

DIATOM AND PROTOZOAN COMMUNITY ANALYSIS
AND COLONIZATION ON ARTIFICIAL
SUBSTRATES IN LENTIC HABITATS

by

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(ABSTRACT)

The purpose of this research was to examine the colonization process and relationship of physico-chemical parameters to diatom and protozoan communities colonizing polyurethane foam (PF) artificial substrates in lentic habitats. This was the first study to utilize multivariate techniques for comparison of protozoan and diatom communities.

The following hypotheses were examined in this study:

1. diatom and protozoan species accrual is similar because the organisms are approximately the same size and share similar ecological conditions,
2. protozoan assemblages are influenced by the physico-chemical parameters of their environment, and
3. diatoms and photosynthetic protozoans are more closely related to the physico-chemical parameters of their environment than are the protozoans of all trophic groups.

PF substrates were placed in the littoral zone of lentic habitats. Substrates were sampled through a time

series and examined for their diatom and protozoan species' presence-absences. The first hypothesis was tested by using the MacArthur-Wilson equilibrium model and by fitting the data to the model by non-linear least squares regression. Protozoan species accrual fit the model in most cases, while diatom species accrual did not. The second part of the research dealt with five lentic habitats in northern lower Michigan which were sampled as described above and concurrent with organismal sampling several physico-chemical parameters were sampled. These environmental parameters included pH, alkalinity, conductivity, temperature, and concentrations of dissolved oxygen, chloride, silica, ammonia, and total and ortho-phosphate. Protozoan communities were examined using reciprocal averaging ordination. It was found that the bog and marsh had distinct communities, while the three lakes did not. Several physico-chemical parameters and factors correlated significantly with axes generated by samples in species space. The final section tested the degree of relationship among diatoms, autotrophic protozoans, and protozoans to the physico-chemical parameters and factors. pH had the highest correlations with the first axes for each group. Diatom communities had the greatest degree of relationship to the physico-chemical parameters, evidence for this is provided by the greatest number of correlations between ordination axes and the physico-chemical parameters and factors.

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Introduction

Ecological theories are of two types: they can be specific for a particular area, group of organisms, or time; or be general, equally applicable across ecosystems and groups of organisms. Several of the many ecological theories include colonization theory and that physico-chemical parameters influence the distribution of organisms. The present study is a comparison of these two general theories for two groups of aquatic organisms in lentic habitats: the diatoms and the protozoans. This is the first study to simultaneously examine these two groups.

This report begins with an examination of work performed to date on diatom and protozoan ecology. The present study is divided into three chapters. Chapter 1 deals with a comparison of the colonization dynamics of diatoms and protozoans on introduced substrates in lentic habitats. Chapter 2 is a first examination of the physico-chemical parameters that are related to the distribution of the entire protozoan community. As will be seen, the sheer size and complexity of these communities lend themselves to utilization of multivariate statistics, tools developed for data reduction and interpretation. Chapter 3 compares the physico-chemical parameters that are related to the distribution of diatom and protozoan communities. A third group, the autotrophic protozoans, also included in the protozoans, are examined. An additional dimension was added to this chapter, and this is to compare the relative degree

of relationship of the different communities to physico-chemical parameters. This is made possible by interpretation of multivariate axes using correlational techniques.

Concerning diatom ecology, no one in the field has contributed as much to the knowledge that exists today as have Ruth Patrick and her colleagues. For example, they have shown the effect of pollution on the species distributions of diatoms on glass slides. Pollutational stress caused the number of species in the mode, when a plot of species per interval was made over individuals per species (octaves), to be less than half of an unpolluted site (Patrick et al. 1954). In this same study it was shown that 75-85% of the species found in overall collections were also found on the slides.

In a river not adversely affected by pollution, the majority of species are represented by a relatively small number of specimens, and thus are rarely collected. On the other hand a small number of species are represented by a fairly large number of specimens. In a polluted river, the more sensitive species are eliminated. Tolerant species thus spread out and occupy a greater proportion of the now available habitat. If the pollutational stress is too severe, the entire flora is eliminated (Patrick et al. 1954).

Patrick (1967) has studied the effect of invasion rate, size of the species pool, and size of area (glass slides) on the structure of the diatom community. From this study it is evident that area, number of species in the species pool

available for colonization, and the rate of invasion by the organisms greatly influence the number of species and diversity of the community found on the slides.

Additional research with diatoms has included their use in the assessment of water quality (Patrick 1967; Lange-Bertalot 1979; and Descy 1979). These studies have often centered on the concept of indicator species to determine the type of water being tested. The indicator species concept has been challenged and another method developed that employs the entire community to indicate the health of the water. Cairns (1974) discusses both methods and points to weaknesses in the indicator species approach, seeming to prefer the community structure method.

Several multivariate techniques have been used in an attempt to determine the environmental parameters that influence diatom communities. These include a study performed to examine the degree to which the diatom flora can be partitioned into discrete associations and to relate the community composition to selected physical properties (McIntire 1973). In the estuary studied it was shown that the distribution of attached diatoms is primarily regulated by such physical factors as salinity, exposure, light, temperature, and by biological interactions.

Additional work has been done on the edaphic diatoms in salt marshes. Sullivan (1975) suggested that the difference between five measured communities was closely related to differences in temperature and elevation between the

habitats, and was also the result of diatom-filamentous algae interactions.

A recent thesis (Stewart 1983) focused on diatom community structure in gravel pit ponds. In these ponds there were no clear cut gradients. With the use of factor analysis to reduce the dimensionality of a complex data set and ordination techniques (Gauch 1977), approximately 25% of the pond separation in species space could be explained by a productivity factor made up of loadings from productivity and phosphorus measurements.

Cairns and Ruthven (1970) have determined the relationship between substrate size and species richness within a minimal size range. Smaller substrates generally had fewer species than the larger ones. They found a linear relationship between log volume and number of species.

Yongue and Cairns (1971) demonstrated that the number of species colonizing foam units reached an asymptote fairly quickly, this number then oscillated due to the appearance and disappearance of transient species. This is similar to the equilibrium theory of island biogeography (MacArthur and Wilson 1963, 1967) with the suggestion that the biota of any island is in a dynamic equilibrium between immigration of new species onto an island and extinction of species already present. Similar results were found with arthropods when a group of small red mangrove islands were defaunated (Simberloff 1969; Simberloff and Wilson 1969, 1970; Wilson and Simberloff 1969).

Other studies of protozoan colonization have shown no clear differences in pattern, related to depth, of colonization or species diversity from the surface to 6 m depth in a rather well-mixed epilimnion (Cairns and Yongue 1974). Also (Cairns et al. 1976a) has shown that there were no major qualitative differences in the colonization process of protozoans at different points in a lake at approximately the same point in time.

Cairns' group has also demonstrated that generally good replication of protozoan colonization exists between substrates in a set (Cairns et al. 1976b). Yongue and Cairns (1978) demonstrated that a pioneer community exists (flagellates) reaching equilibrium much earlier than other taxonomic groups.

Various experiments have been performed with protozoans as the test organisms. The effect of island size, distance, and epicenter (source) maturity on colonization has been demonstrated (Henebry and Cairns 1980). Herein they suggest their results indicate agreement with the tenets of the MacArthur-Wilson model. Hairston et al. (1968) performed an experiment to test the relationship between species diversity and stability using protozoa and bacteria. Their findings indicated that sometimes simpler communities could be more stable than complex ones. However they concluded that much more experimental work is necessary.

Protozoans have also been successfully used to monitor stream pollution (Henebry and Cairns 1980). A sublethal

dose of copper sulfate has also been shown to have decreased the rate of protozoan colonization of both mature and immature systems (Cairns et al. 1980).

It can be seen from this brief survey that many questions concerning protozoan ecology and colonization have been approached. It is essential that both groups be examined simultaneously in order to understand their interactions. Very few studies have been done on both diatoms and protozoans at the same time, in the same laboratory, by the same investigator. An exception to this statement is the preliminary work done on the colonization of diatoms and protozoans (Cairns et al. 1983). This paper suggests that the link between diatoms and protozoans at the species level is not a strong one, at least at the early stages of colonization.

The purpose of this project was to examine the colonization processes of both diatoms and protozoans. This research led to investigation of the important physico-chemical parameters that influence the two types of organisms under investigation.

Hypothesis

The hypotheses under investigation are that:

1. colonization dynamics for diatoms and protozoans are similar since the organisms are approximately the same size and share the same ecological conditions,
2. the same environmental parameters (including possibly

temperature, pH, conductivity, hardness, alkalinity, nutrient levels, and oxygen) are related to both protozoan and diatom communities. These basic trends exist for both a small eutrophic pond, and a series of lakes of different physical-chemical composition, and

3. diatoms are more closely related to the physico-chemical parameters of their environment than are the protozoans.

Objectives

The objectives of this project were to:

1. determine if a relationship exists between colonization dynamics for diatoms and protozoans on artificial substrates,
2. examine the physico-chemical parameters that are related to the distribution of the protozoan community in divergent lentic habitats, and
3. compare the physico-chemical parameters and degree of relationship between diatom and protozoan components of the aquatic community and their physico-chemical environment.

CHAPTER I

DIATOM AND PROTOZOAN SPECIES ACCRUAL ON ARTIFICIAL SUBSTRATES IN LENTIC HABITATS

Abstract

The objectives of this study were to examine the colonization process for diatoms and protozoans in a variety of Michigan lakes and in a southwest Virginia pond, and to examine artificial substrate colonization during the first day of immersion. We hypothesized that diatom and protozoan species accrual would be similar because the organisms are approximately the same size and share similar ecological conditions. Polyurethane foam substrates were placed in the littoral zone of these lakes, and species accrual was monitored after 1, 3, 7, 14, and 21 days of exposure. The species-time data were fitted to the MacArthur-Wilson equilibrium model using non-linear least squares regression. Protozoan species accrual fit the model in most cases; however, the diatom data did not. Further evaluations of species accrual by short-term (<1 day) exposure revealed a high number of diatom species in the water column. These results suggest that diatom species accrual on polyurethane foam artificial substrates does not follow MacArthur-Wilson predictions. It appears that diatoms are present in the water column and do not traverse inhospitable terrain but are merely sampled by the substrates. Protozoan species accrual appears to follow predictions of the MacArthur-

Wilson model. Sampling and study methods must be carefully selected even for closely related taxonomic groups.

Introduction

In this investigation, we compared diatom and protozoan colonization processes for communities developing on polyurethane foam (PF) substrates placed in the littoral zone of several lentic systems. Earlier studies suggested that examination of the colonization process may be a better indicator of the chemical-physical status of a lake than protozoan species composition (Cairns et al., 1979; Henebry & Cairns, 1984). Similar measures of diatom species accrual over time in lakes have been lacking. In lotic systems, Stevenson (1983) examined diatom immigration rates. He found species specific effects of current velocity and microhabitat conditions related to size and cell growth habits. We postulated that diatom and protozoan colonization processes are similar because the organisms are approximately the same size and share similar ecological conditions. It is also interesting to examine sampling methods to determine if diatoms and protozoans can be sampled in the same fashion.

A previous study (Cairns et al., 1983) used cluster analysis to examine different ages of colonizing diatom and protozoan communities in 14 lakes in northern lower Michigan. This study indicated that most of the diatom samples from any given lake clustered, while the corresponding protozoan samples did not exhibit such clustering. Cairns et al. (1983) concluded that no strong relationship exists between the two groups of organisms at

the species level during the early phase of artificial substrate colonization.

The objectives of the present study were: (1) to examine the colonization process for diatoms and protozoans in a variety of northern Michigan lakes and in a southwest Virginia pond; and (2) to examine artificial substrate colonization during the first day of exposure.

Materials and Methods

The methods used investigating the 14 Michigan lakes have been described previously (Cairns et al., 1983). The southwest Virginia pond examined was Pandapas Pond, located approximately 10 km west of Blacksburg. Pandapas Pond is a small, soft-water impoundment in the Jefferson National Forest and has been studied previously by Hall et al. (1975).

The sampling techniques used for Pandapas Pond were similar to those used in the northern Michigan lakes. Polyurethane foam (PF) substrates were carefully removed from the littoral zone of the pond after 1, 3, 6, 15, and 21 days of exposure, immediately placed in collecting jars, and returned to the laboratory. Contents were then squeezed into wide-mouth jars and allowed to settle. Reliable individual counts for protozoans are difficult to make since the organisms must be examined while active (for discussion, see Cairns, 1982). Because one of the objectives of this study was to compare the two groups of organisms, similar procedures of enumeration were considered to be appropriate

for the Panadapas Pond segment of the study. In these samples, the living diatom community was examined (430x) after several reference slides were examined using conventional taxonomic methods (cleaning, mounting, examining at 1000x). This avoided including non-living cells as part of the community; e.g., a diatom present on day 1 that dies would be counted as part of the community at day 21 if conventional techniques of cleaning and mounting were used. Therefore, living diatoms (bearing protoplasts) were counted using methods identical to those used for protozoons. Probably, this is adequate for determining the number of species present for comparative purposes. Although this method is not adequate for precise taxonomic identification of diatoms, increased error from including dead cells may mask important ecological processes (Bahr, 1982). The level of separation obtained by a less rigorous approach addresses the more fundamental question of the relative number of different living species. Species enumerations were plotted against individuals encountered; counts were terminated when an apparent asymptotic point was reached (Cairns & Dickson, 1971; de Caprariis et al., 1981; Heck et al., 1975). This usually required systematic examination of 2-4 slides for protozoons and two slides for diatoms.

Additional PF substrates were placed in Pandapas Pond and sampled over a 24 h time period. Two substrates were removed and examined for protozoons and diatoms using the

same techniques as before at 0, 1, 3, 6, 12, and 24 h of exposure. Time 0 signifies immediate extraction of the PF substrate after immersion. Other PF substrates were soaked overnight in distilled water, placed into Pandapas Pond, and examined at 0 and 72 h of exposure. During placement into the pond, one substrate for each time period was squeezed; the other was placed into the water as gently as possible. In addition, a 125 ml grab sample was taken and examined in an identical manner to the sample obtained when the 72 h PF substrates were returned to the laboratory.

Data analysis

The species-time data were fitted to the MacArthur-Wilson equilibrium model (MacArthur & Wilson, 1967) using non-linear least squares regression (Helwig & Council, 1979). The model equation is

$$S_t = S_{eq} (1 - \exp^{-Gt}),$$

where: S_t = the number of species at time t ,

S_{eq} = the equilibrium number of species,

G = a fitted rate constant, and

t = time.

The resulting fitted curves were tested for significance of regression using Draper and Smith (1966). Estimates of equilibrium species member (S_{eq}) and the colonization rate constant (G) were obtained directly from analysis. An estimate of time to 90% of equilibrium species

number ($t_{90\%}$) was derived as $t_{90\%} = 2.303/G$ (MacArthur and Wilson, 1967). This estimate is more easily understood as a measure of the rapidity of colonization.

Results

Protozoan colonization for the 14 Michigan lakes was adequately explained by the MacArthur-Wilson model. Figure 1 shows the colonization curves for both protozoons and diatoms in a Michigan lake that was considered typical. On day 1, 77 diatom species were present. This number decreased over time and indicated probable lack-of-fit to the MacArthur-Wilson model. Similar patterns of colonization were observed in other Michigan lakes. On very few occasions, diatom colonization was adequately described by the model, but most of the time it was not. Species maxima for diatoms were commonly reached on day 1 or 3, indicating extremely rapid accrual. In general, species richness decayed following the early peak as has been previously observed (Brown, 1973; Brown and Austin, 1973; Hoagland et al., 1982). Table 1 summarizes these results for the Michigan lakes. Particulary noteworthy are the following: (1) all but three of these lakes have high r^2 values for protozoons, while only two of the lakes' diatom communities have high r^2 ; and (2) estimates of G generally are much lower for protozoan samples than for diatoms, and, therefore, $t_{90\%}$ generally is smaller for diatoms than for protozoons.

Similar patterns were observed for Pandapas Pond (Figure 2). Sampling here was restricted to identification of "living" diatoms, but the same patterns were evident. Adequate fit to the model equation was not obtained for diatoms (Table 2). For protozoans, G values were lower (t90% longer) than for diatoms, and r^2 values were highly significant, indicating adequate fit to the MacArthur-Wilson model. The diatom data are described by larger G (shorter t90%) and low r^2 , suggesting that the model does not adequately describe the data obtained by diatom species accrual.

Further evaluation of species accumulations by short-term substrate exposure with substrates either filled (squeezed) or not filled with pond water revealed a high species density in the water column (Fig. 3, Table 3). A small amount of diatom species accrual occurred over 3 days; however, more than 85% of species richness was attained at 0 h. A 125 ml grab sample revealed species richness in the water column (32 diatom species, 6 protozoan species) to be essentially identical to that of the substrates (Table 3).

Discussion

Protozoons colonize PF substrates placed in lakes as predicted by the MacArthur-Wilson equilibrium model (as shown by this study and others; e.g., Cairns et al., 1969). Diatoms sampled from PF substrates do not show increasing species numbers over time, suggesting that if diatom

colonization of PF substrates occurs, it occurs very rapidly. However, examination of diatom species accrual over 24 and 72 h reveals essentially instantaneous diatom presence. The same number of species (32) was found in the grab sample as was found on 72 h PF substrates (32, 34). Apparently, PF substrates merely collect diatoms from the water column. This does not imply that changes in species composition and relative abundance (i.e., succession) and later colonization or arrival of new species do not occur.

These results suggest two possibilities: (1) diatom colonization of PF substrates in lentic systems does not conform to the MacArthur-Wilson predictions; and (2) PF substrates do not behave as islands for diatoms in lake plankton as they appear to be distributed throughout the water column.

The predictions of MacArthur and Wilson (1967) may not hold for all taxonomic groups in all situations. Detailed analyses of the colonization process as described here are lacking for most taxa, and theoretical predictions based on simplistic assumptions have been soundly criticized (Gilbert, 1980). Our study provides evidence for further question of the theoretical basis for colonization.

Colonization as predicted by MacArthur and Wilson has been confirmed for other groups (e.g., protozoons). Obviously, a more extensive investigation of diatom species accrual is needed, particularly in the context of the widespread use of periphytometers.

The possibility of verifying rapid colonization by decreasing sampling periods is improbable because of the high species richness of diatom flora. Large numbers of diatoms of both planktonic and tychoplanktonic (littoral-benthic) origin are common in the water column (e.g., 1,000-2,000 cells/ml), whereas other groups, such as protozoans, are comparatively rare. For example, Beaver & Crisman (1982) reported 10-200 ciliates/ml in zooplankton samples. Prescott (1962) estimated 10 chlorophyte cells/ml for Lake Mendota. This suggests that diatom colonization does not occur on PF artificial substrates. Because live cells are common and species richness of water column samples great, the movement of species from a habitat patch to a newly created island is unlikely to occur.

Simberloff (1974) has defined an island as ". . . any patch of habitat isolated from similar habitat by different, relatively inhospitable terrain transversed only with difficulty by organisms of the habitat patch." Thus, the PF substrates are indeed islands to protozoans, since the protozoans are much less abundant than diatoms and appear more substrate-oriented. Diatoms are present in large numbers in the water column in most lakes and need not traverse inhospitable "terrain"; they are merely sampled by the PF substrate. Colonization theory is not specifically invalidated because the rapid accumulation of diatom species on the new substrate does not represent a strictly defined colonization process.

It appears that diatoms and protozoons cannot be sampled in the same fashion at all times. The purpose of this study was to compare colonization of artificial substrates in lentic systems, and it was deemed appropriate to sample in exactly the same fashion. The results show that these organisms are distributed unequally, which makes identical sampling inappropriate for colonization studies. However, for other types of studies e.g., comparing the effects of physico-chemical factors on communities, these two groups need to be sampled identically to determine the distribution of species present and the parameters that influence community composition. Since diatoms are present in the water column and need not travel over "inhospitable terrain" in these systems, as this paper suggests, perhaps it is necessary to examine other experimental systems to examine colonization processes of these organisms.

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TABLE 1

Estimates of protozoan and diatom Seq, $G(d^{-1})$, $t_{90\%}(d^{-1})$,
and r^2 values for 14 Michigan lakes.

Lake	Protozoons			
	Seq	G	$t_{90\%}$	r^2
Burt	62.5	0.639	3.60	0.916
Coch	42.2	0.483	4.76	0.543
Dog	45.7	0.742	3.10	0.292
Douglas	43.8	0.397	5.79	0.264
Hoop	36.5	0.350	6.57	0.777
Lancaster	59.1	0.334	6.89	0.875
Larks	37.0	0.436	5.28	0.818
Long	47.4	0.225	10.22	0.839
Munro	46.8	1.329	1.73	0.329
Paradise	44.1	0.663	3.47	0.621
Vincent	54.7	0.180	12.78	0.525
Walloon	38.7	0.238	9.66	0.991
Webb	44.8	0.241	9.54	0.899
Wycamp	74.7	0.300	7.67	0.686

TABLE 1 (cont.)

Lake	Diatoms			
	Seq*	G*	t90%	r ²
Burt	64.5	1.95 x 10 ⁴	<1	0.0
Coch	45.0	5.98 x 10 ¹	<1	0.0
Dog	43.5	2.479	0.93	0.085
Douglas	51.1	1.917	1.20	0.150
Hoop	28.0	1.32 x 10 ²	<1	0.0
Lancaster	49.0	1.18 x 10 ¹²	<1	0.0
Larks	57.0	3.27 x 10 ⁷	<1	0.0
Long	42.2	6.54 x 10 ⁸	<1	0.0
Munro	34.0	9.36 x 10 ¹	<1	0.0
Paradise	53.2	0.789	2.92	0.689
Vincent	22.8	1.16 x 10 ²	<1	0.0
Walloon	38.8	1.18 x 10 ⁸	<1	0.0
Webb	43.1	0.842	2.73	0.549
Wycamp	47.0	5.75 x 10 ¹	<1	0.0

*Note that if G is large, the model is probably not valid over the time measured, making invalid estimates of Seq, G, and t90%. They are included here for comparison.

TABLE 2

Estimates of protozoan and diatom values for Seq, $G(\bar{d}^{-1})$, r^2 , and p-values for five colonization periods from Pandapas Pond.

Protozoons					
Colonization run	Seq	G	t90%	r^2	p
November 1982	55.1	0.256	8.98	0.716	<u><0.001</u>
January 1983	37.0	0.208	11.1	0.663	<u><0.001</u>
February 1983	-	-	-	-	-
March 1983 - Site 1	45.1	0.174	13.22	0.805	<u><0.001</u>
March 1983 - Site 2	39.1	0.213	10.80	0.741	<u><0.005</u>
Diatoms					
Colonization run	Seq	G	t90%	r^2	p
November 1982	-	-	-	-	-
January 1983	37.9	8.94×10^5	<1	0.0	<u>>0.75</u>
February 1983	51.0	0.753	3.1	0.073	<u>>0.50</u>
March 1983 - Site 1	37.6	2.320	0.99	0.230	<u>>0.25</u>
March 1983 - Site 2	37.6	2.667	0.86	0.075	<u>>0.50</u>

TABLE 3

Number of diatom and protozoan species found in PF substrates and a grab sample at time = 0 and time = 72 h (SQ, squeezed; NS, not squeezed).

Time(hrs.)	Diatoms		Protozoons	
	SQ	NS	SQ	NS
0	27	27	6	4
72	32	34	-	-
Grab sample	32		6	

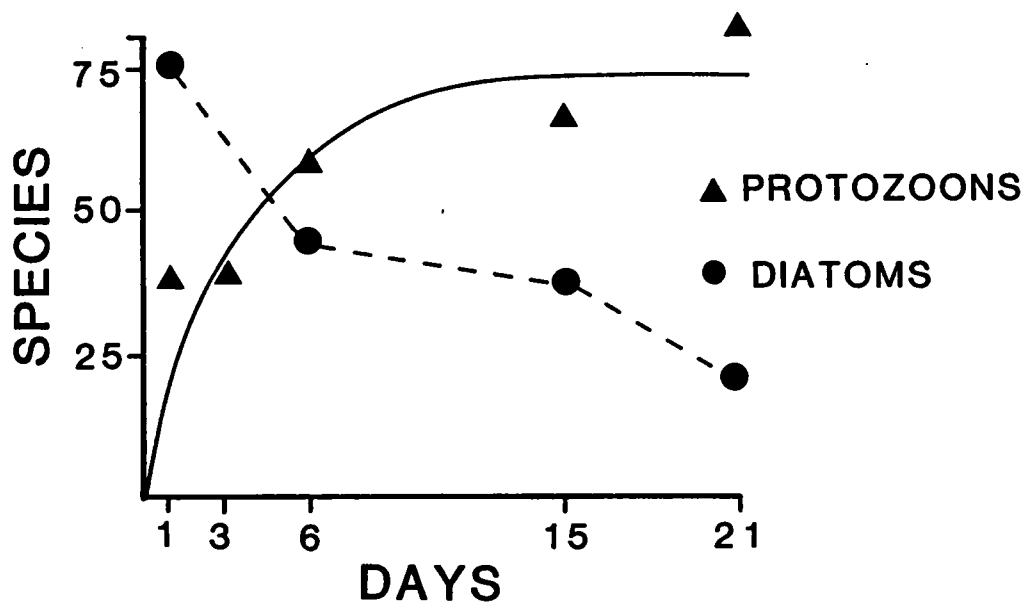


Figure 1. Diatom and protozoan species accrual in a Michigan lake (Lake Wycamp).

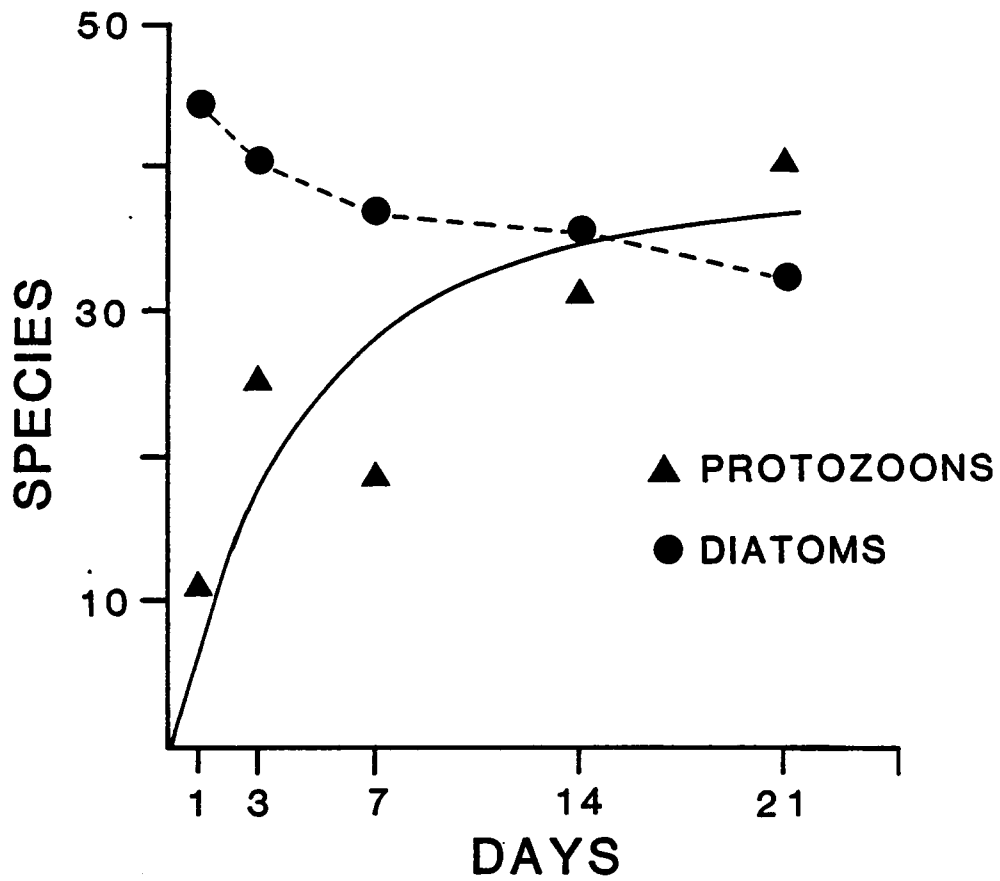


Figure 2. Diatom and protozoan species accrual in Pandapas Pond, Virginia. Plotted points are means of triplicate samples.

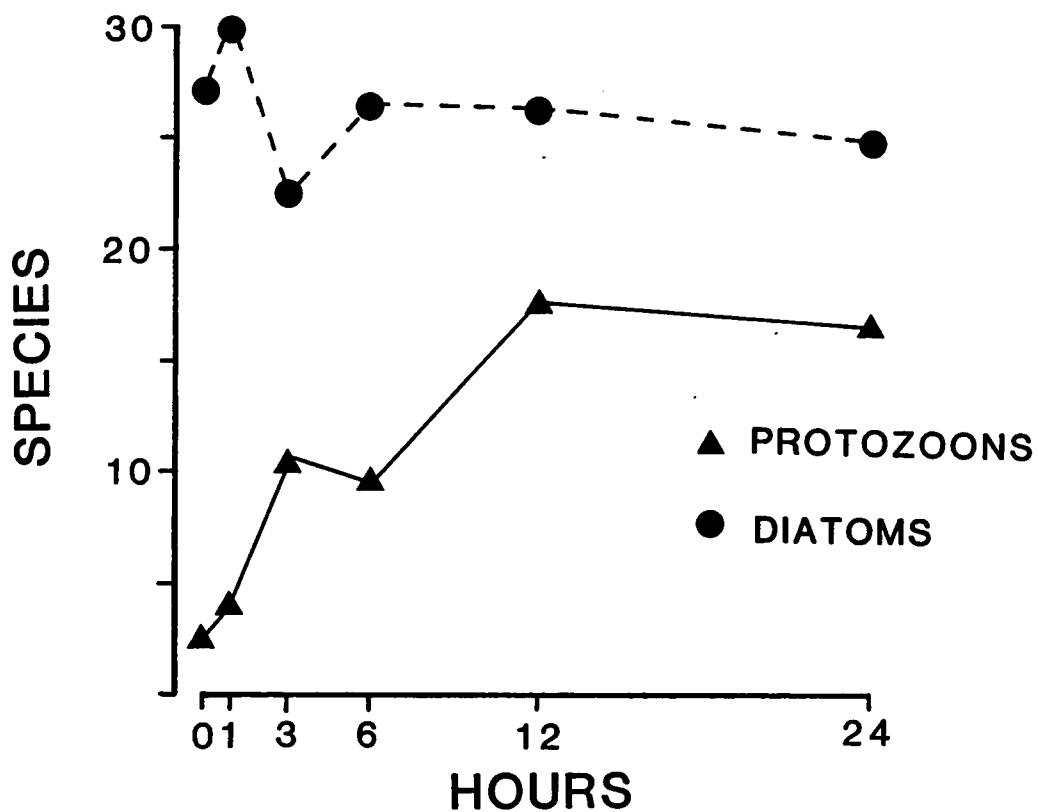


Figure 3. Diatom and protozoan species accrual during a 24-hour period from Pandapas Pond, Virginia. Plotted points are means of duplicate samples.

CHAPTER II

THE STRUCTURE OF PROTOZOAN COMMUNITIES IN LENTIC SYSTEMS

Abstract

The purpose of this research was to examine the roles of physico-chemical parameters in structuring protozoan communities that colonize artificial substrates. Polyurethane foam (PF) substrates were placed in five lentic systems in northern lower Michigan during summer 1983. These lentic habitats represented a range of trophic states and included three lakes, a bog, and a marsh. Triplicate PF substrates were sampled after 1, 3, 7, 14, 21, and 42 days of exposure. During this study, 90 living protozoan samples were examined for the number and kinds of species. Water samples were analyzed concurrent with protozoan collections for several physico-chemical parameters.

A total of 546 protozoan species was recorded. Only seven species were found in over 50% of the samples and 121 species were found in only one sample. The 96 most common species were examined in relation to environmental parameters using several multivariate statistical procedures. Factor analysis (principal components with varimax rotation) performed on the total environmental data set showed that three composite factors explained 85% of the data set variability. A reciprocal averaging ordination (RAO) was used to reduce species presence/absence data and

to separate samples graphically by their species composition. Significant correlations, with RAO generated axes from all five systems, were found for pH, oxygen, and a nutrient factor to axis 1.

Examination of factor analysis on the physico-chemical parameters of the three lakes showed that three factors explained 71% of the environmental data set variability. The RAO generated axis (axis 1) was correlated with silica, ortho-phosphate, and Factor 2, which was primarily comprised of loadings from ortho-phosphate. The bog and marsh physico-chemical data had three factors that explained 93% of the data set variability. The RAO generated axis (axis 1) was related to alkalinity, silica, conductivity, Factor 1 (ion) , and Factor 2 (nutrients). Axis 2 was correlated with Factor 3 (temperature). These techniques support the hypothesis that a limited number of environmental parameters strongly affect protozoan community composition.

Introduction

Examination of factors affecting community organization is one frontier in ecology. Some ecologists believe that communities are highly integrated and structured; others maintain that species are grouped randomly. Picken (1937) first suggested that protozoans occur in communities that have a considerable degree of "social" organization and that simple mechanical factors determine the origin, persistence, and decay of such communities. Evidence for this view has been presented for the occurrence of endogenously determined communities and that these communities are composed of resident species, oscillating colonizers, and transient invaders (Pratt et al. in press; Yongue 1972).

The purpose of this investigation was to examine the relationship between physico-chemical parameters and protozoan communities that colonize polyurethane foam (PF) artificial substrates in three lakes, a bog, and a marsh. The hypothesis was that protozoan communities are assemblages of organisms strongly influenced by habitat parameters in their environment.

Multivariate analyses have made important contributions to several areas of science, including psychology, education, and biology. Biological uses of multivariate analyses have been especially productive in the study of wildlife habitat and its relationship to bird communities (Capen 1980). Green (1979, 1980) has written a selective review of statistical techniques for environmental

biologists covering many of the more commonly used techniques. Several examples of multivariate analyses of interest to community ecologists are discussed below. Many phyto-sociological studies support the hypothesis that certain environmental parameters structure algal and diatom communities (Allen 1971, Allen and Koonce 1973, Bartell et al. 1978, Baybutt and Markarewicz 1981, Cook and Whipple 1982, Karenz and McIntire 1977, Levandowsky 1972, McIntire 1978, Stevenson and Stoermer 1981, Sullivan 1975, 1978, 1982). For example, Levandowsky noted in a study of phytoplankton populations and hydrographic variables in two transient beach ponds and in Long Island Sound, New York that two of the resulting principal axes appear related to salinity and temperature from a comparison of a three-dimensional ordination and habitat parameters. Baybutt and Makarewicz (1981) used several multivariate techniques to show that an increase in blue-green algae could be linked to increases in sodium concentration, phosphorus enrichment, carbon dioxide availability, and several other parameters. Karenz and McIntire (1977) demonstrated that distributional patterns of diatoms in the plankton were related to climatic and hydrographic factors in an estuary. Community distribution was strongly influenced by seasonal rainfall, variable light energy, and temperature. McIntire (1978) was able to explain 41% of the variability in estuary diatom data as associated with salinity, temperature, light energy, and length of exposure.

These studies and others illustrate the utility of multivariate analyses in discerning community patterns. For example, ordination, a method that can be used to separate samples by their species composition, can be used to relate samples and species to environmental gradients and to study patterns of communities as related to patterns of environmental factors (Carleton 1984, Gauch 1977). Examination of protozoan communities has only recently involved multivariate statistical methods for examining community structure. Madoni (1984) examined populations of ciliated Protozoa and delineated ecological relationships between the stations, cenotic affinities, and the biotypology of the watercourses studied. Cairns et al. (1983) performed a cluster analysis on the matrix of Jaccard's coefficients on protozoan and diatom samples from 14 lakes, including several lakes from this present study. Protozoan samples from each lake did not cluster as well nor were they as similar to each other as were diatom samples taken at the same site and time, indicating little relationship between diatom and protozoan communities.

Yongue et al. (1973) examined protozoan communities in chemically disparate, geographically close lentic habitats. Some species were present in both habitats, and other species were found only at one site or the other. The results of their study possibly indicate (a) that some protozoan species exhibit a broad range of environmental tolerances, and (b) that a large random component exists in

the distribution of protozoans. Cairns and Yongue (1973) studied protozoan communities from several areas in a river in conjunction with 23 physico-chemical parameters. Inspection of the protozoan communities with regard to the physico-chemical parameters showed no relationship between these physico-chemical parameters and species distribution. No multivariate analyses were performed as that study was intended primarily as a baseline against which future conditions could be assessed. The present study is designed to examine protozoan communities in relation to physico-chemical parameters using several multivariate statistical techniques.

Materials and Methods

This study was conducted near the northern tip of Michigan's lower peninsula [for a detailed map see Cairns et al. (1983), Henebry and Cairns (1984), or Henebry et al. (1981)]. Colonizing protozoan communities in five lentic ecosystems were examined along with selected physico-chemical parameters. The systems studied included three lakes: Douglas Lake (site of the University of Michigan Biological Station), Lake Munro, and Walloon Lake. These lakes are mesotrophic and are, as shown through this investigation, quite similar in their physico-chemical composition at the sites examined (Fig. 1, 2, 3). Bryant's Bog is a small kettlehole pool surrounded by a floating mat of Sphagnum spp. and Chamaedaphne calyculata and is

located along the southwestern shore of Douglas Lake, Cheboygan County, Michigan. Cheyboygan Marsh is located northwest of the mouth of the Cheboygan River along the western shore of Lake Huron near Cheboygan, Michigan. It is a typical marsh whose primary emergent vegetation is Typha spp.

Polyurethane foam (PF) substrates were suspended approximately 15 cm below the surface in the littoral zone between two or three floats anchored to the bottom. Triplicate PF substrates were removed after 1, 3, 7, 14, 21, and 42 days of exposure, carefully (to minimize water loss) inserted into whirlpak bags, and returned to the laboratory. At the laboratory, the PF substrates were squeezed into wide-mouth jars and allowed to settle. A 2-3 drop subsample was removed from the bottom for making a wet-mount slide. Protozoans were examined within 10 h of removal from the field to minimize community distortion (Cairns 1982). Subsampling was done 2-4 times until an asymptotic species number was reached. This sampling regimen yielded a total of 90 samples examined over the season---triplicate substrates from each of five lakes, sampled six times. Protozoan species were enumerated while alive since movement is often an integral part of the species identification criteria. Standard taxonomic keys were used (Kahl 1930-35, Kudo 1966, Leidy 1879, Page 1976, and Pascher 1913-1927).

Water samples taken concurrent with artificial substrate collections were analyzed according to standard

methods (APHA 1981). Dissolved oxygen and temperature were measured in the field, and a water sample was returned to the laboratory for analysis of pH, conductivity, and alkalinity. Subsamples were frozen for later analysis of chloride, silica, ammonia, nitrate, total phosphate, and ortho-phosphate.

The species presence/absence data were analyzed using Ordiflex (Gauch 1977). The reciprocal averaging ordination (RAO) used the coefficient of distance (CD) as this is most informative and its use is supported in the literature (Gauch 1977, Gauch et al. 1977, Hill 1973). Additionally, protozoan data were subjected to a cluster analysis using the average linkage method (SAS 1982). The physical-chemical parameters were summarized using canonical variate analysis, factor analysis, and correlation analysis (SAS 1982).

Results

Figures 1 and 2 present the results of the physico-chemical measurements and show divergence of the bog and marsh systems for most parameters. The three lakes are generally quite similar for most physico-chemical parameters.

All ten (10) physico-chemical parameters were examined simultaneously in a canonical variate analysis (CVA). A CVA picks linear combinations of variables that are uncorrelated and provides maximum separation between the groups under examination. The scores on the two canonical axes plotted

in Figure 3 graphically display the differences between the physico-chemical parameters of the samples. The bog samples form a group at the bottom of the figure and the marsh a group at the top left. Most of the separation along canonical axis 1 appears due to alkalinity, pH, chloride, and conductivity. Canonical axis 2 separates the samples by differing conductivity, alkalinity, chloride, pH, and oxygen. Water samples from the three lakes appear quite close together and were not separated well by this technique. However, closer examination of the physico-chemical parameters of the three lakes (Fig. 4) shows that they can be separated when the bog and marsh are excluded from the analysis. When examined alone, the three lakes appear to separate along canonical axis 1, primarily as a result of chloride, conductivity, alkalinity, and pH. Canonical axis 1 is where most of the separation occurs. Canonical axis 2 depicts very little separation of the lakes and was therefore not interpreted.

Table 1 summarizes the distribution of species in the system: 546 species were found in the entire study, and 22% (121) were found in only one of the 90 samples. Included in this table are species most commonly found. No one species was found in all the samples examined.

Several species occurred in specific habitats (Table 2). Synura sphagnicola was found in the bog on each of six sampling dates and was also found on three dates in the marsh. This species and the ciliate Urotricha farcta were

not found in any lake sample. Several widely distributed forms were observed with no apparent habitat preference: Dinobryon divergens, Pleuromonas iaculans, Rhynchomonas nasuta. Several species that did not appear in the bog samples were found commonly in the lakes and less often in the marsh; these were Phacotus lenticularis, Stylonychia mytilis, and Chilodonella cucullulus.

The individual species suggest that patterns exist between protozoan communities in these systems. To examine species presence/absence similarity patterns in a more general manner, cluster analysis was used. The cluster analysis (Figure 5) using average linkage suggests clustering of early colonization samples from the lakes (cluster 1), a clustering of bog and marsh samples (cluster 3), and a group of samples whose interpretation is quite difficult including samples from all three lentic types (cluster 2).

Reciprocal averaging ordination is a method that allows graphical examination of the protozoan samples in species space. Results of an RAO of the most frequently occurring 96 species using presence/absence data and coefficient of distance (Gauch 1977, 1982) are shown in Figure 6 where the axes represent combinations of species. Bog samples clustered together with very little overlap with marsh samples in species space. Cheboygan Marsh samples also were clustered and appeared intermediate between bog and lakes in their community composition. Protozoan samples from the

three lakes appeared intermixed, showing similar species composition. There was generally good agreement between the results of the protozoan sample ordination and that of the physico-chemical parameters of the sample ordination. Most of the separation occurred on axis 1.

Tables 3, 4, and 5 present the results of factor analysis with varimax rotation (SAS 1982) of the physico-chemical parameters for the five systems examined, the three lakes, and the bog and marsh, respectively. To investigate associations between the physico-chemical parameters and presence/absence species data, correlations were computed between the physico-chemical parameters and combined factors with the reciprocal averaging axes of the samples. Table 6 shows correlations of the physico-chemical parameters and factors against the coordinates generated for the protozoan samples (in species space) from the RAO previously discussed.

Evidence presented in Table 6 indicates that protozoan samples from five ecosystems appear separated primarily by pH and dissolved oxygen. This observation is doubly supported by correlations of pH, dissolved oxygen, and Factor 3 (temperature, pH, and dissolved oxygen) with axis 1.

When protozoan samples from the three lakes were examined without the bog and marsh samples, they showed significant correlations between silica, orthophosphate, and axis 1, and between Factor 2 (ortho-phosphate) and axis 1.

Bog and marsh protozoan samples appeared to be separated and correlated negatively with alkalinity, pH silica, and conductivity. Axis 1 also correlated with Factor 1 and Factor 2. Axis 2 correlated only with Factor 3 (temperature).

Discussion

The three lentic system types examined in this study were quite different in many of the 10 environmental parameters recorded. Alkalinity, pH, and conductivity appear to cause most of the divergence, as indicated by the CVA and factor analysis.

Of the 546 species observed in this study, 22.2% were seen in only one sample. Only seven species occurred in over 50% of the samples. This is in contrast with other studies that show a greater number of species in common (Yongue 1973). This is probably due to the wide range of lentic types examined in this study.

Several habitat forms were observed, including species not observed in the lakes, some widely distributed forms, and several species not observed in the bog. Interestingly, the bog and marsh, while so diverse in most chemical parameters, shared many species. This may have resulted from a greater number of "extreme" forms present in these systems or could be supportive of the hypothesis that oxygen and pH are very important. The marsh and bog were lowest in these two environmental parameters.

The cluster analysis appears to provide support for the concept of an early successional community, as reported previously by Cairns and Henebry (1982). The dendrogram showed clustering of the bog and marsh protozoans and the lakes as well. This provides evidence that when many species are considered simultaneously (the 96 most common species), the lentic systems appear to cluster in a logical fashion.

Results of the RAO of 90 samples with 96 species support the idea that lentic systems can be separated by their species composition. Marked similarity occurred between the clusters of the bog, marsh, and the three lake protozoan samples and that of the CVA for the physico-chemical parameters. This suggests that the organisms are cueing on the physico-chemical parameters that make these lentic habitats unique.

Protozoan species composition of the five lentic habitats examined in this study appears to be related to oxygen, pH, and nutrients. This is supported by the correlation of the ordination coordinates with oxygen and pH, which contribute to Factor 3, and nutrients, which comprise Factor 2.

The species of protozoans found in the three lakes appear to be most closely related to ortho-phosphate (Factor 2) and to silica. Perhaps silica influences diatoms, and, consequently, influences protozoans indirectly.

The bog and marsh protozoan communities, like their environmental parameters, appear the most distinct. These

communities relate clearly to Factor 1 and are correlated with alkalinity, pH, conductivity, silica, and nutrients. Axis 2 appears somewhat related to temperature.

Conclusions

Correlations are not causation; however, it is interesting that the correlations between several of the physico-chemical parameters, factors, and the ordination axes (especially axis 1) are fairly strong. This is in spite of the highly stochastic nature of these systems: only seven species were found in over 50% of the samples. Further work of this nature may discern which, or which combination of, parameters influence protozoan communities directly. It will be desirable to investigate these parameters in controlled experiments to determine their effect in a laboratory situation.

Several conclusions can be made from this study:

- (a) The three lentic types examined in this study are of widely divergent physico-chemical properties.
- (b) Canonical variate analysis examines all physico-chemical parameters simultaneously. The bog and marsh are easily separated from the three lakes, which appear similar in their physico-chemical properties.
- (c) A cluster analysis of the 96 most common species suggests that several lake samples form an early successional fauna, while the bog and marsh cluster together.
- (d) the coordinates of the samples along the ordination axes

correlate with several physico-chemical parameters and composite factors. This suggests that the differences between all five communities are related to pH and oxygen levels. The three lakes appear to be separated along an orthophosphate and silica gradient. Separation of the bog and marsh communities appears related to pH, alkalinity, conductivity, and silica, which contribute to an ion factor.

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TABLE 1

Species distribution and the most common species in study.

Category	Number of species
Total study	546
Only one sample	121
Over 50% of samples	7
Over 33.3% of samples	36

Most common species	Number of samples observed
<u>Cyathomonas truncata</u>	79
<u>Cryptomonas erosa</u>	73
<u>Cinetochilum margaritaceum</u>	67
<u>Monas sp.</u>	56
<u>Entosiphon sulcatum</u>	53
<u>Bodo rostratus</u>	51
<u>Anisonema pusillum</u>	47

TABLE 2

Protozoan habitat forms including species found in only the bog and marsh, only the lake and marsh, and widely distributed forms. Numbers refer to the number of sampling dates a species was found. D = Douglas Lake, M = Lake Munro, W = Walloon Lake, C = Cheboygan Marsh, B = Bryant's Bog.

Category/ Species	Habitat				
	D	M	W	C	B
Bog and marsh forms					
<u>Synura sphagnicola</u>	0	0	0	3	6
<u>Urotricha farcta</u>	0	0	0	5	6
Widely distributed forms					
<u>Dinobryon divergens</u>	5	2	2	4	2
<u>Pleuromonas jaculans</u>	4	3	6	5	3
<u>Rhynchomonas nasuta</u>	4	3	3	5	5
Lake forms					
<u>Phacotus lenticularis</u>	5	6	4	1	0
<u>Stylonychia mytilis</u>	5	4	4	1	0
<u>Chilodonella cucullulus</u>	3	4	5	2	0

Table 3

Factor analysis (with varimax rotation) of five lentic habitats. Total variance explained by the three factors in this table = 84.88%. Only factor loadings > 0.69 are reported. Cond = conductivity, Alk = alkalinity, Cl = chloride, Si = silica, T-PO₄ = total phosphate, NH₃ = ammonia, O-PO₄ = ortho-phosphate, Temp = temperature, DO = oxygen.

Factor Loadings						
		Factor 1		Factor 2		Factor 3
		(ion)		(nutrient)		(TOP)
Loadings	Cond	0.934	T-PO ₄	0.911	Temp	0.794
	Alk	0.914	NH ₃	0.867	DO	0.775
	Cl	0.887	O-PO ₄	0.775	pH	0.727
	Si	0.868				
Variance						
explained		39.12%		26.43%		19.34%

TABLE 4

Factor analysis (with varimax rotation) of three lakes.
 Total variance explained by the three factors reported =
 70.83%. Only factor loadings greater than 0.69 are reported.
 For abbreviation explanation see table 3.

Factor loadings						
		Factor 1	Factor 2		Factor 3	
		(ion)	(nutrient)		(TOS)	
Loadings	Cond	0.950	O-PO4	0.877	Temp	0.724
	Cl	0.905			DO	-0.696
	Alk	0.898			Si	0.814
	pH	-0.769				
Variance explained		33.71%	18.69%		18.24%	

TABLE 5

Factor analysis (with varimax rotation) of bog and marsh samples. Total variance explained by the three factors reported = 93.27%. Only factor loadings greater than 0.69 are reported.

Factor loadings			
	Factor 1 (ions)	Factor 2 (nutrients)	Factor 3 (temp)
Loadings	pH 0.950	T-PO4 0.979	Temp 0.970
	Alk 0.941	NH3 0.896	
	Cond 0.933	O-PO4 0.714	
	Cl 0.923		
Variance explained	54.28%	27.06%	11.93%

TABLE 6

Correlation of ordination coordinates with physico-chemical parameters and factors. These are the results of separate ordinations, factor analyses, and correlation procedures.

Only correlations with $p \leq 0.01$ are reported.

	5 systems		3 lakes		Bog and marsh	
	Axis		Axis		Axis	
	1	2	1	2	1	2
Oxygen	0.51	-	-	-	-	-
pH	0.84	-	-	-	-0.90	-
Silica	-	-	0.52	-	-0.95	-
Ortho-phosphate	-	-	0.50	-	-	-
Alkalinity	-	-	-	-	-0.94	-
Conductivity	-	-	-	-	-0.92	-
Factor 1	-	-	-	-	-0.86	-
Factor 2	-0.42	-	-0.37	-	0.40	-
Factor 3	0.69	-	-	-	-	0.57

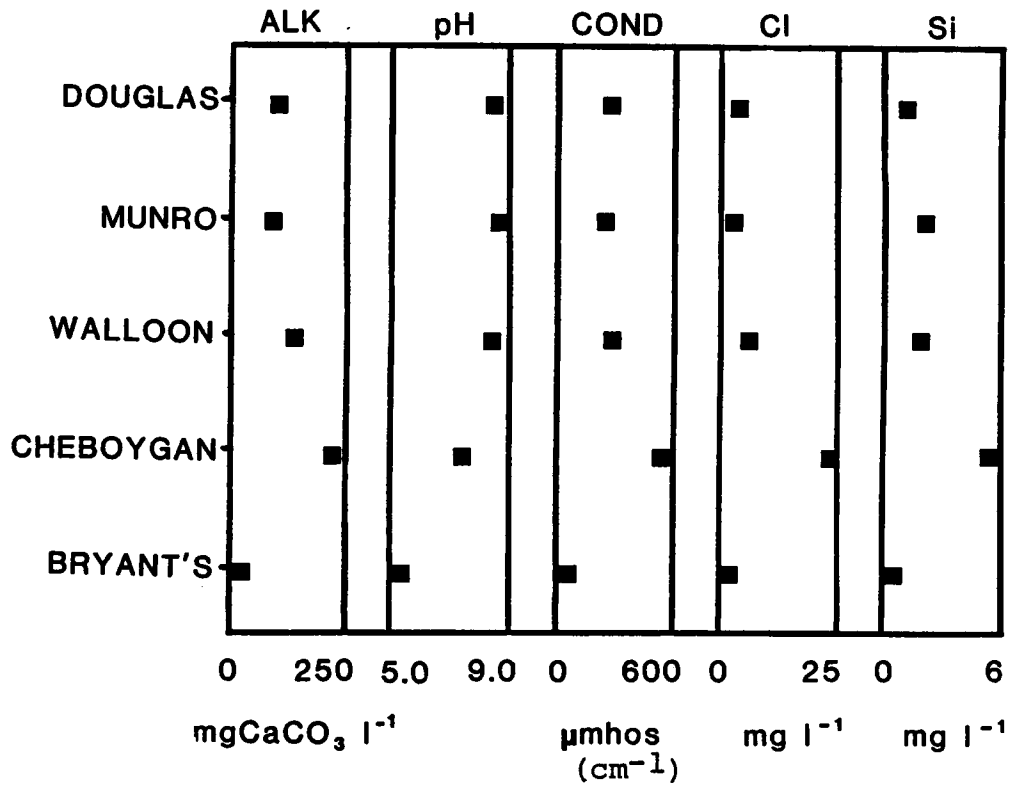


Figure 1. Several physico-chemical parameters from five lentic systems. ALK = alkalinity, pH = hydrogen ion concentration, COND = conductivity, Cl = chloride, Si = silica.

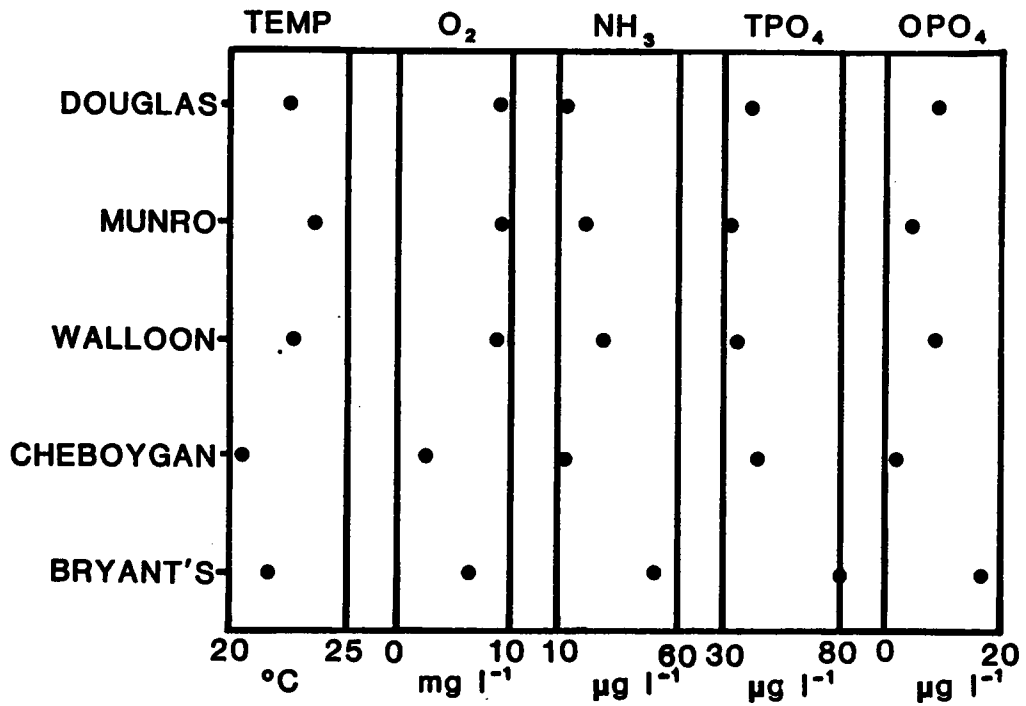


Figure 2. Several physico-chemical parameters from five lentic systems. TEMP = temperature, O₂ = dissolved oxygen, NH₃ = ammonia, TPO₄ = total phosphate, OPO₄ = ortho-phosphate.

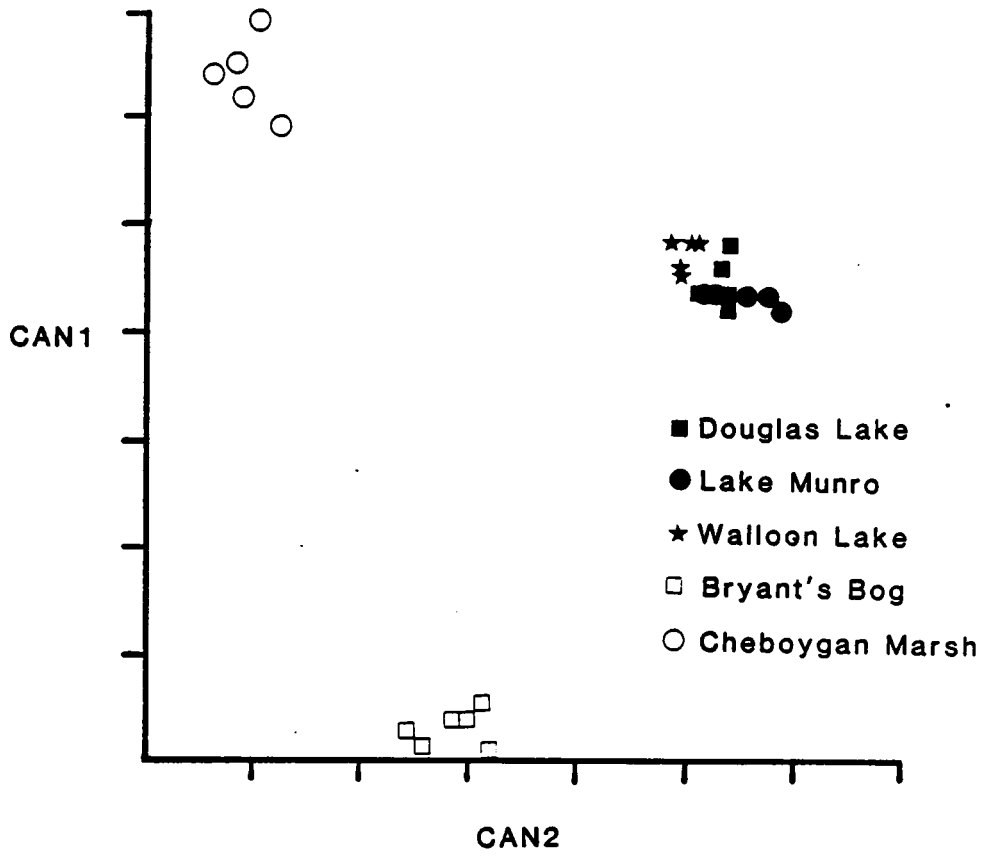


Figure 3. Canonical variate analysis of lake, bog, and marsh physico-chemical parameters.

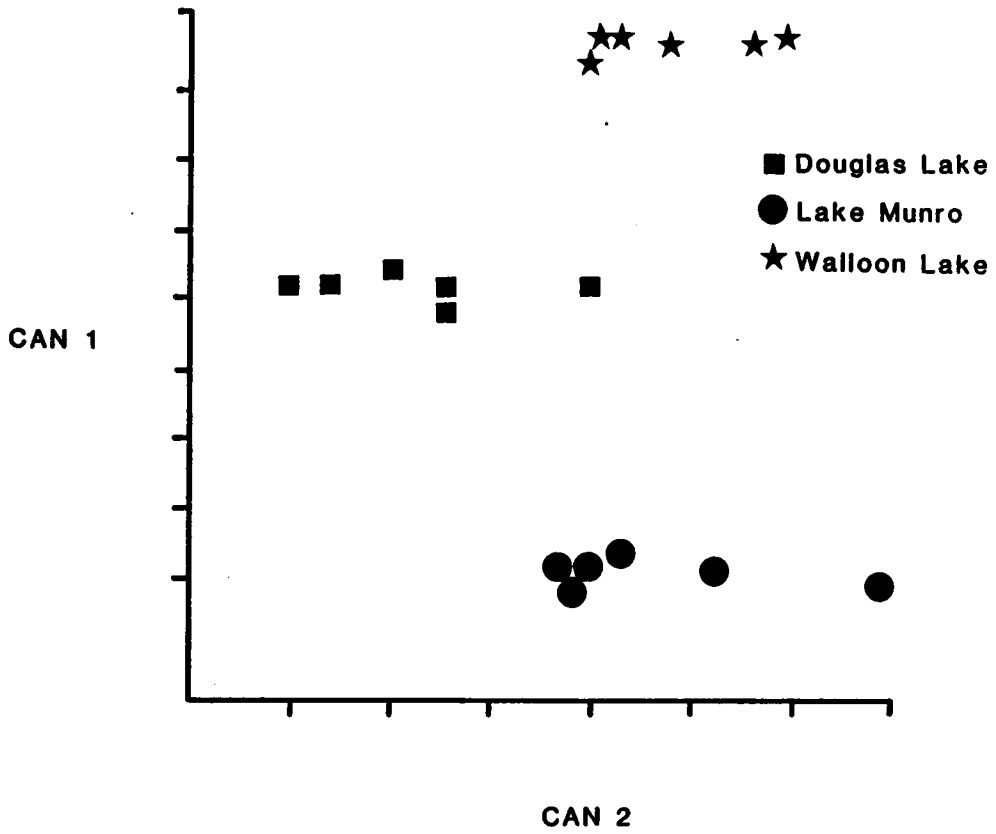


Figure 4. Canonical variate analysis of three lake physico-chemical parameters.

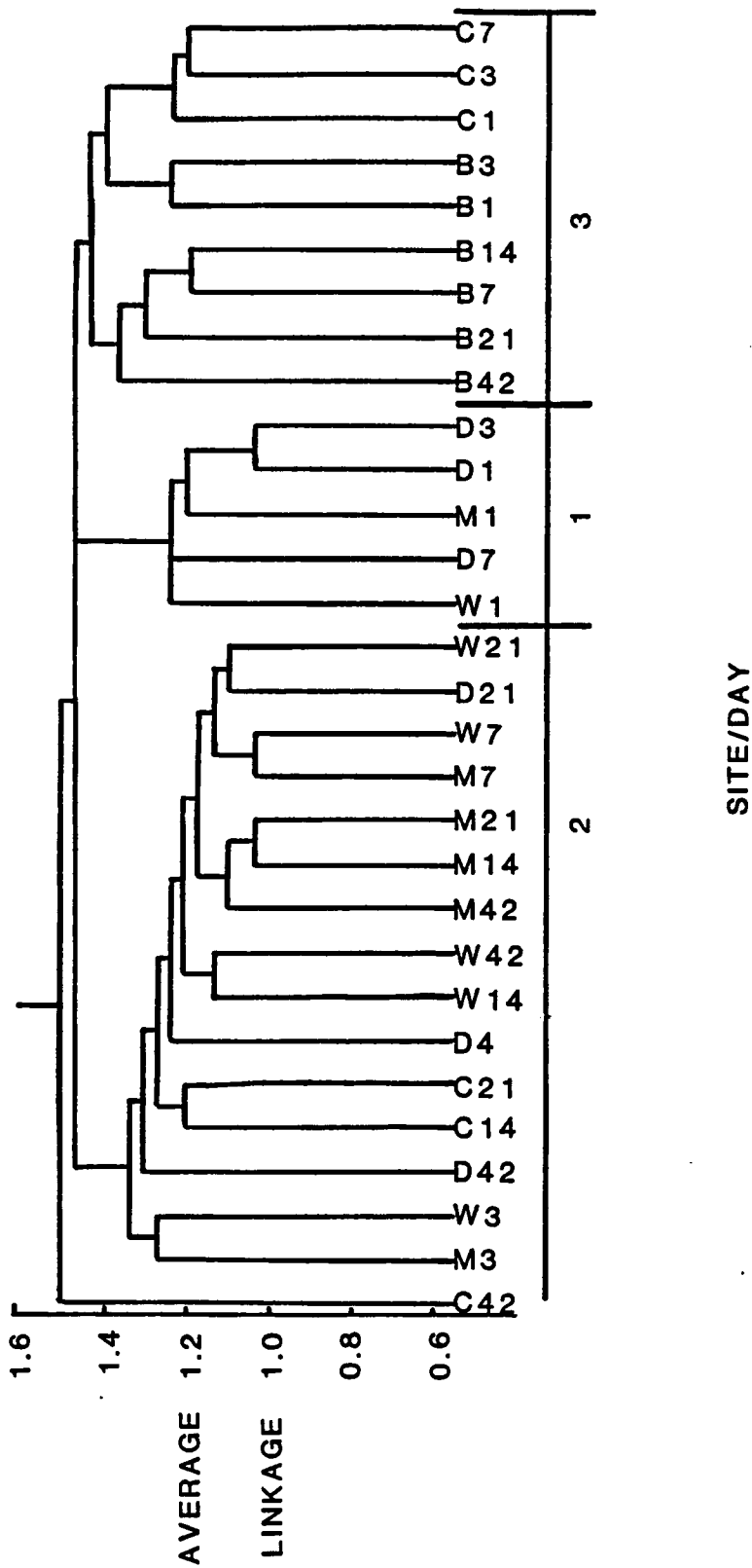
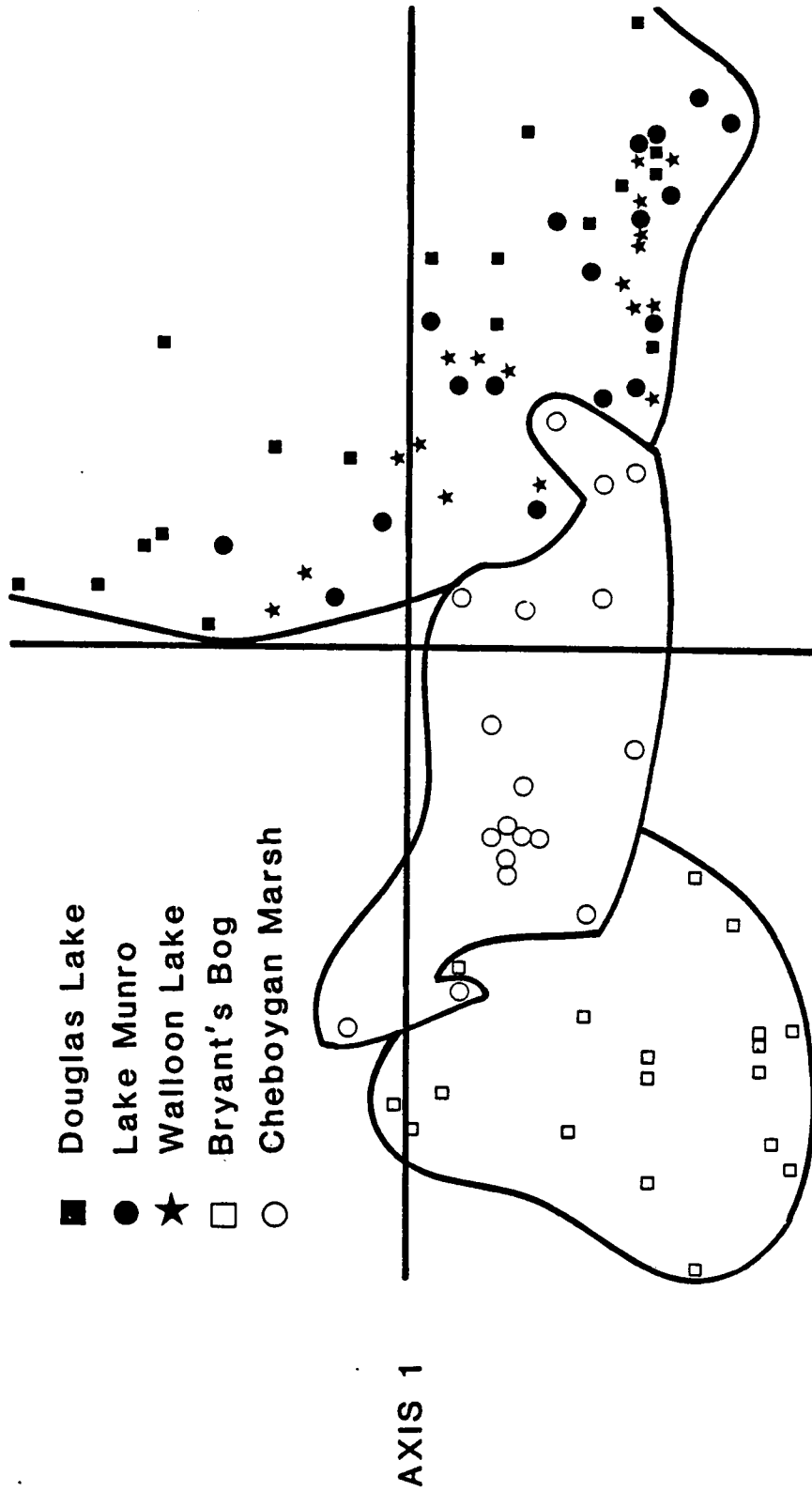


Figure 5. Cluster analysis of combined triplicate samples using protozoan presence/absence data for the 96 most common species. The letter and number refer to the lentic system and collection day. D1 = Douglas Lake sample on day 1, etc.



AXIS 2

Figure 6. Reciprocal averaging ordination of all protozoan samples using presence/absence data and coefficient of distance. The most common 96 species were used in this procedure.

CHAPTER III

RELATIONSHIP OF PHYSICO-CHEMICAL PARAMETERS AND FACTORS TO DIATOM AND PROTOZOAN COMMUNITIES: A MULTIVARIATE APPROACH

Abstract

The purpose of this investigation was to compare the physico-chemical parameters that are possibly important to diatom, autotrophic protozoans, and protozoan communities, and to examine the relative degree of relationship between these parameters and the communities. Polyurethane foam substrates were placed at approximately 15 cm depth in five lentic habitats in northern Michigan during the summer of 1983. These sites were divergent systems including three lakes, a bog, and a marsh. Triplicate substrates were removed after 1, 3, 7, 14, 21, and 42 days of field exposure and protozoan species presence was recorded. Diatoms were enumerated later from preserved samples. Concurrent with PF substrate removal, water samples were collected and analyzed for pH, temperature, alkalinity, conductivity, dissolved oxygen concentrations, and concentrations of chloride, silica, ammonia, and ortho and total phosphate. Examination of physico-chemical parameters singly and collectively revealed the bog and marsh to be quite different, while the three lakes were similar in their physico-chemical composition. Factor analysis revealed three factors that together explained 84.89% of the environmental data set

variability. Detrended correspondence analysis (DCA) performed on the biological presence-absence data revealed unique clusters of diatom assemblages in each of the lentic habitats. Protozoan DCA plots suggest that bog and marsh samples were basically unique while the three lake samples were intermixed. DCA results for autotrophic protozoans were quite similar to that for protozoans. It appears that pH had the strongest relationship between all three community divisions. DCA sample scores, when correlated against the environmental parameters showed that diatom scores had the greatest number of significant correlations with the environmental parameters and factors. This, coupled with the greater clustering of the diatom samples, implied a greater degree of relationship between diatom communities and their physico-chemical environment.

Introduction

Diatoms and protozoans are important components of aquatic food webs. The photosynthetic protozoans and diatoms account for a large proportion of carbon fixation in lentic habitats. Protozoans (Picken 1937, Yongue 1972) and periphyton (Hoagland et al. 1982) are thought to occur in structured communities. Periphyton communities have been shown to exhibit a pattern of structural heterogeneity developing in time analogous to that of terrestrial plant succession (Hoagland et al. 1982).

The purpose of this investigation was to compare the physico-chemical parameters that are found to be important in influencing the structure of diatom and protozoan components of aquatic communities. The hypothesis under investigation was that diatoms and photosynthetic protozoans are more closely related to the physico-chemical parameters of their environment than are the protozoans of other functional groups. See Pratt and Cairns (in press) for a more detailed discussion of protozoan functional groups. This type of study is of necessity a multivariate one due to the complexity of the component communities with hundreds of species co-existing and interacting with many environmental parameters.

Multivariate analyses were utilized to examine community similarity and compare it to measured physico-chemical parameters (see Green 1980 for a review of these procedures). Diatoms have been shown to respond to various

environmental parameters such as elevation and height of the spermatophyte canopy (Sullivan 1982). Stevenson and Stoermer (1981) examined diatom distribution along a depth gradient in Lake Michigan and found different benthic algal communities to be related to the depth of sampling.

Multivariate studies of the relationship between protozoans and the physico-chemical parameters of their environment have been lacking in the literature. The few that exist include Madoni's (1984) investigation of ciliated protozoan populations to determine the ability to characterize watercourses by their ciliate species composition.

The protozoans and microscopic algae are a most appropriate group for examining ecological hypotheses (Allen 1977). The present study extends previous research by investigating diatom and protozoan communities simultaneously to determine the important physico-chemical parameters that influence both groups of organisms.

The specific objectives of this study were: 1) to compare the physico-chemical parameters that are related to the distribution of diatom and protozoan communities including the autotrophic protozoans, and 2) to examine diatoms and protozoan communities (simultaneously) in order to compare the relative degree that diatom and protozoan communities are related to their physico-chemical environment.

Methods

The lakes studied were located at the northern tip of Michigan's lower peninsula (Figure 1). The study sites included three mesotrophic lakes, a bog, and a marsh. An attempt was made to examine divergent habitat types for a broad range of environmental conditions. Douglas Lake is one of the study sites and is the site of the University of Michigan's Biological Station. Also included is nearby Lake Munro and Walloon Lake which is located further south and are "typical" northern mesotrophic lakes. Bryant's Bog is a small kettle hole pool circled by a floating mat of Sphagnum spp. and is located near Douglas lake. Cheboygan Marsh is located on Lake Huron at the mouth of the Cheboygan River near Cheboygan, Michigan. It's primary emergent vegetation is composed of Typha spp.

Polyurethane foam substrates (PF substrates) were suspended in the littoral zone at approximately 15 cm depth in all lentic habitats during the summer of 1983. The substrates were attached to a plastic clothes line and suspended between floating buoys kept in place by weights on the bottom. Three substrates were removed and carefully (to minimize water loss) placed into whirlpak bags after 1, 3, 7, 14, 21, and 42 days of in-site immersion for a seasonal examination. Collected PF substrates were immediately returned to the laboratory and the contents squeezed into wide-mouthed jars and allowed to settle. A wet-mount slide was made with two to three drops of the bottom material.

Protozoans species were identified while living and within 8 hours of collection to minimize community distortion (for a more detailed explanation of several problems encountered during protozoan sampling, see Cairns 1974 and 1982). Two to four subsamples were examined at 200-450X magnification for their species presence-absence data. Protozoan counts were terminated when an apparent asymptotic species number was reached.

The remaining sample was decanted and preserved with formalin for later diatom identification. The samples were cleaned using standard techniques (van der Werff 1953, Patrick and Reimer 1966) and mounted in Hyrax for enumeration. Diatom identifications were made at 1000x and 500 frustules were counted in each sample. This number of frustules is normally enough to reach an asymptotic curve when number of species is plotted against number of individuals. Two samples were quite depauperate and counts were terminated after 100 frustules were identified. Proportional abundances of all diatom species encountered were recorded, although this report utilizes only presence-absence data in order to make valid comparisons with protozoan presence-absence data. Presence-absence data has been shown to yield satisfactory results in community analysis (Hill 1972). Several advantages of presence-absence data are that the dominant species's importance and overall data set variability are reduced.

Concurrent with PF substrate removal from the lentic

habitats under investigation, several environmental parameters were recorded using standard methods (APHA 1981). These include pH, temperature, and dissolved oxygen in the field; and alkalinity, conductivity, chloride, silica, ammonia, ortho and total phosphate, and nitrate at the laboratory.

The water chemistry data were analyzed with several multivariate procedures designed for data reduction and simplification. These include canonical variate analysis and factor analysis. The protozoan data were analyzed both by using all trophic groups combined, and by examination of only the photosynthetic or autotrophic protozoans. These two groups, and the diatoms were analyzed using detrended correspondence analysis (Decorana, DCA) which is an improvement over reciprocal averaging ordination by eliminating compression of axis ends and the arch or horseshoe problem that plagued reciprocal averaging ordination (Hill 1979, Hill and Gauch 1980). DCA results were compared to the physico-chemical parameters and factors by utilizing correlational techniques. This was done to determine which parameters were related to diatoms, autotrophic protozoans, and protozoan sample distribution and to determine which group of organism's DCA scores had the greatest number of correlations with the environmental parameters and factors.

Results

Environmental variables

Table 1 summarizes the environmental variables measured in this study. The values reported are the mean and standard deviations based on six sampling dates. It can be seen that temperature was similar for all 5 lentic habitats. Dissolved oxygen was lowest for the marsh and approximately three times higher for the lakes which were quite similar to each other. pH was lowest in the bog, intermediate in the marsh, and highest in the lakes. Alkalinity, conductivity, silica, and chloride were lowest in the bog, highest in the marsh, with the three lakes having intermediate values. Nutrient values are as follows: ammonia was lowest in Douglas Lake and Cheboygan Marsh, the other two lakes had intermediate values, and the bog had the highest value. Orthophosphate was lowest in the marsh, highest in the bog, and intermediate in the lakes. The lakes had lowest values for total phosphate followed closely by the marsh, with highest values found in the bog samples. Nitrate was at non-detectable levels in most samples, thus not included in further analyses.

Examination of all physico-chemical parameters measured was carried out with canonical variate analysis (Figure 2, Table 2) and factor analysis (Table 3). Canonical variate analysis is a separation technique while factor analysis is a data reduction technique. Figure 2 is the plot of the samples' environmental parameters on the axes of the first

two canonical variates. The marsh samples form a cluster at the top left corner of the figure, the bog samples at the bottom, with the three lakes clustered to the right. This figure supports the single variable analysis which suggested that the lakes were quite similar in their physico-chemical makeup for most of the measured variables. Table 2 presents within canonical structure values for the physico-chemical parameters. Canonical axis 1 was primarily composed of loadings from alkalinity, pH and conductivity. Canonical axis 2 was formed from pH, oxygen, and negative loadings from chloride with lesser contributions from conductivity, and alkalinity. Canonical axis 3 and canonical axis 4 both have very low eigenvalues thus accounting for very little of the data set variability and need not be explained (Table 2).

Factor analysis (principal components with varimax rotation) results of the environmental data are presented in table 3. Factor 1 explains 39.12% of the environmental data set variability and was primarily comprised of loadings from conductivity, alkalinity, chloride and silica. Factor 2 explains 26.43% of the variability and includes loadings from total and ortho-phosphate, and ammonia. Factor 3 explains 19.34% of the environmental data set variability and has high loadings on temperature, dissolved oxygen and pH. These three factors cumulatively explain 84.89% of the environmental data set variability.

Species presence-absence

There were a total of 861 taxa identified in this study. The taxa have been divided into three groups. These are the protozoans (including all trophic groups), autotrophic (photosynthetic) protozoans, and the diatoms. There were 546 protozoan species and 315 species of diatoms identified in the study. General distributions (Table 4) and the most common species of each type are summarized (Table 5).

Detrended correspondence analysis (DCA) was performed on the three groups of organisms disregarding those species that occurred in only one of 90 samples. Thus 425 protozoan species were examined, 228 diatom species, and 116 photosynthetic protozoan species were analyzed using presence-absence data from the five lentic habitats. Table 6 presents eigenvalues of the first four axes of samples in species space.

Figure 3 is a plot of DCA scores for axis 1 versus axis 2 for the protozoan samples. Note the clustering of Bryant's Bog samples, below which there is a cluster of Cheboygan Marsh samples. The lakes are intermingled but one Walloon Lake sample falls between the bog and the marsh samples. Plots of axis 1 vs 3 and axis 1 vs 4 show similar groupings and are not included. Other combinations of axes plots were uninformative with scattering of all samples but are further examined for their relationship to physico-chemical parameters and factors by correlational techniques.

DCA plots of scores for axis 1 vs axis 2 for

photosynthetic protozoans (116 sp.) are shown in figure 4. Some clustering can be discerned, but these clusters are not as pronounced as for the protozoans. Bryant's Bog samples are somewhat clustered near the bottom of the figure, above that comes Cheboygan Marsh, and above that Walloon and Lake Munro. Most of the highest samples are from Douglas Lake. As before, similar patterns occur in plots of other axes and are not shown.

Figure 5 is a plot of DCA scores from a comparison of presence-absence data for 228 diatom species. Unique sample clusters exist for all lentic habitats examined. Note that Bryant's Bog is separate from all other samples along axis 1. Good separation of lakes and marsh samples occurs along axis 2 while axis 1 mainly separates the bog samples from the other systems.

Table 7 presents correlations between DCA axes and physico-chemical parameters and factors. Axis 4 was not significantly correlated with any of the variables or factors recorded and thus was discarded. Diatom Decorana scores for axis 1 and 2 were significantly correlated in 19 instances ($p < 0.01$ 17 times) with the physico-chemical parameters. The highest correlations for axis 1 were with pH ($r = -0.92$, $p < 0.01$), alkalinity (-0.73 , $p < 0.01$) conductivity ($r = -0.65$, $p < 0.01$), factor 1 ($r = -0.55$, $p < 0.01$), and factor 2 (-0.57 , $p < 0.01$). Diatom DCA axis 2 was correlated highest with dissolved oxygen ($r = -0.80$, $p < 0.01$), chloride ($r = 0.75$, $p < 0.01$), and factor 3 ($r = -0.62$, $p < 0.01$).

Axis 3 and 4 were not significantly correlated with any of the physico-chemical parameters or factors.

The DCA axes for autotrophic protozoans correlated significantly in 14 instances against the physico-chemical parameters and factors. Eight of these correlations were strong with a p -value ≤ 0.01 . DCA axis 1 correlated highest with pH ($r=0.72$, $p<0.01$), and factor 3 ($r=0.57$, $p<0.01$). Axis 2 was correlated with silica ($r=-0.61$, $p<0.01$) and factor 1 ($r=-0.59$, $p<0.01$).

The DCA axes from protozoan analyses had only eight significant correlations with the physico-chemical parameters. Six of these correlations had a p -value less than 0.01. pH was highly correlated ($r=-0.84$, $p<0.01$) with axis 1, and so was factor 3 ($r=-0.58$, $p<0.01$). Axis 2 correlated with silica ($r=0.63$, $p<0.01$).

These results show that diatom DCA axes have more and higher significant correlations with physico-chemical parameters than do the other groups of organisms. Autotrophic protozoans are next, but the correlations are generally not as high as those of the diatoms and protozoans. Protozoans have the least number of significant correlations, most of which are slightly higher than those of the autotrophic protozoans.

Discussion

Examination of environmental parameters singly and in combination utilizing a canonical variate analysis (CVA)

show that the three lakes were quite similar in most of the physico-chemical parameters measured, while the bog and marsh were divergent. The three lakes clustered closely in the CVA and it will be interesting to examine general patterns of sample separation by examining DCA results for diatoms, autotrophic protozoans and protozoans.

There were more species of protozoans observed (546) than diatoms (315). Yet several diatom species occur in the most number of samples. Examination of the community shows greater variability in the protozoan samples than the diatoms. This is probably due to the greater number of protozoan species available. For instance, a protozoan that occurs in one system can have the same role as one that occurs in another causing a greater number of species and less occurrence of a particular species in the study. Diatoms, on the other hand are in the same trophic role, that of producers, and there is much greater redundancy available to satisfy the niche openings.

DCA eigenvalues for protozoan communities are more even, and less dominated by a few species than are diatom components of the community. Diatom eigenvalues appear to be dominated by a few species, thus causing the eigenvalue of the first axis to be larger than the others. This presents no problem in this study since axis 3 and 4 are not correlated significantly with environmental parameters and are thus not important.

The samples clustered closely in the plots of axis 1 vs

axis 2 for diatoms, much less so for protozoans and autotrophic protozoans. This suggests that diatom communities are more closely associated with the physico-chemical parameters of their environment, and form more distinct clusters than do protozoan samples. This provides evidence of greater similarity between diatom samples from a given lentic habitat. One can infer from these data that diatom communities are more closely affected by their physico-chemical environment, thus exhibit a greater degree of similarity between samples from the same system. The protozoans show, surprisingly so, a greater degree of clustering than do the autotrophic protozoans. This apparent anomaly will be discussed in light of further evidence.

Evidence for the hypothesis that diatoms are more closely related to the physico-chemical parameters of their environment is provided by the greater number of and higher correlations between DCA axes and physico-chemical parameters and factors. The photosynthetic protozoans have correlations of similar magnitude to those of the protozoans, but have an intermediate number, between the diatoms and protozoans. This suggests that the diatom communities are most closely related to their environmental conditions followed by the autotrophic protozoans. This is logical as diatoms use nutrients and other physico-chemical parameters directly, while protozoans are affected by many of these indirectly through foods such as bacteria, algae,

and other protozoans (Pickens 1937; Noland 1925, 1967). What is surprising is the conflicting evidence for the autotrophic protozoan's relationship with the environment. The DCA plots of autotrophic protozoans suggest less similarity between samples from a lentic habitat than that for all protozoans combined. On the other hand, more (14) versus (8) significant correlations existed for DCA axes scores for autotrophic protozoans than for all protozoans combined. These conflicting data indicate a need for further research subdividing the protozoans into the various functional groups and examining their relationships to their physico-chemical environment.

pH had the highest correlations with DCA scores for axis 1 for all groups of organisms. This could be related to humic acid concentrations in the bog and marsh reflecting the amount of light available to the organisms. This is important information in reference to the continued spread of acid precipitation and the decline of average precipitation from 5.00 in 1955-56 to 4.70 in 1972-73 in the Northern Michigan area (Likens 1976, Likens et al. 1979). As in our study, pH and conductivity were shown to be important for interpreting lake location from diatom assemblages (Huttunen and Merilainen 1983). Axis 1 from the diatom DCA was also correlated with alkalinity, conductivity, factor 1 (loadings from conductivity and alkalinity), and a nutrient factor. Autotrophic protozoan axis 1 was also most closely related to pH and factor 3. It

is interesting to note that silica was correlated to diatom DCA axes less than it was to the axes for autotrophic protozoans and all protozoans.

Data from this and other studies (Cairns et al. 1983) indicates greater variability in protozoan communities than diatom communities. This could in part explain the lower and fewer significant correlations found for the protozoan samples scores against the environmental parameters. This evidence could also indicate that individual diatom species are less environmentally specific.

Conclusions

- 1) The three lakes in this study were more similar in their physico-chemical composition than the bog and marsh. Results from diatom, photosynthetic protozoa, and all protozoa; when run in a DCA, and plotted supported these differences and similarities generally resulting in the formation of clusters of bog, marsh, and lake samples.
- 2) More species of protozoans were identified than diatoms. However, many diatoms were more widely distributed than were the protozoans and autotrophic protozoans.
- 3) Diatoms appear to be more closely in tune with their physico-chemical environment than are the protozoans. This makes sense in reference to greater intimacy and closer utilization of environmental parameters and the more divergent trophic structure of the entire protozoan community. pH (possibly related to humic acid content and light avail-

ability) showed the greatest degree of relationship with the first axis for each community type. This suggests the importance of pH in determining community structure and yields a warning for future changes due to acidic deposition in the Northern Michigan area.

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Table 1

Mean and standard deviation of physico-chemical parameters from five lakes in northern Michigan. Values are from six readings during summer 1983. D = Douglas Lake, M = Lake Munro, W = Walloon Lake, B = Bryant's Bog, and C = Cheboygan Marsh.

Environmental Parameter					
	Temperature (°C)	Dissolved Oxygen (mg l ⁻¹)	pH	Conductivity (umhos cm ⁻¹)	Alkalinity (mgCaCO ₃ l ⁻¹)
<u>Site</u>					
D	22.6(1.1)	9.0(0.5)	8.2(0.2)	260.4(6.9)	118.0(4.6)
M	23.5(2.2)	9.1(0.3)	8.5(0.1)	214.0(7.4)	101.0(7.7)
W	22.9(1.6)	8.9(0.7)	8.2(0.1)	291.1(5.9)	130.5(4.5)
B	21.6(1.5)	6.5(1.3)	5.2(0.5)	24.0(7.4)	5.2(0.8)
C	20.5(2.1)	2.9(1.5)	7.3(0.04)	527.0(101.5)	216.4(32.)

	Ammonia (ug l ⁻¹)	Ortho- phosphate (ug l ⁻¹)	Total- phosphate (ug l ⁻¹)	Silica (mg l ⁻¹)	Chlorine (mg l ⁻¹)
<u>Site</u>					
D	10.6(15.2)	7.8(9.9)	42.0(24.2)	1.3(1.1)	3.7(0.5)
M	22.0(7.4)	3.9(2.8)	30.7(8.2)	2.4(1.2)	2.2(0.3)
W	28.1(8.8)	7.1(8.6)	34.1(14.9)	2.2(0.9)	5.6(0.2)
B	51.6(37.0)	16.9(8.7)	80.9(49.2)	0.2(0.1)	0.8(0.2)
C	11.7(7.3)	2.3(1.4)	44.4(8.5)	5.2(0.7)	24.2(8.5)

Table 2

Within canonical structure loadings for five lentic habitats and ten environmental parameters. Asterisk marks the variables of greatest importance separating the axes.

Variable	Within Canonical Structure			
	Can1	Can2	Can3	Can4
Temperature	0.0067	0.0771	0.0797	0.1209
Dis. Oxygen	-0.0006	0.2996*	-0.1640	0.2505*
Alkalinity	0.4729*	-0.2293*	-0.2833*	-0.0807
pH	0.4651*	0.3266*	0.3966*	0.1532
Conductivity	0.3658*	-0.2389*	-0.2372*	-0.0546
Ammonia	-0.0764	0.0031	-0.0375	0.3731*
Ortho-phosphate	-0.0926	-0.0082	-0.1597	0.2314*
Total phosphate	-0.0614	-0.0376	-0.0773	-0.1407
Silica	0.1534	-0.1233	0.3561*	0.2713*
Chloride	0.1618	-0.2733*	-0.0123	-0.0381
Eigenvalue	108.1999	74.3862	1.2682	0.7175
Variance expl. (%)	58.62	40.03	0.69	0.39
Cumulative(%)	58.62	98.65	99.34	99.73

Table 3

Factor analysis (with varimax rotation) of five lentic habitats. Asterisk refers variables with important loadings in factor.

<u>Variable</u>	Rotated Factor Pattern		
	Factor 1	Factor 2	Factor 3
Temperature	-0.11768	0.00004	0.79423*
Dis. Oxygen	-0.49500	-0.15039	0.77462*
pH	0.41321	-0.40836	0.72684*
Alkalinity	0.91395*	-0.34908	0.07192
Conductivity	0.93351*	-0.30957	-0.02187
Ammonia	-0.29119	0.86669*	-0.01677
Ortho-phosphate	-0.38471	0.77485*	-0.07918
Total-phosphate	-0.04686	0.91057*	-0.21514
Silica	0.86773*	-0.21661	-0.08537
Chlorine	0.88744*	-0.09138	-0.32972
Eigenvalue	3.91185	2.64301	1.93362
Variance expl.(%)	39.12	26.43	19.34
Cumulative (%)	39.12	65.55	84.89

Table 4

Species distributions for the two main groups in this study. Autotrophic protozoans are included in the protozoans. Parenthesis encloses the percent of former number to total.

<u>Category</u>	Group		Total
	Protozoan	Diatom	
Total	546	315	861
More than 1 sample	425	228	653
Only 1 sample	121(22.2%)	87(27.6%)	208
Over 33.3% samples	36(6.6%)	41(13.0%)	77
Over 50.0% samples	7(1.3%)	18(5.7%)	25

Table 5

The most common species found in study and the number of samples in which they occur.

Most common species	Number samples found
A. Protozoans	
<u>Cyathomonas truncata</u>	79
<u>Cryptomonas erosa</u>	73
<u>Cinetochilum margaritaceum</u>	67
<u>Monas sp.</u>	56
<u>Entosiphon sulcatum</u>	53
<u>Bodo rostratus</u>	51
<u>Anisonema pusillum</u>	47
B. Diatoms	
<u>Achnanthes minutissima</u>	81
<u>Cyclotella comensis</u>	74
<u>Nitzschia palea</u>	70
<u>Tabellaria fenestrata</u>	67
<u>Navicula radiosa</u>	66
<u>Navicula radiosa var parva</u>	66
<u>Anomoeoneis vitrea</u>	62
C. Autotrophic protozoans	
<u>Cryptomonas erosa</u>	73
<u>Chromulina pascheri</u>	43
<u>Chroomonas caudatus</u>	37
<u>Dinobryon sertularia</u>	36
<u>Trachelomonas volvocina</u>	36
<u>Chlamydomonas gracilis</u>	35
<u>Cryptomonas ovata</u>	35
<u>Cryptomonas commutata</u>	34

Table 6

Eigenvalues and percent explained for the first four axes (parenthesis) from detrended correspondence analysis for protozoans, autotrophic protozoans, and diatoms.

	Eigenvalues		
	Protozoans	Autotrophic	Diatoms
Axis 1	0.277(33.17)	0.353(36.32)	0.610(56.07)
Axis 2	0.252(30.18)	0.231(23.77)	0.278(25.55)
Axis 3	0.177(21.20)	0.211(21.70)	0.112(10.29)
Axis 4	0.129(15.45)	0.177(17.59)	0.088(8.09)

Table 7

Correlations of Decorana axes and physico-chemical parameters and factors for three groups of organisms. Asterisk after r-value indicates $0.05 > p > 0.01$, no asterisk means that $p < 0.01$. Minus- indicates no significant correlation at $p < 0.05$. Number at bottom, for example (19/17) refers to 19 significant correlations, 17 of them less than 0.01. Temp = temperature, O2 = dissolved oxygen, Cond = conductivity, Alk = alkalinity, Cond = conductivity, NH3 = ammonia, OPO4 = ortho-phosphate, TPO4 = total phosphate, Si = silica, Cl = chloride. Not included in table are weak values for correlations between autotrophic protozoan axis 3 vs alkalinity and factor 3.

Parameter	Correlation					
	Diatom		Autotroph		Protozoan	
	axis1	axis2	axis1	axis2	axis1	axis2
Temp	-	-0.47	-	-	-	-
O2	-	-0.80	0.51	0.39*	-0.53	-
pH	-0.92	-0.38*	0.72	-	-0.84	-
Alk	-0.73	0.47	-	-0.49	-	-
Cond	-0.65	0.55	-	-0.50	-	-
NH3	0.52	-	-0.46*	-	0.46*	-
OPO4	0.55	-	-	-	0.42*	-
TPO4	0.56	-	-0.42*	-	0.48	-
Si	-0.50	0.55	-	-0.61	-	0.63
Cl	-	0.75	-	-0.44*	-	-
F1	-0.55	0.57	-	-0.59	-	-
F2	0.46*	-	-0.48	-	0.52	-
F3	-0.57	-0.62	0.57	-	-0.58	-
	(19/17)		(14/8)		(8/6)	

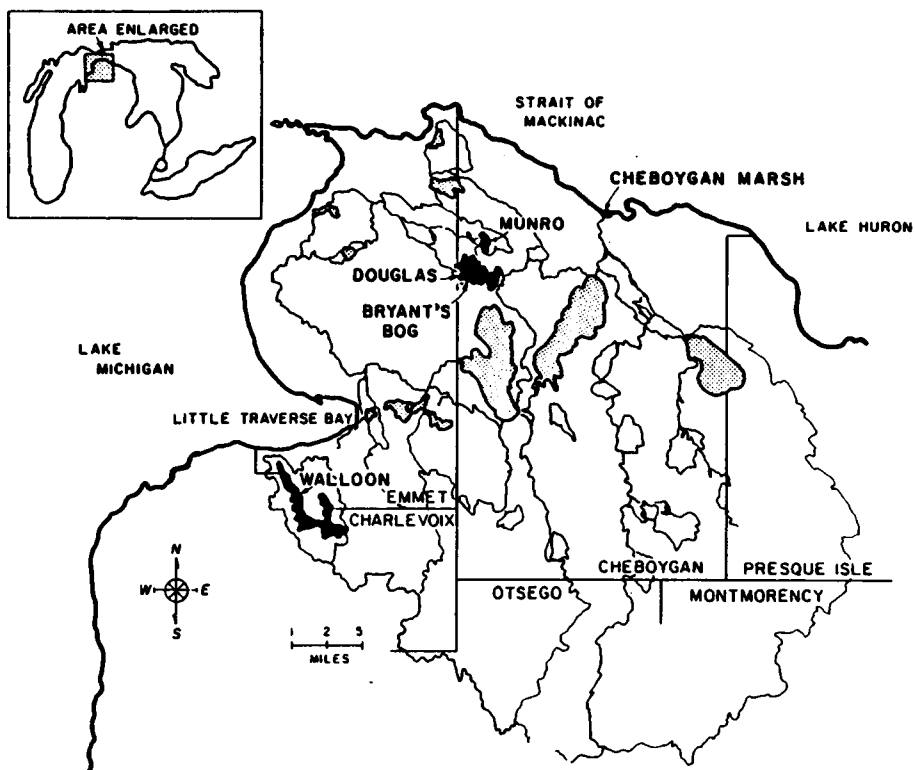


Figure 1. Location of the five northern Michigan lakes used in this study.

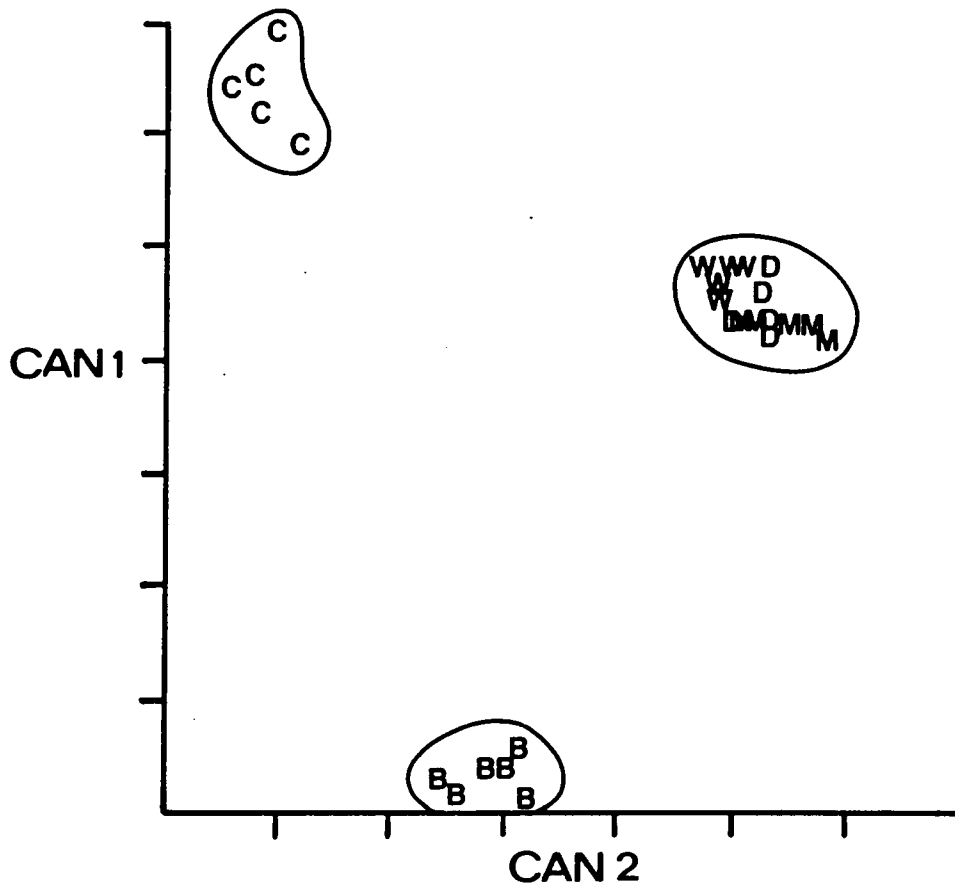


Figure 2. Plot of canonical variate axis 1 versus canonical variate axis 2 for five lentic habitats. D = Douglas Lake, M = Lake Munro, W = Walloon Lake, B = Bryant's Bog, C = Cheboygan Marsh.

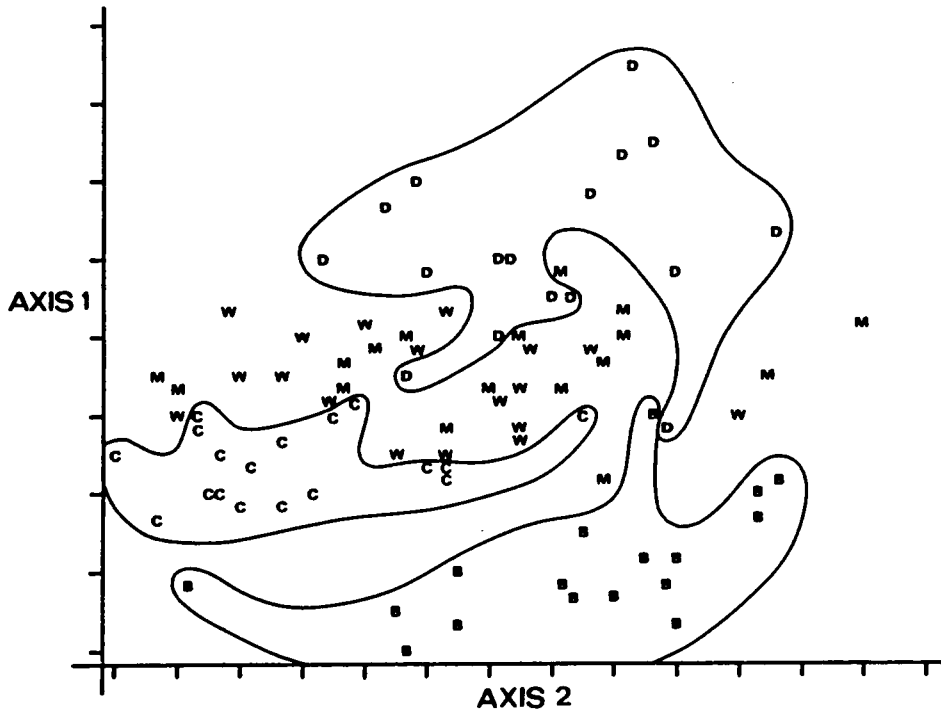


Figure 3. Detrended correspondence analysis scores for axis 1 versus axis 2 using 425 protozoan species presence-absence data. D = Douglas Lake, M = Lake Munro, W = Walloon Lake, B = Bryant's Bog, C = Cheboygan Marsh.

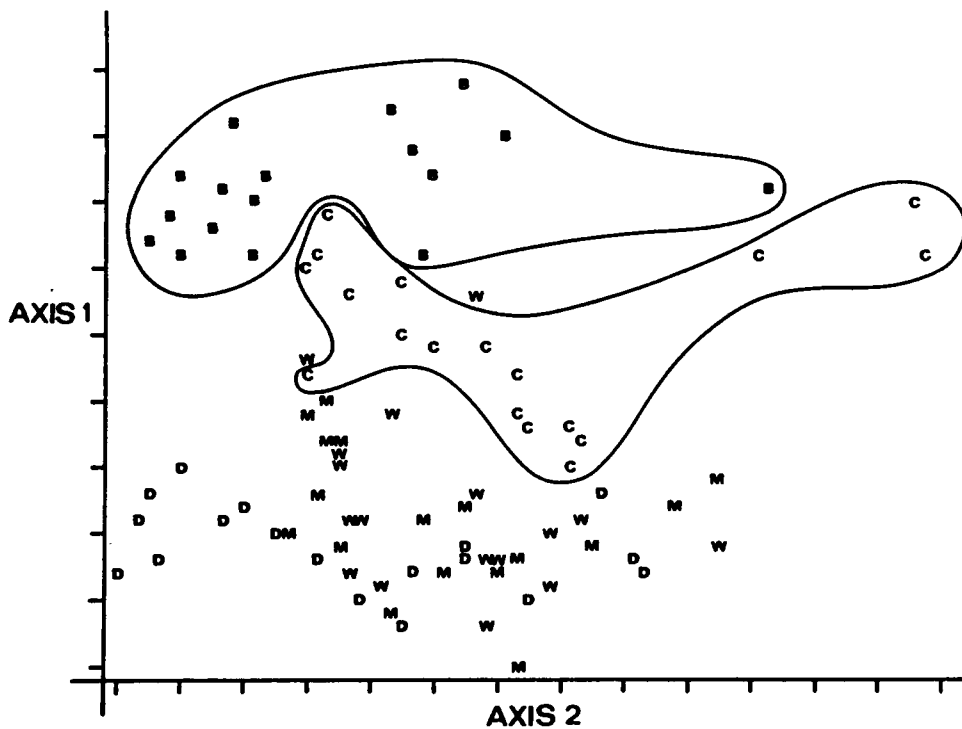


Figure 4. Detrended correspondence analysis scores for axis 1 versus axis 2 using 116 species of photosynthetic protozoans presence-absence data. D = Douglas Lake, M = Lake Munro, W = Walloon Lake, B = Bryant's Bog, C = Cheboygan Marsh.

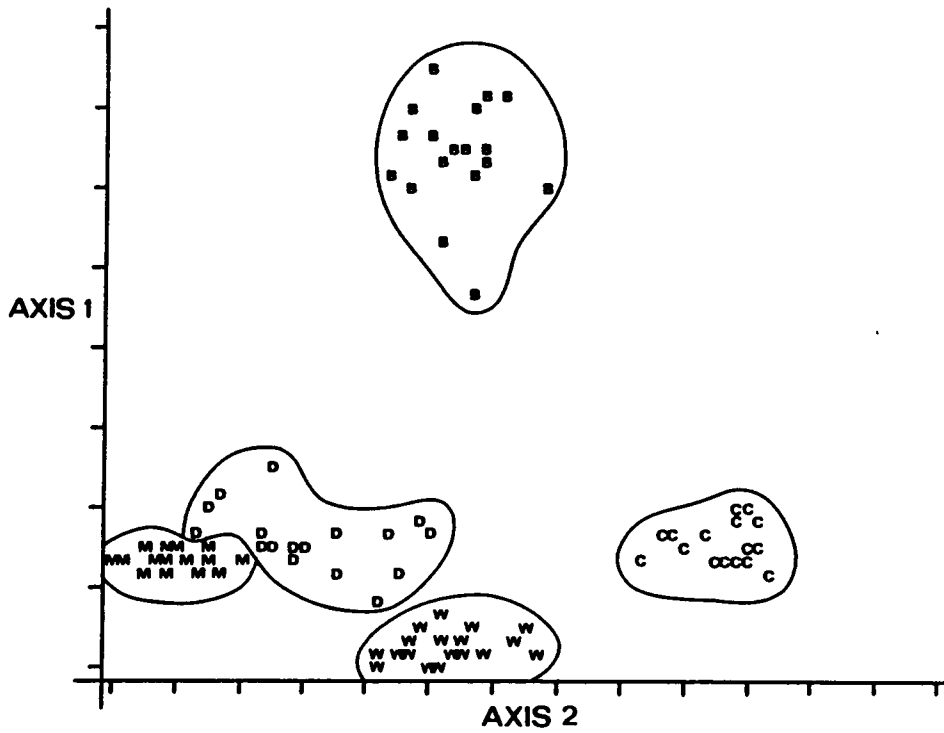


Figure 5. Detrended correspondence analysis scores for axis 1 versus axis 2 using 228 diatom species presence-absence data. D = Douglas Lake, M = Lake Munro, W = Walloon Lake, B = Bryant's Bog, C = Cheboygan Marsh.

Summary and Conclusions

This research provides evidence for similarities and differences between diatom and protozoan communities. The first chapter presents evidence that different groups of organisms, i.e., diatoms and protozoans, do not necessarily have the same colonization dynamics. Chapter 1 also suggests that sampling procedures for two groups of approximately the same size and from the same site cannot always be identical. Diatom communities are present in the water column, thus appearing to be at equilibrium species number (S_{eq}) almost immediately. Most lakes lentic habitats fit the MacArthur-Wilson equilibrium model for protozoan, but not for diatom colonization. Estimates of colonization rate (G) generally were much lower for protozoans than for diatom samples from the Michigan lakes and for Pandapas Pond. Species accrual during short term, < 1 day exposure, also revealed that protozoans fit the model, while diatoms did not. A grab sample revealed that diatoms are present in the water column in large numbers, and probably as a group do not traverse inhospitable terrain to substrates but are merely sampled. Since diatoms are present in the water column, perhaps it is necessary to examine other experimental systems to examine colonization processes of these organisms.

Chapter 2 examined the roles of physico-chemical parameters in structuring protozoan communities. This paper examined the entire protozoan community in divergent lakes simultaneously to determine the effect of environmental

examined the entire protozoan community in divergent lakes simultaneously to determine the effect of environmental influence. Many species (546) were found in the course of this examination representing divergent trophic (functional) groups. These include bacterivores, autotrophs, and predators. Most species were rare: 121 were found in only one sample and only seven were found in over 50% of the samples. This great variability in species composition is most probably due to the functional redundancy that exists in protozoan communities. Many species can fill similar trophic roles, and these different species are seen in different samples and systems.

The physico-chemical parameters were subjected to multivariate analyses for data reduction. Canonical variate analysis results revealed that the bog and marsh samples were quite divergent, while the lakes were similar forming one large cluster showing similarity in their physico-chemical parameters. Factor analysis of the five lentic ecosystems revealed that three composite factors explained 84.88% of the data set variability. Other factors for all three lakes, and factors for the bog and marsh were similar again explaining a high proportion of the data set variability.

Cluster analysis of the 96 most frequently occurring species revealed an early lake community, while the bog and marsh samples tended to cluster indicating similarity. Reciprocal averaging ordination (RAO) suggested similarities

in the bog samples by clustering, and the marsh samples were intermediate. The three lake protozoan samples were intermingled mimicing the apparent similarity of the physico-chemical samples from the lakes. This suggests that protozoan communities from different lentic habitats track the physico-chemical parameters of their environment. This is supported by the correlations of samples scores from the RAO with several physico-chemical parameters and factors. The highest correlation was with pH and factor 3 (temperature, oxygen, and pH) for all five lentic systems; the correlations were not very high for the three lakes, but were very high for the bog and marsh, with pH, silica, alkalinity, conductivity, and factor 1 (pH, alkalinity, conductivity, and chloride) having high correlations with the first axis.

The third and final chapter examines which physico-chemical parameters influence the distribution of diatoms, autotrophic protozoans, and all protozoans. In addition the relative degree of relationship is examined through correlational procedures. An improved statistical procedure called detrended correspondence analysis (DCA) was utilized in this examination that allows inclusion of all species of more than one occurrence. In this fashion 228 diatom species were utilized, 116 species of autotrophic protozoans, and 425 species of protozoans were included. Canonical variate analysis and factor analysis was the same as mentioned in chapter 2.

Correlations between DCA coordinates for diatom, autotrophic protozoan, and protozoan samples revealed that diatom samples consistently revealed a higher degree of relationship between the community and physico-chemical parameters. In addition, examination of plots of DCA scores clearly shows a greater degree of similarity between diatom samples and the other two categories. Finally, the number of significant correlations between diatom DCA scores and the physico-chemical parameters and factors is greatest, while autotrophic protozoans are next, with all protozoans last. This suggests that diatom communities are more closely related to the physico-chemical parameters of their environment than are the autotrophic protozoans and all protozoans.

Conclusions

1. Diatom species accrual on PF substrates does not follow MacArthur-Wilson predictions. It appears that diatoms are present in the water column in lentic habitats and do not need to traverse inhospitable terrain, but are merely sampled by the PF substrates. Protozoan species accrual appears to follow predictions of the MacArthur-Wilson model.
2. Many species of protozoans (546) were found in this study. Many (121) were found in only one sample and only seven were found in over 50% of the samples.
3. Canonical variate analysis and factor analysis are useful tools designed for data reduction and interpretation. In

this study they revealed that the bog and marsh were divergent in physico-chemical composition while the lakes were similar. Much of the environmental data set variability could be explained by three composite factors.

4. Cluster analysis of the most commonly occurring protozoans suggests that several lake samples form an early successional fauna, while the bog and marsh tend to cluster together.

5. The location of protozoan samples along ordination axes correlates with several physico-chemical parameters and factors. This suggests that differences between all five lentic habitats are related to pH and oxygen, the three lake's protozoan samples appear separated along an ortho-phosphate and silica gradient, and the bog and marsh appear to be separated by an ion factor, pH, alkalinity, conductivity, and silica. In addition, similarities between plots of environmental parameters in a canonical variate analysis and plots of ordination scores supports also the conclusion that protozoan communities are influenced by their physico-chemical environment.

6. pH was most highly correlated with the first axis for all community types, this indicates the possible importance of pH in the distribution of organisms in the lentic habitats examined.

7. Diatoms appear to be more closely in tune with the physico-chemical parameters of their environment than are the autotrophic protozoans and protozoans.

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GENUS	SPECIES	1A	1B	1C	3A	3B	3C	7A	7B	7C	14A	14B	14C	21A	21B	21C	42A	42B	42C	42D	
ACHANTHES	LAPPONICA VAR. NINCKEI	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
	LEVANDERI	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	LEWISIANA	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	LINEARIS	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	LINEARIS F. CURTA	10	11	11	19	14	12	15	15	9	2	11	3	15	6	2	2	17	3	6	1
	MARGINULATA	243	3	5	4	2	1	2	0	4	1	3	4	6	9	2	0	1	1	0	0
	MINUTISSIMA	31	2	3	15	16	4	13	0	0	0	8	8	18	9	4	18	12	17	11	19
	OESTRUPHII	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	PINNATA	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
			2	2	4	2	5	0	5	7	8	35	12	21	64	68	24	162	152	130	0
		27	37	29	40	50	37	47	34	48	46	78	86	70	82	72	166	130	121	0	
		63	104	92	79	68	52	89	58	86	49	84	89	77	91	71	133	109	136	0	
		2	1	0	2	2	2	0	0	1	0	1	0	1	0	1	3	6	0	0	
		11	65	64	50	20	2	7	14	16	26	50	32	34	26	31	18	18	20	0	

GENUS	SPECIES	1A	1B	1C	3A	3B	3C	7A	7B	7C	14A	14B	14C	21A	21B	21C	42A	42B	42C	42C	
CALONEIS	SHUMANNIANA VAR. LANCETTULA	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
CALONEIS	SILICULA	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
CALONEIS	SILICULA VAR. TRUNCATULA	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
CALONEIS	VENTRICOSA	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
CALONEIS	VENTRICOSA VAR. TRUNCATULA	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
CALONEIS	SPI	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
COCCONEIS	DIMINUTA	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
COCCONEIS	PEDICULUS	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
COCCONEIS	PLACENTULA VAR. LINEATA	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
		0	2	3	0	1	3	0	1	2	2	0	1	0	1	0	2	0	1	0	1
		0	2	0	1	0	1	1	1	3	3	0	5	1	8	2	4	1	0	0	0
		4	8	11	27	34	4	6	18	23	4	9	13	1	7	7	24	24	10	0	0

GENUS	SPECIES	1A	1B	1C	3A	3B	3C	7A	7B	7C	14A	14B	14C	21A	21B	21C	42A	42B	42C	
DIPLONEIS	ELLIPTICA	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
DIPLONEIS	PUELLA	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
ENTOMONEIS	ORNATA	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
EPITHENIA	ADNATA	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
EPITHENIA	ARGUS VAR. PROTRACTA	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
EPITHENIA	SMITHII	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
EPITHENIA	SOSEX	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
EPITHENIA	TURGIDA	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
EPITHENIA	TURGIDA VAR. GRANULATA	5	4	52	13	16	22	6	62	53	3	5	7	0	8	6	10	28	11	0

GENUS	SPECIES	1A	1B	1C	3A	3B	3C	7A	7B	7C	14A	14B	14C	21A	21B	21C	42A	42B	42C	
NEIDIUM	SP1	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
NITZSCHIA	ACICULARIS	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
NITZSCHIA	AMPHIBIA	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
NITZSCHIA	ANGUSTATA	0	1	0	5	4	0	0	0	1	0	0	0	0	0	0	0	0	0	0
NITZSCHIA	ANGUSTATA VAR. ACUTA	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
NITZSCHIA	ANGUSTATA VAR. FINNATA	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
NITZSCHIA	BREVISSIMA	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
NITZSCHIA	CAPITELLATA	2	3	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
NITZSCHIA	CLAUSII	33	5	2	4	1	1	0	1	10	22	47	5	123	35	7	35	40	9	0

GENUS	SPECIES	1A	1B	1C	3A	3B	3C	7A	7B	7C	14A	14B	14C	21A	21B	21C	42A	42B	42C	
	<i>PINNULARIA MESOLEPTA</i> VAR. <i>ANGUSTA</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	<i>PINNULARIA MICROSTAURON</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	<i>PINNULARIA STOMATOPHORA</i>	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	<i>PINNULARIA SUBCAPITATA</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	<i>PINNULARIA UNDULATA</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	<i>PINNULARIA VIRIDIS</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	<i>PINNULARIA</i> SP1	0	5	5	0	2	2	3	1	3	1	0	0	0	0	0	0	0	0	0
	<i>RHOICOSPHERIA CURVATA</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	<i>RHOPODIA GIBBA</i>	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
		0	10	20	20	45	4	1	1	54	50	31	66	26	78	55	73	46	175	0

GENUS	SPECIES	A	1	2	3	4	5	6	7	8	9	0B	1	2	3	4	5	6	7	8	9	0C	1	2	3	4	5	6	7	8	9	0	
CYRTOLOPHOSIS	ELONGATA	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
		0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0	1	0	0	
		0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
CYRTOLOPHOSIS	MUCICOLA	0	0	0	1	0	0	0	1	1	0	0	0	1	0	1	1	1	1	1	0	1	0	0	0	1	0	0	1	1	1	1	
		1	1	1	0	1	1	0	0	0	1	1	0	1	1	1	1	1	1	1	0	1	1	0	1	0	0	0	0	1	1	0	
		1	0	1	1	1	0	1	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	
DENDROMONAS	VIRGANIA	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
		0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
		1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
DEREPYXIS	SP	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
		0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
		0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	
DIFFLUGIA	ACUMINATA	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
		0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	
		0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
DIFFLUGIA	CONSTRICATA	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
		0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
		0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
DIFFLUGIA	CORONA	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
		0	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
		0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
DIFFLUGIA	GLOBOSA	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0	0	0	0	0	
		0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0	0	0	
		0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	
DIFFLUGIA	OBLONGATA	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
		0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
		0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	
DIFFLUGIA	SP	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
		1	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	
		0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	1	1	0	1	1	1	0	0	1	1	0	0	1	1	
DIFFLUGIA	URCEOLATA	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
		0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
		0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
DILEPTUS	AMERICANUS	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
		1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0	0	0	0	0	
		0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
DILEPTUS	AMPHILEPTUS	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
		0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
		0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
DILEPTUS	ANSER	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
		0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	1	0	0	0	0	
		0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	
DILEPTUS	SP	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
		0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
		0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
DIMORPHA	SP	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
		0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
		0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
DINOBYRON	BAVARICUM	1	1	1	1	1	0	0	0	1	1	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
		0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
		0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0	

GENUS	SPECIES	A1	2	3	4	5	6	7	8	9	0B1	2	3	4	5	6	7	8	9	0C1	2	3	4	5	6	7	8	9	0		
STICHOTRICHA	SP	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0		
		0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	
		0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	1	0	0	0	1	
STOKESIELLA	LEPTOSTOMAS	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0		
		0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0		
		0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0		
STRIAMOEBIA	SP	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	
		0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
		0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	
STRIAMOEBIA	QUADRILINEATA	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
		0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
		0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
STROBIDIUM	SP	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
		0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
		0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
STROBILIDIUM	GYRANS	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
		0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
		0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
STYLONYCHIA	MYTILUS	0	0	0	1	0	0	1	0	1	1	1	1	1	1	0	0	1	0	0	0	0	0	0	1	0	1	0	1	1	
		1	0	1	1	1	0	0	0	0	0	1	0	0	0	1	0	1	1	1	1	1	1	0	0	0	0	0	0	0	
		0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
STYLONYCHIA	PUSTULATA	0	0	0	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
		0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
		0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
STYLONYCHIA	GRANDIS	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
		0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	
		0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
STYLONYCHIA	PUTRINA	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
		0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
		0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
STYLONYCHIA	SP	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
		0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	
		0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
SUCTORIA	SP	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
		0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
		0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
SYNURA	VOLVOX	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
		0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
		0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
SYNURA	ADAMSI	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
		0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
		0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
SYNURA	SP	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
		0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
		0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
SYNURA	SPHAGNICOLA	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
		0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
		1	1	1	1	1	1	0	1	0	1	0	1	0	1	0	1	0	1	0	1	0	1	0	0	0	0	0	0	0	0
SYNURA	UVELLA	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
		0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
		0	1	0	0	0	0	0	0	0	0	0	1	1	0	1	1	1	1	1	0	0	0	0	0	0	1	0	0	0	

The 7 page vita has been
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document