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LAKE SEDIMENT CHRYSOPHYTE SCALES FROM THE NORTHEASTERN U.S.A. AND THEIR RELATIONSHIP TO ENVIRONMENTAL VARIABLES[1]

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Chrysophyte scale assemblages were analyzed in the surface sediments (0–1 cm) of 146 lakes sampled in the U.S. Environmental Protection Agency's (EPA) Environmental Monitoring and Assessment Program–Surface Waters (EMAP-SW) in the northeastern U.S.A. Chrysophyte data from the EMAP lakes were combined with a previous study of 71 Adirondack PIRLA (Paleoecological Investigation of Recent Lake Acidification) lakes and collectively analyzed to examine the indicator potential of scaled chrysophytes in the northeastern U.S.A. with respect to several environmental variables. Canonical correspondence analysis (CCA) was used to determine which environmental variables influenced the distributions of species. Forward selection and Monte Carlo permutation tests showed that 51% of the variance in the chrysophyte assemblages was related to pH. The other six significant variables (conductivity, chloride, total phosphorus [TP], elevation, lake depth, and watershed area) contributed an additional 31% of the total (82%) variance explained by the seven forward-selected variables. Similar to previous studies, many taxa showed distinct distribution patterns with respect to pH. Partial and constrained CCAs indicated that, although all seven variables explained significant proportions of variation in the species data, a reliable inference model could be developed only for lake-water pH. The strength of this model (R^2 = 0.78, $RMSE_{boot}$ = 0.47 of a pH unit) is comparable to a recently constructed diatom-based model for the EMAP lakes. The use of both models in paleolimnological and biomonitoring studies would be advantageous because they would provide two independent lines of evidence of environmental change.

Key index words: **algal microfossils; biomonitoring; chrysophytes; inference models; lake sediment; northeastern U.S.A.; paleolimnology**

Chrysophyceae and Synurophyceae taxa that are covered by siliceous scales are commonly referred to as scaled chrysophytes (Anderson 1987). The indicator potential of scaled chrysophytes (hereafter referred to as chrysophytes) was initially recognized in lake eutrophication studies; however, major advances occurred within the last 15 years as paleolimnological studies gained prominence in lake acidification research (reviewed in Smol 1995). Studies in Canada (e.g. Dixit et al. 1989b, c), the U.S.A. (e.g. Dixit et al. 1990, Siver and Hamer 1990, Cumming et al. 1992a), and Europe (e.g. Cumming et al. 1991) quantitatively related the distributions of scaled chrysophyte assemblages to lake-water pH and provided historical assessments of change to lake-water pH. Chrysophyte assemblages have also been found to be correlated with conductivity (Siver 1993), certain metals (Dixit et al. 1989a, Cumming et al. 1992a), and nutrients (Siver and Marsicano 1996).

Scaled chrysophytes have many characteristics that make them ideal biomonitors for environmental assessments (Siver and Smol 1993). For example, their siliceous scales are often found in high abundance and are generally well preserved in lake sediments. The taxonomy of scaled chrysophytes is based mainly on the morphological characteristics of their scales and bristles, which can often be identified to the species level under the light microscope once their identity is established by electron microscopy. Within the last 10 to 15 years, it has become possible to standardize the taxonomy of common scaled chrysophytes to the degree at which they can be applied to water quality assessment studies. These features have allowed researchers to quantitatively study large numbers of water bodies for species assemblages in both limnological and paleolimnological studies (Siver 1995, Smol 1995).

Because scaled chrysophytes are planktonic and have rapid immigration and replication rates, their populations respond quickly to changes in the aquatic environment, including shifts in other biotic communities. For these reasons, chrysophytes have been recognized as reliable early warning indicators, especially in lake acidification reconstruction studies (e.g. Steinberg and Hartmann 1986, Dixit et al. 1989b, Cumming et al. 1994).

In 1988, the U.S. Environmental Protection Agency (EPA) initiated the Environmental Monitoring and Assessment Program (EMAP) to provide information on the current status and long-term trends in the condition of the nation's major ecological resources (Hunsaker and Carpenter 1990). Surface Waters (SW) was one of the seven ecological resource groups (Agroecosystems, Arid Ecosystems, Estuaries, Forests, Great Lakes, Surface Waters, and Wetlands) considered in EMAP and consisted of

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lake and stream components (Paulsen 1992). In EMAP-SW, sedimentary diatoms, zooplankton, macrobenthos, fish, and riparian birds were selected as lake biological indicators for evaluation and implementation in the northeastern U.S.A.

In addition to the diatom component of EMAP (Dixit et al. 1999), we also studied the indicator potential of scaled chrysophytes for the lakes in the northeastern U.S.A. Because chrysophyte scales are siliceous and share many features with diatoms, no additional field sampling or laboratory preparations were required. In comparison to studies in which either diatom or chrysophyte data are used, combined diatom–chrysophyte data have provided more robust interpretations of temporal and spatial water quality status trends for surface waters in many lake regions (Cumming et al. 1992b, Dixit et al. 1992). Our study is also an extension of PEARL's earlier chrysophyte research in the Adirondacks, New York (e.g. Smol et al. 1984, Cumming et al. 1992a), which focused on the distribution of chrysophyte assemblages to measured environmental variables, especially pH.

The objectives of the present study were (1) to explain why chrysophyte scales are absent or rare in some lakes, (2) to analyze chrysophyte scales in the top sediment samples (0–1 cm) of the EMAP lakes in the northeastern USA, (3) to examine the relationship between chrysophyte species and measured environmental variables, and (4) to develop chrysophyte-based inference models for limnologically important variables for lakes in the Northeast. Because our data set provides large spatial coverage and contains gradients to multiple environmental variables that are related to the distribution of chrysophytes, inference models developed from this study should be widely applicable in assessing the water quality changes in northeastern U.S.A. lakes. Similar to this study, we had previously combined the EMAP and the Adirondack PIRLA diatom data for developing diatom-based inference models (Dixit et al. 1999).

Among the 241 EMAP-SW lakes considered in this study, sediments of only 146 lakes contained sufficiently abundant chrysophyte scales for statistical analysis. Study lakes were sampled during July and August 1991 to 1994 in the northeastern U.S.A. The location of these lakes and the 71 Adirondack PIRLA lakes is shown in Figure 1 and Appendix 1, and further details of lake selection and the study region are presented in Dixit et al. (1999) and Cumming et al. (1992a) for the EMAP-SW and the Adirondack lakes, respectively. Following the ecoregion classification scheme of Omernik (1987), the study area can be broadly divided into the Adirondacks, New England Uplands, and Coastal Lowlands/Plateau ecoregions. The use of this ecoregion approach in assessing water quality and setting management goals for restoration efforts has been encouraged (Lillie 1990). Our EMAP diatom study has shown that the extent of cultural impact has been quite variable among the ecoregions. For example, the Adirondack region has experienced extensive acidification, whereas eutrophication was greatest in the Coastal Lowlands/Plateau ecoregion (Dixit et al. 1999).

MATERIALS AND METHODS

Field sampling. The sediment samples from the EMAP lakes were collected using a modified K-B gravity corer (Glew 1989) from the deep, central area of the lake, where the bottom is relatively flat. The 71 Adirondack PIRLA lakes were sampled at the deepest basin using a modified Cushing and Wright (1965) piston corer or a modified K-B corer (Glew 1989). All EMAP surface samples represent the top 1-cm interval of the cores, whereas the PIRLA Adirondack samples came from the top 0.5- or 1-cm sections of the cores. The details of field sediment sampling and limnological measurements and chemical analyses performed on water samples are given in Baker et al. (1997) and Cumming et al. (1992a) for the EMAP and Adirondack PIRLA lakes, respectively. For the lakes that were sampled more than once during the sampling program, averages of measurements are used in this study. Morphometric and chemical data are summarized in Table 1. Data for EMAP lakes also can be found on EMAP's Web site (http://www.epa.gov/emap/html/dataI/surfwatr/data/nelakes).

Chrysophyte analysis. Sediment samples were digested in a solution of nitric and/or sulfuric acid and potassium dichromate, and the resulting suspensions were centrifuged and washed with distilled water until the sample was acid free (Cumming et al. 1992a, Dixit et al. 1999). A known volume of the cleaned slurry was then poured into Battarbee (1973) trays. On drying, coverslips were mounted on glass slides using Hyrax® or Naphrax® mounting media. These procedures have been standardized and were approved by the EPA for both the EMAP and the PIRLA projects.

An attempt was made to identify and count at least 300 chrysophyte scales in transects for each surface sample at 1250× magnification, under oil immersion. Because of the scarcity of scales in seven EMAP lakes, the minimum counts were at least 100 scales for these lakes. Identifications were made to the lowest possible taxonomic level, using standardized taxonomic literature (e.g. Takahashi 1978, Nicholls 1982, 1988, Wee 1982, Kling and Kristiansen 1983, Asmund and Kristiansen 1986, Siver et al. 1990) and numerous publication/photographs available at PEARL. Light micrographs of scales of most of the taxa we observed are in Smol (1986). For distinguishing difficult taxa, we used the same criteria that were used for the Adirondack PIRLA lakes (Cumming et al. 1992a). Thus, taxonomic consistency has allowed us to combine both data sets for the present study.

Data analysis. Chrysophyte taxa that were present in at least three surface samples and had at least 1% relative abundance in at least one lake were used for the ordination analysis and the development of the calibration models. This selection criteria provided us with 36 identified taxa/groups from the surface samples of 217 study lakes (Table 2). The total number of ''taxa'' encountered was actually higher than 36 because some taxa/groups listed in Table 2 are represented by more than one species (see footnote to Table 2).

Birks (1995) summarizes the statistical treatments we used in this study. Canonical correspondence analysis (CCA), with forward selection, was used to explain how much of the species variation could be attributed to the measured environmental variables (Table 1). In CCA, square-root transformations were used for the species data, and rare species were down-weighted. In CCA, forward selection and Monte Carlo permutation tests (99 unrestricted permutations) were used to identify significant environmental variables in the 217 lake data set. All ordinations were performed using the CANOCO computer program (Ter Braak 1990).

To identify which environmental variables can be reliably reconstructed using chrysophyte assemblage data, the relative strengths of forward selected variables were evaluated using a series of constrained and partial CCAs (Ter Braak 1988). When a CCA is constrained to a single variable, it determines the amount

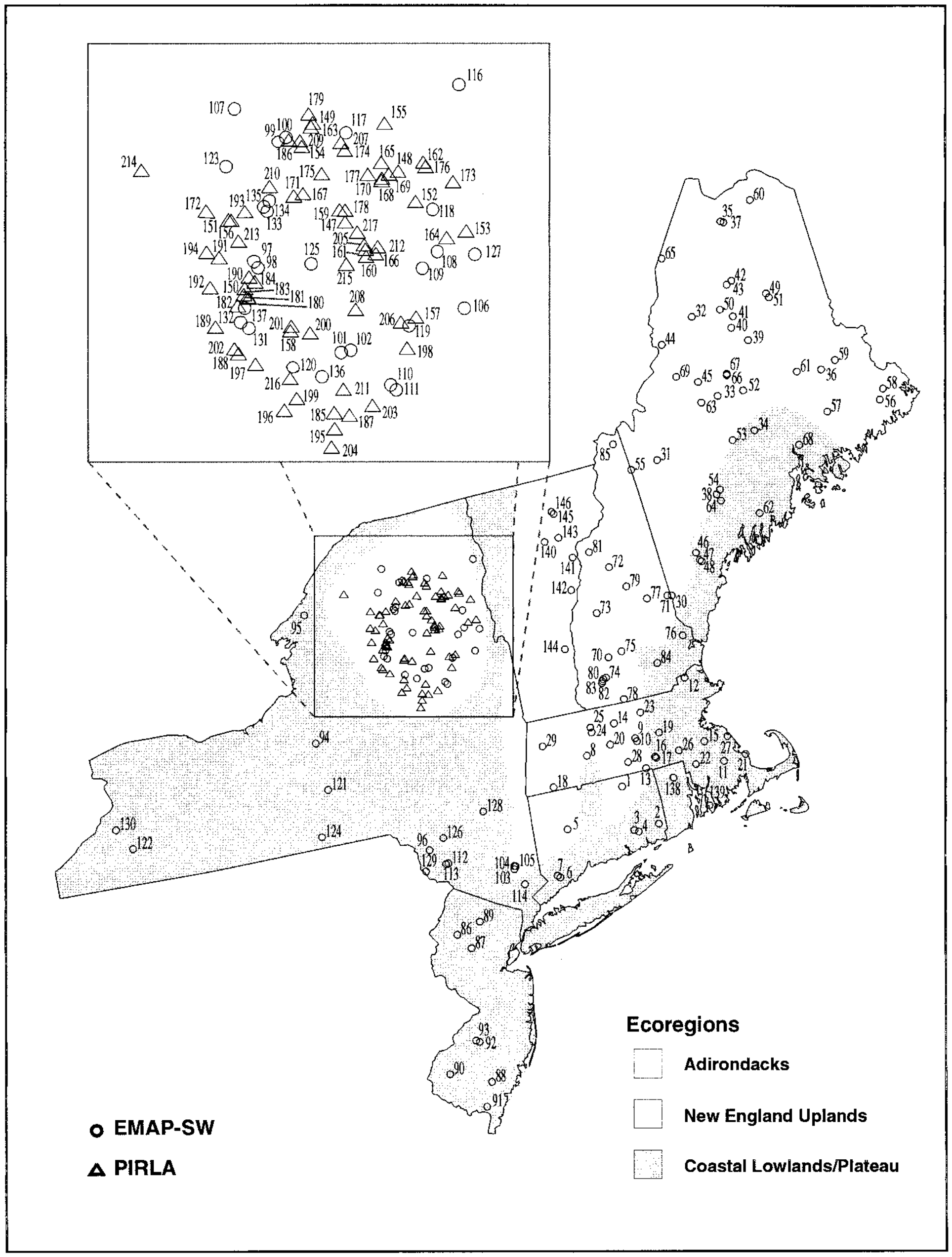


FIG. 1. Study area and location of the 146 EMAP (Environmental Monitoring and Assessment Program) and 71 Adirondack PIRLA (Paleoecological Investigation of Recent Lake Acidification) lakes studied for scaled chrysophytes in the northeastern U.S.A. Lake names that correspond to lake numbers on the map are given in Appendix 1.

of variation that can be accounted by that variable (axis 1 scores). All other axes are termed ''unconstrained.'' The environmental variable that can explain most of the variance in the species data will have a higher eigenvalue for axis 1 than for axis 2. The additional variance in the chrysophyte data explained by other environmental variables was examined by running a series of constrained CCAs when the remaining variables are retained as covariables (in this case, all other forward-selected variables).

Weighted-averaging regression and calibration (WACALIB version 3.3) was used to develop inference models, and the bootstrap error estimation approach was applied to assess errors in our models (Line et al. 1994). Bootstrapping is a computer-intensive resampling procedure in which a subset of calibration samples that is of the same size as the original set is randomly selected with replacement (Birks 1995). After 1000 bootstrap cycles, error estimates are generated for each sample.

RESULTS AND DISCUSSION

Presence of scales in the study lakes. Initially, we planned to study chrysophyte scales in the surface sediment samples of all of the 241 EMAP lakes that were initially sampled in the northeast for diatoms (Dixit et al. 1999). However, because no scales were present in the samples from 62 lakes and only a trace number (i.e. <10 scales counted while counting at least 500 diatom valves in the same slide) of scales were encountered in the samples from 33 lakes, data from only the remaining 146 EMAP lakes are presented in detail here. This was in sharp contrast to the Adirondack PIRLA lakes, where scales

TABLE 1. Minimum, maximum, mean, and median values of morphometric and chemical characteristics for study lakes. The environmental variables for each lake were used as potential explanatory variables for the distribution of surface sediment chrysophyte assemblages. N = number of measurements, ANC = acid-neutralizing capacity.

Variables	Minimum	Maximum	Mean	Median	N
Elevation (m)	2.0	1151.9	371.9	387.0	217
Sampling depth (m)	1.3	46.9	11.4	8.1	217
Lake area (ha)	0.4	3293.5	154.4	24.8	217
Watershed area (ha)	9.2	262,216.4	6427.4	458.4	217
Secchi depth (m)	0.5	13.3	3.9	3.6	217
pH (air-equilibrated)	4.4	8.6	7.0	7.3	217
Gran ANC ($\mu eq \cdot L^{-1}$)	−39.0	3049.6	226.5	114.3	217
Total aluminum ($\mu g \cdot L^{-1}$)	0.5	719.5	74.4	24.4	214
Conductivity ($\mu S \cdot cm^{-1}$)	12.6	1073.9	64.8	32.1	217
Calcium ($\mu eq \cdot L^{-1}$)	35.2	9044.3	292.1	151.9	217
Magnesium ($\mu eq \cdot L^{-1}$)	14.8	3132.8	104.9	61.2	217
Sodium ($\mu eq \cdot L^{-1}$)	5.3	4816.5	176.2	47.4	217
Potassium ($\mu eq \cdot L^{-1}$)	1.0	109.0	16.0	9.7	217
Chloride ($\mu eq \cdot L^{-1}$)	4.0	5323.1	175.1	21.0	217
Sulfate ($\mu eq \cdot L^{-1}$)	6.8	8517.5	161.4	111.2	217
Total nitrogen ($\mu g \cdot L^{-1}$)	3.0	1701.8	291.3	274.9	200
Total phosphorus ($\mu g \cdot L^{-1}$)	0.2	115.8	13.6	8.0	189
Silica ($mg \cdot L^{-1}$)	0.0	15.3	3.0	2.5	216
Dissolved organic carbon ($mg \cdot L^{-1}$)	0.3	15.6	4.4	3.8	217
Dissolved inorganic carbon ($mg \cdot L^{-1}$)	0.3	39.5	3.3	1.6	176
Color (PCU)	1.0	150.4	20.4	14.5	216

were found in countable numbers in all 71 lakes (Cumming et al. 1992a). In general, the preservation of scales was good in the surface sediment samples, and the absence of scales in a number of EMAP lakes cannot be attributed to preservation problems alone because thinly silicified diatom valves were well preserved in these lakes. The few scales that were present in these samples were also well preserved.

To explore why scales were absent or rare in 95 of the EMAP lakes, we first divided the 241 lakes into two groups (scales present vs. scales absent or rare). Then we performed a discriminant analysis to see whether these two groups could be distinguished on the basis of the measured environmental data. The forward-selection option indicated that [Ca], depth, and [K] captured 14% of the total variance in the two groups. In the EMAP data set, [Ca] and [K] were strongly correlated with conductivity ($R = 0.87$) and Na ($R = 0.80$), respectively, whereas lake depth was strongly related to trophic variables (Secchi depth and total phosphorus [TP]). Although all three forward-selected variables were significant ($P \leq 0.01$), considerable overlap existed between sites. Thus, on the basis of the CVA, we could not clearly determine why scales were absent or rare in 95 of our study lakes.

We further analyzed the two groups of lakes by plotting their percent distributions against selected environmental variables (Fig. 2). Frequency histograms in Figure 2 provide some insight on lake types that were likely to contain fewer chrysophyte scales. The proportion of lakes with no/few scales is higher at high TP and TN (total nitrogen) and lower Secchi depth. For example, about half of the more productive lakes (TP $\geq$ 10 $\mu g \cdot L^{-1}$, TN > 400 $\mu g \cdot L^{-1}$, Secchi depth < 2 m) have no scales, whereas in less productive water (TP < 10 $\mu g \cdot L^{-1}$, TN < 200 $\mu g \cdot L^{-1}$, Secchi depth > 4 m), only a small percentage of lakes lack scales. The pattern compares well with the Adirondack PIRLA lakes, which were mostly oligotrophic and contained high abundances of chrysophyte scales. The proportion of lakes with fewer scales also generally increases at high pH (>8), DOC (>6 $mg \cdot L^{-1}$), conductivity (>200 $\mu S \cdot cm^{-1}$), chloride (>500 $\mu eq \cdot L^{-1}$), and Ca (>400 $\mu eq \cdot L^{-1}$). Smaller (lake size <10 ha) and shallower (<4 m) lakes tended to have fewer scales as well. No specific pattern could be observed for Si and elevation. Although it is difficult to ascertain the relative importance of any single variable, a general observation is that sediment of lakes with high pH that are small, shallow, colored, turbid, and productive generally have fewer chrysophyte scales.

Species richness and diversity. In our 217 lake data set, the species richness (number of taxa) ranged between 5 and 25, and the mean richness was 15. We used Hill's (1973) N2 diversity numbers as measures of species diversity. Advantages of using Hill's diversity over other diversity indices are discussed in Ludwig and Reynolds (1988). The species richness and diversity of chrysophytes in our data set were examined against measured lake-water pH, TP, TN, silica, Secchi depth, conductivity, Cl, and lake size and depth. Relationships were examined using both linear and nonlinear functions. In our study, significant nonlinear trends (Fig. 3) were observed between lake-water pH and species richness ($R = 0.51$, $F = 38.17$, $P < 0.0001$) and diversity ($R = 0.48$, $F = 38.47$, $P < 0.0001$). However, no significant ($R = 0.06$–0.16, $F = 0.13$–2.72, $P = 0.10$–0.64) trends were observed for any other selected limnological

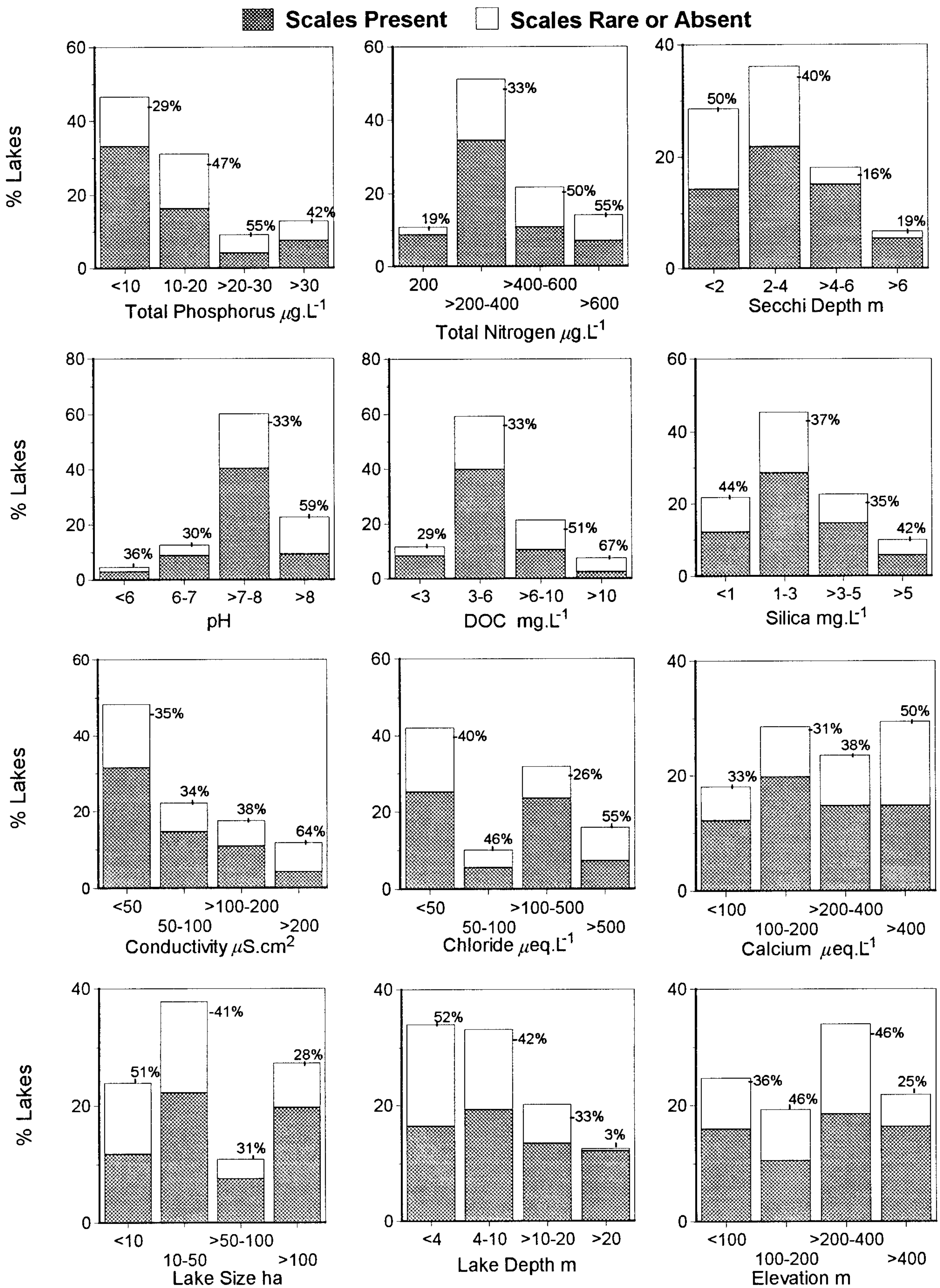
TABLE 2. The number of occurrences, maximum and mean abundances, and pH optima and tolerance values for chrysophyte taxa or groups that were found in at least three lakes and had greater than 1% abundance in at least one of the study lakes.

Taxon name	Taxon code	Number of occurrences	Maximum abundance	Mean abundance	pH optima	pH tolerance
Chrysodidymus synuroideus Prowse	CSYNU	49	11.7	1.3	5.8	0.9
Chrysosphaerella Lauterborn[a]	CHRYS	138	55.6	4.8	7.0	0.8
Mallomonas acaroides var. *muskokana* Nicholls[b]	MACAR	128	33.2	5.4	6.4	1.0
M. akrokomos Ruttner *in* Pascher	MAKRO	32	7.8	1.2	7.0	0.8
M. allorgei (Defl.) Conrad	MALLO	54	24.8	3.3	7.3	0.6
M. alpina Pascher et Ruttner	MALPI	75	49.8	1.8	7.4	0.7
M. caudata Ivanov *em.* Krieger	MCAUD	199	96.7	16.3	7.3	0.8
M. crassisquama (Asmund) Fott	MCRAS	177	59.1	14.1	7.4	0.6
M. duerrschmidtiae Siver, Hamer, et Kling	MDUER	122	85.9	18.8	6.2	1.0
M. elongata Reverdin	MELON	88	55.2	2.2	7.5	0.5
M. hamata Asmund	MHAMA	161	49.2	4.5	6.4	1.0
M. heterospina Lund	MHETE	34	2.7	0.6	7.5	0.6
M. hindonii Nicholls	MHIND	34	69.8	11.0	5.0	0.5
M. insignis Penard	MINSI	18	9.7	1.6	7.8	0.5
M. lelymene Harris et Bradley	MLELY	11	2.8	1.0	7.0	0.8
M. 'medium' group[c]	MMEDI	88	11.4	2.2	7.6	0.5
M. oviformis Nygaard	MOVIF	12	2.2	0.7	7.5	0.4
M. ouradion Harris et Bradley	MOURA	3	1.0	0.8	7.6	0.9
M. peronoides (Harris) Momeu et Péterfi	MPERO	3	6.4	2.4	7.7	0.3
M. pseudocoronata Prescott	MPSEU	136	79.1	13.7	7.5	0.5
M. pugio Bradley	MPUGI	6	8.4	1.6	7.2	0.7
M. punctifera Korsh.	MPUNC	116	16.6	2.5	6.7	0.9
M. 'small' group[d]	MSMAL	179	26.8	4.0	6.8	0.9
M. torquata Asmund et Cronberg[e]	MTORQ	113	10.2	1.5	6.9	0.9
M. transsylvanica Péterfi et Momeu	MTRAN	61	9.9	1.0	6.8	0.8
Paraphysomonas deSaedeleer	PARAP	31	5.1	1.0	7.7	0.3
Spiniferomonas Takahashi	SPINI	33	2.9	0.8	7.4	0.5
Synura curtispina (Pet. et Han.) Asmund	SCURT	119	93.0	6.6	7.5	0.5
S. echinulata Korsh.	SECHI	189	84.4	13.2	6.9	1.1
S. lapponica Skuja	SLAPP	31	2.8	0.7	7.3	0.6
S. mollispina (Pet. et Han.) Péterfi et Momeu	SMOLL	55	48.6	3.2	7.6	0.5
S. petersenii Korsh.	SPETE	175	79.7	10.4	7.2	0.8
S. sphagnicola Korsh.	SSPHA	140	80.4	6.9	6.6	1.0
S. spinosa Korsh.	SSPIN	143	60.2	4.7	7.2	0.6
S. spinosa f. *longispina* Pet. et Han.	SLONG	11	8.5	2.9	6.8	0.8
S. uvella Stein *em.* Korsh.	SUVEL	118	16.5	2.4	7.4	0.5

[a] Includes *C. brevispina* Korshikov and *C. longispina* Lauterborn *em.* Nicholls.
[b] May include the nominate variety because differentiating these two taxa under light microscope was difficult given their overlapping characteristics.
[c] Includes all unidentified scales that are bigger than *M.* 'small' (see below) and may include taxa such as *M. intermedia* Kisselew and *M. corymbosa* Asmund et Hilliard.
[d] Includes scales of small *Mallomonas* such as *M. galeiformis* Nicholls, *M. tonsurata* Teiling *em.* Krieger, *M. calceolus* Bradley, *M. papillosa* Harris et Bradley, and others.
[e] Also includes taxa belonging to *Torquatae* series such as *M. dickii* Nicholls and *M. doignonii* Bourrelly *em.* Asmund et Cronberg.

variables. Species richness data show that, in general, fewer numbers of chrysophyte taxa occur in acidic lakes and that diversity is generally low in these waters (Fig. 3). Richness and diversity increase with pH and reach a maximum at a pH of about 7.0 to 7.5 and then decline. In very alkaline lakes, the values were as low as the acidic lakes. In Danish lakes, Nielsen (1996) also observed an increase in species richness from acid to neutral and alkaline lakes and then a decrease at the most alkaline localities. Siver and Hamer (1989) observed a similar trend; however, in absolute terms, they found maximum species richness (mean of 8.5 taxa per collection) at a pH range between 5.5 and 6.0.

Chrysophytes are more abundant in terms of both species richness and biomass in oligotrophic waters (Siver 1995). Cronberg (1982) observed higher chrysophyte numbers in lakes where phosphorus levels declined as a result of restoration efforts. However, these observations do not always hold true because large increases in nitrogen (levels reaching to 1510 $\mu g \cdot L^{-1}$) might be advantageous to scale-bearing chrysophytes, and the highest richness of scaled chrysophytes might occur at medium phosphorus concentrations and not at the lowest phosphorus (Nielsen 1996). Similarly, in a highly eutrophic Danish lake (TP 151–378 $\mu g \cdot L^{-1}$), Kristiansen (1988) recorded 33 scaled chrysophyte species and suggested that the presence of few species indicate oligotrophy, whereas a rich chrysophyte assemblage generally indicates eutrophic conditions. However, Siver and Hamer (1989) observed no significant difference in the number of scaled chrysophytes along a total phosphorus gradient. The available literature


Scales Present
Scales Rare or Absent
% Lakes
29%
47%
55%
42%
<10
10-20
>20-30
>30
Total Phosphorus μg.L^{-1}
19%
33%
50%
55%
200
>200-400
>400-600
>600
Total Nitrogen μg.L^{-1}
50%
40%
16%
19%
<2
2-4
>4-6
>6
Secchi Depth m
36%
30%
33%
59%
<6
6-7
>7-8
>8
pH
29%
33%
51%
67%
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3-6
>6-10
>10
DOC mg.L^{-1}
44%
37%
35%
42%
<1
1-3
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Silica mg.L^{-1}
35%
34%
38%
64%
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50-100
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Conductivity μS.cm^2
40%
46%
26%
55%
<50
50-100
>100-500
>500
Chloride μeq.L^{-1}
33%
31%
38%
50%
<100
100-200
>200-400
>400
Calcium μeq.L^{-1}
51%
41%
31%
28%
<10
10-50
>50-100
>100
Lake Size ha
52%
42%
33%
3%
<4
4-10
>10-20
>20
Lake Depth m
36%
46%
46%
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<100
100-200
>200-400
>400
Elevation m

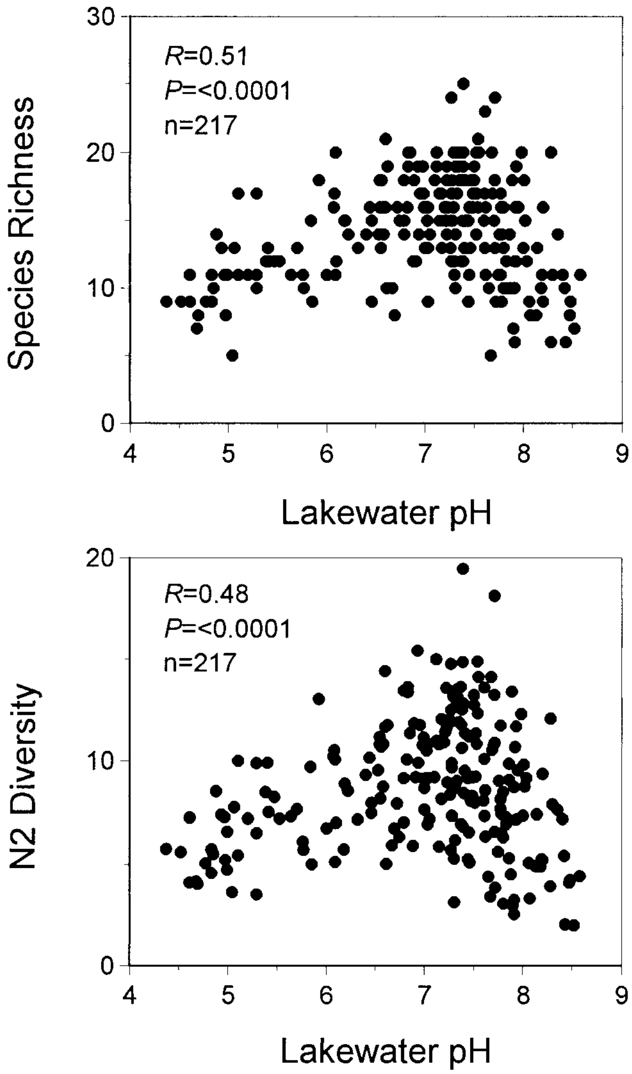

FIG. 3. Species richness and diversity of scaled chrysophyte assemblages in the 217 study lakes plotted against measured lake-water pH.

and the lack of a relationship with trophic variables in our study indicate that no consistent pattern exists between the diversity/richness of scaled chrysophytes and nutrients. The differences that we observed might be due to different gradient lengths that might have been used in other studies. However, the importance of lake-water pH is evident.

Multivariate analysis. Ordination analysis is one of the most effective means to examine the relationship between scaled chrysophytes and lake-water quality. The surface sediments of the 217 study lakes represent the last few years of sediment accumulation and thus contain considerable autecological and synecological information that can subsequently be used to characterize environmental conditions on the basis of the species composition of a sample (Dixit et al. 1989c, 1990, Cumming et al. 1991, 1992a).

To directly relate the distributions of chrysophyte taxa to environmental variables, we used CCA (Ter Braak 1988), which produces simultaneous ordinations for both samples and taxa that can be related directly to environmental variables. The simultaneous influences of multiple environmental variables can also be explored using this technique. In an exploratory CCA using all 21 environmental variables listed in Table 1, the eigenvalues for axes 1 (0.28) and 2 (0.10) explained 20% of the cumulative variance in the species data, and both axes were significant ($P \leq 0.01$). The species–environmental correlations were high for axes 1 (0.91) and 2 (0.75). Many environmental variables were closely correlated (Table 3) in our data set. Thus, high variance inflation factor (VIF) values ($\geq$10) were recorded for pH, ANC (acid-neutralizing capacity), conductivity, Ca, Mg, Na, and K. Not surprisingly, lake-water ANC was strongly correlated with pH ($R = 0.91$) and Ca ($R = 0.93$), and Na was highly correlated with Cl ($R = 0.97$). The correlation matrix data (Table 3) showed that our high-pH lakes generally have high ion concentrations and low Al and that these lakes are located at lower elevation areas. The high-TP lakes also have high TN ($R = 0.66$). Because the Secchi depth is inversely related to TP ($R = -0.68$), DOC ($R = -0.55$), and color ($R = -0.58$), it suggests that lake-water clarity is a function of both nutrients and organics. The lakes that have large surface areas are generally deep ($R = 0.62$) and have large watersheds ($R = 0.75$).

The forward-selection option in CCA was used to select the minimum number of significant environmental variables that can explain the maximum amount of variation in the species data. This analysis identified seven environmental variables as significant ($P \leq 0.01$), capturing 82% of the total variance explained (20%) by the original 21 variables. The contributions of these variables in explaining the species data, in descending order, were pH (51%), TP (9%), depth (6%), conductivity (4%), chloride (4%), watershed area (4%), and elevation (4%). The eigenvalues for axes 1 and 2 were 0.27 and 0.10, respectively, and both axes were significant ($P \leq 0.01$). With the exception of conductivity (VIF 5) and chloride (VIF 6), VIFs for forward-selected variables were low (<3). The variables that were very highly correlated and did not independently influence chrysophyte distributions were successfully ex-

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FIG. 2. Frequency histograms showing distributions of two EMAP (Environmental Monitoring and Assessment Program) lake groups (scales present vs. scales absent/rare) versus selected limnological characteristics. Percentage values associated with ''scales absent/rare'' class refer to percentage within that category.

TABLE 3. Correlations among the 21 environmental variables selected for the exploratory canonical correspondence analysis. Correlation values more than 0.23 are significant at $P = 0.001$.

	Elevation	Lake area	Watershed area	Depth	Secchi	Conductivity	ANC	pH	DIC	DOC	Color	Ca	Mg	Na	K	Cl	SO_4	Al	Total P	SiO_2	Total N
Elevation	1.00																				
Lake area	−0.21	1.00																			
Watershed area	−0.36	0.75	1.00																		
Depth	0.03	0.62	0.35	1.00																	
Secchi	0.28	0.14	−0.07	0.55	1.00																
Conductivity	−0.57	0.02	0.20	−0.06	−0.31	1.00															
ANC	−0.49	0.16	0.31	0.06	−0.28	0.76	1.00														
pH	−0.55	0.26	0.36	0.12	−0.23	0.64	0.91	1.00													
DIC	0.19	−0.11	−0.11	−0.13	−0.07	0.00	0.00	−0.13	1.00												
DOC	−0.21	0.05	0.17	−0.33	−0.55	0.09	0.17	0.14	−0.02	1.00											
Color	−0.02	−0.13	0.05	−0.46	−0.58	−0.09	−0.02	−0.06	0.22	0.71	1.00										
Ca	−0.41	0.08	0.23	0.08	−0.21	0.85	0.93	0.81	0.02	0.09	−0.10	1.00									
Mg	−0.56	0.07	0.22	−0.05	−0.36	0.86	0.86	0.77	0.00	0.23	0.03	0.86	1.00								
Na	−0.71	0.10	0.27	−0.11	−0.33	0.87	0.57	0.58	−0.10	0.12	−0.06	0.60	0.70	1.00							
K	−0.66	0.11	0.24	−0.06	−0.34	0.76	0.52	0.49	−0.10	0.15	−0.02	0.53	0.66	0.80	1.00						
Cl	−0.69	0.11	0.27	−0.08	−0.31	0.86	0.54	0.52	−0.10	0.09	−0.07	0.57	0.68	0.97	0.78	1.00					
SO_4	−0.05	−0.16	−0.12	0.01	−0.01	0.54	0.27	0.15	0.17	−0.20	−0.21	0.48	0.47	0.33	0.36	0.35	1.00				
Al	0.55	−0.26	−0.20	−0.19	0.03	−0.45	−0.57	−0.69	0.30	0.13	0.39	−0.49	−0.51	−0.51	−0.41	−0.49	−0.08	1.00			
Total P	−0.48	−0.10	0.11	−0.46	−0.68	0.44	0.36	0.34	0.06	0.52	0.39	0.27	0.47	0.52	0.50	0.52	0.03	−0.21	1.00		
SiO_2	0.13	−0.11	0.09	−0.04	0.01	0.07	0.18	0.11	0.34	−0.08	0.17	0.21	0.12	−0.06	−0.06	−0.10	0.18	0.19	−0.10	1.00	
Total N	−0.55	0.28	0.45	−0.10	−0.41	0.42	0.37	0.40	−0.13	0.41	0.09	0.27	0.41	0.53	0.55	0.54	−0.01	−0.29	0.66	−0.14	1.00

ANC = acid-neutralizing capacity, DIC = dissolved inorganic carbon, DOC = dissolved organic carbon.

TABLE 4. Interset correlations between first two species axes and forward selected environmental variables in canonical correspondence analysis.

Variable	Axis 1 (λ_1 = 0.27)	Axis 2 (λ_2 = 0.10)
pH	−0.86	−0.04
Total phosphorus	−0.42	0.51
Conductivity	−0.57	0.23
Chloride	−0.60	0.20
Depth	−0.11	−0.55
Elevation	0.64	−0.14
Watershed area	−0.39	0.02

cluded by the forward-selection option in CCA. For example, because ANC was highly correlated with pH (R = 0.91) and Na was highly correlated with Cl (R = 0.97), both ANC and Na could not be selected as significant variables after pH and Cl had already been selected.

The species–environmental correlations for CCA axis 1 (0.89) and axis 2 (0.70) were high and statistically significant ($P \leq 0.01$). Lake-water pH, conductivity, chloride, elevation, and watershed area were most strongly related to species axis 1, whereas TP and lake depth were most strongly related to axis 2 (Table 4). Because in ordinations both taxa and lakes were arranged similarly, we are confident that the measured environmental variables account for a large proportion of the explainable variation in the weighted averages of the chrysophyte data.

On the CCA biplot, the length of environmental arrows indicates their relative importance, and the orientation shows their approximate correlations to the ordination axes. In the environmental–lake score biplot, the lake scores are weighted averages of the taxon scores (Fig. 4). The positioning of lakes in relation to environmental arrows closely corresponds to the limnological characteristics and associated ecoregion patterns for the study lakes. The lakes positioned to the left have high pH, conductivity, and chloride and large watersheds. These lakes are distributed mainly in the New England Uplands and Coastal Lowlands/Plateau ecoregions. The lakes positioned to the right have low pH, conductivity, and chloride. These lakes generally have low ion concentrations and are located in high-elevation areas. With respect to geographical distribution, these lakes are most common in the Adirondack ecoregion. The distribution of study lakes on axis 2 appears to track lake depth and TP. The high-pH lakes that have high scores for axis 2 (positioned on upper-left quadrant) are generally shallower and have high TP values. These lakes are more eutrophic and are widely distributed in the Coastal Lowlands/Plateau region. The high-pH lakes that are generally deep and more oligotrophic are in the lower-left quadrant. A higher proportion of lakes in this quadrant are located in the New England Uplands.

The chrysophyte taxa scores and forward-selected environmental variables are shown in the environ-

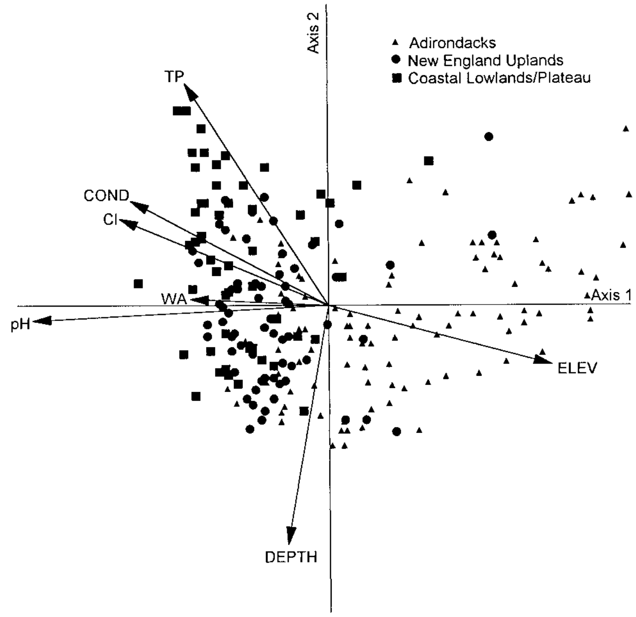


FIG. 4. Canonical correspondence analysis (CCA) ordination biplot showing significant forward-selected environmental variables (arrows) and sample scores of the 217 study lakes.

mental–species CCA biplot (Fig. 5). The position of each taxon on the biplot approximates its weighted-average optimum relative to other taxa. Because pH was the most important variable in our data set, the weighted-averaging pH optima and tolerances of chrysophyte taxa in our data set are presented in Table 2. Because axis 1 represents mainly the pH gradient, taxa that commonly occur in high-pH wa-

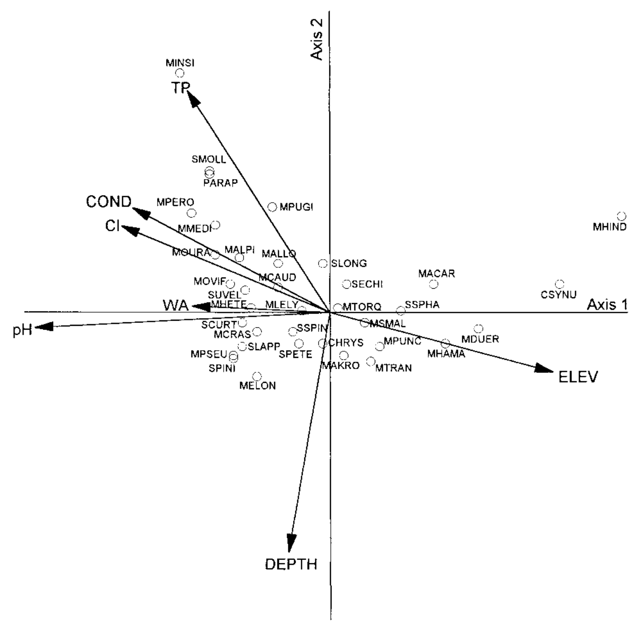


FIG. 5. Canonical correspondence analysis (CCA) ordination biplot showing the significant forward-selected environmental variables (arrows) and species scores of the 37 chrysophyte taxa listed in Table 2.

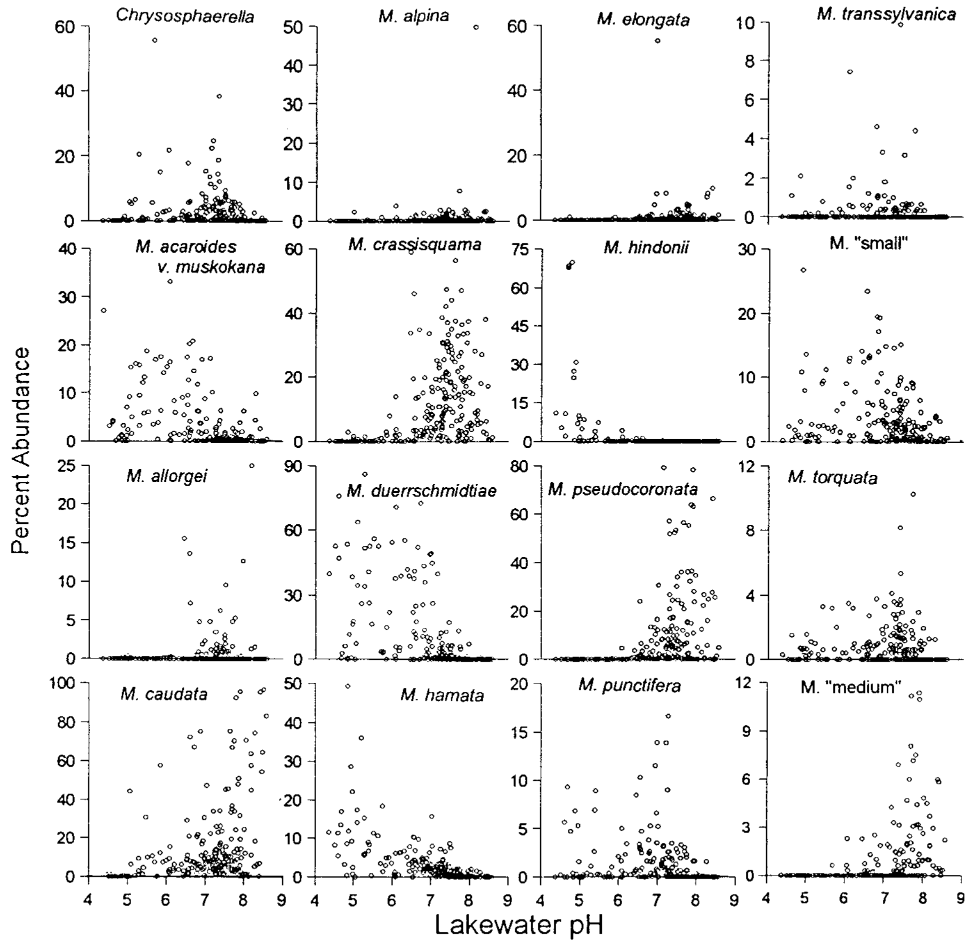


FIG. 6. Percentage composition of scales of *Chrysosphaerella* and selected *Mallomonas* species versus measured lake-water pH in the 217 study lakes.

ters (also high conductivity and chloride) are positioned on the left, whereas taxa found in low-pH waters (also low conductivity and low chloride) are located on the right.

Scatter plots of the most common chrysophyte taxa (Figs. 6, 7) also illustrate the pH-indicator status of these algae. Many chrysophyte taxa encountered in our study have well-defined distribution patterns along a continuum of pH. For example, in our data set, *Mallomonas hindonii* and *M. hamata* were found mainly in low-pH waters (Fig. 6), and *M. acaroides* var. *muskokana* and *M. duerrschmidtiae* occurred mainly in moderate- to low-pH waters. *Mallomonas crassisquama,* the *M.* ''small'' group, *M. allorgei, M. elongata,* and *M. caudata* generally occurred in higher abundances at circumneutral pH, whereas *M. pseudocoronata, M. torquata, M. alpina,* and the *M.* ''medium'' group were more common in high-pH (>7.5) lakes. The occurrence of *Chrysosphaerella, M. punctifera,* and *M. transsylvanica* in both acidic and alkaline waters suggests that they are pH generalists (and thus poor pH indicators).

Among the *Synura* species (Fig. 7), *S. echinulata* and *S. sphagnicola* were tolerant to a wide range of pHs. This is in contrast to some previous studies (e.g. Smol et al. 1984, Dixit et al. 1989c, 1990, Siver and Hamer 1989) where these taxa were reported mainly in acidic waters. Scales of *S. spinosa* and *S. petersenii* were more abundant at about pH 7, whereas scales of *S. mollispina, S. uvella, S. curtispina, Spiniferomonas,* and *Paraphysomonas* were common in high-pH lakes (Fig. 7).

In addition to pH and associated variables, we can also relate the distribution of chrysophyte taxa to trophic variables associated with axis 2 (Fig. 5). For example, taxa that are positioned on the upper-left quadrant of axis 1 (e.g. *M. insignis, Paraphysomonas,* and *S. mollispina*) were more common in high-pH waters that have high nutrients, whereas taxa positioned on the lower-left quadrant (e.g. *M. elongata, M. pseudocoronata,* and *S. spinosa*) were commonly found in high-pH lakes that have relatively low nutrients.

Earlier ordination studies in the northeastern U.S.A. (Dixit et al. 1990, northern New England; Cumming et al. 1992a, Adirondack Mountains) also showed that lake-water pH and related variables (e.g. Al) significantly influenced the distribution of chrysophytes. The calibration lakes used in these studies were selected mainly to address questions related to lake acidification, and thus the influence of nutrients could not be evaluated. The overriding in-

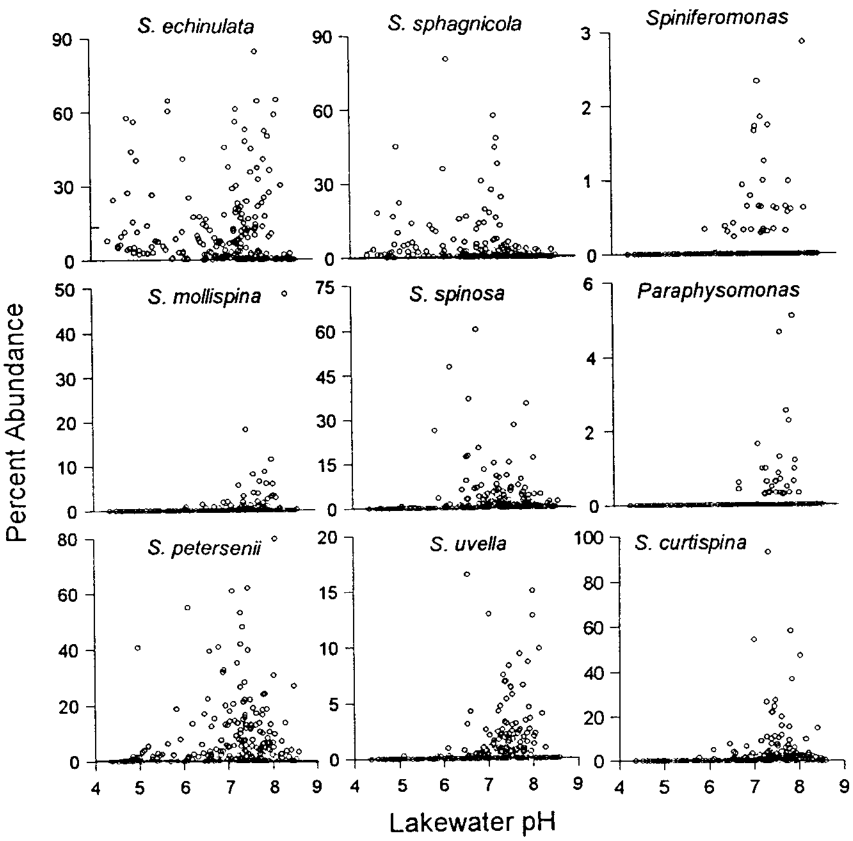


FIG. 7. Percentage composition of scales of selected *Synura, Spiniferomonas,* and *Paraphysomonas* species versus measured lake-water pH in the 217 study lakes.

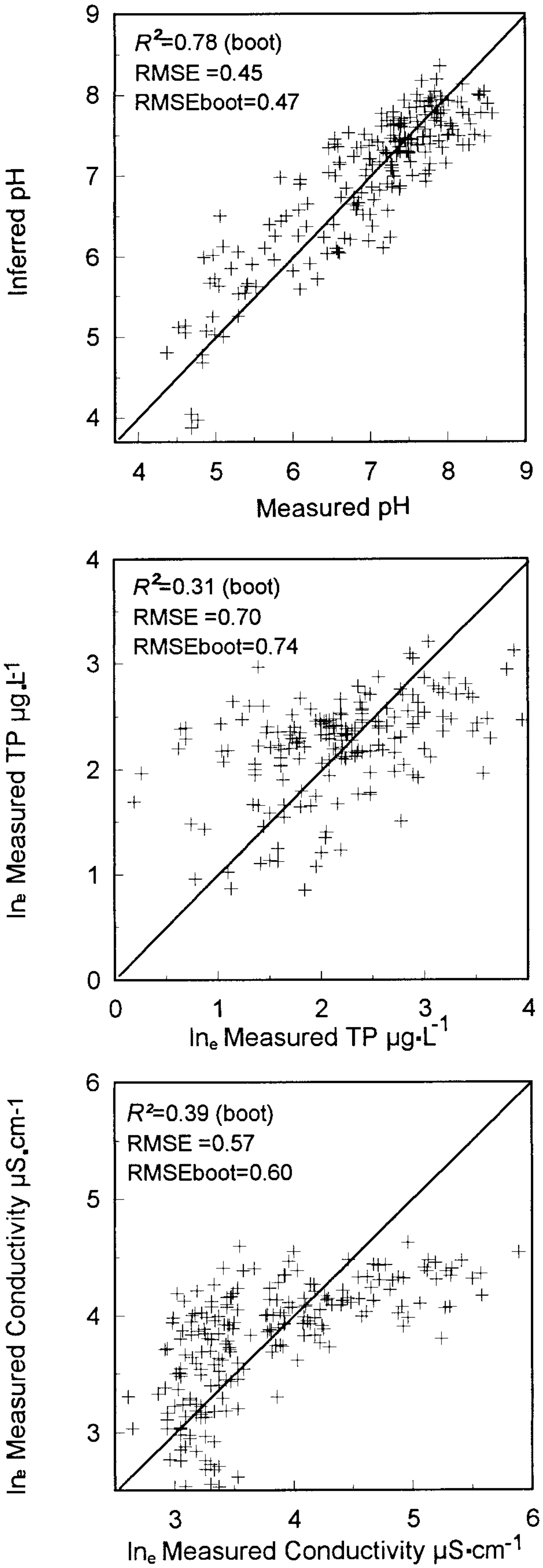
fluence of pH in our 217 lake data set, which included 146 EMAP lakes that were selected via a randomized systematic design and contained trophic and other watershed disturbance variables, provides the most convincing evidence that lake-water pH is the most important environmental variable influencing the distributions of scaled chrysophytes in the northeastern U.S.A.

TABLE 5. Constrained and partial canonical correspondence analysis (CCA) results identifying the strength and partial independence of forward-selected environmental variables. Significance values are based on 99 unrestricted Monte Carlo permutation tests. λ_1 = eigenvalue for axis 1, λ_2 = eigenvalue for axis 2.

Variable	λ_1	λ_1/λ_2	$\leq P$
Constrained CCA			
pH	0.25	1.69	0.01
Total phosphorus	0.09	0.30	0.01
Conductivity	0.12	0.51	0.01
Chloride	0.12	0.48	0.01
Depth	0.04	0.13	0.01
Elevation	0.14	0.67	0.01
Watershed area	0.07	0.22	0.01
Partial CCA			
pH	0.10	0.73	0.01
Total phosphorus	0.02	0.11	0.01
Conductivity	0.03	0.18	0.01
Chloride	0.02	0.13	0.01
Depth	0.02	0.18	0.01
Elevation	0.02	0.13	0.01
Watershed area	0.02	0.12	0.01

Weighted-averaging calibration. The relationship between surface sediment chrysophytes and environmental variables (e.g. pH and Al) can be quantified to a high level of accuracy. In addition to pH, Siver (1993) and Siver and Marsicano (1996) were able to quantify chrysophyte assemblages of southern New England lakes to conductivity and trophic status, respectively. In our data set, we had many significant variables that each explained only a small portion of the total variance. Thus, we further evaluated the significance of these variables in environmental reconstructions by constraining the CCA to one environmental variable at a time and running partial CCAs (Ter Braak 1988). Ratios of the first constrained eigenvalue (λ_1) to the second unconstrained eigenvalue (λ_2) in a constrained CCA indicate the relative importance of the forward-selected environmental variable in explaining the species data (Table 5). Strong inference models can be developed for environmental variables that have high λ_1/λ_2. Although all forward-selected chemical variables were significant ($P \leq 0.01$), pH had the maximum λ_1/λ_2 value, followed by conductivity, chloride, and TP.

We examined the influence of individual environmental variables on chrysophyte species distributions, in addition to other environmental variables (Table 5), using partial CCAs and unrestricted Monte Carlo permutation tests. Here the first ordination axis was constrained to a single environmental vari-



able after the effects of the other six variables were removed (partial CCA). The partial CCAs suggested that there is a significant ($P \leq 0.01$) additional signal from all the variables selected in the forward-selection option of CCA. The high λ_1/λ_2 for pH in the constrained and partial CCAs (Table 5) strongly suggests that pH is the most important environmental variable in this data set and that it accounts for a large and significant proportion of variation that is not present in other forward-selected environmental variables. Our constrained and partial λ_1/λ_2 values for pH are considerably higher than the values reported by Cumming et al. (1992a) for the Adirondack lakes. This is likely due to the larger data set and broader environment gradients that we had available in our present calibration set. However, the low λ_1/λ_2 values for conductivity, TP, and chloride suggest that inference models for these variables would be relatively weak.

We used the weighted-averaging regression and calibration approach to construct inference models for pH, conductivity, and TP. The weighted-averaging approach assumes a unimodal relationship between the inferred variable (pH) and chrysophyte distributions. The available autecological data suggest that for chrysophytes this is a valid ecological assumption. The basic logic in weighted averaging is that at a given environmental value, taxa that have optima nearest to that value will be most abundant. For example, the pH optimum for a taxon would be an average of all the pH values of lakes in the calibration data set in which the taxon occurred, weighted by its relative abundance (regression step). Computed optima of various taxa can then be used to infer any specific environmental variable by taking an average of the taxa abundances in a sample, each weighted by its optimum (calibration step). Because in weighted averaging averages are taken twice (once in the regression step and again during calibration), this results in shrinkage of the range of inferred values. This is normally corrected by a linear deshrinking regression (''classical regression''). An ''inverse regression'' approach can be also applied to deshrink the inferred values because this reduces the root mean squared error (RMSE).

Weighted averages can be also calculated using the tolerance values of individual taxa. The tolerance value for a taxon is the distribution of the taxon around the optimum. When tolerance values of taxa for an environmental variable vary substantially, taxa can be weighted by their squared tolerance in a weighted-averaging equation. Taxa that have a narrow tolerance can be given more weight in weighted averaging than taxa with a wide tolerance (Cum-

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FIG. 8. Weighted-averaging calibration models for lake-water pH, total phosphorus (TP), and conductivity for the 217 study lakes.

ming et al. 1992a). Ideally, tolerance down-weighting should provide more accurate inferences, but in large data sets it has been shown that, although tolerance down-weighting gives a lower apparent RMSE than weighted averaging, it does not improve RMSE in cross-validation or bootstrapping. Thus, weighted averaging without tolerance corrections have generally been applied.

We assessed the strengths of inference models by the R^2 between the measured and inferred values and the bootstrap root mean squared errors ($RMSE_{boot}$) of prediction. The weighted-averaging pH model (without tolerance down-weighting), using inverse regression, proved to be the best model for inferring lake-water pH in our data set. The inference model was robust ($R^2_{boot} = 0.78$), and the data points were fairly evenly distributed on both sides of the 1:1 lines (Fig. 8). As we expected from the CCA results (Table 5), weighted-averaging conductivity ($R^2 = 0.39$) and TP ($R^2 = 0.31$) models were relatively weak (Fig. 8) and are not discussed further.

The error in the pH model was relatively small (RMSE = 0.45; $RMSE_{boot} = 0.47$). The $RMSE_{boot}$ was further split into predictive error that is associated with each sample (s_1) and a constant error (s_2) for the entire data. Because the s_1 value (0.07) was substantially lower than the s_2 value (0.46), it is likely that most of the error associated with our pH model is due to the inherent natural variation in the data set. The chrysophyte pH model that we have developed for the entire northeastern U.S.A. has stronger statistics than the one developed for only the Adirondack Park lakes ($R^2 = 0.72$, $RMSE_{boot} = 0.69$; Cumming et al. 1992a) and is comparable to the diatom-inferred pH model ($R^2 = 0.89$, $RMSE_{boot} = 0.36$) developed for the northeastern U.S.A. lakes in EMAP-SW (Dixit et al. 1999).

CONCLUSIONS

Diverse assemblages of scaled chrysophytes are present in the lakes of the northeastern U.S.A. We identified a number of environmental variables that were important in determining the distribution of species; however, lake-water pH had an overriding influence. We developed a statistically significant pH inference model that can be applied to a large region of lakes. With the availability of regional scale diatom and chrysophyte inference models for the northeastern U.S.A., it will be possible to infer past lake-water conditions with greater confidence. These data will be critical in assessing the timing, rate, and magnitude of acidification and any possible recovery that may have occurred in acid sensitive lakes because of reductions in acidic precipitation. Chrysophyte data will also be useful in identifying the influence of watershed activities on well-buffered lakes, as it has been generally observed that these lakes are becoming more alkaline because of anthropogenic activities in the drainage basin.

Sedimentary diatoms have remained the mainstay of most paleolimnological studies dealing with lake management, and undoubtedly they will continue to occupy this role. However, the use of chrysophytes as environmental markers offers a valuable tool for the monitoring and protection of our water resources because chrysophyte scales are often well represented in sedimentary deposits of oligotrophic lakes, and they can be studied using the same preparation and microscopic techniques developed for diatoms. Our chrysophyte data will provide a useful and important addition to our diatom study in EMAP, where they would provide confirmatory as well as supplementary information on long-term environmental trends. It has been repeatedly shown that using both diatom valves and chrysophyte scales provides more accurate inferences of lake-water pH changes than those provided by diatoms alone in very acidic lakes. Moreover, because chrysophyte changes often pre-date diatom-based assessments (e.g. episodic acidification and recovery in acid-sensitive lakes), planktonic chrysophytes can be used as early warning indicators in environmental monitoring and assessment studies.

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APPENDIX 1. The listing of the 217 study lakes along with their latitudes and longitudes. Lake numbers correspond to numbers in Figure 1.

No.	Lake name	Latitude (°N)	Longitude (°W)
1	Bissonette Pond	41.9242	72.2189
2	Wyassup Lake	41.4883	71.8728
3	Oxoboxo Lake	41.4878	72.2015
4	Wheeler Pond	41.4637	72.1489
5	Lake Plymouth	41.6520	73.0476
6	Hemlock Reservoir	41.2187	73.2919
7	Aspetuck Reservoir	41.2411	73.3190
8	Lithia Springs Reservoir	42.2958	72.5664
9	Kendall Reservoir	42.3431	71.8903
10	Holden Reservoir	42.3114	71.8789
11	Savery Pond	41.9125	70.8403
12	Kenoza Lake	42.4700	71.6000
13	Webster Lake	42.2800	71.5000
14	Queen Lake	42.5341	72.1152
15	Holbrook Lake	42.1441	71.0203
16	Swans Pond	42.1229	71.7003
17	Whitins Pond	42.1095	71.6887
18	Mirror Lake	42.0780	73.0965
19	Williams Lake	42.3388	71.5684
20	Muddy Brook Pond	42.3433	72.2317
21	Scokes Pond	41.9222	70.5430
22	Barrowsville Pond	41.9519	71.2065

Appendix 1. Continued.

No.	Lake name	Latitude (°N)	Longitude (°W)
23	lake Whalom	42.5734	71.7412
24	Lake Wyola	42.5014	72.4310
25	Wickett Pond	42.5511	72.4316
26	Kingsbury Pond	42.1223	71.3739
27	Little Creeks Pond	42.1342	70.7106
28	Walker Pond	42.1380	72.0612
29	Windsor Reservoir	42.4863	73.1067
30	Moose Pond	43.5881	70.9339
31	Mountain Pond	44.8950	70.6442
32	Loon Lake	46.1450	69.6481
33	Bear Pond	45.3389	69.6042
34	Alder Brook Stream	44.9183	69.2506
35	Gardner Pond	46.9611	68.8889
36	Upper Sysladobsis Lake	45.3056	68.1411
37	Upper Pond	46.5600	68.5100
38	Torsey Lake	44.2400	69.5900
39	First Debsconeag Lake	45.4600	68.5800
40	Harrington Lake	45.5600	68.0900
41	Nesowadnehunk Lake	46.0200	69.0400
42	Munsungan Lake	46.3768	68.9771
43	Big Reed Pond	46.3527	69.0574
44	Long Pond	45.9628	70.1570
45	Indian Pond	45.5210	69.8111
46	Panther Pond	43.9261	70.4700
47	Chaffin Pond	43.8482	70.4436
48	Collins Pond	43.8316	70.4257
49	Hot Pond	46.1628	68.5661
50	Midnight Pond	46.1377	69.2420
51	Upper Shin Pond	46.1197	68.5421
52	Mill Brook Pond	45.3222	69.2447
53	Bog Pond	44.8855	69.5748
54	Ingham Pond	44.4542	69.9279
55	Sturtevant Pond	44.8668	71.0207
56	Second Lake	44.8582	67.4943
57	Upper Middle Branch Pond	44.8959	68.2282
58	Lake Cathance	44.9517	67.4086
59	Pleasant Lake	45.3540	67.9230
60	Square Lake	47.0824	68.4069
61	Mattanawcook Pond	45.3532	68.4670
62	Damariscotta Lake	44.1310	69.4966
63	Moxie Pond	45.3190	69.8457
64	Maranacook Lake	44.3491	69.9557
65	Depot Lake	46.7704	69.8329
66	Horseshoe Pond	45.5089	69.4040
67	Mountain Brook Pond	45.5225	69.4004
68	Thurston Pond	44.6632	68.7237
69	Long Pond	45.6268	70.0834
70	Contention Pond	43.1658	71.9656
71	Ivanhoe Pond	43.6003	70.9922
72	Russell Pond	44.0000	71.3900
73	Tewksbury Pond	43.3600	71.5800
74	Nubanusit Lake	42.5800	72.0300
75	French Pond	43.1100	71.4600
76	Barbadoes Pond	43.1901	70.9330
77	Mirror Lake	43.6224	71.2659
78	Pratt Pond	42.7394	71.9074
79	Kusumpe Pond	43.7870	71.4939
80	Tolman Pond	42.9749	72.1048
81	Pearl Lake	44.1997	71.8671
82	Chesham Pond	42.9388	72.1352
83	Childs Bog	42.9572	72.1227
84	Massabesic Lake	42.9937	71.3549
85	Second Connecticut Lake	45.1551	71.1715
86	Cranberry Lake	40.9092	74.7644
87	Pleasant Valley Lake	40.7510	74.6237
88	Harding Lakes	39.4507	74.7552
89	Splitrock Reservoir	40.9824	74.4402
90	Daretown Lake	39.6117	75.2538

Appendix 1. Continued.

No.	Lake name	Latitude (°N)	Longitude (°W)
91	East Creek Pond	39.2262	74.8846
92	Medford Lakes	39.8537	74.7928
93	Oakwood Lakes	39.8730	74.8341
94	White Lake	43.0064	76.0417
95	Hyde Lake	44.2444	75.8342
96	Briscoe Lake	41.7647	74.8731
97	Little Lilly Pond	43.9111	74.7758
98	Upper Sister Lake	43.8836	74.7619
99	Willis Pond (E)	44.3533	74.4983
100	Windfall Pond	44.3644	74.4492
101	Lake Pleasant	43.4842	74.4211
102	Sacandaga Lake	43.4839	74.3661
103	Oscawanna Lake	41.3997	73.8486
104	Clear Lake	41.4294	73.8408
105	Wiccopee Reservoir (N)	41.4244	73.8225
106	Trout Lake	43.5422	73.7033
107	Twin Ponds (E)	44.5197	74.6934
108	Schroon Lake	43.7847	73.7773
109	Hidden lake	43.7344	73.8783
110	Bennett Lake	43.3154	74.1945
111	Alexandra Lake	43.2907	74.1708
112	Melody Lake	41.5992	74.6711
113	St. Josephs Lake	41.5977	74.7041
114	New Croton Reservoir	41.2350	73.7596
115	Ringneck Marsh	43.6331	74.7394
116	Highlands Forge Lake	44.4098	73.4443
117	Moody Pond	44.3291	74.1188
118	Palmer Pond	43.9518	73.7468
119	Garnet Lake	43.5253	74.0224
120	No Name	43.4689	74.6978
121	No Name	42.5436	76.0118
122	Timber Lake	42.3530	78.6789
123	Wolf Pond	44.3040	74.8104
124	No Name (Owego)	42.1112	76.2187
125	Blue Mountain Lake	43.8519	74.4714
126	Neversink Reservoir	41.8509	74.6626
127	Swede Pond	43.7393	73.5783
128	Kingston Reservoir #4	42.0108	74.0732
129	Davis Pond	41.5724	74.9820
130	Clear Lake	42.5615	78.8519
131	Horseshoe Pond	43.6590	74.8837
132	Little Moose Lake	43.6891	74.9212
133	Trout Pond	44.0942	74.6427
134	Hitchins Pond	44.1144	74.6548
135	Horseshoe Lake	44.1319	74.6190
136	Piseco Lake	43.4084	74.5526
137	Forth Chain Lake	43.7409	74.8816
138	Mountaindale Reservoir	41.8828	71.5369
139	Watson Reservoir	41.5375	71.1769
140	Sabin Pond	44.4025	72.4183
141	Ticklenaked Pond	44.1100	72.0500
142	Fairlee Lake	43.5200	72.1300
143	Joes Pond	44.2400	72.1300
144	North Springfield Reservoir	43.3468	72.5065
145	Tildy's Pond	44.6440	72.2043
146	Shadow Lake	44.6687	72.2250
147	Arbutus Lake	43.5858	74.1408
148	Avalanche Lake	44.0752	73.5311
149	Bear Pond	44.2345	74.1712
150	Big Moose Lake	43.4902	74.5123
151	Cat Mountain Pond	44.0541	74.5137
152	Clear Pond	43.5950	73.4950
153	Clear Pond	43.5016	73.3540
154	Copperas Pond	44.1856	74.2230
155	Copperas Pond	44.1945	73.5354
156	Cowhorn Pond	44.0530	74.5050
157	Crane Mountain Pond	43.3310	73.5828
158	Deep Lake	43.3648	74.3952

Appendix 1. Continued.

No.	Lake name	Latitude (°N)	Longitude (°W)
159	Deer Lake	44.0204	74.1506
160	Dunk Pond	43.4952	74.1001
161	Frank Pond	43.5133	74.0939
162	Giants Washbowl	44.0838	73.4420
163	Green Pond	44.2256	74.1802
164	Gull Pond	43.4951	73.4229
165	Heart Lake	44.1050	73.5803
166	Huntley Pond	43.4957	74.0639
167	Jenkins Pond	44.0750	74.2855
168	Lake Arnold	44.0745	73.5625
169	Lake Colden	44.0709	73.5859
170	Livingston Pond	44.0637	73.5918
171	Long Pond	44.0748	74.2546
172	Nick's Pond	44.0839	74.5803
173	Parch Pond	44.0225	73.3612
174	Pine Pond	44.1544	74.0852
175	Rock Pond	44.1126	74.1810
176	Round Pond	44.0726	73.4357
177	Upper Wallface Pond	44.0847	74.0315
178	Wolf Lake	44.0142	74.1316
179	Black Pond	44.2603	74.1756
180	Bubb Lake	43.4630	74.5048
181	Dart's Lake	43.4736	74.5213
182	Lake Rondaxe	43.4523	74.5500
183	Moss Lake	43.4652	74.5111
184	Constable Pond	43.5000	74.4745
185	Chub Lake	43.1530	74.3150
186	Dry Channel Pond	44.2110	74.2615
187	Duck Lake	43.1408	74.2709
188	Fourth Lake (Bisby)	43.3415	74.5815

Appendix 1. Continued.

No.	Lake name	Latitude (°N)	Longitude (°W)
189	Grass Pond	43.4135	75.0340
190	Gull Lake (South)	43.5122	74.4915
191	Hawk Pond	43.5725	74.5730
192	Hitchcock Lake	43.5100	75.0230
193	John Pond	44.0645	74.4550
194	Middle South Pond	43.5922	75.0106
195	Nine Corner Lake	43.1145	74.3300
196	North Branch Lake	43.1845	74.4740
197	South Lake	43.3054	74.5332
198	St. John Lake	43.2630	74.0340
199	Trout Lake	43.2048	74.4250
200	Whitney Lake	43.3515	74.3345
201	Wolf Lake	43.3745	74.3915
202	Woodhull Lake	43.3530	74.5913
203	Woods Lake	43.1510	74.1900
204	Mud Pond	43.0739	74.3520
205	Cheney Pond	43.5240	74.0945
206	Fish Pond	43.3250	74.0340
207	Kiwassa Lake	44.1745	74.0930
208	Long Pond	43.3815	74.1720
209	Middle Pond	44.2020	74.2245
210	Mt. Arab Lake	44.1118	74.3603
211	Mud Lake	43.2026	74.2714
212	Nate Pond	43.5130	74.0530
213	Partlow Lake	44.0015	74.5000
214	Trout Lake	44.2147	75.1608
215	Unknown Pond	43.4910	74.1700
216	Wilmurt Lake	43.2545	74.4330
217	Zack Pond	43.5600	74.1100