The distribution of scaled chrysophytes along a pH gradient[1]

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Frequency distributions versus pH and weighted mean pH values are reported for 25 and 40 species of scaled chrysophytes, from water bodies in Connecticut and the Adirondacks, respectively, and are compared with those assembled from a survey of the literature. For most species, similar distributions with respect to a pH gradient and weighted mean pH values were found. However, in Connecticut and Adirondack lakes, *Mallomonas punctifera* and *Synura spinosa* were more restricted to slightly acidic conditions and *M. hamata* was more abundant in conditions below a pH of 5.5. Groups of taxa with similar distributions with respect to pH were clearly defined. One group, consisting of *Mallomonas acaroides* var. *muskokana, M. paludosa, M. pugio, M. canina, M. hindonii, S. sphagnicola*, and *S. echinulata*, was dominant in waters with a pH < 5.5. Another group, including *M. acaroides* var. *acaroides, M. corymbosa, M. tonsurata, M. psuedocoronata*, and *M. alpina*, was primarily restricted to pH values above 6.5. A third group, including *M. punctifera, M. akrokomas, M. crassisquama, M. galeiformis, M. caudata, Spiniferomonas bourrellyi, Sp. serrata, S. spinosa*, and *Chrysosphaerella longispina*, had a significant decline in occurrence as the pH lowered to the 5–5.5 interval. The importance of scaled chrysophytes as a group in the biomonitoring of acid deposition is discussed.

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Les distributions des fréquences versus le pH et les valeurs moyennes pondérées du pH sont rapportées pour 25 et 40 espèces de Chrysophycées écailleuses respectivement, provenant d'étendues d'eau du Connecticut et des Adirondacks, et sont comparées à celles élaborées à partir d'une revue de la littérature. Pour la plupart des espèces, des distributions semblables par rapport au gradient de pH et aux valeurs moyennes pondérées du pH ont été notées. Cependant, dans les lacs du Connecticut et les Adirondacks, les *Mallomonas punctifera* et *Synura spinosa* n'étaient pas restreints aux conditions légèrement acides et le *M. hamata* était plus abondant à un pH de moins de 5,5. Des groupes de taxons ayant des distributions semblables en ce qui concerne le pH était bien définis. Un groupe comprenant les *M. acaroides* var. *muskokana, M. paludosa, M. pugio, M. canina, M. hindonii, S. sphagnicola* et *S. echinulata* était dominant à un pH < 5,5. Un autre groupe incluant le *M. acaroides* var. *acaroides, M. corymbosa, M. tonsurata, M. pseudocoronata* et *M. alpina* était restreint surtout à des valeurs de pH supérieures à 6,5. La présence d'un troisième groupe incluant les *M. punctifera, M. akrokomas, M. crassisquama, M. galeiformis, M. caudata, Spiniferomonas bourrellyi, Sp. serrata, S. spinosa* et *Chrysosphaerella longispina* a accusé un déclin important au cours d'une diminution du pH à l'intervalle de 5 à 5,5. L'auteur discute de l'importance des chrysophycées écailleuses comme groupe indicateur dans le bio-contrôle de l'acidification.

[Traduit par la revue]

Introduction

Practically every sample of freshwater plankton will contain species of scaled chrysophytes, and it is not uncommon to find greater than eight taxa at any one instant in time (Siver 1989*a*). As such, scaled chrysophytes form an integral component of many freshwater ecosystems (Kristiansen 1986; Roijackers and Kessels 1986). Recently, the importance of scaled chrysophytes in the reconstruction of ancient lake-water conditions, especially past pH conditions, has been well documented (Smol 1986; Charles and Smol 1988).

The Chrysophyceae have long been considered to be restricted to cool, oligotrophic waters (Kristiansen and Takahashi 1982). Such a broad statement is no longer considered valid (Kristiansen 1986; Siver and Hamer 1989). Recent evidence clearly indicates that lake-water pH is perhaps the primary factor that controls the distribution of scaled chrysophytes (Smol et al. 1984*a*; Roijackers and Kessels 1986; Kristiansen 1986; Charles and Smol 1988), especially at the species (Siver and Hamer 1989) and even subspecies (Siver 1989*b*) levels.

Much of the data describing the distributions of species with respect to pH comes from paleolimnological investigations where the siliceous remains of species in surface sediments are compared with current lake-water conditions. Many of the pH distributional records for living populations are either qualitative in nature or are scattered throughout the literature; only a few comprehensive studies (e.g., Kristiansen 1975; Takahashi 1978) exist (Kristiansen 1986).

The purpose of this paper is to document the distributions of common taxa of scaled chrysophytes in Connecticut and Adirondack lakes along a pH gradient and to compare the distributions with those constructed from literature records. Unless indicated, all records are based on living populations.

Materials and methods

A total of 332 samples (293 from Connecticut and 39 from the Adirondack Mountains region of New York) from 62 localities (45 from Connecticut and 17 from the Adirondacks) were analyzed with electron microscopy for the presence of taxa of scaled chrysophytes. Methods for the collection and preparation of samples for observation with scanning electron microscopy (SEM) were as described in previous papers (Siver 1987, 1988*a*). All identifications were made using SEM as previously described (Siver 1987). The pH was measured immediately in the field with a Fisher Accumet model 640A meter.

Frequency graphs were prepared to describe the distributions of taxa with respect to a pH gradient and to calculate weighted mean pH values. The pH means were weighted according to the frequency of the organism in each of nine pH intervals using the following equation:

[1]This paper is dedicated to Dr. George Schumacher in honor of his retirement.

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$$pH = \sum_{i=1}^{9} P_i (X_i) / \sum_{i=1}^{9} P_i$$

where pH is weighted mean pH, P_i is frequency of occurrence of the taxon in the *i*th pH interval, and X_i is the pH midpoint of the *i*th interval. The pH intervals were <5, >8.5, and the seven 0.5 gradations between 5 and 8.5. Taxa were assigned to the following pH groupings defined by Hustedt (1939): acidobiontic, organism occurs only in acidic environments and has an optimum distribution at pH values below 5.5; acidophilic, mostly distributed below a pH of 7.0; indifferent, distributed around a pH of 7.0; alkaliphilic, mostly distributed above a pH of 7.0; and, alkalibiontic, organism occurs only at pH values greater than 7.0.

A total of 207 collections surveyed from the literature were also used to analyze the distributions of species along a pH gradient and to calculate weighted mean pH values. Only literature studies where documentation of species was made with electron microscopy and where the presence–absence of the species observed were reported for each collection were used for quantitative purposes. The studies that were utilized in this manner are listed in the Note in Table 1. Where appropriate, weighted mean pH values were also compared with those reported by Charles and Smol (1988) which were based on analysis of surface sediment remains.

Results and discussion

Autecology of selected species

Mallomonas acaroides Perty em. Iwanoff Figs. 1G, 5A, 5B

Recent works have resulted in discrepancies concerning the distribution of *M. acaroides* along a pH gradient. In lakes from the Adirondack mountain region of New York, *M. acaroides* has been reported to be one of the most common taxa, to be acidobionitic in nature, and to have a weighted mean pH of 5.25 (Smol et al. 1984*a*; Charles and Smol 1988). Dixit (1986) and Dixit et al. (1987) observed *M. acaroides* to be most common between a pH range of 5.5 to 6.0. In contrast, other studies have found *M. acaroides* from more alkaline localities (Asmund 1959; Cronberg and Kristiansen 1980; Roijackers and Kessels 1986; Kristiansen 1986). Roijackers and Kessels (1986) reported *M. acaroides* to occur in localities with a mean pH close to 7.5 and placed this taxon into the alkaliphilic–alkalibiontic category.

The discrepancies in the distribution of *M. acaroides* along a pH gradient were of a taxonomic nature (Siver 1989*b*). A new variety, *M. acaroides* var. *muskokana*, recently described by Nicholls (1987), was found to be primarily restricted to acidic waters (Fig. 1G), while *M. acaroides* var. *acaroides* favored alkaline habitats (Fig. 5A) (Siver 1989*b*). The weighted mean pH reported for *M. acaroides* var. *muskokana* of 5.3 was essentially equal to that reported by Charles and Smol (1988) (Table 1). In Connecticut water bodies, samples containing *M. acaroides* var. *acaroides* were found to have a weighted mean pH of 8.1, similar to the 8.4 value calculated from the literature for those reports believed to represent var. *acaroides* (Table 1; Fig. 5B).

Mallomonas akrokomos Ruttner in Pascher Figs. 2C, 2D

Mallomonas akrokomos was found in 26 and 28% of the collections from this study and the literature survey, respectively. *Mallomonas akrokomos* has a rather wide distribution along a pH gradient and is best described as a pH indifferent taxon, although it has a slightly greater occurrence below pH 7 (Figs. 2C, 2D). The weighted mean pH values found in this study, calculated from the literature, and reported by Charles and Smol (1988) were 6.5, 6.7, and 6.6, respectively (Table 1). In Connecticut lakes the occurrence of *M. akrokomos* was maximal between pH 5.5 and 6.0 (45% of the collections) and decreased steadily as the pH increased to 8.0 (Fig. 2C); a similar distribution was observed by Roijackers and Kessels (1986). A wider distribution was found in the literature (Fig. 2D). In all of the studies, the occurrence of *M. akrokomos* dropped significantly at a pH of about 5.5, and live populations of the species have not been recorded in waters below pH 5.3.

Mallomonas canina Kristiansen, *Mallomonas hindonii* Nicholls and *Mallomonas pugio* Bradley

These species are rare and primarily reported from acidic habitats. *Mallomonas canina*, originally described by Kristiansen (1982) from an acidic locality (pH 4.4–4.9), was found three times from Connecticut lakes, each with a pH < 5.0. It has also been found at pH 5.6 (Eloranta 1985) and 4.7 (Siver 1988*a*). Tolonen et al. (1986) reported an increase in the occurrence of *M. canina* in the surface sediments of small Finnish lakes that had become acidified. A similar increase in abundance was found in a small acidic lake in the Bavarian Alps (Hartmann and Steinberg 1986). Thus, based on available data, *M. canina* is acidobiontic.

Since Nicholls (1982) originally described *M. hindonii*, it has only been documented once (at pH 5.4) from live material (Siver 1988*a*). It was found from one Connecticut lake at pH 4.6. In surface sediments from Adirondack lakes, this organism was found to be an acidobiont with an abundance weighted mean pH of 4.9 (Smol et al. 1984*a*; Charles and Smol 1988). In addition, the relative importance of *M. hindonii* has increased in the recent sediments of three clear, acidic lakes (Deep Lake, Smol et al. 1984*b*; Upper Wallface Pond, Christie and Smol 1986; Big Moose, Charles et al. 1987). *Mallomonas hindonii* appears to be lacking from bog habitats (Smol et al. 1984*a*).

Mallomonas pugio, listed by Charles and Smol (1988) as an acidobiontic taxon with an abundance weighted mean pH of 5.25, was also found in very acidic localities in Connecticut lakes. In addition, Hartmann and Steinberg (1986) observed increases of *M. pugio* in recent sediments from a small acidic lake. Jacobsen (1985) reported *M. pugio* in six localities from western Greenland that ranged from pH 5.9 to 7.3. Thus, this organism may have a wider pH tolerance range than either *M. canina* or *M. hindonii*.

Mallomonas caudata Iwanoff em. Krieger Figs. 3E, 3F

Mallomonas caudata was common, found in 27% of the collections surveyed from the literature and in 53% of the samples from Connecticut lakes. This species was found to have a wide distribution along a pH gradient in both the present study (Fig. 3E) and the literature survey (Fig. 3F); in both cases a significant decrease in the occurrence of *M. caudata* below pH 5 was observed and viewed as an indication of increased lake acidity. Since similar weighted mean pH values were found in the present study (6.7), the literature survey (6.6), and the study reported by Charles and Smol (1988) (7.0), this species is best described as pH indifferent (Takahashi 1978) (Table 1).

Several paleolimnological studies have noted recent shifts in dominance from *M. crassisquama* to *M. caudata* that have been attributed to increased nutrient loadings (Munch 1980; Smol et al. 1983; Haworth 1984; Smol and Boucherle 1985).

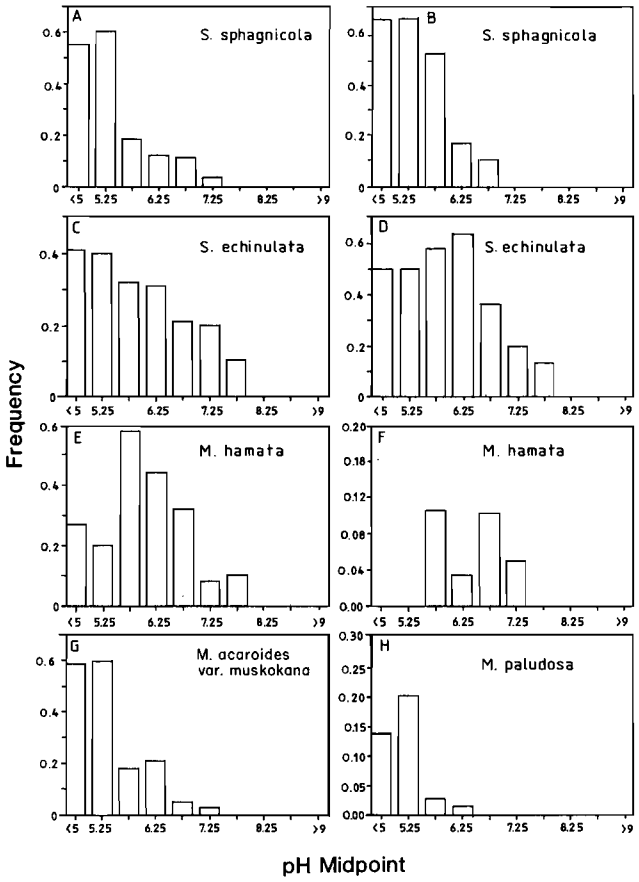

FIG. 1. The frequencies of occurrence along a pH gradient for six common species of scaled chrysophytes. Plots represent results from collections made in water bodies from Connecticut and the Adirondack mountain region of New York (Ct/Ad) or from collections surveyed from the literature. For *S. sphagnicola, S. echinulata*, and *M. hamata*, the left and right graphs represent results from the Ct/Ad and literature survey studies, respectively, while the graphs of *M. acaroides* var. *muskokana* and *M. paludosa* represent data from the Ct/Ad data set only.

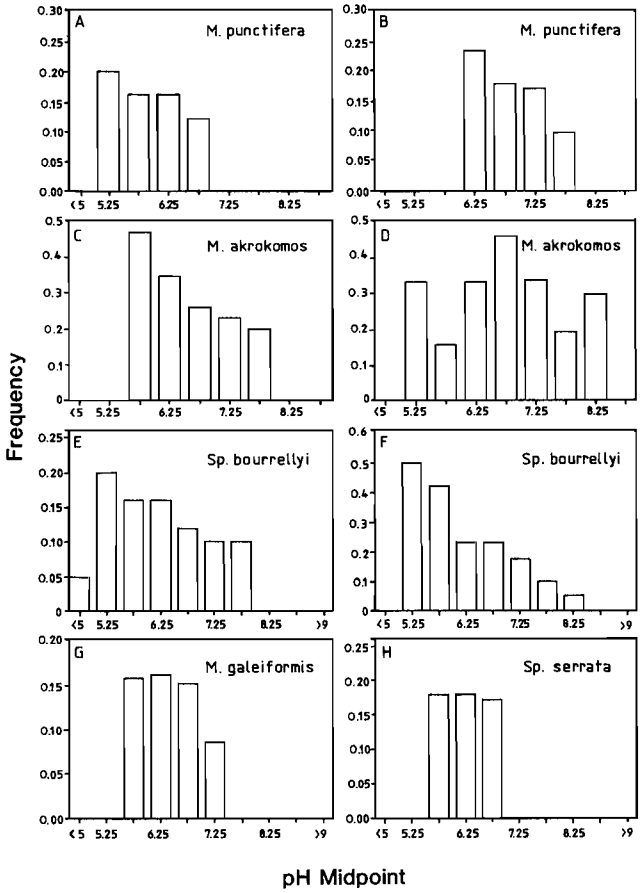

FIG. 2. The frequencies of occurrence along a pH gradient for five common species of scaled chrysophytes. For *M. punctifera, M. akrokomos*, and *Sp. bourrellyi*, the left and right graphs represent results from the Ct/Ad and the literature survey studies, respectively, while graphs of *M. galeiformis* and *Sp. serrata* represent data from the Ct/Ad data set only.

Mallomonas crassisquama (Asmund) Fott Figs. 3C, 3D

Mallomonas crassisquama, one of the most widespread and often encountered species of *Mallomonas*, has been recorded in 30 to 35% of all collections from Connecticut (Siver and Skogstad 1988), Norway (Siver and Skogstad 1988), the Adirondacks (Siver 1988*a*), and the literature (present study). This taxon was found to have a wide tolerance to pH in both the current study (Fig. 3C) and the literature review (Fig. 3D) and weighted mean pH values of 6.9 and 6.6, respectively (Table 1). Charles and Smol (1988) reported a weighted mean pH of 6.4 for *M. crassisquama*. These results are in agreement with those of Roijackers and Kessels (1986) and Dixit (1986) who described *M. crassisquama* as pH indifferent.

One of the most obvious features of the distribution of *M. crassisquama* was its virtual disappearance in water bodies with a pH <5 (Figs. 3C, 3D). Such an absence has been well documented from both living collections (Siver and Skogstad 1988) and the paleo records (Smol et al. 1984*a*; Hartmann and Steinberg 1986; Dixit 1986). The limitation of this species in localities below pH 5 was viewed as an indication of increased lake acidity (Siver and Skogstad 1988).

Mallomonas elongata Reverdin Figs. 5G, 5H

Mallomonas elongata was rare, observed in only 2% of the collections from Connecticut lakes, and reported as 4% in the literature. This organism was found over a pH range of 5.5 to 8.5, however, was lacking from extreme acidic and alkaline environments (Figs. 5G, 5H). *Mallomonas elongata* has often been reported to be more abundant in slightly alkaline waters (Asmund 1959; Asmund and Hilliard 1961; Wujek et al. 1977; Roijackers 1981; Roijackers and Kessels 1981; Smol et al. 1984*a*). The weighted mean pH values for *M. elongata* found in this study, calculated from the literature, and reported by Charles and Smol (1988) were 7.4, 6.8, and 7.0, respectively (Table 1). This taxon is best described as pH indifferent with alkaliphilic tendencies.

Mallomonas galeiformis Nicholls Fig. 2G

With the exception of a recent paper by Siver (1988*b*), no ecological data on living populations exist for *M. galeiformis*, a species recently described by Nicholls (1988). Although initially reported by Smol et al. (1984*a*) and Charles and Smol (1988) as *M. trummensis, M. galeiformis* has been found to be common in the surface sediments of a number of lakes in the Adirondack mountain region (J. P. Smol, personal communication). Siver (1988*b*) found *M. galeiformis* to be a warm-

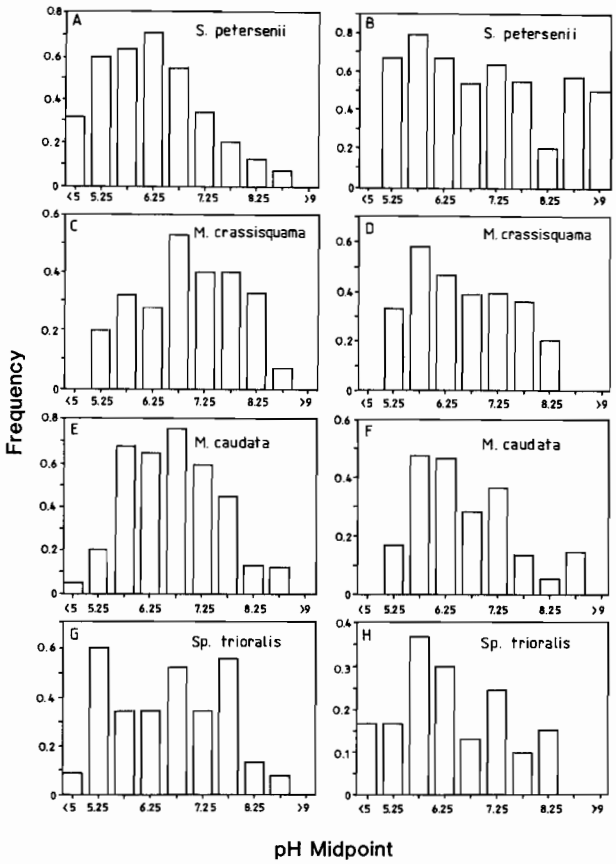

FIG. 3. The frequencies of occurrence along a pH gradient for four common specieis of scaled chrysophytes. Plots represent results from collections made in water bodies from the Ct/Ad study (left-side graphs) and from collections surveyed from the literature (right-side graphs).

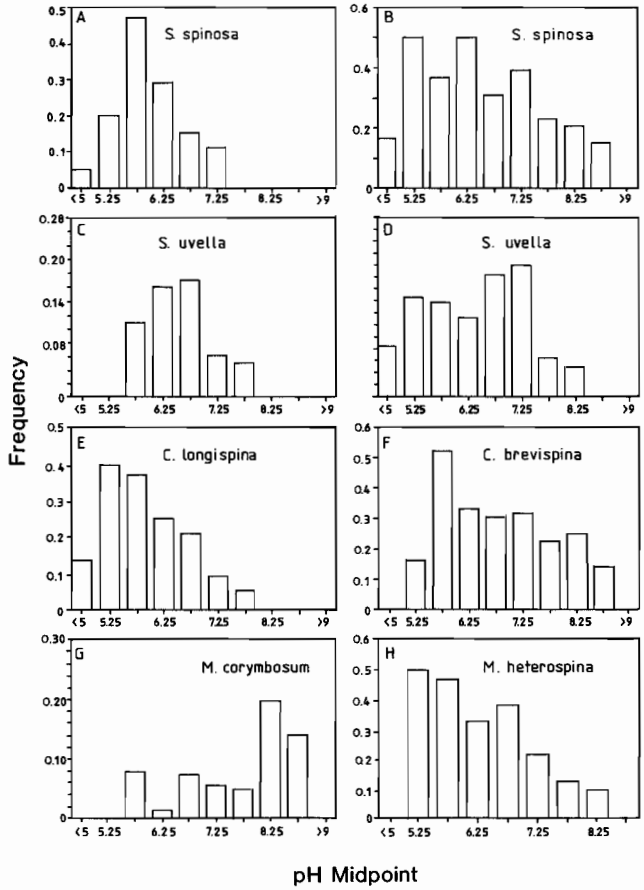

FIG. 4. The frequencies of occurrence along a pH gradient for six common species of scaled chrysophytes. For *S. spinosa* and *S. uvella*, the left and right graphs represent results from the Ct/Ad literature survey studies, respectively. Graphs for *C. longispina*, *M. corymbosa*, and *M. heterospina* represent data from the Ct/Ad set, while the graph for *C. brevispina* represents data from the literature survey data set.

water species that required low specific conductance and slightly acidic conditions. In the present study, *M. galeiformis* had a narrow pH tolerance range of 5.6 to 7.1 (Fig. 2G) and a weighted mean pH of 6.3 (Table 1). An identical weighted mean pH of 6.3 was reported by Charles and Smol (1988).

Mallomonas galeiformis has also been reported (as *M. trummensis*) to have appeared, probably as a transitional species as the pH lowered, and later disappeared in the paleolimnological records of several lakes that are currently very acidic in nature (Christie and Smol 1986). These results support the hypothesis that *M. galeiformis* is an acidophilic organism that forms populations under slightly acidic conditions, but disappears as the pH drops below about 5.6.

Mallomonas hamata Asmund Figs. 1E, 1F

Mallomonas hamata was found to have a maximum frequency of occurrence between pH 5.5 and 6.5, where it was present in approximately 50% of all samples (Fig. 1E). Although it remained in a significant percentage of the collections below pH 5.5, it was rarely reported above pH 7.0 (Fig. 1E). The weighted mean pH was 5.9 (Table 1). Based on initial findings, *M. hamata* is believed to be lacking from localities high in humic content, i.e., bogs (Smol et al. 1984*a*; Dixit 1986; Siver 1988*a*). When the bog lake samples were removed from the current data set, *M. hamata* was found to have a recalculated weighted mean pH of 5.5, close to the 5.4 figure reported by Charles and Smol (1988), and to be present in 50% of the collections below pH 5.5.

Mallomonas hamata is primarily restricted to and most commonly reported from poorly buffered, dilute water bodies that are acidic in nature (Asmund 1959; Nygaard 1979; Green 1979, 1980; Cronberg and Kristiansen 1980; Nicholls 1982; Smol et al. 1984*b*; Dixit 1986; Dixit et al. 1987; Siver 1988*a*). This is especially true in the Adirondacks (Siver 1988*a*; Charles and Smol 1988) and Ontario (Nicholls 1982) where *M. hamata* was found to be one of the most common species. However, *M. hamata* was found in only 4% of the samples from the literature; it was still found primarily below pH 7 (Fig. 1F).

It is concluded that *M. hamata*, best described as an acidobiontic–acidophilous species, is a most valuable indicator of pH. There is initial evidence that *M. hamata* may be particularly sensitive to high levels of trace metals (Dixit 1986), however, more work is necessary to substantiate or refute this finding.

Mallomonas heterospina Lund Fig. 4H

This taxon was found in approximately 50% of all collec-

TABLE 1. The frequency of occurrence, weighted mean pH values, and pH classification for scaled-chrysophyte taxa that are potentially valuable as pH indicator organisms

	Frequency (%)			Weighted mean pH			
	Ct/Ad	Literature survey	Charles and Smol	Ct/Ad	Literature survey	Charles and Smol	Hustedt's classification
Mallomonas							
M. acaroides var. *acaroides*	3	15	—	8.1	8.4	—	AIKB
M. acaroides var. *muskokana*	12	—	70	5.3	—	5.25	ACB
M. akrokomos	26	28	11	6.5	6.7	6.6	IND
M. canina/hindonii	1	1	28	4.9[a]	4.9[a]	4.93	ACB
M. pugio	2	—	15	4.9	—	5.25	ACB
M. caudata	53	27	64	6.7	6.6	7.0	IND
M. crassisquama	30	35	85	6.9	6.6	6.4	IND
M. elongata	2	4	17	6.9	6.8	7.0	IND, ALKF
M. galeiformis	10	—	74	6.3	—	6.3	ACF
M. hamata	27	4	68	5.9	6.4	5.4	ACB, ACF
M. heterospina	7	26	8	6.3	6.3	6.2	ACF
M. pseudocoronata	10	—	26	7.3	—	7.4	AIKF
M. punctifera	8	11	60	5.9	6.8	6.6	IND, ACF
M. tonsurata	16	30	—	7.6	8.1	—	AIKF, AIKB
M. paludosa	2	1	—	5.1[a]	5.1[a]	—	ACB
M. transsylvanica	5	3	23	6.4[a]	6.4[a]	6.6	ACF
M. calceolus	1	12	—	—	6.4	—	ACF
M. allorgei	1	0.5	8	—	—	6.8	ACF
M. alpina	4	13	—	7.7	8.0	—	AIKB
M. corymbosa	5	2	—	7.7	7.0	—	AIKF
M. portae-ferreae	2	—	—	7.1	—	—	AIKF
M. papillosa	3	21	—	6.4	6.6	—	IND
M. annulata	1	12	—	—	6.4	—	IND
M. striata	1	16	—	—	7.8	—	AIKF
Synura							
S. echinulata	15	30	91	6.0	5.9	5.7	ACF, ACB
S. petersenii	36	54	60	6.2	7.0	6.2	IND, ACF
S. sphagnicola	4	15	64	5.3	5.4	5.9	ACB
S. spinosa	17	33	51	6.1	6.5	6.5	ACF, IND
S. uvella	9	14	36	6.6	6.4	6.8	IND
S. curtispina	1	6	13	—	7.1	7.2	IND
Spiniferomonas							
Sp. bilacunosa	12	11	—	6.5	6.6	—	IND
Sp. bourrellyi	10	19	—	6.1	6.1	—	ACF
Sp. coronacircumspina	11	11	—	6.7	6.6	—	IND
Sp. trioralis	33	19	—	6.7	6.8	—	IND
Sp. crucigera	0.5	1	—	5.3[a]	5.3[a]	—	ACB, ACF
Sp. serrata	10	2	—	6.4	6.9	—	ACF
Chrysosphaerella							
C. brevispina	9	28	66[b]	6.2	6.8	6.6[b]	IND, ACF
C. longispina	17	5	66[b]	5.9	6.3	6.6[b]	ACF
Chrysodidymous							
Ch. synuroides	—	2	51	—	6.6	5.5	ACB

NOTES: Data from the Connecticut and Adirondak study (Ct/Ad), the literature survey, and a study by Charles and Smol (1988) are presented (see the text for details). Literature references included Cronberg and Kristiansen (1980), Dürrschmidt (1982), 1984; Eloranta (1985), Green (1979), Gretz et al. (1979, 1983), Kristiansen (1978), Roijackers (1981), Roijackers and Kessels (1981, 1986), Skogstad (1982), Wujek and Hamilton (1972, 1973), and Wujet et al. (1975, 1977). The pH categories according to Hustedt's (1939) system are as follows: ACB, acidobiontic; ACF, acidophilous; IND, pH indifferent; AIKF, aklaliphilous; AIKB, alkalibiontic.

[a]Data for Ct/Ad and literature survey were combined.

[b]Includes both *C. brevispina* and *C. longispina*.

tions from the literature with a pH between 5.0 and 6.0, however, at significantly lower frequencies as the pH increased to 8.5 (Fig. 4H). Unlike other members of the series Heterospinae, *M. heterospina* was clearly absent at a pH < 5.0. The weighted mean pH values calculated in the present study, the literature, and reported by Charles and Smol (1988) were 6.3, 6.3, and 6.2, respectively (Table 1), indicative of an acidophilous species.

Mallomonas heterospina is often reported from eutrophic habitats (Kristiansen 1981, 1986; Smol and Boucherle 1985; Smol et al. 1984*a*). Perhaps its lower occurrence in Connecticut lakes (7%, present study) and Adirondack lakes (8%,

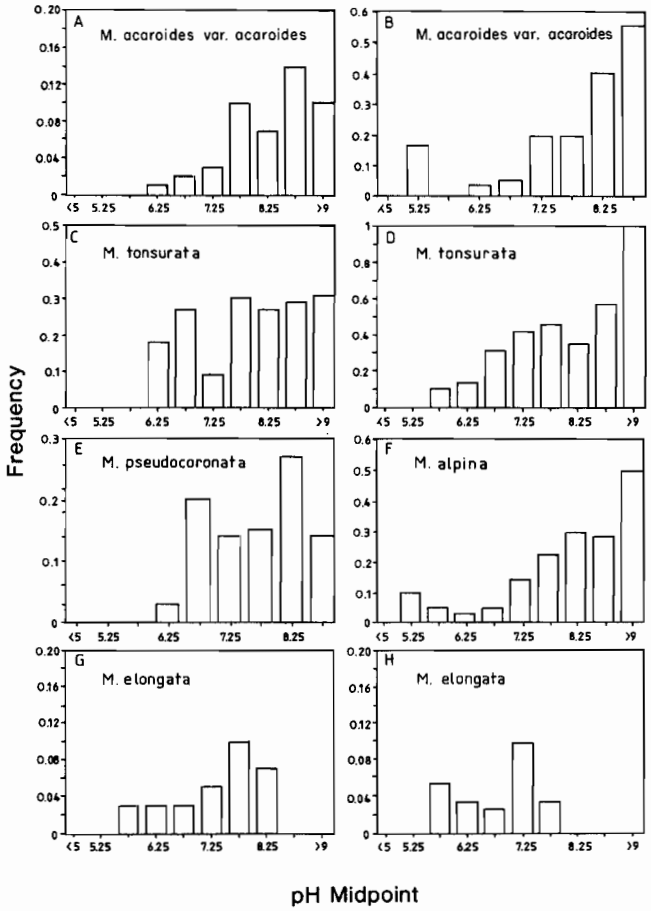

FIG. 5. The frequencies of occurrence along a pH gradient for five common species of scaled chrysophytes. For *M. acaroides* var. *acaroides*, *M. tonsurata*, and *M. elongata* the left and right graphs represent results from the Ct/Ad and literature survey studies, respectively. The graph for *M. pseudocoronata* represents data from the Ct/Ad data set, while the graph for *M. alpina* represents data from the literature survey data set.

Charles and Smol 1988) was due to the smaller percentage of eutrophic water bodies represented in those studies.

Mallomonas pseudocoronata Prescott Fig. 5E

Although recently reported from the sediments of a lake in Europe (Smol 1988), *M. pseudocoronata* is primarily restricted to North American localities.

All available evidence suggests that this taxon is alkaliphilic in nature. The weighted mean pH values reported by Charles and Smol (1988) and found in the present study were 7.37 and 7.25, respectively (Table 1). The bulk of its distribution was found above pH 6.5 and live populations were not recorded in lakes below pH 6.0 (Fig. 5E). This is in agreement with paleolimnological data from the Sudbury area (Dixit 1986) and the few data available from the literature. Therefore, the presence of *M. pseudocoronata* is a clear signal of noncritical levels of hydrogen ions.

Mallomonas punctifera Korsh. Figs. 2A, 2B

In this present study, *M. punctifera* was found over a narrow pH range of 5 to 7, had a weighted mean pH of 5.9, and was distinctly absent from all collections with a pH less than 5.0 (Fig. 2A). A similar pH range (5.2–6.6) was noted by Smol et al. (1984*a*) from the surface sediment of 38 Adirondack lakes.

Although this taxon has not been reported from habitats with a pH greater than 8, Kristiansen (1986) suggested that *M. punctifera* would be expected from a higher pH range than reported by Smol et al. (1984*a*) or found in the current study. This argument is supported by results from the literature survey where *M. punctifera* was found over a pH range of 6 to 8 (Fig. 2B) and had a higher weighted mean pH of 6.8 (Table 1).

Based on initial findings that indicate that *M. punctifera* may be a more acidophilous species in northern New England waters, Charles and Smol (1988) suggested the possibility that perhaps different ecotypes or undescribed varieties exists. Such an idea may be supported, in part, by the fact that in the present study *M. punctifera* was found primarily in warm water, while Roijackers and Kessels (1986) reported this species to favor water temperatures less than 11°C.

Mallomonas tonsurata Teiling em. Kreiger Figs. 5C, 5D

Mallomonas tonsurata is most common in localities with a pH > 7.0 and is rare in soft-water lakes (Figs. 5C, 5D). In the present study, *M. tonsurata* was found in 27% of the collections with a pH of > 7.5 and was absent in all collections with a pH < 6.0 (Fig. 5C). A similar pattern was observed in the literature where *M. tonsurata* was found in 45% of the collections with a pH > 7.5 and in none of the collections with a pH < 5.5 (Fig. 5D). The weighted mean pH calculated from Connecticut localities and from the literature survey were 7.6 and 8.1, respectively (Table 1).

Findings from the present study are in agreement with those of Roijackers and Kessels (1986) who found *M. tonsurata* to have a maximum occurrence above pH 7.0 and classified this species as alkaliphilous. Kristiansen (1986), Smol et al. (1983), and Smol and Boucherle (1985) also observed *M. tonsurata* above pH 8.0.

Other Mallomonas taxa

Mallomonas paludosa Fott is a rare species that appears to be acidobiontic in nature (Péterfi and Momeu 1976; Cronberg and Kristiansen 1980; Kling and Kristiansen 1983; Roijackers and Kessels 1986; Siver 1988*a*). This taxon has not been observed above pH 5.6 (Fig. 1H) and based on all available data has a weighted mean pH of 5.1 (Table 1). *Mallomonas paludosa* has been reported from bog habitats (Péterfi and Momeu 1976; Cronberg and Kristiansen 1980), as well as very clear, acidic lakes (Hartman and Steinberg 1986; Siver 1988*a*).

Mallomonas transsylvanica Péterfi and Momeu and *M. calceolus* Bradley are primarily restricted to a pH range between 5 and 7 and are best classified as acidophilous (Bradley 1964; Kristiansen 1978; Cronberg and Kristiansen 1980; Dürrschmidt 1982; Kling and Kristiansen 1983). In the present study and the literature survey, *M. transsylvanica* had a pH tolerance range of 5.7 to 7.3 and 5.5 to 7.0, respectively. Such a distribution with respect to a pH gradient was similar to its close relative, *M. punctifera*. Thus, initial acidification events may trigger increased numbers of *M. transsylvanica*, however, this species would probably not survive extreme acidification episodes (i.e., those less than 5.0).

Although *M. calceolus*, present in 12% of the collections, was found primarily between pH 5.0 and 7.0, it was reported once at a pH < 5.0 (Roijackers and Kessels 1986) and at a pH as high as 8.8 (Roijackers and Kessels 1981). Hartmann and

Steinberg (1986) found an increase in scales of *M. calceolus* in the recent sediments of a small alpine lake when the water body first began to acidify; it disappeared in recent sediments when the inferred pH dropped below 5.0. Cronberg and Kristiansen (1980) suggested that *M. calceolus* preferred humic conditions.

Mallomonas allorgei (Deflandre) Conrad and *M. lychenensis* Conrad are closely related taxa that are difficult to separate on the basis of isolated scales (Harris and Bradley 1960; Nicholls 1982; Asmund and Kristiansen 1986). As a result, taxonomic overlap most likely exists in the distributional records of these two organisms. Both taxa are rare and primarily reported from slightly acidic habitats (Cronberg and Kristiansen 1980; Smol et al. 1984*a*). *Mallomonas lychenensis* was present in only 4% of the literature collections, had a pH tolerance range from 4.1 (Cronberg and Kristiansen 1980) to 7.0 (Skogstad 1982), and was often found in humic localities (Cronberg and Kristiansen 1980). *Mallomonas allorgei* was rarer than *M. lychenensis*, was most common between pH 6.5 and 7 (Dixit et al. 1987), and had an abundance weighted mean of 6.85 (Charles and Smol 1988). Based on the available records, both *M. allorgei* and *M. lychenensis* are best classifed as acidophilous species.

Mallomonas alpina (Pascher and Ruttner) em. Asmund and Kristiansen, *M. corymbosa* Asmund and Hilliard, and *M. portae-ferreae* Péterfi and Asmund all have weighted mean pH values above 7.0 and are classified as either alkaliphilic or alkalibiontic (Table 1). *Mallomonas alpina*, the most common of the three, had a weighted mean pH of 8.0, the highest of all species surveyed from the literature (Table 1). Even though a few isolated records for *M. alpina* exist below pH 6.5, the vast majority exist at a pH well above 7.0 (Fig. 5F). *Mallomonas alpina* appears to be a true alkalibiontic taxon.

Mallomonas corymbosa and *M. portae-ferreae* had weighted mean pH values of 7.7 and 7.1, respectively, in Connecticut lakes (Table 1) and were more commonly found above pH 7. As such, they are best described as alkaliphilic (Table 1). A recently proposed subspecific taxon, *M. portae-ferreae* var. *reticulata* Gretz, Sommerfeld and Wujek, was also described from an alkaline locality (Gretz et al. 1985).

Mallomonas papillosa Harris and Bradley is a widely distributed species (Kling and Kristiansen 1983) described by Takahashi (1978) as an acidobiont. A variety, *M. papillosa* var. *monilifer* Harris, was suggested to be acidophilous (Hartmann and Steinberg 1986). However, based on the literature survey, *M. papillosa* had a much broader distribution with respect to a pH gradient, ranging from 4.2 (Roijackers and Kessels 1986) to 9.0 (Dürrschmidt 1984). *Mallomonas papillosa* was found in 35% of the collections between pH 6 and 7, yet was still found in over 15% of the collections above and below this range; it had a weighted mean pH of 6.6 and is best classified as pH indifferent (Table 1). It is possible that the discrepancy in the position of this species within Hustedt's pH categories is the result of a real difference at the subspecific level.

Although based on the literature survey *M. annulata* (Bradley) Harris had a weighted mean pH of 6.4, it was reported below pH 5 as often as it was above pH 7.5 (Table 1). It is tentatively classified as pH indifferent. *Mallomonas striata* Asmund, present in 16% of the collections surveyed in the literature, was also widely distributed along a pH gradient from 5.2 (Roijackers and Kessels 1986) to over 9.0 (Kristiansen 1985). Because *M. striata* was much more common above pH 7 and had a weighted mean of 7.8 (Table 1), it is classified as an alkaliphilous species.

Hartmann and Steinberg (1986) suggested that *M. allantoides* Harris (i.e., *Mallomonas clavus* Bradley) and *M. flora* Harris and Bradley were acidobiontic or acidophilic in nature. Takahashi (1978) placed *M. actinoloma* Takahashi into the acidophilous category. Although the distributional records for these three species are few, they support the observations of Hartmann and Steinberg (1986) and Takahashi (1978); none of these species has been found above pH 7.0.

Mallomonas eoa Takahashi was much more tolerant of a pH gradient than originally suggested by Takahashi (1978). *Mallomonas concortica* (Kalina) Péterfi and Momeu and *M. doignonii* Bourrelly em. Asmund and Cronberg are rare species that may have affinities for acidic, possibly humic, localities (Asmund and Cronberg 1979; Péterfi and Momeu 1976; Skogstad 1982; Donaldson and Stein 1983; Roijackers and Kessels 1986).

Synura echinulata Korsh. Figs. 1C, 2D

Although *S. echinulata* has been reported over a wide pH range (e.g., pH 4 to 9; Kristiansen 1975), it is most commonly found in acidic habitats (Takahashi 1967; Wee 1981; Smol et al. 1984*a*, 1984*b*; Roijackers and Kessels 1986; Dixit 1986; Dixit et al. 1987; Siver 1988*a*). *Synura echinulata* had a maximum frequency at all pH intervals below 6.5; its occurrence dropped steadily as the pH increased to the 7.5 to 8.0 pH interval, where it was found in approximately 10% of all collections (Figs. 1C, 1D). Since the weighted mean pH values for *S. echinulata* in this study, calculated from the literature and reported by Charles and Smol (1988), were very similar at 6.0, 5.9, and 5.7, respectively, this taxon is best placed into the acidophilic category (Table 1).

Like *S. sphagnicola, S. echinulata* has been found in both bog and clear-water lakes (Kristiansen 1975; Smol et al. 1984*b*; Siver 1988*a*), in low alkaline waters (Smol et al. 1984*a*; Roijackers and Kessels 1986), and in oligotrophic lakes (Smol 1986). In lakes from the Netherlands, Roijackers and Kessels (1986) found that both *S. sphagnicola* and *S. echinulata* formed a distinct cluster whereby each species easily tolerated habitats with low pH and alkalinity.

Synura petersenii Korsh. Figs. 3A, 3B

In many lake regions *S. petersenii* has been reported as the most frequently encountered species within the genus (e.g., Kristiansen 1975; Wee et al. 1976; Takahashi 1978; Wee 1981; Wujek et al. 1981; Skogstad 1982; Wujek and Weis 1984; Dürrschmidt 1984; Siver 1987); it was recorded in 54% of the collections surveyed from the literature. However, in lake regions with a predominance of poorly buffered water bodies that are low in alkalinity, *S. echinulata* and *S. sphagnicola* were as important as *S. petersenii* (Smol et al. 1984*a*; Nicholls and Gerrath 1985; Dixit 1986; Siver 1988*a*).

Synura petersenii has been found over a very wide pH gradient and reported to be a pH indifferent species (Kristiansen 1975; Takahashi 1978; Roijackers and Kessels 1986; Dixit 1986). This is in agreement with the results from the literature where *S. petersenii* occurred in a large percentage of the collections between pH 5.5 and 9 (Fig. 3B) and had a weighted mean pH of 7.0 (Table 1). However, results from the present study (Fig. 3A) and those of Charles and Smol (1988) suggest that *S. petersenii* is more abundant in water bodies with a pH less than 7 and report a lower weighted mean of 6.2 (Table 1);

S. petersenii had a maximum frequency between 5 and 7 where it was present in over 55% of the collections (Fig. 3A). Similar results were reported by Dixit et al. (1987) who found the highest abundances of *S. petersenii* between pH 6 and 7.

Synura sphagnicola Korsh. Figs. 1A, 1B

Synura sphagnicola is common in and primarily restricted to acidic waters (Takahashi 1967; Wujek and Hamilton 1972; Kristiansen 1975; Green 1979; Takahashi 1978; Smol et al. 1984*a*; Roijackers and Kessels 1986; Dixit 1986; Siver 1988*a*). In the present study (Fig. 1A) and the literature survey (Fig. 1B), *S. sphagnicola* was found in over 55% of all collections with a pH less than 5.5 and its frequency of occurrence diminished rapidly above pH 6.0. The weighted mean pH values for *S. sphagnicola* reported by Charles and Smol (1988), found in the present study, and calculated from the literature, were 5.9, 5.3, and 5.4, respectively (Table 1). Based on all available data, *S. sphagnicola* is best classified as acidobiontic and represents an excellent biological indicator for pH.

Synura sphagnicola has been reported to be common in both clear and humic stained (bog) acid lakes (Dürrschmidt 1980; Kristiansen 1981; Smol et al. 1984*a*; Roijackers and Kessels 1986; Dixit 1986; Siver 1987, 1988*a*) and to be restricted to water bodies with low alkalinity (Roijackers and Kessels 1986; Siver 1988*a*).

Dixit (1986) believed that since *S. sphagnicola* was more common in humic stained as opposed to clear water bodies it could potentially be used to elucidate historical changes in lake-water acidity resulting from organic versus mineral acids.

Synura spinosa Korsh. Figs. 4A, 4B

Most studies indicate that *S. spinosa* is usually found above pH 6 and is very rare in localities with a pH < 5. *Synura spinosa* was reported to occur mainly between pH 6 and 8 (Kristiansen 1975) and to be pH indifferent (Takahashi 1978). Roijackers and Kessels (1986) found this species to have a maximum abundance between pH 6 and 7 and to be less tolerant at pH levels below 5. In this survey, *S. spinosa* had a maximum frequency of occurrence between pH 5.5 and 6.5 (Fig. 4A). However, a much wider pH tolerance range with a maximum from 5.0 to 7.5 was observed from the literature survey (Fig. 4B). In both data sets a significant decrease in abundance occurred in collections with a pH < 5.0 (Figs. 4A, 4B).

The weighted mean pH values for *S. spinosa* reported by Charles and Smol (1988) and the present study, and calculated from the literature were 6.54, 6.14, and 6.5, respectively (Table 1). Because this taxon has a maximum development between pH 5 and 7, yet is very rare below pH 5 and has been found at pH values greater than 8.5 (Kristiansen 1986), it is difficult to place it into one of Hustedt's categories; it is probably best described as acidophilous with a tendency towards being pH indifferent.

Synura uvella Stein em. Korsh. Figs. 4C, 4D

The frequency of maximum occurrence for *S. uvella* in the present study was found to be between pH 6 and 7 (Fig. 4C), however, at a slightly higher interval, pH 6.5 to 7.5, based on data from the literature (Fig. 4D). Like *S. spinosa*, the importance of *S. uvella* is greatly reduced above pH 7.5 as well as below pH 5 (Figs. 4D). If the data from the present study and the literature are combined, *S. uvella* was found in only 1 of the 47 collections below pH 5.5 and in 4 of the 109 collections above pH 7.5. This is not in agreement with the study by Kristiansen (1975) who found *S. uvella* to occur often at a pH of 7 to 8.

The weighted mean pH values for *S. uvella* reported by Charles and Smol (1988), found in the present study, and calculated from the literature, were 6.8, 6.6, and 6.4, respectively (Table 1). These values are in agreement with the study by Roijackers and Kessels (1986). Since the distribution of this taxon is centered around pH 7, it is best classified as a pH indifferent species. Like *S. spinosa*, the presence of *S. uvella* in a sample from a poorly buffered lake will most likely indicate pH values above 5.5.

Other Synura taxa

There are a number of rarer species of *Synura* that are noteworthy as potential indicators of pH. *Synura curtispina* (Petersen and Hansen) Asmund and *S. mollispina* (Petersen and Hansen) Péterfi and Momeu both originally described as forms of *S. spinosa*, were found in only 6 and 2%, respectively, of the collections surveyed from the literature. *Synura curtispina* appears to be a pH indifferent taxon with weighted mean pH values of 7.05 (literature) and 7.19 (Charles and Smol 1988) (Table 1). *Synura mollispina* also appears to be more abundant at a pH near or above 7, however, too few data were available to make an accurate assignment of its distribution along a pH gradient.

Synura mammillosa Takahashi has body and posterior scales that are morphologically very similar to and difficult to distinguish from *S. echinulata* (Takahashi 1978). Because Takahashi (1978) reported *S. mammillosa* as being acidobiontic and Roijackers and Kessels (1986) found it at pH levels of 4.4, 4.7, and 5.6, it is a potentially valuable indicator; its value depends on its absolute occurrence and the abilities of researchers to distinguish it from *S. echinulata*. *Synura macracantha* (Petersen and Hansen) Asmund is another taxon that may have affinities for low acidic localities (Charles and Smol 1988), however, it is rarely reported in the literature.

Spiniferomonas bilacunosa Takahashi

Spiniferomonas bilacunosa has been recorded in habitats with a pH as low as 5.3 (Green 1979) and as high as 8.2 (Skogstad 1982). In the present study it had a maximum occurrence (31%) between pH 6.5 and 7.0. The weighted mean pH values reported by Siver (1988*a*) and calculated from the literature were 6.5 and 6.6, respectively, and the species is classified as pH indifferent (Table 1). The presence of *Sp. bilacunosa*, primarily a warmwater species (Siver 1988*c*), will signal pH conditions above 5.0 and more likely above 5.5.

Spiniferomonas bourrellyi Takahashi Figs. 2E, 2F

Spiniferomonas bourrellyi was as common in the collections surveyed from the literature as *Sp. trioralis* (Table 1). In both the current study and lakes surveyed from the literature, *Sp. bourrellyi* had a maximum frequency of occurrence between pH 5 and 6 (Figs. 2E, 2F), a weighted mean pH of 6.1 (Table 1), and was rare below pH 5.0. It was found in 45% of all collections from the literature survey that were between pH 5 and 6. As a result, this species is best classified as acidophilous.

Spiniferomonas bourrellyi has a wide temperature range, however, it is more common in localities low in total phosphorus and specific conductance and slightly humic in nature

(Siver 1988*c*). As such, it would be expected to be a common member of floras in lakes from poorly buffered regions, provided the pH was above 5.0.

Spiniferomonas coronacircumspina (Wujek and Kristiansen) Nicholls

Spiniferomonas coronacircumspina, reported in 11% of the collections surveyed from the literature review (Table 1), has been found at pH values as low as 4.6 (Siver 1988*a*) and as high as 8.6 (Skogstad 1982). In the present study it had a maximum occurrence in the 5 to 5.5 pH interval where it was found in 33% (literature survey) and 20% (Connecticut and Adirondack lakes) of all collections; however, it was still present in over 10% of the samples above pH 8.0. In addition, Siver (1988*a*) found this organism as the dominant species in a small, clear, acidic (pH = 4.6) lake during midsummer. Since *Sp. coronacircumspina* has a weighted mean pH of 6.6 and is clearly distributed over a wide pH gradient, it is best described as a pH indifferent species (Table 1).

Spiniferomonas trioralis Takahashi Figs. 3G, 3H

Spiniferomonas trioralis, considered to be the most common species in the genus (Takahashi 1973; Wujek et al. 1975; Gretz et al. 1979; K. H. Nicholls 1981; Wee 1982; Skogstad 1986; Siver 1988*c*), was found in 33, 19, and over 40% of the collections from the present study, the literature survey, and Ontario (Nicholls 1981), respectively (Table 1).

Spiniferomonas trioralis has been recorded from localities with a pH < 5 (Eloranta 1985; and Roijackers and Kessels 1986) as well as in ones with a pH > 8 (Wujek et al. 1975; Dürrschmidt 1984; Kristiansen 1985). In the present study it was found to be common above pH 7 and had a weighted mean pH of 6.6 (Figs. 3G, 3H; Table 1). Thus, although Takahashi (1978) reported this species as acidophilous, it is more appropriately classified as pH indifferent. The idea that *Sp. trioralis* is restricted to eutrophic waters (Stoermer and Sicko-Goad 1977) is no longer considered valid (Nicholls 1981; Siver 1988*a*).

Other Spiniferomonas taxa

Spiniferomonas crucigera Takahashi is a rare species that has been reported only once from North America (Siver 1988*c*). Based on available records (n = 7), *Sp. crucigera* is restricted to soft-water, acidic habitats with a pH tolerance range of 4.8 to 6.7 (Kristiansen 1978; Ito and Takahashi 1982; Eloranta 1985; Siver 1988*a*) and has a weighted mean pH of 5.3 (Table 1).

Spiniferomonas serrata Nicholls is another relatively rare taxon with affinities for primarily soft-water habitats (Nicholls 1981; Kling and Kristiansen 1983; Siver 1988*c*). In Connecticut and Adirondack water bodies, *Sp. serrata* was restricted to a pH range of 5.6 to 6.9 (Fig. 2H) and had a weighted mean pH of 6.2 (Table 1). Based on this initial data, *Sp. serrata* appears to be acidophilous, however, it has been found at a pH of 7.8 (Skogstad 1982).

Spiniferomonas abei Takahashi, suggested by Nicholls (1981) to have affinities for acidic habitats, has been reported primarily at pH levels below 7 (Kristiansen 1978; Skogstad 1982; Ito and Takahashi 1982; Roijackers and Kessels 1986). However, it has also been observed in localities from southern Chile (Dürrschmidt 1982) and western Greenland (Jacobsen 1985) at or above pH 7.7.

In the literature review *Sp. cornuta* Balonov was distributed over a pH gradient of 5.4 to 8.0 (Roijackers and Kessels 1981; M. Nicholls 1981; Skogstad 1982; Roijackers and Kessels 1986; Siver 1988*c*).

Chrysosphaerella brevispina Fig. 4F

In the literature survey, *C. brevispina*, found in 28% of the collections, was much more common and had a broader distribution along a pH gradient than *C. longispina* (Figs. 4E, 4F) (Kristiansen 1981; Kling and Kristiansen 1983). On the other hand, *C. brevispina* was much rarer than *C. longispina* in soft-water habitats (Smol et al. 1984*a*; Dixit 1986; Siver 1988*a*).

Based on the literature review, the distribution of *C. brevispina* was similar on each side of pH 7 and it had a weighted mean pH of 6.8 (Table 1). Thus, *C. brevispina* should be classified as pH indifferent. In Connecticut water bodies, however, *C. brevispina* was more abundant in acidic localities and had a weighted mean pH of 6.2 (Table 1).

Chrysosphaerella longispina Fig. 4F

Chrysosphaerella longispina has most often been encountered in soft-water, oligotrophic localities that were acidic in nature (Péterfi 1967; Cronberg and Kristiansen 1980; Kling and Kristiansen 1983; Dixit 1986). In the literature survey, *C. longispina* was rare, present in only 5% of the collections; however, this species was quite common in lakes in the Adirondack Mountains where it was observed in 47 (Siver 1988*a*) and 60% (Charles and Smol 1988) of the study localities, respectively (Table 1). In the present study, *C. longispina* had a peak occurrence at pH 5 to 6 and decreased steadily as the pH increased to above 6 (Fig. 4E); this taxon was rare in water bodies with a pH above 7.5 and below 5.0. A similar distribution was reported for *C. longispina* in lakes from Romania (Péterfi 1967), Sweden (Cronberg and Kristiansen 1980), Canada (Dixit 1986), and Finland (P. Eloranta, personal communication). Since the weighted mean pH values for *C. longispina* were 5.9 (present study) and 6.3 (literature review) and the organism is primarily distributed below 7, it should be classified as acidophilous. This is in agreement with the results of Takahashi (1978) and Dixit (1986).

Conclusions

It is clear that many species of scaled chrysophytes have distinct patterns of distribution with repsect to pH and that most can be placed into one of the pH categories described by Hustedt (Table 1). For most of the taxa, frequency distributions and weighted mean pH values reported in the present study were similar to those assembled from the literature (live populations) as well as ones reported from paleolimnological investigations. Groups of taxa are easily identified on each end of a pH gradient representing natural conditions. *Mallomonas acaroides* var. *muskokana*, *M. canina*, *M. hindonii*, *M. pugio*, *M. paludosa*, *S. echinulata*, *S. sphagnicola*, and perhaps *M. hamata* form a distinct group found primarily in acidic waters. With further research, additional species such as *Sp. crucigera* may be added to this group. On the other end of the pH gradient, *M. corymbosa*, *M. tonsurata*, *M. alpina*, *M. acaroides* var. *acaroides*, and *M. pseudocoronata* were all characteristic of higher pH conditions, had weighted mean pH values above 7.0, and were rarely reported below pH 6.5. There is another group of taxa that are acidophilic or pH indifferent in nature, yet clearly disappear between pH 5 and 5.5. Species in this group, transitional taxa in sensu Smol (1986), include *M. punctifera*, *M. akrokomos*, *M. galeiformis*, *M. crassisquama*, *M. caudata*, *S. spinosa*, *S. uvella*,

Sp. bourrellyi, Sp. serrata, and *C. longispina*. With further research additional taxa will inevitably be placed into this group. As with *Mallomonas acaroides* var. *muskokana* (Siver 1989*b*) and *M. galeiformis* (Siver 1988*b*), refinement of the distributions with respect to pH of some taxa will depend on refinements in their taxonomy.

As indicated in previous research (Smol et al. 1984; Charles and Smol 1988; Christie and Smol 1986), it is clear that scaled chrysophytes represent a valuable tool for indicating changes in lake-water pH. The use of scaled chrysophytes in reconstructing historical pH conditions has been successful (Charles and Smol 1988). Since similar distributions for most taxa, based on live populations, were found in the present study, it is reasonable to conclude that live scaled chrysophytes would also be an effective tool in studying episodic events (e.g., spring snowmelt) and the effects of liming, and in long-term biomonitoring programs. Smol (1986) concluded that even though the Mallomonadaceae were perhaps more sensitive to pH changes than diatoms, they were a "relatively unexplored" group. The results of the present study will allow for a greater utilization of scaled chrysophytes in biomonitoring projects.

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