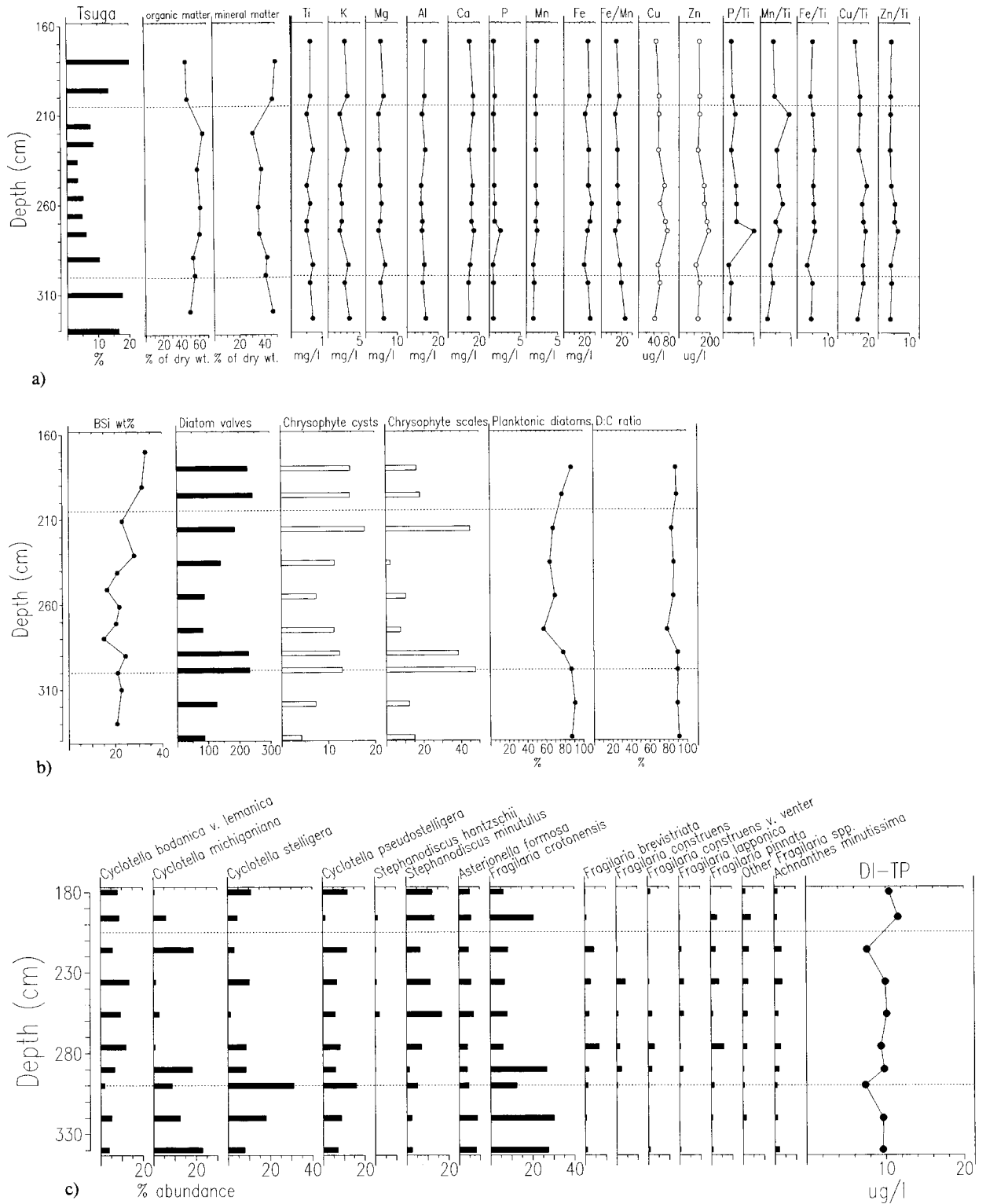


Fig. 2. Stratigraphic profiles from the Burrigde L. sediment core (see caption for Figure 1 for details).

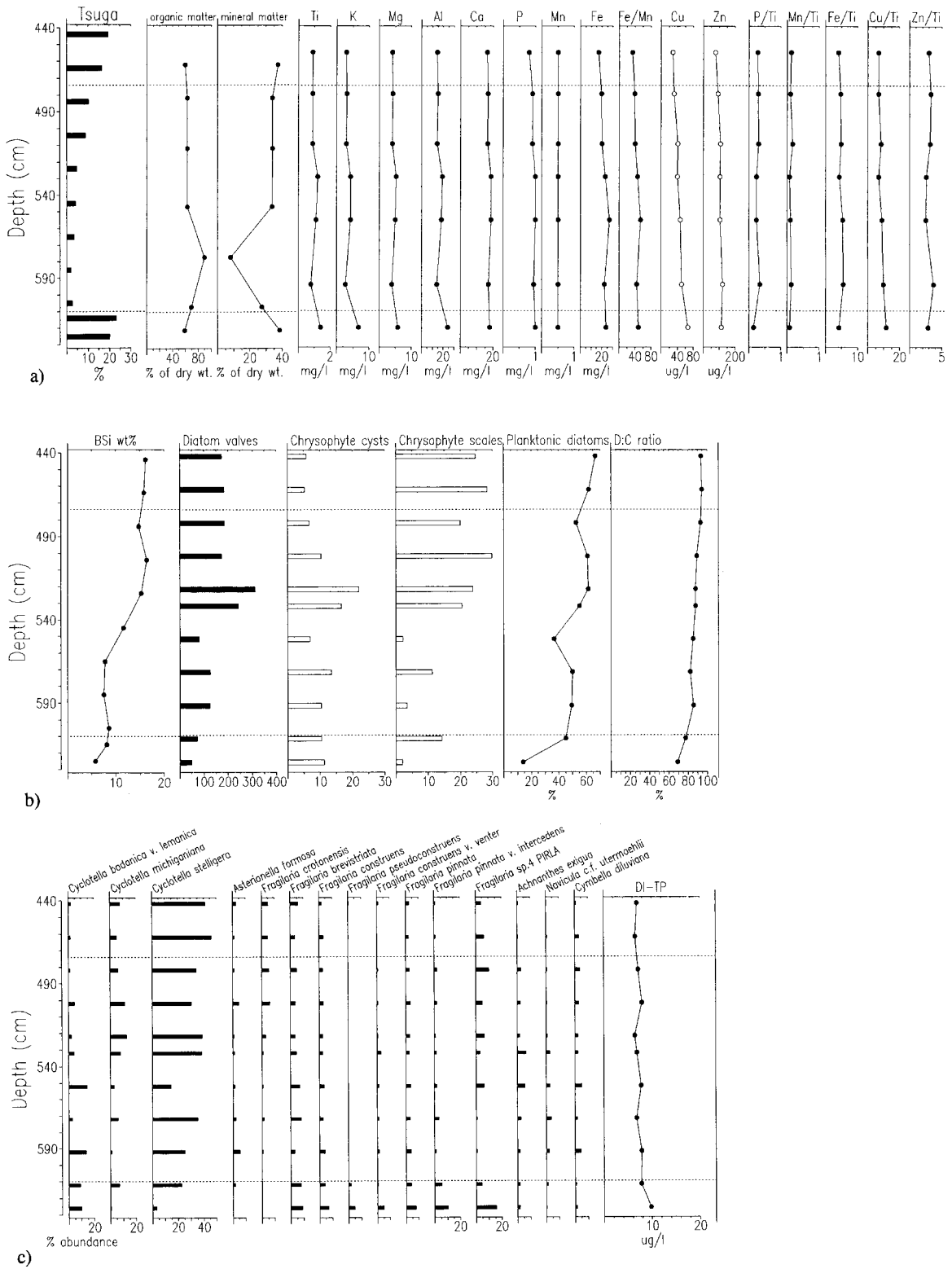


Fig. 3. Stratigraphic profiles from the Gunter L. sediment core (see caption for Figure 1 for details).

exigua Grun., *Ac. minutissima* Kütz., *Navicula* cf. *utermoehlii* Hust., and *N. vitabunda* Hust., and may indicate an expansion of macrophytes and/or changes in hydrologic conditions. Sharp increases in *C. stelligera* percent abundance (Fig. 3c) and microfossil and biogenic silica concentrations (Fig. 3b) occurred again at 530 cm, and remained at high values during the remainder of the hemlock recovery. These increases were larger in magnitude than the changes during the hemlock decline.

Diatom assemblages inferred relatively stable lake-water TP concentrations during the entire period of hemlock decline and recovery (Fig. 3c). The decline and recovery of hemlock appears to have exerted relatively minor influences on lake trophic status, despite striking shifts in algal communities and organic matter loading to the sediments.

Flower Round Lake

The hemlock decline and recovery (275 to 220 cm) appears to have been associated with major disturbances in the watershed and strong limnological changes. Hemlock declined suddenly between 280 and 270 cm (Fig. 4a). Sediment mineral content increased by 20% during the initial hemlock decline (280 to 275 cm), and organic content correspondingly declined (Fig. 4a). Geochemical elements associated primarily with bedrock and mineral erosion (Ti, K, Mg, and Al) all increased sharply at a depth of 275 cm (Fig. 4a). Peak concentrations of these elements occurred during the hemlock decline, and remained high through most of the zone. These trends suggest the hemlock decline was associated with a sharp increase in catchment erosion. Concentrations of Cu and Zn increased 4- and 3-fold, respectively, at the hemlock decline. Ratios of Cu and Zn to Ti showed similar trends, indicating that organic matter decomposition may have occurred at elevated rates. Paludification and acidification of the catchment soils may have enhanced the solubility and transport of these elements from catchment soils.

The hemlock decline was associated with major limnological changes in Flower Round L. The siliceous algal microfossils indicate a large increase in lake productivity during the hemlock decline. Diatom and biogenic silica concentrations doubled between 285 and 270 cm, and quadrupled between 285 and 260 cm (Fig. 4b). Algal communities changed dramatically. Chrysophyte microfossil concentrations (both cysts and scales) declined 3-fold at the time of the hemlock decline. Diatom abundance increased sharply relative to chrysophyte cysts (Fig. 4b), a shift likely indicative of eutrophication (Smol, 1985). Planktonic diatom abundance more than doubled during the hemlock decline. These changes were accompanied by large taxonomic shifts within the diatom community. The expansion of planktonic diatoms was almost entirely due to increases in *Aulacoseira ambigua* (Grun.) Simonsen (Fig. 4c). *F. crotonensis* and *Asterionella formosa* Hasall also increased during this period. Coincidentally, benthic diatoms declined, particularly benthic *Fragilaria* taxa (*F. construens*, *F. construens* var. *venter*, *F. lapponica* Grun., *F. pinnata*). These changes are consistent with a period of eutrophication between 285 and 260 cm, as *Au. ambigua*, *F. crotonensis*, and *As. formosa* all had high weighted averages for TP concentration (Hall & Smol, 1992), and are commonly associated with elevated nutrient concentrations (e.g. Bradbury, 1975; Birks *et al.*, 1976; Christie, 1993). Diatom-inferred TP increased $14 \mu\text{g l}^{-1}$, to a peak of $27 \mu\text{g l}^{-1}$ (Fig. 4c), indicating that the lake became eutrophic.

The above eutrophication trend reversed sharply between 260 and 250 cm. Diatom and biogenic silica concentrations decreased (Fig. 4b), and diatom-inferred TP concentration declined by $11 \mu\text{g l}^{-1}$ (Fig. 4c).

During the remainder of the forest recovery period and re-establishment of hemlock, aquatic productivity increased. The relative abundance of planktonic diatoms, concentrations of diatom valves and biogenic silica, and diatom-inferred TP all increased between 250 and 220 cm (Fig. 4b,c).

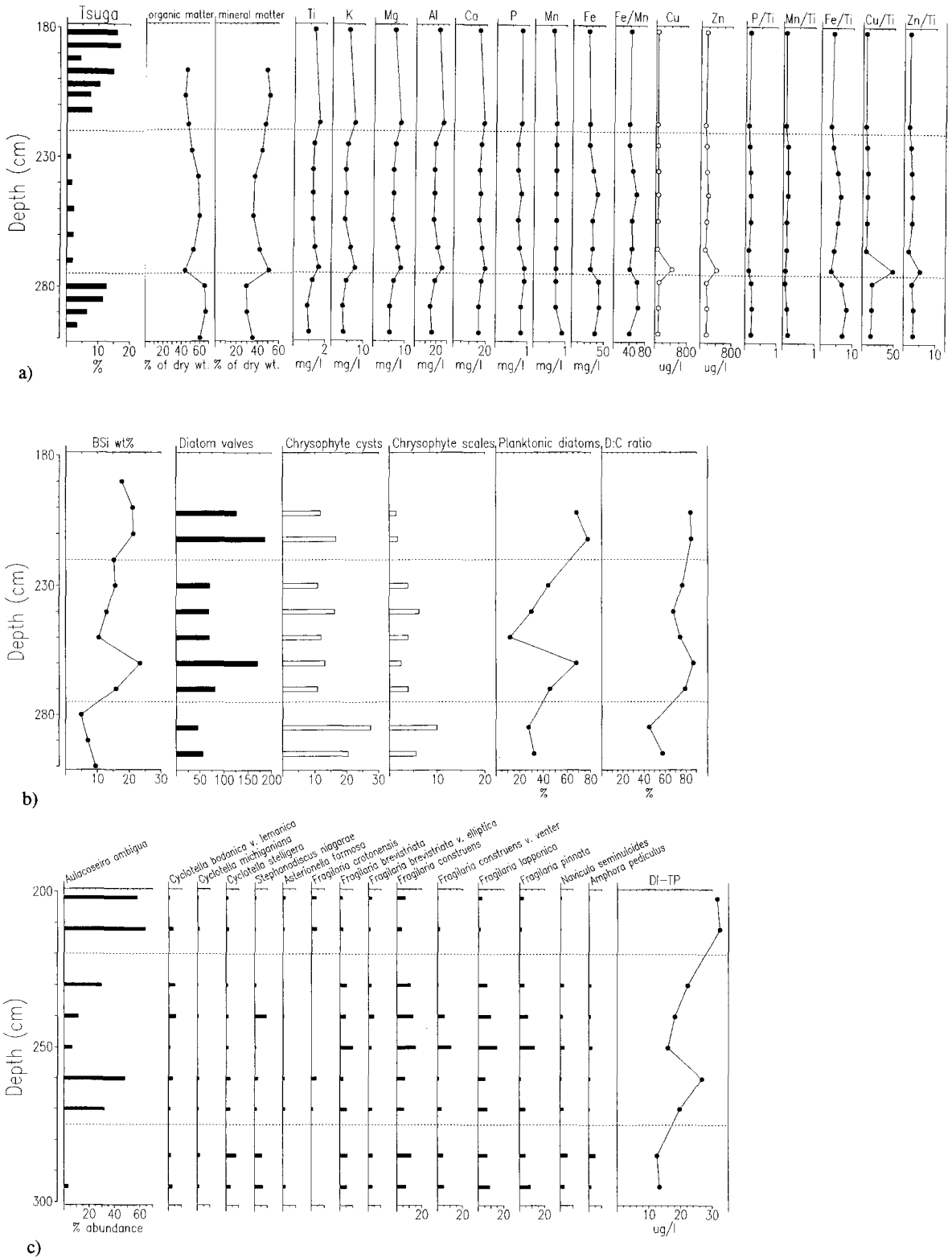


Fig. 4. Stratigraphic profiles from the Flower Round L. sediment core (see caption for Figure 1 for details).

Singleton Lake

The hemlock decline and recovery occurred between 467 and 287 cm (Fig. 5a). Hemlock pollen declined sharply between 475 and 460 cm, and increased gradually above 415 cm (Fig. 5a). Despite the dramatic change in forest composition, the sediments did not record changes in catchment erosion or organic matter input (Fig. 5a).

The aquatic community exhibited a weak response to the decline and recovery of hemlock. Algal microfossils displayed a high degree of variability during most of the Holocene, including the period of hemlock decline (Hall, 1993). Nevertheless, some trends were evident. A small, brief increase in diatom concentration occurred during the hemlock decline (Fig. 5b). Abundances of eutrophic diatoms doubled, including *F. crotonensis*, *As. formosa*, and *Ac. minutissima* (Fig. 5c). *Stephanodiscus hantzschii* Grun. and *Au. ambigua* also increased slightly. The increased abundance of *Ac. minutissima*, an epiphyte, may have resulted from an expansion of aquatic macrophytes (Stockner & Armstrong, 1971). Diatom-inferred TP concentration increased slightly, perhaps indicating a moderate increase in nutrient supply during the hemlock decline (Fig. 5c).

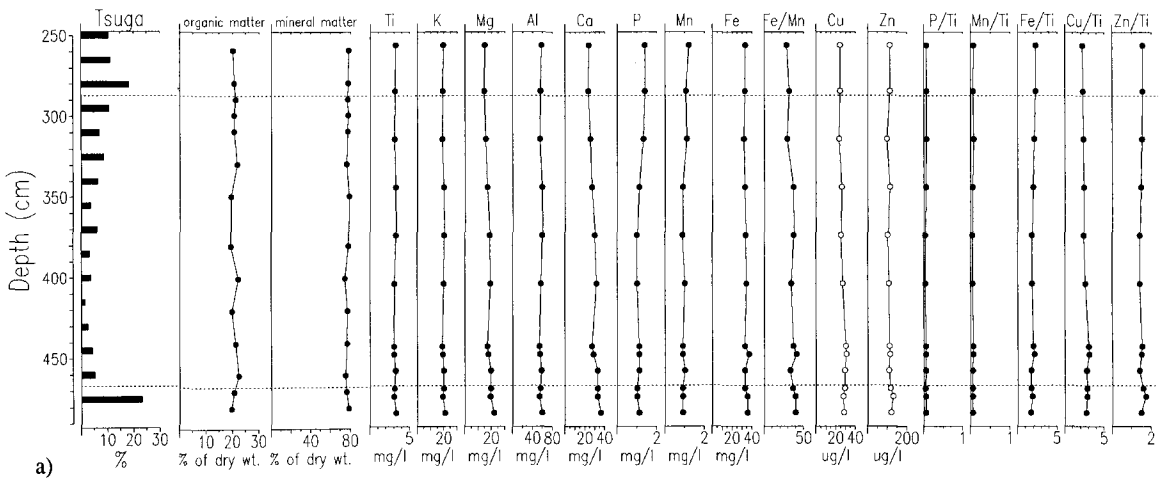
Relative abundances of *F. crotonensis*, *As. formosa* and *S. minutulus* (Kütz.) Cleve & Möll. declined briefly between 455 and 420 cm, and diatom-inferred TP concentrations declined by $8 \mu\text{g l}^{-1}$ (Fig. 5c).

Above 380 cm depth, *Au. ambigua* relative abundance fluctuated widely, and influenced the changes in planktonic diatom abundance and diatom-inferred TP concentration profiles. The reasons for these changes are unknown, but are of similar magnitude to changes that occurred during the hemlock decline and recovery. It therefore appears that the hemlock decline exerted relatively minor influences on aquatic productivity in Singleton L. The initial disturbance was associated with increased algal productivity, whereas forest recovery (stabilization of the catchment with largely hardwood taxa) was associated with a slight reduction in lake trophic status.

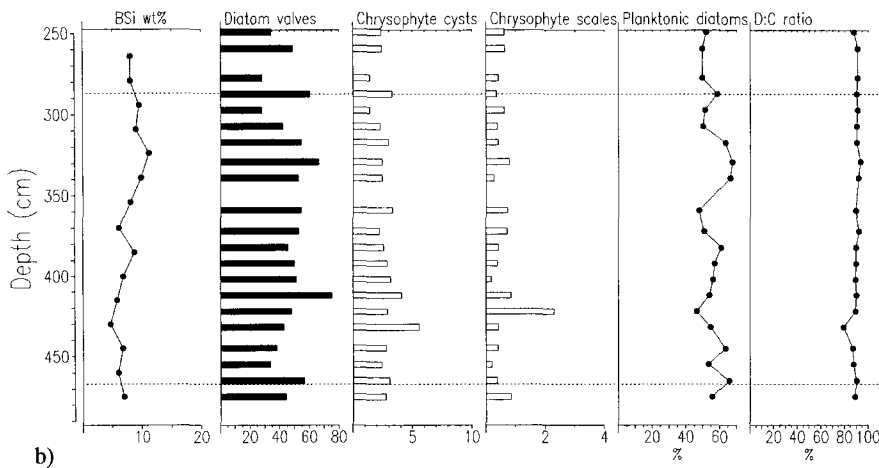
General discussion and synthesis

Paleolimnological analyses of lacustrine sediments have routinely been used to assess lake eutrophication in response to anthropogenic activity (e.g. Brugam, 1978; Engstrom *et al.*, 1985; Anderson *et al.*, 1990; Smol, 1992). The investigation of long-term natural changes in lacustrine productivity has proved more difficult. The magnitude of natural eutrophication events is generally much lower than that caused by human activity, and is more easily masked by background natural variability inherent in freshwater ecosystems. Natural eutrophication also occurs over long time periods (centuries, as opposed to decades or years), and paleolimnological records may be complicated by unrelated changes in climate, soil development, and weathering (e.g. Engstrom & Hansen, 1985), and meromixis (Smol & Boucherle, 1985). The hemlock decline provides a unique opportunity in eastern North America to investigate the effects of a natural forest disturbance that occurred over a relatively short time period (Allison *et al.*, 1986) on lake conditions.

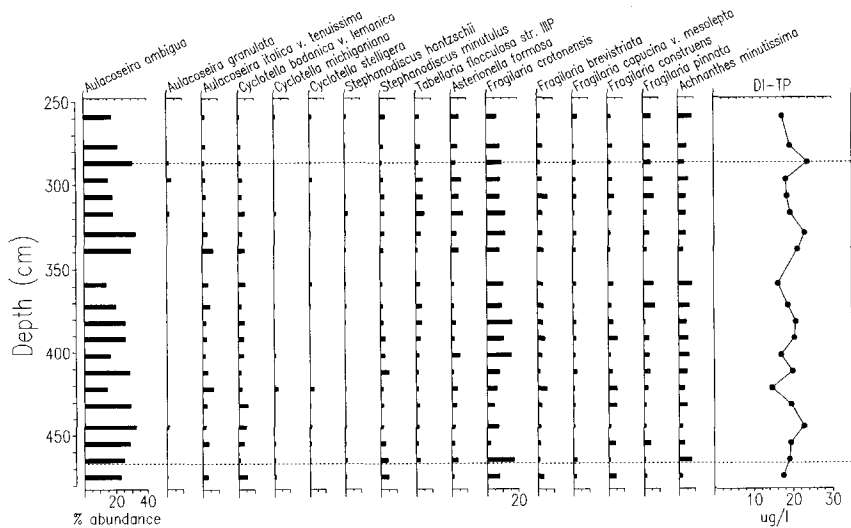
An underlying assumption of this study is that all watersheds had hemlock growing in them at the time of the regional decline, and that the percent of hemlock trees in the catchments was proportional to the percent of hemlock pollen. While it is extremely difficult to ascertain that hemlock trees were equally represented within all catchments 4,800 BP, several lines of evidence suggest hemlock distributions were probably reasonably homogenous. First, hemlock contributes a relatively high percent, between 13 and 23%, of the pollen sum in all lakes prior to the hemlock decline, and indicates that hemlock trees probably grew within their catchments (Dr. Steve Jackson, Northern Arizona University, pers. comm.). Second, hemlock is one of the more poorly dispersed pollen types (Jackson, 1990). The hemlock pollen source radius for our lakes is approximately 5 km (Dr. S. Jackson, pers. comm.), and therefore, a large portion of the pollen was probably produced by trees growing in their catchments. Third, the study lakes are situated close



a)



b)



c)

Fig. 5. Stratigraphic profiles from the Singleton L. sediment core (see caption for Figure 1 for details).

together (within 100 km of each other), encompass a small elevational gradient (200 m; Table 1), & have similar local physiography (Chapman & Putnam, 1984). Hemlock trees prefer cool, moist habitats and grow most densely along riparian channels, lake shores, and on north and northeast facing slopes (Fowells, 1965; Hosie, 1979). These attributes do not differ widely between the catchments, and present day patterning of hemlock is not noticeably different between the sites. For these reasons, hemlock abundance was probably sufficiently homogenous among the sites to justify our interpretations of limnological changes associated with the decline of hemlock.

Limnological consequences of the hemlock decline

The limnological responses during the hemlock decline varied widely among the five lakes included in this study. Our data indicate that not all lakes were equally susceptible to eutrophication during the hemlock decline. Only one of the five study lakes (Flower Round L.) showed marked eutrophication. Therefore, the hemlock decline does not appear to have had a profound, widespread influence on southeastern Ontario lakes, especially those with small catchment-to-lake area ratios.

The degree of eutrophication appears to be related to the size and slope of the catchment area. The hemlock decline generally had the smallest influence on aquatic productivity and diatom-inferred TP concentrations in lakes with the smallest relative catchment area [e.g. Long L. (relative catchment size = 1.0), Burr ridge L. (1.2), and Gunter L. (4.5); Table 1]. Only Flower Round L., which has a large relative catchment area (13.5; Table 1) and strong topographic relief, exhibited marked eutrophication accompanied by a $14 \mu\text{g l}^{-1}$ increase in diatom-inferred TP concentration (Fig. 4c). This observation may help explain why previous studies have demonstrated different magnitudes of lake trophic status change during the hemlock decline. Algal microfossil records from lakes with small catchment size relative to lake area, e.g. Mirror L. (Likens &

Davis, 1975), McKay L. (Boucherle *et al.*, 1986), Long L., and Burr ridge L., have generally demonstrated only minor lake trophic status changes during the hemlock decline. These lakes have similar surface area-to-catchment ratios (SA:C) of 15, 18, 22, and 18% respectively (Table 1). Eutrophication and accompanying changes in algal assemblages tend to be more striking in lakes with larger relative catchment size. For example, Little Round L. [SA:C ratio = 6.8% (Boucherle *et al.*, 1986)] and Flower Round L. (SA:C = 1.8%, Table 1) both experienced marked eutrophication during the hemlock decline.

The relationship between catchment area and lake trophic status in our five lakes, however, is not straight-forward. Several factors complicate the relationship. For example, the lakes were not ecologically homogeneous prior to the hemlock decline. Their ontogenies and trophic status had diverged earlier during the Holocene (Hall, 1993). Furthermore, Singleton L. possesses the largest catchment area of all the lakes in this study, but the magnitude of limnological change was only intermediate. The majority of Singleton L.'s catchment lies within an area of very low topographic relief, and the flow of water through the catchment was probably much slower than that of Flower Round L. As a result, the ability to erode and transport nutrients to the lake may have been relatively low. In addition, the drainage pattern into Singleton L. is very complex, and precipitation falling on the outer reaches of the catchment may never actually reach the lake. Singleton's catchment includes land draining into the Rideau Canal system, but the large majority of the Canal's flow does not pass through Singleton L. Also, low relief and slow water flow through the catchment may have allowed much of the water to evaporate before it could have entered the lake. For this reason, the actual or 'effective' catchment area may be considerably smaller than the area we calculated from topographic maps. The supply of nutrients from the catchment of Singleton L. may therefore be much lower than one would expect on the basis of the catchment area we reported (Table 1).

Catchment slope also appears to play an im-

portant role in determining both the quantity and the quality of external inputs into lakes. Burr ridge L. and Long L. have almost identical catchment areas and catchment area-to-lake volume ratios (Table 1). Despite these similarities, their limnological responses to the hemlock decline differed considerably. Sediment organic matter increased 5% in Burr ridge L., but declined 10% in Long L. This difference may have been due to differences in the slopes of their catchments. Qualitatively, Long L.'s catchment has a more pronounced topography, steeper slopes, thinner soils, and a greater proportion of exposed bedrock compared to Burr ridge L. These differences may have allowed a higher degree of soil and bedrock erosion, and hence mineral transport to Long L. The hemlock decline coincided with an inferred TP concentration increase of $4 \mu\text{g l}^{-1}$ in Long L., and a decrease of $2 \mu\text{g l}^{-1}$ in Burr ridge L. These differences in nutrient loading may have resulted directly from differences in catchment relief. Several researchers have also stressed the importance of slope in regulating the quantity and quality of nutrient loading into lakes (Dillon & Kirchner, 1975; Prairie & Kalff, 1986).

The lakes with more gentle catchment relief (Burr ridge L., Gunter L., Singleton L.) generally experienced an increase in sediment organic content during the hemlock decline. Sediment from lakes with steeper relief, on the other hand, received greater mineral matter supplies. For example, sediment mineral matter content increased 10 and 21% during the hemlock decline in Long L. and Flower Round L., respectively (Fig. 3a, 5a). Faster water runoff from steeper catchments may have provided the mechanism for elevated soil and bedrock erosion and the increased transport of mineral matter relative to organic matter. Catchments with more gentle relief may have permitted greater organic matter decomposition (possibly through paludification and acidification of soils, and changes in aerobic versus anaerobic decomposition), and therefore may have supplied relatively greater amounts of particulate organic matter relative to mineral matter.

Despite the differences in the extent of eutrophication, the hemlock decline was associated with

similar patterns of change in the algal communities of the study lakes. Abundances of planktonic diatoms increased in several lakes at the time of the hemlock decline. Planktonic diatoms increased by 30% in Gunter L., by 40% in Flower Round L., and by 10% in Singleton L. Also, diatoms tended to increase relative to chrysophyte cysts, a shift usually indicating eutrophication (Smol, 1985). The magnitude of these changes generally followed differences in catchment area, and the increase in the diatom to cyst ratio was greatest in Flower Round L. (40%). Only Burr ridge L. and Long L. exhibited contradictory trends, and they have the smallest relative catchment sizes (Table 1). In these two lakes, abundances of planktonic diatoms actually decreased and diatom to cyst ratios did not change.

Lake-watershed interactions during forest recovery

Ecosystem research at the Hubbard Brook Experimental Forest (New Hampshire) has contributed towards the development of the Biomass Accumulation Model (e.g. Bormann *et al.*, 1968; Hobbie & Likens, 1973; Bormann *et al.*, 1974; Bormann & Likens, 1979; Gorham *et al.*, 1979). This model describes changes in forest structure and function following a catastrophic disturbance, and is based on measured and projected changes in total biomass following clear-cutting. It recognizes four distinct successional phases following a severe forest disturbance: (1) a period of 'reorganization', lasting one or two decades, during which the ecosystem loses total biomass and releases large quantities of nutrients; (2) an 'aggradation' period of up to 200 years during which the ecosystem accumulates total biomass and retains nutrients; (3) a 'transition' phase (of variable time length) when total biomass declines, and nutrient release increases again; and (4) a 'steady state-shifting mosaic' phase when total biomass fluctuates about a stable mean (Bormann & Likens, 1979).

Paleolimnological records from our five study lakes generally provide evidence in support of this model. Flower Round L. showed the most pro-

nounced limnological changes, and trends in all paleoindicators provided evidence of an initial increase in nutrient supply during the hemlock decline. These trends may reflect the 'reorganization' phase described by the Biomass Accumulation Model. Mineral erosion and organic matter decomposition appear to have increased during this period. Diatom production and lake-water TP concentration more than doubled, Flower Round L. became eutrophic. Lake trophic status similarly increased (but to lesser extents) in Long and Singleton lakes. Sediment dating and sampling resolution were insufficient to evaluate the exact duration of this 'reorganization' phase, but the limnological effects were relatively short-lived.

Shortly after this eutrophication, a subsequent period of forest recovery also appears to have had a profound effect on the trophic status of Flower Round L. While the hemlock decline was recorded in a 15-cm sediment interval (280–275 cm), the adjacent 20-cm interval records a period of recovery within the catchment forest during which hardwood and pine populations expanded. Sediment mineral content declined 15% during this period (Fig. 4a), indicating a reduction in erosion and transport of catchment minerals. Aquatic productivity decreased, and biogenic silica and diatom valve concentrations declined 2-fold (Fig. 4b). Scaled chrysophytes, a group of algae generally more common in oligotrophic lakes (Sandgren, 1988), increased over 2-fold in population size. Meanwhile, planktonic diatoms virtually disappeared and *Au. ambigua* declined from 48 to 6% of the total diatom assemblage. All these changes tend to indicate a reduction in aquatic productivity, and the diatom-inferred TP concentration declined by $11 \mu\text{g l}^{-1}$ (Fig. 4c). These changes are consistent with a period of nutrient retention associated with the 'aggradation' phase of forest succession and ecosystem development (Bormann & Likens, 1979).

Evidence from Flower Round L. suggests that the supply of nutrients became strongly reduced shortly after the initial eutrophication event. Forest trees and bushes may have expanded rapidly into open spaces left by the dead hemlock trees. The growth of new vegetation may have stabilized

catchment soils, reduced erosion, and decreased runoff by increasing evapotranspiration. As the forests grew, nutrients may have been actively retained in new plant biomass, and nutrient supplies to the lakes may have become sharply reduced. While Flower Round L. exhibited the most striking trends, nutrient supplies appear to have decreased in two other lakes in this study. Diatom-inferred lake-water TP concentrations decreased by $2 \mu\text{g l}^{-1}$ in Long L., and by $8 \mu\text{g l}^{-1}$ in Singleton L. Associated with these inferences, planktonic diatom communities generally declined. In Flower Round L., planktonic diatoms declined from 68 to 12% of the total assemblage. Planktonic diatoms also declined sharply in Gunter L. (50–36%) and, to lesser extents, in Singleton L. (63–46%) and Burrigge L. (78–57%).

Our paleolimnological data indicate that aquatic productivity increased in Long L., Burrigge L. and Flower Round L., as hemlock pollen abundance increased to pre-decline values about 3,500 BP. These trends suggest the hemlock recovery was generally associated with increased nutrient supply to lakes, and may support the occurrence of a 'transition' phase during terrestrial ecosystem development, as suggested by Bormann & Likens (1979). However, there is no clear evidence of the fourth phase of the Biomass Accumulation Model, or a 'steady state-shifting mosaic', during the 2,000 year record of hemlock decline and recovery. Nevertheless, our results provide circumstantial evidence that the Biomass Accumulation Model may accurately describe the response of forest ecosystems to a wide range of disturbance types, from anthropogenic clear-cutting to natural events such as the hemlock decline. Our data clearly demonstrate that lakes interact closely with their surrounding landscape, and are sensitive to changes within forest ecosystems.

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