Climatic influences on algal populations of boreal forest lakes in the Experimental Lakes Area

Abstract—We examined long-term phytoplankton data records for four oligotrophic boreal lakes situated in the Experimental Lakes Area (ELA), western Ontario, for responses to climatic change. ELA experienced a cyclical wet–dry–wet pattern from 1968 to 1998, with the early 1970s and 1990s having above-average precipitation and the 1980s being a period of drought with a 2° C increase in air temperature. During this drought, the length of ice-free season, duration of stratification, depth of the euphotic zone, and light extinction increased while precipitation and nutrient inputs to the lakes decreased. Phytoplankton assemblages of four study lakes were temporally coherent. During the drought, phytoplankton biomass and the number of phytoplankton species increased despite decreased nutrient inputs. There was a noticeable shift in species composition to greater abundances of dinoflagellates and large chrysophytes—mixotrophic species capable of cycling through the deeper, lower light, high-nutrient waters, presumably to consume bacteria as an alternative to autotrophic production. These species have slow turnover times; therefore, suspended nutrients were held in the water column for a longer period of time. Phytoplankton photosynthesis was less responsive.

Global climate warming has become a major environmental issue in recent years (Magnuson et al. 2000). If atmospheric carbon dioxide concentrations continue to increase as they have over the past 50 yr, models predict that the Canadian boreal ecozone will be among the regions most affected by climate warming, with temperature increases of 5–8°C (Environment Canada 1994). Although at this time it is difficult to distinguish between long-term climatic cycles and global warming, the potential consequences of climate change are so great that it is prudent to determine them now.

Climatic changes are expected to have significant and complex effects on aquatic ecosystems (Magnuson et al. 1997). Changes in temperature and precipitation will alter hydrological processes, resulting in floods in some areas and droughts in others, which, in turn, will trigger a variety of physical and chemical changes. Schindler et al. (1990) provided the first glimpse of such changes: during a prolonged period of drought and increase in mean air temperature on the Boreal Shield in western Ontario, precipitation, snow depth, and run-off declined. In one small lake at the Experimental Lakes Area (ELA), L239, ice-free season length, thermocline depth, secchi depth, water residence time, and phytoplankton biomass increased over a 19-yr period.

Algal communities are extremely sensitive to environmental changes (Reynolds 1984). Two major factors affecting algal community biomass and composition are nutrients and light, both of which will be altered by climate change (Schindler et al. 1996; Magnuson et al. 1997). Therefore, shifts in community composition and biomass should occur in response to climatic variation.

The ELA is located in an area of the boreal ecozone that is minimally affected by anthropogenic atmospheric inputs (Schindler et al. 1991). Our objective is to extend the analysis of Schindler et al. (1990) by determining how the phytoplankton communities in four oligotrophic lakes within the ELA responded to changes in climate over a period of 30 yr, for which chemical, physical, meteorological, and phytoplankton data are available.

Methods—Study site: Sites L224, L239, L373, and L382 are dimictic and oligotrophic lakes situated within 15 km of each other. All are headwater lakes, except L224, which receives input from one upstream lake (Beaty and Lyng 1989). These lakes have been intensively monitored as reference systems, with the exception of L382, which was subjected to low-level Cd additions from 1986 to 1992. There was no detectable effect of the Cd additions on the phytoplankton community (Findlay et al. 1996) and continued monitoring indicates there has been no long-term chronic effect to date (D. Findlay unpubl. data). The surrounding catchments are typical boreal forest dominated by jack pine (*Pinus banksiana* Lamb), red pine (*Pinus resinosa* Ait.), and black spruce (*Picea mariana* Mill.). The watersheds of L239 and L382 have experienced fires: in 1974 and 1980, 71% and 100%, respectively, of the L239 watershed was burned (Schindler et al. 1990). In 1979, 8% of the L382 watershed was burned (Findlay et al. 1996). Table 1 gives the morphometric characteristics of the lakes.

Meteorological observations: Daily minimum and maximum air temperatures, wind speed, precipitation, wet and dry deposition, evaporation, and hours of sunlight were collected from a station 1 km from the shore of L239. These records extend continuously from 1969 to the present.

Phytoplankton: L224 and L239 were sampled for phytoplankton at midmorning every 2 wk throughout the ice-free season from 1974 to 1998 (25 yr). Monthly samples were obtained from L382 during 1977–1980 and 1982–1998 (21 yr) and L373 during 1983–1987 and 1990–1998 (14 yr). Water samples from the epilimnion (EPI) and metalimnion (BEPI) were obtained from the deepest station of each lake using an integrating sampler (Shearer 1978). The epilimnion was defined as the upper water layer of uniform temperature in each lake (ignoring any shallow, temporary, diurnal stratification phenomena). BEPI was defined as the layer from the bottom of the epilimnion to the 0.5% light level depth (bottom of the euphotic zone). Euphotic zone biomass estimates were calculated by volume-weighting the epilimnion and BEPI estimates and summing.

Cells were enumerated by the same person for the entire data set using the Ütermohl technique as modified by Nauwerck (1963). Cell counts were converted to wet weight bio-

Table 1. Morphometric characteristics and annual water residence times of the four study lakes. Residence time = lake volume/runoff (K. Beaty, unpubl. data).

Lake	Depth (m) Mean	Depth (m) Maximum	Surface area (ha)	Volume (10^5 m^{-3})	Residence time (y) 1974–1979	Residence time (y) 1980–1989	Residence time (y) 1990–1998
L224	11.6	27.4	25.9	30.1	na	na	na
L239	10.0	30.4	56.1	57.1	6.7($\pm$1.9)	13.6($\pm$5.5)	7.9($\pm$7.1)
L373	10.7	21.5	27.6	30.1	na	na	19.6($\pm$9.9)
L382	5.8	13.1	37.1	21.3	na	8.4($\pm$3.9)	4.7($\pm$2.6)

mass by approximating cell volume. Estimates of cell volume for each species were obtained by measurements of up to 50 cells of an individual species and applying the geometric formula that best described the shape of the cell (Vollenweider 1968; Rott 1981). A specific gravity of 1 was assumed for cellular mass.

Some species of phytoplankton are mixotrophic; that is, they can consume alternative sources of carbon (Caron et al. 1993; Isaksson et al. 1999). Several dinoflagellate species lack characteristic chloroplasts (Canter-Lund and Lund 1995), a feature distinguishable under a light microscope that indicates a mixotrophic species. To quantify the proportion of mixotrophic dinoflagellates in L224 and L239, dinoflagellates lacking chloroplasts were enumerated in decadal composite samples. Composite samples for L224 and L239 were created by combining 2-ml aliquots from each biweekly sample, thus representing decadal samples for the 1970s, 1980s, and 1990s. A 10-ml subsample from each decadal sample was extracted for qualitative bacterial analysis. Samples were titrated with 25 μl of sodium thiosulfate solution ($Na_2S_2O_3$) to clear the Lugol's preservative, stained with 4′,6-diamidino-2-phenylindole (DAPI, Pomroy 1984), and analyzed using epifluorescence microscopy.

Phytoplankton photosynthesis was measured using the ^{14}C radiotracer method described by Shearer et al. (1985). Briefly, fresh whole-lake samples were incubated in a light gradient in a laboratory incubator and in situ rates were calculated by combining these data with transparency and solar radiation data (Fee 1990). Up to 1986, each replicate was individually spiked with ^{14}C. In 1986, a single aliquot of inorganic ^{14}C was added to a 1-liter water sample that was then mixed and siphoned into replicate incubation bottles. This change reduced the variance among replicates but did not result in significantly different production estimates (Fee et al. 1992).

Chemical sampling and analysis: Samples for water chemistry were taken from the integrated phytoplankton samples. Dissolved and suspended fractions of carbon (C), nitrogen (N), and phosphorus (P) were routinely measured. Totals of C, N, and P are the sums of the dissolved and suspended fractions for each element. Chlorophyll was extracted using a mixture of methanol, acetone, and water and measured fluorometrically. Analytical methods are described by Stainton et al. (1977). All data are presented as annual means over the ice-free season.

Data analysis: We used the ratios of annual mean/long-term mean (A_{mean} : Lt_{mean}) to examine long-term trends for

phytoplankton biomass, number of species, photosynthesis, euphotic zone volume, and nutrients. Time series analysis presented in Figs. 2, 6, and 7 have been partitioned (vertical lines) into three groupings of years (1970–1979, 1980–1989, 1990–1998) based on climatic changes observed in degree days (a simplistic temperature index calculated by summing the mean daily temperatures observed at the meteorological station over the ice-free season), annual precipitation, and length of the ice-free season; henceforth, they will be referred to as decades (Fig. 1).

Community changes at the species level were assessed by correspondence analysis (CA). Mean ice-free season monthly biomass from 1974 to 1998 was calculated for each phytoplankton species in each lake for both the EPI and BEPI strata. This resulted in a matrix of 818 lake–stratum–year–month by 280 species. Very rare species are problematic because they result in a large number of zeroes in the matrix. Therefore, only species that contributed >1% to total biomass in at least one lake–stratum–year–month were retained for analysis (213 species). Biomass values were transformed by log(100 biomass + 1). Preliminary analysis showed that results were still highly influenced by rare species and final CA included a further down-weighting of rare species. In brief, if Amax is the frequency of the commonest species, then the abundance of a species rarer than Amax/5 is reduced in proportion to its frequency. The frequency of species j is

$$f_j = \left(\sum a_{ij} \right)^2 \Big/ \sum a_{ij}^2$$

where a_{ij} is the abundance of species j in sample i. If f_j for species j is greater than Amax/5, then its weighting factor is 1; otherwise, it is f_j/(Amax/5).

A two-way analysis of variance (ANOVA) (lake, decade) was performed on the logs of annual means of each of the major taxonomic groups; total phytoplankton biomass; total C, N, and P; dissolved organic carbon (DOC); and N : P and C : P ratios. If the ANOVA resulted in a significant decade effect, then Duncan's multiple range test was used to determine significant differences among the three decadal means.

To test for temporal coherence (i.e., the correlation or synchrony between time series), we used the intraclass correlation coefficient (Rusak et al. 1999). A two-way ANOVA was used to factor out variation due to differences among lakes. Thus, synchrony is quantified for phytoplankton biomass, major taxonomic groups, and number of species over time, excluding variation due to differences in means among lakes. All statistical analyses were performed using SAS (Statistical Analysis Systems Institute).
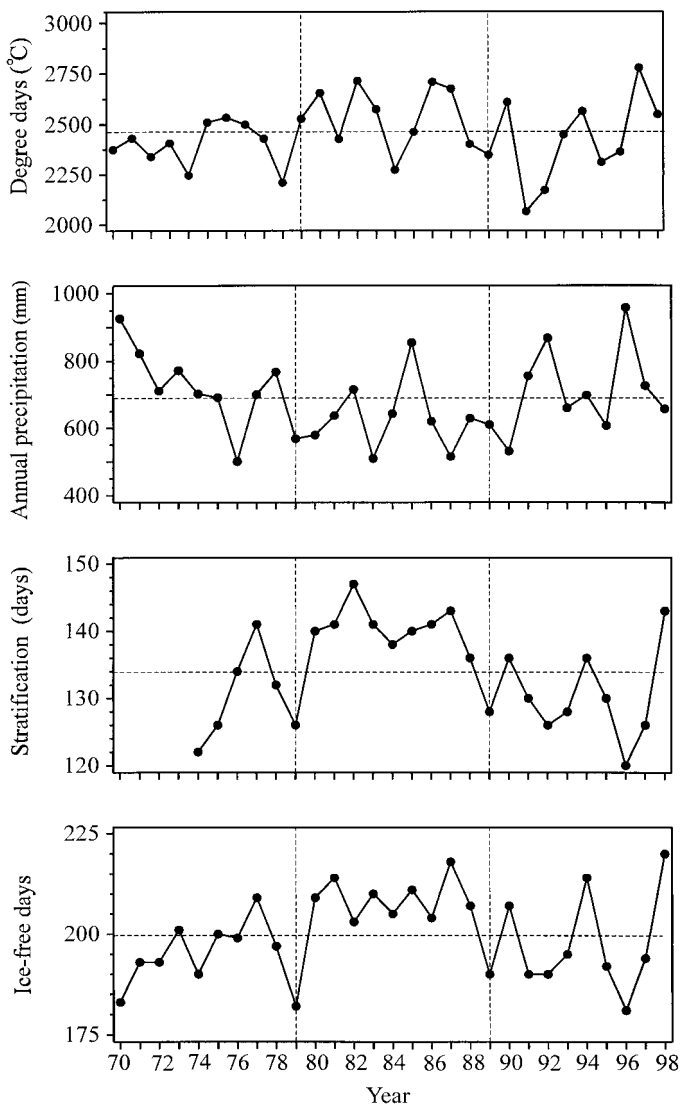
Fig. 1. Mean annual precipitation (mm), number of days of stratification, degree days, and number of ice-free days during 1970–1998 for the ELA region. Vertical lines are reference markers based on changing climatic trends observed in degree days, annual precipitation, and length of the ice-free season. The horizontal line indicates the long-term mean.

Results—Meteorological records from 1969 to 1998 indicated the ELA region experienced a cyclical wet–dry–wet pattern in which the early 1970s and much of the 1990s had above-average precipitation and the 1980s was a period of drought (Fig. 1). Within the period of record, there are several unique years of extreme climatic events: during the drought period of the 1980s, annual precipitation in 1984–1985 was very high because the fall of 1984 and the spring of 1985 were exceptionally wet. The ice-free seasons of 1984–1985, in contrast, had long periods of below-normal precipitation (K. Beaty unpubl. data), preserving the character of the decade in these years.

Phytoplankton biomass and the number of species changed synchronously among lakes (Fig. 2). Temporal coherence among the four lakes was highly significant for total

biomass ($r = 0.70$, $P < 0.01$) and number of species ($r = 0.86$, $P < 0.01$). During the wetter years of the 1970s and 1990s, phytoplankton biomass, number of species, and photosynthesis were significantly lower (Table 2) than during the drought (Fig. 2). For example, average total biomass for L239 increased from 2,182 mg m^{-2} in 1974–1979 to 3,288 mg m^{-2} in 1980–1989, then decreased to 1,596 mg m^{-2} in 1989–1998. A similar pattern was evident in the BEPI layer and in the other study lakes (for details see Web Appendix 1: http://www.aslo.org/lo/toc/vol_46/issue_7/1784a1.pdf).

Compositionally, the phytoplankton communities of the four lakes were similar. Chrysophytes dominated, but there were also substantial populations of cyanobacteria, cryptophytes, chlorophytes, diatoms, and dinoflagellates (Web Appendix 1). However, from 1980 to 1988, dinoflagellates (*Peridinium pusillum* Lemmermann, *P. inconspicuum* Lemmermann, and *Gymnodinium mirabile* Penard) increased in abundance, and the abundance of the dominant chrysophycean species (*Dinobryon cylindricum* Imhof, *D. sertularia* Ehrenberg, *D. bavaricum* Imhof, *D. accuminatum* Ruttner, and *Chrysochromulina laurentiana* Kling) changed noticeably. These increases were observed in both the epilimnion and the BEPI (Web Appendix 1).

Correspondence analysis was performed using species assemblages of all four lakes. The first four axes of the CA accounted for 17.2, 9.4, 6.8, and 3.3%, respectively, of the total inertia (1.399, $\chi^2 = 321907$, df 173,204). Results are shown in Fig. 3, where for clarity, lakes have been plotted separately and years have been connected in chronological order. The species scores (Fig. 4) generated from the CA apply to all lake–year panels and can be overlaid on them. The CA analysis revealed several striking features common among the lakes. First, the time trends for the four lakes are similar, and community composition shifted over time; CA lake–year scores for the 1970s were located in the upper right quadrant, whereas the 1990s scores were located in the lower left. Three periods of relative community stability were apparent, 1974–1977 (observable in L239 and L224 because of the length of record), 1979–1988, and 1990–1998. In each lake, the greatest shift in community composition occurred between 1988 and 1990. Second, there was little difference between the EPI and BEPI assemblages, and both had similar trends over time (Fig. 3a). The species influencing community shifts over time are shown in Fig. 4. The CA coordinates for a species locates its maximum abundance. Maximum abundances for mixotrophic species occur in the plot areas corresponding to the 1980s and 1990s, compared to the 1970s.

Because of these species changes, the relative abundances of mixotrophic and autotrophic species shifted (Fig. 5). Prior to the drought, mixotrophs represented 20–40% of the total biomass; this increased to 50–60% during and after the drought. In the 1970 composite decadal samples for L224 and L239, 11 and 19%, respectively, of the dinoflagellates lacked chloroplasts (i.e., were mixotrophic). In the 1980 decadal samples for L224 and L239, the proportion of mixotrophic dinoflagellates increased to 34 and 39%, respectively. In addition, *Dinobryon* spp., which are also capable of mixotrophy, contained bacteria in all three decadal samples in all lakes. In addition to this qualitative change, *Dinobryon*
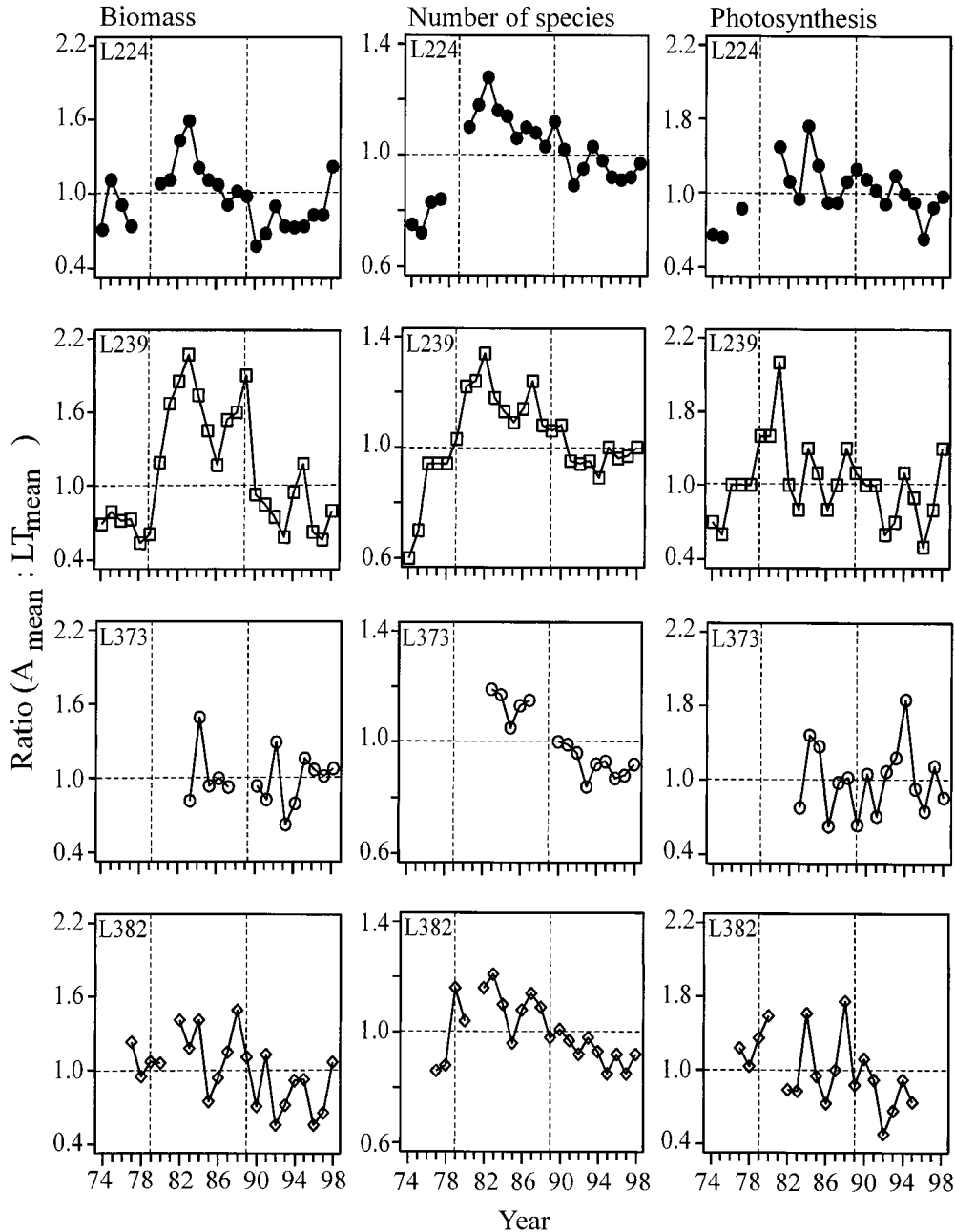
Fig. 2. Ratio of the annual mean to long-term mean ($A_{mean} : Lt_{mean}$) for euphotic zone phytoplankton biomass, number of species, and phytoplankton photosynthesis for L224, L239, L373, and L382 during 1974–1998. Vertical lines indicate different climatic periods based on degree days, annual precipitation, and length of the ice-free season (Fig. 1). The horizontal line indicates the long-term mean.

abundance increased by 51% in L239 and 60% in L224 in the 1980s.

In order to maintain growth, phytoplankton require both nutrients and light. Precipitation and direct runoff are the major source of nutrient inputs to the ELA lakes (Schindler et al. 1996). Lake concentrations of total N and P from 1974 to 1979 were not significantly different (a wet period) compared to 1980–1989 (a period of drought) (Fig. 6, Table 2), even though total N and P increased by 10–15% in 1984–

1985 because of one of the highest precipitation years on record (Fig. 1). However, concentrations of P significantly differed in the 1990s (Table 2) compared to the previous decades (Fig. 6). The resource ratios of suspended C, N, and P were not significantly different in the wet and dry periods (Table 2). The C:P and N:P ratios indicated that the algal communities of the four lakes were severely P limited, even with the increase in P in 1984–1985 (Fig. 6).

Dissolved organic carbon (DOC), a major constituent of

Table 2. Results of ANOVA on the phytoplankton and chemical variables for the four study lakes. Years are grouped into three decades. *P* is the probability (from ANOVA) that at least one decade is significantly different. Lowercase letters (a, b, c) indicate significantly different means between decades as determined by Duncan's multiple range test ($\alpha = 0.05$).

| Variable	1974–1979	1980–1989	1990–1998	*P*
Total biomass	3.32 a	5.06 b	3.41 a	0.0001
Cyanobacteria	0.30 a	0.37 a	0.30 a	0.0500
Chlorophytes	2.40 a	0.53 b	0.28 c	0.0010
Chrysophytes	1.99 a	2.51 b	1.76 a	0.0008
Diatoms	0.34 a	0.59 b	0.47 b	0.0001
Cryptophytes	0.27 a	0.41 b	0.43 b	0.0004
Dinoflagellates	0.35 a	0.86 b	0.56 c	0.0001
Number of species	33.18 a	44.49 b	36.90 a	0.0001
Primary production	22.21 a	27.25 b	22.21 a	0.0105
Total P	6.18 a	6.88 a	5.12 b	0.0001
Total N	305.25 a	312.93 a	254.03 b	0.0078
Total C	1,167.24 a	1,127.50 a	1,115.51 a	0.2720
DOC	451.84 a	400.43 b	394.39 b	0.0450
N:P	9.78 a	11.13 a	11.37 b	0.0730
C:P	6.76 a	6.95 a	4.76 a	0.3330
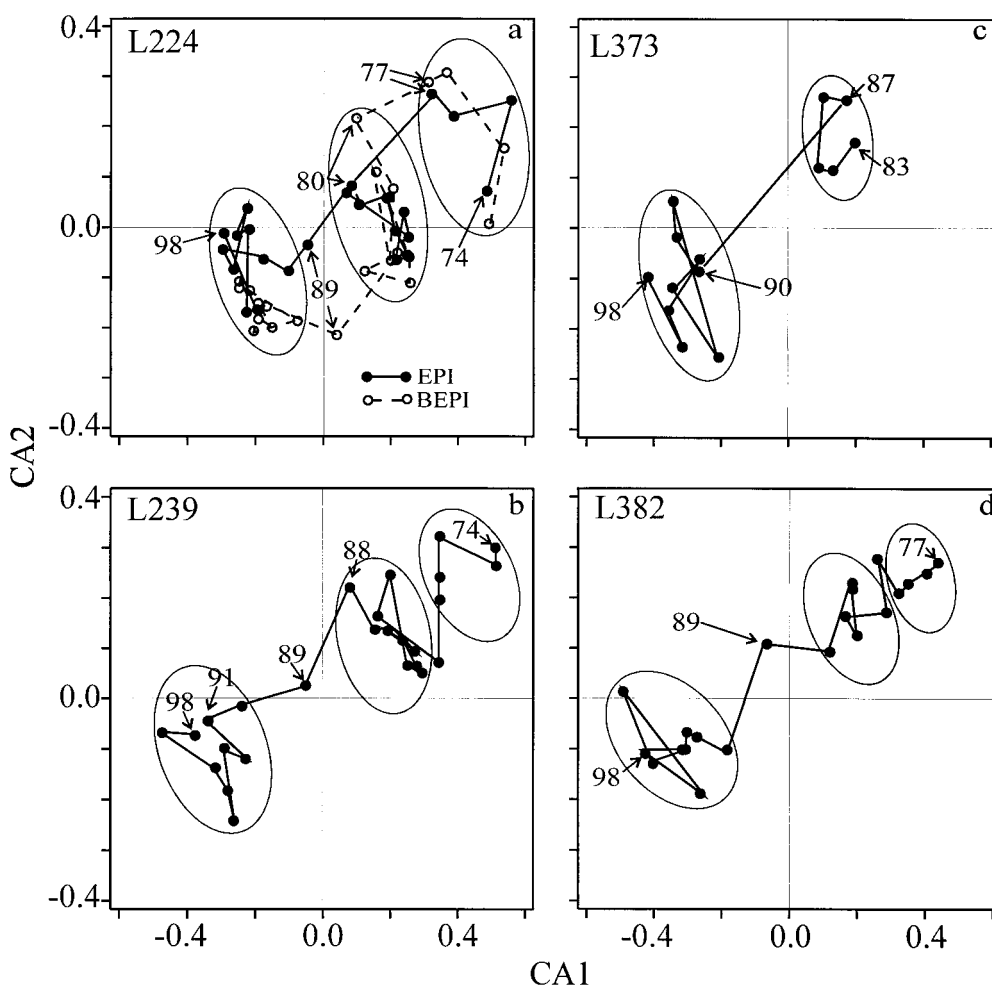
Fig. 3. Lake–year scores of a correspondence analysis of L224, L239, L373, and L382 phytoplankton communities, 1974–1998. Ellipses indicate years of similarity.
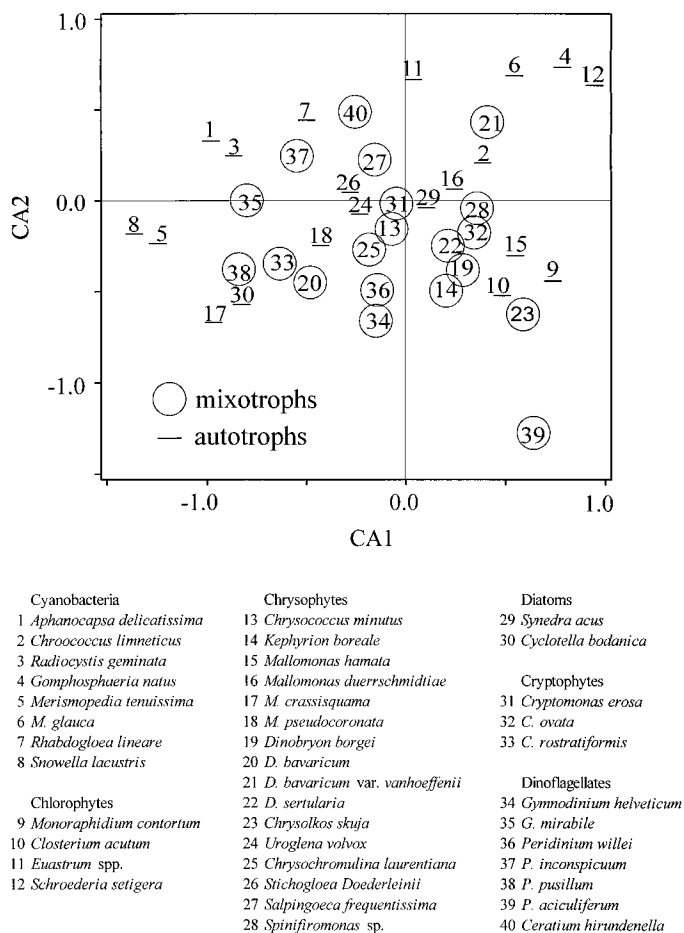
Fig. 4. Species scores of a correspondence analysis of L224, L239, L373, and L382 epilimnetic phytoplankton communities, 1974–1998. To reduce congestion, only species with >25% representation on the first three axes are shown. Numbers correspond to species listed above.

Cyanobacteria	Chrysophytes	Diatoms
1 *Aphanocapsa delicatissima*	13 *Chrysococcus minutus*	29 *Synedra acus*
2 *Chroococcus limneticus*	14 *Kephyrion boreale*	30 *Cyclotella bodanica*
3 *Radiocystis geminata*	15 *Mallomonas hamata*	
4 *Gomphosphaeria natus*	16 *Mallomonas duerrschmidtiae*	Cryptophytes
5 *Merismopedia tenuissima*	17 *M. crassisquama*	31 *Cryptomonas erosa*
6 *M. glauca*	18 *M. pseudocoronata*	32 *C. ovata*
7 *Rhabdogloea lineare*	19 *Dinobryon borgei*	33 *C. rostratiformis*
8 *Snowella lacustris*	20 *D. bavaricum*	
	21 *D. bavaricum* var. *vanhoeffenii*	Dinoflagellates
Chlorophytes	22 *D. sertularia*	34 *Gymnodinium helveticum*
9 *Monoraphidium contortum*	23 *Chrysolkos skuja*	35 *G. mirabile*
10 *Closterium acutum*	24 *Uroglena volvox*	36 *Peridinium willei*
11 *Euastrum* spp.	25 *Chrysochromulina laurentiana*	37 *P. inconspicuum*
12 *Schroederia setigera*	26 *Stichogloea Doederleinii*	38 *P. pusillum*
	27 *Salpingoeca frequentissima*	39 *P. aciculiferum*
	28 *Spinifiromonas* sp.	40 *Ceratium hirundenella*

clude that nutrients, not temperature, are the factors of greatest importance in determining phytoplankton growth and abundance in Shield lakes. The increased depth and volume of the euphotic zone may contribute to the observed increases in the mean annual mass of phytoplankton that we observed. On average during the drought years, epilimnetic depth increased by 1 m, and the depth of the euphotic zone increased by 0.5 m (Fig. 2). Schindler et al. (1990) also documented thermocline depth increasing during the 1980s.

Associated with the increased biomass was an increase in the total number of species present and a shift to more flagellated mixotrophic species (i.e., dinoflagellates (*Peridinium pusillum, P. inconspicuum, Gymnodinium mirabile*) and chrysophytes (*Chrysochromulina laurentiana, Dinobryon cylindricum, D. sertularia, D. bavaricum, D. accuminatum*); Figs. 3, 4). Climate-induced physical and chemical changes apparently created new phytoplankton niches (Fig. 2). In particular, dinoflagellate species have unique pigments that could give them a competitive advantage in high-light environments, which result from decreased DOC (Schindler et al. 1996). Leavitt et al. (1997) examined sediments from an acidified lake (L302S, ELA) and showed significant concentrations of algal degradation products of scytonema-like compounds related to photoprotective pigments. Findlay et al. (1999) documented the ability of dinoflagellates to thrive in acidic waters that also had increased UV-B penetration because of decreased DOC.

Another explanation for an increase in the abundance of mixotrophs is that they can consume bacteria (Caron et al. 1993; Isaksson et al. 1999), giving them an advantage when resources are diminished by drought. Dinoflagellate and chrysophyte species are highly motile and are capable of selecting an appropriate light and nutrient environment in the water column (Fee 1976). Generally, light intensity is an important factor for photosynthesis, but mixotrophic species are freed from this limitation, and they migrate deeper in the water column to consume bacteria as a C source (Bird and Kalff 1987; Isaksson et al. 1999). Caron et al. (1993) found that *Dinobryon cylindricum,* a common species in our study lakes, required bacteria for sustained growth. Based on C, N, and P budgets, they estimated that ingested bacteria accounted for 25% of the organic carbon and concluded that bacterivory by *Dinobryon cylindricum* provided nutrients essential for photosynthetic growth. Isaksson et al. (1999) suggest that when availability of dissolved nutrients is restricted, as during the period of drought (Schindler et al. 1996), phagotrophy permits mixotrophs, which are less competitive at high nutrient concentrations, to outcompete other phytoplankton. Although inputs of P decreased during the drought period (Schindler et al. 1996), there was no associated decrease in water column concentrations of P. We postulate that the sustained concentration of P in the water column was due to increased recycling of P by migration of mixotrophs into deeper nutrient-rich environments. Mixotrophs increased by 30% during the drought. These algal species are large, colonial, very motile, or have protective mucilage or plates, making them less desirable as a food for grazers (Fee 1976); furthermore, based on their biomass : productivity ratios, they have slower turnover times and therefore retain nutrients in the water column longer. The BEPI layer ac-

direct runoff to the four study lakes, differed significantly (*P* = 0.045) in 1974–1979 compared with 1980–1989 and 1990–1998 (Table 2). During the drought period, the A_{mean} : LT_{mean} ratios for DOC concentrations decreased by as much as 35% (Fig. 7), then rebounded through the 1990s.

DOC concentrations in L224, L239, L373, and L382 were significantly correlated with light attenuation (r^2 = 0.87, *P* = 0.0001). DOC adds color to freshwater lakes, acting as a natural ultraviolet (UV) blocking agent. As DOC and light attenuation decreased (Fig. 7) during the drought period, the maximum depth and volume of the euphotic zone increased (Fig. 7).

Discussion—Climatic changes observed over 30 yr at the ELA influenced algal communities. During drought, phytoplankton biomass increased, as did the number of species. The increase in phytoplankton biomass during drought periods was unexpected because nutrients decreased during that time (Schindler et al. 1996). Magnuson et al. (1997) suggests that increased epilimnion temperatures might cause a slight increase in phytoplankton biomass, the number of species present, and annual production; however, they con-
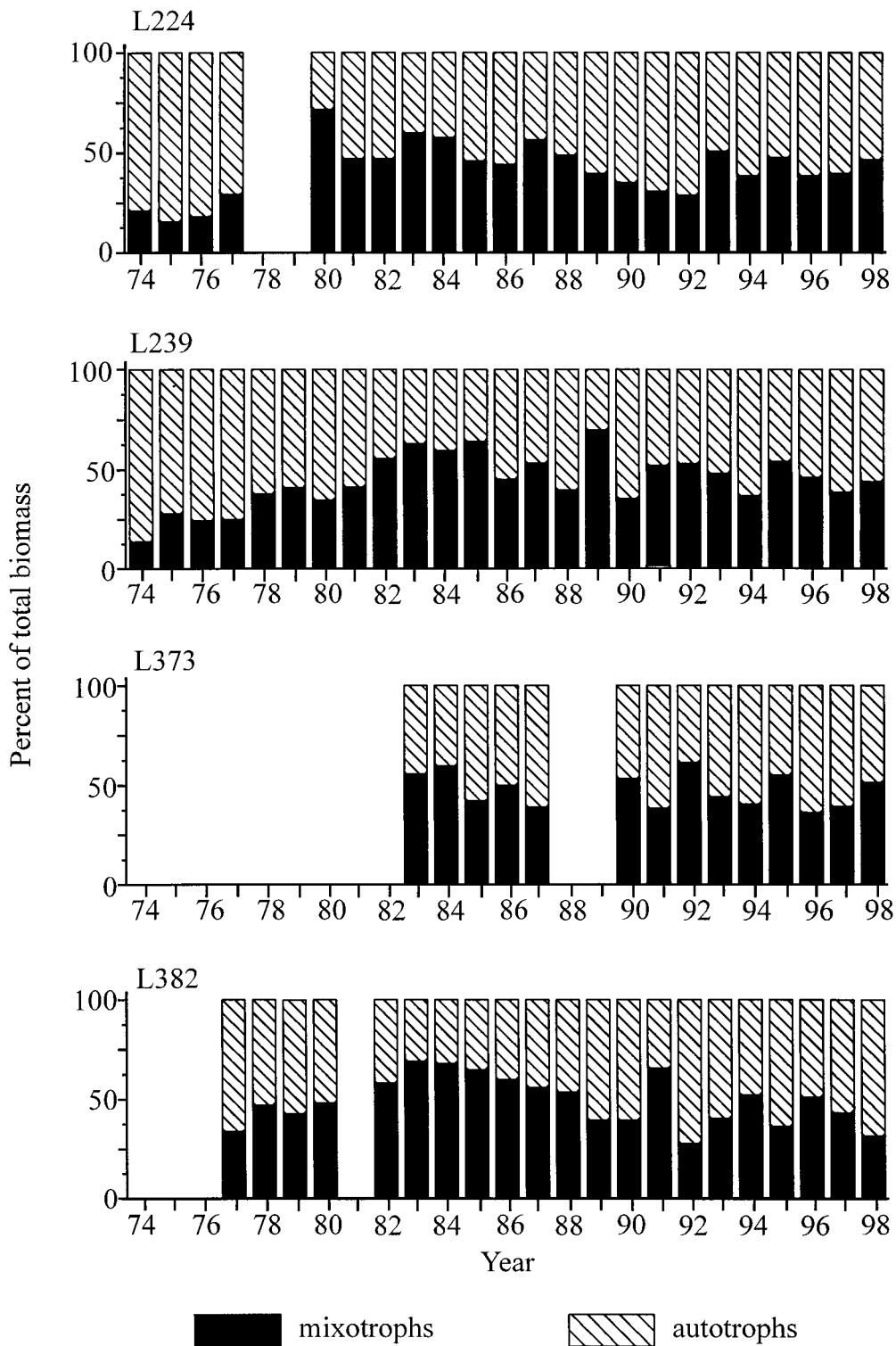
Fig. 5. Percentage of the total biomass of autotrophic and mixotrophic phytoplankton species in the euphotic zone, 1974–1998.

counts for almost half of the algal biomass but contributes less than 25% of the carbon turnover, estimated using ^{14}C uptake. This could be because the phytoplankton were relying on bacterial C, and ^{14}C uptake thus underestimated C turnover.

Changes in the phytoplankton communities observed over the three decades were driven by changes in nutrient and light regimes. There is no evidence to suggest that other factors, such as food web alteration or physical mixing, influenced phytoplankton composition or biomass. Mills et al.
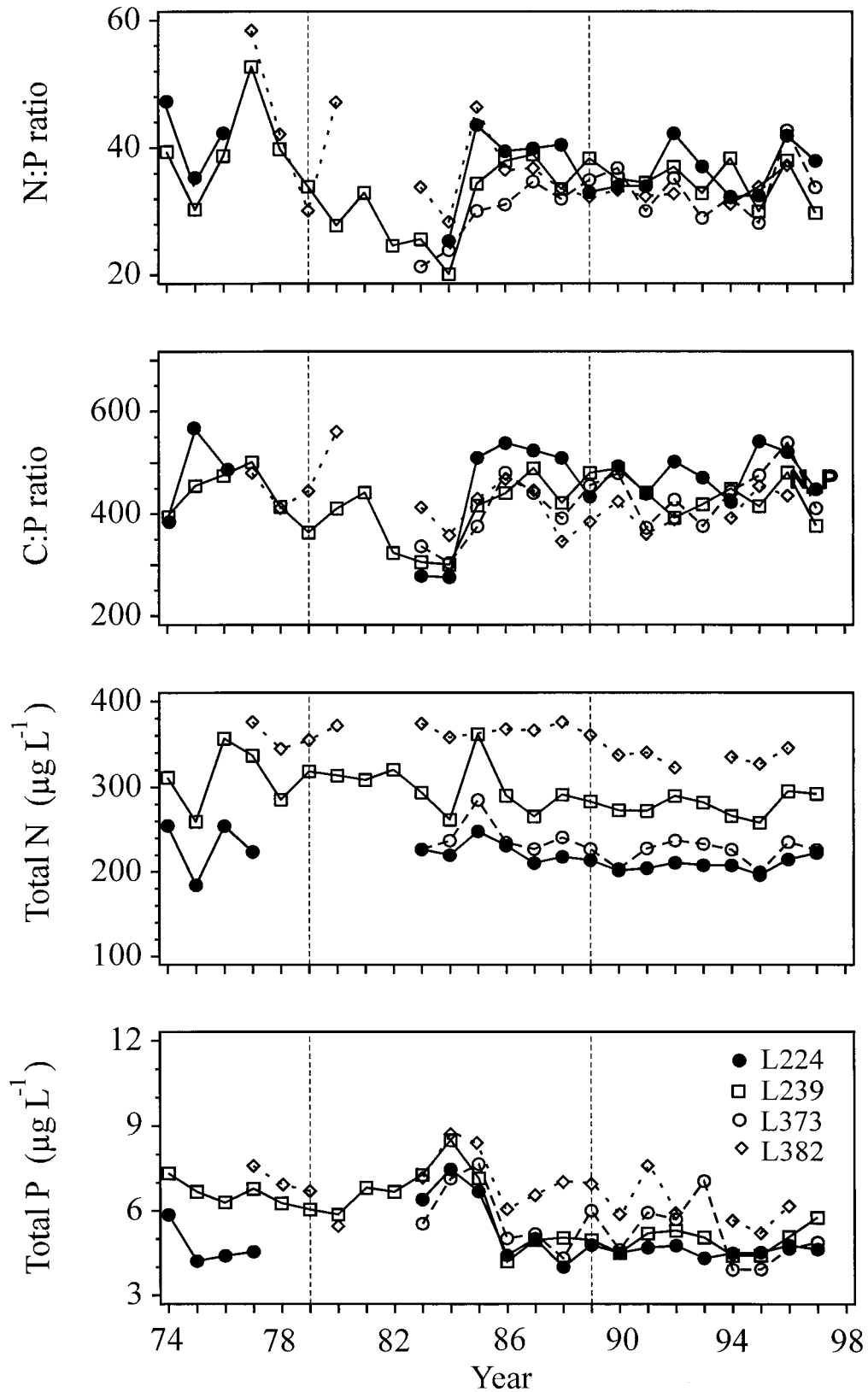
Fig. 6. Ice-free mean concentrations of total phosphorus (P) and total nitrogen (N) and nutrient resource ratios of carbon : phosphorus (C : P) and nitrogen : phosphorus (N : P), 1973–1998. Vertical lines indicate different climatic periods based on degree days, annual precipitation, and length of the ice-free season (Fig. 1).
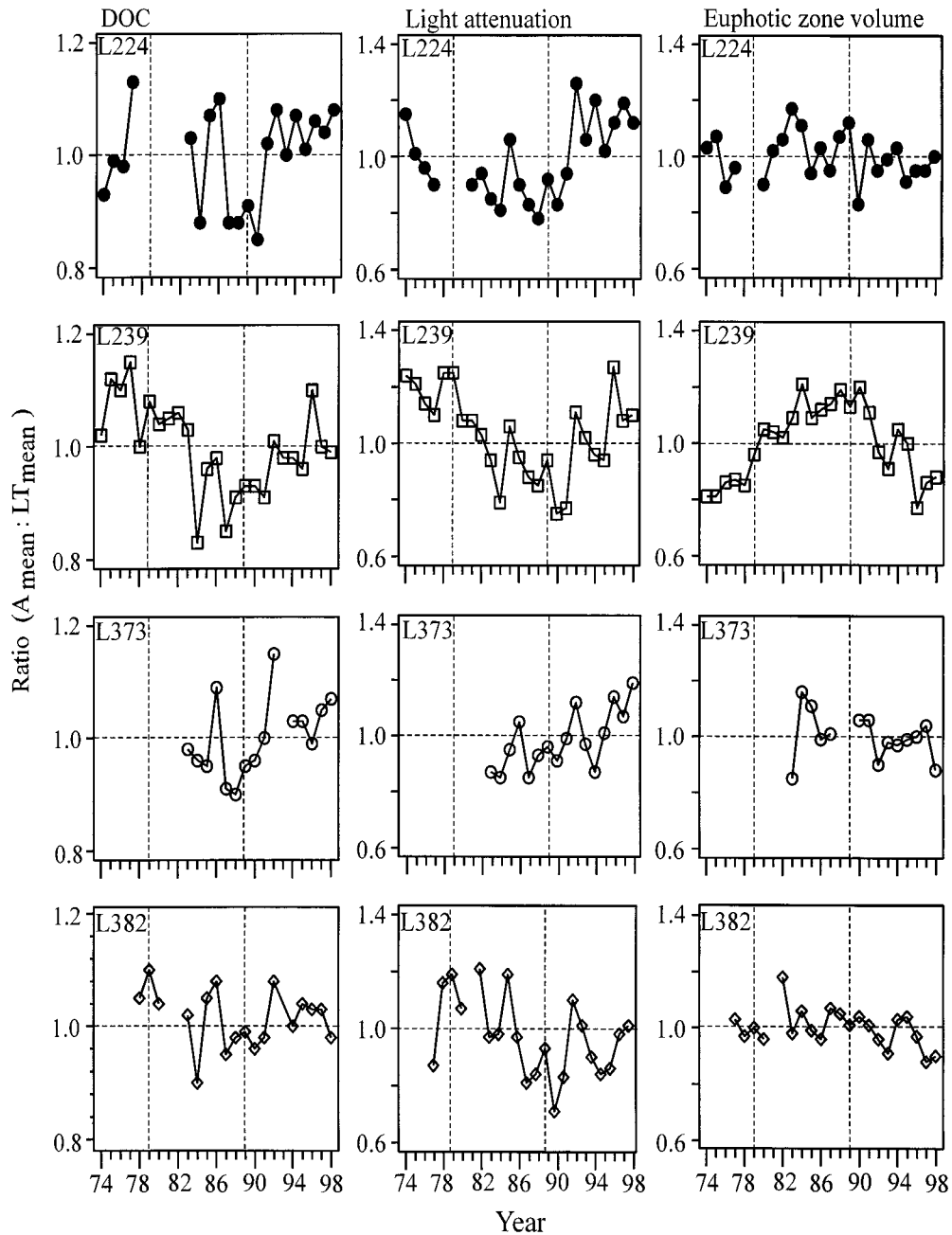
Fig. 7. Ratio of annual mean : long-term mean (A_{mean} : Lt_{mean}) dissolved organic carbon (DOC), light attenuation, and euphotic zone volume, 1974–1998. Vertical lines indicate different climatic periods based on degree days, annual precipitation, and length of the ice-free season (Fig. 1). The horizontal line indicates the long-term mean.

(2000) showed that there was no significant change in fish populations in L224 from 1972 to 1996. Shifts in phytoplankton composition could affect zooplankton; however, the zooplankton community in L239 does not appear to have changed over time (M. Paterson pers. comm.). This is not to say that individual species were not affected. Fee (1976) described peaks of chlorophyll (dominated by mixotrophic species) existing at the 1% light level in many ELA lakes and concluded that during the summer these lakes had extremely stable stratification (eddy diffusion coefficients that

are the lowest reported for lakes). Thus, mixing is an unlikely factor causing the changes we observed in phytoplankton communities.

Schindler et al. (1991) showed that the results from ELA study sites are comparable to results from other boreal ecozone sites. Fee et al. (1992) reached the same conclusion based on studies of the Northwest Ontario Lake Size Series (NOLSS) (including Lake Nipigon and Superior) and ELA and also showed that it applied to all sizes of lakes. Rusak et al. (1999) examined zooplankton populations from eight

lakes in southern Ontario and reported a temporally coherent pattern in the population abundances of three zooplankton species. They concluded that intrinsic factors are important but extrinsic ones, such as climatic signals, must not be ignored. Our detailed phytoplankton data bolster all these conclusions, suggesting that other boreal Shield lakes exposed to these climatic perturbations would respond in a similar manner.

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