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WISCONSIN DESMIDS. III. DESMID COMMUNITY COMPOSITION AND DISTRIBUTION IN RELATION TO LAKE TYPE AND WATER CHEMISTRY

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Abstract

This investigation summarizes quantitative data on the generic composition of the euplankton and aufwuchs desmid communities of 61 Wisconsin lakes, and analyzes the information with respect to 1) the role of the various genera in terms of frequency, density, and relative importance, 2) the suitability of various lake types for harboring desmid communities, and 3) the relationships between chemical parameters and desmid distribution. The genera *Staurastrum, Cosmarium,* and *Closterium* are of wide occurrence, appear to play major roles in the communities of all lake types, and are the most tolerant of varying chemical conditions. Most euplankton genera are of importance only in acid bogs, but aufwuchs genera generally are more widely distributed. Both the euplankton and the aufwuchs communities appear to be composed of 1-4 desmid assemblages, each with a differing range of importance values. Based on biological criteria, acid bogs appear to be the most suitable lake type for harboring desmid communities and calcareous spring ponds the least suitable type. High generic diversity of desmids appears to be correlated with low conductivity, calcium and alkalinity levels, pH values of 5.1-7.0, and the presence of free CO_2. The evidence attending various hypotheses concerning water chemistry and desmid distribution appears contradictory, and further studies are needed to help clarify the situation.

Previous articles in this series have considered the role of desmids (Desmidiales, Chlorophyta) as a group in the euplankton and aufwuchs communities of selected acid bog lakes, alkaline bog lakes, and closed bogs (Woelkerling 1976), and of selected soft water lakes, hard water lakes, and calcareous spring ponds (Cough & Woelkerling, 1976) in Wisconsin. Although qualitative data on the occurrence of the various desmid genera has been included for the 61 study sites encompassed by these investigations, other aspects of desmid community composition and distribution have yet to be considered. This paper summarizes quantitative information on the generic composition of the euplankton and aufwuchs desmid communities in selected Wisconsin lakes and analyzes the data with respect to the role of the various genera in terms of frequency, density, and relative importance, the suitability of various lake types for harboring desmid communities, and the relationships between chemical parameters and desmid occurrences. The significance of these results is also considered in connection with current hypotheses concerning water chemistry and desmid distribution.

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Materials and Methods

The data presented here have been gathered during the course of summer studies on the 61 Wisconsin lakes (Fig. 1) discussed in the first two parts of this series. Geographical, chemical, and biological information for these localities is summarized in the tables of those papers, and the methods utilized in gathering, processing, and analyzing the data already have been outlined elsewhere (Woelkerling, 1976). In addition to the above mentioned data, detailed quantitative records (based on Sedgwick-Rafter cell analyses) have been kept on the generic composition of the desmid component of both the euplankton community and the aufwuchs communities associated with the various macrophytes at each locality. These data are summarized in Tables 1 and 6 in the present study.

The relative importance of a particular genus in lakes of a given type has been assessed by determining importance values using the formula

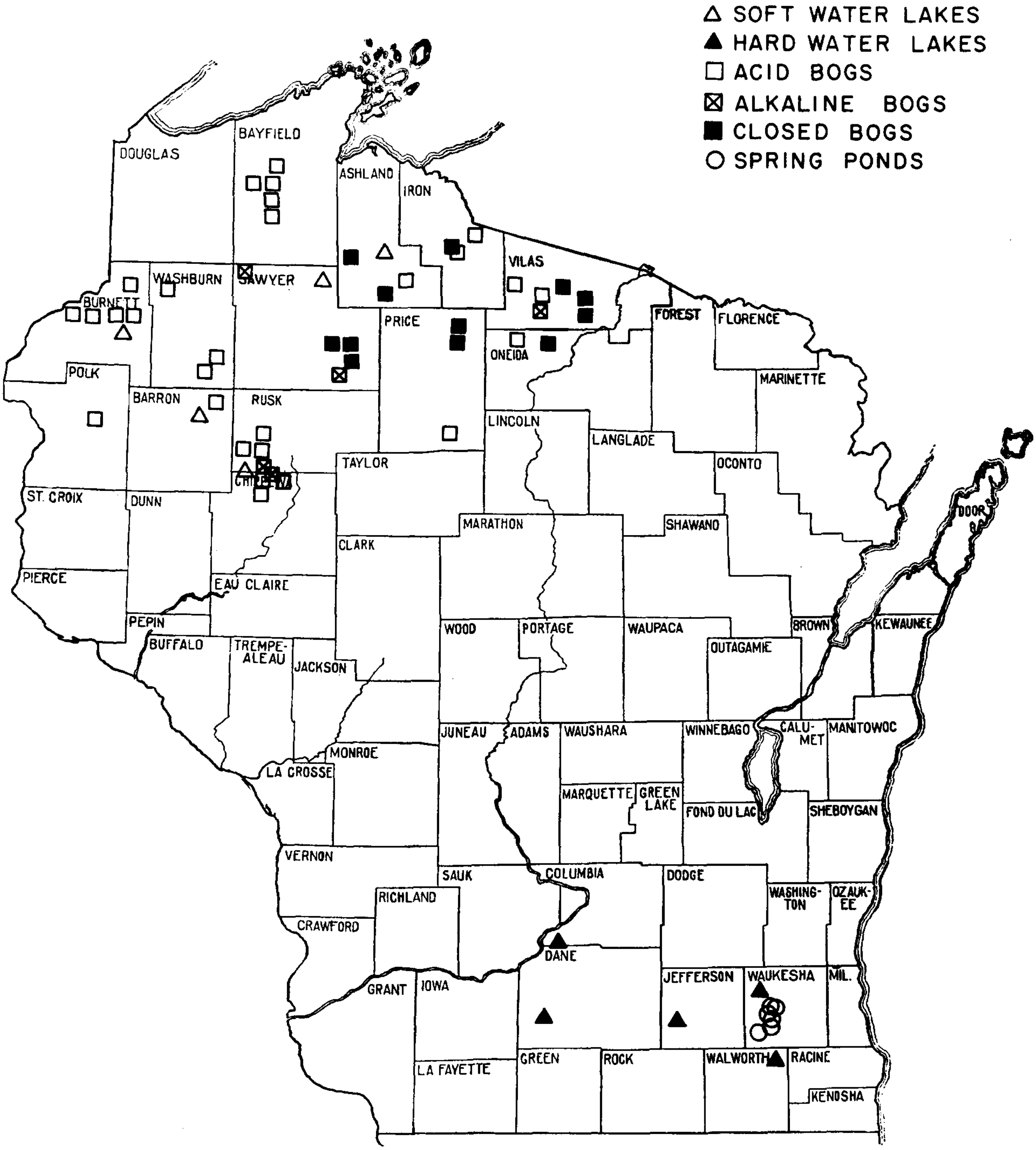

Fig. 1. Location of Study Sites within Wisconsin.

$$\text{(1)} \quad I.V. = (3F_A + 2RD_R + RD_U)/6$$

where I.V. is the importance value in units, F_A is the absolute frequency of the genus in a given lake type, RD_R is the mean relative density of the genus in those lakes where it occurs, and RD_U is the mean relative density in all lakes of the type in question. Absolute frequencies are defined by the formula

$$\text{(2)} \quad F_A = (A/B)100$$

where F_A is the absolute frequency as a percentage, A is the number of lakes in which a taxon occurs, and B is the total number of lakes under consideration. The ratio A/B is multiplied by 100 to express F_A as a percentage. Relative density is defined by the formula

$$(3)\quad RD = (C/D)100$$

where RD is the relative density as a percentage, C is the mean population density, and D is the mean total desmid population density. I.V. values range from 0-100; the higher the reading, the greater is the apparent importance of the taxon.

The formula for I.V. has been derived on the rationale that F_A is the most important criterion since it summarizes presence/absence data. Such data are considered more reliable (in terms of importance) than standing crop determinations from which RD_R and RD_U values are calculated. The RD_R value, in turn, is given more weight than the RD_U value since the former provides a better indication of the relative role of the taxon in those lakes where it occurs. The RD_U values have been included to insure some measurement of all localities of a given type and to reduce emphasis of taxa with prominent populations in only one or several of the total number of lakes of a given type.

Relative frequencies (F_R) have been employed in comparing the importance of a particular genus from one lake type to another and are defined by the formula

$$(4)\quad F_R = (G/H)100$$

where F_R is relative frequency as a percentage, G is het number of lakes in which a particular desmid occurs, and H is the total number of occurrences of all desmid taxa in those lakes. Higher F_R values indicate greater apparent importance than lower F_R values.

Absolute frequencies (Formula 2) have been employed in assessing the potential of particular taxa to occur in and to be restricted to lakes of a given type. Special attention has been paid to those genera present in acid bog lakes and absent in one or more of the other lake types.

Four biological criteria have been utilized to help assess the suitability of a particular lake type for harboring desmid communities. These include:

A. The mean absolute density of the total desmid population (i.e. $AD_M = \Sigma T/N$ where AD_M is the absolute mean density, ΣT is the total desmid population density for all localities, and N is the number of localities) for lakes of the type in question;
B. The total number of desmid genera present in lakes of type in question;
C. The number of desmid 'assemblage orders' present in lakes of the type in question; and
D. The number of genera present in each assemblage order.

In general, higher numerical values for each of these criteria mean a greater apparent suitability for harboring desmids. The first two criteria are self-explanatory; the latter two represent an outgrowth of a hypothesis on desmid community structure (based on importance values) which is outlined below in the discussion on euplankton community composition.

The overall suitability of a lake type has been assessed by assigning ranks to each of the lakes for each of the above four criteria. The highest value of a given criterion received a rank of 1, the next highest 2, etc. Tied values received rank numbers equal to $^1/_2$, $^1/_3$, etc. the sum of the relevant integers. (For further details on assigning rank numbers, consult Wilcoxon & Wilcox, 1964). The sum of the rank numbers for all criteria then represents an index of a lake type's suitability for harboring desmids; the lower the rank number total, the greater is the suitability of the lake type. Results of the suitability analyses are summarized in Table 5 and Table 10.

Results and Discussion

Euplankton Community Composition

Of the nineteen desmid genera encountered in the euplankton (Table 1), *Staurastrum* is by far the most widely distributed, and it assumes primary quantitative importance more frequently than any other desmid genus. Taxa of *Staurastrum* occurred in 36 of the 49 euplankton communities analyzed (the 12 closed bogs lack open water by definition). It was the only genus recorded from the plankton of calcareous spring ponds and hard water lakes and was the sole desmid genus present in the plankton of 3 of the five soft water lakes. It contributed at least 25% to the total desmid population in the five alkaline bogs and accounted for over 80% of the total in three of those localities. Among the 28 acid bogs studied, *Staurastrum* occurred in 24 cases, accounted for at least 50.0% of the total desmid population in 10 localities, and contributed 25.0% or more to the total desmid population in 18 plankton communities.

Six other desmid genera occurred in 12 or more of the 49 plankton communities. Of these, *Xanthidium* was restricted to acid bog lakes, *Arthrodesmus* and *Bambusina* appeared only in acid bogs and alkaline bogs, *Closterium* and *Desmidium* occurred only in acid bogs and soft

Table 1. The percentage composition of the euplankton desmid populations at the study sites.

Data expressed as % of the total desmid population in column 3.

Locality	Lake Type	Total Desmid Population Density (# organisms/ ml)	Taxon: Arthrodesmus	Bambusina	Closterium	Cosmarium	Desmidium	Euastrum	Gonatozygon	Hyalotheca	Micrasterias	Netrium	Penium	Phymatodocis	Pleurotaenium	Sphaerozosma	Spondylosium	Staurastrum	Tetmemorus	Triploceras	Xanthidium
A	Spring Pond	5.30×10^{-1}	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	100.0	--	--	--
B	" "	Absent	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--
C	" "	Absent	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--
D	" "	Absent	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--
E	" "	Absent	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--
F	" "	Absent	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--
Beulah	Hard Water	Absent	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--
Brunner's	" "	Absent	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--
Fish	" "	2.0×10^{0}	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	100.0	--	--	--
Fowler	" "	Absent	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--
Ripley	" "	3.0×10^{0}	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	100.0	--	--	--
Ike	Soft Water	2.30×10^{1}	--	--	12.5	50.0	--	--	--	--	--	--	--	--	--	--	--	37.5	--	--	--
Pine	" "	1.62×10^{1}	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	100.0	--	--	--
Zielke	" "	1.74×10^{1}	--	--	--	--	--	--	--	--	--	--	-	--	--	--	--	100.0	--	--	--
15-12	" "	1.25×10^{1}	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	100.0	--	--	--
20-12A	" "	1.53×10^{1}	--	--	--	--	100.0	--	--	--	--	--	--	--	--	--	--	--	--	--	--

Table 1 continued

Locality	Lake Type	Total Desmid Population Density (# organisms/ ml)	Arthrodesmus	Bambusina	Closterium	Cosmarium	Desmidium	Euastrum	Gonatozygon	Hyalotheca	Micrasterias	Netrium	Penium	Phymatodocis	Pleurotaenium	Sphaerozosma	Spondylosium	Staurastrum	Tetmemorus	Triploceras	Xanthidium
26-9	Acid Bog	$1.07x10^0$	40.0	--	20.0	--	--	--	--	--	20.0	--	--	--	--	--	--	20.0	--	--	--
13-2d	" "	$1.36x10^1$	--	--	1.6	3.1	6.3	1.6	23.4	12.5	1.6	3.1	--	--	1.6	1.5	--	43.7	--	--	--
11-5	" "	$1.63x10^{-1}$	100.0	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--
Evelyn	" "	$4.08x10^{-1}$	--	--	100.0	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--
Unnamed (Price)	" "	$5.10x10^0$	--	--	4.2	25.0	4.2	--	--	--	--	--	--	--	4.2	--	--	41.6	--	--	20.8
Round	" "	$2.74x10^2$	37.3	--	--	--	--	--	--	--	--	--	--	--	--	--	--	62.7	--	--	--
Saxton	" "	$1.46x10^1$	--	--	--	--	--	2.3	--	--	--	--	--	--	--	--	--	97.7	--	--	--
School	" "	$1.04x10^1$	49.2	--	--	--	--	--	--	--	--	--	--	--	--	--	--	50.8	--	--	--
Spruce	" "	$2.39x10^0$	12.5	--	--	--	--	--	--	--	--	--	--	--	--	--	--	68.7	--	18.8	--
Unnamed (Vilas)	" "	$5.10x10^{-1}$	--	16.7	--	--	--	--	--	50.0	--	--	--	--	--	--	--	33.3	--	--	--
Washburn:																					
Unnamed-1	" "	$3.14x10^0$	5.4	5.4	5.9	21.6	2.7	10.8	--	--	--	2.7	--	--	--	2.7	--	35.2	--	--	8.1
Unnamed-2	" "	$2.69x10^1$	3.2	25.4	--	4.8	12.7	4.8	--	9.5	--	1.6	1.6	--	1.6	--	1.6	31.6	--	--	1.6
Unnamed-3	" "	$1.96x10^0$	8.7	4.3	4.3	4.3	17.4	--	--	13.0	--	4.3	--	--	4.3	--	--	30.8	--	4.3	4.3
Bog	Alkaline Bog	$4.76x10^0$	14.3	--	--	--	--	--	--	--	--	--	--	--	--	--	--	85.7	--	--	--
Bullhead	" "	$1.02x10^0$	33.3	--	--	33.4	--	--	--	--	--	--	--	--	--	--	--	33.3	--	--	--
Cedar	" "	$2.10x10^0$	--	--	--	75.0	--	--	--	--	--	--	--	--	--	--	--	25.0	--	--	--
Hegmeister	" "	$1.02x10^0$	--	16.7	--	--	--	--	--	--	--	--	--	--	--	--	--	83.3	--	--	--
Mystery	" "	$5.1x10^{-1}$	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	100.0	--	--	--

Table 1 continued

Locality	Lake Type	Total Desmid Population Density (# organisms/ml)	Taxon: Arthrodesmus	Bambusina	Closterium	Cosmarium	Desmidium	Euastrum	Gonatozygon	Hyalotheca	Micrasterias	Netrium	Penium	Phymatodocis	Pleurotaenium	Sphaerozosma	Spondylosium	Staurastrum	Tetmemorus	Triploceras	Xanthidium
Trout	Acid Bog	$8.16x10^{-2}$	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	100.0
7-9d	" "	$5.95x10^{1}$	--	0.7	13.7	--	82.0	--	--	1.4	--	--	--	--	--	--	--	2.2	--	--	--
17-5	" "	$1.18x10^{0}$	14.3	--	7.1	14.3	14.3	--	--	--	35.8	7.1	--	--	--	--	--	--	--	--	7.1
7-2	" "	$1.97x10^{0}$	18.1	--	--	27.3	--	--	--	9.1	--	--	--	--	--	--	--	27.3	--	9.1	9.1
33-14(Bayfield)	" "	$1.42x10^{1}$	3.0	6.0	--	17.9	11.9	4.5	--	--	--	1.5	--	--	--	--	--	55.2	--	--	--
1-16c	" "	$1.10x10^{0}$	--	7.7	--	--	--	--	--	--	--	7.7	--	--	--	--	--	76.9	--	--	7.7
6-10d	" "	$7.65x10^{0}$	--	5.6	13.9	13.9	52.6	2.8	--	--	--	--	--	2.8	--	2.8	--	5.6	--	--	--
9-2	" "	$4.41x10^{1}$	4.8	2.4	1.2	6.0	14.3	2.4	--	--	4.8	--	--	--	--	--	--	53.4	--	--	10.7
10-6	" "	$1.74x10^{1}$	5.9	--	2.9	14.7	32.4	8.8	--	--	--	--	--	--	--	--	--	23.5	--	--	11.8
16-2	" "	$1.19x10^{1}$	3.6	7.2	--	17.6	3.6	--	--	3.6	--	--	--	--	--	7.2	--	50.0	--	--	--
17-4	" "	$1.60x10^{1}$	6.1	3.0	3.0	27.3	--	--	--	--	--	--	--	--	--	--	--	42.4	3.0	--	15.2
33-14	" "	$1.98x10^{0}$	--	--	--	--	--	--	--	--	--	--	--	--	--	--	25.0	75.0	--	--	--
Larrabee	" "	$5.10x10^{-1}$	16.7	--	--	16.7	--	--	--	--	--	--	--	--	--	--	16.7	49.9	--	--	--
Leo Joerg	" "	$2.11x10^{1}$	1.0	16.8	11.9	16.8	18.7	3.0	--	3.0	1.0	1.0	--	--	--	--	2.0	14.9	--	--	9.9
2-8	" "	$5.10x10^{0}$	--	--	--	8.3	--	16.7	--	--	8.3	--	--	--	4.2	--	--	16.7	--	45.8	--

Table 2. Importance values of euplankton desmid genera within lakes of a particular type

Genus	Spring Ponds	Hard Water	Soft Water	Acid Bog	Alkaline Bog
Arthrodesmus	0	0	0	38.9	29.5
Bambusina	0	0	0	24.9	16.1
Closterium	0	0	14.6	29.0	0
Cosmarium	0	0	28.3	34.9	41.7
Desmidium	0	0	46.7	33.1	0
Euastrum	0	0	0	20.3	0
Gonatozygon	0	0	0	10.0	0
Hyalotheca	0	0	0	19.4	0
Micrasterias	0	0	0	16.7	0
Netrium	0	0	0	15.9	0
Penium	0	0	0	2.4	0
Phymatodocis	0	0	0	3.0	0
Pleurotaenium	0	0	0	10.2	0
Sphaerozosma	0	0	0	8.3	0
Spondylosium	0	0	0	11.0	0
Staurastrum	46.2	60.0	79.4	63.0	82.8
Tetmemorus	0	0	0	3.0	0
Triploceras	0	0	0	14.0	0
Xanthidium	0	0	0	28.5	0

water lakes, and *Cosmarium* was present in all 3 of the above lake types. All six genera contributed over 50% to the total desmid plankton population of at least one of the study sites. The remaining 12 genera were detected only in acid bog lakes and occurred in less than 25% of the euplankton samples analyzed.

The importance values (I.V.) of the various genera within the desmid euplankton communities of each of the five lake types are summarized in Table 2. These I.V. readings suggest the possibility that up to four desmid assemblages, each with a different range of I.V. readings, may exist within the euplankton communities. In all five lake types, a single genus – *Staurastrum* – occupies the first assemblage order and has I.V. readings at least 24.1 units greater than any other desmid. Thus the first order assemblage is sharply delimited from the lesser orders.

In spring ponds and hard water lakes, the lesser assemblage orders are absent. The second order in both soft water lakes and alkaline bogs is occupied by a single genus – *Desmidium* in the first lake type and *Cosmarium* in the second lake type. In acid bogs, however, the second assemblage order is occupied by a group of five genera including *Arthrodesmus, Closterium, Cosmarium, Desmidium*, and *Xanthidium*.

A similar situation exists in the third and fourth assemblage orders. In soft water lakes the third and fourth orders are occupied by *Cosmarium* and *Closterium* respectively. In alkaline bogs these orders are occupied by *Arthrodesmus* and *Bambusina* respectively. In both of these lake types, the various assemblage orders appear sharply delimited from each other and are separated by I.V. readings of at least 12 units.

In acid bog lakes, in contrast, assemblages of the second and succeeding levels all contain groups of genera and are not as distinctly separated from one another in terms of I.V. figures. Thus *Bambusina* (I.V. = 24.9) occupies a transition zone between the 5 genera of the second order mentioned above (I.V. readings of 28.5-38.9) and the four genera (*Euastrum, Hyalotheca, Micrasterias, Netrium*) present in the third order (I.V. readings of 15.9-20.3). Similarly *Triploceras* (I.V. = 14.0) lies in the transition zone between the third and fourth orders, the latter containing seven genera (*Gonatozygon, Penium, Phymatodocis, Pleurotaenium, Sphaerozosma, Spondylosium*, and *Tetmemorus*) with I.V. readings of 2.4 to 11.0.

It cannot be emphasized too strongly that the data which suggested the hypothesis concerning the existence of possible desmid assemblages in euplankton communities comes from a limited number of lakes in one geographic region. Moreover, the conclusions are based on an arbitrary method of determining generic importance. Further studies on additional lakes in this region and/or on lakes elsewhere may result in considerable modification or complete rejection of the hypothesis.

Table 3. The relative frequencies for euplankton desmid genera within lakes of particular types

Genus	Spring Ponds	Hard Water	Soft Water	Acid Bog	Alkaline Bog
Arthrodesmus	0	0	0	11	20
Bambusina	0	0	0	7	10
Closterium	0	0	14	8	0
Cosmarium	0	0	14	10	20
Desmidium	0	0	14	8	0
Euastrum	0	0	0	6	0
Gonatozygon	0	0	0	1	0
Hyalotheca	0	0	0	5	0
Micrasterias	0	0	0	4	0
Netrium	0	0	0	5	0
Penium	0	0	0	1	0
Phymatodocis	0	0	0	1	0
Pleurotaenium	0	0	0	3	0
Sphaerozosma	0	0	0	2	0
Spondylosium	0	0	0	2	0
Staurastrum	100	100	58	16	50
Tetmemorus	0	0	0	1	0
Triploceras	0	0	0	2	0
Xanthidium	0	0	0	7	0

The same applies to the use of desmid assemblages elsewhere in this paper.

Based on relative frequency (F_R) values (Table 3), the majority of desmid genera are of no importance outside of acid bog lakes. In all six cases where a genus occurs in two or more lake types, the lowest F_R value, and thus the least important role for that genus, occurs in conjunction with acid bog lakes. *Cosmarium,* for example, plays a more significant role in the alkaline bogs studied (F_R = 20) than in the soft water lakes studied (F_R = 14), and it plays a more important role in soft water lakes than in acid bog lakes (F_R = 10). Similarly *Staurastrum* is of far less importance in acid bog euplankton communities (F_R = 16) where it is one of 19 genera present than in soft water (F_R = 58) or alkaline bog (F_R = 50) communities where it is one of only 4 genera present or in spring ponds (F_R = 100) or hard water lakes (F_R = 100) where it is the only genus present. It follows, then, that among lake types, the relative importance of a given genus decreases as the number of genera in the community increases.

The absolute frequency data (Table 4) suggest that certain genera found only in acid bogs during this study have a higher potential of being found in other lake types than do certain other genera. Thus *Gonatozygon, Penium, Phymatodocis,* and *Tetmemorus* all were of rare occurrence (F_A's of 4, F_R's of 1) and could be present in other lake types in such small numbers that they were missed in the collection and/or analysis solely by chance. Because of their apparent rarity and consequent low impor-

Table 4. The absolute frequencies for euplankton desmid genera within lakes of particular types

Genus	Spring Ponds	Hard Water	Soft Water	Acid Bog	Alkaline Bog
Arthrodesmus	0	0	0	61	40
Bambusina	0	0	0	43	20
Closterium	0	0	20	46	0
Cosmarium	0	0	20	57	40
Desmidium	0	0	20	46	0
Euastrum	0	0	0	36	0
Gonatozygon	0	0	0	4	0
Hyalotheca	0	0	0	29	0
Micrasterias	0	0	0	25	0
Netrium	0	0	0	29	0
Penium	0	0	0	4	0
Phymatodocis	0	0	0	4	0
Pleurotaenium	0	0	0	18	0
Sphaerozosma	0	0	0	14	0
Spondylosium	0	0	0	14	0
Staurastrum	17	40	80	86	100
Tetmemorus	0	0	0	4	0
Triploceras	0	0	0	14	0
Xanthidium	0	0	0	43	0

Table 5. Summary of data relating to the suitability of particular lake types for harboring euplankton desmid communities

Criterion	Spring Ponds		Hard Water		Soft Water		Acid Bog		Alkaline Bog	
	Value	Rank	Value	Rank	Value	Rank	Value	Rank	Value	Rank
Mean Absolute Population Density	1.06×10^{-1}	5	1.00×10^{0}	4	1.69×10^{1}	2	1.91×10^{1}	1	1.88×10^{0}	3
Total # desmid Genera present	1	4.5	1	4.5	4	2.5	19	1	4	2.5
Number of assemblage Orders present	1	4.5	1	4.5	4	2	4	2	4	2
Number of genera Present in each Assemblage order:										
1	1	3	1	3	1	3	1	3	1	3
2	0	4.5	0	4.5	1	2.5	5	1	1	2.5
3	0	4.5	0	4.5	1	2.5	4	1	1	2.5
4	0	4.5	0	4.5	1	2.5	7	1	1	2.5
Rank Total		30.5		29.5		17		10		18
Suitability Rank		5		4		2		1		3

tance (I.V. readings of 2.4-10), genera such as these offer little value as potential biological indicators.

Certain other genera, in contrast, appear to have a higher potential of being confined solely to acid bogs. Thus *Xanthidium* (F_A = 43), *Euastrum* (F_A = 36), *Hyalotheca* (F_A = 29), and *Netrium* (F_A = 29) all have reasonably high acid bog F_A values and do not occur (i.e. F_A = 0) in any of the other lake types. This suggests that these taxa may be characteristic of acid bog euplankton communities and, therefore, may have good potential value as biological indicators of acid bog lakes. Again, caution must be exercised in carrying such generalizations too far since the data bank forming the basis for these observations involves only 61 lakes in one geographic region. Further studies may require modification of these hypotheses. Moreover, the absence of any one or several of these taxa does not eliminate the possibility of the locality being an acid bog. The presence of one or more, however, appears to be a good potential indicator of acid bog conditions.

Data relating to the suitability of a particular lake type for harboring an euplankton desmid community are summarized in Table 5. Based on these criteria, acid bog lakes are far more suitable for harboring desmids in the euplankton than are soft water lakes or alkaline bog lakes, and these two lake types, in turn, are much more suitable than are spring ponds or hard water lakes. The relationships between the relative biological suitability of a lake type for harboring desmids and the factors in the chemical environment are discussed in Section 3 below.

Aufwuchs Community Composition

Within the 61 study lakes, the aufwuchs communities of 107 macrophyte hosts were analyzed (Table 6), including 10 from spring ponds, 19 from hard water lakes, 12 from soft water lakes, 35 from acid bogs, 16 from alkaline bogs, and 15 from closed bogs. Since, as determined in parts 1-2 of this series on Wisconsin Desmids, each of these hosts has the potential to harbor a unique algal association, the desmid community of each macrophyte is considered as a distinct entity, even though the hosts may have come from the same locality. The macrophytes of the spring ponds studied did not harbor desmid communities and will not be considered further.

Among the 23 genera recorded from the aufwuchs communities analyzed during this investigation (Table 6), *Cosmarium* and *Staurastrum* appear to be the two most widely distributed taxa and often are the two most conspicuous taxa present; both were found in all five lake types which harbored aufwuchs desmids. Plants of *Cosmarium* occurred in 71 of the 97 aufwuchs samples analyzed. It was the sole genus present in 11 cases, accounted for at least 50% of the desmid population in 32 instances, and contributed 25% or more to the total desmid population in 48 communities. *Staurastrum* was recorded from 60 macrophytes, but was the sole aufwuchs genus present on only two occasions. It contributed over 50% of the total desmid population to 13 aufwuchs communities and over 25% to 31 aufwuchs communities.

Closterium was the only other genus recorded from all five lake types and appeared in 39 of 97 samples. In two samples, it was the sole desmid present, in five samples it dominated with over 50% of the desmid population, and in eleven samples it accounted for 25% of more of the desmid population. Two other genera occurred in at least one-quarter of the total number of aufwuchs communities. *Euastrum*, with 32 occurrences, was found in all lake types except for hard waters. *Netrium*, with 28 occurrences, was detected in acid bogs, alkaline bogs, and soft water lakes. Both genera contributed over 50% to the total desmid population in at least one aufwuchs community.

The remaining 18 genera occurred in less than 25% of the samples analyzed and for the most part were found in only two or three of the lake types. None occurred in hard water lakes. Four genera (*Docidium, Gonatozygon, Spinoclosterium, Spirotaenia*) were confined to acid bog lakes, and one genus (*Roya*) was detected only in soft water lakes.

The importance values of the various desmid genera in the aufwuchs communities of each of the five lake types are summarized in Table 7. These I.V. readings suggest the possibility that the aufwuchs communities, like the euplankton communities, contain up to 4 desmid assemblage orders of varying importance. In hard water lakes only two desmid assemblages occur. The first order contains *Cosmarium* (I.V. = 81.8), and the second order includes *Closterium* and *Staurastrum* (I.V. = 16.0-18.3). The closed bogs as a group harbored 3 desmid assemblages, the first order containing only one genus (*Staurastrum*, I.V. = 49.1), the second order including seven genera (*Bambusina, Closterium, Cosmarium, Cylindrocystis, Euastrum, Netrium, Penium*) with I.V. readings of 17.6-34.3, and the third order having four genera (*Arthrodesmus, Desmidium, Hyalotheca, Tetmemorus*) with I.V. readings of 5.7-12.1.

The remaining 3 lake types all contain 4 desmid assemblages. In soft water lakes the first order includes only

Table 6. The percentage composition of the aufwuchs desmid populations at the study sites of the various lake types. Date expressed as a % of the total desmid population in the right hand column.

A. Data For Hard Water Lakes

County	Locality	Host	Closterium	Cosmarium	Staurastrum	Total Desmid Population Density org/mg host dry wt
Dane	Bruner's Pond	Ceratophyllum	--	---	--	Absent
		Myriophyllum	12.1	87.9	--	$3.02x10^3$
		Potamogeton	--	100.0	--	$1.39x10^3$
	Fish Lake	Ceratophyllum	--	---	--	Absent
		Myriophyllum	--	93.9	6.1	$1.96x10^3$
		Nuphar	--	100.0	--	$3.20x10^1$
		Utricularia	--	94.5	5.5	$5.94x10^3$
Jefferson	Ripley	Myriophyllum	--	81.0	19.0	$2.73x10^2$
		Nuphar	--	---	--	Absent
		Potamogeton	--	100.0	--	$7.10x10^1$
		Utricularia	3.4	73.7	22.9	$1.10x10^4$

Table 6 continued

A. Data For Hard Water Lakes

County	Locality	Host	*Closterium*	*Cosmarium*	*Staurastrum*	Total Desmid Population Density org/mg host dry wt
Walworth	Beulah	*Anacharis*	--	100.0	--	$2.20x10^1$
		Myriophyllum	--	100.0	--	$3.70x10^1$
		Potamogeton	--	100.0	--	$1.60x10^1$
		Utricularia	--	100.0	--	$7.70x10^1$
Waukesha	Fowler	*Anacharis*	--	---	--	Absent
		Chara	16.0	68.0	16.0	$3.69x10^2$
		Myriophyllum	27.6	72.4	--	$4.61x10^2$
		Potamogeton	--	100.0	--	$5.61x10^2$

Table 6 continued

B. Data for Soft Water Lakes

County	Locality	Host	*Closterium*	*Cosmarium*	*Desmidium*	*Euastrum*	*Hyalotheca*	*Micrasterias*	*Netrium*	*Pleurotaenium*	*Roya*	*Sphaerozosma*	*Spondylosium*	*Staurastrum*	*Triploceras*	*Xanthidium*	Total Desmid Population Density org/mg host dry wt
Sawyer	Ike	*Potamogeton*	---	33.0	--	--	-	-	-	67.0	-	--	-	--	-	-	$2.14x10^4$
		Utricularia	22.7	59.2	--	4.5	-	-	-	4.5	9.1	--	-	--	-	-	$4.86x10^4$
Chippewa-Rusk	Pine	*Hygroamblystegium*	3.2	35.7	--	20.6	6.5	3.2	-	1.8	-	12.9	-	12.9	3.2	-	$1.87x10^4$
		Potamogeton	---	56.6	--	7.5	7.5	-	1.5	--	-	7.5	-	19.4	-	-	$1.82x10^4$
		Sphagnum	---	62.5	12.5	18.8	-	-	-	--	-	--	-	6.2	-	-	$1.73x10^4$
		Utricularia	2.2	37.3	4.4	12.1	9.9	-	2.2	1.1	-	9.9	-	19.8	-	1.1	$3.96x10^4$
Ashland	Zielke	*Nitella*	25.0	25.0	--	50.0	-	-	-	--	-	--	-	--	-	-	$2.39x10^4$
		Utricularia	100.0	--	--	--	-	-	-	--	-	--	-	--	-	-	$4.74x10^4$
Burnett	Lk 15-12	*Equisetum*	---	60.5	--	12.1	3.0	-	-	6.1	-	--	-	15.1	-	3.0	$1.04x10^4$
		Utricularia	1.5	34.7	1.5	18.5	1.5	-	-	3.1	-	7.7	1.5	25.5	1.5	-	$4.78x10^4$
Barron	Lk 20-12A	*Riccia*	---	60.0	--	--	-	-	-	--	-	20.0	-	20.0	-	-	$2.74x10^4$
		Utricularia	13.6	40.9	4.5	--	-	9.1	-	--	-	--	-	31.9	-	-	$4.93x10^4$

Table 6 continued

C. Data for Acid Bog Lakes

County	Locality	Host	*Arthrodesmus*	*Bambusina*	*Closterium*	*Cosmarium*	*Cylindrocystis*	*Desmidium*	*Docidium*	*Euastrum*	*Gonatozygon*	*Hyalotheca*	*Micrasterias*	*Netrium*	*Penium*	*Pleurotaenium*	*Spinoclosterium*	*Spirotaenia*	*Sphaerozosma*	*Spondylosium*	*Staurastrum*	*Tetmemorus*	*Triploceras*	*Xanthidium*	Desmid Population Density
Ashland	Trout	*Sphagnum*	--	18.2	--	--	--	9.1	--	--	--	9.1	--	9.1	9.1	--	--	--	--	--	45.4	--	--	--	$9.16x10^2$
Barron	Lk 7-9d	*Sphagnum*	12.5	--	--	--	--	--	--	--	--	--	--	12.5	25.0	--	--	--	--	--	37.5	--	12.5	--	$1.73x10^2$
		Utricularia	7.7	7.7	15.3	7.7	--	7.7	--	--	--	--	--	7.7	--	--	--	--	--	--	46.2	--	--	--	$4.24x10^3$
Bayfield	Lk 7-5	*Sphagnum*	--	--	--	--	--	--	--	--	--	42.8	--	--	14.3	--	--	--	--	--	28.6	14.3	--	--	$4.45x10^2$
	Lk 7-2	*Sphagnum*	--	6.3	6.3	6.2	--	--	--	--	--	--	6.2	50.0	21.9	--	--	--	--	--	--	--	3.1	--	$2.15x10^3$
	Lk 33-14	*Utricularia*	--	4.3	--	23.9	--	2.2	2.2	15.0	--	--	2.2	4.3	2.2	2.2	--	--	--	--	41.3	--	--	2.2	$3.49x10^3$
	Lk 1-16c	*Utricularia*	--	--	25.0	41.8	--	--	--	8.3	--	--	--	8.3	--	--	--	--	--	--	8.3	--	--	8.3	$2.18x10^3$
	Lk 6-10d	*Utricularia*	--	--	3.7	33.4	--	--	--	7.4	3.7	--	--	3.7	3.7	--	--	--	7.4	--	33.3	--	--	3.7	$2.06x10^3$
Burnett	Lk 9-2	*Utricularia*	2.0	--	21.5	23.5	--	2.0	--	7.8	2.0	--	--	2.0	--	3.9	--	--	--	11.8	23.5	--	--	--	$9.81x10^3$
	Lk 10-6	*Utricularia*	--	--	17.1	31.4	--	7.1	--	12.9	--	--	--	1.4	1.4	1.4	--	--	--	2.9	24.3	--	--	--	$1.45x10^4$
	Lk 16-2	*Utricularia*	2.4	3.9	3.9	43.9	--	2.4	--	3.9	2.4	2.4	2.4	--	--	--	--	--	--	7.3	22.0	--	--	--	$5.87x10^3$
	Lk 17-4	*Sphagnum*	8.3	--	75.0	8.4	--	--	--	--	--	--	--	--	--	8.3	--	--	--	--	--	--	--	--	$8.23x10^2$
		Utricularia	3.4	--	6.8	37.5	--	--	1.1	2.3	2.3	--	1.1	1.1	2.3	1.1	--	--	--	--	36.4	--	2.3	2.3	$1.63x10^4$
	Lk 33-14	*Sphagnum*	--	--	62.5	--	--	--	--	--	--	--	--	6.2	--	--	--	25.0	--	--	--	6.3	--	--	$8.62x10^2$
Chippewa	Larrabee	*Utricularia*	20.0	--	--	33.3	--	6.7	--	13.3	--	--	--	6.7	--	--	--	--	--	--	20.0	--	--	--	$2.21x10^3$

Table 6 continued

C. Data for Acid Bog Lakes

County	Locality	Host	Arthrodesmus	Bambusina	Closterium	Cosmarium	Cylindrocystis	Desmidium	Docidium	Euastrum		Hyalotheca	Micrasterias	Netrium	Penium	Pleurotaenium	Spinoclosterium	Spirotaenia	Sphaerozosma	Spondylosium	Staurastrum	Tetmemorus	Triploceras	Xanthidium	Desmid Population Density
	Leo Joerg	Brasenia	--	10.7	--	64.3	--	3.6	--	10.7	--	--	--	--	--	--	--	7.1	--	--	--	--	--	3.6	8.15×10^2
		Sphagnum	--	14.3	14.3	14.3	--	--	--	14.3	--	--	--	42.8	--	--	--	--	--	--	--	--	--	--	3.21×10^2
		Utricularia	--	3.3	13.3	26.8	--	3.3	--	10.0	--	--	3.3	--	--	--	--	--	--	--	40.0	--	--	--	4.01×10^3
	Lk 2-8	Utricularia	--	18.2	4.5	9.1	--	11.4	--	27.2	--	2.3	4.5	--	--	4.5	--	--	--	4.5	9.1	2.3	--	2.3	2.97×10^3
Iron	Lk 26-9	Sphagnum	--	2.0	5.9	52.9	11.8	--	--	--	--	--	--	5.9	17.6	--	--	--	--	--	3.9	--	--	--	1.50×10^3
		"Moss"	--	--	--	4.9	7.3	--	--	--	--	--	--	4.9	4.9	--	--	--	--	--	78.0	--	--	--	6.66×10^3
	Lk 13-2d	Potamogeton	--	20.0	6.7	13.2	--	20.0	--	6.7	--	--	--	--	--	--	--	--	--	--	26.7	--	--	6.7	7.92×10^2
		Sphagnum	--	--	--	57.1	--	--	--	14.3	--	--	--	--	--	--	--	--	--	--	28.6	--	--	--	2.10×10^2
		Utricularia	--	3.4	8.6	15.5	--	3.4	--	12.1	--	--	--	1.7	--	3.4	--	--	--	--	51.9	--	--	--	1.10×10^4
Oneida	Lk 11-5	Sphagnum	13.8	--	--	7.7	--	--	--	1.5	--	--	67.8	1.5	1.5	--	--	--	--	--	6.2	--	--	--	8.87×10^3
Polk	Evelyn	Utricularia	--	--	50.0	20.0	--	--	--	--	--	--	--	10.0	--	--	--	--	--	--	10.0	--	--	10.0	1.33×10^3
Price	Unnamed	Sphagnum	--	--	--	40.0	--	--	--	--	--	--	20.0	20.0	--	--	--	--	--	--	--	20.0	--	--	2.74×10^2
Rusk	Round	Utricularia	41.1	--	--	--	--	--	--	--	--	--	--	1.5	--	--	--	--	--	--	57.4	--	--	--	8.31×10^3
	Saxton	Sphagnum	--	--	--	--	--	--	--	--	--	--	--	20.0	--	--	--	--	--	--	80.0	--	--	--	1.69×10^2
	School	Utricularia	31.6	--	26.4	11.8	--	--	--	--	--	--	--	--	--	1.3	--	--	--	1.3	27.6	--	--	--	6.58×10^3
Vilas	Spruce	Sphagnum	11.1	--	11.1	11.2	--	--	--	--	--	11.1	--	11.1	--	--	--	--	--	--	11.1	11.1	11.1	11.1	9.30×10^2

Table 6 continued

C. Data for Acid Bog Lakes

County	Locality	Host	*Arthrodesmus*	*Bambusina*	*Closterium*	*Cosmarium*	*Cylindrocystis*	*Desmidium*	*Docidium*	*Euastrum*	*Gonatozygon*	*Hyalotheca*	*Micrasterias*	*Netrium*	*Penium*	*Pleurotaenium*	*Spinoclosterium*	*Spirotaenia*	*Sphaerozosma*	*Spondylosium*	*Staurastrum*	*Tetmemorus*	*Triploceras*	*Xanthidium*	Desmid Population Density
	Unnamed	*Sphagnum*	45.6	18.1	--	--	--	--	--	--	--	--	4.5	--	4.5	--	--	--	--	--	27.3	--	--	--	2.20×10^3
Washburn	Unnamed(1)	*Potamogeton*	--	--	20.0	20.0	--	--	--	--	--	--	--	--	--	20.0	20.0	--	--	--	20.0	--	--	--	5.08×10^2
	Unnamed(2)	*Utricularia*	7.9	3.1	9.2	12.3		21.5		15.4	--	--	--	1.5	1.5	4.6	--	--	--	1.5	20.0	--	--	1.5	1.90×10^3
	Unnamed(3)	*Sphagnum*	2.8	17.2	8.6	8.6	2.8	5.7		2.8	--	--	8.6	8.6	8.6	--	--	--	--	--	22.9	--	2.8	--	2.80×10^3

Table 6 continued

D. Data for Alkaline Bog Lakes

County	Locality	Host	Arthrodesmus	Closterium	Cosmarium	Cylindrocystis	Desmidium	Euastrum	Micrasterias	Staurastrum	Xanthidium	Total Desmid Population Density
Rusk	Bog Lake	Potamogeton	--	--	14.3	---	--	--	--	85.7	--	$2.5x10^2$ org/mg d.w.
Sawyer	Bullhead Lake	Chara	--	--	21.4	---	--	21.4	--	57.2	--	$4.65x10^2$
		Nojas	--	--	80.0	---	--	--	--	20.0	--	$4.28x10^1$
		Potamogeton	--	--	85.7	---	--	--	--	14.3	--	$2.09x10^2$
		Utricularia (Lk)	3.8	--	38.5	---	--	11.5	--	46.2	--	$1.97x10^3$
		Utricularia (Mat)	--	--	10.0	---	10.0	--	10.0	60.0	10.0	$1.32x10^3$
Chippewa	Cedar Lake	Ceratophyllum	--	42.9	14.2	---	--	--	--	42.9	--	$8.33x10^2$
Sawyer	Hegmeister Lk	Myriophyllum	--	--	---	---	--	--	--	100.0	--	$6.26x10^1$
		Potamogeton A	--	--	---	---	--	--	--	---	--	---
		Potamogeton B	--	--	100.0	---	--	--	--	---	--	$3.83x10^1$
		Potamogeton C	--	--	---	---	--	--	--	---	--	---
		Sphagnum A	--	--	100.0	---	--	--	--	---	--	$3.46x10^1$
		Sphagnum B	--	--	---	100.0	--	--	--	---	--	$2.05x10^1$
		Utricularia	20.0	20.0	60.0	---	--	--	--	---	--	$1.53x10^3$
Vilas	Mystery Lake	Carex	--	11.1	66.7	---	--	--	--	22.2	--	$6.96x10^2$
		Sphagnum	--	--	11.1	---	--	--	11.1	77.8	--	$7.29x10^2$

Table 6 continued

E. Data for Closed Bogs

County	Locality	Host	Arthrodesmus	Bambusina	Closterium	Cosmarium	Cylindrocystis	Desmidium	Euastrum	Hyalotheca	Netrium	Penium	Staurastrum	Tetmemorus	Population Density
	1	*Sphagnum* A	--	--	---	---	--	--	---	--	100.0	---	--	--	$6.06x10^1$
		Sphagnum B	--	--	---	---	50.0	--	---	--	33.3	---	16.7	--	$6.29x10^2$
	2	*Utricularia*	--	--	100.0	---	--	--	---	--	---	---	--	--	$2.94x10^2$
	3	*Sphagnum*	--	--	---	---	--	--	---	--	---	---	100.0	--	$5.25x10^2$
	4	*Sphagnum*	--	--	---	---	--	--	---	--	---	---	---	--	---
	5	*Sphagnum*	--	--	---	62.1	37.9	--	---	--	---	---	---	--	$1.12x10^3$
	6	*Sphagnum*	--	--	---	---	--	25.0	---	--	---	50.0	---	25.0	$2.40x10^2$
	7	*Sphagnum*	--	12.5	12.5	12.5	--	--	---	6.3	---	---	56.2	--	$9.40x10^2$
	8	*Sphagnum*	--	--	---	100.0	--	--	---	--	---	---	---	--	$1.12x10^3$
		Potamogeton	--	--	25.0	50.0	--	--	---	--	---	---	25.0	--	$1.44x10^2$
	9	*Sphagnum*	--	33.3	---	---	--	--	33.3	--	---	---	33.4	--	$1.93x10^2$
	10	*Sphagnum*	25.0	--	---	---	--	--	12.5	--	---	---	62.5	--	$1.85x10^2$
	11	*Sphagnum*	--	--	---	---	--	--	100.0	--	---	---	---	--	$8.15x10^1$
		Carex	--	16.7	---	33.3	--	--	16.7	--	---	---	33.3	--	$2.22x10^2$
	12	*Sphagnum*	--	--	---	---	--	--	---	---	---	---	100.0	--	$1.75x10^1$

Table 7. Importance values of aufwuchs desmid genera within lakes of a particular type

Genus	Hard Water	Soft Water	Acid Bog	Alkaline Bog	Closed Bog
Arthrodesmus	0	0	26.5	10.7	12.1
Bambusina	0	0	25.6	0	17.6
Closterium	16.0	39.3	39.7	18.5	26.8
Cosmarium	81.8	67.0	50.6	62.7	34.3
Cylindrocystis	0	0	6.7	37.4	22.9
Desmidium	0	14.3	23.0	6.4	12.1
Docidium	0	0	3.6	0	0
Euastrum	0	42.9	29.7	12.4	26.6
Gonatozygon	0	0	6.4	0	0
Hyalotheca	0	23.1	11.8	0	5.7
Micrasterias	0	10.7	19.1	10.2	0
Netrium	0	9.2	39.1	0	30.2
Penium	0	0	23.3	0	20.7
Pleurotaenium	0	30.8	16.5	0	0
Roya	0	7.2	0	0	0
Spinoclosterium	0	0	8.3	0	0
Spirotaenia	0	0	8.5	0	0
Sphaerozosma	0	26.1	4.0	0	0
Spondylosium	0	4.5	10.3	0	0
Staurastrum	18.3	42.5	55.3	59.3	49.1
Tetmemorus	0	0	10.9	0	12.1
Triploceras	0	9.4	9.3	0	0
Xanthidium	0	9.3	16.5	6.4	0

Cosmarium (I.V. = 67.0), but in acid bogs and alkaline bogs both *Staurastrum* and *Cosmarium* occur in the first order. The I.V. range in acid bogs is 50.6-55.9 and in alkaline bogs 59.3-62.7. The second and succeeding orders of soft water lakes and acid bogs all contain more than one genus. In soft water lakes the second order includes *Closterium, Euastrum,* and *Staurastrum* (I.V. 39.3-42.9), the third order contains *Hyalotheca, Pleurotaenium,* and *Sphaerozosma* (I.V. 23.1-30.8), and the fourth order contains *Desmidium, Micrasterias, Netrium, Roya, Spondylosium, Triploceras,* and *Xanthidium* (I.V. 4.5-14.3). The second order assemblage in acid bogs includes *Closterium* and *Netrium* (I.V. 39.1-39.7), the third order contains *Arthrodesmus, Bambusina, Desmidium, Euastrum,* and *Penium* (I.V. 23.0-29.7), and the fourth order includes the remaining 12 genera (I.V. 3.6-16.5, see Table 7). *Micrasterias* (I.V. = 19.5) occupies a transition zone between the third and fourth orders in acid bogs.

In alkaline bogs, the second and third orders have only one genus each (*Cylindrocystis* [I.V. = 37.4] in 2, *Closterium* [I.V. = 18.5] in 3), a situation which contrasts to that of the other lake types. The fourth order, however, is occupied by an assemblage of 5 genera including *Arthrodesmus, Desmidium, Euastrum, Micrasterias,* and *Xanthidium* (I.V. = 6.4-12.4).

Based on relative frequency values (Table 8), *Closterium, Cosmarium* and *Staurastrum* are the three most important genera in all lake types except acid bogs, where *Netrium* replaces *Closterium* as the third most important taxon. *Closterium* and *Cosmarium* reach their maximum F_R values in hard water lakes while *Staurastrum* attains maximum relative importance in alkaline bogs. *Netrium,* in contrast, has its highest F_R value in acid bogs and was not detected in hard water lakes or alkaline bogs.

The maximum relative importance (based on F_R values) for two genera (*Closterium, Cosmarium*) occurs in hard water lakes, for five other genera (*Hyalotheca, Pleurotaenium, Roya, Sphaerozosma, Triploceras*) in soft water lakes, for 8 genera (*Docidium, Gonatozygon, Micrasterias, Netrium, Penium, Spinoclosterium, Spirotaenia, Xanthidium*) in acid bogs, and for 4 genera (*Bambusina, Cylindrocystis, Euastrum, Tetmemorus*) in closed bogs. *Staurastrum* is the only genus to reach a maximum F_R in alkaline bogs, although *Arthrodesmus* had maximum F_R values of 6 for both acid and alkaline

Table 8. The relative frequencies for aufwuchs desmid genera within lakes of particular types

Genus	Hard Water	Soft Water	Acid Bog	Alkaline Bog	Closed Bog
Arthrodesmus	0	0	6	6	3
Bambusina	0	0	6	0	9
Closterium	17	11	9	9	9
Cosmarium	63	17	12	37	16
Cylindrocystis	0	0	1	3	6
Desmidium	0	6	6	3	3
Docidium	0	0	1	0	0
Euastrum	0	13	7	6	14
Gonatozygon	0	0	2	0	0
Hyalotheca	0	8	2	0	3
Micrasterias	0	3	4	3	0
Netrium	0	3	10	0	6
Penium	0	0	6	0	3
Pleurotaenium	0	8	4	0	0
Roya	0	2	0	0	0
Spinoclosterium	0	0	0.5	0	0
Spirotaenia	0	0	1	0	0
Sphaerozosma	0	8	0.5	0	0
Spondylosium	0	2	2	0	0
Staurastrum	20	13	12	30	25
Tetmemorus	0	0	2	0	3
Triploceras	0	3	2	0	0
Xanthidium	0	3	4	3	0

bogs. Similarly *Desmidium* and *Spondylosium* had identical maxima in acid bogs and soft water lakes.

The absolute frequency data (Table 9) suggest that *Closterium, Cosmarium,* and *Staurastrum* are 'weedy' taxa with moderate to high F_A values in all five lake types. Similarly, the six genera (*Docidium, Gonatozygon, Roya, Spinoclosterium, Spirotaenia, Tetmemorus*) found in only one lake type exhibit the potential for weediness since they all have low F_A values (3-14) and thus could have been missed in collection or analysis of samples by chance alone.

The biological indicator potential (in terms of lake type) for all of the above genera appears low since the first three are ubiquitous and the remaining ones are of apparent infrequent occurrence and have low I.V. readings (3.6-10.9). Indeed, the absolute frequency data offer few clues as to which aufwuchs genera, if any, may have biological indicator potential. *Pleurotaenium* appears to be characteristic only of soft water lakes and acid bogs where it has F_A values of 50 and 29 respectively, whereas it has F_A values of 0 in the other lake types. The remaining genera appear to be distributed over three or more lake types and/or have low F_A's, thus showing little apparent potential as indicators. Whether particular species within

Table 9. The absolute frequencies for aufwuchs desmid genera within lakes of particular types

Genus	Hard Water	Soft Water	Acid Bog	Alkaline Bog	Closed Bog
Arthrodesmus	0	0	40	13	7
Bambusina	0	0	43	0	20
Closterium	21	58	63	19	20
Cosmarium	79	92	80	75	33
Cylindrocystis	0	0	9	6	13
Desmidium	0	25	40	6	7
Docidium	0	0	6	0	0
Euastrum	0	67	51	13	27
Gonatozygon	0	0	11	0	0
Hyalotheca	0	42	14	0	7
Micrasterias	0	17	29	13	0
Netrium	0	17	69	0	13
Penium	0	0	40	0	7
Pleurotaenium	0	50	29	0	0
Roya	0	8	0	0	0
Spinoclosterium	0	0	3	0	0
Spirotaenia	0	0	6	0	0
Sphaerozosma	0	42	3	0	0
Spondylosium	0	8	17	0	0
Staurastrum	26	67	83	63	53
Tetmemorus	0	0	14	0	7
Triploceras	0	17	14	0	0
Xanthidium	0	17	29	6	0

Table 10. Summary of data relating to the suitability of particular lake types for harboring aufwuchs desmid communities

Criterion	Hard Water		Soft Water		Acid Bog		Alkaline Bog		Closed Bog	
	Value	Rank	Value	Rank	Value	Rank	Value	Rank	Value	Rank
Mean Absolute Population Density	1.33×10^3	3	2.60×10^4	1	3.66×10^3	2	5.13×10^2	4	3.85×10^2	5
Total # desmid genera present	3	5	14	2	22	1	9	4	12	3
Number of assemblage orders present	2	5	4	2	4	2	4	2	3	4
Number of genera present in each assemblage order:										
1	1	4	1	4	2	1.5	2	1.5	1	4
2	2	3.5	3	2	2	3.5	1	5	7	1
3	-	5	3	3	5	1	1	4	4	2
4	-	4.5	7	2	12	1	5	3	-	4.5
Rank Total		30		16		12		23.5		23.5
Suitability Rank		5		2		1		3		3

Table 11. Range of chemical conditions under which desmid genera occurred in Wisconsin lakes. Chemical tolerance range for each genus.

Genus	Conductivity	pH	CO_2	O_2	PO_4-P	Total P
Arthrodesmus	14-112	4.2-8.6	1-21	2-15	<.005-.104	.02-.16
Bambusina	14-96	4.0-9.1	0-21	2-17	.012-.147	.02-1.40
Closterium	15-490	4.0-8.8	0-21	2-15	<.005-.468	.02-1.13
Cosmarium	16-490	4.0-8.8	0-21	2-15	<.005-.747	.02-1.61
Cylindrocystis	17-50	4.3-6.7	(4)	(10)	.024-.967	.03-1.90
Desmidium	14-53	5.6-7.0	0-21	2-15	.019-.446	.04-2.12
Docidium	14-18	5.7-5.9	10-16	5-6	.028-.048	.04-.06
Euastrum	14-56	4.0-7.0	0-21	2-13	<.005-.519	.02-1.40
Gonatozygon	17-23	5.9-6.6	3-16	5-10	.028-.048	.04-.12
Hyalotheca	16-50(-180?)	4.3-7.0	2-20	6-15	.001-.147	.02-.20
Micrasterias	14-28	5.7-7.0	3-16	5-13	.026-.072	.03-.22
Netrium	14-48	4.7-7.0	0-21	2-15	.012-.967	.02-1.90
Penium	14-53(-180?)	5.6-6.8	0-21	4-11	.025-.051	.04-2.12
Pleurotaenium	14-56	5.6-7.0	3-21	4-12	<.005-.058	.02-.11
Phymatodocis	(15)	(6.5)	(0)	(11)	(.026)	(.06)
Roya	(56)	(6.9)	(6)	(7)	(<.005)	(.02)
Spinoclosterium	(18)	(5.7)	(21)	(2)	(.019)	(.04)
Spirotaenia	14-24	5.7-6.3	7-10	6-10	.028-.058	.04-.07
Sphaerozosma	15-22	5.7-7.0	0-21	2-12	.019-.058	.04-.11
Spondylosium	14-28	5.6-7.0	3-21	4-12	.025-.058	.04-.12
Staurastrum	14-520	4.0-9.1	0-28	2-17	<.005-.967	.02-1.40
Tetmemorus	14-39	5.6-6.8	3-16	5-12	.023-.052	.04-.09
Triploceras	17-38	5.8-7.0	3-16	5-15	.001-.058	.02-.11
Xanthidium	14-48(-180?)	5.6-7.0	2-21	2-13	.001-.058	.02-.11

these genera exhibit more restricted distributions and/or have greater indicator potential remains to be determined.

Data relating to the suitability of a particular lake type for harboring an aufwuchs desmid community are summarized in Table 10. As was the case for euplankton communities, acid bog lakes appear to be the most suitable type for aufwuchs desmids, and soft water lakes are the second most suitable. Following these, alkaline bogs and closed bogs appear to have a similar degree of suita-

Table 11 continued

Genus	Ca^{++}	Mg^{++}	K^{+}	Na^{+}	Cl^{-}	$SO_4^{=}$
Arthrodesmus	0-15.7	<2.0-7.6	<0.5-2.2	<1.0-20.4	2-28	3-12
Bambusina	0-17.8	<2.0-6.8	<0.5-2.2	<1.0-10.2	2-13(-26?)	1-31(-69?)
Closterium	0-63	<2.0-5.5	<0.5-3.7	<1.0-11.4	2-27	3-40
Cosmarium	0-63	<2.0-55	<0.5-2.4	<1.0-10.2	2-27	1-40)139?)
Cylindrocystis	0.3-3.4	<2.0-3.1	<0.5-2.2	<1.0-5.1	7-15	4-25(139?)
Desmidium	0-7.6	<2.0-4.7	<0.5-6.6	<1.0-10.2	9-18(26?)	1-21
Docidium	1.0-2.0	(<2.0)	<0.5-1.4	<1.0-1.7	4-9	3-6
Euastrum	0-9.1	<2.0-5.2	<0.5-2.2	<1.0-20.4	2-28	3-31(-69?)
Gonatozygon	0.9-1.3	(2.0)	<0.5-1.8	<1.0-1.7	3-9(26?)	4-7
Hyalotheca	0-6.2	<2.0-2.2	<0.5-2.1	<1.0-7.3	2-39	3-21
Micrasterias	0.3-4.8	(<2.0)	<0.5-1.8	<1.0-1.7	3-10)26?)	3-7
Netrium	0-8.0	<2.0-3.7	<0.5-2.2	<1.0-5.1	3-15	3-25
Penium	0-6.4	<2.0-4.7	<0.5-6.6	<1.0-4.2	2-39	3-21
Pleurotaenium	0-9.1	<2.0-5.2	<0.5-2.1	<1.0-10.2	2-18	1-8
Phymatodocis	(0)	(2.1)	(2.0)	1.0	(3)	(6)
Roya	(9.1)	(5.2)	(2.0)	(2.2)	(2)	(6)
Spinoclosterium	(2.2)	(2.5)	(2.2)	(<1.0)	(3)	(6)
Spirotaenia	2.0-3.7	(<2.0)	<0.5-0.6	(<1.0)	(4)	3-4
Sphaerozosma	0-3.2	<2.0-2.5	<.5-2.2	<1.0-2.7	3-18	3-6
Spondylosium	0-4.8	<2.0-2.2	<.5-1.6	<1.0-1.8	2-5(-26?)	3-8
Staurastrum	0-50	<2.0-37.7	<0.5-3.7	<1.0-83.1	2-140	1-40)-69?)
Tetmemorus	0.9-3.7	(<2.0)	<0.5-1.8	<1.0-10.2	3-13	1-6
Triploceras	1.0-3.7	(<2.0)	<0.5-2.1	<1.0-5.1	3-18	4-6
Xanthidium	0-8.0	<2.0-2.5	<0.5-2.2	<1.0-10.2	2-39	1-10

bility, and hard water lakes show the least suitability. Spring ponds, with a total absence of aufwuchs desmids, also appear unsuitable.

Chemical Considerations in Wisconsin Lakes

The relative suitability of lakes of a given type to harbor desmid communities may be governed in part by the range of chemical conditions present and in part by the ability of various desmids to survive under those conditions. The occurrence of desmid genera in the 61 Wisconsin localities in relation to chemical parameters is summarized below; the bearing these results have on various

Table 11 continued

Genus	NO_2-N	NO_3-N	NH_3-N	Org-N	Total-N	Total Alkalinity
Arthrodesmus	<.002-.021	<.04-.27	<.03-.27	.24-1.64	.33-1.97	0-41
Bambusina	<.002-.62	.04-2.21	<.03-.26	.27-6.60	.38-7.34	0-50
Closterium	.002-.04	<.04-.95	<.03-.20	.36-3.64	.54-4.83	0-324
Cosmarium	<.002-.058	<.04-3.22	<.03-1.62	.44-3.64	.54-4.83	0-324
Cylindrocystis	.004-.06	<.04-3.22	<.03-1.62	.66-12.63	.67-13.30	0-1
Desmidium	<.002-.12	.04-3.44	<.03-2.26	.27-6.14	.38-11.96	0-6
Docidium	<.002-.005	.04-.08	.03-.05	1.03-1.07	1.10-1.20	0-1
Euastrum	<.002-.62	.04-2.21	<.03-.27	.44-6.60	.54-7.42	0-19
Gonatozygon	.002-.006	.04-.09	<.03-.05	.92-1.07	1.06-1.20	0-2
Hyalotheca	.002-.02	.04-.45	<.03-.27	.24-1.96	.33-2.52	0-6
Micrasterias	<.002-.013	<.04-.13	<.03-.27	.66-1.31	.67-1.58	0-6
Netrium	<.002-.06	.04-.29	<.03-.32	.72-12.63	.81-13.30	0-18
Penium	<.002-.12	.04-3.44	.03-2.26	.8-6.14	.96-11.96	0-4
Pleurotaenium	<.002-.013	.04-.13	<.03-.15	.27-1.29	.38-1.58	0-19
Phymatodocis	(.004)	(.06)	(.04)	(1.85)	(1.95)	(0)
Roya	(.004)	(.10)	(<.03)	(.44)	(54)	(19)
Spinoclosterium	(.004)	(.08)	(<.03)	(.81)	(.89)	(2)
Spirotaenia	<.002-.008	.04-.10	.03-.26	1.03-1.05	1.10-1.42	1-6
Sphaerozosma	.002-.013	.05-.13	<.03-.15	.72-1.85	.81-1.95	0-2
Spondylosium	<.002-.014	.04-.11	.03-.27	.73-1.23	.98-1.42	0-6
Staurastrum	<.002-.62	<.04-2.72	<.03-.70	.34-12.63	.33-13.30	0-247
Tetmemorus	<.002-.008	.04-.10	.03-.26	.24-1.07	.33-1.42	0-6
Triploceras	.004-.013	.04-.14	<.03-.26	.24-1.29	.33-1.58	0-6
Xanthidium	<.002-.013	.04-.15	<.03-.27	.27-1.85	.38-1.95	0-18

hypotheses concerning desmid distribution and water chemistry then will be considered.

The range in chemical conditions under which the various desmid genera occurred is summarized in Table 11. To determine overall relative tolerance of the genera, the extent of the range (i.e. the difference between maximum and minimum values) of each parameter for each genus was calculated from Table 11. Then the genera were ranked for each parameter, with the widest range given a rank of 1, the next widest a rank of 2, etc. The ranks for each genus were then summed and relative tolerance ratings assigned, the lowest rank sum receiving a tolerance rating of 1, the second lowest 2, etc. These results appear in Table 12.

Considering relative tolerance to all chemical parameters simultaneously, *Staurastrum* appears to be by far the most tolerant of the desmid genera encountered. Its ability to survive a wide range of chemical conditions may account, in part, for its prominence in the euplankton and/or aufwuchs of all six lake types in terms of frequency, density, and importance values. *Cosmarium*, with the second highest tolerance rating, and *Closterium*, with the fifth highest tolerance rating, occurred in the euplankton and/or aufwuchs communities of all lake types except for spring ponds. *Bambusina* (tolerance rating of 3) was one of the more prominent desmids in the 3 types

Table 12. Tolerance Ranges and Tolerance Ratings of Desmid Genera.

Genus	Conductivity		pH		CO_2		O_2		PO_4 - P	
	Range	Rank	Range	Rank	Range	Rank	Range	Rank	Range	Rank
Arthrodesmus	98	4	4.4	5	20	10	13	5	.104	9
Bambusina	85	5	5.1	1.5	21	5.5	15	1.5	.135	8
Closterium	475	2	4.8	3.5	21	5.5	13	5	.468	5
Cosmarium	474	3	4.8	3.5	21	5.5	13	5	.747	3
Desmidium	39	8.5	1.4	10.5	21	5.5	13	5	.427	6
Docidium	4	19	0.2	19	6	19	1	19	.020	18.5
Euastrum	42	6.5	3.0	7	21	5.5	11	8.5	.519	4
Gonatozygon	6	18	0.7	18	13	16.5	5	18	.020	18.5
Hyalotheca	34	10	3.7	6	18	13	9	12	.146	7
Micrasterias	14	15	1.3	13.5	13	16.5	8	14	.046	13
Netrium	14	15	2.3	8	21	5.5	13	5	.955	2
Penium	39	8.5	1.2	16	21	5.5	7	16.5	.026	17
Pleurotaenium	42	6.5	1.4	10.5	18	13	8	14	.058	11
Sphaerozosma	7	17	1.3	13.5	21	5.5	10	10.5	.039	14
Spondylosium	14	15	1.4	10.5	18	13	8	14	.033	15
Staurastrum	506	1	5.1	1.5	28	1	15	1.5	.967	1
Tetmemorus	25	12	1.2	16	13	16.5	7	16.5	.029	16
Triploceras	21	13	1.2	16	13	16.5	10	10.5	.058	11
Xanthidium	30	11	1.4	10.5	19	11	11	8.5	.058	11

Genus	Na^+		Cl^-		$SO_4^{=}$		Rank Total	Tolerance Rating
	Range	Rank	Range	Rank	Range	Rank		
Arthrodesmus	20.4	2.5	26	5.5	9	10.5	139.0	8
Bambusina	10.2	7.5	11	13	50	4	95.5	3
Closterium	11.4	4	25	7.5	57	3	95.5	5
Cosmarium	10.2	7.5	25	7.5	59	1.5	78.0	2
Desmidium	10.2	7.5	9	15	20	7	105.0	4
Docidium	1.7	18	5	18	3	17	316.0	19
Euastrum	20.4	2.5	26	5.5	28	5	97.5	6
Gonatozygon	1.7	18	6	17	3	17	298.5	18
Hyalotheca	7.3	11	37	3	18	8.5	163.0	10
Micrasterias	1.7	18	7	16	4	15	235.5	14
Netrium	5.1	12.5	12	12	22	6	129.5	7
Penium	4.2	14	37	3	18	8.5	138.5	9
Pleurotaenium	10.2	7.5	16	9	7	12	184.0	12
Sphaerozosma	2.7	15	15	10.5	3	17	232.0	15
Spondylosium	1.8	16	3	19	3	13.5	249.0	16
Staurastrum	83.1	1	138	1	59	1.5	37.0	1
Tetmemorus	10.2	7.5	10	14	3	13.5	251.5	17
Triploceras	5.1	12.5	15	10.5	2	19	229.0	13
Xanthidium	10.2	7.5	37	3	9	10.5	166.0	11

Table 12 continued

Genus	Total N		Total Alkalinity		Ca^{++}		K^+	
	Range	Rank	Range	Rank	Range	Rank	Range	Rank
Arthrodesmus	1.64	10	41	5	13.7	5	2.2	8.5
Bambusina	6.96	5	50	4	17.8	4	2.2	8.5
Closterium	4.29	7.5	324	1.5	63	1.5	3.7	3.5
Cosmarium	4.29	7.5	324	1.5	63	1.5	2.4	5
Desmidium	11.58	3	6	12.5	7.6	10	6.6	1.5
Docidium	.10	19	1	19	1.0	18	1.4	19
Euastrum	6.88	6	19	6.5	9.1	6.5	2.2	8.5
Gonatozygon	.14	18	2	17.5	.4	19	1.8	16
Hyalotheca	2.19	9	6	12.5	6.2	12	2.1	13
Micrasterias	.91	16	6	12.5	4.5	14	1.8	16
Netrium	12.49	2	18	8.5	8.0	8.5	2.2	8.5
Penium	11.0	4	4	16	6.4	11	6.6	1.5
Pleurotaenium	1.20	13	19	6.5	9.1	6.5	2.1	13
Sphaerozosma	1.14	14	2	17.5	3.2	15	2.2	8.5
Spondylosium	.44	17	6	12.5	4.8	13	1.6	18
Staurastrum	12.97	1	247	3	50	3	3.7	3.5
Tetmemorus	1.09	15	6	12.5	2.8	16	1.8	16
Triploceras	1.25	12	6	12.5	2.7	17	2.1	13
Xanthidium	1.57	11	18	8.5	8.0	8.5	2.2	8.5

Genus	Total P		NO_2 - N		NO_3 - N		NH_3 - N		Org-N	
	Range	Rank	Range	Rank	Range	Rank	Range	Rank	Range	Rank
Arthrodesmus	.14	11	.019	10	.025	19	.27	8	1.40	11
Bambusina	1.38	6	.618	2	2.17	5.5	.26	11.5	6.33	3
Closterium	1.11	8	.02	9	.95	7	.20	15	3.28	7
Cosmarium	1.59	4	.056	8	3.22	3	1.62	3	3.20	8
Desmidium	2.08	1.5	.118	4	3.40	1.5	2.26	1	5.86	5
Docidium	.02	19	.003	19	.01	18	.02	18.5	.04	19
Euastrum	1.38	6	.618	2	2.17	5.5	.27	8	6.16	4
Gonatozygon	.08	15.5	.004	18	.05	17	.02	18.5	.13	18
Hyalotheca	.18	10	.018	11	.41	8	.27	8	1.72	9
Micrasterias	.19	9	.013	13	.13	10	.27	8	.65	16
Netrium	1.88	3	.06	7	.25	9	.32	5	11.91	2
Penium	2.08	1.5	.12	6	3.40	1.5	2.23	2	5.34	6
Pleurotaenium	.09	13	.13	5	.09	13	.15	16.5	1.02	14
Sphaerozosma	.07	17	.011	14.5	.08	14	.15	16.5	1.13	12
Spondylosium	.08	15.5	.014	12	.07	15	.24	13	.50	17
Staurastrum	1.38	6	.618	2	2.72	4	.70	4	12.29	1
Tetmemorus	.05	18	.006	17	.06	16	.23	14	.83	15
Triploceras	.09	13	.009	16	.10	12	.26	11.5	1.05	13
Xanthidium	.09	13	.011	14.5	.11	11	.27	8	1.58	10

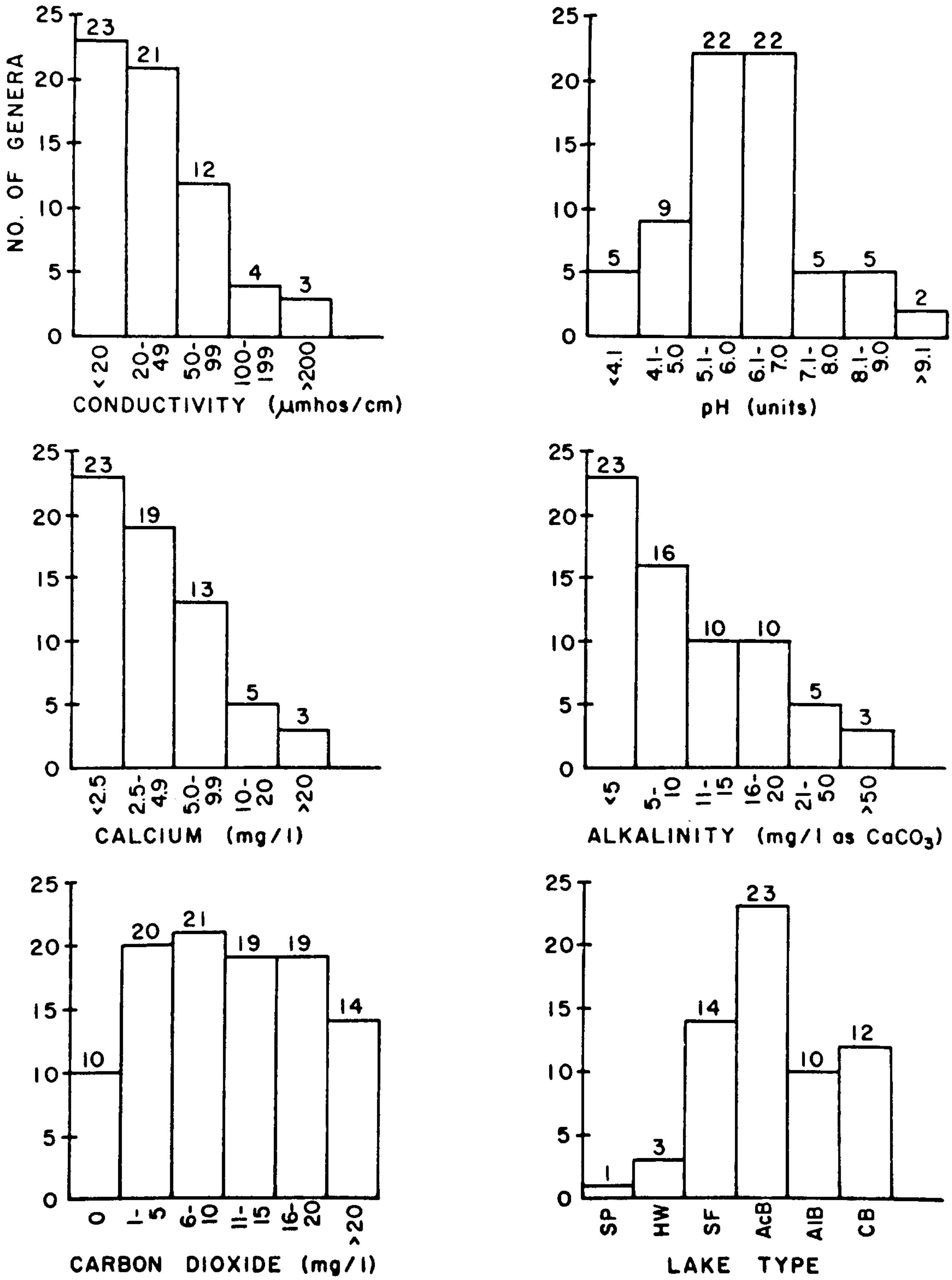

Fig. 2. Relationships between the occurrence of desmid genera and particular environmental parameters. (Numbers on top of each bar indicate the number of desmid genera present.)

of bog environments, and *Desmidium* (tolerance rating of 4) was among the more prominent desmids of soft water lakes and acid bogs. It also occurred in closed bogs and alkaline bogs.

The five least tolerant genera were detected in only 1 or 2 lake types, one of which was the acid bog. In most cases these genera did not play a prominent role in terms of frequency, density or relative importance. It was not possible to calculate tolerance ratings for *Phymatodocis, Roya,* and *Spinoclosterium* because of their presence at only 1 locality. Similarly, overall tolerance ratings could not be computed for *Cylindrocystis* and *Spirotaenia* because of incomplete data or very low levels of certain chemical species at all localities where the taxa were recorded.

Apparent correlations exist between the number of desmid genera present at a locality and the levels of certain chemical parameters in that locality (Fig. 2). Thus the greatest number of genera occur when conductivity levels are under 20 μmhos/cm, the pH is 5.1-7.0, calcium levels are less than 2.5 mg/l, alkalinity readings are below 5 mg/l (expressed as $CaCO_3$), and CO_2 levels are 1-20 mg/l. Five or fewer genera, in contrast, were detected in waters where conductivity levels exceeded 100 μmhos/cm, and/or pH readings were over 7.0, and/or calcium levels surpassed 10 mg/l, and/or alkalinity readings were greater than 20 mg/l. Similarly only 10 genera were recorded from waters where carbon dioxide levels of 0 mg/l occurred.

Of the six lake types covered in these investigations, the chemical environments (Table 13) of acid bogs most nearly correspond to the apparent optima for the occurrence of desmids. This assessment supports the suitability rating of acid bogs based on biological criteria (Table 5, 10) and concurs with the observed qualitative richness of desmid genera in acid bogs (Table 4, 9). Conversely, the chemical environments of spring ponds and hard water lakes differ sharply from the apparent chemical optima for the occurrence of desmids, and this correlates with their low biological suitability rating (Table 5, 10) and the paucity of desmid genera present.

Apparent correlations also occur between the number of desmid genera present and the levels of Mg^{++}, K^+, Na^+, Cl^-, and $SO_4^=$ in the water (see Table 11). All of these ions, however, contribute to the conductivity levels which have been discussed above. In general, higher levels of the various ions correspond to the occurrence of fewer desmid genera.

Meaningful relationships between levels of the various nitrogen and phosphorous species and the occurrence of desmid genera are difficult to detect because the chemical readings reflect only the amounts present in the water and do not necessarily take into account any nitrogen or phosphorous bound up in biological tissues or in the sediments.

Desmid Distribution and Water Chemistry

The apparent correlation between desmid distribution and certain factors in the chemical environment has been recognized for many years, and a number of hypotheses (see Hutchinson 1967, pgs. 330-333 and Prescott 1946, pgs. 667-670 for reviews) have been offered to account for the observed situation. The most widely accepted views suggest that calcium concentrations (or calcium and magnesium concentrations), or pH-conductivity relations, or pH-bicarbonate-CO_2 relations govern desmid distributions.

A number of investigators (e.g. Hutchinson, 1967; Hutchinson & Pickford, 1932; Strom, 1921; Wade, 1957) have postulated that desmids are calciphobic and that desmid diversity and abundance decrease as calcium concentrations increase. Thus, environments with low calcium levels (e.g. acid bogs, soft water lakes) presumably favor desmid development while environments with high calcium levels (e.g. spring ponds, hard water lakes) presumably retard desmid development.

Other studies (e.g. Mevius, 1924; Ruttner, 1963) suggest that total electrolyte content in conjunction with pH control the distribution of many organisms, including desmids, by affecting the permeability of the plasmalemma. According to this hypothesis, alkaline pH's greatly increase plasmalemma permeability. Increased permeability in environments where electrolyte content (as measured by conductivity) is high results in the cells being flooded by excess ions, and this, in turn, causes death. Such flooding does not occur in situations where conductivity levels are high but pH values are acidic because of reduced plasmalemma permeability. Similarly ionic flooding does not occur in situations where conductivity levels are low, regardless of pH. Thus, hard water lakes and spring ponds (alkaline pH, high conductivity) are supposedly unsuitable for desmid development in comparison with soft water lakes and acid bogs (acid pH, low conductivity).

A third hypothesis (Moss, 1972, 1973a-c) suggests that desmid distribution is controlled by the availability of free CO_2 for photosynthesis. At acidic pH levels, most carbon available for photosynthesis will be in the form of

Table 13. Summary of water chemistry conditions in the various lake types.

All values expressed as mg/l except for conductivity (μmhos/cm) and pH (units). N.A. = data not available.

Parameter	Spring Ponds		Hard Water Lakes		Soft Water Lakes		Acid Bogs		Lake Samples Alkaline Bogs		Mat Samples Alkaline Bogs		Closed Bogs	
	Range	Mean	Range	Mean	Range	Mean	Range	Mean	Range	Mean	Range	Mean	Range	Mean
Conductivity	520-619	584	228-490	375	16-56	32	14-61(180?)	27	37-103	79	41-78	59	30-429	104
pH	7.3-7.5	7.4	8.30-8.80	8.58	6.5-7.0	6.8	5.6-7.0	6	7.1-9.1	8.0	4.4-7.3	5.7	4.0-5.9	4.5
CO_2	24-32	29	N.A.	N.A.	3-6	4	0-21	8	0-10	4	40-54	45	N.A.	N.A.
O_2	4.0-9.0	7.7	N.A.	N.A.	7-13	11	2-15	9	9-17	12	2-11	4	N.A.	N.A.
PO_4-P	.014-.030	.020	.014-.051	.023	<.005-.072	.040	.011-.058	.033	<.005-.104	.051	.017-.095	.068	.015-.967	.310
Total P	.03-.06	.04	.01-.08	.04	.02-.22	.09	.02-.12	.06	.02-.13	.08	.03-.16	.25	.04-2.12	.85
NO_2-N	.002-.021	.010	.000-.032	.007	.004-.013	.009	<.002-.014	.06	.003-.021	.011	.002-.036	.019	.01-.62	.09
NO_3-N	2.35-2.94	2.61	<.04-.39	.12	.07-.28	1.36	<.04-.27	.08	<.04-.27	.06	.04-1.94	.60	.16-3.44	1.02
NH_3-N	.05-.23	.14	<.03 .12	N.A.	<.03-.15	.07	<.03-.27	.06	<.03-.70	N.A.	.04-.94	.29	<.03-2.26	.44
Org. N	.34-.66	.56	.64-1.48	.96	.44-1.31	.97	.24-1.85	.90	.34-1.36	.77	.72-3.53	1.9	.95-12.63	3.96
Total N	3.07-3.63	3.34	.76-1.53	1.12	.54-1.58	1.18	.33-1.95	1.06	.39-2.25	1.00	.80-6.43	2.91	1.19-13.30	5.52
Total Alkalinity	247-290	271	110-324	196	1-19	8	0-21	2	14-50	38	12-39	20	0-17	1
Ca^{++}	50-74	66	35-63	48	2.7-9.1	5.0	0-99	3	7.5-20.8	14.8	<2.0-12.0	8.7	2.3-12.3	5.7
Mg^{++}	25-43	36	N.A.	N.A.	N.A.	N.A.	<2.0-2.5	N.A.	<2.0-7.6	5.1	<2.0-7.9	4.5	<2.0-5.2	3.2
K^+	N.A.	N.A.	N.A.	N.A.	N.A.	N.A.	<.5-2.2	N.A.	<.5-1.9	1.0	<.5-2.1	1.4	<.5-6.6	2.1
Na^+	N.A.	N.A.	N.A.	N.A.	N.A.	N.A.	<1.0-11.5	N.A.	<1.0-4.8	2.4	<1.0-4.7	3.1	<1.0-83.1	14.8
Cl^-	21-32	26	13-27	18	2-18	7	2-39	6	4-28	10	5-8	6	2-140	27
$SO_4^=$	27-32	29	3-30	18	6-14	8	1-12	5	3-8	6	3-35(92?)	17.7	7-40	21

free CO_2 (see Hutchinson, 1957, p. 657). At alkaline pH levels, more and more of the carbon becomes bound as bicarbonate or carbonate and less and less remains as free CO_2 under most circumstances (an important exception occurs in calcareous spring ponds; its bearing on this hypothesis is discussed below). Assuming most desmids require free CO_2 (i.e., they cannot utilize HCO_3^-) for photosynthesis, acidic environments with a ready source of free CO_2 (e.g., acid bogs) would favor desmid development whereas alkaline environments with low or nonexistent free CO_2 (e.g., hard water lakes) would retard desmid development.

In addition to the above three hypotheses, a fourth idea, developed in conjection with experimental work on *Sphagnum* (Clymo, 1973), merits consideration. Clymo (*op. cit.*) found that alkaline pH's (7.6) acting in concert with high levels of calcium (100 mg/l) caused the death of *Sphagnum* plants, whereas high pH or high calcium alone did not adversely affect the plants. Similarly, low pH and low calcium in concert did not adversely affect *Sphagnum* growth. If desmids as a group respond similarly to varying combinations of pH and Ca^{++}, then environments with high pH and Ca^{++} (e.g., spring ponds, hard water lakes) would retard desmid development whereas environments low in either or both pH and Ca^{++} (e.g., acid bogs with surrounding *Sphagnum* mats) would tend to favor desmid development.

The available field and laboratory data do not provide a clear indication as to which of the above hypotheses, if any, most accurately accounts for observed desmid distributions. Field data collected during the investigations of Wisconsin lakes show an inverse relationship between calcium levels and desmid diversity (Fig. 2C) and thus supports the hypothesis that most desmids may be calciphobic. Tassigny (1971), working with axenic cultures of four desmids, found the growth was markedly reduced in the three species normally found in oligotrophic environments (see Moss, 1973c for definitions of oligotrophy and eutrophy) when calcium levels were increased. The species normally found in eutrophic environments prospered equally well at all calcium levels. Thus Tassigny's results also suggest that most desmids are calciphobic. Moss (1972), however, concluded from laboratory experiments on a variety of algae (including 11 desmids) that calcium concentration (range of 0.02-100.0 mg/l) does not affect the growth of desmids regardless of their natural distribution and that, consequently, experimental evidence does not support the hypothesis that most desmids are calciphobic. The current evidence regarding relationships between calcium levels and desmid distribution therefore appears to be contradictory.

The second hypothesis implicating pH-conductivity relations as a controlling factor in desmid distribution is also attended by apparently contradictory evidence. The Wisconsin field studies, which confirm the observations of a number of earlier investigators, indicate that a marked reduction in desmid diversity occurs in environments (e.g., spring ponds, hard water lakes) with alkaline pH's and conductivity levels over 100 μmhos/cm. Desmid diversity is greatest where pH values are acidic and conductivity levels are low (acid bogs, soft water lakes). Intermediate diversities occur under acidic conditions with increased conductivity levels (alkaline bogs, closed bogs). A drastic reduction in desmid diversity occurs when pH values go above 7.0, a condition which Ruttner (1963) states is almost invariably accompanied by increased conductivities in natural environments. Experiments conducted by Moss (1973a) on three desmids, however, suggest that conductivity levels in excess of 100 μmhos/cm when combined with alkaline pH readings do not always adversely affect survival and growth rates. Indeed, Moss (1973a, p. 168) concludes that '...the possibility of toxicity of high ionic content has been experimentally eliminated.'

The third hypothesis – that desmid distribution is controlled by availability of free carbon dioxide – gains support from the experimental studies of Moss (1972, 1973a-c). Based on extensive laboratory investigations, Moss presumably eliminated calcium concentrations and conductivity-pH relations as control factors in desmid distribution, assumed that most desmids require free CO_2 for photosynthesis, and, using known pH-bicarbonate-CO_2 relations (see Hutchinson 1957, p. 657), concluded that pH indirectly governs desmid distribution by controlling the amount of free CO_2 available. Thus the desmid flora should reach its greatest diversity in environments with readily available free CO_2 and should be comparatively depauperate in environments poor in free CO_2, regardless of calcium concentrations or conductivity levels.

Field data gathered during the course of investigations of Wisconsin desmid communities apparently do not support CO_2 availability as the sole factor in controlling desmid distributions. Thus 10 genera (Table 11) were encountered in situations where free CO_2 levels apparently were 0. Included were genera (e.g., *Cosmarium, Staurastrum*) found in a number of lake types and genera (e.g., *Phymatodocis, Sphaerozosma*) confined to one or two lake types. Moreover, the six Wisconsin spring ponds all had plentiful levels of CO_2 (which supposedly makes them conducive to desmid development), but their desmid flora was the most depauperate of all six lake types studied. Indeed, plants of only one genus (*Staurastrum*) were encountered in only one of the six ponds. Thus field observations are not supportive of the hypothesis that CO_2 levels alone govern desmid distribution.

The recent experimental work of Clymo (1973) on *Sphagnum* suggests the possibility that alkaline pH values in concert with high (ca. 100 mg/l) calcium concentrations may affect desmids adversely. This combination of factors exists in Wisconsin spring ponds and hard water lakes where the desmid diversities are low. Similarly, the open waters of alkaline bog lakes (pH 7.1-9.1; Ca^{++} 7.5-20.8) have a much less diverse flora than the mats (pH 4.4-7.3; $Ca^{++} < 2.0$-12.0) [see Woelkerling, 1976]. In acid bogs and soft water lakes, pH is acidic, Ca^{++} levels are low (Table 13), and desmid diversity is high. All this data support the experimental observations of Clymo (1973). The work of Moss (1972), however, indicates that at least some desmids naturally present in acid waters with low Ca^{++} levels can also survive and grow in alkaline waters with Ca^{++} levels up to 100 mg/l. Thus the hypothesis that alkaline pH and high Ca^{++} levels act in concert to adversely affect desmid diversity also is attended by apparently contradictory evidence.

Concluding Remarks

The problem of accounting for observed desmid distributions in natural environments appears complex and has not been resolved. All hypotheses involving apparent correlations between certain chemical parameters and desmid diversity have both favorable and unfavorable evidence associated with them, and obviously more research is needed.

Part of the current dilemma stems from attempts to extract sweeping generalizations from experiments on an extremely limited number of taxa. To conclude, for example, that high conductivity levels do not adversely affect desmids (Moss, 1973a, p. 164, 168) on the basis of experiments on only three of the thousands of described species seems, to these investigators at least, to be exceedingly presumptuous. Meaningful conclusions can be drawn, it seems, only from far more broadly based experimentation. Carefully planned laboratory studies are needed on a wide variety of desmids to determine to what extent, if any, various species are calciphobic, to elucidate to what extent, if any, ionic content (i.e., conductivity) affects desmids, to establish whether none, some, most, or all desmids require free CO_2 for photosynthesis, and to gain insight into the role, if any, played by pH.

While the above chemical parameters are most commonly implicated in explaining desmid distributions, other factors also could be involved. Thus little is known about the effects of other chemical parameters. For example, to what extent, if any, is bicarbonate toxic to desmids? Moss (1973a, p. 164 and Fig. 4) found, for instance, that the growth of two desmids was suppressed when 420 mg/l $NaHCO_3$ was added to the cultures. Likewise, little is known about the ability of desmids to utilize the various nitrogen species (see, however, Moss, 1973b), and more work is needed.

The role of various biological factors also remains largely unexplored. Little is known about the ability of desmids to compete with other algae for available nutrients. Perhaps the environments of acid bogs give desmids a greater competitive advantage than do those of hard water lakes or spring ponds. There also is a paucity of information on desmid-bacterial relations. Perhaps desmids are favored by an association with bacteria which are largely restricted to certain types of environments. These and many other questions must be answered before the problem of explaining desmid distributions is finally resolved.

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