

STRUCTURE OF ARTHROPOD COMMUNITIES IN SOME SALINE LAKES
OF CENTRAL BRITISH COLUMBIA

By

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ABSTRACT

Aquatic arthropods communities were examined with respect to factors determining species distributions and community structure in a series of eight lakes on the Chilcotin Plateau of British Columbia. Climate, altitude, physical location, water temperature and basin shape were similar for all lakes, and although size differed, no evidence was found for the influence of basin morphology on community structure. Salinity and vegetation characteristics differed widely among lakes, so three major processes were investigated: the association of (1) salinity with faunal communities, (2) salinity with floral communities, and (3) faunal with floral communities. These relationships were examined in light of diversity-stability hypotheses.

The severity component of environmental stability was represented by salinity, and mean surface water conductivity ranged from 56 to 13115 $\mu\text{S cm}^{-1}$ at 25 °C. Salinity variations among lakes were determined primarily by the ions Na, HCO_3 , CO_3 , Cl and K.

Two classification schemes (taxonomic and ecological) and several analytical techniques (community parameters and cluster analysis) indicated that the distribution and structure of faunal and floral communities were related to salinity. In total, 84 arthropod taxa and 26 macrophyte species were found and divided into three groups: those characteristic of high salinities ($>5000 \mu\text{S}$), of moderate or low salinities ($<5000 \mu\text{S}$), or tolerant of all salinities. Faunal assemblages in all lakes were dominated by filter feeders, and predators were more abundant in saline lakes. Shredders, collectors and predators were found in all the lakes, but saline lakes had fewer size groups. Floating leaved macrophytes occurred only in

freshwater lakes, submerged forms were rare in highly saline lakes, and emergent forms were found in all lakes, although they were less abundant at high salinities.

Generally, this study supports the hypothesis that saline habitats have less diverse communities than freshwater ones. In all floral and faunal sample sets, increased salinity was accompanied by a decrease in species richness. Virtually all measures of macrophyte community diversity and productivity were inversely correlated with salinity. Faunal subgroups must be examined separately when measures of community structure incorporate relative abundances. Patterns of association observed in the entire faunal community were dictated by the numerically dominant entomostracan subcommunity, and patterns in other subgroups were masked. Zooplankton trophic level diversity increased with decreasing salinity and changes in community composition were analogous to those of eutrophication. In both coleopteran and hemipteran communities, diversity decreased and density increased with increasing salinity. Possible causal mechanisms structuring each community are hypothesized.

Faunal distributions corresponded to their known habitat preferences in terms of macrophyte communities. It was difficult to distinguish between the influence of salinity or macrophyte communities on animal communities as animal communities were often associated with both.

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GENERAL INTRODUCTION

Inland saline lakes comprise only a very small fraction of the total aquatic environment, yet they have intrigued biologists for many years. These unusual habitats confront potential colonizing organisms with extremely severe osmotic problems, but nevertheless they contain some characteristic inhabitants (Bayly, 1972). Questions of how aquatic organisms are affected by water salinity can be approached at an ecological or physiological level: physiologically, environmental factors "act" at the organismal level whereas ecologically, higher levels of community organization can be considered an integration of all the direct individual-environment relations (Scott, 1974). This investigation does not deal with the physiological processes of osmotic regulation and tolerance, but concentrates on the ecological level of community structure in saline lake series.

Lakes of the Chilcotin Plateau region of British Columbia present an ideal opportunity to study the effects of salinity on aquatic organisms as they cover a wide range of salinity, while many other factors such as climate, altitude and geographical location are similar for all lakes. Previous studies comparing saline lake flora and fauna have encompassed ranges of climate, altitude, or permanence, so several major environmental factors other than salinity may have affected the biota of these lakes (Beadle, 1943; Rawson & Moore, 1944; Moore, 1952; Bayly & Williams, 1966; Hammer et al., 1975; Geddes et al., 1981; Brock & Shiel, 1983; Galat & Robinson, 1983; Timms, 1983; van Vierssen & Verhoeven, 1983). Timms (1981) studied three lakes that had similar physiographical and physiochemical features except salinity, but more than three lakes are required to

adequately describe patterns in community structure and correlate them with environmental variables.

It has been established that the salinity gradient present in these Chilcotin lakes influences the distribution of organisms, i.e. aquatic angiosperms (Reynolds & Reynolds, 1975), Hirudinea (Scudder & Mann, 1968), arthropods (Scudder, 1969a), crustacean zooplankton (Reynolds, 1979), Odonata (Cannings et al., 1980; Cannings & Cannings, 1985), Corixidae (Scudder, 1969b; 1983), and Chironomidae (Cannings & Scudder, 1978). However, virtually no work has been done on community structure or the relationship between plant and animal communities in these lakes.

There are three major processes which need to be investigated simultaneously in order to understand the community structure and species interactions of saline lake ecosystems: (1) the effects of salinity on animal communities, (2) the effects of salinity on plant communities, and (3) the relationship between plant and animal communities. There have been a number of studies on saline lake fauna and saline lake flora, but few have attempted to relate the two, as this study does.

One of the difficulties accompanying studies of community structure along environmental gradients is how best to quantify and describe both the environment and community. In order to provide a complete picture and avoid a biased perspective, several different and complementary techniques should be employed. In this study, abiotic and biotic aspects of the lakes were described in two general ways: simple quantitative parameters and multivariate techniques. Multivariate techniques objectively search for patterns among communities that may correspond to environmental gradients, whereas quantitative comparisons of numerical parameters test for specific relationships between the abiota and biota. In this study, comparisons

between biotic and abiotic numerical parameters are perhaps best viewed in terms of the diversity-stability concept, a topical and controversial area of ecology.

The concept of a relationship between diversity and stability has been prevalent in ecological literature for the past 30 years, and much of the controversy associated with this topic is attributed to the wide spectrum of meanings covered by the terms "diversity" and "stability". Diversity and stability are related not by one hypothesis, but rather a whole family of hypotheses depending on whether these terms are applied to either the abiotic environment or the biotic community. Some general hypotheses are:

1. Diverse communities are more (or less) stable than less diverse communities.
2. Diverse environments have more (or less) stable/diverse communities than less diverse environments.
3. Stable environments have more (or less) stable/diverse communities than less stable environments.

A short paper by MacArthur (1955) that attempted to relate community stability to food web structure (diversity), stimulated a plethora of studies testing Group 1 type hypotheses. Goodman (1975) reviews much of the early literature on this topic and finds no evidence supporting MacArthur's hypothesis. Hypotheses dealing with diverse environments (Group 2) often focus on the relations between spatial or substrate heterogeneity and community structure, as seen in studies on bird species diversity (MacArthur & MacArthur, 1961; MacArthur et al., 1966). Tests of Group 3 hypotheses examine relations between environmental gradients and biotic communities, a common topic in ecology, although many such studies are not discussed in the framework of diversity-stability theory. Some

studies successfully confuse these groups of hypotheses, thereby adding to the controversy. Zaret (1982) attempted to relate Group 1 and Group 3 type hypotheses, but appears to have fallen short of his goal, partly owing to a carelessness of terminology (Kimmerer, 1984), although Kimmerer himself uses some fallacious arguments.

This particular study uses a saline lake series primarily to test the hypothesis that stable environments have more diverse faunal (and floral) communities than less stable ones (Group 3). Secondly, it examines the hypothesis that more diverse floral communities host more diverse faunal communities (Group 2). Zaret (1982) deems Group 3 hypotheses trivial because the impetus for diversity-stability questions came from observed latitudinal diversity gradients. There are few, if any studies, however, that unequivocally demonstrate such trends or that attempt to elucidate the mechanisms producing such a trend. More specifically, many studies of saline lakes suggest that increasing salinity is accompanied by decreasing community diversity, but none has rigorously tested the hypothesis or examined it in light of the diversity-stability concept.

The hypothesis that stable environments have more diverse communities than less stable ones can be expanded into an even larger number of sub-hypotheses depending on exactly how "diversity" and "stability" are defined. Environmental stability can be defined as the severity, variability, or predictability of abiotic factors. Hence, the hypothesis assumes that less diverse communities are found in habitats with severe abiotic conditions, variable conditions, unpredictable conditions, or combinations thereof. Community diversity generally refers to the structural complexity of a community in terms of the number or relative abundance of species or morphs. Diversity can be measured or estimated

from community censuses; this topic will be discussed in more detail in Chapter 2. I make no attempt to examine community stability as it cannot be measured directly, its presence can only be inferred from changes in the community through time. Community stability can be defined in a variety of ways, but usually refers to the tendency of a system to remain near, or return to, an equilibrium point after a perturbation (Orians, 1975).

STUDY SITE

The study site, Becher's Prairie, is in the Chilcotin Plateau region of central British Columbia: west of the Fraser River and near Riske Creek (Fig. 1). Environmental parameters such as physical location, altitude and climate are similar for all lakes. The lakes are at 950 m elevation and lie 250 to 2000 m apart, within a 5 km radius, among many other small water bodies in pine-aspen parkland. The climate is characterized by relatively low annual temperatures with large seasonal and daily fluctuations (-11.6 and 13.7 °C mean daily temperature for January and July respectively), and low precipitation (35 cm annually) (Cannings *et al.*, 1980). The lakes are under ice-cover from mid-October to late April (Cannings & Scudder, 1978). The water level is relatively stable during any one season as lakes lack inlet or outlet streams, are not connected with the main drainage system, and hence are not subject to flooding (Munro, 1945).

The eight study lakes vary both in size and chemical character: larger, more saline lakes are generally dominated by NaHCO_3 while in smaller, fresher ones MgCO_3 often predominates (Cannings & Scudder, 1978). Detailed physical and chemical properties of the water bodies are given in Topping & Scudder (1977). All are athalassic in ionic origin, as defined by Bayly (1967), i.e. they have no present or historic associations with a marine environment [see Williams (1981a) for further discussion of terms]. The complexity of the geology in central British Columbia and general lack of geological data from the study area preclude a detailed geological interpretation of lake water chemistry (Topping & Scudder, 1977). Surface water salinity usually varies seasonally and annually both within and between lakes. These variations are owing to changes in the

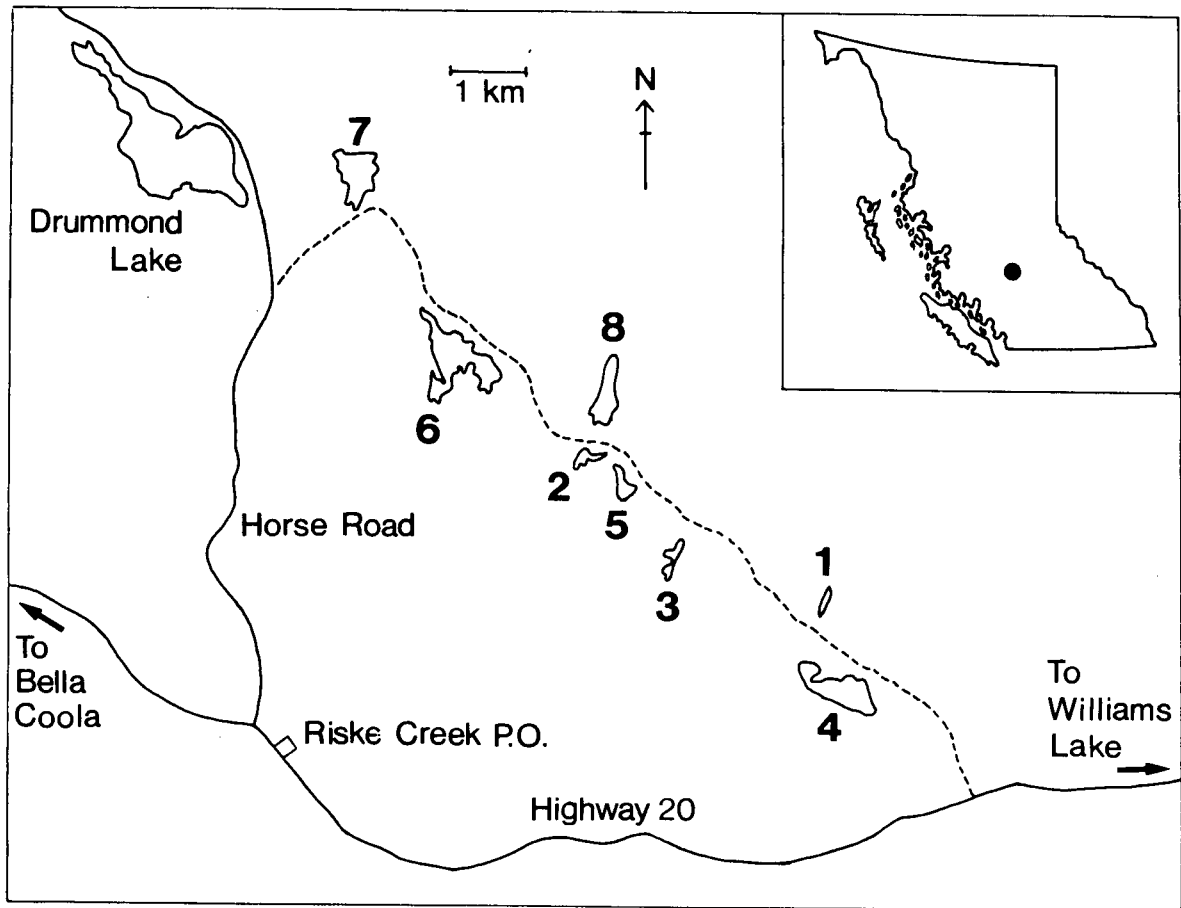


Fig. 1. Study area. Numbers 1-8 = lakes studied: 1 = Box 27, 2 = Barkley L., 3 = Near Opposite Crescent, 4 = Rock L., 5 = L. Jackson, 6 = L. Lye, 7 = Round-Up L., 8 = Barnes L.

volume and time of spring run-off, and to different amounts of mixing between surface and lower, more saline water (Scudder, 1969a; Topping & Scudder, 1977).

There are differences in the vertical distribution of temperature in different lakes. In general, lakes are homeothermal in the upper 2 m, and lakes shallower than 3-4 m, or with conductivities less than 5500 μS , are essentially isothermal throughout (Scudder, 1969a; Topping & Scudder, 1977).

The eight lakes examined in this study are all permanent, lack fish predators, and were specifically chosen to obtain a wide range of salinities: in 1978 mean conductivity ranged from 56 to 13115 $\mu\text{S cm}^{-1}$ at 25 °C. For convenience, lakes were numbered from 1 to 8 in order of increasing salinity (Fig. 1). All lakes are situated in depressions in the rolling prairie (Plate 1). The two most freshwater lakes studied are both small, shallow, and have extremely soft shorelines (Plate 2), whereas others have firm margins, often with precipitated salts (Plate 3).



Plate 1. 14.ix.84. Lake 2 (Barkley L.) situated in a depression in the rolling prairie.



Plate 2. 14.ix.84. Lake 2 (Barkley L.) with a shallow soft shoreline.



Plate 3. 12.viii.84. Lake 7 (Round-Up) with a firm gravelly bottom and white precipitated salts on emerged rocks.

CHAPTER 1: PHYSIOCHEMICAL FEATURES

Introduction

Ecological studies of aquatic fauna must consider the physical and chemical nature of the waters as well as the fauna because aquatic ecosystems are intimately coupled with and affected by the abiotic environment (Williams, 1967). This study is concerned with faunal community differences in a saline lake series and the physiochemical (or other) factors that contribute to these differences. The objective of this first chapter is to characterize the physiochemical properties of the study lakes.

Although the main difference between study lakes is salinity, a variety of abiotic factors could influence the biota. The study lakes are all close enough together that they have the same geological origin, are at the same altitude, and are subject to the same climate. Consequently, these factors, often significant in lake metabolism (Hutchinson, 1957; Wetzel, 1975), were not considered with respect to differences in the biota. Local factors such as water temperature, chemistry and basin morphometry, however, may vary and affect the biota, and therefore were examined.

Temperature is a key environmental factor directly influencing life-history patterns of aquatic animals, and indirectly influencing their food supply through changes in the phytoplankton community. Sweeney (1984) provides an excellent review of the life-history literature on aquatic insects; Hutchinson (1967) reviews crustacean zooplankton and phytoplankton. Therefore, the possibility of water temperature differences affecting biological communities in the study lakes must be considered.

Water salinity, in terms of both the total and proportionate concentrations of ions, varies among lakes and can influence the metabolism of many organisms through osmotic stress and consequently affect community structure. Every organism has a critical range of salt concentrations within which the integrity of biochemical mechanisms of the organism is ensured; variations above or below this range can be fatal. Some organisms avoid the problems of osmotic stress by being tolerant of a wide range of conditions, such as most zooplankton (Hutchinson, 1967; Brand, 1981), or by regulating their internal environment through selective absorption and excretion of ions, as in several dipteran species (Phillips et al., 1978) and brine shrimp (Croghan, 1958a; 1958b; 1958c; 1958d; Geddes, 1975a; 1975b; 1975c). Although salinity acts at the organismal level, its effects may be manifest on an ecological scale, as many studies have indicated (Beadle, 1943; Rawson & Moore, 1944; Moore, 1952; Bayly & Williams, 1966; Scudder, 1969a; Savage, 1971; Reynolds, 1975; Cannings & Scudder, 1978; Williams, 1978; Cannings et al., 1980; Geddes et al., 1981; Timms, 1981; 1983; Brock & Shiel, 1983). Few studies, however, have examined the role of ionic proportions to the ecology of faunal groups although they may well be important as suggested by Bayly (1969), Paterson & Walker (1974) and Williams (1981b). Although this investigation does not deal directly with the physiological processes of osmotic regulation and tolerance, salinity is obviously a factor important to aquatic communities.

One of the ecological questions addressed in this study requires that salinity be expressed in terms of environmental stability, as mentioned in the General Introduction. Salinity is readily quantified in terms of the three components of environmental stability: severity as mean or maximum salinity, variability as the range or deviation within one year, and

predictability as the variation between years. This is a convenient way to quantify the seasonal and annual variations in salinity known to occur in the study lakes (Scudder, 1969a; Topping & Scudder, 1977).

The morphology of lake basins can have important effects on biotic communities in terms of productivity, the species/area phenomenon, and the relative contribution of littoral processes to the whole lake. The shape of lake basins is often reflected by productivity: steep sided basins are usually deep and unproductive whereas shallow depressions with a greater percentage contact of water with the sediments generally exhibit moderate to high productivity (Wetzel, 1975). A number of studies have focused on the importance of lake morphometry to lake productivity (Rawson, 1952; 1955; Hayes & Anthony, 1964), so I included basin shape in lake characterization. Secondly, the theory of island biogeography postulates that the size of an island is directly proportional to the number of inhabiting species (MacArthur & Wilson, 1967), and it has been shown to be true in some cases [see summary and early references in Simberloff (1974); Fryer (1985) for a more recent example]. The lakes on Becher's Prairie can be considered islands of various sizes situated close enough together that all species have equal potential for dispersal to all lakes, as suggested for Corixidae (Scudder, 1969b). Therefore, I examined lake size with respect to faunal community structure. Thirdly, biotic communities can be influenced by the relative contribution of littoral processes to the whole lake, especially in small lakes such as those in this study (Westlake, 1963; 1965). Littoral flora constitute a major site for the synthesis of organic matter which contributes significantly to the productivity of lakes and to the regulation of metabolism of the whole lake ecosystem (Kowalczewski, 1975; Wetzel, 1975). Morphometric components of a lake

determine the potential for littoral processes to influence the ecosystem, and should be considered a possible influence on biotic communities.

Materials and Methods

There are many ways to describe physical and chemical aspects of a lake, and I used composite measures of the environment in the form of single numerical parameters and pictorial dendograms produced by multivariate methods. The necessary raw data for these characterizations were assembled from a variety of sources: unpublished chemical and temperature data collected by R.A., R.J. & S.G. Cannings in 1978, physiochemical data from 1966 published by Topping & Scudder (1977), and some of my own map measurements.

TEMPERATURE. Water temperature was measured at 1 m depth with Ryan model-D underwater continuous chart recorders from May to October, 1978.

CHEMISTRY. Among the simplest measures of salinity are total ion concentration, TDS (total dissolved solids), and conductivity. Total ion concentration is the sum of the concentrations of the eight major cations and anions, Ca, Mg, Na, K, HCO_3 , CO_3 , SO_4 and Cl, analyzed independently [see Topping & Scudder (1977) for techniques]; TDS is an estimate of all inorganic materials dissolved in water; conductivity (specific conductance) is a measure of the resistance of a solution to electric current. A study of 32 B.C. lakes, including those in this study, showed conductivity to be a significant linear function of TDS and a significant curvilinear function of total ion content (Topping & Scudder, 1977). Consequently, this study considered only conductivity to indicate salinity as it was the most convenient and readily available measure.

Conductivity at 1 m depth was measured with a Radiometer CD 2 conductivity meter monthly, from May to October 1978.

One drawback of total salinity measures is that individual ions lose their unique identity when anonymously lumped together. To avoid this problem I used multivariate ordination techniques that consider both ionic composition and concentration simultaneously and equally, yet produce a quantitative linear arrangement of lakes. Ordination is a mathematical treatment designed to produce an objective numerical arrangement of samples (lakes) reflecting the similarity of their constituent variables (ions). It aims to resolve the total variation in a set of variables into linearly independent composite variables which successfully account for maximal variability in the data (Sinha, 1977). In this way one can objectively examine whether most of the information in the data can be expressed by a few axes. The first axis contains the largest share of statistical variation in the original data; the second and subsequent components are unique and uncorrelated with preceding ones, and express decreasing amounts of total variation in the data (Gates et al., 1983). Component scores for each lake on these axes can then be used as a composite measure of salinity in terms of environmental severity, but not variability or predictability unless an element of time is included.

In addition, it is possible to determine which variables (ions) combine to define each component by looking for correlations between individual ions and component scores. Any associations between component scores and biotic parameters might give some indication of which ions are physiologically limiting to species.

Of the many ordination techniques available, principal components analysis (PCA), as provided by BMDP (Frane et al., 1983), was used to

ordinate the lakes from their ionic composition. The necessary data on ion concentrations were predicted for 1978 from values in Topping & Scudder (1977). Given that conductivity is closely related to total ion content (Topping & Scudder, 1977), and since the relative proportion of ions in each lake is comparatively similar from year to year (Scudder, personal communication), it is possible to predict individual ion concentrations in any other year from a measure of conductivity. Predicted concentrations of the eight major ions in each lake constituted the raw data matrix from which a covariance matrix was calculated and subjected to PCA. A covariance matrix was used because all variables are in the same units, and because this matrix extracts more information than one based on correlations only.

MORPHOMETRY. The simplest and perhaps best composite measure of lake size is mean depth, calculated as the ratio of lake volume to surface area. Morphometric measures of lake surface area, volume, and mean depth were taken from Topping & Scudder (1977).

The morphometric measure of shoreline development reflects potential for the development of littoral communities in proportion to lake volume (Wetzel, 1975), and hence its contribution to the whole lake. Values for shoreline development are only comparable among lakes if area is constant (Hutchinson, 1957). Because lake area is not constant among lakes, I modified the shoreline development formula so different lakes would be comparable. Shoreline development (D_L) is the ratio of lake perimeter (shorelength, L) to the circumference of a circle of area equal to that of the lake. When corrected for area (A) the ratio (D_{LA}) is as follows:

$$D_{LA} = \frac{L}{2A \sqrt{A\pi}}$$

High values of D_{LA} indicate high potential for littoral processes to affect the whole lake, and vice versa for low values. I measured shoreline length with a chartometer on a 1:50,000 map and normalized results according to Håkanson (1981). These data were then used to calculate shoreline development (D_L) and the ratio of D_L to area (D_{LA}).

CLASSIFICATION. Multivariate classification techniques, like ordination, permit a simultaneous and equal examination of both ionic composition and concentration. These techniques group similar entities (lakes) together in clusters by means of similarity or dissimilarity indices. Hierarchical classifications arrange groups into hierarchical dendrograms indicating relationships among groups.

The unweighted pair-groups method using arithmetic averages, UPGMA, as provided by NT-SYS (Rohlf et al., 1980) and recommended by Sneath & Sokal (1973), was used to cluster the eight lakes. This method follows a polythetic agglomerative hierarchical strategy clustering similar lakes together and arranging the groups into a hierarchical dendrogram. Euclidean distance, a dissimilarity measure, was used to group lakes as it tended to produce the least amount of distortion when numerical data were converted to pictorial dendrograms. The cophenetic correlation coefficient (Sokal & Rohlf, 1962; Rohlf, 1974; Romesburg, 1984) was used to evaluate the amount of distortion associated with clusters. This technique computes the correlation between the original similarity coefficients, on which the dendrogram is based, and the cophenetic values which are a matrix of coded similarity values extracted from the dendrogram. A perfect correlation ($r=1.00$) between the original similarity coefficients and cophenetic values indicates no distortion on converting data into a dendrogram. A correlation of $r=0.80$ is usually considered the cut-off for acceptable

dendrograms, although there may still be some distortion (Romesburg, 1984).

Two dendrograms were drawn, the first from concentrations of the eight major ions alone, and the second with the addition of total conductivity and six morphometric variables: surface area, volume, mean depth, shoreline length, shoreline development, and the shoreline development/area ratio.

Results and Discussion

TEMPERATURE. Evidence suggests that temperature is not a factor affecting the distribution of organisms among lakes as all eight lakes had similar temperature profiles at 1 m depth. Similar results were found by Scudder (1969a), Jansson & Scudder (1974), and Cannings *et al.* (1980). Fig. 2 presents a plot of temperatures recorded in Lake 1 showing marked seasonal variation, with a recorded minimum of 6 °C and maximum of 23 °C, and is representative of temperature profiles in the other study lakes.

CHEMISTRY. Of the three components of environmental stability, (severity, variability and predictability), only severity can be represented by salinity. This study does not examine the effects of environmental predictability as biological data were available for only one season, although evidence suggests that salinity has gradually increased over the past 20 years (Table 1). Surface water salinity varied seasonally, generally increasing from spring to autumn, but it is difficult to separate environmental variability from severity as mean, range and maximum conductivity are all highly correlated (Fig. 3). Mean conductivity, ranging from 56 μS in Lake 1 to 13115 μS in Lake 8, was used to represent environmental stability in the form of severity.

Fig. 2. Daily temperature range in Lake 1 (Box 27) at 1 m depth in 1978.

Fig. 3. Seasonal conductivity ($\mu\text{S cm}^{-1}$, 25 °C) in each lake in order of increasing salinity. (See Fig. 1 for lake names; see Appendix A for numerical values).

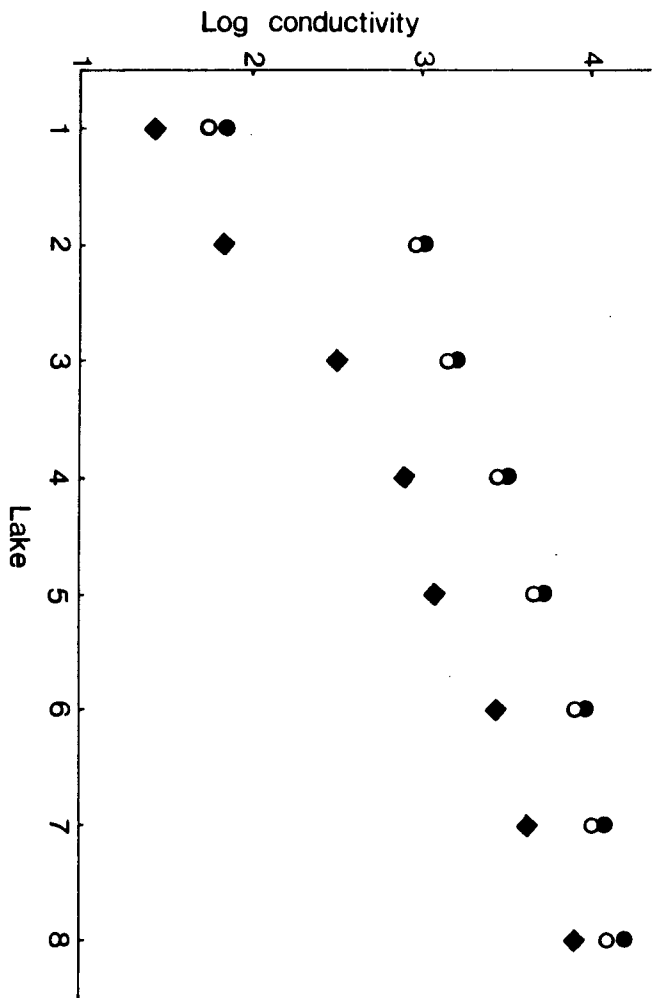
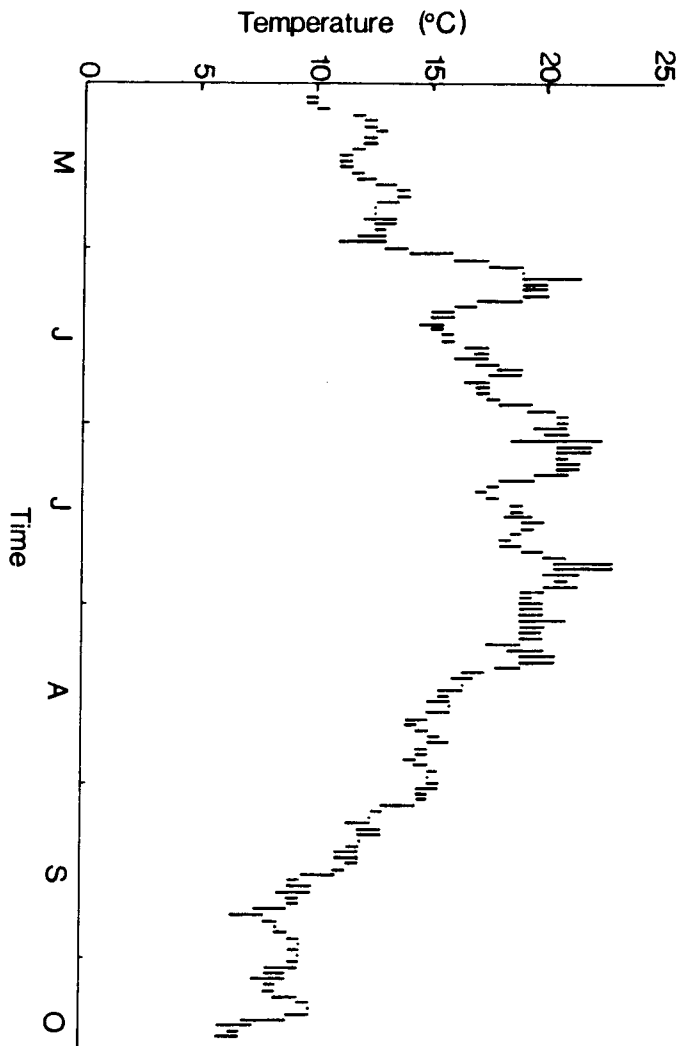


Table 1. Annual variations in mean surface conductivity of study lakes.
($\mu\text{S cm}^{-1}$, 25 °C). (See Fig. 1 for lake names).

Lake	year							
	1963	1966	1967	1969	1972	1978	1983	1984
1				40	40	56	42	65
2				592	720	932	740	956
3				810	830	1437	1443	1762
4				1496	1500	2759	2723	3038
5				2766	3230	4544	4443	5014
6	7125	5350	6448	6548	6550	8281	8067	9348
7				6885	6890	10365	10667	11942
8	13000	8343	10938	11816	11820	13115	12117	14580

Table 2. Mean conductivity and predicted ion concentrations in 1978.
(See Fig. 1 for lake names).

Lake	mean	milliequivalents per liter							
	conductivity ($\mu\text{S cm}^{-1}$ 25°C)	Na	K	Ca	Mg	CO ₃	HCO ₃	Cl	SO ₄
1	56	0.13	0.14	0.32	0.22	0.14	0.41	0.14	0.13
2	932	3.09	0.98	0.60	8.08	0.69	9.02	0.38	0.63
3	1437	5.98	1.06	1.72	7.81	1.44	11.39	0.62	2.38
4	2759	27.50	1.81	1.14	3.21	7.97	22.78	2.90	0.33
5	4544	26.60	2.51	2.33	26.53	3.42	9.86	5.93	39.25
6	8281	88.05	6.46	0.94	3.72	19.94	49.96	27.91	8.84
7	10365	110.86	7.90	0.90	4.59	22.37	48.49	38.24	17.07
8	13115	145.59	14.87	0.48	3.27	55.01	59.85	41.40	28.68

Table 3. Principal component scores for lakes and ions, plus Pearson's product moment correlation of ion PC scores with ion concentrations, calculated from data in Table 2. (** = $p < 0.01$). (See Fig. 1 for lake names).

Lake	PC1	PC2	ion	PC1	r	PC2	r
1	-0.927	-0.480	Na	56.00	1.00**	0.11	0.00
2	-0.844	-0.328	HCO ₃	22.20	0.97**	-3.57	-0.16
3	-0.787	-0.275	Cl	17.80	0.99**	-0.39	-0.02
4	-0.416	-0.706	CO ₃	17.70	0.94**	-0.20	-0.01
5	-0.442	2.361	K	4.90	0.97**	0.30	0.06
6	0.672	-0.655	SO ₄	7.52	0.50	12.90	0.86**
7	1.030	-0.163	Mg	-1.91	-0.23	7.58	0.92**
8	1.710	0.246	Ca	-0.18	-0.27	0.46	0.68

Table 4. Morphometric properties of study lakes (area, volume and mean depth data from Topping & Scudder, 1977). (See Fig. 1 for lake names).

Lake	surface area (ha)	volume (m ³ x 10 ³)	mean depth (m)	shoreline length (m)	shoreline development	shoreline development/ area ratio
1	4.30	23.0	0.5	846	1.15	0.27
2	4.55	32.8	0.7	1184	1.57	0.35
3	6.88	99.2	1.4	1022	1.10	0.16
4	34.64	387.5	1.1	3433	1.65	0.05
5	5.81	79.9	1.4	1397	1.63	0.28
6	46.52	1283.2	2.8	4597	1.90	0.04
7	30.84	787.6	2.6	2721	1.38	0.05
8	17.19	348.4	2.0	2626	1.79	0.10

Table 5. Correlations among abiotic variables. * = $p < 0.10$; ** = $p < 0.05$; *** = $p < 0.01$.

Variable	variable			
	conductivity	PC1	PC2	mean depth
PC1	0.99***			
PC2	0.12	0.00		
mean depth	0.83**	0.81**	-0.02	
D _{LA}	-0.63*	-0.66*	0.38	-0.75**

Ordination results indicate that variations in salinity among the eight lakes were determined primarily by the following ions: Na, HCO_3 , Cl, CO_3 and K; the remaining ions, SO_4 , Mg and Ca, have little influence. Mean conductivity values and predicted concentrations of eight major ions based on the relative proportions presented in Topping & Scudder (1977), and used in ordination, are presented in Table 2. PCA summarized ionic composition on two principal component axes, each representing a different group of ions (Table 3). The first component accounted for 93% of the total variance in the data, the second added only 5% more, indicating that this one projection more than adequately represents the structure of the data matrix. Table 3 shows correlations between individual ions and calculated principal component scores. There is a significant correlation of PC1 with Na, HCO_3 , CO_3 , Cl and K; PC2 with SO_4 and Mg. Principal component scores calculated for each lake are also measures of salinity or environmental severity.

MORPHOMETRY. All the study lakes were of similar form despite variations in size. Morphometric properties of the lakes (Table 4) differed considerably with areas ranging from 4.30 to 46.52 ha, volumes from 23.0 to $1283.2 \times 10^3 \text{ m}^3$, and shoreline length from 846 to 4597 m. Mean depth measures indicate that all the basins were relatively "saucer shaped". The lakes in this study were too small to use mean depth as an indicator of lake productivity, as inverse relationships between mean depth and productivity hold only for large lakes, and deteriorate among small lakes (Wetzel, 1975). Shoreline development values indicate that lakes ranged from almost circular to more elliptical, but none were very convoluted. Not surprisingly, small lakes tended to have higher values of D_{LA} indicating a greater potential for littoral processes to affect the

whole lake. This may well be an indicator of productivity.

RELATIONSHIPS BETWEEN VARIABLES. The eight lakes were characterized according to five composite abiotic parameters: mean conductivity, two principal component axes based on ionic composition, mean depth and the ratio of shoreline development to area. Relationships among these five variables are shown in Table 5, in terms of Pearson's product-moment correlation coefficient (Sokal & Rohlf, 1981). Not surprisingly, conductivity is significantly correlated with PC1, but neither is correlated with PC2 as PC2 is by definition orthogonal to any other component axes produced in the analysis.

The results in Table 5 show a significant positive correlation between mean depth and both conductivity and PC1. This association is probably incidental rather than causal as the relationship did not hold when the test was repeated using mean depth and conductivity data from 29 lakes in Topping & Scudder (1977) ($r=0.01$; $p>0.05$). This chance association is not a serious drawback to the study. Because a positive correlation exists between lake size and salinity, a positive association of community structure with mean depth will probably be accompanied by a positive association with salinity, and likewise for negative associations. Island biogeography predicts a positive relationship between community parameters and lake size, but a negative relationship is predicted between community parameters and salinity. As it is impossible to simultaneously have significant but opposite associations of community structure with both lake size and salinity, only one hypothesis can be supported at a time.

There is a significant inverse relationship between shoreline development/area ratio and mean depth which is not totally unexpected as lake size is used to calculate D_{LA} . D_{LA} tends to be negatively

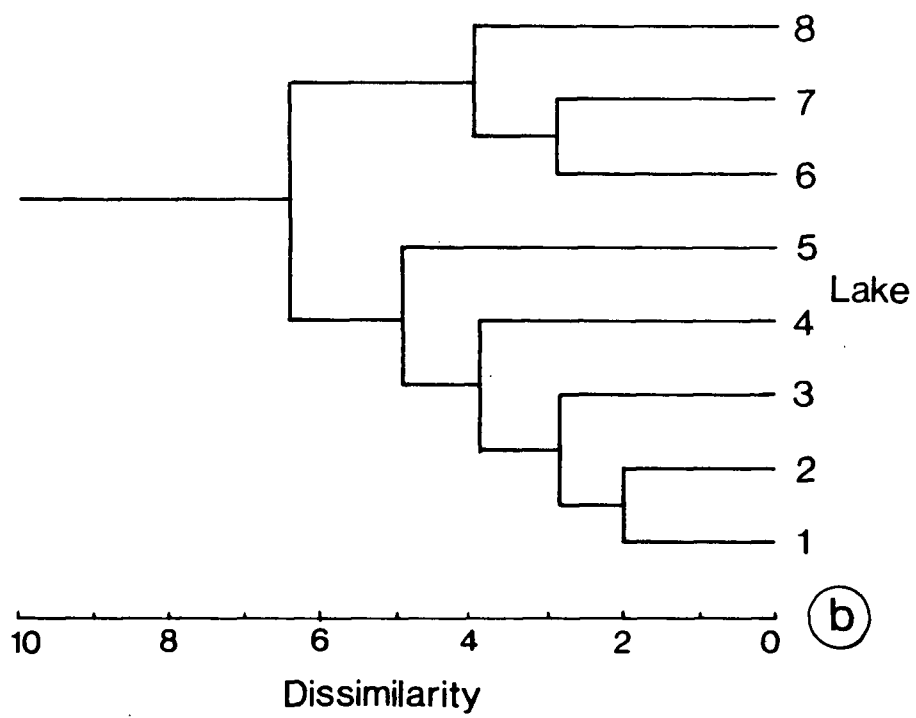
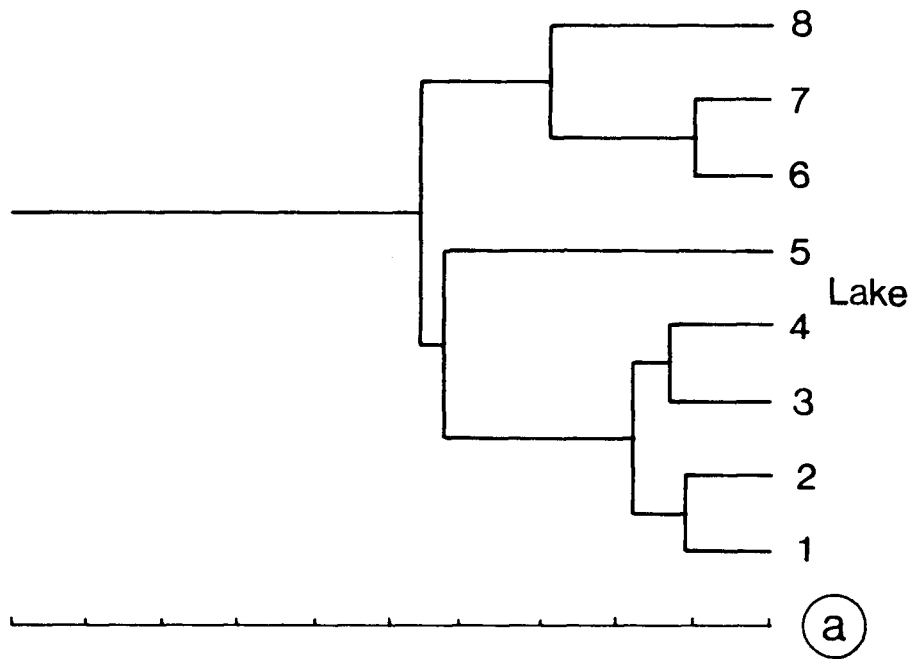
associated with both conductivity and PC1 ($0.05 < p < 0.10$ in both cases), also probably an incidental relationship owing to the positive correlation between lake size and salinity. This association may be a handicap in interpreting biological data as an inverse relationship is predicted between community structure and both salinity and D_{LA} .

CLASSIFICATION. The numerical classification results of predicted chemical data (Table 2) and chemical plus morphometric data (Tables 2+4) are shown in Fig. 4. In both cases, the cophenetic correlation coefficients are greater than the critical level of acceptance so dendrograms are considered adequate representations of the original data.

In general, the dendrograms indicate one major dichotomy of lake types with two branches: one containing saline Lakes 6, 7 and 8; the other containing the more freshwater Lakes 1 to 5. In both instances (with and without morphometric variables) Lakes 6 and 7 are grouped together before Lake 8 is added. Details of the clustering of Lakes 1 to 5 are dependent to some extent on whether or not morphometric variables are included. When lakes are clustered solely on the basis of ionic composition (Fig. 4a), Lakes 1 to 4 are all tightly clustered and Lake 5 is considered relatively dissimilar, probably owing to its extraordinarily high concentrations of Mg and SO_4 (Table 2). With the addition of morphometric variables (Fig. 4b), Lakes 1 and 2 are considered least dissimilar with Lakes 3, 4 and 5 sequentially added to the cluster at more or less regular intervals. This difference is probably attributable to the influence of lake size. None of the resulting dendrograms are surprising even though no a priori assumptions about ranking could be developed from the original data.

Fig. 4. Cluster analysis of study lakes based on dissimilarity of
(a) 1978 predicted ionic composition, cophenetic correlation
coefficient $r=0.813$, and (b) 1978 predicted ionic composition
plus morphometric characters, $r=0.867$. (See Fig. 1 for lake
names).

Note: Least dissimilar (most similar) lakes are joined together
first, and more dissimilar ones are added to the cluster
later.



Summary

This first chapter briefly discusses some hypotheses of how environmental factors can influence biotic communities, and characterizes physiochemical properties of the study lakes in light of these hypotheses. Evidence suggests that temperature was not an important factor influencing biotic communities as all lakes had similar temperature profiles. Of the three components of environmental stability, only environmental severity was represented by salinity data. Salinity varied markedly among lakes and ordination results indicate that these variations were determined primarily by the ions Na, HCO_3 , Cl, CO_3 and K. Morphometrically, all lakes were of similar form, varying mainly in size. Five composite abiotic parameters characterize the lakes and relationships among parameters are discussed. These abiotic variables can now be used in numerical comparisons with biotic community parameters. Multivariate cluster diagrams pictorially represent abiotic similarities among lakes and are clearly related to salinity. These dendrograms act as templates against which to compare dendrograms produced from purely biological data.

CHAPTER 2: FAUNAL COMMUNITIES

Introduction

This chapter examines the relationship between water salinity and faunal community structure, in terms of the diversity-stability hypothesis. As defined in the General Introduction, this hypothesis states that environmentally stable habitats have more diverse communities than less stable ones, where salinity defines environmental stability in terms of severity (Chapter 1). It is well known that many organisms are physiologically affected by water salinity (Bayly, 1972), yet few studies have examined its effects on community structure. The main difference between my study lakes is salinity, but a variety of abiotic factors could influence the biota. Consequently, abiotic measures of basin morphometry are also compared to the faunal community to test for the possible effects of other processes (Chapter 1).

A thorough investigation of lake communities should consider both the entire fauna plus subsets of the fauna, and consider communities in the different lake zones (limnos, littoral, benthos) in concert. In work with a single taxon one must always consider whether observations are an artefact of the taxon, or whether the entire fauna might present a different picture (Simberloff, 1974). Conversely, generalizations about the entire community may mask patterns in its component subsets that may be important factors controlling community structure. Experimental studies by Hall et al. (1970) suggest that communities in different lake zones are not functionally independent but intimately interrelated with each other. This study examines the structure of both the entire faunal community and its subsets, in both the limnetic and littoral zones of several lakes.

It is now generally agreed that several different measures of community structure must be used simultaneously to provide true representation of a community and avoid the loss of valuable information. Therefore, I used a variety of methods to measure community structure to provide a complete picture of the communities and perhaps insight into the various possible mechanisms controlling community structure. Methods of analyzing community structure fall into two broad categories: simple quantitative parameters and multivariate techniques. Community parameters fall under the general heading "diversity" but include species richness, diversity indices, hierarchical diversity, and a new family of super community indices I have developed. Multivariate techniques used in community ecology include direct gradient analysis, classification, and ordination (Gauch, 1982).

Traditionally, studies on the diversity-stability phenomenon interpret diversity in terms of taxonomic species; this study additionally considers an ecological classification in which individuals are categorized according to their feeding ecology and size. Both Walker (1973) and Paterson & Walker (1974) state that low trophic diversities are characteristic of saline waters, yet no one has quantitatively examined the trophic structure of saline lake communities. All measures of community structure can be applied to both taxonomic species and ecological categories.

QUANTITATIVE PARAMETERS

To date, most investigators of saline lake communities used species richness (number of species) to imply decreasing diversity with increasing salinity (Beadle, 1943; Rawson & Moore, 1944; Moore, 1952; Bayly & Williams, 1966; Scudder, 1969a; Hammer et al., 1975; Williams, 1978;

Reynolds, 1979; Wiederholm, 1980; Geddes et al., 1981), but richness may not be the best measure of community diversity. Firstly, species richness may be highly dependent on sampling effort, i.e. observed richness may increase with more or larger samples. This is probably not a significant problem in most saline lake studies as the unusual nature of these habitats has led to more extensive sampling of saline lakes than freshwater ones, yet they appear to have fewer species (Rawson & Moore, 1944; Bayly & Williams, 1966; Scudder, 1969a; Timms, 1981; and others). More importantly, species richness may be the simplest, most fundamental measure of a community and it does perhaps indicate the number of species physiologically capable of surviving in an environment, but alone it is not a useful method for making inferences about community structure. Two communities can have the same number of species yet have quite different relative proportions, niches, interspecific relationships, etc. Unless one assumes that these properties are similar, although the identity of particular species may be different, there is no real basis for comparing the richness of two communities as a gauge of community structure (Peet, 1974). For example, Timms' (1981) results indicate that particular animal species occupy broader niches in saline lakes, hence the nature of biological interactions may vary and species richness may not be a suitable measure of community structure. This drawback of comparing species richness was one motivation for attempting to create a more appropriate measure of community structure, such as a diversity index.

Diversity indices elegantly combine species richness and abundance in a single measure of community structure. Mathematically there are many ways to combine richness and abundance in a single diversity index, and the literature contains many reviews of this topic (Hurlbert, 1970; Peet, 1974;

Pielou, 1975; Routledge, 1979; Washington, 1984). Indices based on information theory are perhaps best known among ecologists, particularly the Shannon-Wiener index. Some advantages of this index are that it is appropriate for measuring community diversity from samples of the total population (Pielou, 1975), it is independent of sample size (MacArthur, 1965), and it is hierarchically additive (Pielou, 1974; 1975).

A formula for hierarchical diversity (Pielou, 1974; 1975) may extract even more information about a community when individuals are classified in more than one way. Unfortunately, hierarchical diversity does not often appear in the literature and those who have used it were restricted to taxonomic classifications and offered limited biological interpretation of findings (Lloyd et al., 1968; Kaesler & Herricks, 1979; Osborne et al., 1980; Ben-Eliahu & Safriel, 1982). There is no reason to restrict classifications to taxonomy, and categorization according to trophic level, size, or growth form may be much more revealing biologically. For example, animals can be classified into both taxonomic and trophic groupings. This method may provide insight into what mechanisms control community structure in saline lake ecosystems. There are several possible explanations of how physiochemical factors could directly or indirectly control the structure of animal communities, and some plausible scenarios are as follows: (1) the distributions of all organisms are directly attributed to physiological limitations, (2) predators and/or competitors controlling herbivore populations are physiologically restricted, (3) herbivores are distributed according to their osmotic tolerance, or (4) the distribution and/or abundance of food for herbivores is affected by salinity. A hierarchical division of diversity could help tease apart these possibilities. If a community shows decreasing species diversity within each trophic level, but

not decreasing trophic level diversity, one might suspect physiological constraints play a more important role than food resources. In the reverse situation one might suspect food quality or quantity to be related to salinity and important in structuring the community. Observations of this sort do not provide definitive explanations of causal relationships, but do suggest areas for further study.

A diversity index is a single descriptive statistic and offers a limited amount of information by itself. Communities can be compared to each other on the basis of their diversity indices, but one would prefer comparisons with an independent reference point. There have been several attempts at "evenness" or "equitability" indices which compare observed diversities to a theoretical maximum for that particular community (Lloyd & Ghelardi, 1964; Pielou, 1966; 1975; Hurlbert, 1970). The major flaw to all evenness indices, however, is that they must presuppose a specific species-abundance distribution, be it geometric, lognormal, or MacArthur's broken stick distribution (May, 1975; Southwood, 1978). Evenness indices have not been very popular in ecological studies because there is no agreement on which species-abundance distribution is appropriate. I propose a new approach to this problem by creating a theoretical maximum "super community" determined by sample communities themselves, not a presupposed species-abundance distribution.

The super community indices I have developed are conceptually very simple: given any series of discrete communities, each one is independently compared, by means of similarity indices, to a theoretical super community. The super community contains all species from all communities in the series, at the maximum density known for each species. The super community itself, like all theoretical maxima, is probably not biologically feasible,

but it does employ an intuitively more realistic species-abundance distribution than other theoretical models. This type of analysis is feasible for only a specific variety of community studies, such as spatially distinct communities where all species are capable of occurring at all sites, or communities that are separated in time but not space. This particular study falls into the first category: the lakes on Becher's Prairie are islands situated close enough together that all species have equal potential for dispersal to all lakes. Biologically, these indices measure the number of species present in a lake relative to the total number available for colonization, or they measure the complexity of a sample community relative to the most complex community possible.

The main advantages of super community indices are that (1) they compare sample communities to a reference point determined by the samples themselves and not some presupposed species-abundance distribution, (2) a variety of similarity indices can be used to compare samples to super communities depending on the nature of the data and personal philosophy of the researcher, (3) indices are comparable to other community parameters and are appropriate for use in simple descriptive statistics, i.e. correlations with environmental parameters, and (4) indices are easily interpreted biologically.

MULTIVARIATE TECHNIQUES

Multivariate techniques of analysis have long been popular among phytosociologists and more recently have received much attention from animal ecologists (Sprules, 1975; Sprules & Holtby, 1979; Gates et al., 1983; Townsend et al., 1983). There are three complementary methods of multivariate analysis: direct gradient analysis, ordination, and

classification. Direct gradient analysis examines the distribution of individual species populations along recognized environmental gradients. Ordination is the objective numerical arrangement of samples or variables along axes that may correspond to environmental gradients. Classification methods group variables into clusters depending on their relative similarities. Two examples of classification used in this study are clustering similar sample sites on the basis of their species composition, and clustering species on the basis of the sample sites that they occurred in. The choice of method depends on study objectives and data set structure.

Materials and Methods

INVERTEBRATE SAMPLING AND ENUMERATION

All samples were collected between May and October 1978, by R.A., R.J. & S.G. Cannings. Limnetic zooplankton were sampled in triplicate every ten days with a 2 litre Van Dorn bottle at 1-2 m depth, mid-lake. Submerged light traps were set between dusk and dawn one night a month in each lake, at 1 m depth just above bottom mud. These simple funnel traps consisted of a 1.4 litre (48 oz.) can, affixed to an upright post, with a funnel opening and a Cyalume light stick inside to attract animals. Littoral zone fauna were sampled with sweep nets every ten days. To ensure that sweep samples were quantitative and comparable, samples were always taken at the same point along the lake shore and each sample consisted of 5 or 10 standardized sweeps, depending on faunal density. All specimens were stored in 70% ethanol.

One difficulty inherent to all community studies is how to delimit a

community: taxonomically, temporally, spatially or by sampling technique. In this study, communities were defined simultaneously by sampling technique and lake zone, as each method was applied to a different lake zone, and defined by taxonomic subsets of total sample sets. Although samples were taken over a period of five months, the time element was largely ignored owing to the highly variable nature of aquatic communities and inadequate number of replicate samples necessary to accurately quantify temporal changes. Instead, community structure was measured in each lake over the entire season. In total, the following communities in each lake were examined and analyzed independently:

water bottle samples: limnetic zooplankton;

light trap samples: all species; Entomostraca; Coleoptera; Hemiptera;

sweep samples: Coleoptera; Hemiptera.

Light traps collect an enormous number and variety of taxa that may not justly be lumped together in numerical analysis of community structure. Therefore, subsets of the total collection were also examined. Littoral sweep samples contained a phenomenal volume of material, but only adult Coleoptera and Hemiptera were enumerated as these individuals were readily removed from samples, possible to identify to species, and complementary to subsets of light trap material.

All individuals were examined and identified to species where possible. Taxonomic identifications employed primarily the following works: (1) Crustacea: Brooks (1957; 1959), Dexter (1959), Wilson (1959), Yeatman (1959) and Pennak (1978); (2) Odonata: Cannings & Stuart (1977); (3) Hemiptera: Hungerford (1948), Scudder (1976) and Truxal (1979); (4) Coleoptera: Wallis (1933), Hatch (1953; 1965; 1971), Anderson (1971; 1976; 1983), Larson (1975), Gunderson (1977) and Colonnelli (1980); (5)

Trichoptera: Wiggins (1977), (6) Diptera: Cook (1956), Coffman (1978) and Belton (1983). Further determinations of Coleoptera were performed by D.J. Larson at the Memorial University of Newfoundland and R.E. Roughley at the University of Manitoba. Voucher specimens and reference material are in the Spencer Entomological Museum at the University of British Columbia.

Foundations for a trophic classification scheme are provided by Cummins (1973; Merritt & Cummins, 1978), and enough information is available in the literature to assign individual species to each feeding ecology group. [Hereinafter, feeding ecology groups will be referred to as trophic levels.] The five trophic levels used are as follows:

- (a) shredder; herbivore: Animals that shred live or decomposing vascular plant material, eg. Haliphus spp.
- (b) collector; filter feeder: Animals that filter suspended fine particulate organic matter from the water column, eg. Daphnia spp.
- (c) collector; sediment feeder: Animals that gather fine particulate organic matter from sediments and deposits, eg. Hyalaea azteca, Chironomini.
- (e) predator; engulfer: Animals that feed on whole live animals (or parts) and have raptorial mouthparts, eg. Dytiscidae, Chaoborus.
- (f) predator; piercer: Animals that feed on live animal cell and tissue fluids and have piercing mouth parts, eg. Corixidae.

Data acquired from the literature were used to assign species to levels. Measures of adult total body length, except in insect orders other than Hemiptera and Coleoptera which employed lengths of last larval instars, were used to designate size groups. These size groups were collated as octaves (logarithmic like intervals) to emphasize subtle size differences

among small species. Approximately ten size groups were determined for each sample set in order to provide a wide enough range of groups for numerical analysis. Trophic level - size groups are referred to as ecological categories.

MEASURES OF COMMUNITY STRUCTURE

To investigate the relationship between salinity and faunal communities, the series of eight lakes was characterized abiotically according to water chemistry and morphometry (Chapter 1), and biotically according to species distribution, richness, abundance, diversity, hierarchical diversity, and super community indices. In addition, lakes were classified into hierarchical cluster diagrams on the basis of their species composition and abundance.

The diversity index I chose is the Shannon-Wiener index (entropy formula) based on information theory (Khinchin, 1957; Margalef, 1968):

$$H' = -\sum p_i \ln p_i$$

where p_i = the proportion of individuals in species i

This formula readily divides total community diversity into the hierarchical components, trophic level diversity and the mean within-trophic level species diversity averaged over all trophic levels, such that:

$$H'(s) = H'(t) + H'_t(s)$$

where $H'(s)$ = total species diversity

$H'(t)$ = trophic level diversity

$H'_t(s)$ = mean within-trophic level species diversity

The mathematical formula is as follows:

$$H'(s) = -\sum p_j \ln p_j + \sum p_j (-\sum p_i \ln p_i)$$

where p_i = proportion of individuals in species i

p_j = proportion of individuals in trophic level j

There are many similarity, or dissimilarity, measures which could be used in a super community index. In this study I considered two contrasting measures: (1) Jaccard's coefficient calculated from binomial species presence/absence data where common and rare species have equal weights, and (2) Euclidean distances calculated from quantitative species abundance data and influenced mainly by numerically dominant species. Super community indices using Jaccard's coefficient are similar to species richness indices; those employing Euclidean distances are more closely related to traditional diversity indices.

Table 6 lists all community parameters and their symbols. Pearson's product-moment correlation coefficient was used to statistically compare each parameter with physiochemical variables discussed in Chapter 1.

Given samples collected over a period of time, there are several ways to determine a single index of community structure: maximum diversity, diversity of pooled samples, diversity measures averaged over time, and statistically estimated diversity. [This problem is discussed in terms of diversity indices, but it applies to most community parameters.] Unfortunately, this study does not provide the large number of samples required to estimate diversity, by either sequentially pooled quadrats (Pielou, 1975) or a jackknife estimate (Zahl, 1977), and to calculate a measure of variance. The maximum diversity found at any point during the season measures a system's potential for supporting species at any one time (Root, 1973), but this measure may be confounded by vagrant species and consequently not indicate the true maximum. The diversity of all samples

Table 6. List of community parameters used to characterize faunal communities.

Symbol	description
D	density (number of individuals per unit volume)
s	species richness (number of species)
ti	ecological category richness (number of ecological categories)
DIVERSITY INDICES	
$H'(s)$	total species diversity
$H'(t)$	trophic level diversity
$H'(ti)$	ecological categories diversity
$H'_t(s)$	mean within-trophic level, species diversity
$H'_t(i)$	mean within-trophic level, size group diversity
$H'_{ti}(s)$	mean within-ecological category, species diversity
SUPER COMMUNITY INDICES	
$Q_J(s)$	Jaccard's coefficient, based on presence/absence of species
$Q_J(ti)$	Jaccard's coefficient, based on presence/absence of ecological categories
$Q_d(s)$	Euclidean distance, based on relative abundance of species
$Q_d(ti)$	Euclidean distance, based on relative abundance of ecological categories

pooled throughout the season accounts for seasonal replacement of species (Root, 1973), and it is not greatly affected by vagrants. Independent diversity measures averaged over time will normally be similar to but lower than pooled measures, and even lower than statistically estimated values (Hendrickson, 1979). Preliminary calculations indicated a strong correlation between pooled and averaged diversities so only one (pooled) was used in this study to calculate a single measure of diversity, over the entire season.

In this study, hierarchical classification was the only multivariate technique employed with any success. Direct gradient analysis was rejected as far too unwieldy; ordination was explored in depth but abandoned as data sets were too discontinuous to analyze without a high degree of distortion, using the available programs. The program used to cluster data on the eight study lakes was UPGMA, as described in Chapter 1. Both taxonomic species and ecological categories were used to produce cluster diagrams. Euclidean distances clustered lakes on the basis of species/categories abundances. Jaccard's coefficient of similarity, calculated from binomial presence/absence data, was used to cluster lakes on the basis of their species or categories composition, and to cluster species on the basis of lakes that they occupied. This latter technique is an objective way of designating species as typical freshwater, euryhaline, or high salinity species. The cophenetic correlation coefficient (Sokal & Rohlf, 1962; Rohlf, 1974; Romesburg, 1984) was used to evaluate the amount of distortion associated with each cluster and to quantitatively compare dendrograms based on biotic and abiotic variables.

Results

DISTRIBUTION

Three principal groups of species, those restricted to saline lakes, to freshwater lakes, and those occurring at moderate salinities or tolerant of a wide range of salinity, were revealed when multivariate classification clustered species according to lakes that they occurred in (Fig. 5). A list of the species present in the samples, their size, trophic level, and distribution is provided in Table 7. Group A at the top of Fig. 5 contains species that are primarily inhabitants of freshwater lakes, and most noticeable is the tight cluster of species that were found only in Lake 1, including Daphnia rosea, D. catawba, Alona quadrangularis, Haliphus leechi and Hydroporus griseostriatus. The centre cluster (Group B) contains species tolerant of all salinities such as Ceriodaphnia quadrangula, Callibaetis spp, Enallagma spp, Notonecta kirbyi, Cenocorixa bifida, Chironomini and Haliphus immaculicollis, plus many other sub-groups such as those species that were found in all lakes less than 5500 μS : Chydorus sphaericus, Cymatia americana, Callicorixa audeni, Hygrotus lutescens and Chaoborus americanus. Group C, at the bottom of the dendrogram, contains species including Branchinecta mackini, Daphnia similis, Moina hutchinsoni, Diaptomus nevadensis, Diaptomus sicilis, Dasycorixa rawsoni, Cenocorixa expleta, Hygrotus masculinus and Hydroporus spenceri, that were found only in saline lakes.

COMMUNITY COMPOSITION

CRUSTACEAN ZOOPLANKTON. Zooplankton species composition and relative abundance differed markedly among lakes (Fig. 6a; 7a), with Cladocera dominant in fresh to moderately saline lakes; calanoid copepods

Table 7. List of species present in samples, their size, trophic class, and distribution.
(See Fig. 1 for lake names).

#	species	mean length (mm)	trophic level	lake							
				1	2	3	4	5	6	7	8
Class Branchiopoda											
Order Anostraca											
1	<u>Branchinecta mackini</u> Dexter	22.5	collector; filter feeder							0	0
Order Diplostraca, Suborder Cladocera											
2	<u>Daphnia magna</u> Straus	5.0	collector; filter feeder					0	0		
3	<u>D. similis</u> Claus	2.8	collector; filter feeder							0	0 0
4	<u>D. rosea</u> Sars	1.33	collector; filter feeder	0							
5	<u>D. pulex/schödleri</u>	1.75	collector; filter feeder			0	0	0	0		
6	<u>D. catawba</u> Coker	1.33	collector; filter feeder	0							
7	<u>Simocephalus vetulus</u> Schödler	3.0	collector; filter feeder	0	0	0	0	0	0	0	
8	<u>Scapholerberis kingi</u> Sars	0.9	collector; filter feeder	0	0	0	0				
9	<u>Ceriodaphnia quadrangula</u> (O.F.Müller)	1.0	collector; filter feeder	0	0	0	0	0	0	0	0
10	<u>Moina hutchinsoni</u> Brehm	1.6	collector; filter feeder								0
11	<u>Leydigia quadrangularis</u> (O.F.Müller)	0.9	collector; filter feeder			0	0				
12	<u>Alona quadrangularis</u> (O.F.Müller)	0.9	collector; filter feeder	0							
13	<u>A. rectangula</u> Sars	0.38	collector; filter feeder	0	0	0	0				
14	<u>Chydorus sphaericus</u> (O.F.Müller)	0.4	collector; filter feeder	0	0	0	0	0			
Class Ostracoda											
15	Species 1	1.0	collector; sediment feeder	0					0		
16	Species 2	1.0	collector; sediment feeder	0	0	0					
Class Copepoda											
17	<u>Diaptomus leptopus</u> Forbes	1.91	collector; filter feeder	0	0	0					
18	<u>D. nevadensis</u> Light	3.73	predator; engulfer							0	0 0
19	<u>D. sicilis</u> Forbes	1.3	collector; filter feeder					0		0	0 0
20	<u>Eucyclops agilis</u> (Koch)	0.95	collector; sediment feeder	0		0					
21	<u>Cyclops vernalis</u> Fischer	1.11	predator; engulfer	0			0	0			
22	<u>C. navus</u> Herrick	1.11	predator; engulfer				0	0			
23	<u>Macrocyclus albidus</u> (Jurine)	1.48	predator; engulfer	0	0			0	0		
Class Malacostraca											
Order Amphipoda											
24	<u>Hyalella azteca</u> (Saussure)	6.0	collector; sediment feeder	0	0	0	0				
25	<u>Gammarus lacustris</u> Sars	20.0	collector; sediment feeder	0	0			0			
Class Insecta											
Order Collembola											
26	<u>Sminthurides</u> sp.	0.75	collector; sediment feeder	0							
Order Ephemeroptera											
27	<u>Caenis</u> spp.	4.5	collector; sediment feeder	0							
28	<u>Siphonurus</u> spp.	14.5	collector; sediment feeder	0							
29	<u>Callibaetis</u> spp.	8.0	collector; sediment feeder	0	0	0	0	0	0	0	0
Order Odonata											
30	<u>Lestes congener</u> Hagen	24.0	predator; engulfer	0	0				0	0	
31	<u>L. disjunctus</u> Selys	26.0	predator; engulfer	0				0			
32	<u>Enallagma</u> spp.	25.5	predator; engulfer	0	0	0	0	0	0	0	0

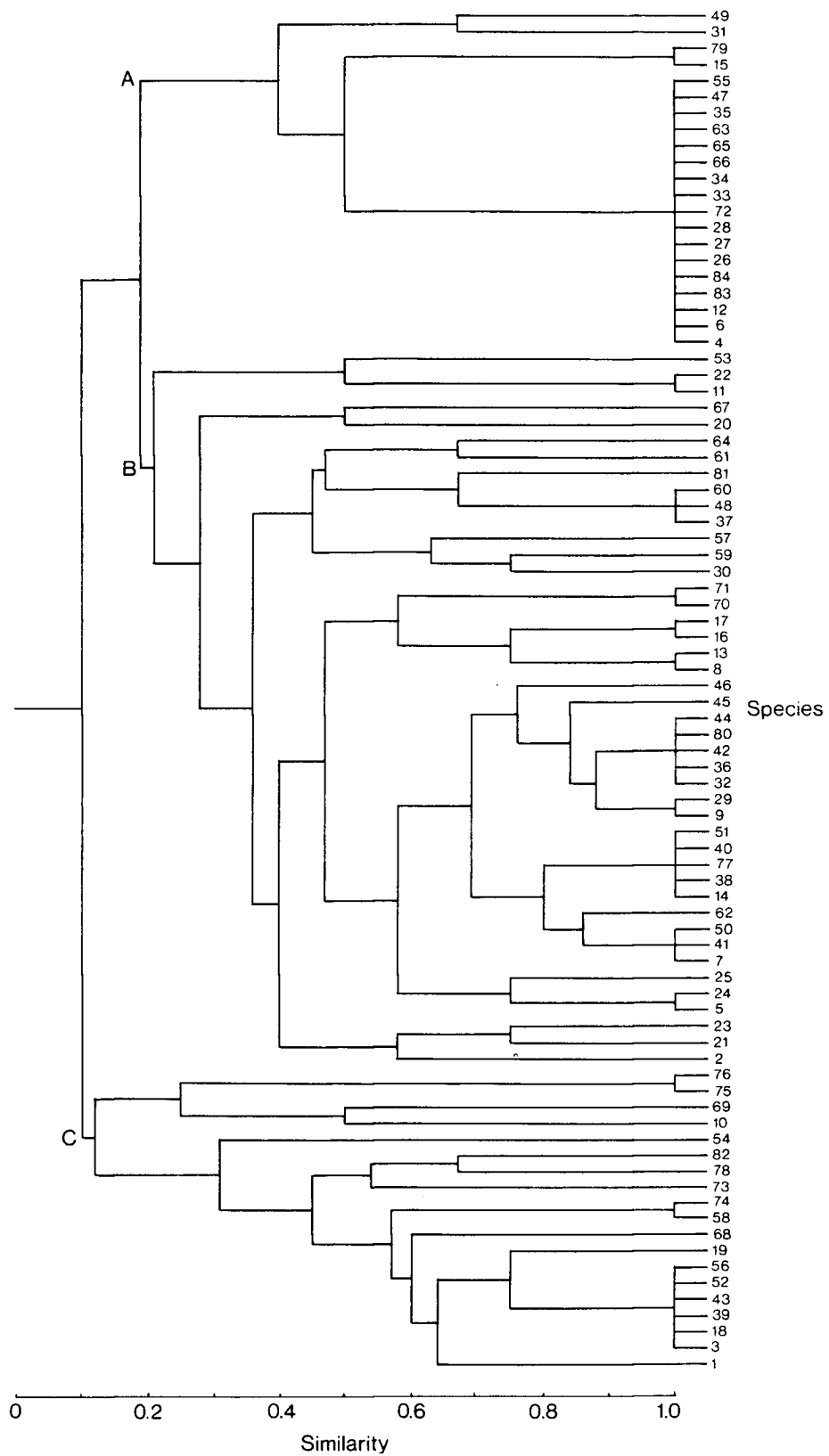
Table 7. CONT.

#	species	mean length (mm)	trophic level	lake							
				1	2	3	4	5	6	7	8
33	<u>Aeshna interrupta</u> Walker	40.5	predator; engulfer	0							
34	<u>Sympetrum</u> spp.	15.0	predator; engulfer	0							
35	Order Plecoptera	12.0	shredder; herbivore	0							
	Order Hemiptera										
	Family Notonectidae										
36	<u>Notonecta kirbyi</u> Hungerford	14.5	predator; piercer	0	0	0	0	0	0	0	0
37	<u>N. undulata</u> Say	14.5	predator; piercer	0	0						
	Family Corixidae										
38	<u>Cymatia americana</u> Hussey	7.0	predator; piercer	0	0	0	0	0			
39	<u>Dasycorixa rawsoni</u> Hungerford	8.19	predator; piercer						0	0	0
40	<u>Callicorixa audeni</u> Hungerford	7.6	predator; piercer	0	0	0	0	0			
41	<u>Hesperocorixa laevigata</u> (Uhler)	10.45	predator; piercer	0	0	0	0	0	0	0	
42	<u>Cenocorixa bifida</u> (Hungerford)	7.35	predator; piercer	0	0	0	0	0	0	0	0
43	<u>C. expleta</u> (Uhler)	6.8	predator; piercer						0	0	0
	Order Coleoptera										
	Family Haliplidae										
44	<u>Haliphus immaculicollis</u> Harris	2.75	shredder; herbivore	0	0	0	0	0	0	0	0
45	<u>H. strigatus</u> Roberts	3.0	shredder; herbivore	0	0	0		0	0	0	0
46	<u>H. stagninus</u> Leech	3.4	shredder; herbivore		0	0	0	0	0	0	
47	<u>H. leechi</u> Wallis	4.25	shredder; herbivore	0							
	Family Dytiscidae										
48	<u>Laccophilus biguttatus</u> Kirby	4.35	predator; engulfer	0	0						
49	<u>Hygrotus sayi</u> Balfour-Browne	3.05	predator; engulfer	0	0			0			
50	<u>H. unguicularis</u> (Crotch)	5.29	predator; engulfer	0	0	0	0	0	0		
51	<u>H. lutescens</u> (LeConte)	3.35	predator; engulfer	0	0	0	0	0			
52	<u>H. masculinus</u> (Crotch)	4.3	predator; engulfer						0	0	0
53	<u>H. impressopunctatus</u> (Schaller)	4.77	predator; engulfer		0						
54	<u>Hydroporus striatellus</u> LeConte	4.06	predator; engulfer						0		
55	<u>H. griseostriatus</u> (DeGeer)	4.86	predator; engulfer	0							
56	<u>H. spenceri</u> (Leech)	5.69	predator; engulfer						0	0	0
57	<u>Agabus ajax</u> Fall	6.92	predator; engulfer	0	0			0			
58	<u>A. griseipennis</u> LeConte	6.93	predator; engulfer						0	0	
59	<u>A. antennatus</u> Leech	7.68	predator; engulfer	0				0	0		
60	<u>I. fraterculus</u> LeConte	10.22	predator; engulfer	0	0						
61	<u>I. subaenus</u> Erichson	10.46	predator; engulfer	0	0			0			
62	<u>Rhantus frontalis</u> (Marshall)	9.57	predator; engulfer	0	0	0	0	0	0	0	0
63	<u>Dytiscus cordieri</u> Aubé	29.0	predator; engulfer	0							
64	<u>D. alaskanus</u> Balfour-Browne	27.4	predator; engulfer		0			0			
65	<u>Graphoderus liberus</u> (Say)	11.54	predator; engulfer	0							
66	<u>G. perplexus</u> Sharp	14.65	predator; engulfer	0							
67	<u>G. occidentalis</u> Horn	12.65	predator; engulfer	0							
	Family Hydrophilidae										
68	<u>Laccobius</u> sp.	2.75	shredder; herbivore						0	0	
69	<u>Enochrus diffusus</u> LeConte	6.0	shredder; herbivore						0		0

Table 7. CONT.

#	species	mean length (mm)	trophic level	lake								
				1	2	3	4	5	6	7	8	
	Family Curculionidae											
70	<u>Lixellus filiformis</u> LeConte	4.4	shredder; herbivore	0	0							
71	<u>Litodactylus griseomicans</u> Redtenbacher	2.8	shredder; herbivore	0	0							
	Order Trichoptera											
72	<u>Lepidostoma</u> spp.	10.0	shredder; herbivore	0								
73	<u>Tranodes</u> spp.	10.0	shredder; herbivore	0	0	0	0	0	0			
	Order Diptera											
	Family Culicidae											
74	<u>Aedes campestris</u> Dyar & Knab	11.5	collector; filter feeder						0		0	
75	<u>A. fitchii</u> (Felt & Young)	11.5	collector; filter feeder					0				
76	<u>A. flavescens</u> (Muller)	11.5	collector; filter feeder					0				
77	<u>Chaoborus americanus</u> (Johannsen)	11.5	predator; engulfer	0	0	0	0	0	0			
	Family Chironomidae											
78	Macropelopiini	10.0	predator; engulfer	0	0				0		0	
79	Pentaneurini	10.0	predator; engulfer	0		0						
80	Chironomini	10.0	collector; sediment feeder	0	0	0	0	0	0	0	0	
81	Tanytarsini	10.0	collector; sediment feeder	0	0					0		
82	Orthocladiini/Metrioconemini	10.0	collector; sediment feeder	0		0	0	0	0	0	0	
	Family Heleidae											
83	<u>Alluaudomyia</u> sp.	5.5	predator; engulfer	0								
84	<u>Bezzia/Probezzia</u> sp.	9.5	predator; engulfer	0								

Fig. 5. Cluster analysis of arthropod species based on similarities of lakes occupied, $r=0.854$. Principal subgroups, designated by stem letters, are discussed in the text. (See Table 7 for species names).



Legend for Figs. 6 - 12:

Composition and relative abundance of arthropod (a) species and (b) ecological categories in the eight study lakes.

— = <5 %  = 5-10 %  = 10-25 %  = 25-50 %  = 50-100 %

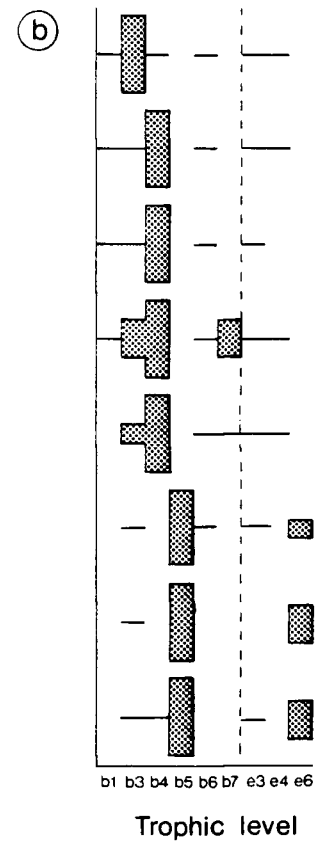
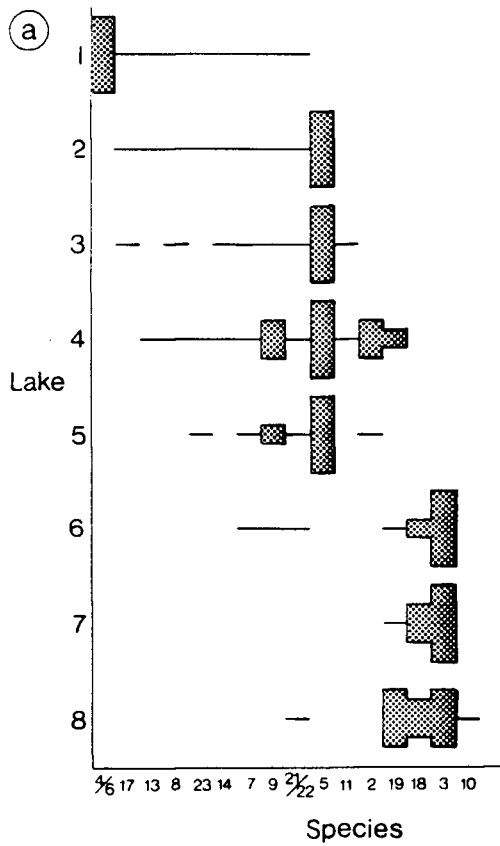
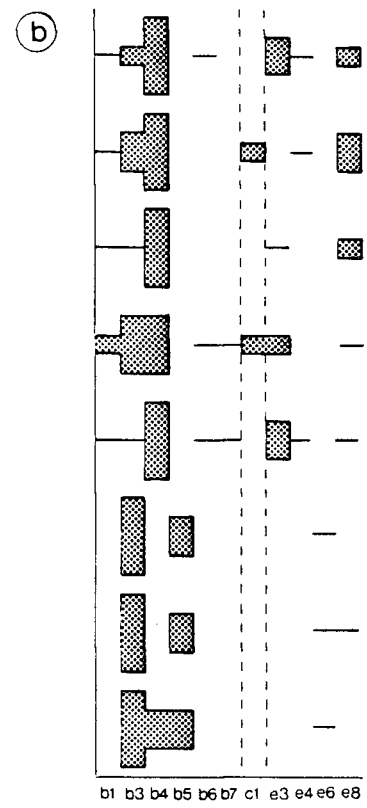
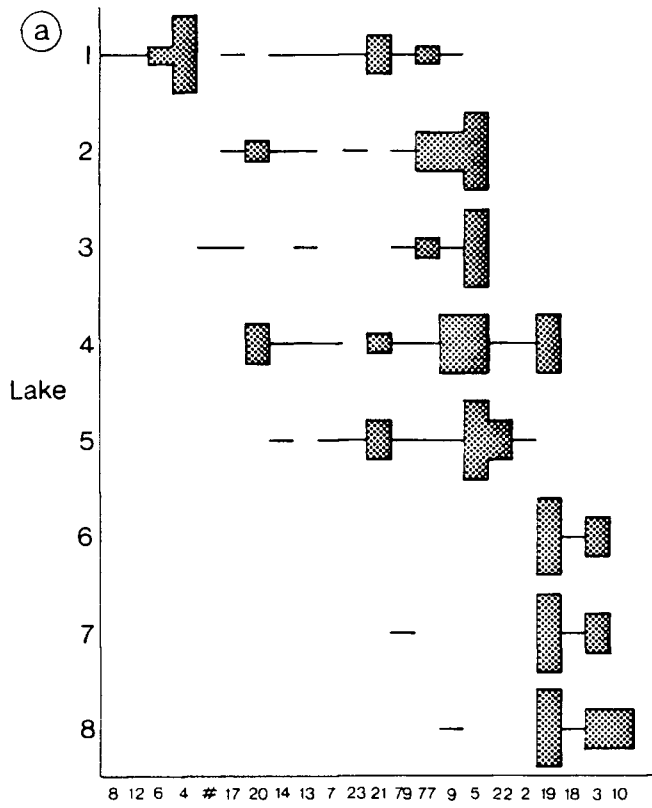
See Fig. 1 for lake names; see Table 7 for species names; trophic levels are as follows:

- a = shredder; herbivore
- b = collector; filter feeder
- c = collector; sediment feeder
- e = predator; engulfer
- f = predator; piercer

Numbers 1-10 accompanying trophic levels refer to increasing body size; these numbers in the various sample sets are not comparable. Dashed lines in (b) part of Figures separate trophic levels. Ecological categories within each trophic level are presented in order of increasing size.

Fig. 6. Limnetic zooplankton collected in Van Dorn bottles. (See pg. 49 for legend; see Appendix B.1 for numerical values).

Fig. 7. Entomostraca collected in light trap samples. (See pg. 49 for legend; see Appendix B.2 for numerical values).



in highly saline ones. In both limnetic and light trap samples, two highly variable species, Daphnia pulex and D. schødleri were lumped together because they were difficult to distinguish morphologically. Two pairs of species, Daphnia rosea/catawba and Cyclops vernalis/navus were also lumped together in light trap samples as the amount of time required to separate these pairs was prohibitive with the volume of material. Lake 1, the most freshwater, is dominated by Daphnia rosea and D. catawba, species unique to this lake, whereas moderately saline Lakes 2-5 all have similar species ensembles dominated by Daphnia pulex/schødleri. These lakes differed from each other in the presence or absence and relative abundance of minor species. For example, only Lakes 4 and 5 supported populations of Daphnia magna, but not as a major component of the community. High salinity Lakes 6, 7 and 8 were dominated by the calanoid copepods Diaptomus sicilis and D. nevadensis, and the cladoceran Daphnia similis; only Lake 8 contained the halobiont cladoceran Moina hutchinsoni.

Entomostraca collections in water bottle and light trap samples were similar, but some differences are as follows: (1) Light trap samples showed Diaptomus nevadensis rather than D. sicilis as the dominant copepod in saline lakes. (2) Several typical littoral species, namely Leydigia quadrangulara, Scapholeberis kingi, Simocephalus vetulus and Macrocyclus albidus, were more common in the littoral than limnetic zone. (3) Water bottle samples included certain dipteran larvae, namely, Chaoborus americanus and chironomids. Chironomids were not identified beyond family level since most were early instars. In the limnetic zone of the study lakes, these Diptera occurred at such high densities (Chaoborus comprised 11% of the community in Lake 2) that I consider them important to the functioning community, even though they are not normally considered members

of the limnetic zooplankton. Although dipterans were present in light trap samples, they were included only in analysis of the entire light trap community, and not in the entomostracan subset.

There was a marked difference in the relative abundance of zooplankton ecological categories between low to moderate and high salinity lakes (Fig. 6b; 7b). Lakes 1-5 all had small filter feeding herbivores (Chydorus, Ceriodaphnia), and were dominated by large filter feeders (Daphnia). More saline lakes are also dominated by large filter feeders (Daphnia), but had no small filter feeders. Limnetic samples showed proportionately more medium sized filter feeders in saline lakes than light traps did, owing to higher catches of Diaptomus sicilis. Fresh to moderately saline lakes have small and large predators (cyclopoids and dipterans respectively), but there were no medium sized ones. Conversely, saline lakes had some medium sized predators (calanoids), but no small or large ones. No large predators are shown in Fig. 7b as the dipteran larvae representing this category were not included in light trap samples. In saline Lakes 6-8, proportionately more medium sized predators were found in light traps than bottle samples owing to higher catches of D. nevadensis.

LIGHT TRAPS. Species composition and relative abundance of the 70 arthropod species collected in light traps differed markedly among lakes (Fig. 8a). All lakes were numerically dominated by species of Cladocera and Copepoda. All individuals were identified to species where possible although there were exceptions. Species lumping of Cladocera and Copepoda is mentioned above. Chironomidae were identified to tribe as further identification was too time consuming or impossible with early instars. Fortunately, most chironomid species within a tribe belong to the same ecological category.

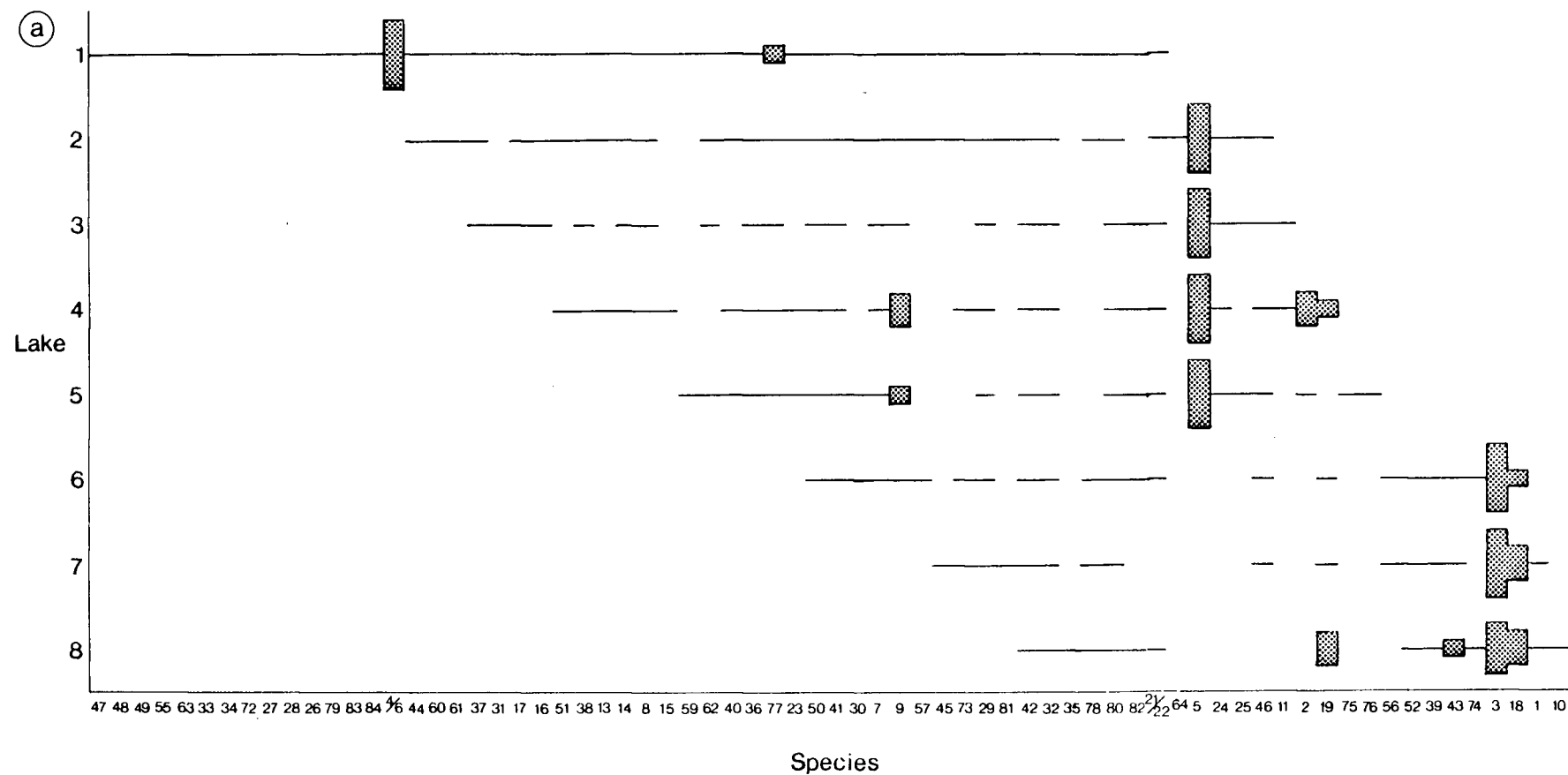


Fig. 8a. All species collected in light trap samples. (See pg. 49 for legend; see Appendix B.2 for numerical values).

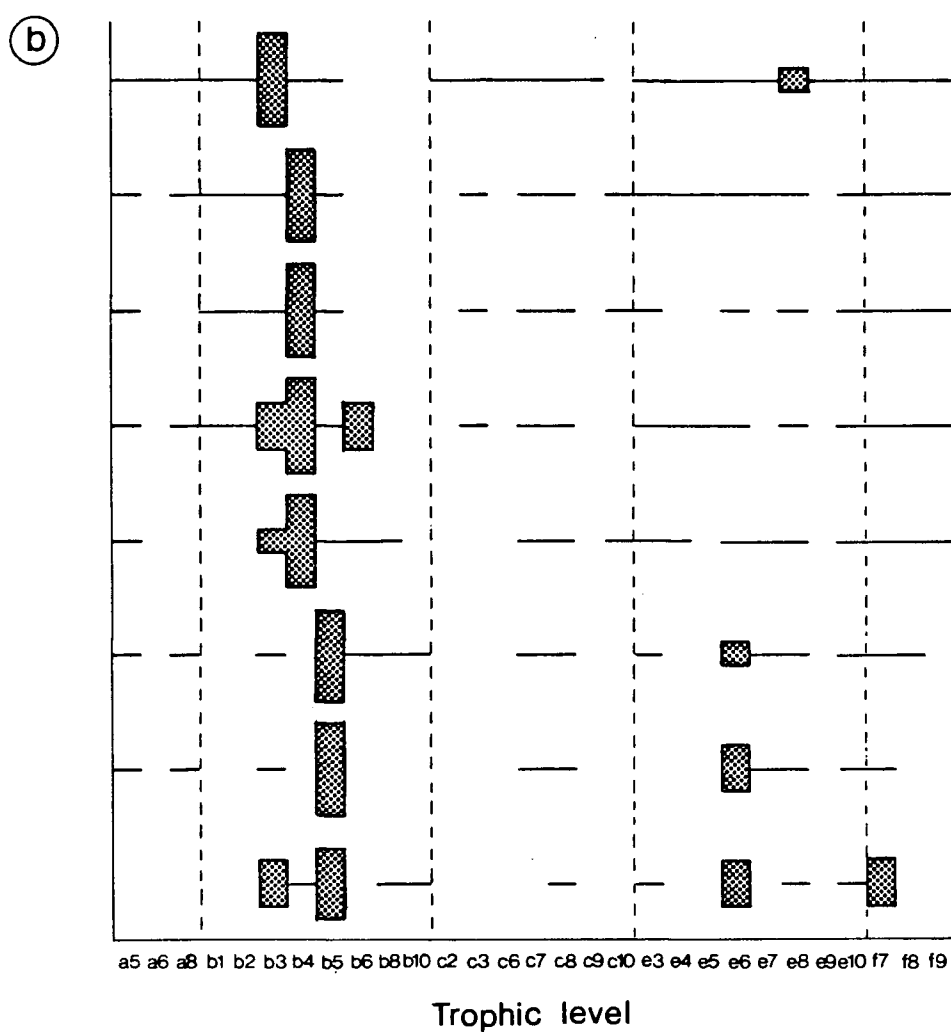


Fig. 8b. All ecological categories collected in light trap samples.

(See pg. 49 for legend; see Appendix B.2 for numerical values).

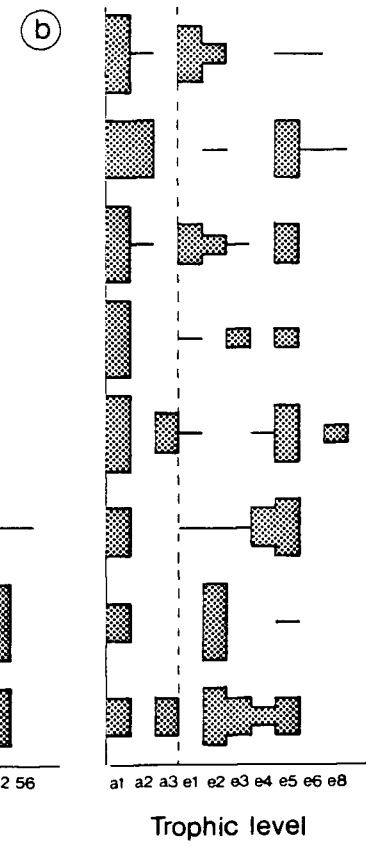
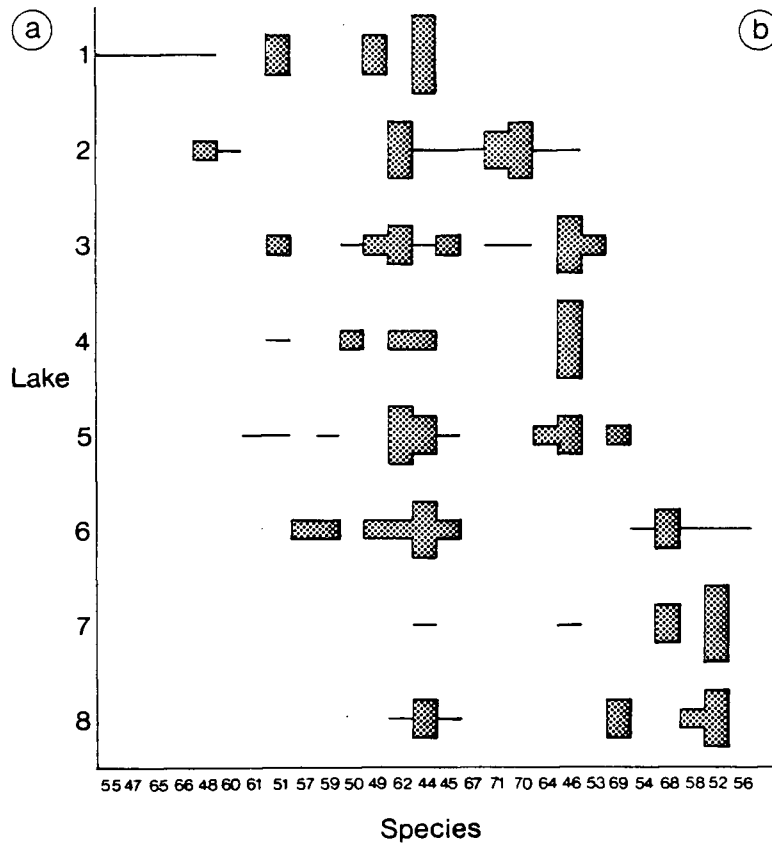
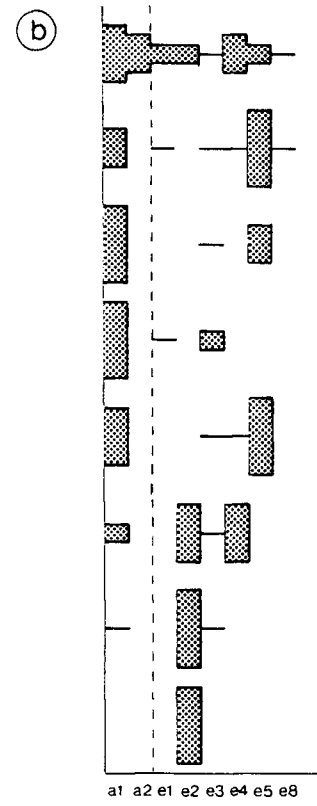
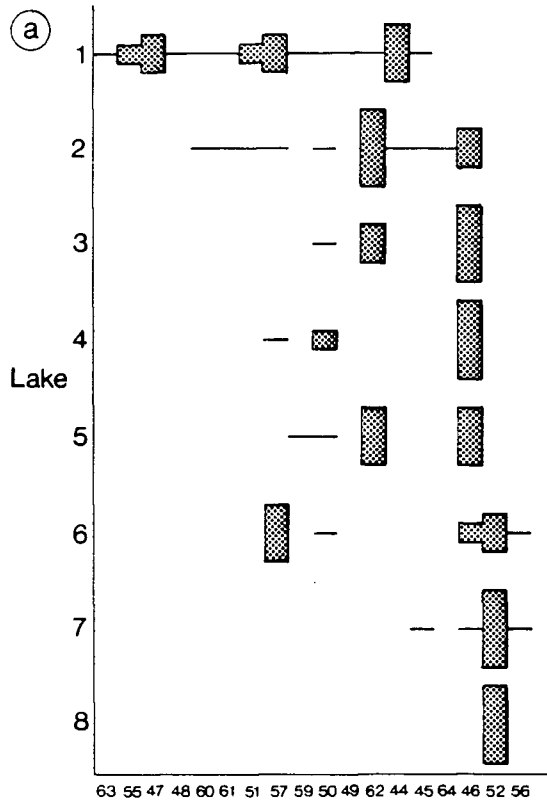
All lakes were numerically dominated by large sized filter feeders (Daphnia), as shown in Fig. 8b presenting the distribution and relative abundance of ecological categories in light trap samples. Low salinity lakes had small filter feeders (Ceriodaphnia, Scapholeberis, Chydorus), but no very large ones and had a wide size range of sediment feeders. Conversely, saline lakes had very large filter feeders (Branchinecta), but no very small ones and only mid-size sediment feeders (Chironomini, Callibaetis). Predators were present in all lakes, but saline lakes had fewer size classes and proportionately more individuals.

COLEOPTERA. Twenty-eight Coleoptera species were collected in the eight lakes, 18 in light traps; 27 in sweep samples, and lakes differ noticeably in their composition and relative abundance (Figs. 9a; 10a). All coleopterans caught in light traps were in the families Haliplidae and Dytiscidae, while sweep nets also caught members of the Hydrophilidae and Curculionidae. Several herbivorous species, Haliphus immaculicollis, H. strigatus, Litodactylus griseomicans, Lixellus filiformis, Enochrus diffusus and Laccobius spp, were more common in sweep samples than light traps. Sweep nets collected more species than light traps, but their numerical abundance was very variable.

Light trap samples of beetle communities in the most saline Lakes 7 and 8 were composed almost exclusively of Hygrotus masculinus, a typical high salinity species that also occurred in Lake 6, but in the company of abundant Agabus ajax and Haliphus stagninus. Lakes 2-5 were characterized by abundant populations of H. stagninus and Rhantus frontalis, except Lake 4 where R. frontalis was not found, but Hygrotus unguicularis was relatively common. Lake 1 was unusual in that it contains more species than any other, several were unique, and two unique species (Haliphus

Fig. 9. Coleoptera collected in light trap samples. (See pg. 49 for legend; see Appendix B.2 for numerical values).

Fig. 10. Littoral Coleoptera collected in sweep nets. (See pg. 49 for legend; see Appendix B.3 for numerical values).



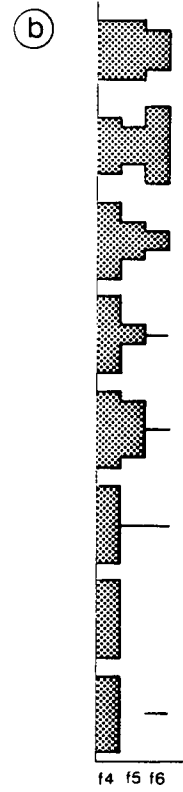
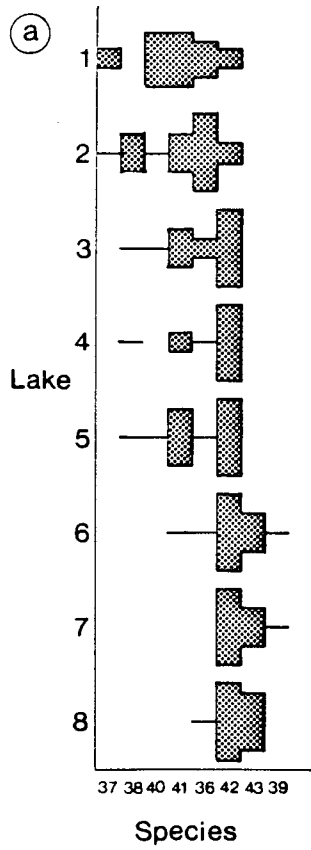
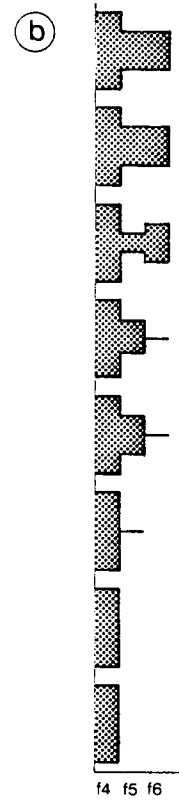
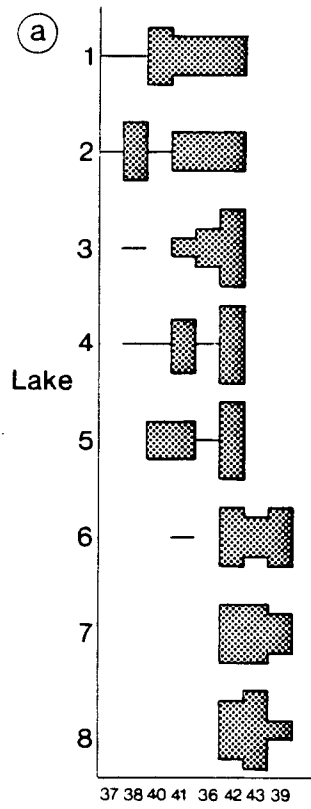
leechi and Hydroporus griseostriatus) were abundant. The composition and relative abundance of ecological categories is shown in Fig. 9b. The division between predators and shredders coincides with a taxonomic division between the families Dytiscidae and Haliplidae. As salinity increased, herbivores (Haliphus spp.) were fewer and smaller. Lake 1 had a wide range of predator sizes occurring with more or less equal abundance, moderately saline lakes also had a wide range of predator sizes but were dominated by medium sized forms (Rhantus), and highly saline lakes were populated almost exclusively by small predators (Hygrotus).

Unlike light trap samples, sweep samples showed no strong pattern in the relative abundance of taxonomic species or ecological categories across lakes (Fig. 10). Lake 1 had some unique species and some species were restricted to highly saline lakes, but no strong pattern is apparent. One important feature, however, is the abundance of herbivores in all lakes.

HEMIPTERA. Compared to other groups, there were relatively few hemipterans in these lakes. Figs. 11 and 12 show the composition and relative abundance of Hemiptera species and ecological categories, in light trap and sweep samples. There was a marked difference in species composition above and below conductivities of 5000 μ S (Lakes 1-5 vs. 6-8) (Figs. 11a; 12a). Cenocorixa bifida was relatively abundant in all lakes, all other species were typical of either high or low salinity lakes. The halobiont, Dasycorixa rawsoni, was caught more often in light traps than in sweep nets, however, both techniques provided similar representations of the hemipteran fauna. All these Hemiptera are in the same trophic level (predator; piercer) so Figs. 11b and 12b present the relative abundance of size categories within this level. Lake 1 contained a wide range of size forms but as salinity increased, only small size classes were represented.

Fig. 11. Hemiptera collected in light trap samples. (See pg. 49 for legend; see Appendix B.2 for numerical values).

Fig. 12. Littoral Hemiptera collected in sweep nets. (See pg. 49 for legend; see Appendix B.3 for numerical values).



Trophic level

COMMUNITY PARAMETERS

Community structure in the 7 sample sets was numerically characterized according to 13 community parameters in each sample set, and these are presented in Table 8. Important features of this table are as follows: (1) Euclidean distances are a measure of dissimilarity so values increase for more dissimilar communities. (2) In general, Lake 1 had the largest number of species and ecological categories yet the lowest density. Notable exceptions were in both limnetic and light trap zooplankton samples where maximum values for most community parameters occurred in the moderately saline Lake 4. (3) Entomostracans made up approximately 95% of all individuals collected in light traps. (4) Total species diversity was generally low, never exceeding 1.96. (5) The density of beetles in sweep samples was very low. (6) The super community index $Q_J(s)$ never achieved the maximum value of 1.00, and $Q_J(ti)$ rarely did.

Table 9 summarizes relationships between community parameters of zooplankton and Hemiptera sets. In general, parameters for limnetic zooplankton are positively correlated with those in light trap Entomostraca communities, and parameters for sweep Hemiptera are correlated with light trap Hemiptera. No light trap and sweep coleopteran community parameters are correlated.

Each faunal community had distinctly different parameters. Fig. 13 shows the mean and variation of limnetic zooplankton diversity in three lakes, representative of the whole series. The 48 samples of each lake were grouped into four groups of four adjacent sample times, each consisting of 12 individual samples. Each lake is undoubtedly different from the others.

Water chemistry appears to be the best abiotic variable for predicting

Table 8. Numerical values for faunal community parameters. Maximum values are in bold type.
(See Fig. 1 for lake names; see Table 6 for explanation of symbols).

lake	D	s	ti	Community parameter						Q _J (s)	Q _J (ti)	Q _d (s)	Q _d (ti)
				H'(s)	H'(ti)	H'(t)	H' _t (s)	H' _t i(s)	H' _t (i)				
WATER BOTTLE - ZOOPLANKTON													
1	41.3	13	7	1.30	1.13	0.52	0.78	0.17	0.61	.591	.700	9.488	6.818
2	21.6	9	6	0.94	0.89	0.56	0.38	0.05	0.33	.409	.600	12.147	8.310
3	37.2	7	5	0.31	0.29	0.25	0.05	0.01	0.04	.318	.500	12.021	8.285
4	158.5	12	8	1.78	1.36	0.58	1.20	0.42	0.79	.545	.800	9.761	5.543
5	86.3	10	8	0.78	0.66	0.48	0.30	0.12	0.18	.455	.800	11.321	6.949
6	26.3	3	3	0.16	0.49	0.00	0.49	0.00	0.65	.136	.300	12.100	7.887
7	74.7	5	4	0.54	0.53	0.08	0.46	0.01	0.45	.227	.400	12.140	7.796
8	47.4	4	4	0.75	0.75	0.04	0.71	0.00	0.71	.182	.400	12.080	8.276
SWEEP - COLEOPTERA													
1	11.4	8	6	1.26	0.98	0.64	0.62	0.28	0.33	.296	.600	12.202	6.458
2	24.9	10	6	1.61	1.34	0.67	0.94	0.27	0.67	.370	.600	12.031	5.112
3	3.0	10	6	1.46	1.31	0.68	0.83	0.15	0.63	.370	.600	13.582	7.643
4	6.3	5	4	0.85	0.62	0.43	0.66	0.23	0.19	.185	.401	13.785	7.346
5	8.2	9	6	1.77	1.28	0.68	1.17	0.49	0.60	.333	.600	12.780	6.601
6	3.2	11	6	1.96	1.31	0.69	1.27	0.65	0.62	.407	.600	12.767	7.237
7	2.1	4	3	0.67	0.62	0.50	0.05	0.05	0.12	.148	.300	14.101	7.798
8	4.1	7	6	1.70	1.69	0.56	1.14	0.01	1.13	.259	.600	13.312	6.461
SWEEP - HEMIPTERA													
1	31.5	5	3	1.38	1.07			0.32		.625	1.00	6.073	3.593
2	49.8	6	3	1.17	0.93			0.25		.750	1.00	6.150	3.071
3	54.5	5	3	0.69	0.56			0.13		.625	1.00	7.213	3.936
4	88.1	4	3	0.34	0.32			0.02		.500	1.00	7.313	3.905
5	41.0	5	3	0.87	0.76			0.11		.625	1.00	7.267	3.911
6	259.3	5	3	0.43	0.05			0.38		.625	1.00	6.666	2.903
7	9.6	3	1	0.47	0.00			0.47		.375	.333	7.698	4.742
8	506.4	3	2	0.69	0.01			0.69		.375	.667	6.896	3.810

Table 8. CONT.

lake	D	s	ti	Community parameter						Q _J (s)	Q _J (ti)	Q _d (s)	Q _d (ti)
				H'(s)	H'(ti)	H'(t)	H' _t (s)	H' _{ti} (s)	H' _t (i)				
LIGHT TRAP - ALL SPECIES													
1	1191	51	25	1.17	1.10	0.68	0.50	0.07	0.43	.729	.862	16.605	11.425
2	11551	36	21	0.55	0.53	0.29	0.26	0.02	0.24	.514	.724	19.262	13.278
3	54356	24	17	0.11	0.10	0.07	0.04	0.01	0.03	.343	.586	20.561	12.679
4	33770	28	20	1.17	1.03	0.18	0.99	0.14	0.86	.400	.690	19.391	11.262
5	17603	24	18	0.73	0.73	0.25	0.49	0.01	0.48	.343	.621	20.35	12.968
6	16988	23	15	0.40	0.39	0.06	0.33	0.01	0.32	.329	.517	21.450	13.810
7	20280	17	13	0.64	0.63	0.05	0.59	0.01	0.58	.243	.448	21.498	13.813
8	10882	16	12	1.51	1.46	0.45	1.07	0.06	1.01	.229	.414	21.024	12.880
LIGHT TRAP - ENTOMOSTRACA													
1	1031	9	6	0.56	0.53	0.16	0.41	0.03	0.38	.563	.750	9.376	7.214
2	10859	9	6	0.26	0.26	0.03	0.23	0.01	0.23	.563	.750	10.014	7.088
3	53758	8	5	0.04	0.02	0.01	0.03	0.01	0.02	.500	.625	9.399	7.140
4	33239	11	7	1.09	0.94	0.09	1.00	0.14	0.86	.688	.875	7.430	4.450
5	17279	6	6	0.62	0.62	0.15	0.47	0.00	0.47	.375	.750	9.513	6.125
6	16812	6	5	0.33	0.32	0.31	0.02	0.01	0.01	.375	.500	10.338	7.265
7	20124	3	3	0.58	0.58	0.53	0.05	0.00	0.05	.188	.375	10.144	7.001
8	9347	5	4	1.10	0.70	0.44	0.66	0.40	0.26	.313	.500	9.762	7.446
LIGHT TRAP - COLEOPTERA													
1	27.4	14	8	1.82	1.58	0.67	1.16	0.25	0.91	.778	1.00	6.860	5.302
2	56.5	10	6	0.88	0.68	0.41	0.47	0.20	0.27	.556	.750	9.307	5.941
3	25.8	3	3	0.64	0.64	0.55	0.09	0.00	0.93	.167	.375	10.870	6.979
4	28.8	3	3	0.41	0.41	0.35	0.06	0.00	0.06	.167	.375	10.518	6.390
5	63.2	4	4	0.76	0.76	0.65	0.11	0.00	0.11	.222	.500	10.408	6.623
6	31.6	5	4	1.03	1.01	0.25	0.78	0.02	0.76	.278	.500	10.518	6.720
7	90.2	4	3	0.06	0.03	0.03	0.03	0.03	0.01	.222	.375	10.705	7.384
8	369.0	1	1	0.00	0.00	0.00	0.00	0.00	0.00	.056	.125	10.995	7.271
LIGHT TRAP - HEMIPTERA													
1	41.6	6	3	1.42	0.85			0.57		.750	1.00	6.815	4.577
2	93.4	6	3	1.41	0.87			0.54		.750	1.00	6.042	3.721
3	179.0	4	3	0.75	0.67			0.09		.500	1.00	6.494	3.157
4	312.0	5	3	0.60	0.50			0.10		.625	1.00	6.265	2.797
5	102.2	4	3	0.71	0.62			0.09		.500	1.00	6.755	4.062
6	169.8	4	2	1.08	0.04			1.05		.500	.667	6.890	4.418
7	153.2	3	1	1.00	0.00			1.00		.375	.333	7.031	4.513
8	347.6	3	1	0.78	0.00			0.78		.375	.333	6.648	4.120

Table 9. Summary of relationships between community parameters, based on Pearson's product-moment correlation coefficient. - = no association. Positive associations: + = $p < 0.10$; ++ = $p < 0.05$; +++ = $p < 0.01$. Negative associations: ** = $p < 0.05$. (See Table 6 for symbol description; Appendix C for numerical values).

		WATER BOTTLE ZOOPLANKTON													
		D	s	ti	H'(s)	H'(t)	H'(ti)	H't(s)	H't(i)	H'ti(s)	Qj(s)	Qj(ti)	Qd(s)	Qd(ti)	
LIGHT TRAP ENTOMOSTRACA	D	-													
	s		++												
	ti			+++											
	H'(s)				+										
	H'(t)					**									
	H'(ti)						+								
	H't(s)							++							
	H't(i)								-						
	H'ti(s)									-					
	Qj(s)										++				
	Qj(ti)											+++			
	Qd(s)												++		
	Qd(ti)													+++	
		SWEEP HEMIPTERA													
		D	s	ti	H'(s)	H'(ti)	H'ti(s)	Qj(s)	Qj(ti)	Qd(s)	Qd(ti)				
LIGHT TRAP HEMIPTERA	D	+													
	s		++												
	ti			+++											
	H'(s)				++										
	H'(ti)					+++									
	H'ti(s)						++								
	Qj(s)							++							
	Qj(ti)								+++						
	Qd(s)									-					
											-				

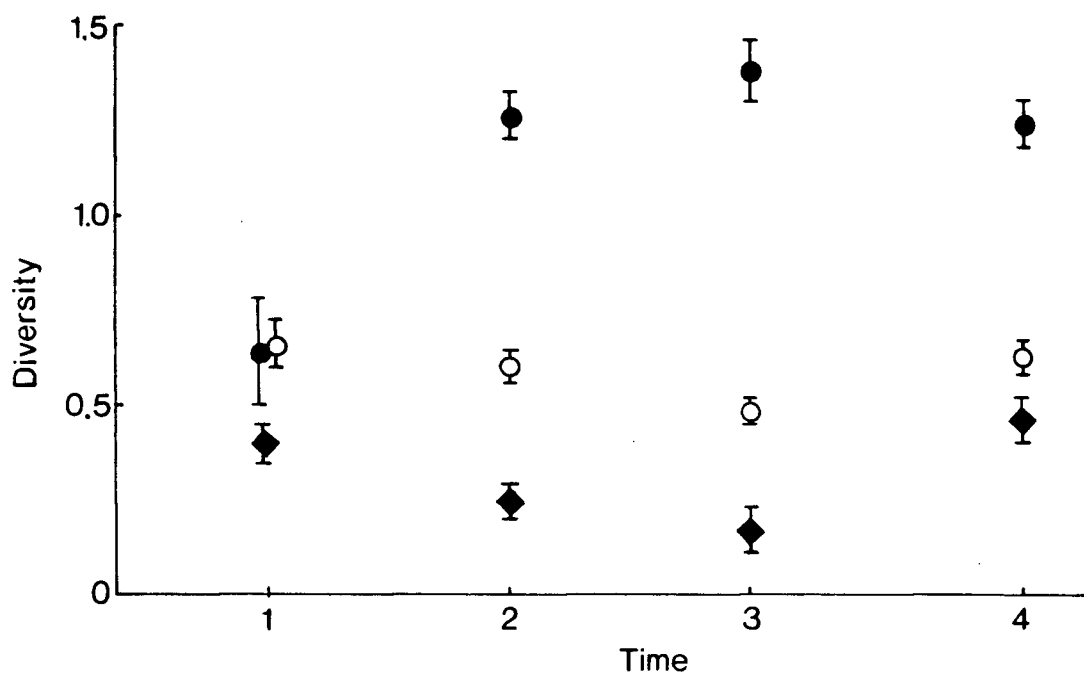


Fig. 13. Mean and standard error of diversity vs time in limnetic zooplankton samples in three lakes. $\blacklozenge$ = Lake 3, $\bullet$ = Lake 4, $\circ$ = Lake 6. (See Fig. 1 for lake names).

Table 10. Summary of relationships between community parameters and physiochemical variables based on Pearson's product-moment correlation coefficient. Negative associations: * = $p < 0.10$; ** = $p < 0.05$; *** = $p < 0.01$; positive associations: + = $p < 0.10$; ++ = $p < 0.05$; +++ = $p < 0.01$. See Table 6 for description of community parameter symbols; k_{25} = conductivity; z = mean depth. (See Appendix D for numerical parameters).

Community parameter													
Variable	D	s	ti	H'(s)	H'(t)	H'(ti)	H' _t (s)	H' _t (i)	H' _{ti} (s)	Q _j (s)	Q _j (ti)	Q _d (s)	Q _d (ti)
WATER BOTTLE - ZOOPLANKTON													
k ₂₅	-	**	*	-	***	-	-	-	-	**	*	-	-
logk ₂₅	-	**	-	-	*	-	-	-	-	**	-	+	-
PC1	-	**	*	-	*	-	-	-	-	**	*	-	-
PC2	-	-	-	-	-	-	-	-	-	-	-	-	-
z	-	***	**	-	***	-	-	-	-	***	**	+	-
D _{LA}	-	-	-	-	+	-	-	-	-	-	-	-	-
SWEEP - COLEOPTERA													
k ₂₅	-	-	-	-	-	-	-	-	-	-	-	-	-
logk ₂₅	-	-	-	-	-	-	-	-	-	-	-	-	-
PC1	-	-	-	-	-	-	-	-	-	-	-	-	-
PC2	-	-	-	-	-	-	-	-	-	-	-	-	-
z	*	-	-	-	-	-	-	-	-	-	-	-	-
D _{LA}	-	-	-	-	-	-	-	-	-	-	-	**	**
SWEEP - HEMIPTERA													
k ₂₅	+	**	**	-	***				++	**	**	-	-
logk ₂₅	-	-	-	**	***				-	-	-	+	-
PC1	++	**	**	-	***				+++	**	**	-	-
PC2	-	-	-	-	-				-	-	-	-	-
z	-	-	-	**	***				-	-	-	-	+
D _{LA}	-	++	-	+++	+++				-	++	-	-	*

Table 10. CONT.

Community parameter													
Variable	D	s	ti	H'(s)	H'(t)	H'(ti)	H' _t (s)	H' _t (i)	H' _{ti} (s)	Q _J (s)	Q _J (ti)	Q _d (s)	Q _d (ti)
LIGHT TRAP - ALL SPECIES													
k25	-	**	***	-	-	-	-	-	-	**	***	++	-
logk25	-	***	***	-	*	-	-	-	-	***	***	+++	+
PC1	-	**	***	-	-	-	-	+	-	**	***	+	-
PC2	-	-	-	-	-	-	-	-	-	-	-	-	-
z	-	**	***	-	*	-	-	-	-	**	**	+++	++
DLA	-	+	+	-	-	-	-	-	-	+	+	-	-
LIGHT TRAP - ENTOMOSTRACA													
k25	-	**	**	-	+++	-	-	-	-	**	**	-	-
logk25	-	*	-	-	-	-	-	-	-	*	-	-	-
PC1	-	**	*	-	+	-	-	-	-	**	**	-	-
PC2	-	-	-	-	-	-	-	-	-	-	-	-	-
z	-	**	**	-	++	-	-	-	-	**	***	-	-
DLA	-	-	-	-	-	-	-	-	-	-	-	-	-
LIGHT TRAP - COLEOPTERA													
k25	++	*	**	*	***	*	-	-	-	*	**	-	++
logk25	-	***	***	**	**	**	*	*	**	***	***	+++	+++
PC1	++	-	*	*	***	*	-	-	-	-	*	-	++
PC2	-	-	-	-	-	-	-	-	-	-	-	-	-
z	-	*	*	-	**	-	-	-	*	*	*	+	++
DLA	***	+	+	-	+	-	-	-	+	+	+	-	*
LIGHT TRAP - HEMIPTERA													
k25	-	***	***	-		***			+	***	***	-	-
logk25	+	***	*	-		**			-	***	*	-	-
PC1	-	**	***	-		***			+	**	***	-	-
PC2	-	-	-	-		-			-	-	-	-	-
z	-	**	**	-		***			+	**	**	+	-
DLA	*	+	+	-		++			-	+	+	-	-

community parameters, as both conductivity and PC1 show significant correlations or trends with several parameters; PC2 is not associated with any parameters. Although mean depth is associated with several parameters, the sign of observed relationships is contrary to predictions. Table 10 summarizes the relationships between community parameters (Table 8) and abiotic variables (Tables 2, 3 and 4). Mean depth is negatively correlated with several parameters and D_{LA} often shows a positive trend with community parameters.

In all but one sample set, increasing salinity is accompanied by a decrease in the absolute number of species $[s]$ and ecological categories $[ti]$, and in the relative number of species $[Q_j(s)]$ and ecological categories $[Q_j(ti)]$, with respect to the total number available for colonization. The sole exception is found in the set of Coleoptera sampled in the littoral zone with sweep nets. Other associations between physiochemical variables and community parameters vary depending on the sample set.

Limnetic zooplankton show a significant negative correlation between salinity and trophic level diversity, $H'(t)$. Curiously, this association is positive in light trap Entomostraca samples, and this contradiction is attributable to the differential sampling of predators by the two techniques. In limnetic samples, the majority of predators were found in freshwater lakes, whereas light traps collected more in saline lakes.

When all species in light trap collections were used to calculate community parameters, the complexity of sample communities, relative to the maximum complexity possible, decreases with increasing salinity. None of the traditional measures of species diversity are associated with salinity, but the new super community index, $Q_d(s)$, is significantly correlated,

and $Q_d(t_i)$ shows a trend. There is a trend for decreasing trophic level diversity with increasing salinity, as seen in the limnetic zooplankton. The relationships between community parameters and salinity for the entire light trap collection are more similar to the entomostracan subset, than Coleoptera or Hemiptera.

Where light trap and sweep net Coleoptera and Hemiptera communities were considered separately, there are many significant relationships between salinity and community parameters. Again, sweep net Coleoptera communities are anomalous showing virtually no associations between abiotic variables and community parameters. For both Coleoptera and Hemiptera, increasing salinity is accompanied by increasing density of individuals, and decreasing diversity in terms of both traditional diversity indices plus the new super community indices. There are some significant associations between D_{LA} and community parameters in sweep samples.

CLASSIFICATION

Results of the numerical classification of taxonomic and ecological species data are shown in Figs. 14 - 20. Most dendrograms are considered adequate representations of the original data as cophenetic correlation coefficients are greater than the critical level of acceptance. The exceptions, Figs. 17d, 18b, 19c, were omitted from further analysis.

Cluster analysis of all sample sets calculated from the presence or absence of species and ecological categories with Jaccard's coefficient of similarity (parts a & b of Figs. 14-20, 18b omitted) produced dendrograms closely related to salinity. In most cases, dendrograms show a major dichotomy of lake types with one branch containing saline Lakes 6-8 and the other containing the more freshwater Lakes 1-5, a pattern similar to

Fig. 14. Cluster analysis of study lakes based on limnetic zooplankton:

- (a) similarity of species composition, $r=0.956$
 - (b) similarity of ecological composition, $r=0.977$
 - (c) dissimilarity of species relative abundance, $r=0.965$
 - (d) dissimilarity of ecological relative abundance, $r=0.914$
- (See Fig. 1 for lake names).

Fig. 15. Cluster analysis of study lakes based on light trap Entomostraca:

- (a) similarity of species composition, $r=0.923$
 - (b) similarity of ecological composition, $r=0.944$
 - (c) dissimilarity of species relative abundance, $r=0.891$
 - (d) dissimilarity of ecological relative abundance, $r=0.896$
- (See Fig. 1 for lake names).

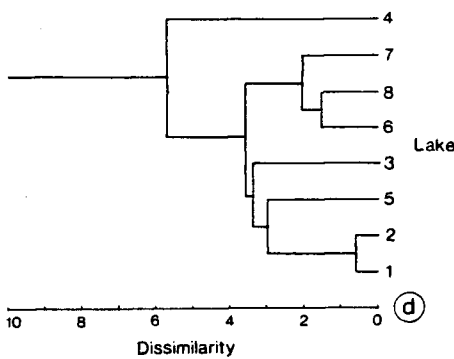
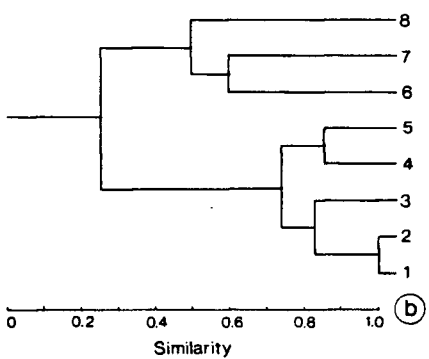
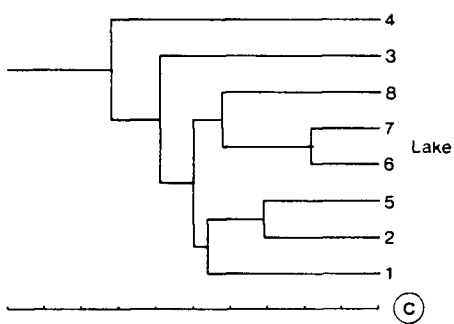
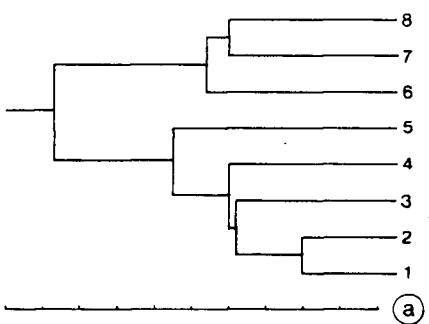
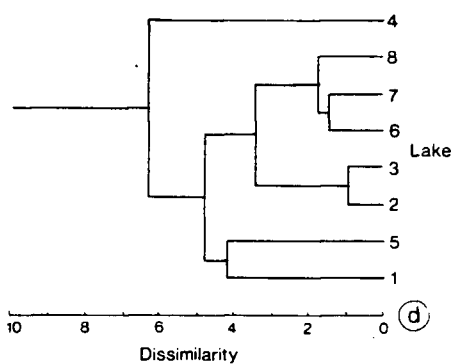
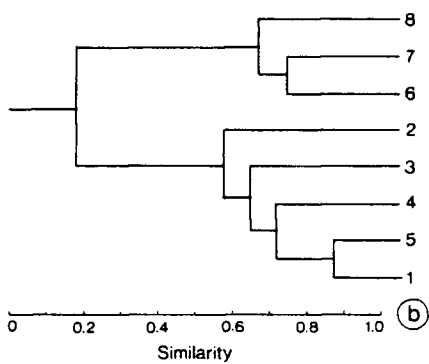
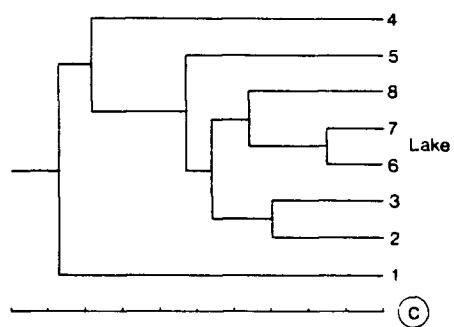
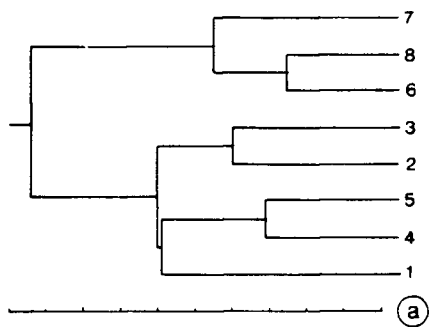


Fig. 16. Cluster analysis of study lakes based on all species in light traps:

- (a) similarity of species composition, $r=0.894$
 - (b) similarity of ecological composition, $r=0.859$
 - (c) dissimilarity of species relative abundance, $r=0.979$
 - (d) dissimilarity of ecological relative abundance, $r=0.924$
- (See Fig. 1 for lake names).

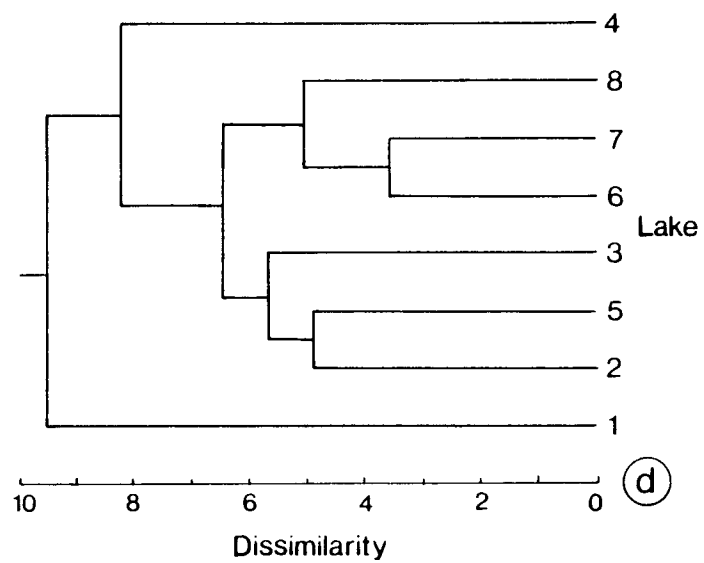
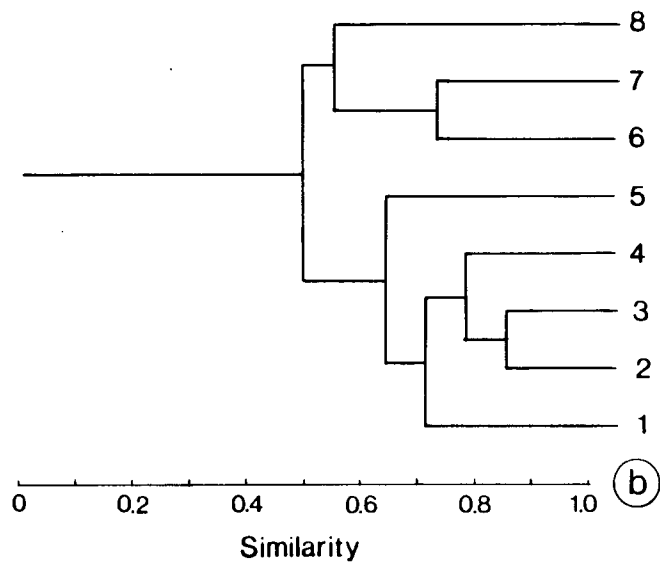
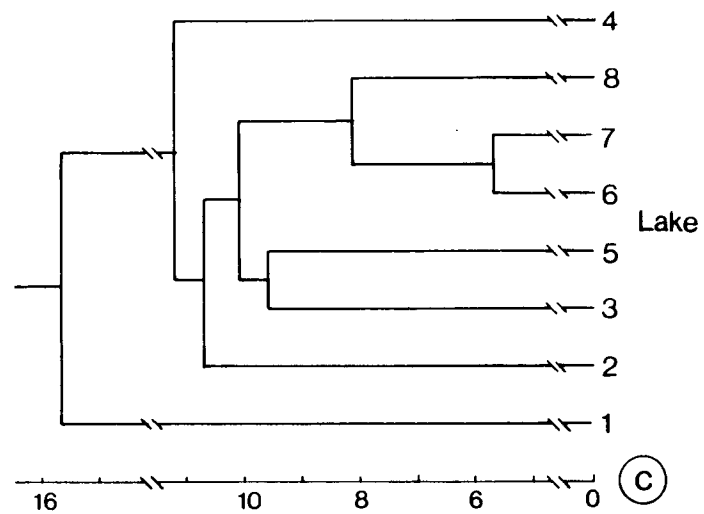
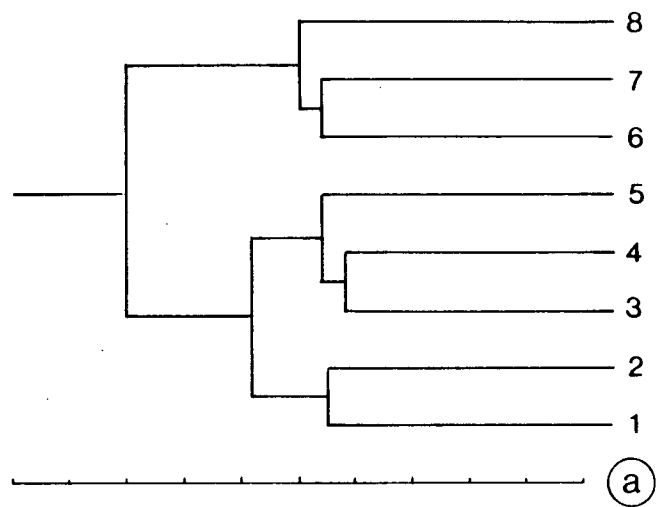


Fig. 17. Cluster analysis of study lakes based on light trap Coleoptera:

- (a) similarity of species composition, $r=0.893$
 - (b) similarity of ecological composition, $r=0.902$
 - (c) dissimilarity of species relative abundance, $r=0.973$
 - (d) dissimilarity of ecological relative abundance, $r=0.789$
- (See Fig. 1 for lake names).

Fig. 18. Cluster analysis of study lakes based on sweep net Coleoptera:

- (a) similarity of species composition, $r=0.907$
 - (b) similarity of ecological composition, $r=0.627$
 - (c) dissimilarity of species relative abundance, $r=0.935$
 - (d) dissimilarity of ecological relative abundance, $r=0.936$
- (See Fig. 1 for lake names).

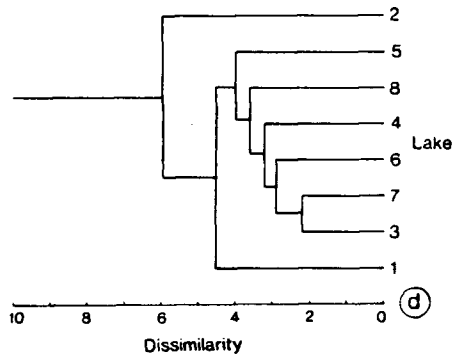
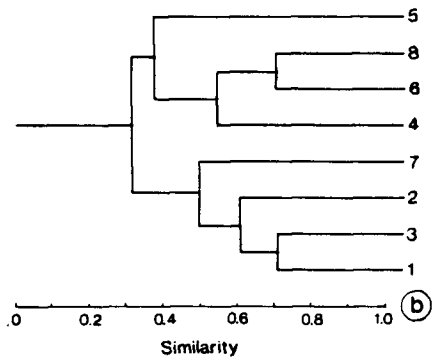
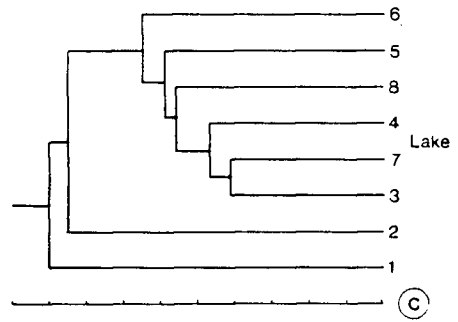
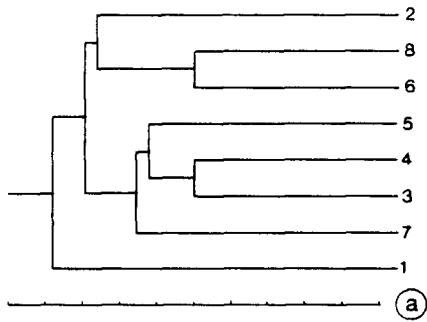
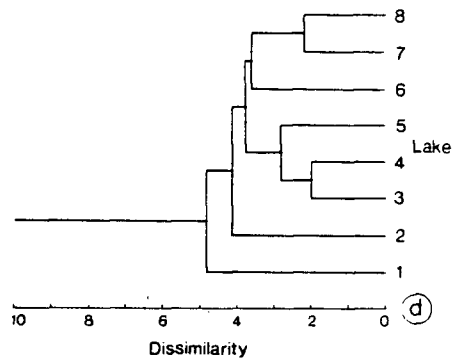
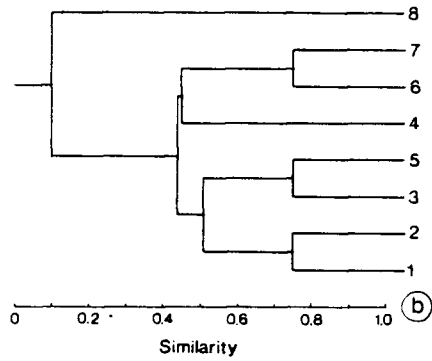
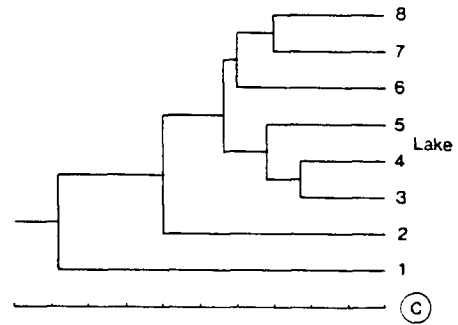
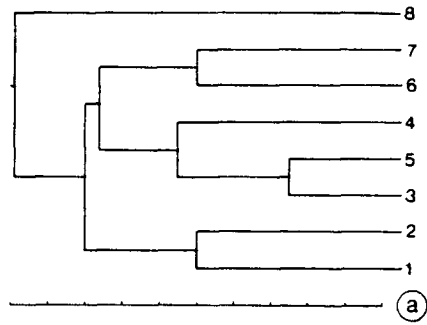
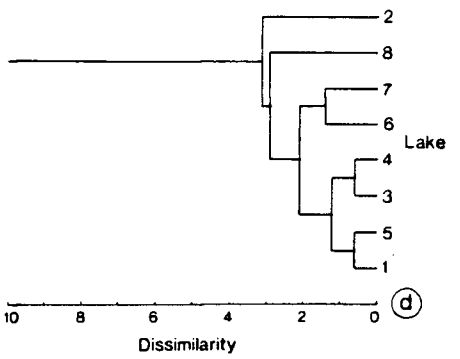
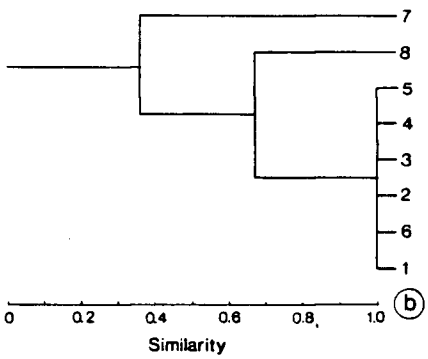
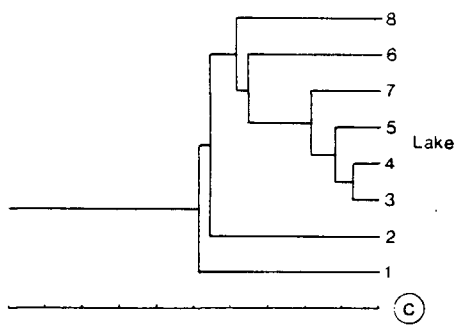
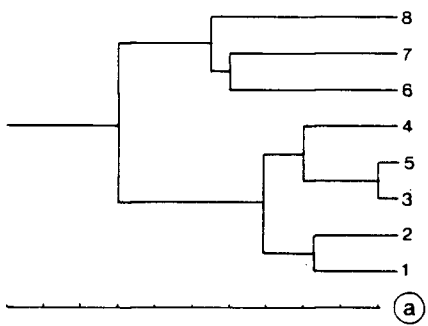
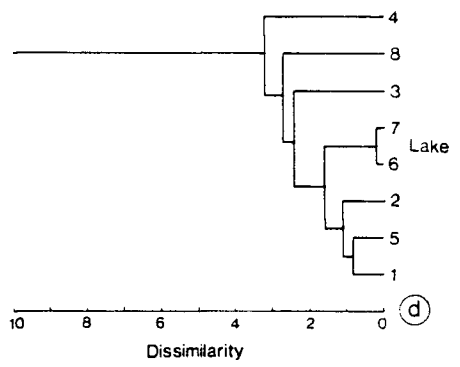
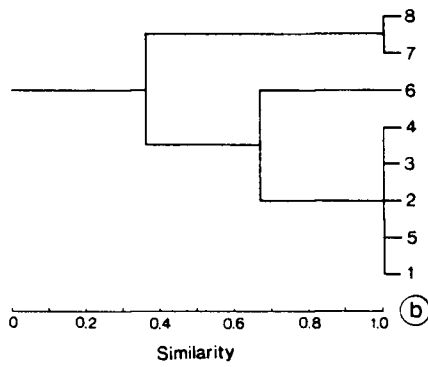
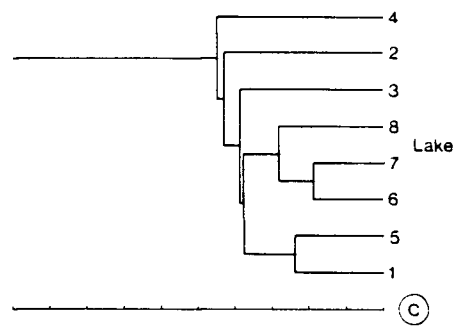
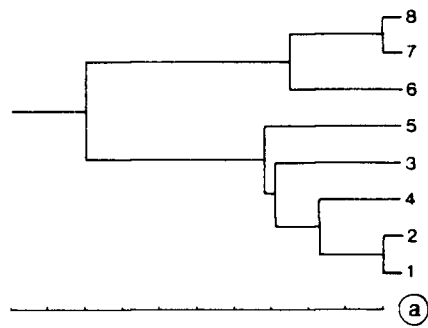


Fig. 19. Cluster analysis of study lakes based on light trap Hemiptera:

- (a) similarity of species composition, $r=0.978$
 - (b) similarity of ecological composition, $r=0.990$
 - (c) dissimilarity of species relative abundance, $r=0.800$
 - (d) dissimilarity of ecological relative abundance, $r=0.886$
- (See Fig. 1 for lake names).

Fig. 20. Cluster analysis of study lakes based on sweep net Hemiptera:

- (a) similarity of species composition, $r=0.901$
 - (b) similarity of ecological composition, $r=0.994$
 - (c) dissimilarity of species relative abundance, $r=0.913$
 - (d) dissimilarity of ecological relative abundance, $r=0.839$
- (See Fig. 1 for lake names).



physiochemical dendrograms (Fig. 4). Details of the clustering of Lakes 1-5 is dependent on sampling technique and whether taxonomic species or ecological categories are employed. Exceptions to this pattern are seen in Coleoptera communities where dendrograms (Figs. 17a, 17b, 18a) are clearly related to salinity, although not in the same manner.

Cluster diagrams derived from Euclidean distances between lakes tend to be different from those based on Jaccard's coefficient owing to the influence of relative species abundance, and are not obviously related to those drawn from physiochemical data. Euclidean based dendrograms fall into three groups. Dendrograms in the first group include limnetic zooplankton (Figs. 14c; 14d), light trap Entomostraca (Figs. 15c; 15d) and all species in light traps (Figs. 16c; 16d). Lake 1 and/or Lake 4 is last to join the cluster in these figures, reflecting the unique species composition and low density of Lake 1, and the extraordinarily high density and diversity of Lake 4. Below this point, figures generally show a dichotomy between high and low salinity lakes. The second group is represented by the dendrogram of light trap beetle species (Fig. 17c) and is clearly related to salinity, although not closely related to those produced using Jaccard's coefficient (Figs. 17a; 17b), nor to those produced from physiochemical data (Fig. 4). The final group includes cluster diagrams of sweep Coleoptera (Figs. 18c; 18d) and Hemiptera (Figs. 19d; 20c; 20d) that are confusing and not readily interpretable in any obvious way.

Cophenetic correlations between physiochemical and faunal dendrograms (Table 11) provide statistical evidence to support the patterns mentioned above. Most faunal dendrograms based on Jaccard's coefficient are correlated with physiochemical ones, except Coleoptera. None of the faunal

Table 11. Cophenetic correlation coefficients between physiochemical and faunal dendrograms. * indicates significant relationships. N.B. Figs. 17d, 18b and 19c are omitted, see text for explanation.

Faunal Dendrogram	Abiotic Dendrogram	
	chemical Fig. 4a	physiochemical Fig. 4b
WATER BOTTLE ZOOPLANKTON		
Fig. 14a	0.666	0.829*
Fig. 14b	0.687	0.841*
Fig. 14c	0.030	0.032
Fig. 14d	0.185	0.114
LIGHT TRAPS Entomostraca		
Fig. 15a	0.873*	0.972*
Fig. 15b	0.720	0.879*
Fig. 15c	0.058	0.155
Fig. 15d	0.171	0.325
All species		
Fig. 16a	0.743	0.873*
Fig. 16b	0.855*	0.867*
Fig. 16c	0.017	0.046
Fig. 16d	0.003	0.053
Coleoptera		
Fig. 17a	0.301	0.377
Fig. 17b	0.353	0.434
Fig. 17c	0.100	0.134
Hemiptera		
Fig. 19a	0.800*	0.924*
Fig. 19b	0.489	0.639
Fig. 19d	0.040	0.133
SWEEP SAMPLES Coleoptera		
Fig. 18a	0.254	0.290
Fig. 18c	0.300	0.388
Fig. 18d	0.123	0.207
Hemiptera		
Fig. 20a	0.646	0.814*
Fig. 20b	0.205	0.296
Fig. 20c	0.103	0.114
Fig. 20d	0.163	0.171

Euclidean dendrograms are correlated with physiochemical ones. The abiotic clusters based on both morphometric and chemical data are more closely related to faunal dendrograms than the one based on only chemical data.

Discussion

In total, 84 taxa of aquatic arthropods were found in the eight Becher's Prairie lakes (Table 7) and species characteristic of high, moderate or low salinities, or tolerant of all salinities were present in the series (Fig. 5). My use of these terms does not imply anything about the nature of mechanisms restricting species to particular waters because many mechanisms are possible, and some are considered in the discussion to follow. Not all arthropod species found in the lakes were censused, only those predisposed to capture with the techniques used. For example, Odonata and Gerridae are common in the area (Scudder, 1971; Cannings et al., 1980; Spence & Scudder, 1980; Cannings & Cannings, 1985), but in my sample sets they were infrequent or absent. For the most part, observed species distributions concurred with those found previously in the same lakes (Scudder, 1969a; Cannings & Scudder, 1978; Reynolds, 1979; Cannings et al., 1980; Cannings & Cannings, 1985). Some exceptions include Enochrus diffusus, Rhantus frontalis and Aedes fitchi that Scudder (1969a) reports in almost all these study lakes whereas my data showed more limited distributions. These discrepancies are owing primarily to the sampling program in this study which was not exhaustive. Furthermore, distributions provided by Scudder (1969a) are based on data obtained over a ten year period, and these patterns are not constant.

Each study lake in the series supported a distinctly different faunal

assemblage, despite the fact that all species are capable of dispersing to all lakes (Scudder, 1969b). These distribution patterns were closely related to salinity (Figs. 6-12). A marked difference in species composition among lakes in a saline lake series has been seen in other surveys (Beadle, 1943; Rawson & Moore, 1944; Bayly & Williams, 1966; Scudder, 1969a; Timms, 1981; and others). Cluster analyses in this study arranged lakes in hierarchical dendrograms based on the presence or absence of animal species and ecological categories (parts a & b of Figs. 14-20). Typically, these dendrograms show one major dichotomy between lakes with conductivities above and below 5000 μS . This pattern is very similar to arrangements of lakes based on their physiochemical properties (Fig. 4), and in most cases, statistically significant correlations exist between lake dendrograms based on faunal composition and on physiochemical properties (Table 11). The one notable exception to this pattern is seen among coleopterans where the arrangement of communities among lakes is clearly related to salinity (Figs. 17a; 17b), but not statistically correlated with the physiochemical clusters (Table 11). This disparity indicates that in order to discern patterns produced by multivariate classification, cluster diagrams should be visually examined as well as statistically compared with predicted or theoretical dendrograms. Those faunal dendrograms (zooplankton, Hemiptera, all species) that are correlated with physiochemical ones, show slightly stronger correlations with dendrograms based on chemical plus morphometric features, than those based only on water chemistry. This suggests that most of the variation in these faunal communities among lakes was related to water chemistry, and morphometric characteristics are less important.

In comparisons between physiochemical variables and community

parameters, water chemistry appeared to be the most important abiotic variable influencing biotic communities and little evidence was found of morphometric correlations. Mean depth, a measure of lake size, was included to test the species/area hypothesis explained in Chapter 1. Island biogeography (MacArthur & Wilson, 1967) predicts positive relationships between community parameters and lake size, therefore, the observed negative associations (Table 10) are owing to the coincidental correlation of mean depth with salinity in the study lakes (Chapter 1). It is not clear if observed positive trends between the potential effects of littoral processes on the whole lake (D_{LA}) and community parameters (Table 10) are secondary associations, primarily attributable to the chance association of D_{LA} with salinity in the study lakes (Chapter 1), or if littoral processes do actually play a significant role in community structure. Of the three ways of measuring salinity (mean conductivity, log mean conductivity, first principal components scores) compared with community parameters, no one consistently showed stronger or more frequent correlations with community parameters (Table 10). This merely indicates that the mathematical nature of relationships between community parameters and salinity are not the same for all faunal groups or types of parameters. All three measures, however, were necessary to reveal all the associations between biota and abiota.

To analyze community structure, this study used two schemes of classification (taxonomic and ecological), multivariate classification techniques, and 13 numerical parameters. No one method was sufficient to summarize the relationship between community structure and environmental severity. Rather, all contributed some information to characterizations and hypotheses, and none were useless. The nature of the relationship

between salinity and community structure is very complex and each data set must be examined separately.

Data from the 7 sample sets examined in this study support the hypothesis that saline habitats have less diverse communities than freshwater ones, when diversity is defined as the absolute or relative number of species or ecological categories in a lake. These associations demonstrate that an increase in salinity is accompanied by a decrease in the number of species or categories capable of surviving in such conditions, and in the number of species or categories able to colonize a lake relative to the total number available for colonization. Most surveys of saline lake series (Beadle, 1943; Rawson & Moore, 1944; Moore, 1952; Bayly & Williams, 1966; Scudder, 1969a; Hammer et al., 1975; Williams, 1978; Reynolds, 1979; Wierderholm, 1980; Geddes et al., 1981) have suggested this inverse relationship between species richness and salinity, but few have performed rigorous statistical tests or attempted to quantify community structure beyond simple species counts.

In a study of three Australian lakes, Timms (1981) found an inverse association between salinity and species richness, but questioned the usefulness of diversity indices as he found that they did not always reflect a decrease in diversity with increasing salinity. My results also indicated that diversity indices did not always decrease with increasing salinity, however, I do not attribute this solely to the inadequacies of diversity indices. Instead, when measures of community structure involve the relative abundance of species, particular groups of animals must be examined separately as the structure of these subcommunities is affected differently by salinity.

In the discussion to follow, community composition and structure of

the three taxonomic groups (zooplankton, Coleoptera, Hemiptera) are considered separately, and then drawn together in a consideration of the entire faunal community.

ZOOPLANKTON COMMUNITIES

Of the three sampling techniques employed to collect animals in this study (van Dorn bottles, sweep nets, submerged light traps), all collected zooplankton, but van Dorn bottles best represent a functional zooplankton community. Littoral sweep nets were not suitable as it was impractical to enumerate the enormous number of small crustaceans gathered. Light trap collections were numerically feasible to work with, but they do not necessarily represent functional ecological communities so results must be interpreted with caution. Actively swimming animals with positive phototactic responses are selectively sampled in light traps, so observed relative abundances may not be realistic. The number of animals collected in the limnetic zone with van Dorn bottles was suitable for enumeration, and more representative of the true densities and relative abundances of animals in the community. Even though aquatic environments are highly variable in time and space, and sample replicates were probably not numerous enough to show seasonal population changes, these samples were adequate to measure zooplankton community structure in each lake over the entire season.

Cladocera, Copepoda and Rotifera are commonly considered the dominant components of freshwater zooplankton (Wetzel, 1975), yet in analyzing the limnetic zooplankton I included the dipteran larvae Chaoborus americanus, the only species of phantom midge found, and chironomids. These larvae often occurred in the limnetic zone in high densities so I deem them

important members of the functioning community. In general, highly predaceous Chaoborus larvae exhibit diurnal migration patterns; remaining at lake bottom during the day and ascending to the surface to prey on zooplankters at night (Northcote, 1964; LaRow, 1968; Goldspink & Scott, 1971), but this pattern does not always hold true. Fedorenko & Swift (1972) reported the occurrence of all four instars of C. americanus at or near the surface all day, i.e. above 5 m. Although chironomids are normally considered members of the benthos, it is reasonable to include them in the zooplankton community as their regular appearance and activity in the limnetic zone has been reported (Mundie, 1959; Davies, 1974; 1976). Dipterans were not included with light trap Entomotraca as light trap collections do not necessarily represent a functional community, and it is impossible to determine which, or how many, dipterans collected in traps actually interacted with crustaceans. In addition, because the study lakes are relatively small and shallow, cladoceran species such as Alona and Chydorus, usually designated inhabitant of the littoral zone (Chengalath, 1982), could not be omitted from analysis of limnetic communities.

Zooplankton community composition differed markedly among lakes (Figs 6; 7). Lake 1 showed a freshwater species assemblage dominated by Daphnia rosea and D. catawba. Moderately saline lakes 2-5 all had a similar composition dominated by D. pulex/schødleri. A peculiar co-occurrence of a large cladoceran, Daphnia similis, with a large and small diaptomid, Diaptomus nevadensis and D. sicilis, occurred in lakes with conductivities over 5000 μS and is characteristic of extreme conditions around the world (Hutchinson, 1937; Moore, 1952; Anderson, 1970; Reynolds, 1979). To date, no one has examined this phenomenon or speculated on its existence. Moina hutchinsoni was found only in the most saline lake, in accordance with

findings of others (Hutchinson, 1937; Moore, 1952; Reynolds, 1979).

Virtually no experimental evidence is available on the salinity tolerances of species found in the study lakes, although species could be limited by simple osmoregulatory stress as shown by Brand (1981) for Calamoecia clitellata, a planktonic copepod endemic to Australian athalassic saline waters.

When measures of diversity include the relative abundance of species or ecological categories, there is virtually no evidence that the diversity of zooplankton species or categories decreased with increasing salinity. For the most part, diversity parameters for limnetic and light trap samples are positively correlated with each other (Table 9), indicating that both sampling techniques provide a good representation of the zooplankton community. One factor disrupting the predicted association between salinity and diversity was the extremely high density and diversity of zooplankton in the moderately saline Lake 4. It is not simply the case that this high diversity is a function of the number of individuals sampled because Lake 1 had low densities and relatively high diversity.

Dendrograms clustering lakes on the basis of the relative abundance of zooplankton species or categories all show this odd lake as the last or penultimate one to join the cluster (Figs. 14; 15). Other than this one aberration, the arrangement of lakes in the dendrograms is related to salinity. Why Lake 4 was so unusual is a mystery.

A highly significant inverse association exists between salinity and the trophic level diversity of limnetic zooplankton (Table 10). The contradictory positive association indicated by light trap samples is a distortion owing to the differential sampling of predators by the two techniques. Predatory diaptomid copepods inhabiting saline lakes were

collected in large numbers by light traps, but were much less numerous in limnetic bottle samples. Most likely, this predator was attracted to light or to the abundant prey attracted to light, and hence appeared in much higher densities than normal. Therefore, the positive association between trophic level diversity and salinity indicated by light trap samples is probably an artefact, and the negative relationship suggested by water bottle samples represents the real situation. This inverse association suggests that salinity may be important in structuring zooplankton communities through its effects on food quantity or quality, rather than simple physiological constraints.

Shifts in species composition and ecological categories of zooplankton from saline to fresh waters are analogous to changes seen with eutrophication. Taxonomically, cladocerans were abundant in all study lakes, calanoid copepods were abundant only in saline lakes, and cyclopoids were found only in fresh to moderate salinities. Similarly, oligotrophic systems are typified by populations of calanoid copepods, whereas cladocerans and cyclopoid copepods are relatively more abundant in eutrophic conditions (Patalas, 1972; McNaught, 1975; Allan, 1976; Gliwicz, 1977; Gannon & Stemberger, 1978; Fry & Osborne, 1980; Blancher, 1984; Richard et al., 1985). Prevalent explanations for this change are that the type and concentration of food in eutrophic conditions may be adequate for small cladocerans, but not for large Cladocera or copepods which are better adapted for oligotrophic conditions. Furthermore, Gannon & Stemberger (1978) report that zooplankters primarily considered littoral species often become more abundant in the limnetic zone of eutrophic waters. This pattern was also observed in the limnetic zone of the more freshwater lakes. Although our understanding of this phenomenon is limited, here it

may simply be because freshwater lakes happen to be relatively small and shallow. Ecologically, saline lakes were typically populated by large herbivores and carnivores, whereas freshwater lakes had proportionately more small herbivores and predators. Both Gannon & Stemberger (1978) and Richard et al. (1985) report that under conditions of nutrient enrichment, the average size of zooplankters often decreases as smaller species with simpler life histories and more rapid rates of reproduction appear. Sprules & Holtby (1979) found that the most important variation in the ecological structure of limnetic zooplankton, in a series of Ontario lakes, was from a predominance of small herbivores to large herbivores and carnivores. Furthermore, they correlated this pattern with morphometric indicators of lake productivity.

The success of calanoids or cladocerans, and large or small herbivores and predators, in an environment ultimately depends on the abundance and seasonality of the food supply and the ability of species to survive such conditions. Topping (1975) suggests that primary productivity decreases with increasing salinity in these Chilcotin lakes, thereby indicating reduced food supply in saline lakes that may account for the observed zooplankton distribution pattern. Although zooplankton employ a variety of feeding mechanisms and eat many types of food, phytoplankton productivity can be used as an indicator of food supply (Patalas, 1972). The majority of limnetic zooplankters are herbivores feeding on suspended fine particulate organic matter and these filter feeders, in turn, are preyed upon by predatory species.

Some zooplankton life history characteristics involved in producing the observed distribution patterns include feeding ability and competition, plus predator escape potential (McNaught, 1975; Allan, 1976; Gannon &

Stemberger, 1978; Blancher, 1984; Richard et al., 1985). A possible explanation for the phenomenon observed in the study lakes is as follows. Calanoid copepods predominate in saline or oligotrophic lakes because of their superior filtering capacity and high ingestion rate at low cell densities, and high ingestion efficiency at small cell size, whereas cladocerans are more efficient in freshwater or eutrophic conditions because of their feeding efficiency on small and large cells alike (McNaught, 1975). Small herbivores are restricted to fresher waters by their feeding requirements (Gannon & Stemberger, 1978), and small predators are restricted to the same lakes as this is where their potential prey are. Large filtrators do well in all lakes as there are no vertebrate predators and size makes them less vulnerable to invertebrate predators (Zaret, 1980). Large herbivores, however, tend to be bigger and more abundant in saline or oligotrophic lakes as they are better adapted to food conditions there i.e. colonial and filamentous blue-green algae they are known to avoid are less abundant (Wetzel, 1975), and are not subject to competition from smaller forms.

In summary, changes in the taxonomic and ecological composition of zooplankton communities with decreasing salinity in this series of lakes are analogous to those reported with increasing eutrophy. This suggests that the mechanisms shaping zooplankton community structure are primarily related to food supply and species' nutritional requirements and secondarily to osmoregulatory stress, although salinity may ultimately affect the trophic status of lakes. Because most of the evidence to support this hypothesis is circumstantial, further investigations of salinity tolerances and food requirements of inhabiting zooplankters, and the effects of salinity on food availability are now necessary.

COLEOPTERAN COMMUNITIES

A total of 28 aquatic Coleoptera species were found in the series of eight study lakes. Analysis of community structure was limited to adult forms as there is no good key for larval forms. Without a good key to the larvae or an in-depth study of the beetles, it is impossible to be sure if distribution records for adults indicate that species were breeding in the various lakes or were simply temporary inhabitants since many Coleoptera are known to be strong fliers. Larson's (1985) work on predaceous diving beetle communities indicates that all dytiscids encountered in this study are typical inhabitants of grassland and parkland ponds. Therefore, even though there is no evidence of breeding, it is likely that all these species are indigenous to the aspen parkland ponds found on Becher's Prairie.

In this study, aquatic Coleoptera were collected with both submerged light traps and sweep nets. Light traps attracted large numbers of the free swimming, predaceous Dytiscidae, that exhibit positive phototactic responses. They did not, however, well represent the herbivorous haliplids nor catch any herbivorous hydrophilids and curculionids as were found in sweep samples, as these species tend to be poor swimmers and remain closely associated with the macrophytes they feed upon. Sweep net samples included all but one of the species collected in light traps. They caught relatively more herbivores than light traps and collected ten additional species including several rare predaceous dytiscids (Graphoderus spp.), herbivorous curculionids (Litodactylus griseomicans, Lixellus filiformis) and hydrophilids (Enochrus diffusus, Laccobius spp.).

Although sweep nets collected more beetle species than light traps, any generalizations drawn about the community from the data set are

questionable because total densities and relative abundances were very variable. Aiken & Wilkinson (1985) also found sweep netting unsatisfactory for collecting quantitative samples of aquatic Coleoptera. The highly variable nature of sweep net samples is reflected by dendrograms and community parameters: no pattern is apparent in cluster diagrams of lakes based on beetles caught in sweep nets (Fig. 18), no community parameters are correlated with parameters calculated from light trap samples, and virtually none of the community parameters shows an association or trend with abiotic variables (Table 10). The only exception is where the complexity of beetle communities relative to the theoretical maximum is negatively associated with the potential for littoral processes to affect the whole lake. This may indicate the importance of littoral processes in structuring Coleoptera communities, or it may be an artefact of sampling technique. Sweep nets are obviously a useful sampling device as they appeared to collect all, or most, of the species inhabiting a lake, but a much more extensive sampling program would be required to provide reliable numerical data. Consequently, much of the following discussion is based on the numerically more realistic data provided by submerged light traps.

The composition of aquatic coleopteran communities in the study lakes is clearly related to salinity. The eight lakes fall into three groups based on the relative abundance of species in each community, as shown by relative abundance charts and cluster diagrams (Figs. 4a; 17c). The most freshwater Lake 1 was unique in the series. It had the most species; its dominant species, Haliphus immaculicollis, was found in all lakes but is abundant only in this one; and several co-dominant species, namely H. leechi and Hydroporus griseostriatus, were unique to this lake. The second group is composed of the fresh to moderately saline Lakes 2-5 that were

characterized by large populations of Haliphus stagninus and Rhantus frontalis. High salinity Lakes 6-8, with conductivities over 5000 μS , had few species and were dominated by Hygrotus masculinus. Little information is available on the salinity tolerance ranges of aquatic beetles, although H. masculinus is known to be a typical inhabitant of saline ponds (Hatch, 1953; Scudder, 1969a; Anderson, 1983; Larson, 1985). The successional sequence of Hygrotus species seen with increasing salinity in these lakes, H. lutescens, H. unguicularis, H. sayi, H. impressopunctatus, H. masculinus, is in accordance with the pattern found by Larson (1985) in Alberta ponds, although H. lutescens is not known to occur in Alberta (Anderson, 1983). Clearly, more documentation on the salinity tolerances of Coleoptera is required.

Three groups of lakes, equivalent to those mentioned above, are seen in analysis of the relative abundance of ecological categories in each beetle community (Figs. 9b; 17d). Lake 1 had a wide size range of predaceous Dytiscidae occurring with more or less equal abundance, Lakes 2-5 also had a wide range of sizes but were dominated by medium-sized predators, and high salinity Lakes 6-8 were populated almost exclusively by small predators. Small and large herbivores were abundant in Lake 1, only small herbivores were present and were abundant in Lake 2-5, and small forms were present but relatively rare in saline lakes. Body size may be related to the potential osmoregulatory capacity of Coleoptera as only relatively small species appear tolerant of all salinities or are found at high salinities. Alternatively, Larson (1985) suggests that species-rich coleopteran faunas with a variety of abundant size groups are typical of seasonal habitats or shallow vegetation-rich sites with strong seasonal nutrient and production pulses. If so, then macrophyte faunas and primary

production may affect coleopteran community structure in concert with salinity.

This study showed increased densities of Coleoptera with increased salinity. One possible explanation of this phenomenon suggests that few organisms are adapted to extreme salinities, but those few are often found in enormous numbers owing to lack of competition (Beadle, 1943). Furthermore, Simberloff & Wilson found that islands with relatively few species (in their case owing to dispersal limitations), have abnormally large populations of those species owing to absence of competitors and predators [see Simberloff (1974) for summary]. Therefore, competition and predation may be factors important in structuring Coleoptera communities in freshwater lakes.

Coleoptera community parameters, from light traps, support the hypothesis that saline lakes have less diverse communities than freshwater ones. All traditional diversity indices and the new super community indices show inverse trends or significant inverse correlations with salinity in terms of taxonomic species, ecological categories, and trophic levels (Table 10). Super community indices demonstrate that with increasing salinity, the complexity of aquatic beetle communities decreases relative to the maximum complexity possible, in terms of both species and ecological categories. The hierarchical division of traditional diversity indices revealed a highly significant decrease in trophic level diversity with increasing salinity, but only a trend of decreasing species diversity within trophic levels. This suggests that Coleoptera community structure is governed to some extent by physiological constraints, but food resources play a much more important role, even though they are probably related to salinity. Further examination of food resources should include macrophytes

for herbivorous species and potential prey forms for predators.

HEMIPTERAN COMMUNITIES

The distribution pattern of Hemiptera in the Becher's Prairie lake series was that of a primarily freshwater group containing a few taxa that can tolerate moderate or high salinities. Such a pattern was also found with the Odonata (Cannings & Cannings, 1985). One species (Cenocorixa bifida) occurred in all lakes, two species (C. expleta and Dasycorixa rawsoni) occurred in only saline lakes, and were replaced by several species (Cymatia americana, Callicorixa audeni, Hesperocorixa laevigata, Notonecta kirbyi and N. undulata) in more freshwater lakes (Figs. 11a; 12a). All species were indigenous to lakes they were found in, except single records of H. laevigata and C. americana in Lakes 6 and 5 respectively, and species are not known to breed in other lakes within the series (Scudder, 1969a).

The range of salinities inhabited by various Hemiptera can be defined with some precision, but the nature of possible causes determining range limits is less certain. It is probable that the inhibitory effects of salinity on adults (Scudder, 1969a; 1969b; Scudder et al., 1972; Knowles & Williams, 1973; Tones & Hammer, 1975) or eggs (Banks, 1949; Davis, 1966) determine the upper limits of salinity inhabited by the various species, whereas lower limits, if any, are often attributed to biological factors. Perhaps the best documented example is a series of studies on the distribution of two closely related corixids, Cenocorixa bifida and C. expleta, in the study lake series [see Scudder (1983) for review]. These species differ physiologically in their ability to tolerate high salinity, C. expleta occurs at much higher salinities than C. bifida. Although both

species are able to live at low salinities, C. expleta does not occur below 5000 μS as it appears unable to survive mite parasitism. There are numerous other records of ectoparasitic mites on corixids (Davids, 1973; Harris & Harrison, 1974; Martin, 1975). Other possible factors affecting the composition and structure of hemipteran communities in the study lakes include interspecific competition and temporal partitioning of breeding (Istock, 1973), the amount and variety of vegetation cover (Macan, 1938; 1962; Savage, 1971; van Vierssen & Verhoeven, 1983), egg cannibalism (Crisp, 1960; Pajunen, 1970; Scudder, 1976), vertebrate predation (Macan, 1965), and invertebrate predation. Although it is known that invertebrates such as larval Dytiscidae prey on Hemiptera, there has been no intensive study of invertebrate predators.

Ecologically, all aquatic Hemiptera belong to the same trophic level and differ only in size. In this study, variously sized Hemiptera occurred in fresh to moderately saline lakes and small forms occurred in all lakes, but only small forms were found with increasing salinity (Figs. 11b; 12b). Aquatic hemipteran communities in English saline lakes (Savage, 1971) and Dutch supra-littoral pools (van Vierssen & Verhoeven, 1983) have similar patterns of community composition with various conditions of water chemistry. Savage reports the occurrence of Sigara dorsalis (mean length 7 mm) over a wide range of salinities, and an accompanying succession of progressively smaller species with increasing salinity: S. falleni (7.5 mm), S. concinna (7.3 mm), S. stagnalis (6.5 mm). Van Vierssen & Verhoeven (1983) report two small species, S. lateralis (5.8 mm) and S. stagnalis (6.5 mm), occurring over a wide range of chlorinities, and co-occurring with a variety of species including Callicorixa concinna (7 mm), Hesperocorixa linnei (7.5 mm), Corixa affinis (9 mm) and C. punctata (14

mm) at low chlorinities.

Increased densities of Hemiptera were observed with increasing salinity, as also seen in the coleopteran communities above. This association, coupled with the inverse association between the number of species or categories and salinity, suggests that the few Hemiptera adapted to high salinities occur in enormous numbers owing to lack of competition and predation (Beadle, 1943; Simberloff, 1974).

Hemiptera community parameters support the hypothesis that less diverse communities are found in more saline habitats, when measures of diversity incorporate the relative abundance of different animals. For the most part, community parameters for Hemiptera caught in light traps and sweep nets are positively correlated with each other (Table 9), indicating that a good representation of the hemipteran community is provided by both techniques. Of the traditional diversity indices, the diversity of ecological categories shows a much stronger negative association with salinity than the usual species diversity (Table 10). This suggests that an ecological classification of animals may better describe community structure than ordinary taxonomy. The inverse association between salinity and the diversity of ecological categories reflects the fact that variously sized forms were found in fresh to moderately saline lakes, small forms occurred in all lakes, but only small forms were found with increasing salinity. The positive association between salinity and mean species diversity per ecological category demonstrates that although there was a wider range of sizes in freshwater lakes, fewer species belonged to each size group.

One possible explanation of the mechanisms controlling the observed structure of Hemiptera communities in the study lakes is as follows.

Because all species found are typical freshwater insects, the upper limits of species distributions are probably determined physiologically, and only 3 of the species encountered are well adapted to survive the high salinities in this lake series. It is known that Cenocorixa expleta is eliminated from low salinity lakes by mite parasitism (Scudder, 1983), but virtually nothing is known about the biology of Dasycorixa rawsoni and why it occurs only at high salinities. As suggested above for Coleoptera, body size may be related to the potential osmoregulatory capacity of Hemiptera as only relatively small species appear tolerant of all salinities, or are found at high salinities. The fact that hemipterans inhabiting fresh to moderately saline waters cover a wide range of sizes with relatively fewer species per size category suggests that competition may play, or have played, a role in structuring communities in these lakes. This was also suggested by the positive association between Hemiptera density and salinity. Assuming that the ecological niche of an animal is indicated by body size, the wide size range with relatively few species per size group suggests that species have minimal niche overlap, hence reducing the possibility of competition. In high salinities, interspecific competition is not a problem so relatively more species can occupy one size group. Much of this argument is purely speculative, but before one can elucidate the mechanisms controlling community structure in this saline lake series, more detailed autecological studies of aquatic Hemiptera are required.

ENTIRE FAUNAL COMMUNITY

Of the three sampling techniques used in this study, submerged light traps provide the best opportunity to examine the structure of the entire faunal community as they collected the most species and ecological

categories, and they were practical to work with. Sweep net samples collected more species, but in such enormous numbers that they were impossible to work with. Light traps samples do not necessarily represent functioning communities as actively swimming animals with positive phototactic responses are selectively sampled, so results must be treated with caution.

The relative abundance of species and ecological classes in the faunal community differed markedly among lakes (Fig. 8), as seen in other data sets above. All lakes were numerically dominated by species of Cladocera and Copepoda, and ecologically by large sized filter feeders. These groups, their influence on the arrangement of lakes in dendrograms, and the mechanisms controlling their community structure, are discussed above in the section on zooplankton communities. Members of all trophic levels were present in each lake, and Lake 1 had the widest range of size groups in each level. As salinity increased, fewer size categories were represented in each trophic level.

Perhaps the most important conclusion drawn from analysis of the light trap samples of the entire fauna is that observations of the entire fauna present a different picture than those of its component subgroups. This study shows that numerically dominant subgroups can dictate patterns observed in the entire community and mask important patterns in other subgroups. Patterns observed for the entire community appeared much the same as those of the entomostracan subcommunity, and patterns seen in Coleoptera and Hemipetra communities were hidden. Dendrograms illustrating Euclidean distances between lakes based on the entire fauna (Fig. 16), are much the same as those drawn from zooplankton communities (Figs. 14; 15). The most freshwater Lake 1 is last to join the cluster reflecting its

unique, species rich composition and low density; Lake 4 penultimately joins the cluster reflecting its extremely high density and diversity; the remaining lakes are split into two groups of high and low salinity lakes. Associations between abiotic and biotic parameters of the entire fauna are quite different from those found in its component subcommunities (Table 10).

Community parameters calculated from light trap samples of the entire fauna support the hypothesis that habitats of increasing salinity support communities of decreasing diversity, when measures of diversity incorporate the relative abundance of animals. Inverse associations were found between salinity and the new super community indices indicating that with increasing salinity, the complexity of faunal communities decreases relative to the maximum complexity possible. None of the hierarchical diversity indices were correlated with abiotic variables thereby providing no clues to controlling mechanisms.

Summary

This second chapter examines the relationship between water salinity and faunal community structure, and tests the diversity-stability hypothesis that saline habitats have less diverse communities than freshwater ones. Three different sampling techniques, van Dorn bottles, submerged light traps and sweep nets, were used to collect aquatic arthropods in the limnetic and littoral zones of a saline lake series. In total, 84 taxa of aquatic arthropods were found in the eight lakes and species characteristic of high salinities ($>5000 \mu\text{S}$), moderate or low salinities ($<5000 \mu\text{S}$), or tolerant of all salinities were present in the

series. Each study lake supported a distinctly different faunal assemblage and these distribution patterns were closely related to salinity.

The structure of the entire faunal community and its entomostraca, coleopteran and hemipteran subsets were characterized using two schemes of classification (taxonomic and ecological), multivariate classification techniques, and 13 numerical parameters including density, richness, diversity, hierarchical diversity, and new super community indices. No one method was sufficient to summarize relationships between salinity and community structure. Instead, all contributed some information to community characterizations and hypotheses about controlling mechanisms. Water chemistry appeared to be the most important abiotic variable influencing faunal community structure and little evidence was found for morphological correlations. In all sample sets, increased salinity was accompanied by a decrease in the number of species or ecological categories capable of surviving in such conditions, and in the number of species or ecological categories relative to the total number available for colonization. When measures of community structure incorporated relative abundances, each data set had to be examined separately as the structure of these subgroups showed different patterns of association with salinity.

ZOOPLANKTON. Both water bottle and light trap samples presented similar patterns of zooplankton community structure. Evidence suggests that mechanisms shaping zooplankton community structure are primarily related to available food supply and species' nutritional requirements, and secondarily to osmoregulatory stress, although salinity may ultimately affect the trophic status of lakes. Changes in the taxonomic and ecological composition of zooplankton communities with decreasing salinity were analogous to those reported with increasing eutrophication. When

incorporating relative abundances of animals, the only evidence found to indicate that zooplankton diversity decreased with increasing salinity, was an inverse association between salinity and trophic level diversity.

COLEOPTERA. Sweep nets were inadequate to quantitatively sample aquatic Coleoptera, so light trap samples were primarily used to characterize communities. Salinity, competition and food supply could all be important mechanisms controlling the structure of Coleoptera communities. Species rich communities covering a wide range of size groups and trophic levels, were found in freshwater lakes, but only a few relatively small species were found in saline lakes, and only small species were found in all salinities. This may indicate that body size is related to the potential osmoregulatory capacity of Coleoptera. Additionally, a wide size range of species may indicate minimal niche overlap at low salinities, hence reducing the possibility of competition. Decreased trophic level diversity with increasing salinity may indicate that food supply is more varied in freshwater lakes. Coleopteran density increased with increasing salinity, possibly because the few organisms adapted to extreme salinities are often found in enormous numbers owing to lack of competition and predation.

HEMIPTERA. Sweep net and light trap samples provided similar representations of the littoral Hemiptera. Distribution patterns of hemipteran species were of a primarily freshwater group containing a few taxa that can tolerate moderate or high salinities. Upper limits of distribution were probably determined physiologically, and species appearing only in high salinity lakes were probably eliminated from low salinities by biological factors. Body size may be related to potential osmoregulatory capacity as only relatively small species appeared to be

tolerant of all salinities or were found at high salinities. Evidence suggests that competition may play, or have played, a role in structuring hemipteran communities in freshwater lakes, but not saline lakes. The wide size range of Hemiptera and relatively few species per size group at low salinities suggests that species have minimal niche overlap, hence reducing the possibility of competition. Increased density with increasing salinity suggested that the few Hemiptera adapted to extreme salinities were found in enormous numbers owing to lack of competition and predation at high salinities.

ENTIRE FAUNAL COMMUNITY. With increased salinity, the complexity of the entire faunal community decreased relative to the maximum complexity possible. No insight into possible controlling mechanisms was found. Observations of the entire fauna presented a different picture than those of its component subgroups, indicating that numerically dominant subgroups can dictate patterns observed in the entire community and mask important patterns in other subgroups.

CHAPTER 3: MACROPHYTE COMMUNITIES

Introduction

The aim of this chapter is to examine and quantify the relationship between water salinity and aquatic macrophyte communities in a saline lake series. The main objective of this study was to investigate the relationship between salinity and arthropod communities (Chapter 2), but because the fauna is closely related with the flora, I considered it necessary to also investigate the macrophyte community. The relationships between faunal and floral communities will be examined in Chapter 4.

Studies of saline lake flora (Rawson & Moore, 1944; Hammer et al., 1975; Reynolds & Reynolds, 1975; Topping, 1975; Brock, 1981; Timms, 1981; Brock & Lane, 1983; Brock & Shiel, 1983; Hammer et al., 1983; Lieffers & Shay, 1983) provide some evidence to support the hypothesis that saline lakes support fewer and less productive species than fresher ones. It has long been known that water chemistry is perhaps the most important factor influencing the distribution of aquatic plant species within their tolerance ranges (Moyle, 1945; Seddon, 1972). Yet, there is no study providing a comprehensive quantitative analysis of macrophyte community structure in a saline lake series free of confounding abiotic factors.

In this study, the question of how aquatic plants are affected by salinity was viewed in terms of two hypotheses: the diversity-stability hypothesis, and a less complicated productivity-salinity hypothesis. As defined in the General Introduction, this first hypothesis states that environmentally stable habitats have more diverse communities than less stable ones, where salinity defines environmental stability in terms of severity (Chapter 1). The second hypothesis simply predicts reduced

productivity of macrophytes in more saline lakes, as excessive salinity disrupts normal growth and metabolism of plants so that species are unable to survive or at least experience reduced productivity (Waisel, 1972). Topping (1975) found that phytoplankton productivity decreased at higher salinities and Waisel (1972) suggests the same for macrophytes, but this is a much neglected area of study. As the study lakes are small and macrophytes may significantly contribute to total lake productivity (Westlake, 1963; 1965; McNaught, 1975; Wetzel, 1975; Canfield et al., 1983), it may be informative to characterize their macrophyte communities.

Without massive investment of effort or time, macrophyte productivity can be determined by temporal differences in standing crop. It is at best a conservative estimate, i.e. it will underestimate differences among sites, but this is sufficient for the aims of this chapter. Biomass may be synthesized and populations replaced without any change in standing crop, but differences in standing crop can only be attributed to productivity (Topping, 1975). This method of determining annual productivity is particularly suited to communities showing marked annual fluctuations of biomass and subject to few losses during the period of growth (Westlake, 1963). In temperate regions, like the Chilcotin, losses due to natural death are probably very small during the growing season, at least until maximum biomass is attained (Sculthorpe, 1967), so temporal differences in standing crop are not an unreasonable way to estimate relative productivity.

As in Chapter 2, measures of lake morphometry are also compared to macrophyte community structure to test for the possible effects of other processes such as the species/area phenomenon (see Chapter 1 for further discussion).

Materials and Methods

To investigate the relationship between salinity and macrophyte communities, the series of eight lakes was characterized abiotically according to water chemistry and lake morphometry (Chapter 1), and biotically according to macrophyte species distribution, richness, abundance, diversity, hierarchical diversity, super community indices, and productivity. In addition, lakes were classified into hierarchical cluster diagrams on the basis of their macrophyte communities and compared to similar dendrograms produced from abiotic factors.

THE DATA. Species distribution and abundance data used in this section were kindly provided by the Canadian Wildlife Service (CWS) from their 1983 study of the Chilcotin wetlands. Data include relative abundances of each macrophyte species, estimated on the Braun-Blanquet scale (Braun-Blanquet, 1964) at mid-summer, in each of several lake zones classified according to the scheme of Runka & Lewis (1981). Zones are defined with respect to water depth, water level fluctuations, and proportion of emergent plant cover. The original CWS survey covered many water bodies in the Chilcotin, my analysis was restricted to the eight lakes on Becher's Prairie used in my faunal studies. All these raw data are presented in Appendix F.

To measure productivity I collected triplicate littoral plant samples from each of the eight lakes, once a month between May and September 1984. In order that results be comparable with faunal community parameters, samples were taken from the same part of the littoral zone that animals were collected in 1978. One sample consisted of all the aquatic plants within a 0.1 m² quadrat at 20-30 cm depth. Dry weights were determined after washing and drying the vegetation at 100 °C for 24 hours.

Abiotic parameters of the lakes were calculated in the manner outlined in Chapter 1. Salinity parameters were recalculated for 1983 and 1984 as annual variations in salinity are common in the study lakes and these changes may affect the biota. CWS provided conductivity measures for 1983 and I measured conductivity monthly with a Radiometer conductivity meter in 1984. Values for morphometric variables were taken from Topping & Scudder as in Chapter 1.

COMMUNITY PARAMETERS. From the CWS data I was able to calculate species richness, percent cover, species diversity, hierarchical diversity, and two super community indices. For a detailed discussion of these terms see Chapter 2.

Hierarchical diversity was used to tease out the confounding effects of basin morphology. One would expect the unique basin shape of each lake to influence the number and variety of species that can establish and survive, irrespective of water chemistry. Through this technique, diversity of the whole community was divided into zone diversity, an abiotic character of basin morphology, and mean within-zone species diversity averaged over all zones such that:

$$H'(s) = H'(z) + H'_z(s)$$

where $H'(s)$ = total species diversity

$$H'(z) = \text{zone diversity}$$

$$H'_z(s) = \text{mean within-zone species diversity.}$$

One would predict that by subtracting the abiotic measure of basin morphology, any obscured relationship between diversity and salinity would become more obvious. Similarly, total diversity was divided into hierarchical components based on growth form (submerged, floating, emergent).

Super community indices were calculated from species presence/absence data using Jaccard's coefficient of similarity and from cover-abundance data using Euclidean distances.

CLASSIFICATION. The method used to cluster the eight study lakes was UPGMA, as described in Chapter 1. The similarity indices used and methods of comparison were the same as those in Chapter 2.

Results

PHYSIOCHEMICAL FEATURES. The eight lakes were characterized according to five abiotic variables: mean conductivity, two principal component axes based on ionic composition, mean depth, and the ratio of shoreline development to area. Morphometric variables were the same as those in Chapter 1 (Table 4), and other than minor numerical differences, physiochemical features were much the same in 1978, 1983 and 1984. Fig. 21 presents salinity data; Fig. 22 shows dendrograms.

GENERAL DESCRIPTION OF LAKES. All lakes in the series (except Lakes 1 and 7) were surrounded by stands of Juncus and Scirpus, and more freshwater lakes developed heavy algal blooms (Plate 4). All lakes had little or no vegetation early in the season (Plate 5), but Lakes 1-5 developed thick mats of submerged vegetation by mid-summer: Potamogeton natans in Lake 1 (Plate 6), Myriophyllum exalbescens in Lake 2 (Plate 7), and a combination of Potamogeton pectinatus and Ruppia occidentalis in Lakes 3-5 (Plate 8). In 1984 the submerged vegetation of Lake 3 suffered considerable damage between mid-August and mid-September, probably by water fowl or muskrats that favour this lake and use hydrophytes for food and house building (Munro, 1945; Krull, 1970; Danell, 1978; 1979).

Fig. 21. Seasonal conductivity ($\mu\text{S cm}^{-1}$, 25 °C) in each lake in order of increasing salinity (a) for 1983, and (b) for 1984.

● = maximum, ○ = mean, ◆ = range. (See Fig. 1 for lake names; see Appendix E for numerical values)

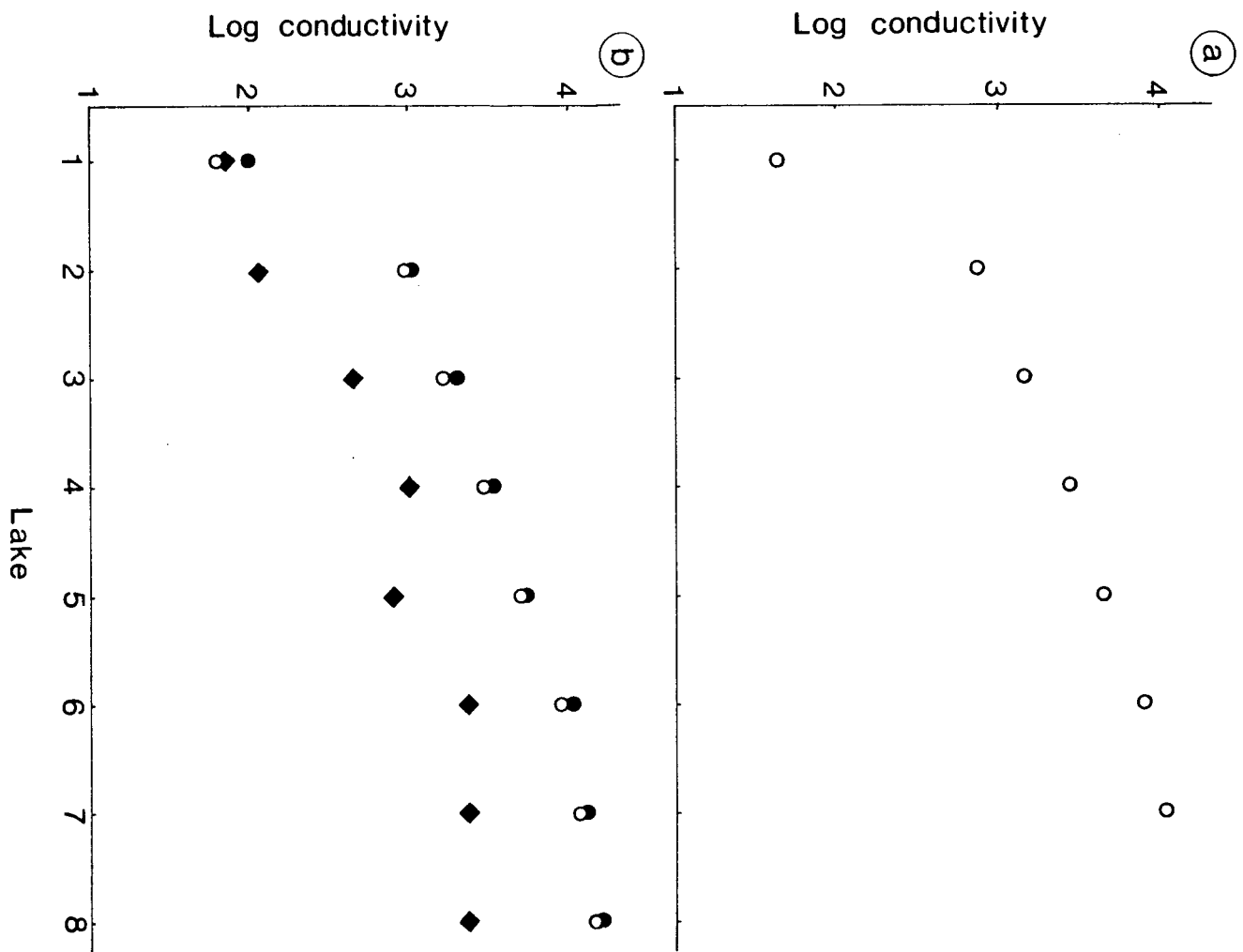


Fig. 22. Cluster analysis of study lakes based on dissimilarity of

(a) 1983 predicted ionic composition, $r=0.826$

(b) 1983 predicted ionic composition plus morphometric
characters, $r=0.881$

(c) 1984 predicted ionic composition, $r=0.786$

(d) 1984 predicted ionic composition plus morphometric
characters, $r=0.866$

(See Fig. 1 for lake names).

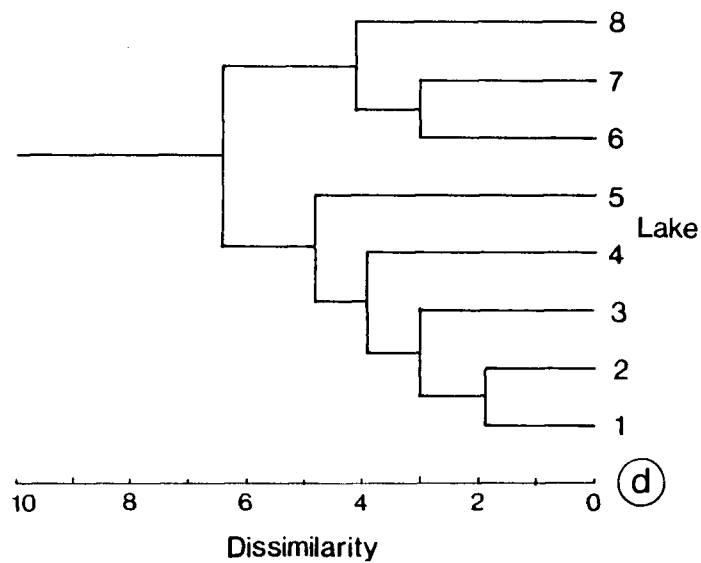
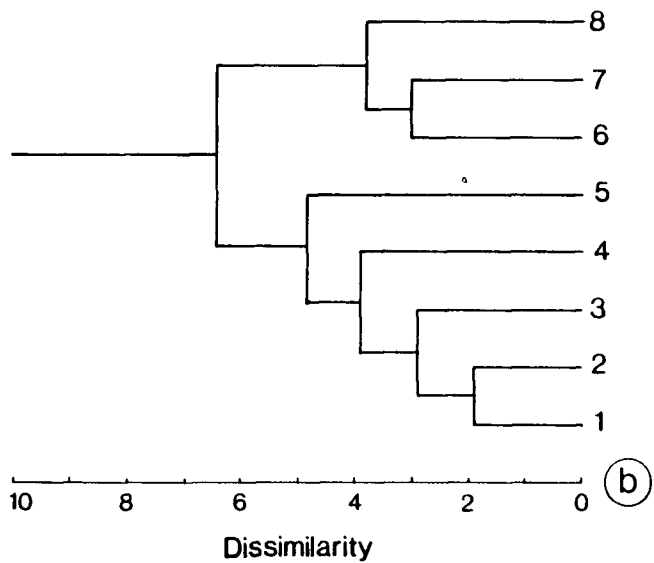
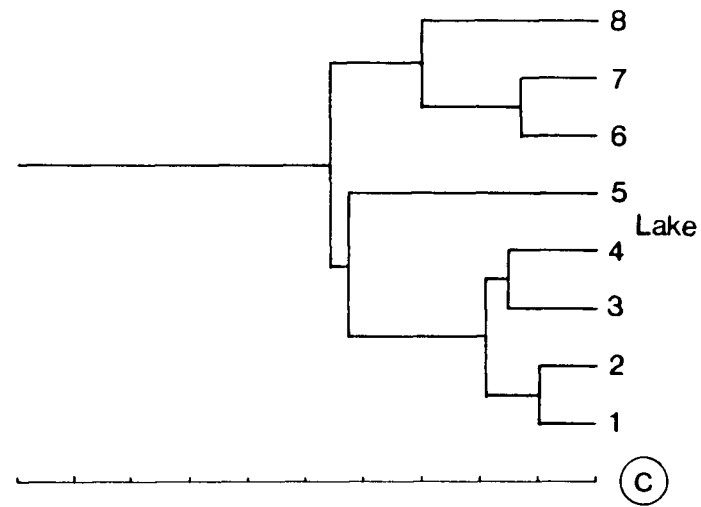
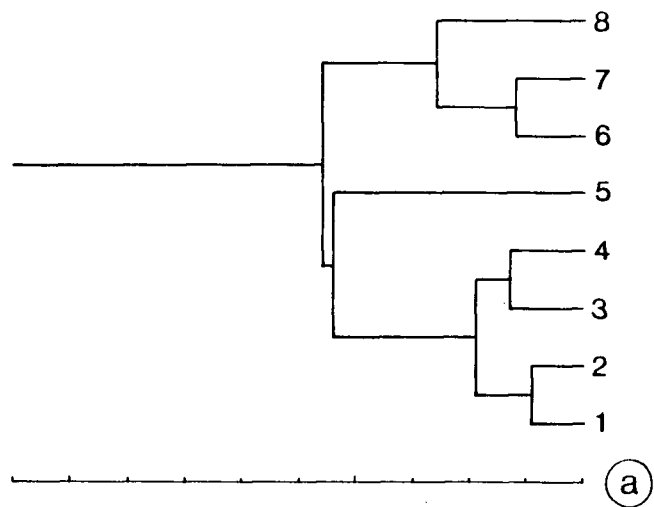




Plate 4. 12.viii.84. Lake 5 (Jackson L.) showing stands of emergent flowering Scirpus lacustris and a heavy algal bloom on water surface.

Plate 5. 12.v.84. Lake 3 (Near Opposite Crescent) in Early spring before any annual plant growth. Dead S. lacustris from the previous year are in the foreground.





Plate 6. 7.vii.84. Lake 1 (Box 27) mid-summer: close-up photograph of extensive mat of Potamogeton natans. Floating leaves are 5-10 cm long.



Plate 7. 13.vi.84. Lake 2 (Barkley L.) with dense submerged Myriophyllum exalbescens early in the season, emergent Juncus balticus is in the foreground.



Plate 8. 7.vii.84. Lake 4
(Rock L.): close-up of submerged
vegetation. Length across
bottom of photograph is
approximately 1.5 m.



Plate 9. 12.viii.84. Lake 8
(Barnes L.) with margin of
emergent Juncus balticus,
standing 50 cm above water
surface.

In general, the three highly saline lakes had no submerged or floating vegetation and no heavy algal blooms typical of fresher waters. Lakes 6 and 8 had well established margins of the perennial Juncus and showed relatively few changes in the littoral zone with season (Plate 9). In these lakes Juncus was rooted below the water level throughout the season whereas in others it usually occurred at or above water level. It is not clear why there was no vegetation in Lake 7, it is not simply owing to water chemistry as healthy macrophyte growth was found in more saline lakes.

SPECIES DISTRIBUTION. Each lake had a unique assemblage of macrophyte species, and although there was some overlap, no species occurred in all lakes and many (14) species in only one lake. A total of 26 plant species was found inhabiting the eight lakes (Table 12). Three principal groups of species, those restricted to saline lakes, to freshwater lakes, and those occurring at moderate salinities or tolerant of a wide range of salinities, were revealed when multivariate classification clustered species according to which lakes they occur in (Fig. 23). At the top of Fig. 23 is a small group, A, of species including Distichlis stricta, a typical halophyte, occurring only in the most saline lake. Group B, with two subgroups, contains species that occurred at moderate salinities or over a wide range of salinities. Subgroup B1 contains species such as Potamogeton pectinatus found in moderately saline lakes, and the most widespread species, Juncus balticus and Scirpus lascastris, found in six of the eight lakes. In subgroup B2 are species found only in Lake 2, including Myriophyllum exalbescens, Ceratophyllum demersum and Beckmannia szygachne. Group C, at the bottom of the dendogram, contains typically freshwater species, including Potamogeton natans, Glyceria borealis, Utricularia vulgaris and

Table 12. Distribution of aquatic plants recorded by CWS.

S = submerged; F = floating; E = emergent.

(See Fig. 1 for lake names)

Number	growth		species	lake							
	form			1	2	3	4	5	6	7	8
1	S		Filamentous algae sp.		o	o	o	o	o		
2	S		<u>Drepanocladus</u> sp.	o							
3	S		<u>Aphanozomenon flosaquatis</u>			o		o			
4	E		<u>Polygonum amphibium</u> L.	o	o						
5	F		<u>Ceratophyllum demersum</u> L.		o						
6	S		<u>Myriophyllum exalbescens</u> (Fern.) Jeps.		o	o					
7	F		<u>Utricularia vulgaris</u> L.	o							
8	E		<u>Sagittaria cuneata</u> Sheld.	o							
9	S		<u>Potamogeton pectinatus</u> L.		o	o	o	o			
10	S		<u>P. pusillus</u> L./ <u>berchtoldi</u> Fieb.		o	o					
11	S		<u>P. richardsoni</u> (Bennett) Rydb.		o						
12	F		<u>P. natans</u> L.	o							
13	S		<u>Ruppia occidentalis</u> L.				o	o			o
14	E		<u>Juncus balticus</u> Willd.		o	o	o	o	o		o
15	E		<u>Carex atherodes</u> Spreng.			o					
16	E		<u>C. rostrata</u> Stokes	o							
17	E		<u>C. lanuginosa</u> Michx.			o					
18	E		<u>Eleocharis palustris</u> (L.) R. & S.	o	o	o					
19	E		<u>Scirpus americanus</u> Pers.				o				
20	E		<u>S. lacustris</u> Vahl.		o	o	o	o	o		o
21	E		<u>Beckmannia szygachne</u> (Stend.) Fern.		o						
22	E		<u>Distichlis stricta</u> (Torr.) Rydb.								o
23	E		<u>Glyceria borealis</u> (Nash) Batch.	o							
24	E		<u>Hordeum jubatum</u> L.								o
25	S		<u>Sparganium</u> sp.	o							
26	F		<u>Lemna minor</u> L.		o						

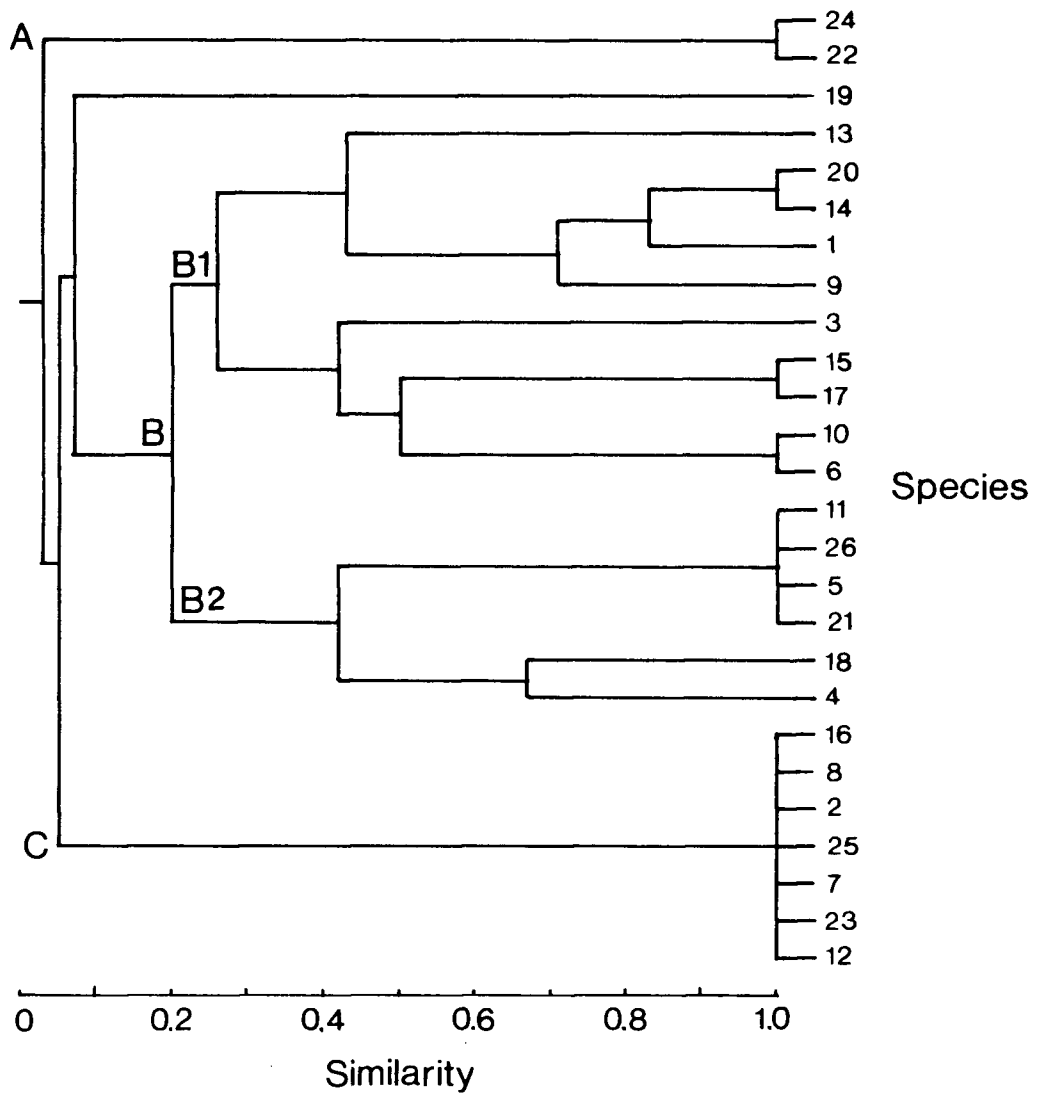


Fig. 23. Cluster analysis of aquatic macrophyte species based on similarities of lakes occupied, $r=0.911$. Principal subgroups, designated by stem letters, are discussed in the text. (See Table 12 for species names).

Sagittaria cuneata, that were found only in Lake 1.

Floating-leaved forms were found only in the two most freshwater lakes whereas emergent and submerged forms occurred in all lakes, as shown in Fig. 24 displaying the relative proportion of each lake covered by emergent, submerged or floating macrophytes. The figure suggests that the relative proportion of emergent plants decreased with increasing salinity.

COMMUNITY PARAMETERS. Values for community parameters varied considerably among lakes (Table 13). All parameters had zero values in Lake 7, as this lake had no vegetation. Maximum values for species richness, diversity, mean within-zone diversity, and both super community indices occurred in Lake 2. Lake 4 had the highest percent cover with an estimated 94% of the lake area covered by aquatic macrophytes.

Water chemistry appears to be the most important variable for predicting community parameters: Table 14 summarizes the relationships between physiochemical variables and community parameters (Table 13). Conductivity and PC1 both show significant associations with five parameters and trends with two more. Of the remaining abiotic variables examined, PC2 shows no association with any parameters; mean depth is correlated with several parameters but the sign (negative) of the observed relationships is contrary to predictions and attributed to the chance correlation of mean depth with salinity (Table 5). This coincidental relation of community parameters with lake size was also seen in comparison with faunal communities (Chapter 2). D_{LA} is associated with some parameters, but in each case salinity measures show a stronger correlation with the same parameter so this phenomenon is likely owing to the chance correlation of D_{LA} with salinity (Table 5), although some other explanation cannot be ruled out.

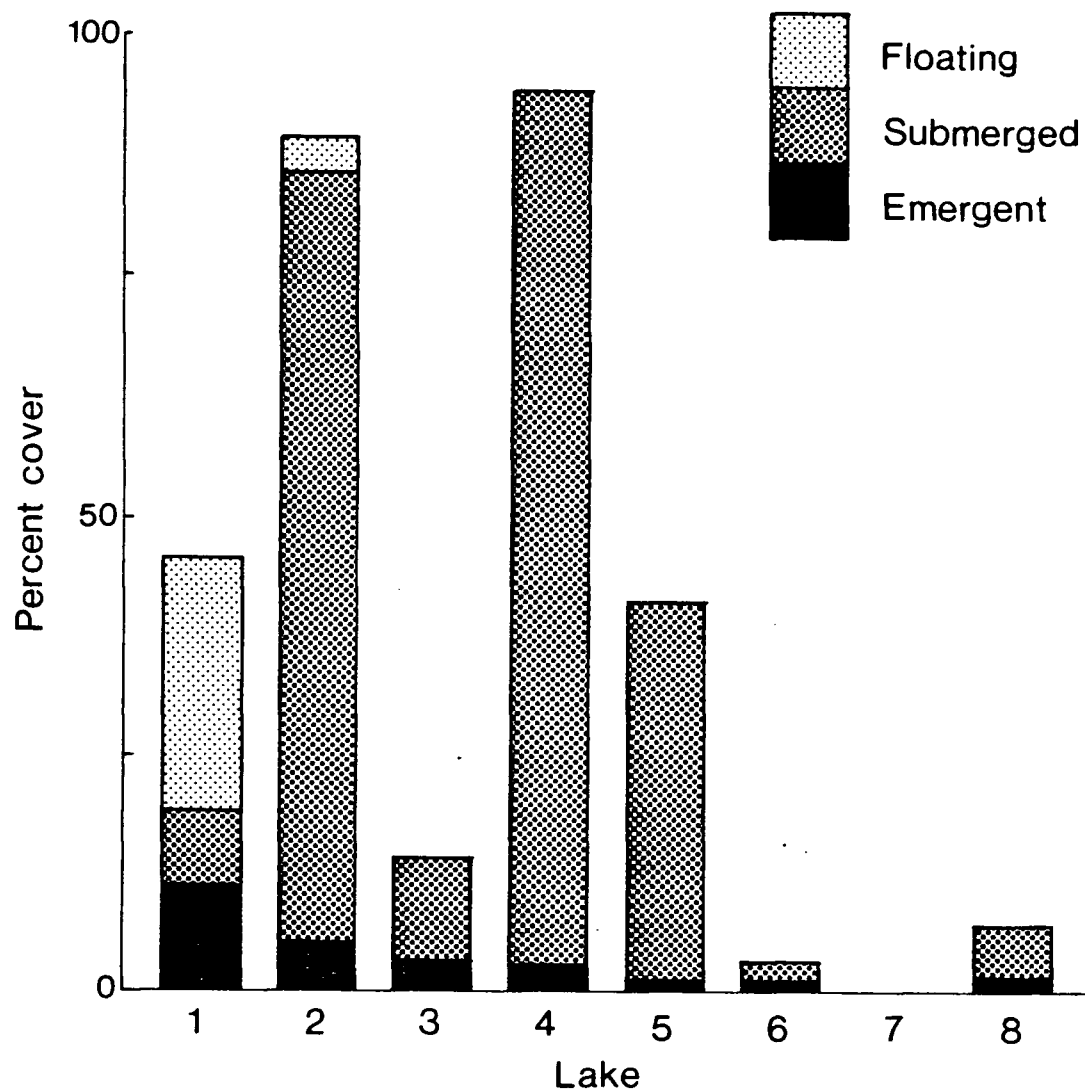


Fig. 24. Relative proportion of floating, submerged and emergent macrophytes in each lakes. Maximum height of bars represents percent of lake area covered by all macrophytes; variously shaded sections represent percent of lake area covered by each growth form. (See Fig. 1 for lake names).

Table 13. Aquatic macrophyte community parameters, maximum values are in bold type. (See Fig. 1 for lake names; see text explanation of symbols).

Lake	s	% cover	community parameter						
			H'(s)	H'(z)	H' _z (s)	H'(f)	H' _f (s)	Q _j	Q _d
1	9	45	1.62	0.69	0.93	0.96	0.66	0.35	11.39
2	12	89	1.82	0.22	1.06	0.36	0.92	0.46	11.15
3	10	14	1.41	0.55	0.86	0.55	0.86	0.39	12.69
4	6	94	1.00	0.33	0.68	0.12	0.88	0.23	12.91
5	6	40	1.09	0.83	0.26	0.10	0.99	0.23	13.25
6	3	30	0.28	0.01	0.27	0.14	0.14	0.12	13.95
7	0	0	0.00	0.00	0.00	0.00	0.00	0.00	14.05
8	5	70	1.05	0.95	0.10	0.42	0.63	0.19	13.20

Table 14. Summary of relationships between physiochemical variables and aquatic macrophyte community parameters based on Pearson's product-moment correlation coefficient. Negative associations: * = p<0.10; ** = p<0.05; *** = p<0.01. Positive associations: + = p<0.10; ++ = p<0.05; +++ = p<0.01. (See text for explanation of symbols; see Appendix G for numerical values).

	s	% cover	community parameter						
			H'(s)	H'(z)	H' _z (s)	H'(f)	H' _f (s)	Q _j	Q _d
k ₂₅	**	*	**	-	***	-	*	**	++
logk ₂₅	*	-	**	-	**	**	-	*	+++
PC1	**	*	**	-	***	-	*	**	++
PC2	-	-	-	-	-	-	-	-	-
z	***	**	**	-	***	-	**	***	+++
D _{LA}	++	-	++	-	+	-	+	++	**

Of the biotic variables examined, species richness, $H'(s)$, $H'_z(s)$, Q_J and Q_d , all show significant associations with water chemistry. When diversity was expressed in a hierarchical form to control for morphologically different basin shapes, i.e. by subtracting $H'(z)$ from $H'(s)$, the association is much stronger. As expected, there is no association between $H'(z)$ and water chemistry. A trend is indicated for decreasing percent cover and $H'_f(s)$ with increasing conductivity and PC1.

CLASSIFICATION. Dendrograms produced by multivariate classification of lakes according to their species composition show an arrangement of lakes clearly related to salinity (Fig. 25). Both dendrograms have acceptable cophenetic correlation coefficients. In the dendrogram based solely on species presence/absence (Fig. 25a), Lake 1 is last to join the cluster owing to its unique freshwater assemblage, and the remainder are joined in pairs of lakes adjacent to each other on the salinity scale. When species relative abundances were considered (Fig. 25b), saline Lakes 6 and 7 are considered least dissimilar and the remaining lakes are sequentially added to the cluster, more or less in order of decreasing salinity. Although both dendrograms show patterns related to salinity, they are not closely related to each other or to dendrograms produced from physiochemical data (Fig. 4) as cophenetic correlations between dendrograms are not significant. The simple matching coefficient was used to cluster binomial data (Fig. 25a) as it is not algebraically possible to use Jaccard's coefficient when a sample (Lake 7) in the series has no species. The one aberration in Fig. 25b is the displacement of Lake 4, probably owing to its extremely high percent cover (Table 13).

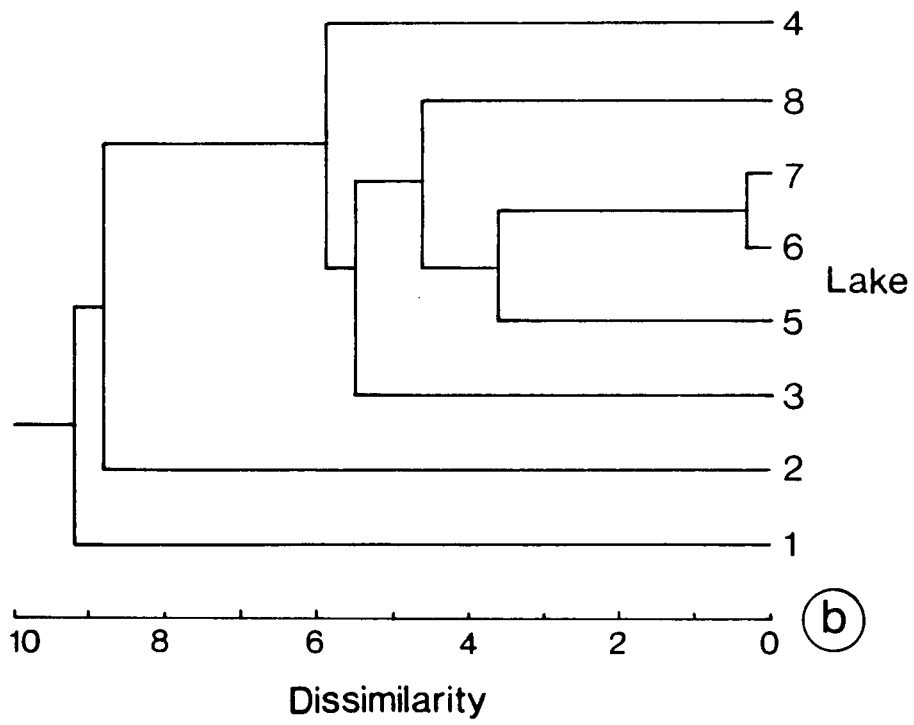
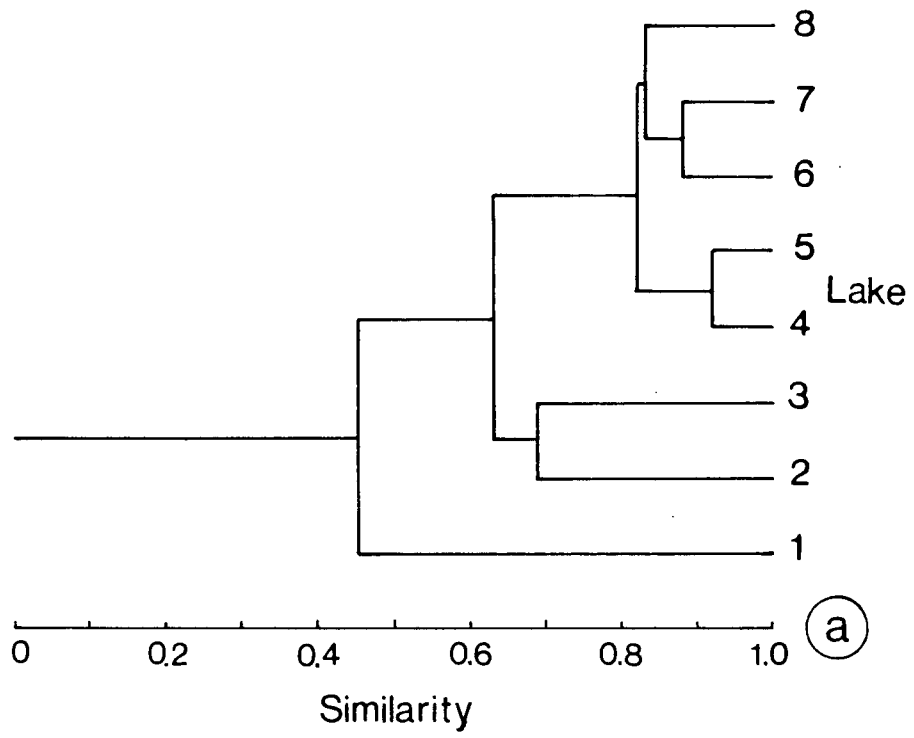
PRODUCTIVITY. The dominant species, and in some cases growth forms,

Fig. 25. Cluster analysis of study lakes based on

(a) similarity of macrophyte species composition, $r=0.899$

(b) dissimilarity of species relative abundance, $r=0.968$

(See Fig. 1 for lake names).



collected in sample quadrats differed among lakes. Samples from lakes with conductivities less than 5000 μS (Lakes 1-5) were dominated by mats of floating and/or submerged vegetation: Potamogeton natans in Lake 1, Myriophyllum exalbescens in Lake 2, and a combination of Potamogeton pectinatus, Ruppia occidentalis plus filamentous algae in Lakes 3, 4 and 5. The littoral zones of Lakes 6 and 8 had no, or virtually no, submerged vegetation, instead they were dominated by the widely spaced thick emergent stems of Juncus balticus. J. balticus was present around the fresher lakes, but not usually in the water so it never entered the sampling area, whereas in Lakes 6 and 8 it was partially submerged all season. No vegetation was found in Lake 7.

Macrophytes in the first five lakes exhibited typical growth curves: low or no biomass early in the season, increasing to a maximum level by mid or late summer, whereas no pattern was evident in the more saline lakes. This is illustrated in Fig. 26 showing the standing crop of aquatic macrophytes in each lake in relation to time. The dramatic drop in biomass of Lake 3 in September reflects damage done by muskrats or water fowl. No growth pattern was evident for the two more saline Lakes 6 and 8 owing to highly variable data. It may be that the sampling technique used was not sensitive enough for the type of plants present in these lakes. One can say, however, that despite high variation, the standing crop of Lake 6 was higher than that of the more saline Lake 8 ($F=39.49$; $df=1,28$; $p<0.01$).

It is difficult to analyze these data in terms of productivity as the dominant macrophyte species differed among lakes and species differ in their life cycle and biomass dynamics. In an attempt to make meaningful comparisons among lakes, the data were rescaled and put on a more even footing. Fig. 27 shows standing crop values of each lake after data were

Fig. 26. Mean and standard error of macrophyte standing crop in the littoral zone of each lake. (#) = lake number. Note : no graph shown for Lake 7. (See Fig. 1 for lake names).

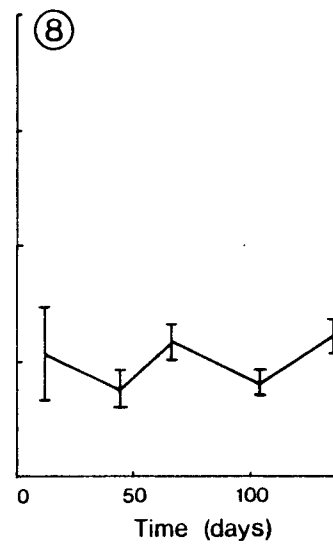
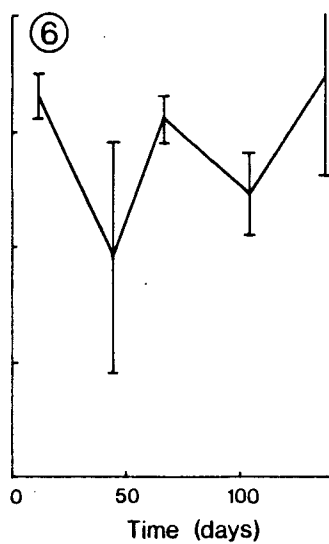
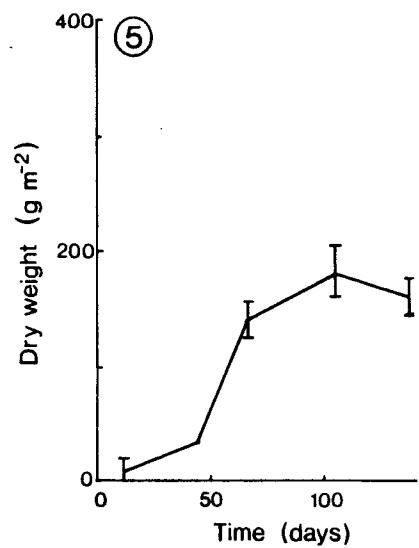
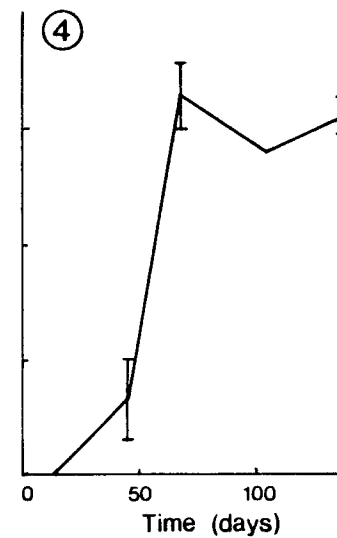
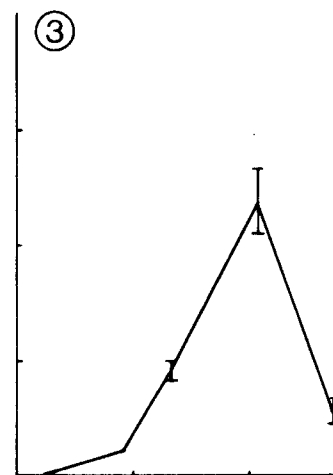
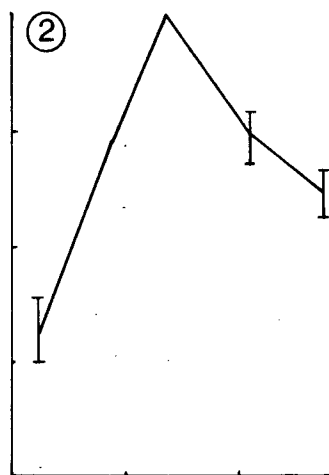
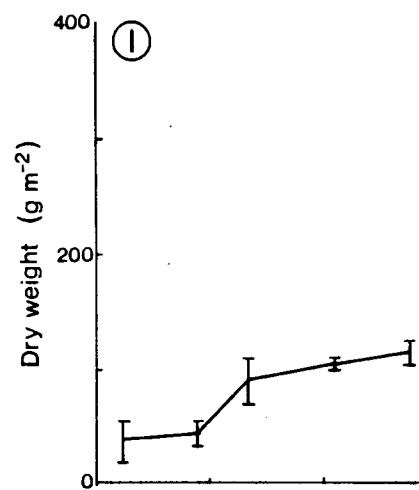
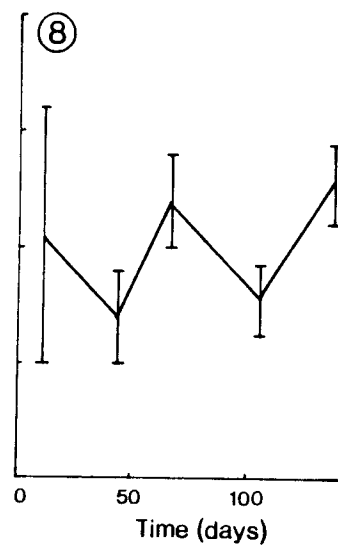
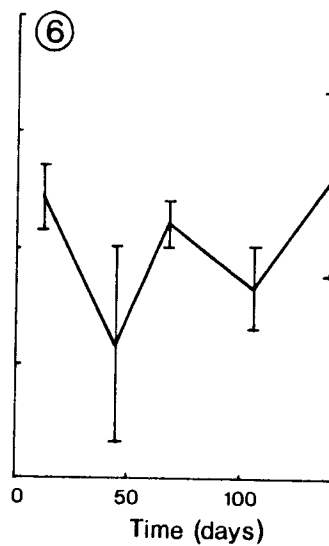
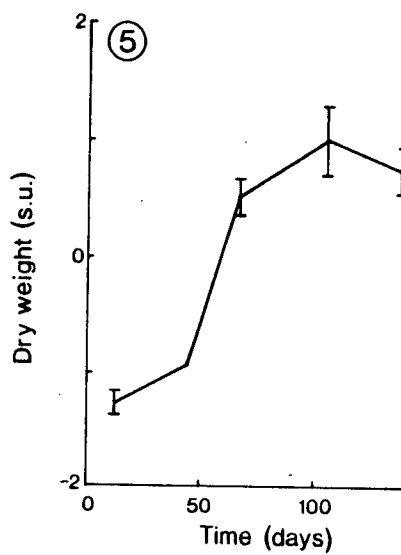
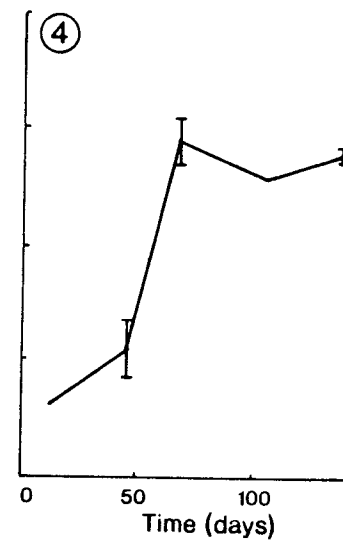
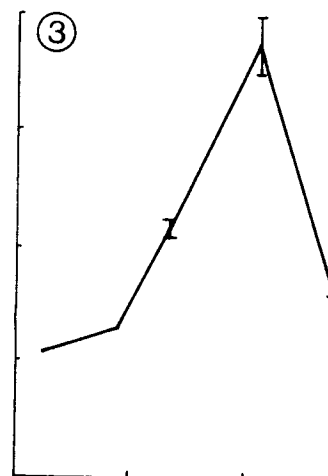
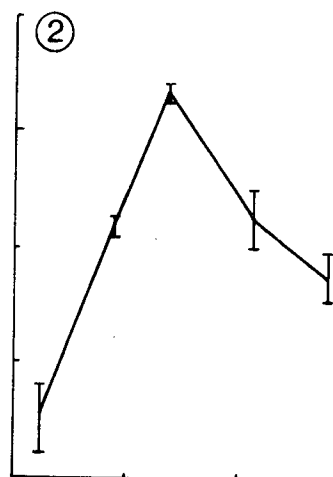
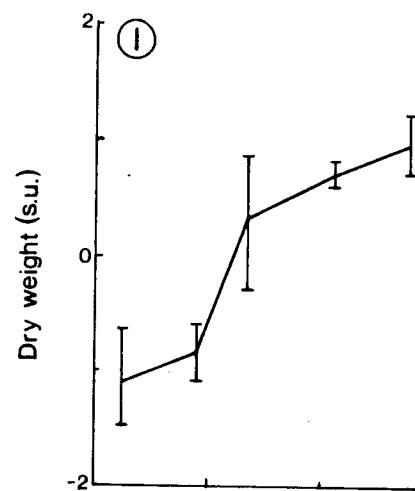


Fig. 27. Mean and standard error, in standardized units, of macrophyte standing crop in the littoral zone of each lake. (#) = lake number. Note : no graph shown for Lake 7. (See Fig. 1 for lake names).



centered and standardized by standard deviation (Noy-Meir et al., 1975).

Macrophyte productivity shows a significant inverse association with conductivity, PC1, and mean depth (Table 15). Productivity was estimated as the difference between maximum and minimum standing crop when expressed in standardized units. Productivity measured in this way has no absolute value, but it does give an indication of relative productivity. It is unrealistic to calculate productivity values for Lakes 6 or 8 because the data were so variable that there was no obvious seasonal maximum or minimum. However, it is not unreasonable to suggest that the Juncus found in these lakes maintained a relatively constant standing crop without any appreciable increase over the season, as the results indicate, in which case net seasonal productivity must be zero. Again, the association with mean depth is contrary to predictions and probably an incidental occurrence.

Discussion

In this study, salinity is inversely correlated with absolute and relative species richness, abundance, diversity, super community complexity and productivity of aquatic macrophytes, therefore supporting both the diversity-stability and productivity-salinity hypotheses. The series of eight lakes was characterized abiotically according to salinity to test these hypotheses, and according to lake morphometry to control for possible effects of other processes.

PROBLEMS. Even though the general conclusions of this study are valid, there were a number of difficulties associated with the data, as with any other study. The main drawback of the data provided by CWS is

Table 15. Aquatic plant productivity measured in 1984 and its relationship to abiotic variables, based on Pearson's product-moment correlation coefficient. All associations are negative: * = $p < 0.10$; ** = $p < 0.05$; *** = $p < 0.01$. (See Fig. 1 for lake names).

Lake	productivity
1	2.024
2	2.879
3	2.651
4	2.259
5	2.308
6	0.0
7	0.0
8	0.0
K ₂₅	***
logk ₂₅	*
PC1	***
PC2	-
z	***
D _{LA}	*

that they reflect the condition of the lakes at only one point in time (mid-summer), and are not necessarily representative of the entire season. From my own visits to Becher's Prairie, it is evident that macrophyte communities do change dramatically over time. It is likely that there would not be large changes in species richness but total cover, relative abundance and hence diversity could change considerably. In addition, there are some weaknesses associated with estimates of abundance on the Braun-Blanquet scale: percent areal cover may be high, but dry weight biomass per unit area is often small (Westlake, 1963; Sculthorpe, 1967), or alternatively, many plant parts such as roots and rhizomes are not visually apparent so cover may be underestimated.

Generally speaking, the method used to determine relative productivity was appropriate (Westlake, 1963), but some problems arose during sampling. The dominant plant species, and in some cases growth form, collected in sample quadrats differed among lakes. As a result, not all lakes were sampled with the same degree of accuracy, and it was difficult to compare lakes without rescaling the data on a somewhat arbitrary scale. In addition, the data do not necessarily represent productivity of the whole lake, only of a small stand. Many of these problems are insurmountable but one must be aware of them. Nevertheless, these methods are probably adequate to reveal relative differences among lakes with a degree of accuracy sufficient for the objectives of this study.

DISTRIBUTION AND COMMUNITY COMPOSITION. In total, 26 aquatic macrophyte species were found inhabiting the eight study lakes (Table 12), and species characteristic of high, low or moderate salinities, or tolerant of all salinities, were present in the series (Fig. 23). There is some conflict between several of the species names found by CWS and those

published previously by Reynolds & Reynolds (1975), but these are mainly taxonomic idiosyncracies. For example: (1) Scirpus lacustris vs S. validus: typical S. lacustris is a Eurasian plant, but in North America it is considered a species-complex with S. validus one of its variations (Hitchcock et al., 1969). (2) Myriophyllum exalbescens vs M. spicatum: according to McGaha (1952) these are the same species, but more recently they have been described as variations of the same species (Hitchcock & Cronquist, 1973). (3) Ruppia occidentalis vs R. maritima: again, these are considered variations of the same species (Hitchcock & Cronquist, 1973). Almost all the species are cosmopolitan or circumboreal in distribution, and many have been noted to occur in brackish water (Hitchcock et al., 1969).

Macrophyte species distributions were apparently determined primarily by upper and lower limits of tolerance to salinity, while the presence or absence of a particular species within that range was owing to some other factor. Each lake had a unique species assemblage and/or dominant species, and although there was some overlap, no species occurred in all lakes and many species occurred in only one lake (Table 12). Similar results were found by Reynolds & Reynolds (1975) in a study that included these eight lakes, and by Seddon (1972) in a series of Welsh lakes. Objective, multivariate classification methods arranged lakes in hierarchical dendrograms on the basis of their species composition and relative abundance (Fig. 25). These dendrograms show an arrangement of lakes clearly related to salinity, but not the same as patterns in the physiochemical clusters (Fig. 4).

The ions Na, HCO₃, CO₃, Cl and K are likely to be important limiting factors for macrophyte survival in the study lakes, although it

was not possible to distinguish between the influence of total salinity or individual ions. Chloride salts are considered the most toxic ions to plants, and most glycophytes (non salt tolerant plants) are physiologically limited at concentrations of NaCl greater than 50 mM (Waisel, 1972). None of the lakes in this study had Cl concentrations this high (Table 2) so species distributions were probably not governed simply to the influence of a single ion, but rather to total salinity or the synergistic effects of several ions. Macrophyte species need not be limited only by a physiological intolerance to salinity. Other factors such as competition may play an important role where plants are subject to less than optimal salinities.

In a discussion of tolerance ranges in these Chilcotin lakes as compared to other saline water bodies, Reynolds & Reynolds (1975) concluded that, at the global level, there are no clear correlations of plant distribution with total conductivity as the particular ion composition and other environmental variables, such as temperature, appear to be important. More information on the relative significance of salinity, and all its associated factors, to specific plants is necessary before species assemblages in different waters can be fairly compared (Sculthorpe, 1967). However, because these Chilcotin lakes were abiotically similar in almost every respect except total salinity, it is reasonable to suggest that within this series, salinity played a major role in limiting the distribution of species.

The distribution of growth forms also appeared to be affected by salinity (Fig. 24): floating-leaved macrophytes were found only in the two most freshwater lakes (primarily in Lake 1), the more saline lakes (over 5000 μ S) had virtually no submerged forms, and emergent plants occurred

throughout the range of salinity, but tended to decrease in abundance with increasing salinity. Brock (1981) suggests that more emergent than floating or submerged macrophytes are tolerant of salinity, yet other factors such as wind action can prevent plants with floating leaves from flourishing (Arber, 1920). The floating-leaved Potamogeton natans dominated the macrophyte community in the most freshwater lake, but this lake was also well protected from prevailing winds, perhaps more so than any other lake in the series. Arber (1920) states the P. natans often dominates calm waters, but in lakes subject to much wind and wave action it may be out-competed by Myriophyllum, whose highly divided foliage is not so susceptible to mechanical damage. As this explanation is in keeping with conditions observed on Becher's Prairie, it is not entirely clear if salinity is the only factor affecting the distribution of floating-leaved forms.

COMMUNITY PARAMETERS. The results support the hypothesis that stable habitats have more diverse communities than less stable ones, where salinity defines environmental stability in terms of severity (Table 14). Little evidence was found to support hypotheses that basin morphometry affects community structure. The inverse association of plant species richness with salinity indicates that fewer species were capable of surviving in high salinity lakes. Species diversity is inversely correlated with salinity and the hierarchical diversity formula (Pielou, 1974; 1975) proved useful to control for differences in basin morphology among lakes and hence revealed an even stronger correlation. The inverse association between the two new super community indices and salinity indicates that although species were capable of dispersing to all lakes, salinity played a significant role in determining which species, how many

species, and their relative abundance, actually established in a particular lake. The general complexity of communities decreased with increasing salinity, as compared to the maximum complexity possible.

PRODUCTIVITY. The data in this study indicate that increasing salinity was accompanied by an overall decrease in lake productivity (Table 15). Freshwater lakes displayed larger changes in macrophyte standing crop biomass than saline lakes. The observed decrease in percent cover of aquatic macrophytes with increasing salinity also indicates decreasing eutrophication (Westlake, 1963; 1965; McNaught, 1975; Wetzel, 1975; Canfield et al., 1983). In addition, the absence of algal blooms and macrophyte growth in more saline lakes indicates their poor trophic state as Gannon & Stemberger (1978) suggest.

Summary

This third chapter examines relationships between salinity and the aquatic macrophyte community in terms of the diversity-stability hypothesis and a productivity-stability hypothesis. In total, 26 species were found and species were characteristic of high ($>5000 \mu\text{S}$), moderate or low salinities, or tolerant of all salinities. Species distribution was apparently determined primarily by upper and lower limits of tolerance to salinity, while the presence or absence of a particular species within that range was owing to some other factor. The distribution of growth forms may be affected by salinity as floating leaved forms occurred only in freshwater lakes, virtually no submerged forms occurred in saline lakes, and emergent forms were found throughout but tended to decrease in abundance with increased salinity. Each lake was characterized abiotically

according to salinity and basin morphometry, and biotically according to macrophyte species richness, abundance, diversity, hierarchical diversity, super community indices and productivity. Salinity appeared to be the most important abiotic factor in association with community parameters, and little evidence was found of morphometric correlations. Inverse associations of salinity with absolute and relative species richness, diversity, hierarchical diversity and super community indices, support the hypothesis that saline environments have less diverse communities than freshwater ones. Inverse associations of salinity with productivity in terms of seasonal biomass changes and percent vegetation cover, support the hypothesis that saline habitats have less productive macrophyte communities than freshwater ones.

CHAPTER 4: RELATIONSHIPS BETWEEN FAUNAL AND FLORAL COMMUNITIES

Introduction

Several studies examining the fauna of saline lake series have acknowledged the need to interpret the observed structure of animal communities in terms of the plant community as well as salinity (Reynolds & Reynolds, 1975; Cannings et al., 1980; Timms, 1981; Brock & Shiel, 1983; van Vierssen & Verhoeven, 1983; Cannings & Cannings, 1985). Evidence presented in Chapter 2 showed that there is a relationship between salinity and the structure of faunal communities, but the nature of the association is quite complex. It may be possible to resolve some of this complexity by comparing the structure of faunal communities (Chapter 2) with the floral communities (Chapter 3) present in the study lakes.

Aquatic macrophytes play many varied and interrelated roles in aquatic ecosystems and their influence can directly or indirectly affect the lives of other organisms. Plants are capable of altering the physical and chemical environment, thereby indirectly influencing the distribution and survival of the fauna. Physically they can alter light penetration, wave action, current velocity and direction, and rate of silting, the latter two being more important in running water than lakes. Macrophyte shading can inhibit phytoplankton development (Goulder, 1969), and alter local distributions of phototactic insects (Lyman, 1956; Hughes, 1966; Hynes, 1970) and limnetic zooplankton (Siebeck & Ringelberg, 1969). Through the metabolic processes of photosynthesis and respiration, macrophytes can affect concentrations of dissolved O_2 , CO_2 and NH_4 , mineral nutrients, and pH (Straškraba, 1965; Sculthorpe, 1967; Wetzel, 1975). Aquatic plants secrete dissolved organic compounds (Wetzel, 1969; Wetzel &

Manny, 1972; Hough & Wetzel, 1975) that can enhance periphyton productivity (Wetzel, 1975) or act as repellents or attractants to certain animals (Pennak, 1973; Hutchinson, 1975; Lloyd, 1976).

More directly, macrophytes provide a substrate for animals to colonize, lay eggs, pupate, seek refuge, hunt for food, and use as building materials (Minshall, 1984). The use of substrate changes throughout the animals' lifecycle, and the degree of dependence varies from obligate to facultative (Soszka, 1975b). Many insects oviposit in or on macrophytes but differ in the extent of their dependence: corixids frequently oviposit on plants (Hungerford, 1948); some Odonata deposit eggs among thick vegetation (Wolfe, 1953) whilst those with ovipositors lay eggs within plant tissues (Corbet, 1962; Cannings & Stuart, 1977); chrysomelids of the Donaciinae oviposit and pupate within plant tissues (Houlihan, 1969; 1970; Crowson, 1981; Otto, 1985) whereas some aquatic weevils complete their lifecycle from egg to adult within plant tissues (McGaha, 1954a; Gaevskaya, 1966; DeLoach et al., 1976; Cordo et al., 1978; 1981; 1982; Forno et al., 1983). Similarly, the Trichoptera and Pyralidae build protective cases with plant material (McGaha, 1954b) whereas some crustaceans simply hide among littoral vegetation to avoid predation (Davies, 1985). The lacunal system of some aquatic plants can even be used as an oxygen source for insect respiration (Houlihan, 1969; 1970; Otto, 1985).

Aquatic macrophytes can enter the trophic system indirectly as a substrate for periphyton communities which many herbivores graze upon, or as a direct food source. A major part of the total primary production in a lake occurs in the littoral vegetation where periphyton grows on the macrophytes (Westlake, 1963; 1965; McNaught, 1975; Canfield, et al., 1983). The aquatic fauna feeding directly on plants consist of obligate

phytophages such as weevils (McGaha, 1954a; Gaevskaya, 1966; DeLoach et al., 1976; Cordo et al., 1978; 1981; 1982; Forno et al., 1983), Donaciinae (Crowson, 1981; Otto, 1985), Pyralidae (McGaha, 1954b; Hynes, 1984), some chironomids and ephydriids (Berg, 1949; Minshall, 1984), and facultative phytophages such as corixids (Reynolds, 1975), some Dytiscidae (Gaevskaya, 1966), and amphipods (Stroikina, 1957 cited by Gaevskaya, 1966). Some aquatic plants are themselves carnivores (Lloyd, 1976; Meyers, 1982).

These specific plant-animal relationships are very complex and many of them are interrelated to form a network of relationships, each of which can influence many others. It is virtually impossible to examine any one community for all these factors and this study does not attempt to, but the sum of all individual plant-animal interactions can be summarized at an ecological level.

Many ecological studies have shown distinct associations between aquatic plant and animal communities (Macan, 1938; Kreckler, 1939; Berg, 1949; McGaha, 1952; Smyly, 1952; 1953; Rosine, 1955; Gerking, 1957; Smyly, 1957; Harrod, 1964; Straškraba, 1965; Whiteside & Harmsworth, 1967; Petr, 1968; Quade, 1969; Krull, 1970; Soszka, 1975a; 1975b; Shiel, 1976; Fry & Osborne, 1980; Palmer, 1981; Brock & Shiel, 1983; van Vierssen & Verhoeven, 1983; Blancher, 1984; Minshall, 1984; Richard et al., 1985). Results of these studies overlap a great deal, therefore, generalized relationships are summarized below without specific references. The distribution of macrophyte species and growth forms is important to animal communities as different plants are associated with different animal species and/or densities. Evidence indicates that the number and variety of animals associated with macrophytes are correlated with the morphological form of the plants: plants with finely divided leaves possess larger and more

varied animal populations than those with simple, entire leaves. The abundance and/or productivity of aquatic macrophytes in a lake has been shown to affect the composition, abundance, richness and diversity of animal communities. With larger areas of plant cover and/or more productive communities, plants have more influence on all physical, chemical and biological processes taking place in the lake. It has been found that more species rich or diverse floral assemblages support more species rich or diverse faunal assemblages, and presumably these phenomena are related to aspects of spatial and substrate heterogeneity. In addition, a contagious (patchy) distribution of animals is a common feature of aquatic (and terrestrial) habitats and probably frequently is a result of a patchy distribution of plants in the environment.

Tests for ecological relationships between floral and faunal communities are Group 2 type hypotheses of the diversity-stability concept (see General Introduction). Specifically, they test the hypothesis that more abundant, rich and diverse plant communities support more abundant, rich and diverse animal communities. This hypothesis was tested with the faunal and floral communities in the Becher's Prairie study lakes. Any patterns revealed through this analysis may help explain observed patterns between faunal communities and salinity (Chapter 2).

Materials and Methods

Species distribution patterns, community parameters and dendrograms, of faunal and floral communities presented in Chapters 2 and 3, were compared. Numerical parameters were statistically compared using Pearson's product-moment correlation coefficient, and dendrograms were compared with

cophenetic correlation coefficients (see previous chapters for details). All associations between plant and animal communities were further summarized with reference to their relationship with salinity. No new data are presented.

Results

Table 16 summarizes the associations between floral and faunal community parameters, and Table 17 illustrates how faunal community parameters relate to both macrophyte communities and salinity. The sign (positive or negative) of all correlations and trends in Table 16 indicate that more diverse plant communities are associated with more diverse animal communities, with one exception. Trophic level diversity [$H'(t)$] of entomostracans caught in light traps shows an inverse correlation with floral community parameters. This parameter was rejected in Chapter 2 as being biased by sampling technique and hence not representative of the true community, therefore, this inverse association is ignored and the parameter is not included in Table 17. The plant community parameter $H'(z)$ is not correlated with any faunal parameters (Table 16) and also has been omitted from Table 17. This parameter is representative of the abiotic environment rather than of macrophyte community structure, and was used in the hierarchical diversity formula to remove the confounding effects of basin morphometry from measures of macrophyte species diversity (Chapter 3). Table 18 presents cophenetic correlation coefficients between faunal and floral dendrograms, and illustrates how faunal community dendrograms relate to both macrophytes and salinity.

In both water bottle and light trap samples of zooplankton

Table 16. Summary of relationships between floral and faunal community parameters based on Pearson's product-moment correlation coefficient. Negative associations: * = $p < 0.10$; ** = $p < 0.05$; *** = $p < 0.01$; positive associations: + = $p < 0.10$; ++ = $p < 0.05$; +++ = $p < 0.01$; - = no association. See Table 6 for description of symbols. See Appendix H for numerical values.

Plant Community		Faunal Community parameter											
Parameter	D	s	ti	H'(s)	H'(t)	H'(ti)	H' _t (s)	H' _t (i)	H' _{ti} (s)	Q _J (s)	Q _J (ti)	Q _d (s)	Q _d (ti)
WATER BOTTLE - ZOOPLANKTON													
S	-	-	-	-	+	-	-	-	-	-	-	-	-
C	-	++	++	++	-	++	+	-	++	-	-	-	-
H'(s)	-	+	-	-	+	-	-	-	-	+	-	-	-
H'(z)	-	-	-	-	-	-	-	-	-	-	-	-	-
H' _z (s)	-	+	-	-	++	-	-	-	-	+	-	-	-
H'(f)	-	-	-	-	-	-	-	-	-	-	-	-	-
H' _f (s)	-	+	++	-	++	-	-	-	-	+	++	-	-
Q _J	-	-	-	-	+	-	-	-	-	-	-	-	-
Q _d	-	*	-	-	*	-	-	-	-	*	-	-	-
P	-	++	+	-	+++	-	-	-	-	++	++	-	-
SWEEP - COLEOPTERA													
S	++	-	+	-	-	-	-	-	-	-	+	*	*
C	++	-	-	-	-	-	-	-	-	-	-	-	*
H'(s)	+	-	+	-	-	-	-	-	-	-	+	*	*
H'(z)	-	-	-	-	-	-	-	-	-	-	-	-	-
H' _z (s)	+	-	-	-	-	-	-	-	-	-	-	-	-
H'(f)	-	-	-	-	-	-	-	-	-	-	-	-	-
H' _f (s)	-	-	-	-	-	-	-	-	-	-	-	-	-
Q _J	++	-	+	-	-	-	-	-	-	-	+	*	*
Q _d	**	-	-	-	-	-	-	-	-	-	-	+	++
P	-	-	-	-	-	-	-	-	-	-	-	-	-
SWEEP - HEMIPTERA													
S	-	++	+	+	-	++	-	-	-	++	+	*	***
C	-	-	-	-	-	-	-	*	-	-	-	-	*
H'(s)	-	+	+	++	-	++	-	-	-	+	+	*	***
H'(z)	-	-	-	-	-	-	-	-	-	-	-	-	-
H' _z (s)	-	++	+	-	-	++	-	-	-	++	+	*	**
H'(f)	-	-	-	++	-	-	-	-	-	-	-	*	-
H' _f (s)	-	-	+	-	-	+	-	-	-	-	+	-	*
Q _J	-	++	+	+	-	++	-	-	-	++	+	*	***
Q _d	-	*	-	***	-	***	-	-	-	*	-	++	++
P	-	+	+	-	-	++	-	-	**	+	+	-	-

Table 16. CONT

Plant Community		Faunal Community parameter											
Parameter	D	s	ti	H'(s)	H'(t)	H'(ti)	H' _t (s)	H' _t (i)	H' _{ti} (s)	Q _J (s)	Q _J (ti)	Q _d (s)	Q _d (ti)
LIGHT TRAP - ALL SPECIES													
S	-	+	+	-	-	-	-	-	-	+	+	-	-
C	-	-	++	-	-	-	-	-	-	-	-	-	-
H'(s)	-	+	+	-	-	-	-	-	-	+	+	*	-
H'(z)	-	-	-	-	+	-	-	-	-	-	-	-	-
H' _z (s)	-	++	++	-	-	-	-	-	-	++	++	*	-
H'(f)	-	++	-	-	++	-	-	-	-	++	-	**	-
H' _f (s)	-	-	-	-	-	-	-	-	-	-	-	-	-
Q _J	-	+	+	-	-	-	-	-	-	+	+	-	-
Q _d	-	***	**	-	*	-	-	-	-	***	**	++	-
P	-	-	++	-	-	-	-	-	-	-	++	-	-
LIGHT TRAP - ENTOMOSTRACA													
S	-	++	+	-	***	-	-	-	-	++	+	-	-
C	-	++	+	-	-	-	++	+	-	+	+	-	-
H'(s)	-	+	+	-	**	-	-	-	-	+	+	-	-
H'(z)	-	-	-	-	-	-	-	-	-	-	-	-	-
H' _z (s)	-	+++	+	-	***	-	-	-	-	+++	+	-	-
H'(f)	-	-	-	-	-	-	-	-	-	-	-	-	-
H' _f (s)	-	+	++	-	**	-	-	-	-	+	++	-	-
Q _J	-	++	+	-	***	-	-	-	-	++	+	-	-
Q _d	-	*	-	-	+	-	-	-	-	*	*	-	-
P	-	++	++	-	***	-	-	-	-	++	++	-	-
LIGHT TRAP - COLEOPTERA													
S	-	-	-	-	+	-	-	-	-	-	-	-	*
C	-	-	-	-	-	-	-	-	-	-	-	-	-
H'(s)	-	-	-	-	+	-	-	-	-	-	-	-	*
H'(z)	-	-	-	-	-	-	-	-	-	-	-	-	-
H' _z (s)	-	+	+	+	+	-	-	-	+	+	+	-	**
H'(f)	-	+	-	+	-	+	-	-	+	+	-	**	-
H' _f (s)	-	-	-	-	+	-	-	-	-	-	-	-	-
Q _J	-	-	-	-	+	-	-	-	-	-	-	-	*
Q _d	-	**	**	-	-	-	-	-	***	**	**	++	++
P	-	-	-	-	++	-	-	-	-	-	-	-	*
LIGHT TRAP - HEMIPTERA													
S	-	++	++	-	-	+++	-	-	-	++	++	**	-
C	-	++	+	-	-	+	-	-	-	-	-	**	-
H'(s)	-	++	+	-	-	+++	-	-	-	++	+	*	-
H'(z)	-	-	-	-	-	-	-	-	-	-	-	-	-
H' _z (s)	-	+++	++	-	-	+++	-	-	-	+++	++	*	-
H'(f)	-	-	-	-	-	-	-	-	-	-	-	-	-
H' _f (s)	-	-	++	-	-	++	-	-	***	-	++	**	*
Q _J	-	++	++	-	-	+++	-	-	-	++	++	**	-
Q _d	-	***	*	-	-	***	-	-	-	***	*	+	-
P	-	+	+++	-	-	+++	-	-	***	+	+++	*	-

Table 17. Summary of relationships between floral and faunal community parameters and salinity. † = both faunal and floral parameters associated with salinity and each other; ■ = faunal parameter associated with flora but not salinity; 0 = fauna associated with salinity but not flora; - = no associations. See Table 6 for description of parameters.

Plant Community		Faunal Community parameter											
Parameter	D	s	ti	H'(s)	H'(t)	H'(ti)	H' _t (s)	H' _t (i)	H' _{ti} (s)	Q _J (s)	Q _J (ti)	Q _d (s)	Q _d (ti)
WATER BOTTLE - ZOOPLANKTON													
s	-	0	0	-	†	-	-	-	-	0	0	0	-
c	-	†	†	■	0	■	■	-	■	0	0	0	-
H'(s)	-	†	0	-	†	-	-	-	-	†	0	0	-
H' _z (s)	-	†	0	-	†	-	-	-	-	†	0	0	-
H'(f)	-	0	0	-	0	-	-	-	-	0	0	0	-
H' _f (s)	-	†	†	-	†	-	-	-	-	†	†	0	-
Q _J	-	0	0	-	†	-	-	-	-	0	0	0	-
Q _d	-	†	0	-	†	-	-	-	-	†	0	0	-
P	-	†	†	-	†	-	-	-	-	†	†	0	-
SWEEP - COLEOPTERA													
s	■	-	■	-	-	-	-	-	-	-	■	■	■
c	■	-	-	-	-	-	-	-	-	-	-	-	■
H'(s)	■	-	■	-	-	-	-	-	-	-	■	■	■
H' _z (s)	■	-	-	-	-	-	-	-	-	-	-	-	-
H'(f)	-	-	-	-	-	-	-	-	-	-	-	-	-
H' _f (s)	-	-	-	-	-	-	-	-	-	-	-	-	-
Q _J	■	-	■	-	-	-	-	-	-	-	■	■	■
Q _d	■	-	-	-	-	-	-	-	-	-	-	■	■
P	-	-	-	-	-	-	-	-	-	-	-	-	-
SWEEP - HEMIPTERA													
s	0	†	†	†		†			0	†	†	†	■
c	0	0	0	0		0			†	0	0	0	■
H'(s)	0	†	†	†		†			0	†	†	†	■
H' _z (s)	0	†	†	0		†			0	†	†	†	■
H'(f)	0	0	0	†		0			0	0	0	†	-
H' _f (s)	0	0	†	0		†			0	0	†	0	■
Q _J	0	†	†	†		†			0	†	†	†	■
Q _d	0	†	0	†		†			0	†	0	†	■
P	0	†	†	0		†			†	†	†	0	-

Table 17. CONT.

Plant Community				Faunal Community parameter									
Parameter D	s	ti	H'(s)	H'(t)	H'(ti)	H't(s)	H't(i)	H'ti(s)	Qj(s)	Qj(ti)	Qd(s)	Qd(ti)	
LIGHT TRAP - ALL SPECIES													
s	-	†	†	-	0	-	-	-	-	†	†	0	0
c	-	0	†	-	0	-	-	-	-	0	0	0	0
H'(s)	-	†	†	-	0	-	-	-	-	†	†	†	0
H'z(s)	-	†	†	-	0	-	-	-	-	†	†	†	0
H'(f)	-	†	0	-	†	-	-	-	-	†	0	†	0
H'f(s)	-	0	0	-	0	-	-	-	-	0	0	0	0
Qj	-	†	†	-	0	-	-	-	-	†	†	0	0
Qd	-	†	†	-	†	-	-	-	-	†	†	†	0
P	-	0	†	-	0	-	-	-	-	0	†	0	0
LIGHT TRAP - ENTOMOSTRACA													
s	-	†	†	-	-	-	-	-	-	†	†	-	-
c	-	†	†	-	-	■	■	-	-	†	†	-	-
H'(s)	-	†	†	-	-	-	-	-	-	†	†	-	-
H'z(s)	-	†	†	-	-	-	-	-	-	†	†	-	-
H'(f)	-	0	0	-	-	-	-	-	-	0	0	-	-
H'f(s)	-	†	†	-	-	-	-	-	-	†	†	-	-
Qj	-	†	†	-	-	-	-	-	-	†	†	-	-
Qd	-	†	0	-	-	-	-	-	-	†	†	-	-
P	-	†	†	-	-	-	-	-	-	†	†	-	-
LIGHT TRAP - COLEOPTERA													
s	0	0	0	0	†	0	0	0	0	0	0	0	†
c	0	0	0	0	0	0	0	0	0	0	0	0	0
H'(s)	0	0	0	0	†	0	0	0	0	0	0	0	†
H'z(s)	0	†	†	†	†	0	0	0	†	†	†	0	†
H'(f)	0	†	0	†	0	†	0	0	†	†	0	†	0
H'f(s)	0	0	0	0	†	0	0	0	0	0	0	0	0
Qj	0	0	0	0	†	0	0	0	0	0	0	0	†
Qd	0	†	†	0	0	0	0	0	†	†	†	†	†
P	0	0	0	0	†	0	0	0	0	0	0	0	†
LIGHT TRAP - HEMIPTERA													
s	0	†	†	-	†	-	-	-	0	†	†	■	-
c	0	†	†	-	†	-	-	-	0	0	0	■	-
H'(s)	0	†	†	-	†	-	-	-	0	†	†	■	-
H'z(s)	0	†	†	-	†	-	-	-	0	†	†	■	-
H'(f)	0	0	0	-	0	-	-	-	0	0	0	-	-
H'f(s)	0	0	†	-	†	-	-	-	†	0	†	■	■
Qj	0	†	†	-	†	-	-	-	0	†	†	■	-
Qd	0	†	†	-	†	-	-	-	0	†	†	■	-
P	0	†	†	-	†	-	-	-	†	†	†	■	-

Table 18. Cophenetic correlation coefficients between faunal and floral dendrograms, and their relationship with salinity. * indicates significant relationships; other symbols are as in Table 17. N.B. Figs. 17d, 18b and 19c are omitted, see text for explanation.

Faunal Dendrogram	Floral dendrogram			
	presence/absence		relative abundance	
	Fig. 24a		Fig. 24b	
WATER BOTTLE Zooplankton				
Fig. 14a	0.162	0	0.087	0
Fig. 14b	0.049	0	0.007	0
Fig. 14c	0.505	-	0.548	-
Fig. 14d	0.114	-	0.227	-
LIGHT TRAPS Entomostraca				
Fig. 15a	0.130	0	0.107	0
Fig. 15b	0.209	-	0.235	0
Fig. 15c	0.005	-	0.206	-
Fig. 15d	0.147	-	0.087	-
All species				
Fig. 16a	0.034	-	0.086	0
Fig. 16b	0.166	0	0.159	0
Fig. 16c	0.804*	■	0.777-	
Fig. 16d	0.549	-	0.588	-
Coleoptera				
Fig. 17a	0.033	-	0.229	-
Fig. 17b	0.204	-	0.041	-
Fig. 17c	0.825*	■	0.772-	
Hemiptera				
Fig. 19a	0.070	0	0.056	0
Fig. 19b	0.257	-	0.339	-
Fig. 19d	0.201	-	0.046	-
SWEEP SAMPLES Coleoptera				
Fig. 18a	0.451	-	0.292	-
Fig. 18c	0.681	-	0.775	-
Fig. 18d	0.409	-	0.721	-
Hemiptera				
Fig. 20a	0.139	-	0.114	0
Fig. 20b	0.303	-	0.389	-
Fig. 20c	0.514	-	0.576	-
Fig. 20d	0.098	-	0.184	-

communities, virtually all faunal community parameters that are correlated with salinity are also correlated with several plant community parameters, namely s , t_i , $H'(t)$, $Q_J(s)$ and $Q_J(t_i)$ (Table 17). Only the super community index $Q_d(s)$ in the limnetic samples is associated with salinity and not the floral community. Additionally, various measures of zooplankton diversity [$H'(s)$, $H'(t)$, $H'_t(s)$, $H'_{t_i}(s)$, $H'_t(i)$] are associated with the amount of aquatic plant cover, but not salinity. As shown in Table 18, cluster diagrams of lakes based on zooplankton communities are not significantly correlated with those based on macrophytes, but those based on the presence or absence of zooplankton species or ecological categories are correlated with salinity.

When all species in light trap samples were considered, virtually all faunal community parameters that are correlated with salinity [s , t_i , $H'(t)$, $Q_J(s)$, $Q_J(t_i)$, $Q_d(s)$] are also correlated with several plant community parameters (Table 17). Only the super community index $Q_d(t_i)$ is correlated with salinity and not plants. The cluster diagram of animal species abundance is significantly correlated with the one based on the presence or absence of aquatic plant species, but no others are associated (Table 18).

Light trap and sweep net samples of Coleoptera present quite different patterns of association with macrophyte communities and salinity. Table 17 shows that parameters calculated for beetle communities sampled in light traps are all associated with salinity, and several show positive trends with plant community parameters. The density of Coleoptera caught in light traps is correlated with salinity but not with any aspects of the macrophyte community. Only the dendrogram based on Coleoptera species presence or absence is correlated with the plant community, and none are

correlated with salinity (Table 18). Community parameters calculated from sweep net samples of aquatic beetles show no correlations with salinity, but several parameters are associated with macrophyte community parameters (Table 17). Specifically, the density, richness, and diversity of plant communities are positively associated with the density, absolute and relative number of ecological categories, and super community complexity measures of coleopteran communities. Dendrograms drawn from sweep net Coleoptera are not correlated with those drawn from macrophyte assemblages or physiochemical properties (Table 18).

Hemiptera communities collected in sweep nets and light traps show similar patterns of association with macrophyte communities and salinity (Table 17). Hemipteran density is not correlated with aspects of the plant community, although it is correlated with salinity. Super community indices of community complexity are correlated with macrophyte community parameters, but not with salinity. The remaining parameters are related to both salinity and the floral community. The results presented in Table 18 show that no cluster diagrams based on Hemiptera assemblages are significantly correlated with those based on macrophytes.

Discussion

In Chapters 2 and 3, both animal and plant species were described as characteristic of high salinities ($>5000 \mu\text{S}$), of moderate or low salinities ($<5000 \mu\text{S}$), or tolerant of all salinities, and the distribution patterns of organisms among lakes was closely related to salinity. It is possible that faunal and floral species could have similar distribution patterns with respect to salinity, and/or plants could directly influence the

distribution of animals. Previous studies of the fauna in these Chilcotin lakes (Scudder & Mann, 1968; Scudder, 1969a; 1969b; Cannings & Scudder, 1978; Reynolds, 1979; Cannings et al., 1980; Scudder, 1983; Cannings & Cannings, 1985) established that the salinity gradient influences faunal distribution, but none have examined faunal distributions or community dynamics with respect to macrophyte communities. The marked difference in communities above and below 5000 μS may represent a critical point in the physiological tolerance levels of both flora and fauna, or it could indicate that animals are partially dependent upon the distribution of plants, which are physiologically constrained by salinities above this point.

The evidence demonstrates that faunal abundance, richness and diversity are frequently, but not always, associated with floral abundance, richness and diversity (Tables 16; 18). Furthermore, these parameters are frequently, but not always, associated with salinity (Tables 17; 18). Four types of associations among faunal communities, floral communities and salinity were observed. (1) Where faunal communities are not associated with floral communities or salinity, the observed pattern is presumably attributed to a factor or combination of factors not used in this study. (2) Associations of animal communities with salinity but not plant communities, indicate that water chemistry may be of primary importance determining the structure of animal communities. (3) In some instances, faunal communities are associated with floral communities, but not with salinity. This implies that macrophyte communities, but not salinity, may be important factors controlling the structure of arthropod communities. (4) Where both faunal and floral communities are associated with salinity and with each other, it is impossible to determine if the structure of

animal communities is affected primarily by salinity, by macrophyte communities which are themselves influenced by salinity, or by the combined effects of both.

This study used several schemes of classification, multivariate techniques, and numerical parameters to characterize and compare the structure of faunal communities, floral communities, and salinity. No one method of was sufficient to summarize the relationships, rather, all contributed some information to characterizations and all were necessary to provide a complete picture of the associations.

Particular groups of animals showed different patterns of association with plant communities and salinity therefore, these subcommunities must be examined separately. In the discussion to follow, the relationships of the four faunal groups (zooplankton, Coleoptera, Hemiptera, all species) with floral communities and salinity, are considered separately. Some possible mechanisms producing the observed patterns are hypothesized. One must remember, however, that field studies can indicate correlations between the biota and abiota, and controlling mechanisms can be hypothesized, but detailed investigations of causal relationships require an experimental approach.

ZOOPLANKTON COMMUNITIES

Associations between faunal and floral community parameters demonstrate that zooplankton richness and diversity decreased with decreasing macrophyte abundance, richness and diversity. Other studies have reported similar patterns in zooplankton communities (Smyly, 1952; 1953; 1957; Whiteside & Harmsworth, 1967; Quade, 1969; Shiel, 1976; Fry & Osborne, 1980; Blancher, 1984; Richard et al., 1985), but many authors do

not explain possible causes of the patterns and the literature on the subject are frequently contradictory.

My data support the hypothesis, proposed in Chapter 2, that mechanisms controlling zooplankton community structure in the Becher's Prairie lakes, are related to the available food supply and nutritional requirements of inhabiting species. Changes in the composition and structure of zooplankton communities observed with decreasing salinity in the study lakes are analogous to those reported with increasing eutrophication (Patalas, 1972; McNaught, 1975; Allan, 1976; Gliwicz, 1977; Gannon & Stemberger, 1978; Fry & Osborne, 1980; Richard et al., 1985) (for further discussion see Chapter 2). The evidence that lake productivity decreased with increasing salinity (Chapter 3), and that the same zooplankton community parameters that were negatively correlated with salinity are positively correlated with the abundance, richness and diversity of macrophyte communities (Table 16; 17), further support this hypothesis. Although my results are consistent with the hypothesis, the evidence is largely circumstantial and a rigorous experimental approach is required to definitively test the mechanisms controlling zooplankton community structure.

Additionally, there is some evidence that habitat preference may play an important role in structuring zooplankton communities. The percent of each lake covered by aquatic vegetation is positively associated with the absolute and relative number of zooplankton species and ecological categories, and with virtually all diversity measures (Tables 16; 17). Although percent cover is negatively associated with salinity (Chapter 3), several of these faunal parameters are not. This suggests that the amount of plant cover may affect some aspects of zooplankton community structure

that salinity does not, although salinity may ultimately be responsible for structuring aquatic macrophyte communities. There are many ways in which aquatic plant communities could influence zooplankton communities.

In the study lakes, littoral species of Cladocera, such as Chydorus sphaericus, Scapholeberis kingi and Alona spp., were more common in freshwater lakes than saline ones. This may be a phenomenon attributable to increased eutrophication in freshwater lakes relative to saline ones (Gannon & Stemberger, 1978), or it may be because freshwater lakes have relatively more macrophyte cover than saline ones. It is well known that littoral species, such as the Chydoridae, are profoundly affected by the composition and dynamics of littoral macrophyte communities (Whiteside & Harmsworth, 1967; Quade, 1969; Goulden, 1971; Shiel, 1976; Whiteside et al., 1978). Most chydorids are poor swimmers and remain in close contact with the substrate, hence they seldom occur where there is no substrate (animate or inanimate). Chydorus sphaericus, the most widespread chydorid, is the only species showing consistent swimming behaviour and is often found among the off-shore plankton, but even it shows a preference for vegetated habitats (Whiteside et al., 1978). Not all littoral species are restricted by simple substrate requirements. For example, Scapholeberis kingi feeds on the neuston [microscopic components of the interface habitat between air and water (Wetzel, 1975)] which is most extensive in sheltered, quiet waters common in littoral vegetation (Quade, 1969). In the study lakes, S. kingi was relatively more abundant in light traps set in the littoral, than in van Dorn bottles set in the limnetic zone, and was found only in lakes with extensive submerged vegetation.

COLEOPTERAN COMMUNITIES

The distribution of Coleoptera species encountered in the study lakes corresponded to their habitat preference in relation to macrophyte communities. There are few studies on the ecology of aquatic coleopteran communities in North America, and most of the information is contained in primarily systematic treatments of various taxa (Wallis, 1933; Hatch, 1953; 1965; 1971; Anderson, 1971; Larson, 1975; Anderson, 1976; 1983). The available data, however, suggest that all the species encountered in this study were found in lakes typical of their preferred habitat. For example, Laccobius biguttatus, Hygrotus sayi, H. lutescens, Ilybius spp. and Graphoderus spp. are typical inhabitants of vegetated ponds (Larson, 1975; 1985), and were found only in the more freshwater lakes which support extensive macrophyte cover. Conversely, Hygrotus masculinus shows a preference for saline ponds with bare bottoms and without vegetation (Larson, 1975; 1985), and was found only in more saline lakes which support relatively little vegetation. The curculionid, Litodactylus griseomicans, was abundant in Lake 2 and one specimen was found in Lake 3. This species is probably restricted by the distribution of its host plant Myriophyllum (Hatch, 1971) which occurred in extensive mats in Lake 2 and in very small amounts in Lake 3, but in no other lake of the series (Table 12). In addition, dendrograms arranging lakes on the basis of the relative abundance of beetle species collected in light traps are significantly correlated with those based on the presence or absence of macrophyte species (Table 18). These observations may reflect the influence of plant distributions on beetle distributions, or simply that beetles and plants have similar distribution patterns with respect to some other factor such as salinity.

The Coleoptera collected in sweep nets and light traps present quite different patterns of association with macrophyte communities and salinity. No community parameters calculated from sweep net samples are correlated with salinity, but the density, absolute and relative number of ecological classes, and super community complexity measures are positively correlated with several macrophyte community parameters (Tables 16; 17). But, generalizations drawn from sweep net samples of Coleoptera are questionable because total density and relative abundance of beetles were low and very variable in these samples (Chapter 2). Therefore, although sweep samples suggest that the structure of beetle communities may be influenced by macrophyte communities, no definite conclusions can be drawn from sweep net samples without more reliable data.

Evidence indicates that salinity may be of primary importance in controlling coleopteran community structure, and macrophytes may have some secondary influence. All community parameters calculated from light trap collections of Coleoptera are associated with salinity, and some are associated with macrophyte community parameters (Tables 16; 17). This is contrary to observations of Cuppen (1983) and van Vierssen & Verhoeven (1983) that habitat structure and the presence of plants play a greater role than chemical factors in influencing aquatic beetle communities. If macrophytes did affect the structure of Coleoptera communities in these study lakes, it was in such a way that coleopteran richness and diversity increased with increasing macrophyte diversity (Table 17). Wilson (1923) suggests that this association existed in Iowa fishponds, but no study has closely examined the ecological relationships between aquatic macrophytes and Coleoptera.

Contrary to predictions, coleopteran density in light trap collections

of this study is not correlated with percentage macrophyte cover. There are two opposing hypotheses of how the percentage vegetation cover present in a lake can influence the density of aquatic Coleoptera. (1) Wilson (1923) and Aiken & Wilkinson (1985) suggest that the greatest density of diving beetles should occur in the absence of aquatic plant growth because very dense vegetation makes swimming and surfacing to breathe very difficult for these animals. (2) Alternatively, Wilson (1923) observed that coleopteran density increased with increasing macrophyte cover, and attributed this to increased habitat heterogeneity. Coleopteran density in light trap samples of this study is not correlated with macrophyte cover (Tables 16; 17), although it is positively related to salinity and there is a trend for decreasing macrophyte abundance with increasing salinity. It is possible that the two opposing processes, mentioned above, were both operating in the study lakes, with the net result that there is no apparent association between macrophyte cover and beetle density. Alternatively, vegetation cover may have no influence on aquatic beetle communities. It may simply be that the few Coleoptera species adapted to high salinities occurred in enormous numbers owing to lack of competition and predation (Beadle, 1943; Simberloff & Wilson, 1974) as suggested in Chapter 2.

HEMIPTERAN COMMUNITIES

The results suggest that both salinity and macrophyte community structure may have influenced the structure of hemipteran communities. Similar patterns of hemipteran community structure were provided in both light trap and sweep net samples (Tables 16; 17; 18). A marked difference was seen in hemipteran community composition between lakes with conductivities above and below 5000 μS (Chapter 2). This may represent a

critical point of salinity tolerances for Hemiptera, as suggested above, or it may be because Hemiptera were influenced by the macrophyte community which changed dramatically at this point (Chapter 3). A distinct ecological succession of corixid species with decreasing salinity, and increasing vegetation cover and accumulation of organic matter has been observed in Europe (Macan, 1938; Savage, 1971; van Vierssen & Verhoeven, 1983), and although a succession is suggested in this study (Chapter 2), none has previously been recorded in North America.

Aquatic Hemiptera, especially Corixidae, are typical inhabitants of the littoral zone and are dependent on its physical structure. Their external air stores used for respiration make them extremely buoyant and therefore they must cling to various submerged objects (such as vegetation) to prevent from bobbing to the surface (Scudder, 1976). Their dependence on external air stores, which need to be renewed periodically, restricts them to rather shallow waters (Scudder, 1976). Consequently, a positive correlation between percentage vegetation cover and hemipteran density is predicted because a more extensive area of suitable habitat would potentially support more individuals. No such correlation was found in this study, perhaps because macrophyte abundance never dropped below a critical point at which it was limiting, and/or because enough inanimate substrate were available. Density is, however, negatively related to salinity which suggests that the few species adapted to high salinities occurred in enormous numbers owing to lack of competition and predation (Beadle, 1943; Simberloff & Wilson, 1974) as was suggested in Chapter 2.

Increased macrophyte diversity may have contributed to increased hemipteran richness and diversity in the study lakes, as all parameters of hemipteran community structure are correlated with the macrophyte community

(Table 16). It is possible that species rich or diverse hemipteran communities were found in dense, rich or diverse plant communities because (1) prey organisms were more abundant in such habitats, (2) plants provided protection from predators (Macan, 1965), or (3) a more diverse substrate was available for holding on to. This later suggestion may account for the wide variety of hemipteran size groups in lakes with diverse plant assemblages if body size is an important factor in substrate preference. My data, however, indicate correlations between hemipteran communities and both macrophyte communities and salinity. Thereby making it impossible to distinguish between causal mechanisms related to plant community structure (above), or salinity (Chapter 2). More detailed investigations are required to distinguish between the processes and examine causal relationships.

ENTIRE FAUNAL COMMUNITY

My data indicate that the structure of the entire faunal community, as represented by all animals caught in light traps, is related to both salinity and the macrophyte community. The relative abundance of animal species differed markedly among lakes in relation to salinity (Fig. 8a), and the dendrogram arranging lakes on the basis of animal species relative abundance is significantly correlated with the dendrogram based on presence or absence of plant species (Table 18). For the most part, the same faunal community parameters that were negatively correlated with salinity are positively correlated with the abundance, richness and diversity of macrophyte communities (Tables 16; 17). These patterns of association are very similar to those of the entomostracan subcommunity, but those of the Coleoptera and Hemiptera were hidden. This demonstrates that numerically

dominant subgroups can dictate patterns observed for the entire community and mask important patterns in other subgroups, as was also seen in Chapter 2. Other studies have reported similar patterns of association between floral communities and the entire faunal community (Krecker, 1939; Rosine, 1955; Harrod, 1964; Petr, 1968; Krull, 1970; Soszka, 1975a; 1975b; Brock & Shiel, 1983), but because the observed patterns are also related to salinity, it is impossible to determine whether salinity and/or plant communities may be of primary importance in structuring the entire faunal community.

Summary

This fourth chapter briefly discusses some of the many ways in which aquatic macrophytes can directly or indirectly influence the distribution and survival of aquatic fauna. Ecological relationships between faunal and floral communities were tested for in the Becher's Prairie study lakes by comparing the faunal and floral communities characterized in Chapters 2 and 3 respectively, and summarizing their relationships with reference to salinity. Evidence indicates that both salinity and macrophyte communities may have played a role in structuring zooplankton, coleopteran, hemipteran, and the entire faunal community. Particular groups of animals show different patterns of association with plant communities and salinity therefore, these subcommunities must be examined separately. Zooplankton richness and diversity decreased with decreasing macrophyte abundance, richness and diversity. Evidence supports the hypothesis that mechanisms controlling zooplankton community structure are related to the available food supply and nutritional requirements of inhabiting species. There is

also some evidence that habitat preference may play a role in structuring zooplankton communities. Salinity may be of primary importance in controlling coleopteran community structure, and macrophytes may have some secondary influence. Contrary to predictions, coleopteran density is not correlated with percent macrophyte cover. Hemipteran richness and diversity increased with increased macrophyte diversity, although it was impossible distinguish between the possible influence of macrophyte communities and salinity.

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APPENDIX A

Seasonal conductivity ($\mu\text{S cm}^{-1}$, 25 °C) at 1 m depth in the study lakes in 1978. (See Fig. 1 for lake names).

Date	Lakes							
	1	2	3	4	5	6	7	8
6-8 May	72	913	1253	2233	3706	6335	7356	7629
5-7 June	58	980	1362	2589	4441	7761	9945	11989
5-7 July	57	913	1457	2852	4564	8446	10490	13214
4-5 Aug.	53	933	1501	2866	4777	8956	11420	14852
3-5 Sept.	49	918	1568	2986	4881	9106	11449	15524
14-15 Oct.	45	933	1483	3027	4892	9083	11532	15481
mean	56	932	1437	2759	4544	8281	10365	13115
range	27	67	315	794	1186	2771	4176	7895
maximum	72	980	1568	3027	4892	9106	11532	15524

APPENDIX B

B.1 Abundance of zooplankton species and ecological categories in Van Dorn bottle samples, (#/2 l summed over entire season). (See Fig. 1 for lake names; Table 7 for species names; text for category description).

	Lake							
	1	2	3	4	5	6	7	8
SPECIES								
2	-	-	-	76	36	-	-	-
3	-	-	-	-	-	356	406	179
4	860	-	-	-	-	-	-	-
5	-	499	1105	1155	2180	-	-	-
6	94	-	-	-	-	-	-	-
7	9	-	-	1	2	-	-	-
8	1	-	-	-	-	-	-	-
9	21	71	1	1645	25	-	1	-
10	-	-	-	-	-	-	-	179
12	11	-	-	-	-	-	-	-
13	4	2	1	12	-	-	-	-
14	31	1	-	146	1	-	-	-
17	17	4	1	-	-	-	-	-
18	-	-	-	-	-	69	37	10
19	-	-	-	1069	-	1376	1946	1147
20	-	39	-	386	-	-	-	-
21	161	-	-	229	231	-	-	-
22	-	-	-	131	251	-	-	-
23	8	1	-	-	3	-	-	-
#	-	-	18	-	-	-	-	-
77	105	74	63	1	31	-	-	-
79	11	3	1	121	1	-	1	-
ECOLOGICAL CATEGORIES								
b1	35	2	1	258	1	-	-	-
b3	126	71	1	1714	25	1376	1946	1147
b4	877	513	1106	1155	2180	-	-	179
b5	-	-	-	-	-	356	406	179
b6	9	-	-	1	2	-	-	-
b7	-	-	-	76	36	-	-	-
c1	-	39	-	386	-	-	-	-
e3	161	-	18	360	482	-	-	-
e4	8	1	-	-	3	-	1	-
e6	-	-	-	-	-	69	37	10
e8	116	77	64	122	32	-	-	-

B.2 Abundance of species and ecological categories in submerged light traps, (#/5 trap nights). (See Fig. 1 for lake names; Table 7 for species names; text for category description).

	lake							
	1	2	3	4	5	6	7	8
SPECIES								
1	-	-	-	-	-	-	36	24
2	-	-	-	54476	7072	-	-	-
3	-	-	-	-	-	243753	247616	71960
4/6 14453	-	-	-	-	-	-	-	-
5	-	163662	856252	356416	234161	-	-	-
7	795	737	272	2788	3596	16	-	-
8	13	100	868	48	-	-	-	-
9	32	8359	1044	70116	22415	8	-	-
10	-	-	-	-	-	-	-	3480
11	-	-	56	1268	-	-	-	-
13	58	6	-	20	-	-	-	-
14	146	181	244	2418	-	-	-	-
15	583	-	-	52	-	-	-	-
16	95	11	16	-	-	-	-	-
17	396	14	1148	-	-	-	-	-
18	-	-	-	-	-	24480	71040	24093
19	-	-	-	35327	-	720	3320	50431
21/22	52	155	244	8912	8641	16	-	20
23	547	536	-	36	580	-	-	-
24	-	800	134	3628	1781	-	-	-
25	-	443	35	-	79	-	-	-
26	1	-	-	-	-	-	-	-
27	1	-	-	-	-	-	-	-
28	2	-	-	-	-	-	-	-
29	15	31	32	88	9	45	11	-
30	3	11	-	-	25	1	-	-
31	8	-	16	-	-	-	-	-
32	27	160	436	464	83	65	4	64
33	1	-	-	-	-	-	-	-
34	1	-	-	-	-	-	-	-
35	3	-	-	-	-	-	-	1
36	34	82	154	8	22	-	-	-
37	3	3	-	-	-	-	-	-
38	5	331	27	4	-	-	-	-
39	-	-	-	-	-	942	319	168
40	139	22	-	40	103	-	-	-
41	56	217	79	509	95	5	-	-
42	166	179	1048	2104	656	762	620	3206
43	-	-	-	-	-	636	925	15571
44	62	2	-	-	-	-	-	-

B.2 CONT.

	Lake							
	1	2	3	4	5	6	7	8
45	1	2	-	-	-	-	1	-
46	-	28	98	128	111	11	1	-
47	21	-	-	-	-	-	-	-
48	5	-	-	-	-	-	-	-
49	2	-	-	-	-	-	-	-
50	2	13	5	12	4	2	-	-
51	17	2	-	4	-	-	-	-
52	-	-	-	-	-	65	458	1861
55	16	-	-	-	-	-	-	-
56	-	-	-	-	-	3	2	-
57	29	1	-	-	-	77	-	-
59	7	-	-	-	3	-	-	-
60	3	3	-	-	-	-	-	-
61	5	7	-	-	-	-	-	-
62	2	294	51	-	309	-	-	-
63	2	-	-	-	-	-	-	-
64	-	5	-	-	-	-	-	-
72	1	-	-	-	-	-	-	-
73	4	4	-	196	-	107	15	-
74	-	-	-	-	-	32	-	2000
75	-	-	-	-	35	-	-	-
76	-	-	-	-	12	-	-	-
77	954	8100	4700	48	311	-	-	-
78	26	84	-	-	-	32	52	20
79	12	-	-	7	-	-	-	-
80	79	214	2346	943	1124	18	34	1196
81	1	16	-	-	-	-	18	-
82	2	-	404	255	427	16	-	20
83	149	-	-	-	-	-	-	-
84	16	-	-	-	-	-	-	-
ALL ECOLOGICAL CATEGORIES								
a5	63	32	98	128	111	11	2	-
a6	21	-	-	-	-	-	-	-
a8	8	4	-	196	-	107	15	-
b1	204	187	244	2438	-	-	-	-
b2	13	100	924	1316	-	-	-	-
b3	14485	8359	1044	105443	22415	728	3320	50431
b4	396	163676	857400	356416	234161	-	-	3480
b5	795	737	272	2788	3596	243769	247616	71960
b6	-	-	-	54476	7072	-	-	-
b8	-	-	-	-	47	32	-	2000
b10	-	-	-	-	-	-	36	24

B.2 CONT.

	Lake							
	1	2	3	4	5	6	7	8
c2	1	-	-	-	-	-	-	-
c3	678	1	16	52	-	-	-	-
c6	1	-	-	-	-	-	-	-
c7	15	831	166	3716	1790	45	11	-
c8	82	230	2750	1198	1551	34	52	1216
c9	2	-	-	-	-	-	-	-
c10	-	443	35	-	79	-	-	-
e3	52	155	244	8912	8641	16	-	20
e4	547	536	-	36	580	-	-	-
e5	19	2	-	4	-	-	-	-
e6	23	13	5	12	4	24547	71498	25954
e7	201	1	-	-	3	80	2	-
e8	1005	8488	4751	55	620	35	52	20
e9	1	-	-	-	-	-	-	-
e10	42	176	452	464	108	66	4	64
f7	310	532	1075	2148	759	2340	1864	18945
f8	56	217	79	509	95	5	-	-
f9	37	85	154	8	22	-	-	-

ENTOMOSTRACAN ECOLOGICAL CATEGORIES

b1	204	187	244	2438	-	-	-	-
b3	14498	8459	1968	106759	22415	728	3320	50431
b4	396	163676	857400	356416	234161	-	-	3480
b5	-	-	-	-	-	243753	247616	71960
b6	795	737	272	2788	3596	16	-	-
b7	-	-	-	54476	7072	-	-	-
e3	52	155	244	8912	8641	16	-	20
e4	547	536	-	36	580	-	-	-
e6	-	-	-	-	-	24480	71040	24093

COLEOPTERAN ECOLOGICAL CATEGORIES

a1	63	32	98	128	111	11	2	-
a2	21	-	-	-	-	-	-	-
e1	11	1	-	4	-	-	-	-
e2	11	-	-	-	-	65	447	1845
e3	1	8	4	12	4	5	2	-
e4	21	1	-	-	3	77	-	-
e5	8	181	27	-	198	-	-	-
e8	1	3	-	-	-	-	-	-

B.2 CONT.

	Lake							
	1	2	3	4	5	6	7	8
HEMIPTERAN ECOLOGICAL CATEGORIES								
f4	141	309	689	1276	403	844	766	1738
f5	30	73	52	276	86	5	-	-
f6	37	85	154	8	22	-	-	-

B.3 Abundance of adult Hemiptera and Coleoptera in sweep net samples, (#/10 standard sweeps summed over entire season). (See Fig. 1 for lake names; Table 7 for species names; text for category description).

	Lake							
	1	2	3	4	5	6	7	8
SPECIES								
36	79	467	54	2	21	33	-	2
37	32	3	-	-	-	-	-	-
38	-	161	6	3	3	-	-	-
39	-	-	-	-	-	6	1	-
40	155	15	17	-	12	-	-	-
41	202	98	92	133	211	3	-	-
42	36	54	704	1270	408	3601	128	4247
43	-	-	-	-	-	506	24	3854
44	114	5	1	7	28	19	1	12
45	-	9	3	-	4	3	-	2
46	-	11	20	77	27	-	1	-
47	8	-	-	-	-	-	-	-
48	4	20	-	-	-	-	-	-
49	21	-	3	-	-	3	-	-
50	-	-	1	9	-	-	-	-
51	25	-	3	2	3	-	-	-
52	-	-	-	-	-	2	27	24
53	-	-	3	-	-	-	-	-
54	-	-	-	-	-	1	-	-
55	7	-	-	-	-	-	-	-
56	-	-	-	-	-	1	-	8
57	-	-	-	-	-	3	-	-
58	-	-	-	-	-	2	-	6
59	-	-	-	-	2	3	-	-
60	-	7	-	-	-	-	-	-
61	-	-	-	-	4	-	-	-
62	-	120	9	7	44	4	-	3
64	-	7	-	-	7	-	-	-
65	2	-	-	-	-	-	-	-
66	2	-	-	-	-	-	-	-
67	-	3	-	-	-	-	-	-
68	-	-	-	-	-	10	5	-
69	-	-	-	-	12	-	-	9
70	-	141	2	-	-	-	-	-
71	-	76	2	-	-	-	-	-
COLEOPTERAN ECOLOGICAL CATEGORIES								
a1	114	111	26	83	58	32	7	17
a2	3	141	2	-	-	-	-	-

B.3 CONT.

	Lake							
	1	2	3	4	5	6	7	8
a3	-	-	-	-	12	-	-	9
e1	46	-	7	2	3	3	-	-
e2	11	20	3	-	-	3	27	24
e3	-	-	1	9	-	1	-	8
e4	-	-	-	-	2	8	-	7
e5	2	127	9	7	32	19	1	12
e6	2	3	-	-	-	-	-	-
e8	-	7	-	-	7	-	-	-
HEMIPTERAN ECOLOGICAL CATEGORIES								
f4	191	229	727	1274	424	4113	153	8101
f5	202	98	92	133	211	3	-	-
f6	111	470	54	2	21	33	-	2

APPENDIX C

Pearson's product-moment correlation coefficients between faunal community parameters. (See Table 6 for symbol description).

WATER BOTTLE ZOOPLANKTON

[illegible]

SWEEP HEMIPTERA

[illegible]

APPENDIX D

Pearson's product-moment correlation coefficients between faunal community parameters and physiochemical variables. See Table 6 for description of community parameter symbols;
 k_{25} = conductivity; z = mean depth.

Variable	D	Community parameter											
		s	ti	H'(s)	H'(t)	H'(ti)	H' _t (s)	H' _t (i)	H' _{ti} (s)	Q _J (s)	Q _J (ti)	Q _d (s)	Q _d (ti)
WATER BOTTLE - ZOOPLANKTON													
k ₂₅	.037	-.792	-.660	-.374	-.848	-.321	.052	.316	-.454	-.792	-.660	.528	.335
logk ₂₅	.270	-.749	-.489	-.393	-.651	-.409	-.102	.029	-.309	-.751	-.496	.647	.246
PC1	.021	-.789	-.696	-.322	-.627	-.259	.010	.297	-.432	-.789	-.696	.489	.551
PC2	.058	.085	.364	-.234	.072	-.276	-.357	-.423	-.106	.087	.364	.132	-.027
z	.048	-.880	-.780	-.548	-.848	-.533	-.182	.033	-.517	-.880	-.780	.616	.351
D _{LA}	-.478	.538	.509	.050	.623	.084	-.337	-.432	-.038	.539	.509	-.118	.123
SWEEP - COLEOPTERA													
k ₂₅	-.559	-.338	-.265	.068	-.286	.217	.041	.341	-.232	-.338	-.265	.463	.285
logk ₂₅	-.505	-.209	-.317	.106	-.266	.160	.164	.169	-.055	-.232	-.345	.584	.352
PC1	-.546	-.357	-.272	.036	-.328	.202	.014	.336	-.274	-.357	-.272	.455	.276
PC2	-.019	.098	.229	.335	.292	.296	.326	.257	.190	.098	.229	-.092	-.148
z	-.685	-.115	-.313	.085	-.095	.049	.009	.086	.093	-.115	-.313	.513	.564
D _{LA}	.814	.452	.553	.316	.569	.302	.212	.179	.142	.452	.553	-.779	-.784
SWEEP - HEMIPTERA													
k ₂₅	.699	-.774	-.725	-.544		-.867			.786	-.774	-.725	.429	.551
logk ₂₅	.490	-.557	-.500	-.790		-.850			.343	-.572	-.528	.668	.523
PC1	.737	-.790	-.724	-.535		-.879			.825	-.790	-.724	.365	.516
PC2	-.049	.028	.015	.151		.185			-.110	.028	.015	.285	.084
z	.418	-.533	-.574	-.723		-.884			.520	-.533	-.574	.518	.690
D _{LA}	-.390	.710	.451	.894		.906			-.277	.710	.451	-.595	-.703

APPENDIX D CONT.

														Community parameter									
Variable D		s	ti	H'(s)	H'(t)	H'(ti)	H' _t (s)	H' _t (i)	H' _{ti} (s)	Q _J (s)	Q _J (ti)	Q _d (s)	Q _d (ti)										
LIGHT TRAP - ALL SPECIES																							
k ₂₅	-.195	-.781	-.901	.282	-.212	.324	.505	.581	-.205	-.780	-.901	.712	.550										
logk ₂₅	.208	-.963	-.915	-.057	-.643	-.032	.325	.391	-.272	-.964	-.919	.938	.622										
PC1	-.213	-.731	-.872	.326	-.166	.363	.535	.603	-.131	-.730	-.872	.662	.499										
PC2	-.087	-.254	-.140	.023	.041	.064	.005	.059	-.374	-.249	-.137	.171	.178										
z	.086	-.788	-.874	-.213	-.605	-.184	.091	.160	-.420	-.788	-.875	.837	.716										
D _{LA}	-.328	.625	.645	-.080	.514	-.061	-.419	-.424	-.229	.625	.645	-.539	-.128										
LIGHT TRAP - ENTOMOSTRACA																							
k ₂₅	-.205	-.813	-.764	.439	.906	.302	-.031	-.312	.554	-.812	-.789	.388	.270										
logk ₂₅	.200	-.634	-.526	.280	.580	.201	-.024	-.195	.336	-.651	-.587	.196	-.063										
PC1	-.223	-.760	-.635	.459	.695	.307	-.103	-.366	.599	-.760	-.789	.364	.387										
PC2	-.091	-.342	.025	.088	.015	.128	.108	.143	-.025	-.346	.092	.123	-.072										
z	.088	-.786	-.733	.026	.764	-.012	-.396	-.533	.093	-.787	-.848	.473	.259										
D _{LA}	-.329	.324	.432	-.356	-.577	-.314	-.065	.078	-.309	.324	.515	.154	.191										
LIGHT TRAP - COLEOPTERA																							
k ₂₅	.736	-.626	-.715	-.680	-.863	-.663	-.409	-.346	-.558	-.626	-.715	.587	.790										
logk ₂₅	.465	-.868	-.866	-.832	-.727	-.781	-.700	-.634	-.832	-.861	-.861	.913	.867										
PC1	.751	-.583	-.692	-.656	-.900	-.646	-.354	-.294	-.502	-.583	-.692	.539	.751										
PC2	.179	-.238	-.145	-.127	.281	-.088	-.344	-.328	-.287	-.239	-.145	.195	.177										
z	.276	-.602	-.613	-.516	-.707	-.460	-.278	-.182	-.639	-.602	-.613	.654	.798										
D _{LA}	-.995	.645	.666	.537	.676	.477	.326	.215	.673	.645	.666	-.581	-.654										
LIGHT TRAP - HEMIPTERA																							
k ₂₅	.548	-.852	-.944	-.314		-.946			.645	-.852	-.944	.523	.415										
logk ₂₅	.607	-.837	-.663	-.598		-.815			.297	-.844	-.679	.216	-.016										
PC1	.584	-.806	-.960	-.262		-.951			.691	-.806	-.960	.493	.406										
PC2	-.174	-.289	.076	-.348		.082			-.352	-.289	.076	.199	.157										
z	.331	-.829	-.777	-.286		-.926			.648	-.829	-.777	.627	.369										
D _{LA}	-.675	.642	.602	.514		.824			-.372	.642	.602	-.394	.068										

APPENDIX E

Mean conductivity ($\mu\text{S cm}^{-1}$, 25 °C) of each study lake in 1983.
(See Fig. 1 for lake names).

	Lake							
	1	2	3	4	5	6	7	8
Conductivity	42	740	1443	2723	4443	8067	10667	12117

Seasonal conductivity ($\mu\text{S cm}^{-1}$, 25 °C) at 1 m depth in the study lakes in 1984. (See Fig. 1 for lake names).

	Lake							
Date	1	2	3	4	5	6	7	8
12 May	90	942	1594	2681	4638	8406	10870	13478
13 June	67	913	1638	2826	4812	8696	11449	13913
7 July	36	1014	2029	3130	5145	9130	12174	14928
12 August	101	1014	1812	3478	5406	9783	12899	15797
14 September	29	899	1739	3072	5072	10724	12319	14782
mean	65	956	1762	3038	5014	9348	11942	14580
range	72	115	435	797	768	2318	2029	2319
maximum	101	1014	2029	3478	5406	10724	12899	15797

APPENDIX F

Relative abundance of macrophyte species, estimated on the Braun-Blanquet scale, at mid-summer, in each of several lake zones classified according to the scheme of Runka & Lewis (1981).

Braun-Blanquet classes of cover:

+	= 0-1 %	3	= 25-50 %
1	= 1-5 %	4	= 50-75 %
2	= 5-25 %	5	= 75-100 %

Lake zones:

SOW	= Shallow open water
MAR	= Marsh

LAKE 1 (Box 27)

Species	zone	
	SOW 1	MAR 1
<u>Drepanocladus</u> sp.		2
<u>Potamogeton natans</u>	3	2
<u>Polygonum amphibium</u>	+	+
<u>Sagittaria cuneata</u>		1
<u>Sparganium</u> sp.	+	
<u>Utricularia vulgaris</u>	+	
<u>Carex rostrata</u>		+
<u>Eleocharis palustris</u>		1
<u>Glyceria borealis</u>		2
Area (m ²)	11160	10868

LAKE 2 (Barkley L.)

Species	zone	
	SOW 1	MAR 1
<u>Ceratophyllum demersum</u>	1	
Filamentous algae	+	
<u>Lemna minor</u>	+	+
<u>Myriophyllum exalbescens</u>	4	
<u>Potamogeton richardsoni</u>	+	
<u>P. pusillus/berchtoldi</u>	2	
<u>P. pectinatus</u>	2	
<u>Polygonum amphibium</u>		1
<u>Beckmannia szygachne</u>		1
<u>Eleocharis palustris</u>		2
<u>Juncus balticus</u>		+
<u>Scirpus lacustris</u>		2
Area (m ²)	25173	3885

LAKE 3 (Near Opposite Crescent)

Species	zone		
	SOW 1	SOW 2	MAR 1
<u>Aphanozomenon flosaquatis</u>	2		
Filamentous algae sp.	+		
<u>Myriophyllum exalbescens</u>	+		
<u>Potamogeton pectinatus</u>	3		
<u>P. pusillus/berchtoldi</u>	1		
<u>Carex lanuginosa</u>			+
<u>C. atherodes</u>			+
<u>Eleocharis palustris</u>			1
<u>Juncus balticus</u>			2
<u>Scirpus lacustris</u>			3
Area (m ²)	4670	18784	1444

LAKE 4 (Rock L.)

Species	zone			
	SOW S	SOW 1	SOW 2	MAR 1
Filamentous algae sp	2		2	
<u>Potamogeton pectinatus</u>	+	3	+	
<u>Ruppia occidentalis</u>	4	2	4	
<u>Juncus balticus</u>				+
<u>Scirpus lacustris</u>				3
<u>S. americanus</u>				1
Area (m ²)	5516	12208	237229	16782

APPENDIX F CONT.

LAKE 5 (Jackson L.)

Species	zone			
	SOW S	SOW 1	SOW 2	MAR 1
<u>Aphanozomenon flosaquatis</u>			3	
<u>Filamentous algae sp</u>	3	3		
<u>Potamogeton pectinatus</u>	1	1		
<u>Ruppia occidentalis</u>	1	1		
<u>Juncus balticus</u>				2
<u>Scirpus lacustris</u>				1
Area (m ²)	641	26866	28890	1116

LAKE 6 (L. Lye)

Species	zone			
	SOW S	SOW 1	MAR 1	
<u>Filamentous algae sp.</u>	1	1		
<u>Juncus balticus</u>				2
<u>Scirpus lacustris</u>				+
Area (m ²)	10638	334292	2131	

LAKE 7 (Round-Up L.)

Species	zone	
	SOW S	SOW 1
Area (m ²)	408	220888

LAKE 8 (Barnes L.)

Species	zone			
	SOW S	SOW 1	SOW 2	MAR 1
<u>Ruppia occidentalis</u>	2	2		
<u>Distichlis stricta</u>				2
<u>Hordeum jubatum</u>				+
<u>Juncus balticus</u>				3
<u>Scirpus lacustris</u>				+
Area (m ²)	8632	18834	150516	3362

APPENDIX G

Pearson's product-moment correlation coefficients between aquatic macrophyte community parameters. See text for explanation of symbols.

	community parameter								
	s	% cover	H'(s)	H'(z)	H' _z (s)	H'(f)	H' _f (s)	Q _j	Q _d
k ₂₅	-.791	-.678	-.720	-.025	-.913	-.478	-.625	-.825	.782
logk ₂₅	-.689	-.169	-.715	-.194	-.810	-.830	-.380	-.694	.847
PC1	-.768	-.646	-.734	-.051	-.863	-.411	-.652	-.757	.730
PC2	-.067	-.101	.041	.550	-.365	-.257	.355	.078	-.025
z	-.848	-.766	-.911	-.408	-.838	-.612	-.802	-.848	.910
D _{LA}	.763	.458	.797	.366	.602	.460	.635	.764	-.795

APPENDIX H

Pearson's product-moment correlation coefficients between floral and faunal community parameters. See Table 6 for description of symbols.

Plant Community		Faunal Community parameter											
Parameter	D	s	ti	H'(s)	H'(t)	H'(ti)	H' _t (s)	H' _t (i)	H' _{ti} (s)	Q _J (s)	Q _J (ti)	Q _d (s)	Q _d (ti)
WATER BOTTLE - ZOOPLANKTON													
s	-.393	.537	.442	.173	.639	.177	-.185	-.322	.144	.537	.442	-.214	.086
c	.357	.762	.759	.773	.568	.748	.602	.509	.740	.421	.463	-.361	-.348
H'(s)	-.341	.621	.540	.277	.652	.290	-.054	-.183	.215	.621	.540	-.330	-.004
H'(z)	-.100	.285	.383	.061	.094	.052	.020	-.009	.077	.286	.383	-.260	-.005
H' _z (s)	-.237	.642	.453	.351	.726	.344	-.004	-.180	.327	.642	.453	-.403	-.115
H'(f)	-.528	.395	.138	.115	.222	.166	.008	.024	-.016	.395	.138	-.414	.094
H' _f (s)	.085	.648	.753	.342	.701	.283	.002	-.234	-.411	.649	.753	-.343	-.262
Q _J	-.392	.537	.442	.173	.635	.175	-.191	-.328	.144	.535	.436	-.215	.088
Q _d	.384	-.659	-.477	-.378	-.694	-.423	-.056	.043	-.224	-.659	-.477	.391	.028
P	-.033	.724	.639	.346	.841	.289	-.132	-.417	.438	.765	.758	-.384	-.280
SWEEP - COLEOPTERA													
s	.709	.527	.615	.277	.438	.333	.286	.256	.006	.527	.615	-.606	-.626
c	.714	-.051	-.018	-.192	-.221	-.275	.002	-.253	.072	-.027	.179	-.342	-.641
H'(s)	.699	.395	.609	.240	.347	.343	.270	.295	-.090	.395	.609	-.613	-.683
H'(z)	-.025	.072	.522	.313	.165	.506	.381	.541	-.219	.072	.522	-.170	-.253
H' _z (s)	.665	.385	.364	.003	.264	-.026	.022	-.111	.052	.385	.364	-.520	-.445
H'(f)	.262	.282	.540	.122	.343	.246	.032	.183	-.172	.282	.540	-.491	-.308
H' _f (s)	.488	.261	.458	.211	.170	.262	.372	.255	-.010	.261	.458	-.328	-.479
Q _J	.709	.527	.614	.276	.437	.332	.285	.255	.005	.536	.619	-.606	-.616
Q _d	-.827	-.286	-.435	-.057	-.263	-.122	-.034	-.062	.091	-.286	-.434	.693	.731
P	.593	.293	.287	-.009	.234	-.061	.068	-.143	.086	.293	.287	-.365	-.376
SWEEP - HEMIPTERA													
s	-.241	.739	.697	.685		.809			-.438	.738	.697	-.625	-.845
c	-.379	.450	.521	.289		.569			-.629	.180	.413	-.413	-.697
H'(s)	-.160	.609	.629	.761		.827			-.345	.609	.629	-.631	-.838
H'(z)	.331	-.081	.207	.407		.307			.081	.081	.208	-.111	-.257
H' _z (s)	-.450	.736	.683	.585		.786			-.559	.736	.683	-.615	-.729
H'(f)	-.007	.307	.349	.744		.598			.076	.307	.350	-.678	-.492
H' _f (s)	-.166	.475	.659	.417		.662			-.597	.475	.659	-.215	-.639
Q _J	-.242	.739	.697	.684		.809			-.439	.744	.703	-.627	-.841
Q _d	.299	-.621	-.509	-.841		-.855			.266	-.622	-.509	.765	.822
P	-.567	.666	.646	.468		.780			-.742	.697	.681	-.258	-.576

Plant Community		Faunal Community parameter											
Parameter D	s	ti	H'(s)	H'(t)	H'(ti)	H' _t (s)	H' _t (i)	H' _{ti} (s)	Q _j (s)	Q _j (ti)	Q _d (s)	Q _d (ti)	
LIGHT TRAP - ALL SPECIES													
s	.099	.630	.687	-.128	.397	-.148	-.415	-.468	.099	.630	.687	-.569	-.408
c	-.054	.535	.710	.201	.227	.156	.126	.058	.554	.286	.377	-.342	-.471
H'(s)	-.049	.659	.702	.113	.592	.098	-.217	-.267	.212	.659	.702	-.666	-.521
H'(z)	-.121	.100	.110	.522	.639	.538	.297	.296	.195	.100	.111	-.312	-.432
H' _z (s)	.142	.776	.830	-.191	.308	-.231	-.443	-.520	.255	.776	.829	-.690	-.519
H'(f)	-.200	.725	.579	.205	.761	.198	-.200	-.247	.199	.726	.578	-.754	-.520
H' _f (s)	.204	.339	.530	.124	.320	.101	-.034	-.080	.296	.338	.531	-.425	-.549
Q _j	.100	.630	.687	-.129	.396	-.149	-.416	-.468	.099	.634	.689	-.571	-.408
Q _d	.247	-.834	-.817	-.117	-.638	-.101	.241	.296	-.228	-.834	-.817	.786	.486
P	.301	.560	.751	-.225	.154	-.259	-.392	-.453	.170	.559	.751	-.544	-.502
LIGHT TRAP - ENTOMOSTRACA													
s	.099	.630	.609	-.128	-.860	-.148	.067	.147	-.122	.719	.667	-.181	.049
c	-.054	.825	.642	.178	-.383	.282	.744	.687	.190	.649	.662	-.512	-.455
H'(s)	-.058	.686	.607	-.172	-.770	-.245	.241	.281	.041	.687	.701	-.241	.021
H'(z)	-.138	.076	.170	.354	-.147	.200	.465	.307	.536	.076	.288	-.195	.047
H' _z (s)	.144	.849	.671	-.416	-.866	-.388	.032	.199	-.319	.849	.699	-.308	-.088
H'(f)	-.203	.395	.204	-.194	-.344	-.296	-.014	-.057	.084	.396	.257	-.005	.407
H' _f (s)	.193	.671	.729	.046	-.805	.011	.495	.560	-.109	.670	.829	-.519	-.388
Q _j	.094	.718	.608	-.380	-.863	-.438	.055	.138	-.123	.719	.663	-.177	.055
Q _d	.249	-.683	-.557	.214	.666	.227	-.137	-.227	.109	-.684	-.648	.153	.080
P	.302	.762	.757	-.315	-.941	-.229	.181	.410	-.374	.761	.840	-.455	-.367
LIGHT TRAP - COLEOPTERA													
s	-.234	.490	.498	.487	.659	.444	.268	.175	.554	.491	.498	-.452	-.654
c	-.349	.369	.405	.237	.403	.189	.080	-.011	.406	.120	.078	-.150	-.465
H'(s)	-.075	.500	.487	.464	.639	.413	.249	.154	.581	.500	.487	-.523	-.673
H'(z)	.501	-.079	-.097	.049	.318	.061	-.126	-.115	-.028	-.079	-.097	-.132	-.067
H' _z (s)	-.512	.634	.652	.607	.661	.561	.431	.343	.653	.635	.652	-.582	-.776
H'(f)	.002	.630	.557	.645	.474	.601	.596	.558	.664	.631	.557	-.741	-.570
H' _f (s)	-.075	.090	.153	.172	.639	.170	-.151	-.205	.133	.091	.153	-.144	-.438
Q _j	-.234	.490	.498	.486	.659	.443	.267	.174	.554	.495	.504	-.456	-.655
Q _d	.202	-.755	-.712	-.588	-.563	-.504	-.465	-.344	-.835	-.756	-.713	.737	.824
P	-.529	.373	.467	.403	.807	.387	.063	-.013	.357	.373	.466	-.340	-.614
LIGHT TRAP - HEMIPTERA													
s	-.311	.738	.757	.332		.879			-.568	.738	.757	-.738	-.424
c	-.072	.782	.684	.130		.679			-.538	.525	.314	-.773	-.450
H'(s)	-.259	.716	.695	.301		.864			-.578	.716	.694	-.683	-.349
H'(z)	.153	-.047	.141	-.280		.250			-.457	-.047	.140	-.034	-.042
H' _z (s)	-.382	.880	.810	.438		.884			-.488	.880	.810	-.691	-.444
H'(f)	-.316	.513	.334	.485		.541			-.128	.513	.334	-.086	.119
H' _f (s)	-.009	.487	.745	-.198		.760			-.873	.487	.745	-.719	-.626
Q _j	-.311	.738	.757	.332		.880			-.569	.739	.760	-.729	-.421
Q _d	.429	-.870	-.632	-.600		-.859			.338	-.870	-.633	.624	.168
P	-.369	.706	.923	.068		.945			-.838	.706	.922	-.692	-.597