

THE UNIVERSITY OF MANITOBA

THE ZOOBENTHIC ASSEMBLAGES OF FOUR CENTRAL CANADIAN LAKES
AND THEIR POTENTIAL USE AS ENVIRONMENTAL INDICATORS

by

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A dissertation submitted to the Faculty of Graduate Studies of
the University of Manitoba in partial fulfillment of the requirements
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The errors inherent in the thesis are my sole responsibility.

ABSTRACT

The characteristics of the benthos of four lakes in central Canada were studied through a one-year cycle. The results showed that in each lake the benthic densities and diversity indices decreased with increasing depth. Temporal changes in both diversity and standing crop sampled were greatest in the littoral zone, and this was interpreted as reflecting the instability of the physical environment.

Faunal assemblages based on the mutual information shared by a number of samples identified to genus and species level were compared to diversity indices and individual taxa as indicators of environmental conditions. From the results it appeared that none of these methods were adequate in describing lake types, but that faunal assemblages at the generic level were the best indicators of within-lake environmental conditions. The environmental factors which appeared to most influence the distribution of benthic assemblages in these four lakes were the organic content of the sediment, depth of the trophogenic zone, and the minimum oxygen levels in the hypolimnion.

INTRODUCTION

In this study, four lakes in central Canada are investigated to describe the macrobenthic faunal assemblages, and to relate the assemblages to the physical characteristics present. An attempt is made to relate these findings to the trophic state of the lake and to the diversity-stability-maturity principles described by MacArthur (1955) and Margalef (1968) and others.

The use of benthic macroinvertebrates to describe conditions in lakes dates back to the early part of the twentieth century. Thienemann (1920), after extensive work in lakes of the Baltic region, concluded that lakes could be characterized by their dominant genera, Tanytarsus found in oligotrophic, well-aerated waters, and Chironomus characteristic of more eutrophic conditions. Between, lay a spectrum of lake types dominated by Stictochironomus and Sergentia. Brundin (1949), commenting on such a characterization, expressed frustration at the fact that some obviously eutrophic lakes held "typically" oligotrophic taxa, and vice versa.

These were followed by studies attempting to find the environmental factors limiting the distribution of specific zoobenthic organisms. Thienemann

(1928), Berg (1938), and Brundin (1951) championed oxygen concentrations. Reed and Klugh (1924), Harp and Campbell (1967), and Bell (1970) described the detrimental effects of low pH on aquatic invertebrates. Lundbeck (1926) and Jonasson (1972) correlated density of zoobenthos to rooted vegetation. Eggleton (1931) and Miller (1941) emphasized the thermocline's role in determining species composition. Adamstone (1924) and Eggleton (1952) attempted to relate zoobenthic distribution to substrate.

Clearly, the emphasis in the literature is upon description of cumulative zoobenthic densities, de-emphasizing distribution of individual species or the co-occurrence of species as in faunal assemblages. Most studies have been done on single lakes, and generally as portions of fisheries studies whose prime concern was the standing crop available as a food source. There is a singular lack of benthic community studies of the type undertaken by Thorson (1957) in the marine environment.

Recently, an increased use has been made of benthic faunas to describe the conditions of aquatic systems. This has resulted either in the search for indicator organisms, usually following the schemes of Thienemann (1920) and Lundbeck (1926), or in the

use of faunal coefficients such as diversity indices as proposed by Wilhm and Dorris (1966) and Wilhm (1967, 1968, 1970). In essence, both of these approaches are searching for biological indicators of environmental conditions. Using organisms as indicators of conditions in fresh water has been widely accepted in the last fifty years. Fishes, phytoplankton, oligochaetes, and chironomids have all been used with limited success (Thienemann 1920, Lundbeck 1926, Brundin 1949, Rawson 1960, Brinkhurst 1966, Odum 1971, Stockner 1971).

Some of the problems encountered in using indicator organisms are: 1) an organism can occur in low numbers or for short periods of time in unfavourable environments, 2) often the presence or absence of an organism can be attributed to zoogeographical distribution patterns rather than contemporary environmental conditions, and 3) for many aquatic invertebrates the identification keys available are grossly inadequate.

Even if the above problems could be ignored, one still needs to recognize the physical factors that limit the animal's distribution. This latter problem can be overcome if much a priori knowledge of the animal's requirements is available. Unfortunately, this is most often lacking for zoobenthic organisms. Green (1971) overcame this deficiency while attempting

to spatially separate the pelecypods of central Canada by using a multivariate method of analysis which may prove useful in these types of studies. He achieved this by defining the Hutchinsonian niche (Hutchinson 1957b) of the animals involved by a series of discriminant functions and the variables contributing to these functions. Probably the major shortcoming of any indicator organism approach is that the concept is based on the presence or absence of the organism in the community. Thus, the abundance of the taxon does not contribute to the results obtained. This approach essentially ignores interspecific interactions, as well as the ability of organisms to survive for limited periods of time under conditions unfavourable for reproduction.

Wilhm (1967, 1968, 1970) felt that "indicator" organisms were unreliable, and instead proposed the use of diversity indices. Believing that diversity indices were "good" indicators of associations of benthic organisms, he felt that this method could simplify the presentation of data concerning taxa and their numerical abundance. However, the application of diversity indices to environmental studies rests on the concepts of the relationships among ecosystem diversity, stability, and maturity. Diversity, whether

denoting the number of species or their frequency distribution, has often been used to measure the complexity of a system. Increases in diversity have been equated with increases in ecosystem maturity, and vice versa. Low maturity systems have been said to have low diversity and also a lower stability, stability being used as a measure of the predictability over time of a system (Margalef 1963).

Margalef also states that "Anything that keeps an ecosystem oscillating retains it in a state of low maturity". MacArthur (1955) suggests a similar relationship between diversity and stability, maintaining that stability is highest in areas of high diversity because during periods of change alternate energy pathways can be utilized.

The idea that diversity, maturity, and stability are correlated has wide acceptance. However, a few investigators (eg. Pielou 1966) have postulated that it is possible for diversity to decrease with maturity.

Communities in some environments, such as the marine benthos, in-depth community studies have been carried out (Sanders 1968, Johnson 1970, Boesh 1972). From diversity values reported in these studies, some predictive use can be made of diversity indices. In

lacustrine zoobenthos, however, no such information is available. Studies of diversity patterns and relationships among diversity, stability, and maturity should be carried out in lakes before the results are utilized in pollution biology. And, although such results can be meaningful, one cannot help but wonder if such an approach is desirable because, as pointed out by R.H. Green (personal communication), much of the information contained in the data becomes lost when it is presented as an index.

- When inferring environmental conditions from biological information, plant ecologists have generally been more successful. This greater success has probably been due to the plant ecologist's tendency to stress the community or floral association concept rather than population dynamics.

An advantage of working at the community or assemblage level is that the composition of the assemblage is the end product of the interspecific interactions. Then it is reasonable to assume that a specific assemblage should be limited in its spatial distribution almost exclusively by the physical environment. Thus the assemblage should be a more accurate environmental indicator. And if the assemblage itself can be identified by its numerically dominant members, then much of the information lost

in diversity indices would be retained.

Lacustrine zoobenthos lends itself to a community type approach partly because of the number of species involved. Moreover, a transect from shore to maximum depth in a lake can be viewed as analogous to a phytosociological transect from a mountaintop to a valley, with all the subtle variations caused by or related to environmental gradients.

The present study was undertaken in four central Canadian lakes representing two distinct geological regions and different trophic types of lakes. This study 1) provides information on the temporal and spatial taxonomic composition of the bottom fauna of the four lakes, 2) seeks to identify groups of benthic organisms which occur together as faunal assemblages, 3) explores the changes in diversity found in lacustrine benthic communities through depth and time, 4) seeks to compare the information that can be gathered from diversity indices and indicator organisms to that from faunal assemblages, and 5) ultimately attempts to relate the individual benthic faunal assemblages to the physical environment that they occupy, and thus form a predictive scheme for water quality.

MATERIALS AND METHODS

Watersheds

Two of the lakes studied, Beautiful and East Blue Lakes, are located in the Duck Mountain Provincial Park, 51°30'N, 101°0'W. The Park is part of the northern portion of the Manitoba Escarpment, which represents the east-facing border of former Lake Agassiz. In the Duck Mountain region, the Escarpment rises approximately 370 m above the old lake bed, and consists of hilly morainic uplands with numerous end moraines (Tyrrell 1888). The facies is Mesozoic Rock, primarily siliceous shale (Elson 1967) of the Cretaceous Riding Mountain Formation.

The area receives an average of 40.6 to 43.1 cm of precipitation per year, and there are 80 to 90 frost-free days (Weir 1960). The region is overlain with grey-wooded soil (Weir 1960). The lakes are surrounded by mixed woods of aspen, spruce, and poplar.

Logging is taking place in the Duck Mountains, but not in the vicinity of the lakes studied.

The other two lakes, Lake 239 and Lake 240, are located at the western border of the Pre-Cambrian Shield in Northwestern Ontario. They are within the Experimental Lakes Area (Johnson and Vallentyne 1971),

a research area of the Freshwater Institute, Department of the Environment, approximately 30 km south-east of Kenora, Ontario, at $49^{\circ}40'N$ and $93^{\circ}45'W$. This region is believed to be located along one of the eastern borders of former Lake Agassiz (Elson 1967).

The study area is reported to have "irregularly distributed deposits of boulder till, stratified sand, silts, and gravel in low-lying areas" (Brunskill and Schindler 1971), with many granitic outcrops covered with thin to no layers of soil or lichens. Brunskill and Schindler (1971) report that there are about 103 frost-free days, and a mean annual precipitation between 50 and 75 cm. A mixed stand of sub-climactic boreal forest surrounds these lakes, and is dominated by black spruce, trembling aspen, and jackpines. Logging takes place in the area, but not within the watersheds of these lakes.

Morphometry of the Lakes

East Blue Lake

East Blue Lake, altitude 700 m above sea level, is situated in a depression of unstratified glacial deposits at $51^{\circ}36'N$, $100^{\circ}55'W$, in the Duck Mountain Provincial Park of western Manitoba.

Approximately 2000 m long and 700 m wide (Figure 1a), the lake has a surface area of 97.1 hectares, a maximum depth of 72 m, and a mean depth of 22.5 m. The basin is oriented on a north-south axis, and is protected from westerly winds while exposed to north-south winds, the prevailing fall winds.

The small drainage area of the lake and lack of inlets or outlets indicate that the drainage is principally spring seepage and runoff.

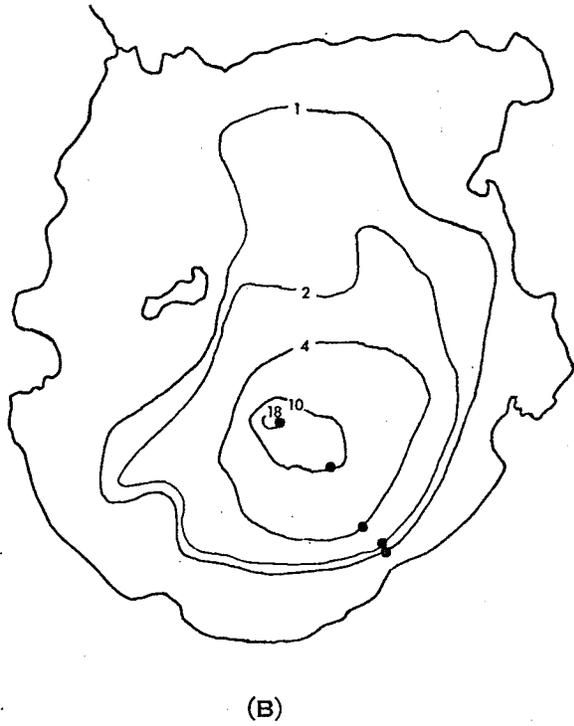
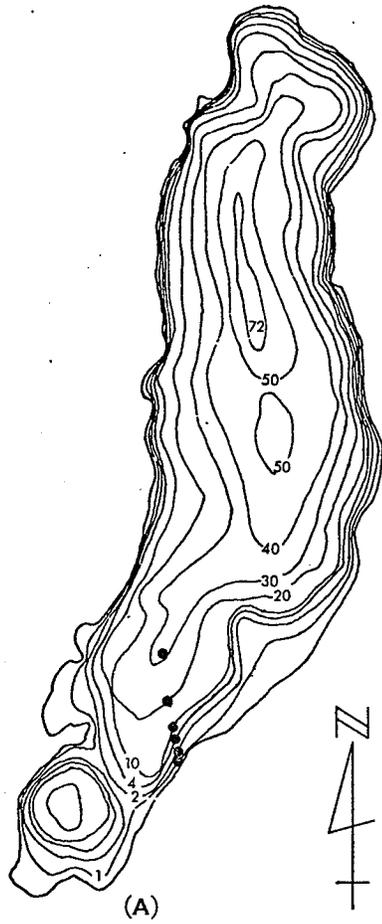
The shoreline to 1 m depth is clear of vegetation, but below this an extensive Chara bed extends to 20 m water depth on the north side of the lake, and to 10 m on the south side. Sediment slumps caused by the basin's steep sides are evident to 10 m at a number of places.

The water is clear, with summer Secchi transparencies of about 10 m, and the lake is pale blue in colour. Gibson (1969, MS personal communication) reported a dissolved solids value of 186 ppm, and summer dissolved oxygen values below 40 m of 3.5 ppm (27% sat.) and 1.9 ppm (14% sat.).

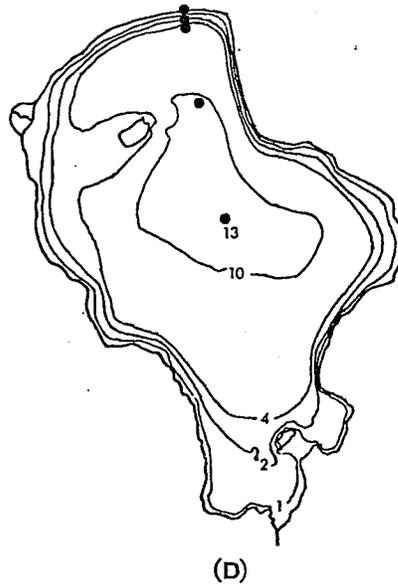
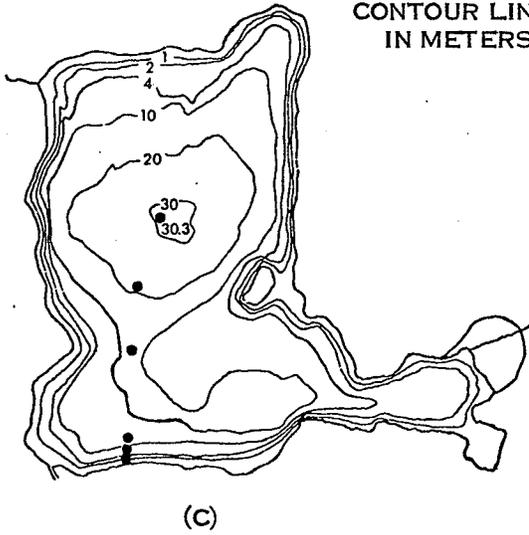
The lake supports a sport fishery for lake trout (Salvelinus namaycush), splake, and rainbow

Figure 1. Bathymetric maps of the four lakes studied, with sampling stations indicated. (a) East Blue Lake; (b) Beautiful Lake; (c) Lake 239; (d) Lake 240.

(Bathymetry of East Blue Lake was reconstructed from Gibson (1969); Beautiful Lake from Fedoruk (1969); and Lakes 239 and 240 from Brunskill and Schindler (1971).)



CONTOUR LINES
IN METERS



trout (Salmo gairdneri), all three of which have been recently introduced. Cottages line the extreme northern portion of the lake along provincial highway 366.

Beautiful Lake

Beautiful Lake is situated at an altitude of 650 m in an unstratified glacial depression at $51^{\circ}33'N$ and $101^{\circ}02'W$ in the Duck Mountain Provincial Park. It lies approximately 6 km west of East Blue.

The lake is roughly circular, about 1700 m long and 1000 m wide (Figure 1b), and relatively unprotected from winds except for the spruce stands surrounding the shoreline. The basin has a surface area of 135 hectares, a maximum depth of 18 m, and a mean depth of only 5.0 m (Fedoruk 1969, MS personal communication). The lake resembles a pond, in that it has an extensive zone shallower than 3 m representing over 60% of the surface area, and a relatively narrow steep-sided depression in the south-east part of the basin which extends to 18 m.

There is a small intermittent stream entering at the north-east corner of the lake draining a boggy area, and there is no effluent.

From shoreline to about 1.5 m water depth, the lake bottom is covered by emergent vegetation, primarily Scirpus. Beyond this depth, a muddy bottom predominates.

The water is brown and usually roiled by wind action, with summer Secchi transparencies around 2 m. Fedoruk (1969, MS personal communication) reported dissolved solids determinations of 290 ppm. He also reported that in April, 1962, the water at middle and bottom was oxygen deficient, and in February, 1963, was "good" for fish survival.

The fish in the lake were eradicated with Toxaphene in 1961, and in 1962 the lake was stocked with kokanee (Oncorhynchus nerka) and muskellunge (Esox masquinongy).

No permanent buildings currently stand in the watershed, and there is little sport fishing.

Lakes 239 and 240

Lakes 239 and 240 are located in the Experimental Lakes Area of northwestern Ontario, at 47°40'N and 93°45'W. Brunskill and Schindler (1971) state that the lakes in this region "probably resulted

from glacial ice excavation and deepening of faulted and jointed bedrock."

Lake 239 is approximately 850 m in length north-south, and from 500 to 1200 m in width (Figure 1c). The basin is protected from east-west winds, but portions of the north and south shores are exposed. Its surface area is 56.1 hectares, its maximum depth 30.3 m, and mean depth 10.5 m (Brunskill and Schindler 1971). Sections of the north and south shores consist of sand deposits, and the remainder of the lake has broken granitic boulders along the shore. At the south-eastern corner is a shallow, boggy bay with rooted vegetation along its edges. Stockner and Armstrong (1971) reported that the bottom was gradually sloping.

There are two boggy inlets to the lake, one at the north-west and one at the south-east. Both are less than 2 km in length.

The south-west portion of the shoreline appears to be a glacial drift dam, through which Lake 239 drains into Lake 240.

The water is humic, having summer Secchi transparencies of 3 to 4 m, and total dissolved solids values reported to be 50 ppm (Cleugh and Hauser 1971).

At the time of the study, there was a cottage at the north-west corner of the lake, and a research camp with accommodations for 32 people at the south-western corner near the outlet. Limited sport fishing for Salvelinus namaycush and Esox lucius took place in the lake.

Lake 240 is located 10 to 20 m south of Lake 239, and probably shares the same geologic origin. It is approximately 1200 m long (north-south), and about 725 m at the widest point (Figure 1d). Its surface area is 44.1 hectares, maximum depth 13.1 m, and mean depth 6.1 m (Brunskill and Schindler 1971). Two island outcrops are present, both with standing vegetation.

The north shore is well exposed to southerly winds, but the south shore is protected by rocky points and the islands. Broken rock and boulders make up the shoreline, except for the exposed north shore which has a sand beach. The west shore of the lake supports rooted emergent vegetation, primarily Scirpus, Carex, and Utricularia.

There are two inlets to the lake, one at the north-east corner draining Lake 239. The other, at the north-west corner, is a stream less than 1 km in length, draining two smaller lakes.

The outlet is at the southern end of the lake, and this eventually drains into Dryberry Lake, and Lake of the Woods.

The water is humic coloured with a Secchi transparency of 3 to 4 m. Total dissolved solids values of 60 ppm were reported by Cleugh and Hauser (1971).

At the time of the study, no buildings were present on the lake, and there was a limited sport fishery for Esox lucius.

Physical and Chemical Factors

The purpose of collecting physical and chemical data was to illustrate the interaction between physical-chemical parameters and the benthic faunal assemblages.

The parameters were chosen so that 1) they be useful in characterizing the trophic state of the lake, 2) they influence the benthic fauna, 3) they be easy to measure under field conditions, and 4) they reflect temporal changes in the benthic environment.

Unless otherwise stated, all the chemical analyses were conducted using kits marketed by the

Hach Chemical Company, because of their compactness and availability.

The sampling programme extended from May, 1970, until July, 1971. Sampling was at monthly intervals during the open water season, and once in winter. A total of nine collections was made, but those of May and June of 1970 were discarded because of sampling inconsistencies.

On each sampling trip, temperature and oxygen profile was taken at the deepest station.

Water for chemical determinations was obtained by means of a Milbrink sampler (Milbrink 1968) at depths below 4 m, and a Maitland corer at shallower stations (Maitland 1969). In every case, the water was withdrawn from the sampler at about 0 to 2 cm above the sediment by means of a 100 ml glass syringe.

Chemical analyses were carried out on samples collected from 2.0 m, 10.0 m, and 30.0 m or maximum depth stations on all sampling dates. The 1.0 m and 4.0 m stations were sampled only in July and September, 1970, and May, 1971.

Where values obtained in chemical determinations were below the limits of detection, they were

arbitrarily set as zero. This was justified because trends were sought within and among lakes, rather than the absolute values.

The parameters chosen were:

(1) Dissolved oxygen — The limiting effect of low oxygen concentrations on the benthic faunal diversity has been discussed by Berg (1938) and Jonasson (1972). It is also useful in characterizing the trophic states of the lakes. Except for the profiles, all determinations were carried out using the modified Winkler method Hach kit OX-2-P, a drop count titration method accurate to 1 ppm. Titration was done in a glass syringe, to avoid aeration. Oxygen and temperature profiles in 1971 were obtained with a YSI Model 54 meter.

(2) pH — Variations in pH have been strongly linked to species composition of communities (Reed and Klugh 1924, Ruttner 1963). Its limiting effects on chironomid larvae are discussed by Curry (1965) and Bell (1970). The test was performed using the colour comparison technique employing the indicators Brom Cresol Purple (for pH 5.0 - 6.3), Brom Thymol Blue (pH 5.5 - 8.5), and Thymol Blue (pH 8.0 - 9.2). The test was accurate to 0.25 pH units.

(3) Alkalinity — Alkalinity was used as a rough indicator of the fertility of the lakes. Generally, an alkalinity greater than 100 mg/l and pH of 7 to 8 is considered capable of supporting a diversified aquatic life. In addition, Northcote and Larkin (1956) found a correlation between alkalinity and the trophic state of a series of lakes in British Columbia. Alkalinity (Total) was measured by the drop titration method using the Brom Cresol Green-Methyl Red indicator. The total alkalinity was expressed as ppm of calcium carbonate. The limit of detection was 7 ppm.

(4) Calcium — Because of the use of calcium in shell formation by invertebrates, calcium is believed to be of some importance as a potential limiting factor in aquatic systems. Calcium was measured as calcium hardness, and determined using the Hach calcium hardness test. The limit of detection was 8.6 ppm, as was the sensitivity.

(5) Magnesium — Magnesium ion was determined from the difference between total hardness and calcium hardness. Hach's Uni-Ver Hardness test was employed for total hardness, and it eliminated interference from copper, iron, and manganese ions. The limits of detection and sensitivity were 8.6 ppm.

(6) CO_2 — Inversely correlated to dissolved oxygen in the hypolimnion, CO_2 is a good indicator of reduction. Estimates of CO_2 concentration were derived from pH and alkalinity data using the table in Ruttner (1963, page 67). The values obtained in low pH-low alkalinity lakes such as those in the Pre-Cambrian Shield are too high because of the table used. However, these values were still used in subsequent analyses since the trends through depth were realistic, and the analyses were sensitive to these trends.

(7) Iron — Iron is present in the bottom waters when reduction is occurring. Its presence in the ferrous form has often been taken to indicate eutrophic conditions. Total dissolved iron was measured using the Hach Ferro-Ver colour comparison technique, with 1,10 Phenanthroline as the indicator. Orthophosphate, metaphosphate, and fluoride do not interfere with this test. The test used up to 1 ppm had a sensitivity of 0.02 ppm; for values between 1 and 10 ppm the sensitivity was 0.2 ppm.

(8) H_2S — Ohle (1955) found that H_2S production is linearly dependent on $\text{SO}_4^{=}$ concentration in lakes. Hutchinson (1957) considered H_2S presence to indicate prolonged stagnation. H_2S was determined using Hach's

Hydrogen Sulphide Test, with a limit of detection of 0.1 ppm and test range 0 - 5 ppm.

(9) Temperature — Of obvious use in classifying lakes and indicating lake conditions, temperature has been shown to greatly affect the metabolic rates and growth of poikilotherms. Previously calibrated Centigrade thermometers, accurate to 0.5°C, were used to obtain readings. Temperature profiles in 1971 were obtained with a YSI thermistor Model 54.

(10) Compensation level — Transparency, which controls the depth to which photosynthetic activity occurs, was used as a possible indicator of types of food available to benthic organisms. Expressed as Secchi depth, transparency was obtained with a 25 cm white disk, following the reading procedures outlined in Tyler (1968). The compensation point was roughly estimated as being twice the Secchi depth.

(11) Mean sediment particle size — A distinct and predictable gradient of particle size exists in most lakes, going from the littoral zone to maximum depth. Although Marzolf (1965) found little correlation between particle size and substrate selectivity for P. affinis in laboratory experiments, others such as Adamstone (1924) and Eggleton (1952) felt that some correlation existed between species distribution and

sediment particle size. Sediment samples were collected, and frozen within four hours of collection. In the laboratory, particle size was determined by the wet sieving method, and the fraction smaller than 0.0625 mm by the hydrometer method (Bouyoucos 1927).

Mean particle size, $\bar{\theta}$, was calculated using the equation:

$$\frac{\theta_{84} + \theta_{50} + \theta_{16}}{3} = \bar{\theta} \quad (1)$$

from Folk (1968).

(12) Sorting coefficient of sediment — This was used to estimate the effect of wave action in an area. The better sorted the sediments are, the more water movement must occur in the area. The importance of sediment types in benthic distribution has been emphasized by many such as Adamstone (1924), Eggleton (1952), and Jonasson (1972).

The sorting coefficient was calculated from the equation:

$$SC = \frac{\theta_{84} - \theta_{16}}{4} + \frac{\theta_{95} - \theta_5}{6.6} \quad (2)$$

from Folk (1968).

(13) Organic content of sediment — This was estimated by loss on ignition at 525°C for one hour, after oven

drying for 24 hours at 100°C, and was expressed as percentage of dry weight.

(14) Presence or absence of rooted vegetation — Although this is not a physical parameter, Gerking (1962) has shown a distinct fauna to be associated with macrophytes. In the analysis the value of 1 was used to indicate presence of macrophytes, and 0 for absence.

Biological Components

When this study was begun, one of the first problems faced was the large number of taxa represented in each lake. Some arbitrary decision had to be made about the taxa on which maximum effort should be placed.

The criteria used in selecting these taxa were:

- (1) Good keys must be available for each
- (2) The taxa must have been discussed in previously published works
- (3) Members of the groups must be large enough in size that even the immature stages may be retained by a 200 μ mesh
- (4) The animal must spend a predictable portion of its life cycle on or in the sediment

(5) Identification must be possible without internal dissection.

The following groups met these criteria: most insects, the mollusks, some amphipods, decapods, and the leeches. The animals were to be studied only during their residence in the lake's sediment.

In each of the four lakes, a series of samples were collected along a transect extending from shore to the deepest point, or 30 m in East Blue Lake. Following a series of exploratory dives and sampling, the transects were chosen so that a gradient would be present, originating from a common littoral zone type (i.e., sand particle size).

The following depths were arbitrarily chosen along the transects: 1.0 m, 2.0 m, 4.0 m, 10.0 m, 20.0 m, 30.0 m or the maximum depth (Figures 1a,b,c,d). The sampling sites, marked with buoys, were so distributed as to insure the more intensive sampling of the littoral zone and the metalimnion; it was felt that the hypolimnion, being more homogeneous, required less intensive sampling.

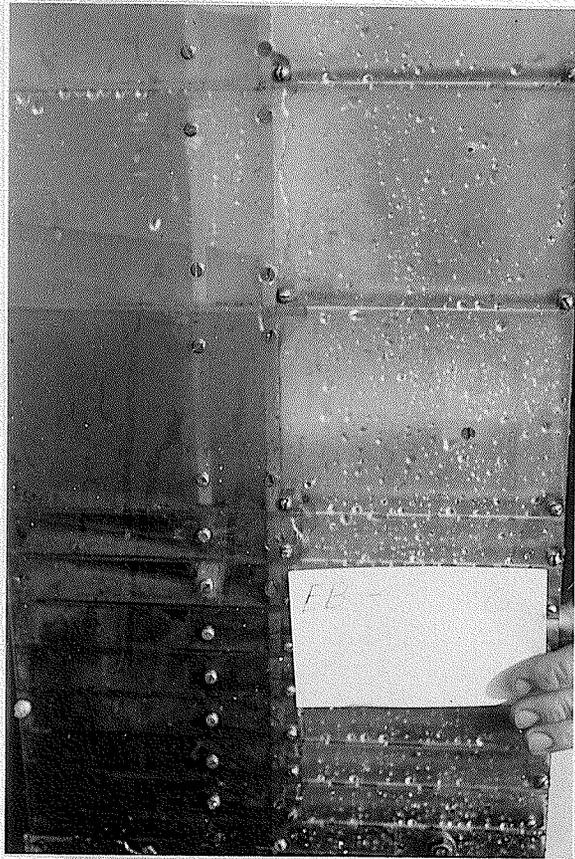
In order to minimize variability resulting from diel migration of organisms, sampling times were restricted to between 0830 and 1730 hr.

Sampling was done at the 1.0 m, 2.0 m, and 4.0 m depth stations using a 7 cm diameter hand-held corer (Figure 2a) (Maitland 1969). The 1.0 m and 2.0 m stations were sampled from a boat using a 2.5 m pipe handle, while at 4.0 m SCUBA was used. The corer was chosen for the littoral zone because it facilitated sampling to the desired depth in the more compact and coarse sediment.

In summer, a Perspex corer tube was used to sample to a 15 cm sediment depth (Figure 2). The sediment column was extruded in 3 cm thick horizons. Poor samples were discarded and re-taken; however, even with extreme care, some mixing of the top two horizons occurred during extrusion of the column. During winter sampling, a brass corer was used.

At depths of 10 m and greater, a Perspex sampler similar to that of Milbrink (1968) was used (Figure 2b). This sampler allows for stratification in situ, and its streamlined design, coupled with complete sample retention during raising, was found by Milbrink (1968) to be more efficient than the standard Ekman in soft sediments. The sampler, with a 1.5 kg lead ballast attached, was allowed to free-fall, and the partitions closed by a messenger.

Figure 2. Samplers used for the collection of benthic samples. (a) Milbrink Sampler; (b) Maitland Sampler.



(A)



(B)

All stations were sampled in triplicate. Immediately after collection, samples were sieved through 200 μ mesh Nitex netting and preserved in 10% formalin. Jonasson (1955) showed that 250 μ retained most of the early Diptera instars. Within two weeks of collection, samples were transferred to 70% ethyl alcohol.

The preserved samples from stations shallower than 10.0 m, where much organic material was present, were floated twice in sugar solution (specific gravity 1.12) as described by Anderson (1959). Gerking (1957) found this method to be 90 to 99% efficient when the Mollusca and Trichoptera are excluded. All of this floating material was retrieved with a 200 μ net and preserved. The remainder of the sample was washed and then subjected to the $ZnCl_2$ flotation method described by Sellmer (1956), which floated the Sphaeriidae and Trichoptera.

All samples, including floated ones from shallow stations, were sorted using a dissecting microscope (16X).

All dipteran larvae were mounted on glass slides using Turtox CMC mounting/clearing medium. The Chironomidae were identified using keys provided

by A.L. Hamilton and O. Saether of the Freshwater Institute, Department of the Environment, Canada (unpublished), and some of the difficult generic identifications were verified by O. Saether. Identifications of Chaoboridae were according to Saether (1972), the Sphaeriidae from Herrington (1962), the Ceratopogonidae from Johannsen (1937), the Ephemeroptera using Burks (1953), and the other taxa according to Ward and Whipple (1959), Pennak (1953), and Usinger (1968).

All dipteran measurements were done using an ocular micrometer using 100X magnification (67 microns per micrometer division). With the Chironomidae, the distance measured was from the anteriormost point of the central tooth of the labial plate to the center of the ventro-posterior margin of the head capsule. This measurement was chosen in favour of the usual capsule length or capsule width because both the length and width can be altered by the pressure used on the cover slip during mounting. The antenna length of the Chaoboridae was measured using the same magnification as above.

With the Amphipoda, the dorsal length of the cephalic segment was measured under 40X magnification (168.5 microns per division). Using this same

magnification, the Sphaeriidae were measured using the greatest distance between the anterior and posterior margins.

The samples collected were converted to numbers per square meter. Diversity indices were estimated using the Shannon-Weaver function proposed by MacArthur (1955)

$$H(S) = - \sum_{i=1}^s p_i \log_2 p_i \quad (3)$$

The modified equation given in Southwood (1966) was used as the working formula for the Shannon-Weaver function

$$H(S) = c \left\{ \log_{10} N - \frac{1}{N} \sum_{r=1}^s n_r \log_{10} n_r \right\} \quad (4)$$

n_r = numbers found in r^{th} species

S = numbers of species

N = total numbers in sample

c = 3.321928, a constant used to change the base of the logarithm from 10 to 2

The Shannon-Weaver measure of diversity (Equation 4) was favoured over simpler ones because a measure of the "faunal heterogeneity" was desired rather than the "faunal richness" which most of the other indices measure.

The diversity function was calculated from the three samples combined. To estimate the dominance ranking of individual taxa to a sample, the function $n_r \log_{10} n_r$ was retained for each taxon in a group. The "information contribution" was expressed by calculating the percent of the H(S) made up of the particular $n_r \log_{10} n_r$. When compared to the arithmetic percentage composition of the sample, this method was found to slightly emphasize the contribution of the more abundant species, a desirable characteristic as it facilitated recognition of dominant species in situations of high diversity.

To identify groups which consistently appear together (assemblages), the mutual information analysis described by Orloci (1968, 1969) was employed. The formula used was

$$2I = 2 \left(\sum_{i=1}^r \sum_{j=1}^c x_{ij} \ln x_{ij} + N \ln N - \sum_{i=1}^r X_i \ln X_i - \sum_{j=1}^c X_j \ln X_j \right) \quad (5)$$

r = row or species

c = columns or samples

x_{ij} = value of i^{th} species in j^{th} sample

N = total number

X_i = row totals

X_j = column totals

This type of analysis, based on information theory, groups together those samples having the most similar taxonomic composition. The end result is that the degree of similarity among all the samples is used to rank all the samples on a relative basis.

One of the problems encountered in community studies is that, in the presence of numerous taxa, one has difficulty in identifying samples or groups of samples which are similar in taxonomic composition. For example, if a simple data matrix is made up of three samples having the same three species per sample (see Figure 3a), it is difficult to decide which two samples are most similar. Typical responses are that all three samples are equally dissimilar or that samples X and Y are most similar because they have common values for the most numerous species (c).

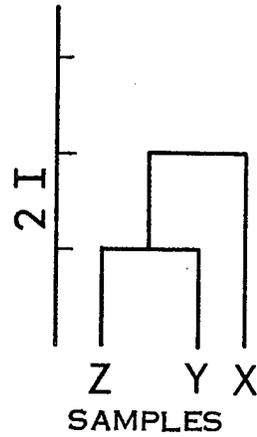
If diversity indices were calculated as is the present vogue in pollution studies, all three samples would have identical diversities, which could be said to reflect similar environmental conditions.

However, if the above data is submitted to the mutual information analysis, a hierarchical ordering of the samples is first constructed, as in Figure 3b. From these data, the dominant taxa are

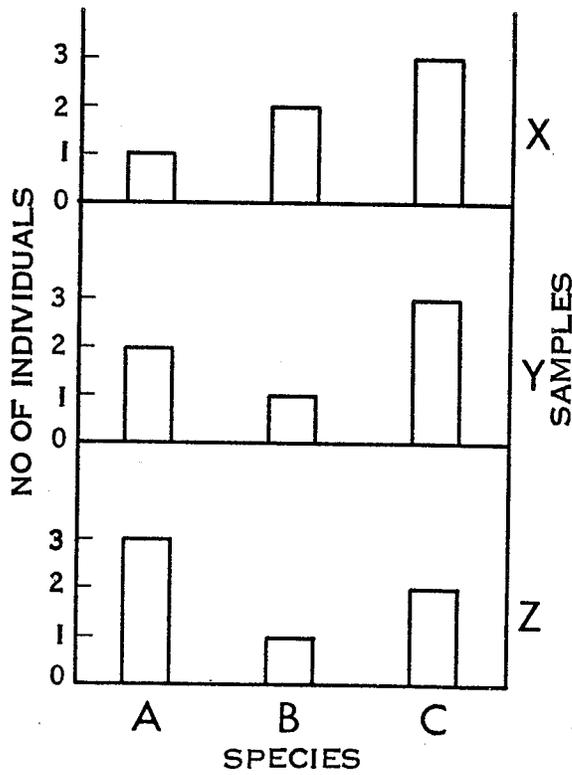
Figure 3. Procedures used in mutual information analysis.

| | A | B | C |
|---|---|---|---|
| X | 1 | 2 | 3 |
| Y | 2 | 1 | 3 |
| Z | 3 | 1 | 2 |

(A) DATA MATRIX



(B) DENDROGRAM RESULTING FROM MUTUAL INFORMATION ANALYSIS



(C) SPECIES DISTRIBUTION

DIVERSITY $\bar{Y} = 1.64$

X
Y
Z

determined in each group of samples and they are used to identify the floral or faunal assemblages. These results are in turn interpreted ecologically. In this case, the results indicate that samples Y and Z are most similar while X is the most dissimilar. The reason for classifying these samples in the above pattern becomes immediately apparent if bar diagrams of the species distribution for the three samples are plotted (Figure 3c). Samples Y and Z have very similar patterns in distribution in that the "community" that they represent is dominated by the same two species, A and C, even though the densities are slightly different. Sample X, on the other hand, is dominated by species C and B, while species A, which was very common in the other samples, plays the part of a rare species.

The sensitivity of this analytical technique in discriminating among samples of taxonomic compositions, even when a large number of taxa are present, makes it extremely useful in community studies.

The analysis was performed for species and then for genera to determine assemblages within lakes and among lakes.

Samples were identified as faunal associations if they shared the same dominant species or

genera and occurred as a group below the same level of fusion. Such a means of distinguishing associations was accepted because it was felt that a change of dominance between two faunas must indicate a change in interaction among species present.

As expected, the first samples retrieved indicated that three replicates did not give accurate estimations of densities (Table 1). This was not considered a serious drawback, however, since the study was designed to rely on the relative taxonomic composition of an area rather than the standing crop or biomass. Following the collections, the adequacy of using three replicates to accurately describe the taxonomic composition was tested using the mutual information analysis. The following criteria were used in evaluating the results:

(1) The three replicates should fuse with one another more often than with other samples

(2) Assuming that changes in assemblages along the transects were gradual, a lumped sample of the three replicates from each point should fuse first with samples collected at points in close proximity.

The results are shown in Figure 4. Based on these results, it appears that although some variation was evident when the test was done on Beautiful Lake

Table 1. Mean number, standard deviation, and coefficient of variation found in the first three replicates collected in June, 1970.

TABLE 1

| EAST BLUE LAKE | | | | LAKE 239 | | | |
|----------------|------------|-----------------------|----------------------------|--------------|------------|-----------------------|----------------------------|
| Depth (m) | Mean No | Standard Deviation | Coefficient ofVariation | Depth (m) | Mean No | Standard Deviation | Coefficient ofVariation |
| 1 | 2.0 | 1.0 | 0.5 | 1 | 18.0 | 5.2 | 0.3 |
| 2 | 19.0 | 18.3 | 1.0 | 2 | 5.7 | 3.2 | 0.6 |
| 4 | 4.7 | 3.8 | 0.8 | 4 | 5.3 | 0.6 | 0.1 |
| 10 | 32.7 | 11.4 | 0.3 | 10 | 13.3 | 11.8 | 0.9 |
| 20 | 63.3 | 22.9 | 0.4 | 20 | 24.7 | 6.4 | 0.3 |
| 30 | 49.7 | 5.7 | 0.1 | 30 | 6.3 | 3.8 | 0.6 |

| BEAUTIFUL LAKE | | | | LAKE 240 | | | |
|----------------|------------|-----------------------|----------------------------|--------------|------------|-----------------------|----------------------------|
| Depth (m) | Mean No | Standard Deviation | Coefficient ofVariation | Depth (m) | Mean No | Standard Deviation | Coefficient ofVariation |
| 1 | 8.3 | 12.7 | 1.5 | 1 | 5.0 | 2.6 | 0.5 |
| 2 | 3.0 | 5.2 | 1.7 | 2 | 6.0 | 2.6 | 0.4 |
| 4 | 2.3 | 4.0 | 1.7 | 4 | 2.0 | 3.5 | 1.8 |
| 10 | 26.7 | 7.8 | 0.3 | 10 | 6.7 | 3.1 | 0.4 |
| 18 | 7.7 | 7.5 | 1.0 | 13 | 3.7 | 0.6 | 0.2 |

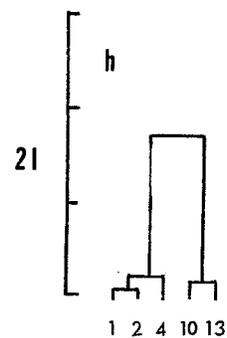
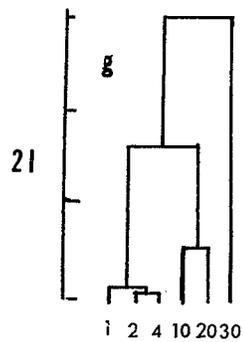
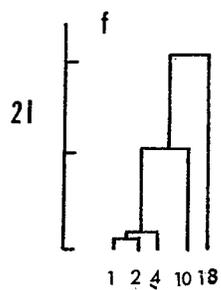
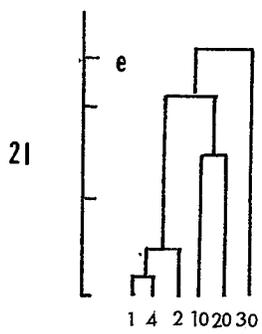
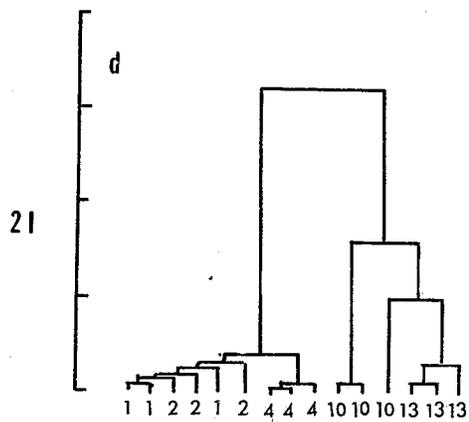
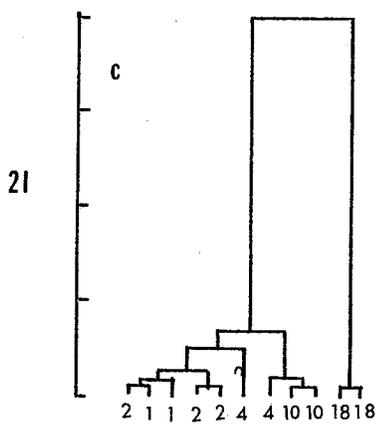
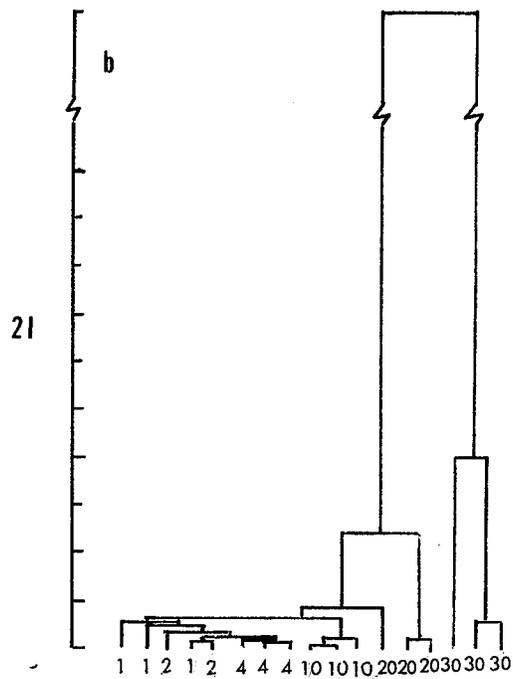
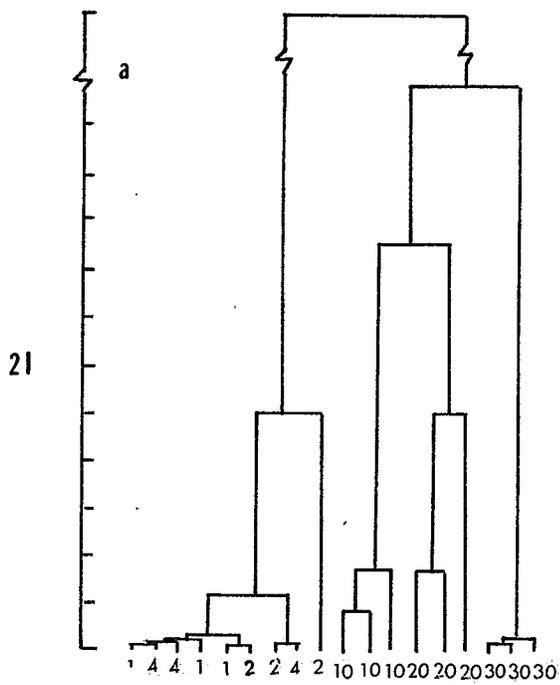
replicates, generally a realistic spatial representation of the taxonomic composition was obtained.

The multiple discriminant analysis model (Rao 1952, Cooley and Lohnes 1962) was chosen as the method of analysis to identify the significant environmental factors best separating the various ecological groups. This method essentially follows the techniques applied by Green (1971) in defining the Hutchinsonian niche of some mollusks of central Canada. The program used, a modification of Lee (1971), was found to yield identical results to the procedures used by Green (1971).

This analysis is subject to the same limitations stated by Green (1971). In addition, because of the temporal sequences in the data, this analysis tends to emphasize the stable physical variables over dynamic ones, resulting in the de-emphasis of such variables as oxygen and temperature, which have large within-group variances due to the seasonal cycles. This limitation is unfortunate, but inevitable, especially when one considers that in biological systems the high and low values occurring for short periods of time during a year are more likely limiting factors than the seasonal mean. Perhaps in the future a method efficiently utilizing both mean and extreme values will be found.

Figure 4. Hierarchical ordination of replicates collected on first sampling trip (June 1970).

(a) East Blue Lake, (b) Lake 239, (c) Beautiful Lake, (d) Lake 240, are dendograms resulting from analysis prior to lumping of replicates. (e) East Blue Lake, (f) Beautiful Lake, (g) Lake 239, (h) Lake 240, are results following lumping of replicates. Numbers correspond to depths sampled. All samples containing 0 organisms were deleted from the analysis.



The discriminant analysis was used in two analyses: 1) to identify the ecological factors which best separate the most numerous taxa in the lakes, 2) to identify the ecological factors which best separate the faunal assemblages previously identified.

Some of the assumptions in discriminant function analysis are 1) that the groups used be discrete a priori groups, and 2) that the groups be independent of each other. In the first analysis the taxa used were discrete groups and, if biological interaction can be ignored, they could also be assumed to be independent. In the second analysis, the assemblages were formed from a classification analysis, and some question on their being discrete groups could be raised. Because of the possibility that the above situations might violate the assumptions, the results of the discriminant analysis cannot be tested. However, even if the assumptions are violated, the use of discriminant function analysis as a descriptive tool is still valuable.

In the analysis, variables such as rooted vegetation, compensation point, and organic content of the sediment were used as possible indicators of the type of food available.

For the discriminant analysis among assemblages, the 14 chemical and physical parameters were used. For the other analysis, H_2S was deleted because it had a standard deviation of 0 within certain groups, and caused the program to malfunction. Also, since measurable amounts of the variable were highly localized, while the groups were not, it was felt that little information was gained by its inclusion.

The physico-chemical variables were logarithmically transformed, assuming a more multiplicative than additive relationship. The variables pH, sediment particle size, and sediment sorting coefficients were not transformed since pH and "phi" units are already logarithmic expressions.

RESULTS

Physical-Chemical Characteristics

According to the thermal classifications of Forel (1895), the four lakes fall into the temperate category. East Blue Lake, Lake 239, and Lake 240 are typically temperate dimictic (Hutchinson and Loffler 1956), but nowhere is the inadequacy of such classifications more evident than in Beautiful Lake with

its erratic circulations. It would have to be classified as temperate oligomictic, temperate because of its inverse stratification, and oligomictic because of the irregularity of its turnovers.

Masked by the trophic classification of the lakes is the fact that the two extreme lakes have in common high alkalinity, total hardness, and calcium hardness, as well as a well-vegetated littoral zone and geographical proximity. The effects of these on the presence of zoobenthic organisms will be discussed later. Lakes 239 and 240 are similar in most characteristics, including similar littoral substrates, shallow thermocline, and water chemistry since they share a common watershed. However, Lake 240 is shallower and suffers severe oxygen depletion. In terms of production, zooplankton (Patalas 1971), and diatom composition (Stockner and Armstrong 1971), these two lakes have been set into separate trophic groups.

The ranges of the physical parameters measured through the sampling period are summarized for each station in Table 2. Further data and discussion of water chemistry appear in Appendix II.

The environments of the zoobenthic organisms in the study areas can be summarized in the following manner.

Figure 5. Temperature profiles at the times of benthic sampling in the four lakes.

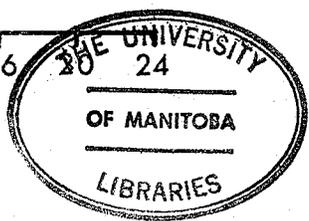
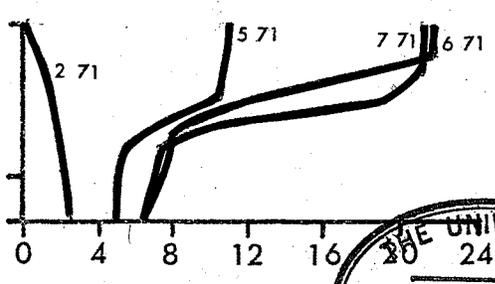
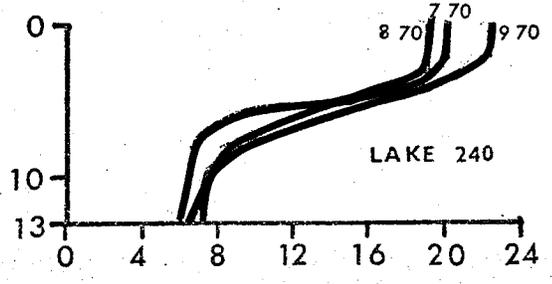
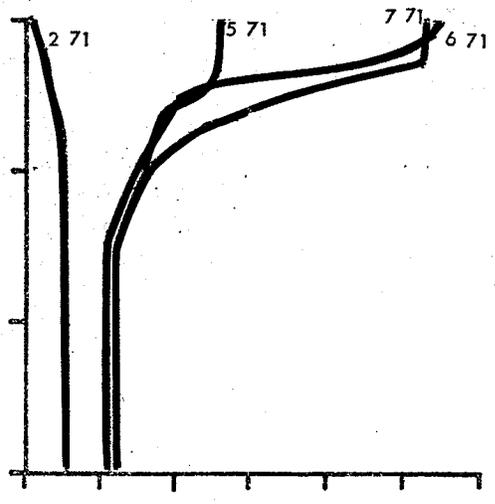
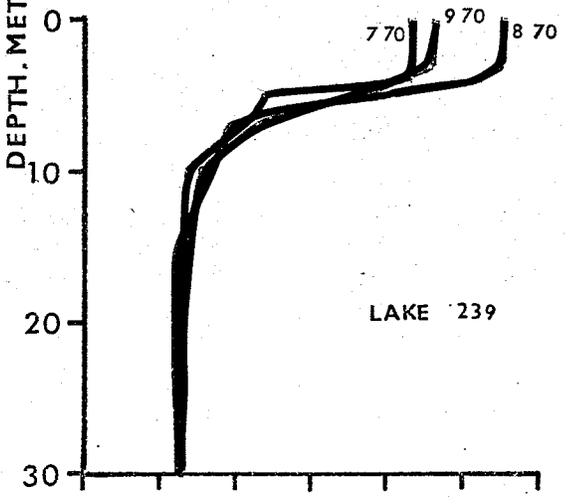
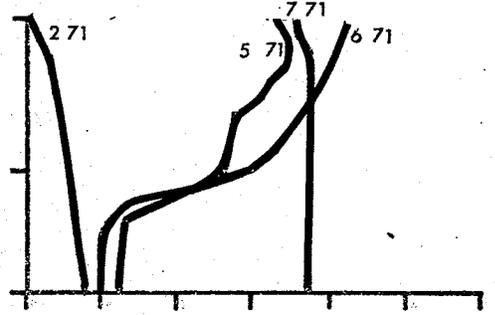
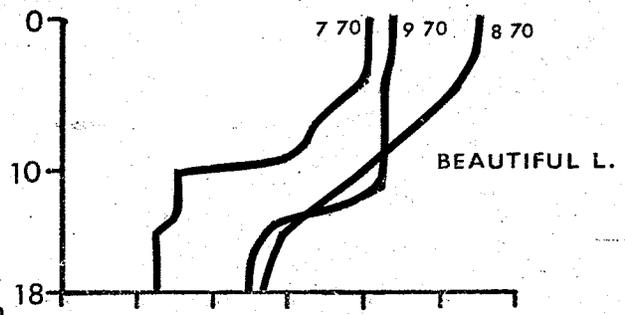
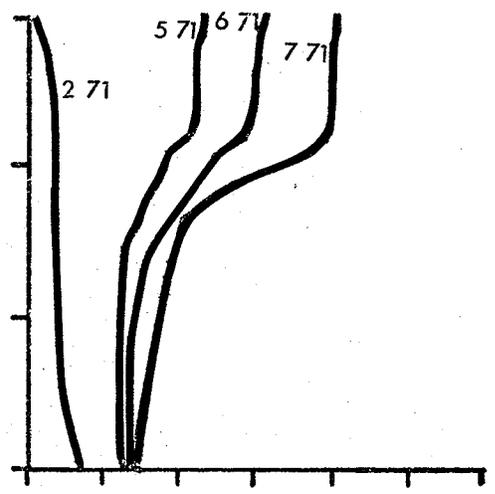
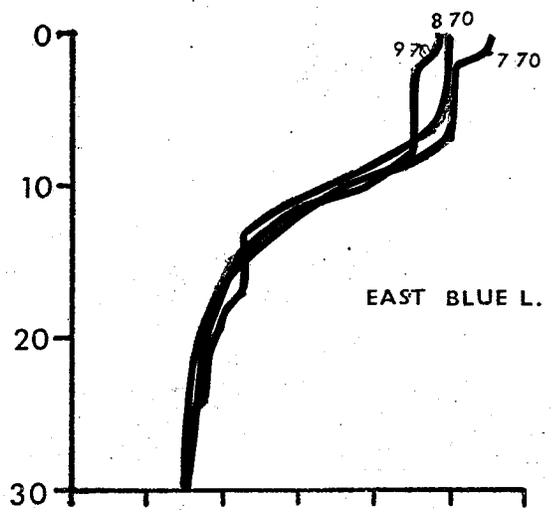
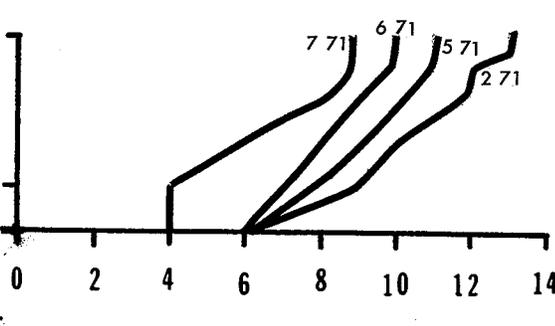
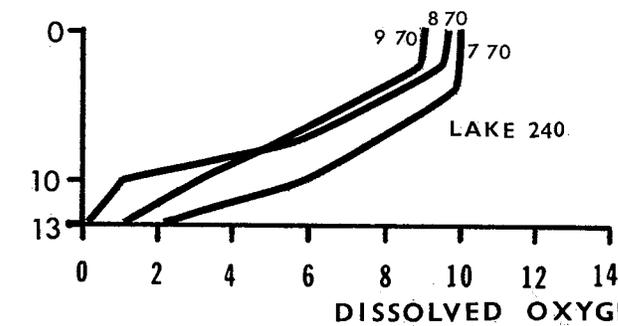
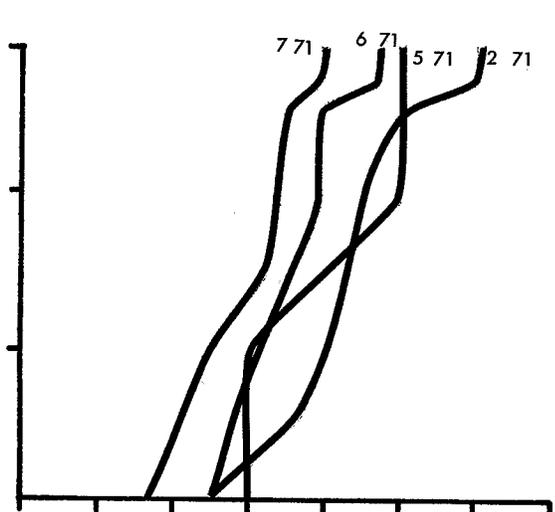
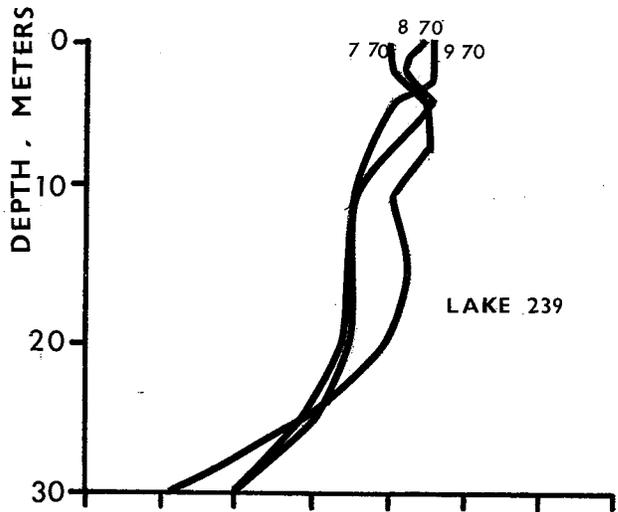
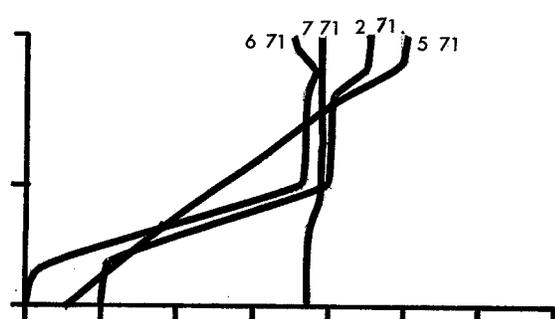
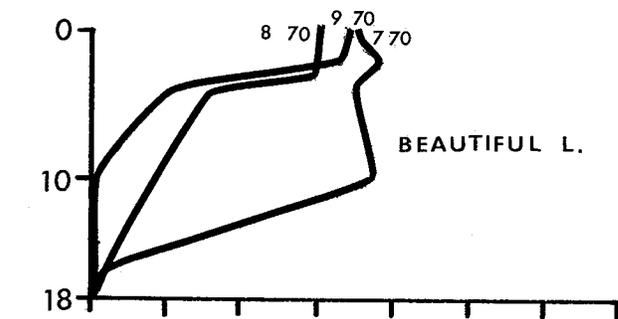
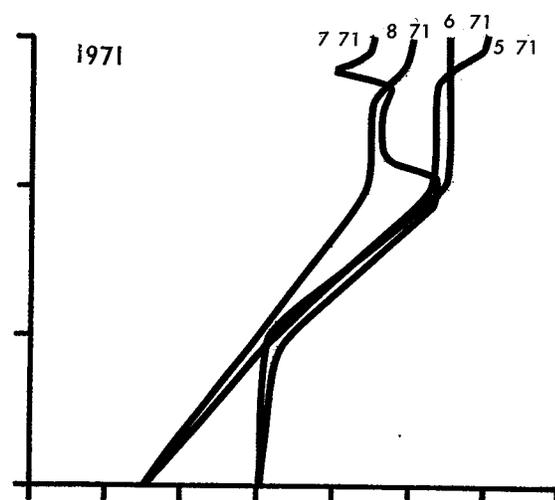
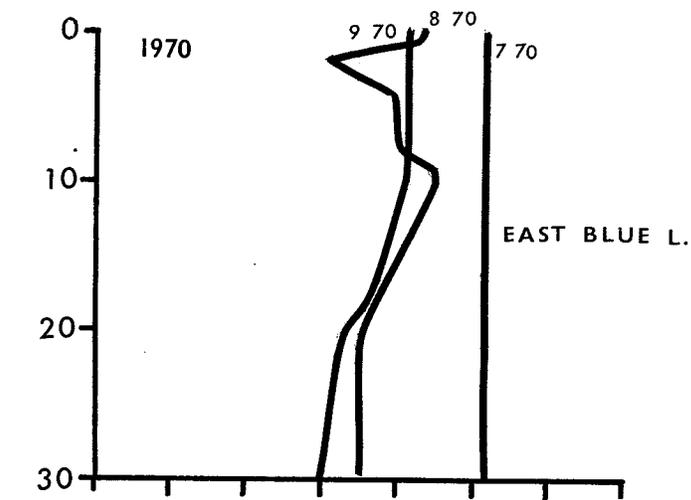


Figure 6. Oxygen profiles at the times of the benthic collections in the four lakes.



DISSOLVED OXYGEN, PPM.

Table 2. Mean seasonal values and ranges of the physical parameters of water collected immediately above the sediment surface at selected depths for each lake.

TABLE 2

| Lake | z (m) | Variables | | | | | | | | |
|-----------|----------|-----------------------|----------------|----------------|-------------------------|--------------|--------------------|----------------|-------------------------|---------------|
| | | O ₂ ppm | pH | Alk. ppm | H ₂ S ppm | Fe ppm | Total Mg ppm | Ca ppm | CO ₂ mg/l | Temp. °C |
| East Blue | 2 | 10.1 7-12 | 8.1 7.5-8.5 | 166 113-296 | 0.0 0 | 0.0 0-0.1 | 95.6 68-120 | 90.8 86-103 | 6.4 1.7-21.9 | 13.4 1-22 |
| | 10 | 10.1 9-11 | 8.3 8.0-8.5 | 153 141-172 | 0.0 0 | 0.1 0-0.1 | 105.1 68-137 | 85.7 68-120 | 2.6 1.7-3.9 | 9.8 1.5-15 |
| | 20 | 7.3 6-10 | 8.1 8.0-8.2 | 169 169-169 | 0.0 0 | 0.1 0-0.1 | 129.7 120-137 | 73.1 68-86 | 3.4 2.8-4.1 | 6.0 1.8-7 |
| | 30 | 6.3 3-11 | 7.8 7.5-8.0 | 167 155-173 | 0.0 0 | 0.1 0-0.2 | 134.2 120-137 | 68.0 68-68 | 6.1 4.1-11.5 | 5.7 5-6 |
| Beautiful | 2 | 8.0 6-10 | 8.2 7.8-8.5 | 139 99-162 | 0.0 0 | 0.1 0-0.5 | 111.0 86-137 | 86.0 69-137 | 2.6 1.9-3.8 | 14.3 1-22 |
| | 10 | 5.4 0-8 | 8.0 7.8-8.2 | 144 127-157 | 0.1 0-0.5 | 0.2 0-0.5 | 112.7 86-154 | 93.1 69-153 | 3.6 2.5-5.4 | 11.0 2-17 |
| | 18 | 1.5 0-7.4 | 7.5 6.8-8.0 | 170 155-211 | 0.2 0-1.5 | 0.2 0-1.0 | 115.1 86-120 | 86.0 69-103 | 20.2 3.7-80.2 | 7.1 4-15 |

TABLE 2 (cont'd)

| Lake | z (m) | Variables | | | | | | | | |
|----------|----------|-----------------------|----------------|-------------|-------------------------|----------------|---------------|----------------|-------------------------|--------------|
| | | O ₂ ppm | pH | Alk. ppm | H ₂ S ppm | Fe ppm | Mg ppm | Ca ppm | CO ₂ mg/l | Temp. °C |
| Lake 239 | 2 | 9.2 8-12 | 6.6 6.2-7.0 | 2 0-7 | 0.0 0 | 0.6 0-2 | 4.9 0-17 | 0 0 | 2.2 0-10.5 | 16.4 1-23 |
| | 10 | 7.7 5-10 | 5.9 5.8-6 | 6 0-14 | 0.0 0 | 2.6 0-5 | 2.4 0-17 | 0 0 | 14.2 0-26.6 | 5.4 2-7 |
| | 20 | 6.9 6-8 | 5.8 5.8-6 | 7 7-7 | 0.0 0 | 2.0 0-5 | 2.4 0-17.1 | 3.7 0-8.6 | 26.2 16.5-26.6 | 4.3 3-6 |
| | 30 | 4.1 2.5-6 | 5.9 5.8-6.2 | 7 7-7 | 0.0 0 | 2.2 0-6.0 | 2.4 0-17.1 | 6.2 0-8.6 | 20.6 10.5-26.6 | 4.4 3-6 |
| Lake 240 | 2 | 10.1 9-12 | 6.6 6.0-6.8 | 3 0-7 | 0.0 0 | 0.9 0-3.8 | 0.0 0 | 8.6 8.6-8.6 | 3.1 0-16.5 | 17.7 1-24 |
| | 10 | 5.4 1-9 | 5.7 5.5-6.5 | 8 0-14.1 | 0.0 0 | 3.8 3.0-5.4 | 9.8 0-17.1 | 8.6 8.6-8.6 | 32.7 0-104.3 | 7.1 3-11 |
| | 13 | 3.6 0-6 | 5.8 5.5-6.5 | 8 0-14 | 0.0 0 | 3.9 0.6-6.0 | 7.4 0-17.1 | 8.6 8.6-8.6 | 26.4 0-104.3 | 6.0 3-8 |

East Blue Lake

The sediment of East Blue was primarily autochthonous in nature, consisting of crushed molluscan and ostracod shells, and Chara remains encrusted with CaCO_3 . Soft, and with a high water content throughout the profile (Table 3), it was light grey in colour down to the thermocline, and brown to black below 10 m water depth.

Both the sorting coefficients and the mean particle size indicated sediment quite homogeneous in nature, poorly sorted, and in the fine sand range.

The percent organic material increased with water depth, especially below the thermocline. The high values in the epilimnion as compared with the other lakes, 8 - 12%, are indicative of the high density of Chara.

The most variable parameter, temperature, fluctuated approximately 20°C per year. Some instability in the sediment at the one meter zone was observed, since wind-driven waves often caused the substrate to shift.

Below the thermocline, little variation ($2 - 4^\circ\text{C}$) in annual temperature occurred. Oxygen did

Table 3. Characteristics of the surficial sediments
in the four lakes.

Table 3

| Lake | Depth m | $\bar{x} \theta$ | S.C. θ | % H ₂ O | % Organic |
|-----------|------------|------------------|---------------|-----------------------|--------------|
| East Blue | 1 | 2.3 | 2.6 | 75.0 | 9.3 |
| | 2 | 3.3 | 2.4 | 92.0 | 9.3 |
| | 4 | 2.2 | 2.0 | 80.0 | 12.0 |
| | 10 | 1.7 | 1.9 | 81.0 | 20.0 |
| | 20 | 2.3 | 2.2 | 81.0 | 32.0 |
| | 30 | 2.7 | 2.3 | 83.0 | 46.0 |
| Beautiful | 1 | 1.3 | 2.1 | 34.9 | 2.5 |
| | 2 | 1.3 | 3.3 | 74.4 | 5.4 |
| | 4 | 2.7 | 1.9 | 75.3 | 22.3 |
| | 10 | 2.7 | 1.9 | 91.3 | 51.7 |
| | 18 | 3.0 | 1.9 | 92.3 | 61.5 |
| Lake 239 | 1 | 0.3 | 2.6 | 27.5 | 1.2 |
| | 2 | 2.0 | 1.0 | 31.6 | 1.1 |
| | 4 | 2.0 | 0.7 | 33.0 | 0.8 |
| | 10 | 2.3 | 1.4 | 82.1 | 30.1 |
| | 20 | 1.3 | 1.2 | 78.8 | 23.5 |
| | 30 | 3.7 | 1.9 | 89.7 | 27.0 |
| Lake 240 | 1 | 2.0 | 1.3 | 52.3 | 7.86 |
| | 2 | 2.0 | 1.2 | 34.5 | 7.61 |
| | 4 | 2.0 | 1.3 | 35.7 | 1.72 |
| | 10 | 3.0 | 1.8 | 84.4 | 24.07 |
| | 13 | 3.0 | 1.7 | 89.1 | 38.84 |

not appear to be low enough to be limiting for the organisms described by Curry (1965), Jonasson (1972), and Walshe (1950). The compensation level was reached between 20 and 30 m, and hence only detrital material and bacteria were available for food. Most of the chemical parameters were similar to those of the ephilimnion (Table 2).

Beautiful Lake

The sediment of this lake was both autochthonous and allochthonous in origin. The 1 m station was composed mainly of coarse sand and small, angular pebbles, poorly sorted because of sheltering from the wind by the reed beds. At 4 m, the particles were in the fine to very fine sand range, and covered by a thin organic layer. It was soft to the touch, had a high water content, and below the surface had the consistency of clay. From 10 to 18 m the sediment consisted primarily of leafy material and reed stems. Over 90% water at this depth (Table 3), the sediment had the consistency of thick soup, and had a very high organic content.

The one meter depth area was sheltered from the wind, except in spring, by the macrophyte bed. The 2 m and 4 m depths were exposed to the wind and disturbed by the waves.

Not enough light for photosynthesis appeared to be present at 10 m and for a short period of the year the water was anoxic, with high CO₂ and iron concentrations (Table 2). Below the thermocline extended anoxic periods occurred, with very high concentrations of CO₂, iron, and some H₂S present during parts of the year. Great temperature fluctuations occurred during unpredictable summer turnovers, and considerable pH changes (eg. pH 8 to 6) were recorded.

Lake 239

Lake 239 sediment varied considerably with water depth. Large particle sizes (Table 3), coarse sand to very coarse sand, characterized the littoral zone to approximately 1.5 m. Beyond 4 m, a thick organic layer covered the sediment, increasing in thickness with water depth. From 10 m on, the sediment was a brown mixture of granular and flocculent material, partly composed of invertebrate fecal pellets. The water content and loss on ignition increased below the thermocline, the latter increasing 25 to 30 times while the former nearly trebled (Table 3).

Littoral zone temperature varied seasonally from 0°C to 23°C, and the area was well oxygenated.

At 10 m the sediment was very soft, overlain by a thin, flocculent, apparently organic layer; the gyttja here was thin because of a granitic shelf extending upwards. Little light penetrated this region. Below 10 m the water was low in oxygen during August and September of some years. Temperatures stayed close to 4°C throughout the year, varying two to three degrees (Appendix II).

The chemical parameters measured, with the exception of oxygen, changed little between epilimnion and hypolimnion or surface and interstitial water. In both cases, acidity and iron increased slightly with depth, probably in response to low oxygen and increased CO₂.

Lake 240

The surface sediments of Lake 240 were similar to those of Lake 239 (Table 3), except for the 1 m zone where the sediment was much better sorted and in the medium to fine sand category. Loss on ignition and percent water content values agreed closely with those given by Brunskill et.al. (1971, Table 8).

The littoral zone at the 1 and 2 m depths consisted of well sorted sand, with a narrow band of rocks (10 to 20 cm diameter) present at 2 m. In late

summer 10 to 20% of the area was covered by rooted vegetation, mainly Carex sp. and Utricularia sp. The area was well exposed to prevailing winds and the sediment in the 1 m zone often appeared to be shifting.

Below 2 m, smaller particles and greater water content created a softer sediment with a thin organic layer. Water chemistry, temperature ranges, and interstitial water resembled those of Lake 239, but with a higher iron content.

Sediment of the hypolimnion was very similar to that of Lake 239, but very low oxygen concentrations occurred and at time anoxic areas occurred below 10 m in the fall. Thus, within a span of four months, oxygen in an area changed from near saturation to zero, and iron from below 1 ppm to over 5 ppm. Temperature fluctuations were five to six degrees Centigrade, from 3°C in winter to 8 or 9°C in late fall.

Trends which were observable in the four lakes were:

- (1) O₂, pH, temperature, and sediment particle size decreased with water depth
- (2) Total dissolved iron, CO₂, and loss on ignition increased with increasing water depth.

Stability of the Physical Environment

As a measure of the stability of the environment, the mean coefficient of variation (Steel and Torrey 1960) was calculated for each sampling site. Only the following variables were used since data for these were available from each sampling period: dissolved oxygen, pH, alkalinity, H_2S , total iron, calcium, magnesium, temperature, presence or absence of macrophytes, and CO_2 . For depths of 1, 2, and 4 m, the values obtained at 2 m were used, except in the cases of dissolved oxygen, pH, temperature, and macrophytes which were determined at each sampling trip. For each variable the mean, standard deviation, and coefficient of variation were calculated. From these, the mean coefficient of variation for all variables was derived. A high mean coefficient of variation was interpreted as indicating a zone of fluctuating environmental conditions, and a low coefficient of variation was interpreted as indicating relatively stable environmental conditions. The results are summarized in Table 4.

From these results, it became apparent that in both East Blue and Lake 239 the shallow zone was more unstable than the hypolimnetic zone. Lake 240 was unstable both in the shallow zone and at maximum

depth; this latter probably was due to the high rates of oxygen depletion during summer and winter stratification as evidenced by the main contributors to the coefficient of variation at 13 m being dissolved oxygen and iron. The most unstable conditions were the shallow water zones, however. Beautiful Lake had conditions reversed from the other lakes, with instability increasing with depth. The primary contributors to the high coefficient of variation at 18 m were dissolved oxygen, H_2S , total iron, temperature, and CO_2 .

The Distribution of Benthic Organisms Between and Within Lakes

The average densities decreased with depth in each lake, generally following the distributions of benthos in lakes first described by Lundbeck in 1926 (Figure 7a,b,c,d).

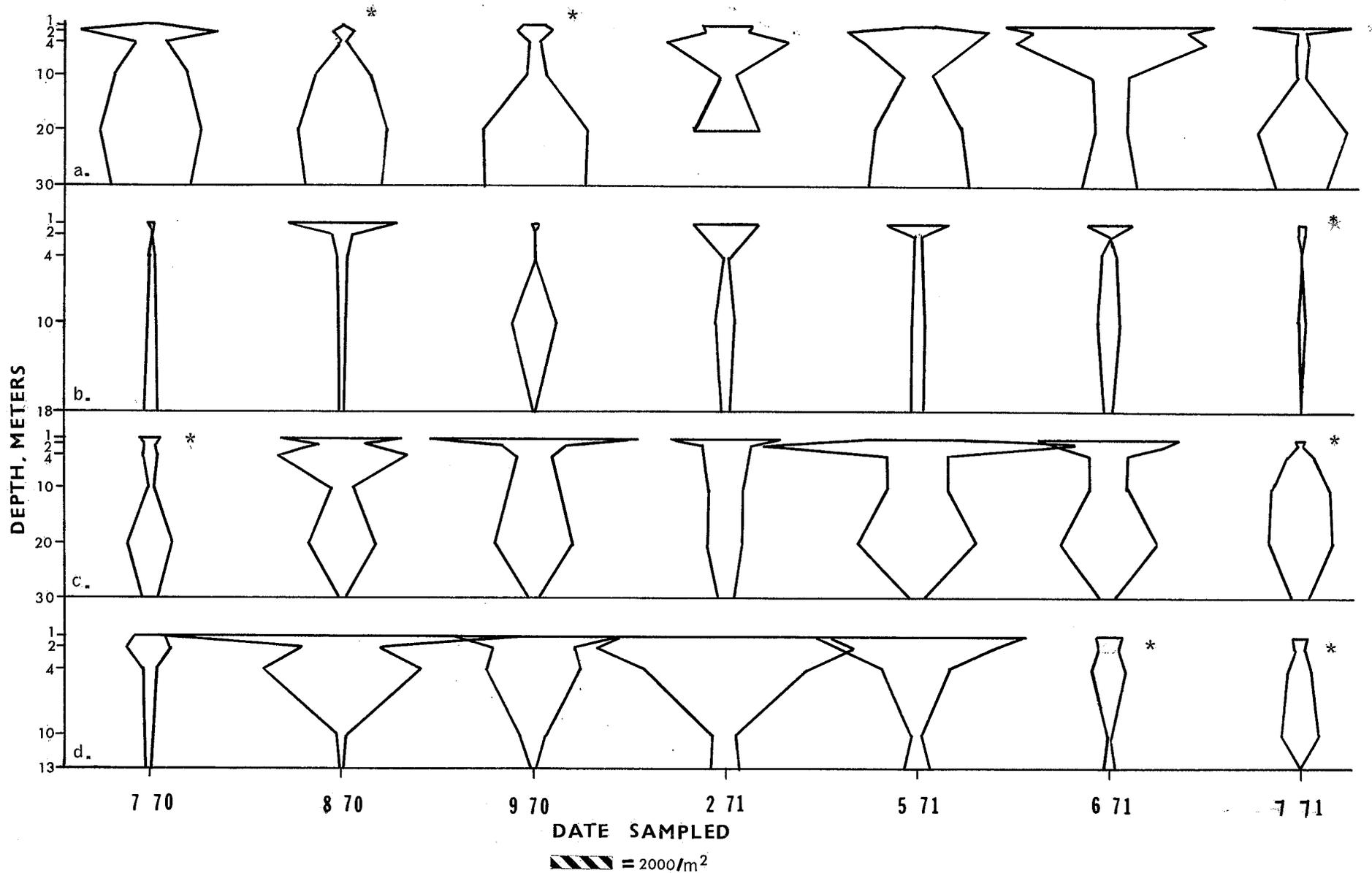
In all lakes, the highest and lowest densities were encountered in the top two meter zones. The periods when the lowest numbers were sampled corresponded closely to the presence of high winds and considerable wave action in the shallow areas (Figure 7a,c,d, asterisked). Whether the wave action resulted in

Table 4. Mean coefficient of variation for all physical and chemical data collected during the sampling year.

TABLE 4

| EAST BLUE LAKE | | LAKE 239 | |
|----------------------------|---|----------------------------|---|
| <u>Depth</u> <u>(m)</u> | <u>Coefficient</u> <u>of Variation</u> | <u>Depth</u> <u>(m)</u> | <u>Coefficient</u> <u>of Variation</u> |
| 1 | 0.57 | 1 | 0.95 |
| 2 | 0.46 | 2 | 0.95 |
| 4 | 0.45 | 4 | 0.95 |
| 10 | 0.16 | 10 | 0.26 |
| 20 | 0.12 | 20 | 0.28 |
| 30 | 0.20 | 30 | 0.28 |
| BEAUTIFUL LAKE | | LAKE 240 | |
| 1 | 0.21 | 1 | 0.56 |
| 2 | 0.26 | 2 | 0.54 |
| 4 | 0.28 | 4 | 0.54 |
| 10 | 0.41 | 10 | 0.28 |
| 18 | 0.72 | 13 | 0.41 |

Figure 7. Bathymetric distribution of benthic organisms in (a) East Blue Lake; (b) Beautiful Lake; (c) Lake 239; (d) Lake 240. Asterisks indicate collections made either during or following windy periods.



organisms being transported to other areas, high mortality, or movement into deeper sediments is not known.

The densities collected in the hypolimnion were, on the average, lower than those collected above the thermocline. The seasonal fluctuations encountered in the hypolimnion were of a lower magnitude than those found in the epilimnion, and the seasonal minima could usually be correlated with the disappearance of the fourth instars of the dominant members of the Chironomidae or Chaoborinae, or reflecting the life history patterns of P. affinis as presented in the following pages.

Results of the zoobenthic identifications and the lakes in which the animals occur are summarized in Appendix I. The ninety taxa recognized will be referred to as species, although some (indicated by an asterisk) represent more than one species. From these results, it appeared that many species were shared between Lakes 239 and 240, some shared between East Blue and Beautiful Lakes, but little similarity existed between the two geological areas.

In the 90 taxa, 41 genera were represented. For the purpose of diversity indices, two taxa were

omitted the oligochaetes because they were not properly identified, and the Hydracarina because of their strongly contagious distribution. The remaining species were distributed as follows: East Blue Lake, 33; Beautiful Lake, 24; Lake 239, 35; Lake 240, 37.

When the distribution of species within lakes was examined, all the species occurring in at least three samples were plotted against depth for each lake (Table 5). Results indicated that the area of the littoral zone to the depth of the summer thermocline usually held the largest number of species, as well as being represented by the largest number of orders and families. Almost all of the Ephemeroptera, Trichoptera, Coleoptera, and Ceratopogonidae came from this region, as well as the few Odonata and Gastropoda (not shown).

Within the Chironomidae, which made up by far the largest number of organisms collected, the greatest diversity below the family level was found at stations in the littoral region. Two to three genera of the tribe Tanytarsini were usually found, several of the Orthocladini, and six to twelve genera of Chironomini.

The sole amphipod abundant in the littoral stations of all four lakes was Hyalella azteca.

Table 5. Species—depth distribution for each lake.

TABLE 5

| East Blue Lake | | 1 m | 2 m | 4 m | 10 m | 20 m | 30 m |
|--------------------------------|------|-----|-----|-----|------|------|------|
| <u>Pagastiella</u> | | x | x | | | | |
| <u>Ephemera varia</u> | | x | x | | | | |
| <u>Cricotopus</u> | sp 1 | | x | x | | | |
| <u>Cricotopus</u> | sp 2 | | x | x | | | |
| <u>Chironomus</u> | sp 1 | x | x | x | x | | |
| <u>Dicrotendipes</u> | sp 1 | x | x | x | | | |
| <u>Polypedilum (Tripodura)</u> | sp 1 | x | x | x | x | | |
| <u>Polypedilum (Tripodura)</u> | sp 2 | x | x | x | x | | |
| <u>Paratendipes</u> | sp | x | | | x | | |
| <u>Cryptochironomus</u> | sp | | x | x | x | | |
| <u>Einfeldia</u> | sp | | x | | x | | |
| <u>Psectrotanypus</u> | sp | | | | x | | |
| <u>Paratanytarsus</u> | sp 2 | x | x | x | | | |
| <u>Paratanytarsus</u> | sp 3 | x | x | x | | x | |
| <u>Pisidium variable</u> | | x | | | | x | |
| <u>Pisidium casertanum</u> | | x | | | x | x | |
| <u>Hyalella azteca</u> | | x | x | x | x | x | |
| <u>Bezzia/Palpomyia</u> | sp 1 | | | x | x | x | |
| <u>Tanytarsus</u> | sp 7 | x | | x | x | x | |
| <u>Cryptocladopelma</u> | sp 2 | | x | | x | x | |
| <u>Heterotanytarsus</u> | sp 1 | | | | | x | |
| <u>Psectrocladius</u> | sp 1 | | | | | x | |
| <u>Ablabesmyia</u> | sp 1 | x | x | x | | | x |
| <u>Tanytarsus</u> | sp 4 | x | x | x | x | x | x |
| <u>Tanytarsus</u> | sp 5 | x | x | x | x | x | x |
| <u>Tanytarsus</u> | sp 7 | x | x | x | x | x | x |
| <u>Chironomus</u> | sp | | | | | x | x |
| <u>Chironomus</u> | sp 5 | | | | x | x | x |
| <u>Chironomus</u> | sp 7 | | | | | x | x |
| <u>Procladius</u> | spp | x | x | x | x | x | x |

TABLE 5 (Cont'd)

| Lake 239 | | 1 m | 2 m | 4 m | 10 m | 20 m | 30 m |
|--------------------------------|-------|-----|-----|-----|------|------|------|
| <u>Cryptocladopelma</u> | sp 1 | x | | | | | |
| <u>Stictochironomus</u> | sp | x | | | | | |
| <u>Micropsectra</u> | sp | x | x | | | | |
| <u>Paratanytarsus</u> | sp | x | x | | | | |
| <u>Heterotanytarsus</u> | sp | x | x | | | | |
| <u>Cricotopus</u> | sp | x | x | | | | |
| <u>Hyalella azteca</u> | | x | x | | | | |
| <u>Elmiidae</u> | | x | x | | | | |
| <u>Polypedilum (Tripodura)</u> | sp | x | x | | | | |
| <u>Dicrotendipes</u> | sp | x | x | x | | | |
| <u>Ablabesmyia</u> | sp 2 | x | x | x | | | |
| <u>Cryptocladopelma</u> | sp | | x | x | | | |
| <u>Paralauterborniella</u> | spp | x | x | x | | | |
| <u>Pagastiella</u> | | x | x | x | | | |
| <u>Cryptochironomus</u> | sp | x | x | x | | | |
| <u>Microtendipes</u> | sp | x | | x | | | |
| <u>Pentapedilum</u> | sp | x | x | x | | | |
| <u>Paratanytarsus</u> | sp 1 | | x | x | | | |
| <u>Ephemera varia</u> | | x | | x | | | |
| <u>Bezzia/Palpomyia</u> | sp | x | | x | | | |
| <u>Heterotrissocladus</u> | spp | x | x | x | x | x | |
| <u>Protanypus</u> | | x | x | | x | x | |
| <u>Tanytarsus</u> | sp | x | x | x | x | x | |
| <u>Tanytarsus</u> | sp 1 | x | x | x | x | x | |
| <u>Mysis relicta</u> | | | | | x | x | |
| <u>Procladius</u> | spp 1 | x | x | x | x | x | |
| <u>Chironomus</u> | sp 4 | | | | | x | x |
| <u>Chironomus</u> | sp 6 | | | | | x | x |
| <u>Pisidium conventus</u> | | | x | x | x | x | x |
| <u>Pontoporeia affinis</u> | | | | x | x | x | x |
| <u>Phaenopsectra</u> | sp 1 | x | x | x | | x | x |

TABLE 5 (Cont'd)

| Lake 240 | | 1 m | 2 m | 4 m | 10 m | 13 m |
|--------------------------------|-------|-----|-----|-----|------|------|
| <u>Stictochironomus</u> | sp 1 | x | | | | |
| <u>Monodiamesa</u> | | x | | | | |
| <u>Leptophlebia</u> | sp | x | | | | |
| <u>Hexagenia limbata</u> | | x | | | | |
| <u>Athripsodes</u> | | x | | | | |
| <u>Microtendipes</u> | sp | x | x | | | |
| <u>Paralauterborniella</u> | spp | x | x | | | |
| <u>Pisidium conventus</u> | | x | x | | | |
| <u>Ablabesmyia</u> | sp 2 | | x | | | |
| <u>Micropsectra</u> | sp | x | x | | | |
| <u>Hyalella azteca</u> | | x | x | | | |
| <u>Elmiidae</u> | | x | x | | | |
| <u>Tanytarsus</u> | sp | x | x | x | | |
| <u>Tanytarsus</u> | sp 1 | x | x | x | | |
| <u>Paratanytarsus</u> | sp | x | x | x | | |
| <u>Pagastiella</u> | sp | x | x | x | | |
| <u>Heterotrissocladus</u> | spp | x | x | x | | |
| <u>Cryptocladopelma</u> | sp | x | x | x | | |
| <u>Cryptocladopelma</u> | sp 1 | x | x | x | | |
| <u>Polypedilum (Tripodura)</u> | sp | x | x | x | | |
| <u>Polypedilum (Tripodura)</u> | sp 1 | x | x | x | | |
| <u>Cryptochironomus</u> | sp 1 | x | | x | | |
| <u>Cricotopus</u> | sp | | x | x | | |
| <u>Heterotanytarsus</u> | sp | | | x | | |
| <u>Heterotanytarsus</u> | sp 1 | | | x | | |
| <u>Pontoporeia affinis</u> | | | | x | | |
| <u>Ephemera gluttulata</u> | | | | x | | |
| <u>Procladius</u> | spp 1 | x | x | x | x | |
| <u>Phaenopsectra</u> | sp | | | | x | |
| <u>Phaenopsectra</u> | sp 1 | | | | x | |
| <u>Chironomus</u> | sp 6 | | | | x | x |
| <u>Chaoborus flavicans</u> | | | | | x | x |
| <u>Chaoborus punctipinnis</u> | | | | | x | x |

TABLE 5 (Cont'd)

| Beautiful Lake | | 1 m | 2 m | 4 m | 10 m | 18 m |
|--------------------------------|------|-----|-----|-----|------|------|
| <u>Pseudochironomus</u> | sp 1 | x | | | | |
| <u>Dicrotendipes</u> | sp 2 | x | | | | |
| <u>Dicrotendipes</u> | sp 3 | x | | | | |
| <u>Cryptochironomus</u> | sp 2 | x | | | | |
| <u>Polypedilum (Tripodura)</u> | sp 1 | x | | | | |
| <u>Psectrocladius</u> | sp 1 | x | | | | |
| <u>Hyallela azteca</u> | | x | | | | |
| <u>Bezzia/Palpomyia</u> | sp 1 | x | x | | | |
| <u>Paratanytarsus</u> | sp 3 | x | x | x | | |
| <u>Tanytarsus</u> | sp 3 | x | x | x | | |
| <u>Tanytarsus</u> | sp 8 | x | x | x | x | |
| <u>Caenis</u> | sp | x | x | x | x | |
| <u>Cryptocladopelma</u> | sp 2 | | x | x | x | x |
| <u>Chironomus</u> | sp 2 | | | | x | x |
| <u>Chironomus</u> | sp 3 | | | | x | x |
| <u>Procladius</u> | spp | x | x | x | x | x |
| <u>Chaoborus punctipinnis</u> | | | | | | x |

Stations below the thermocline were generally characterized by a decrease in the number of taxa. Three genera of chironomids occurred, Chironomus, Phaenopsectra, and Tanytarsus. The other macro-organisms found in large numbers appeared to be specific to particular lakes; these were the phantom midge Chaoborus, the burrowing amphipod Pontoporeia affinis, and the clam Pisidium conventus.

Few species were found in large numbers both above and below the thermocline. Members of the oligochaetes were present at all depths, and several species of the genus Tanytarsus through most depths, though the maximum depth distribution of the latter varied from lake to lake. The primary predatory chironomid, Procladius (Roback 1969), was found in all lakes and at all depths.

Of the 41 genera present in the collection, many were represented by a few individuals distributed over a narrow depth zone.

The genera which were numerically dominant in at least one of the lakes were: Tanytarsus, Paratanytarsus, Micropsectra, Chironomus, Phaenopsectra, Pagastiella, Cryptocladopelma, Procladius, Chaoborus, Pisidium, Hyaella azteca, and Pontoporeia affinis;

their numerical contribution to the samples of each lake and to the total are summarized in Table 6. Of the above, the following are discussed in greater detail: Tanytarsus, Paratanytarsus, Chironomus, Phaenopsectra, Chaoborus, Pisidium, H. azteca, and P. affinis. The numerical importance of each species of the above genera collected at each depth sampled is summarized in Table 7.

Tanytarsus

Tanytarsus is a widespread genus of both North American and European aquatic environments. It has been described as occurring from shallow woodland ponds (Armitage 1968) to deep oligotrophic lakes, and was one of the key genera in the lake faunistic type systems of Thienemann (1928) where it was considered an indicator of oligotrophic conditions.

Armitage (1968, 1970) and Hamilton (1965) describe the genus as being both an algal and detritus feeder. From laboratory observations, Cavanaugh and Tilden (1930) concluded that Tanytarsus dissimilis was feeding almost exclusively on algae.

The genus Tanytarsus was widespread in all four of the lakes studied, with a total of seven species

Table 6. Actual numbers of the dominant taxa collected in each lake during the sampling period.

TABLE 6

| | EAST BLUE LAKE | BEAUTIFUL LAKE | LAKE 239 | LAKE 240 |
|--------------------------------------|---------------------------------|---------------------------------|---------------------------------|---------------------------------|
| | <u>Nos.</u> <u>Collected</u> | <u>Nos.</u> <u>Collected</u> | <u>Nos.</u> <u>Collected</u> | <u>Nos.</u> <u>Collected</u> |
| * <u>Chaoborus flavicans</u> | 0 | 0 | 0 | 64 |
| * <u>Chaoborus punctipinnis</u> | 0 | 3 | 6 | 83 |
| * <u>Chironomus</u> | 1487 | 163 | 131 | 27 |
| <u>Cryptocladopelma</u> | 11 | 33 | 16 | 12 |
| <u>Micropsectra</u> | 0 | 0 | 1 | 11 |
| <u>Pagastrella</u> | 11 | 1 | 47 | 33 |
| * <u>Paratanytarsus</u> | 43 | 28 | 141 | 117 |
| * <u>Phaenopsectra</u> | 0 | 0 | 26 | 159 |
| <u>Polypedilum</u> | 24 | 6 | 29 | 50 |
| <u>Procladius</u> | 129 | 26 | 61 | 67 |
| * <u>Tanytarsus</u> | 727 | 76 | 269 | 355 |
| * <u>Hyalella azteca</u> | 139 | 6 | 23 | 23 |
| * <u>Pentoporeia affinis</u> | 0 | 0 | 745 | 5 |
| * <u>Pisidium conventus</u> | <u>9</u> | <u>0</u> | <u>538</u> | <u>9</u> |
| Column total | 2580 | 342 | 2034 | 1015 |
| Total organisms collected in Lake | 3073 | 510 | 2413 | 1361 |

Table 7. The numerical importance of each major species to the samples collected at each depth. The numerical importance is expressed as percent of total benthos collected at depth.

TABLE 7

| | LAKE 239 | | | | | | LAKE 240 | | | | |
|-----------------------------|------------|------|------|------|------|------|------------|------|------|------|------|
| | Depth in m | | | | | | Depth in m | | | | |
| | 1 | 2 | 4 | 10 | 20 | 30 | 1 | 2 | 4 | 10 | 13 |
| <u>Paratanytarsus</u> sp. 1 | 17.7 | 21.3 | - | - | - | - | 11.4 | 7.6 | 16.4 | - | - |
| <u>Paratanytarsus</u> sp. | | 8.8 | 11.7 | 0.2 | - | - | - | - | - | - | - |
| <u>Tanytarsus</u> sp. | 8.2 | 7.3 | 16.3 | 2.7 | 1.6 | - | 10.6 | 24.5 | 16.5 | 0.9 | - |
| <u>Tanytarsus</u> sp. 1 | 2.7 | 11.8 | 13.0 | 5.2 | 10.3 | - | 16.9 | 23.6 | 21.5 | 0.9 | - |
| <u>Chironomus</u> sp. 6 | - | - | - | - | 1.5 | 42.2 | 0.5 | - | 0.4 | 5.6 | 9.8 |
| <u>Chironomus</u> sp. 4 | - | - | - | - | 0.1 | 30.8 | - | - | - | - | - |
| <u>Phaenopsectra</u> sp. | 0.5 | 0.4 | 0.7 | - | 0.3 | 5.4 | - | 0.4 | 0.8 | 12.4 | - |
| <u>Phaenopsectra</u> sp. 1 | - | - | - | - | - | - | - | - | - | 54.9 | 2.2 |
| <u>C. flavicans</u> | - | - | - | - | - | - | - | - | 0.4 | 4.4 | 39.1 |
| <u>C. punctipinnis</u> | 0.5 | - | - | - | - | 0.6 | - | - | - | 9.7 | 45.9 |
| <u>H. azteca</u> | 5.2 | 1.3 | 0.7 | 0.2 | - | - | 3.8 | 3.0 | - | - | - |
| <u>P. affinis</u> | 0.2 | 0.4 | 1.4 | 38.6 | 53.9 | 12.0 | - | 0.8 | 1.3 | - | - |
| <u>P. conventus</u> | 0.5 | 1.3 | 6.5 | 47.8 | 29.2 | 3.0 | 0.9 | 1.1 | 0.4 | - | - |

TABLE 7 (cont'd)

| | | EAST BLUE LAKE | | | | | | BEAUTIFUL LAKE | | | | |
|------------------------|-------|----------------|------|------|------|------|------|----------------|------|------|------|------|
| | | Depth in m | | | | | | Depth in m | | | | |
| | | 1 | 2 | 4 | 10 | 20 | 30 | 1 | 2 | 4 | 10 | 18 |
| <u>Paratanytarsus</u> | sp. 2 | 2.9 | 9.0 | 1.4 | - | - | - | 10.3 | 19.3 | 36.8 | 0.9 | 2.4 |
| <u>Paratanytarsus</u> | sp. 3 | - | 0.6 | 2.4 | 1.1 | 0.4 | - | - | - | - | - | - |
| <u>Tanytarsus</u> | sp. 7 | 6.6 | 1.3 | 2.6 | 14.0 | 15.1 | 0.1 | - | - | - | - | - |
| <u>Tanytarsus</u> | sp. 3 | - | - | - | - | - | - | 25.3 | 19.3 | 21.0 | - | - |
| <u>Tanytarsus</u> | sp. 4 | 5.8 | 3.1 | 2.6 | 12.0 | 17.4 | 0.4 | - | - | - | - | - |
| <u>Tanytarsus</u> | sp. 8 | - | - | - | - | - | - | 8.0 | 9.7 | 5.3 | 6.9 | 3.6 |
| <u>Tanytarsus</u> | sp. 5 | 0.1 | 1.0 | 2.7 | 7.4 | 13.5 | 1.2 | - | - | - | - | - |
| <u>Chironomus</u> | sp. 5 | - | - | - | 1.4 | 11.5 | 47.6 | - | - | - | - | - |
| <u>Chironomus</u> | sp. 3 | - | - | - | - | - | - | - | - | 5.3 | 38.1 | 47.2 |
| <u>Chironomus</u> | sp. 2 | - | - | - | - | 20.5 | 51.1 | 1.6 | 6.4 | 5.3 | 18.1 | 15.0 |
| <u>Chironomus</u> | sp. 1 | 28.5 | 28.8 | 61.9 | 5.7 | 0.3 | - | - | - | - | - | - |
| <u>C. punctipinnis</u> | | - | - | - | - | 0.1 | - | - | - | - | - | 3.6 |
| <u>H. azteca</u> | | 5.8 | 3.9 | 5.7 | 22.4 | 1.3 | 0.1 | 8.7 | 3.2 | - | - | 1.2 |
| <u>P. conventus</u> | | - | 0.1 | - | 0.1 | - | - | - | - | - | - | - |

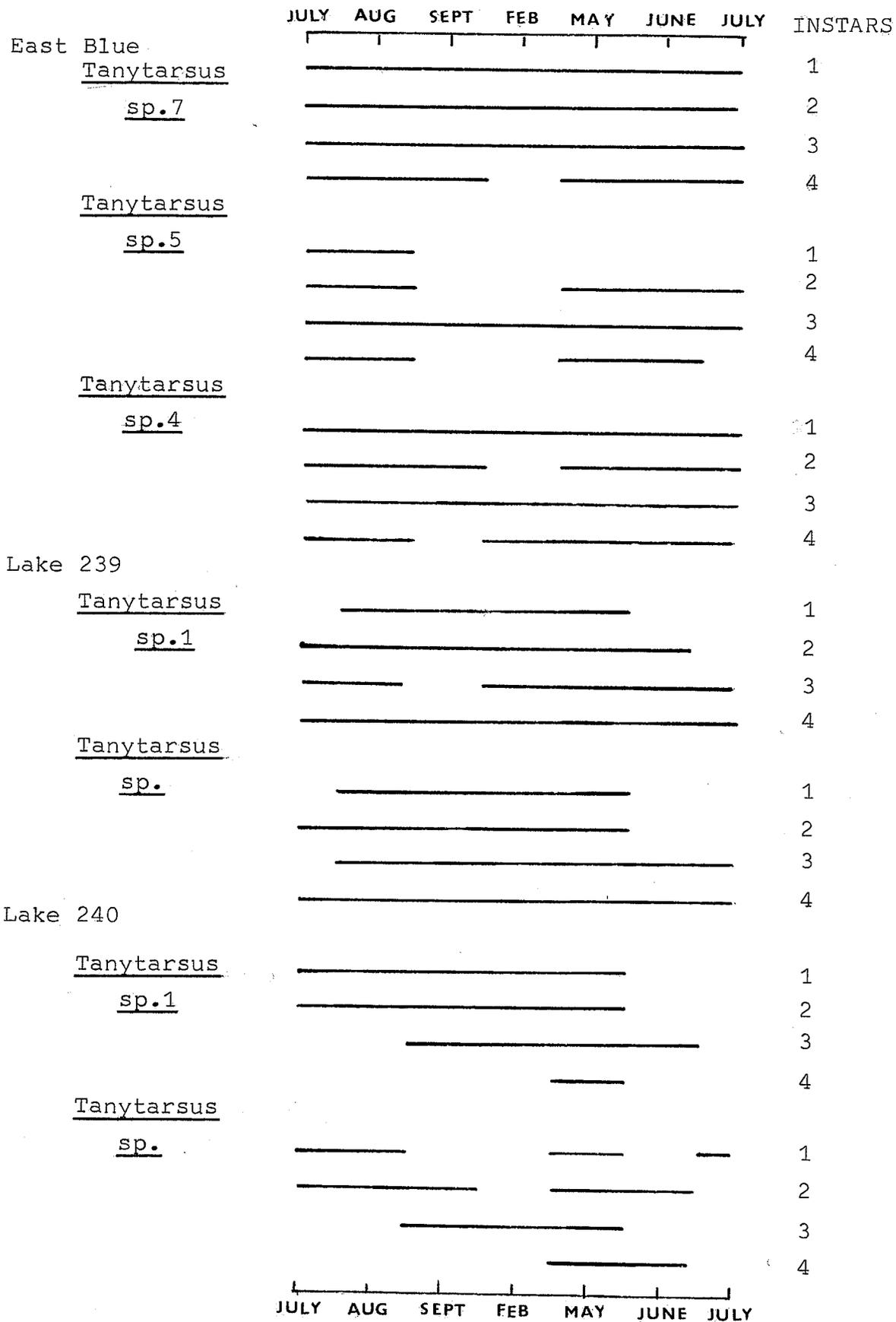
recognized (Appendix III). Three of these, sp. 4, 5, and 7, were found in the East Blue samples, two in Beautiful Lake (sp. 3 and sp. 8), and Tanytarsus sp. and sp. 1 in both Lakes 239 and 240.

In East Blue Lake, a total of 230 individuals of Tanytarsus sp. 7, 271 of Tanytarsus sp. 5, and 226 of Tanytarsus sp. 4 were collected. In Beautiful Lake, only 49 individuals of Tanytarsus sp. 3, and 27 of Tanytarsus sp. 8 were collected. In Lake 239, 145 individuals of Tanytarsus sp. 1 and 124 of Tanytarsus sp. were collected, and in Lake 240 171 individuals of Tanytarsus sp. 1 and 184 of Tanytarsus sp.

Based on the time of disappearance or decrease of fourth instar individuals (Figure 8), it appears that Tanytarsus emerged throughout the open water season. These results are in agreement with the varying emergence periods reported in the literature. For example, Armitage (1970) reported that Tanytarsus emerged randomly throughout the open-water season; Hamilton (1965) found that, of two species in Marion Lake, one emerged in the late summer and one in late fall.

The spatial distributions of the species are shown in Figures 9 and 10. A greater difference in the distribution occurred among lakes, than between species within lakes.

Figure 8. Temporal distribution of the instars of Tanytarsus species collected in the four lakes.



In general, the lowest limits of the distribution of the species depended on the conditions in the lake. They extended to 30 m in East Blue, 20 m in Lake 239, and to 4 m in Lake 240. In Beautiful Lake, they extended to 4 m in 1970 and 18 m in the summer of 1971.

When several species were found in the same lake, they occupied very similar environments and typically overlapped spatially. The greatest separation in these situations occurred in the first and second instars, when the individuals were distributed over different depths or occurred at slightly different times.

In most species, a spatial differentiation occurred for each instar, earlier instars being found in shallower waters while the later instars were deeper. The third and fourth instars always occupied the deepest portion of the genus' range in the lake; few fourth instar individuals were ever found in the shallow water regions. This distribution was common to all the lakes, with the exception of sp. 1 in Lake 240 (Figure 10).

There are reports in the literature of the presence of large larvae in the hypolimnion later in the season than those found in the shallower water (Miller 1941), and this has been interpreted in the

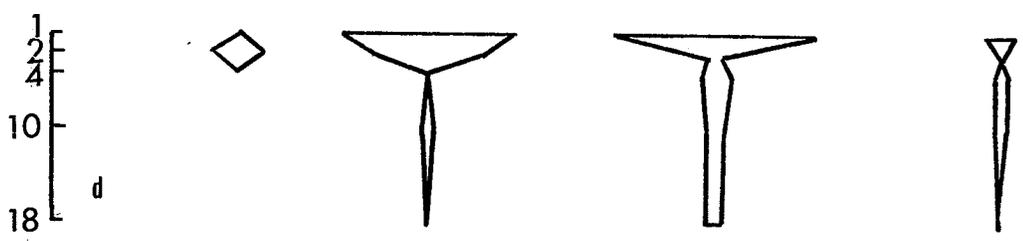
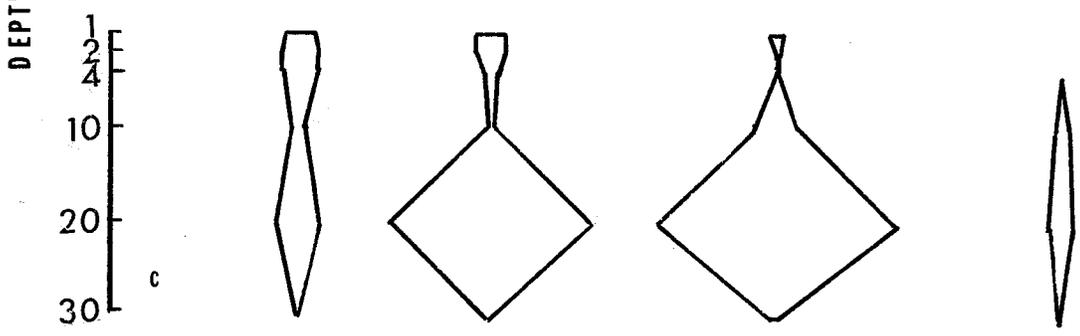
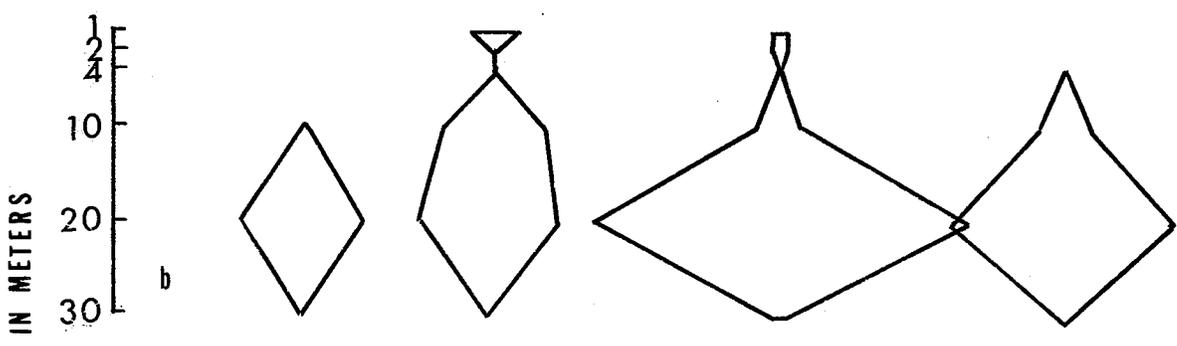
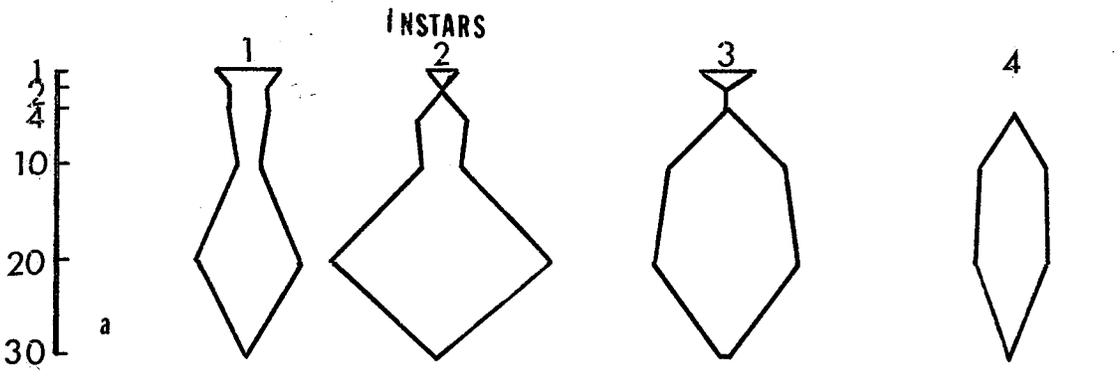
Figure 9. Spatial distribution of the instars of Tanytarsus species collected in East Blue Lake (a, b, c) and Beautiful Lake (d).

a) Tanytarsus sp. 7

b) Tanytarsus sp. 5

c) Tanytarsus sp. 4

d) Tanytarsus spp.



1000

Figure 10. Spatial distribution of the instars of Tanytarsus species collected in Lake 239 (a, b) and Lake 240 (c, d).

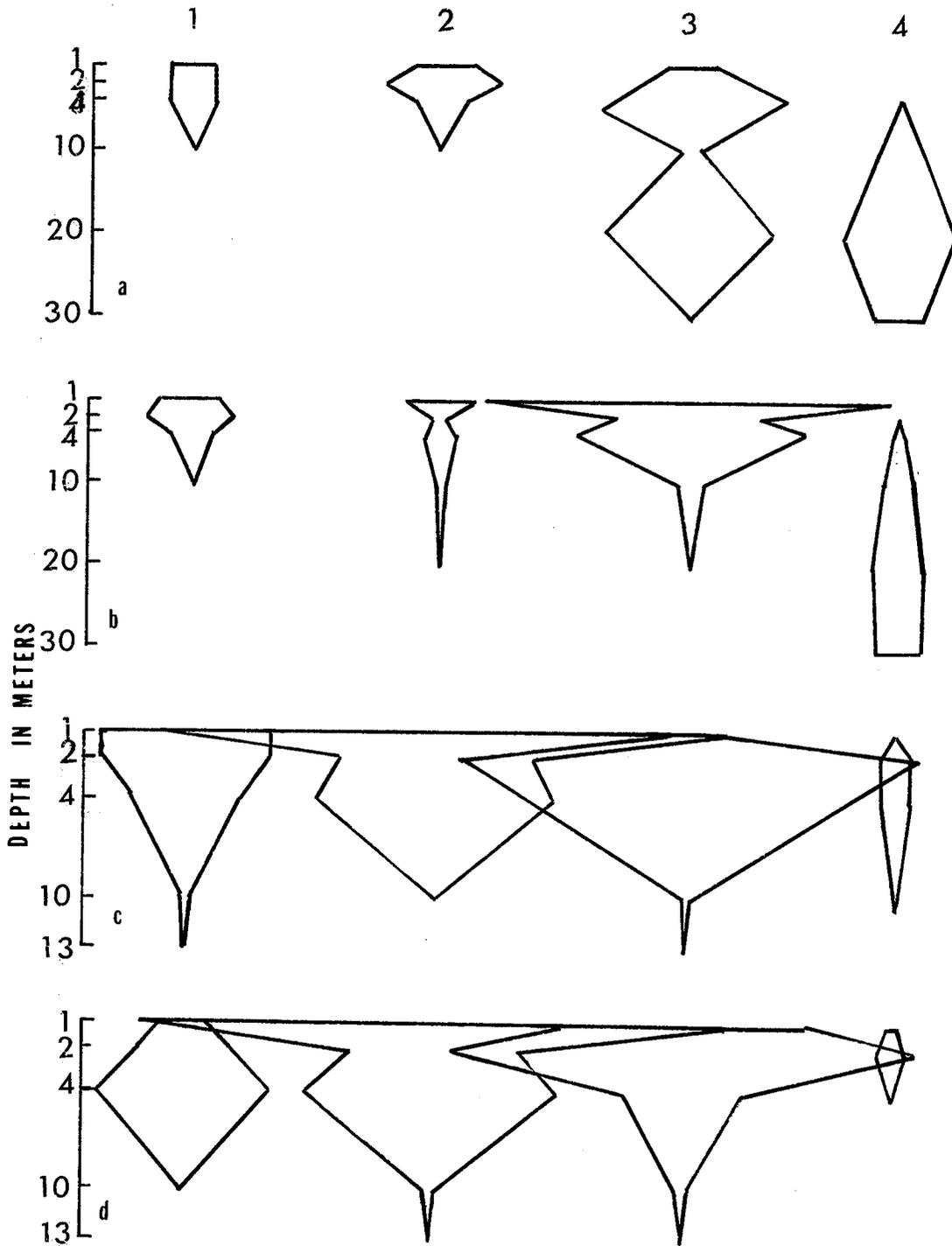
a) Tanytarsus sp. 1

b) Tanytarsus sp.

c) Tanytarsus sp. 1

d) Tanytarsus sp.

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past as reflecting a slower growth rate for individuals inhabiting the cooler hypolimnion water. However, in this investigation, the absence of fourth instars in shallow water at any time of the year strongly suggests that a migration of late instars to deeper water is taking place.

Chironomus

The genus Chironomus is ubiquitous in distribution, and is generally considered a euryoxybiontic group (Brundin 1951). Its tolerance of anaerobic conditions and its predominantly hypolimnetic distribution have led to its use as an indicator of eutrophic conditions.

Hamilton (1965) found that the species of Chironomus in Marion Lake were primarily detritivores, and Rempel (1936) citing Malloch (1915) indicated Chironomus as eating primarily diatoms, algae, and vegetable detritus.

Curry (1965) gives ranges of physical parameters for waters in which the genus has been reported, and includes the following: pH 4.0 to 9.1; temperature 0°C to 32.8°C; 0.0 ppm dissolved oxygen; 61.0 ppm CO₂ maxima. Harp and Campbell (1967) state that it is the only

chironomid genus capable of living and reproducing at a pH lower than 5.0.

The taxonomy at the species level is poorly known. The larval stages are further complicated by the sexual dimorphism displayed by the group (Atchley 1971). In the present study, eight species were recognized on the basis of eye shape, head capsule length, and dental structure; undoubtedly this was a conservative estimate. Of these, four were found in East Blue Lake, three of which were found deeper than 10 m and one below 4 m, two in Beautiful Lake, two in Lake 239, and one in Lake 240.

The eight types of Chironomus could only be positively separated in the third and fourth instars, except for East Blue Lake's Chironomus sp. 1 which had a distinct tooth structure. The distribution of Chironomus is shown as a composite of all species (Figure 11). The bathymetric distribution of Chironomus sp. 1 is shown in Figure 12.

Paratanytarsus

A total of four species were found in the four lakes and their distribution was as follows: East Blue, 2; Beautiful Lake, 1; Lake 239, 1; Lake 240, 2.

Figure 11. Bathymetric distribution of the genus
Chironomus in the four lakes.

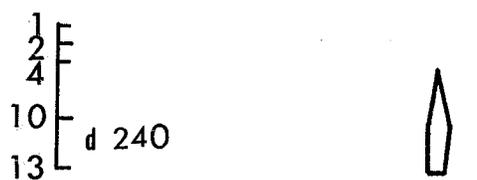
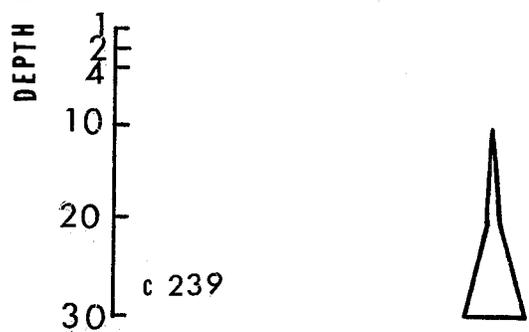
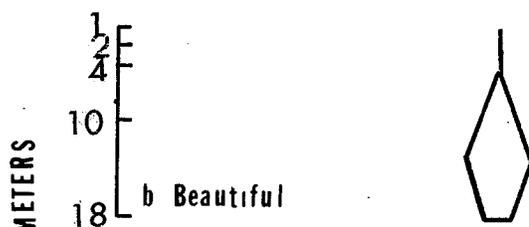
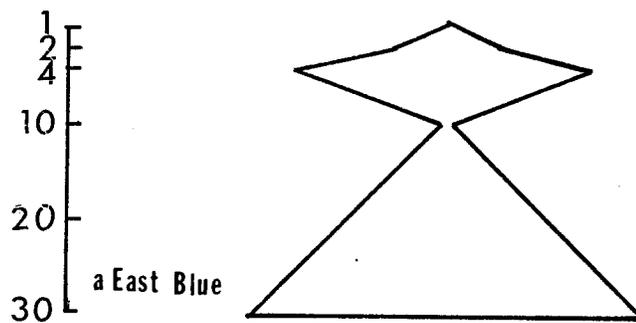
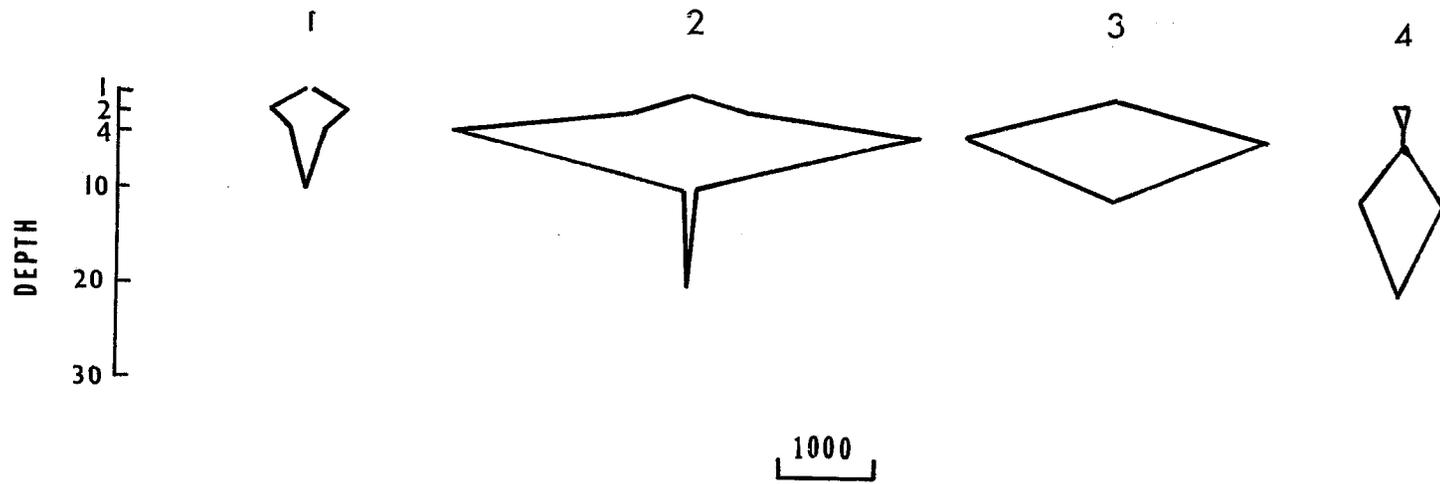


Figure 12. Bathymetric distribution of the four instars
of Chironomus sp. 1 in East Blue Lake.

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Ecological information on this genus is generally lacking, although Berg (1938) found Paratanytarsus spp. confined to the littoral zone of Lake Esrom. In the present study area the genus primarily occupied the littoral zone, rarely extending below 4 m (Figure 13); its high numbers played a dominant role in the littoral zones of the Pre-Cambrian Shield lakes from fall to spring when its densities were very high. Only larvae of the third and fourth instars were collected through July and August, suggesting that adults emerged throughout the summer in all lakes. Maximum numbers coincided with the reappearance of first and second instar individuals in September.

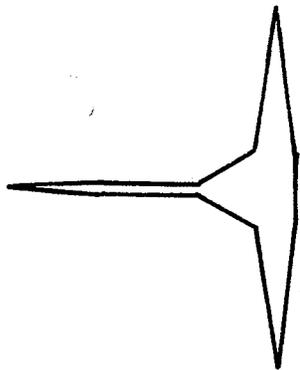
Phaenopsectra

This genus was represented by two species, both of which occurred only in Lakes 239 and 240. Few individuals were found in Lake 239, and these solely at 20 and 30 m. The distribution in Lake 240 centered at 10 m, with few being found at 4 m and only 3 at 13 m.

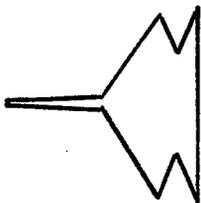
The two species shared the same habitat, wintering as the fourth instar and emerging in the spring. Young individuals, predominantly second instars, returned to the sediment in July, none being found in June. The sole reference on the genus in

Figure 13. Bathymetric distribution of the genus Paratanytarsus in the four lakes sampled.

1
2
4
0
0
0
a

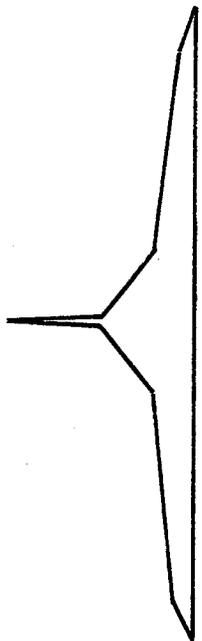


1
2
4
10
18
b

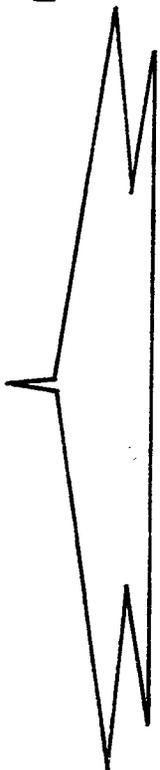


DEPTH IN METERS

1
2
4
10
20
c



1
2
4
10
13
d



1000

this region (Slack 1967) reports that Phaenopsectra shows a preference for highly organic sediments. The bathymetric distribution of the genus in Lake 240 is shown in Figure 14a, and the temporal distribution of each instar is shown in Figure 15a.

Chaoborus (formerly Corethra)

Chaoborus is a widespread genus occurring in most lakes of the northern hemisphere. Thienemann (1920) associated its presence with highly eutrophic conditions and lakes with very low oxygen in their hypolimnia.

Chaoborus are primarily predatory on copepods and cladocerans (Deonier 1943), and they have been reported feeding on oligochaetes as well as other Chaoborus larvae (Berg 1937).

They are the only dipteran larvae known to exhibit diel migrations, with movements in the water column occurring between sunset and dawn (Teraguchi and Northcote 1966, LaRow and Marzolf 1970, LaRow 1969). Roth (1968) indicated that 50% of C. punctipinnis and 80% of C. flavicans populations migrated at night. LaRow (1969) found in a laboratory experiment that as many as 84% of the population were planktonic two hours

after dark. LaRow (1970) isolated oxygen as the dominant factor in controlling the density of the Chaoborus migrants.

In this study, two species of Chaoborus were collected, C. punctipinnis in all the lakes, and C. flavicans only in Lake 240. In Lakes 239, Beautiful, and East Blue very few individuals were found, but in Lake 240 they made up as much as 70% of the fauna below 4 m. Their spatial distributions are shown in Figure 14b and c, and the temporal distributions by instar are shown in Figure 15b and c.

Both C. punctipinnis and C. flavicans in Lake 240 occupied the region below the thermocline. The spatial distributions of the two species overlapped, complementing the findings of Stahl (1966). As expected, the first and second instars were poorly sampled. Teraguchi and Northcote (1966) and LaRow (1970) reported that the first two instars are mainly planktonic. However, from the meager evidence available on the first instar it appears that emergence and reproduction occur at different times for the two species, June for C. punctipinnis and July for C. flavicans (Figures 15b, c, and 16b, c).

The seasonal migrations to the littoral zone reported by Wood (1956) in an Algonquin Park lake, and

the migrations to deeper water in winter reported by Deevey (1941) and Bonomi (1962), failed to materialize. However, the first instar of C. flavicans was always collected in the sediments of shallow water inferring a possible seasonal cycle.

The third and fourth instars generally co-occurred, and appeared to occupy similar habitats.

Minima in population densities were recorded in July and August, corresponding to the times of reproduction.

Pontoporeia affinis

The glacial relict amphipod Pontoporeia affinis is considered to be a predominantly benthic invertebrate in northern lakes. It is known to occupy the brackish waters of the circumpolar region as well as deep or cold lakes of the glaciated portions of the northern hemisphere (Segestråle 1959). It has been shown to exhibit diel migrations in the water column (Larkin 1948), and these have been correlated to light intensity and thermal structure of the lake (Marzolf 1965).

Although the animal has been known to reach a length of 15 mm in brackish water, Green (1965) reports a maximum length of only 10 mm in Cayuga Lake.

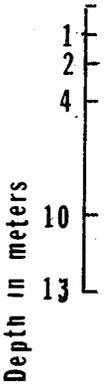
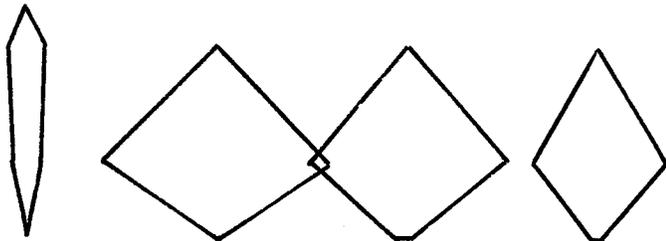
Figure 14. Spatial distribution by instar of
(a) Phaenopsectra; (b) Chaoborus punctipinnis; and
(c) Chaoborus flavicans in Lake 240.

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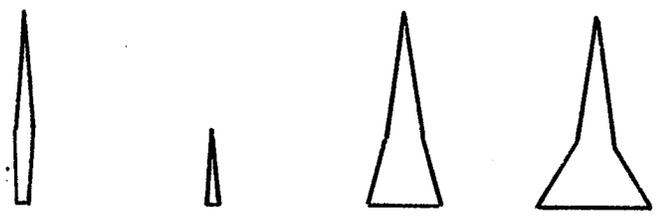
1 2 3 4



a



b



c

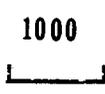
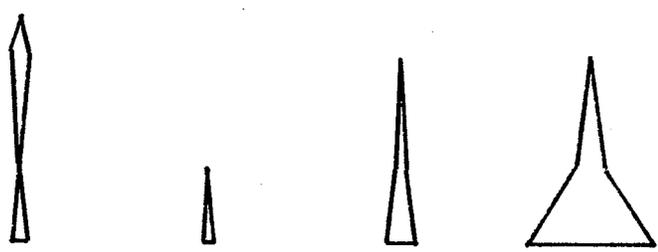


Figure 15. Temporal distribution of the instars of
(a) Phaenopsectra; (b) Chaoborus punctipinnis; and
(c) Chaoborus flavicans in Lake 240.

July Aug Sept Feb May June July

INSTARS

Phaenopsectra



1

2

3

4

C. punctipinnis



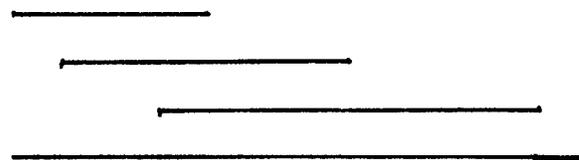
1

2

3

4

C. flavicans



1

2

3

4

July Aug Sept Feb May June July

P. affinis is believed to feed on organic detritus (Marzolf 1965b) in the sediment as well as planktonic organisms (Adamstone 1924, Larkin 1948). Segestråle (1959) reports upper temperature limits in the field between 14 and 20°C, and laboratory limits of 21 - 24°C. Salinity limits have been reported at 13 - 15%. Their bathymetric range is variable, apparently dependent on temperature; in Great Slave Lake they occur from 2 m (personal observation) to 300 m (Larkin 1948). The lowest dissolved oxygen recorded for P. affinis in fresh water is 1 ppm (Juday and Birge 1927).

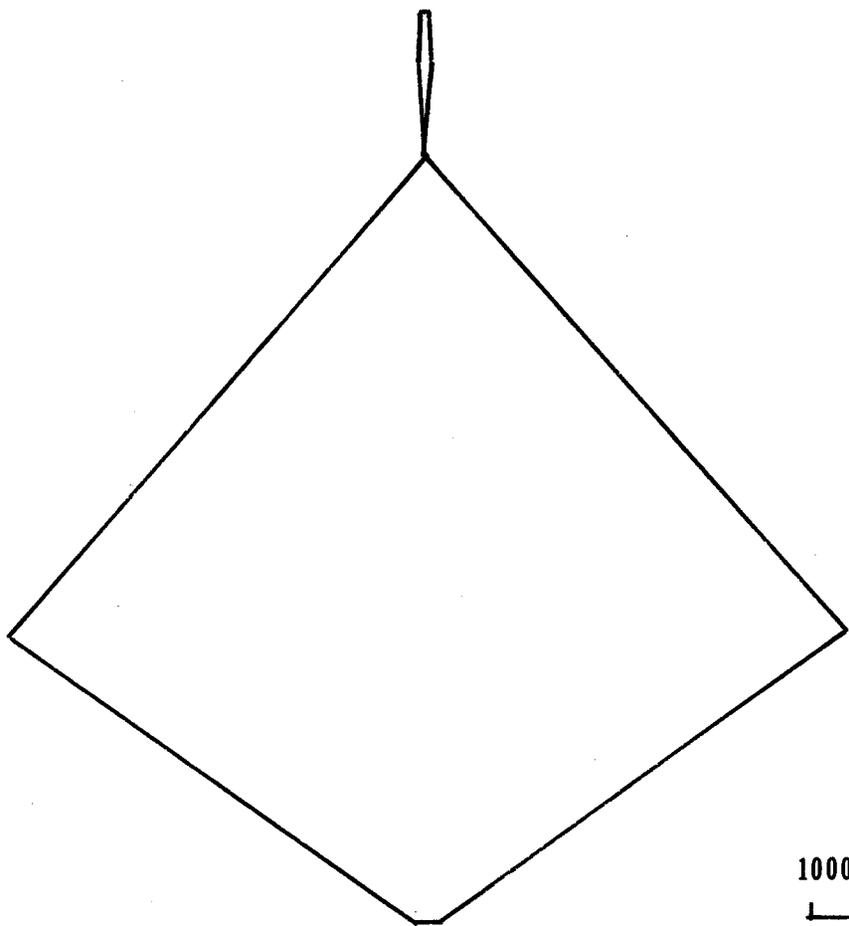
In the present study P. affinis was collected in Lakes 239 and 240, with few individuals collected in the latter. In Lake 239 this species made up over 40% of the profundal fauna. The bathymetric distribution through time is shown in Figure 16.

Based on head length-frequency measurements, the specimens were broken down into seven size classes (Figure 17), although size class VI probably represents two different size classes. Based on the seven size classes, the percent contribution of each instar to the sampled population (Figure 18) was calculated.

Figure 16. Bathymetric distribution of Pontoporeia
affinis in Lake 239 (all samples combined).

1
2
4
10
20
30

Depth in meters



1000/ m²

Figure 17. Length—frequency distribution of Pontoporeia affinis with size group divisions indicated.

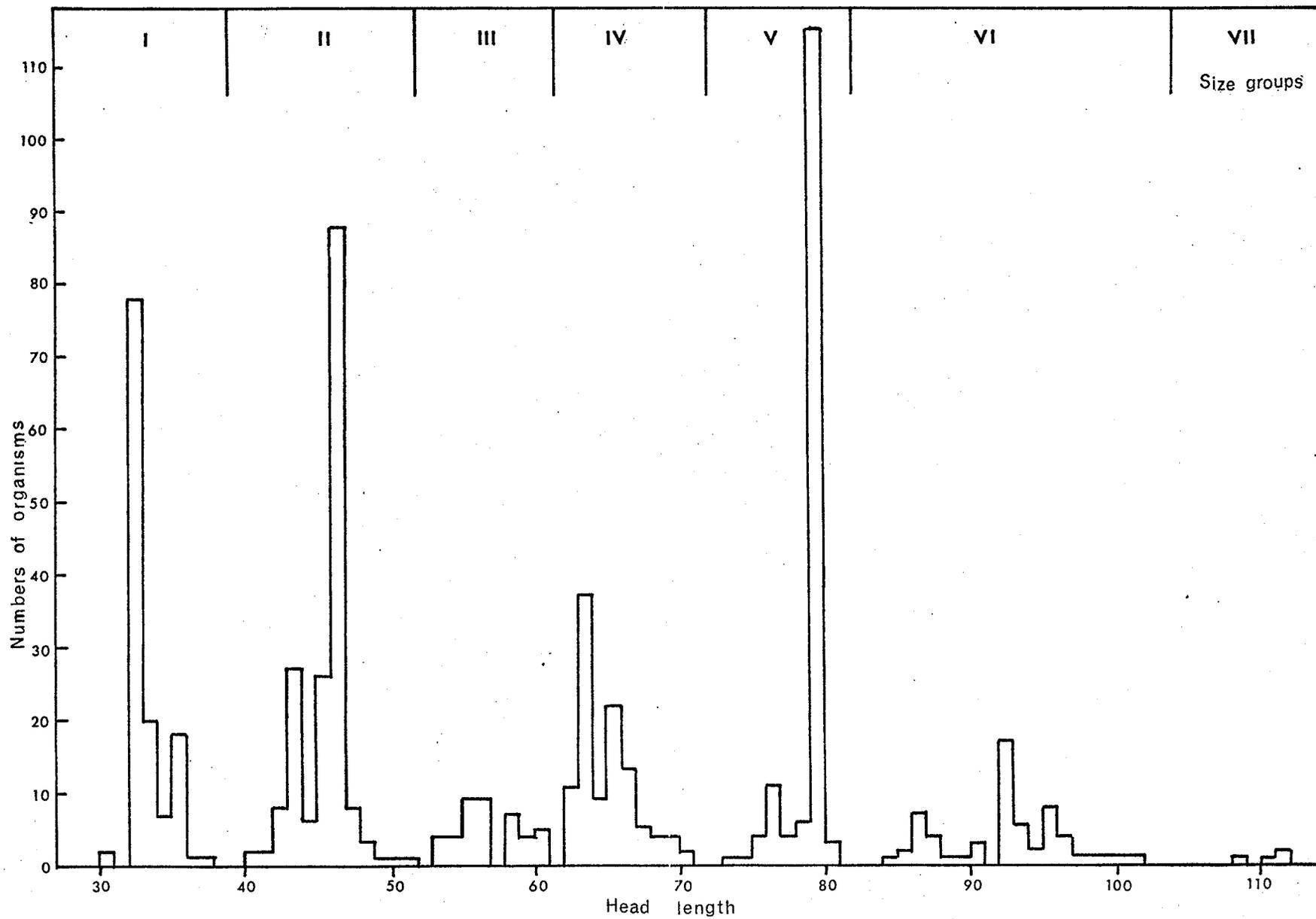
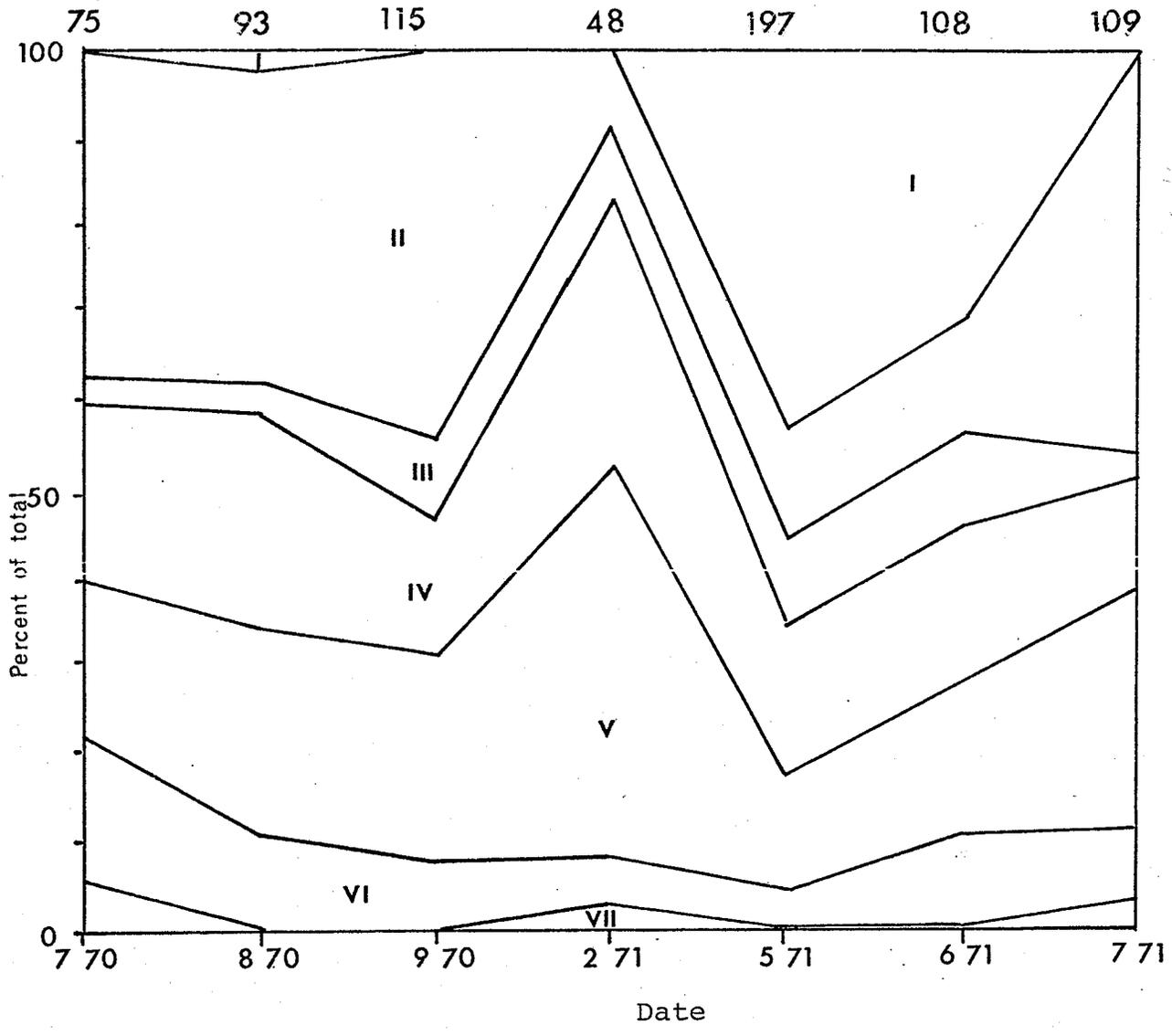


Figure 18. Percent contribution of each size class
to the sampled population of Pontoporeia affinis.

SAMPLE SIZE



The results indicate that in Lake 239 Pontoporeia occupied a region between 10 and 20 m, but extended its distribution to 30 m in mid-summer. Following the spring overturn, individuals were found in the shallowest depth sampled, but moved deeper as the summer progressed.

The population had its lowest density in mid-winter and its highest early in the spring (Figure 18). The maximum coincided with the appearance of the young, which in May accounted for 43% of the sampled population. All first instars disappeared from the samples by July; however, in August, 1970, a few first instar individuals were collected. Whether these were remnants of the spring reproduction, or whether they represented a secondary reproductive peak as described by Green (1965) is not known; if a secondary peak was present, it was made up of very few individuals.

No distinct seasonal pattern in depth distribution was evident. However, individuals of the seventh size group were consistently collected 5 to 10 m shallower than the others.

Hyalella azteca

Hyalella is a widespread amphipod in permanent bodies of water in North America. Although known to

occur primarily in warm standing water, it has been found in cold running streams (Wienert 1950).

Hyaella feeds on algae and plant and animal detritus (Cooper 1965). Biette (1965), citing Holmes (1901) and Phipps (1915), described the species as strongly thigmotactic and negatively phototropic.

Its range of environments includes all waters with monthly mean temperatures over 10°C (Bousfield 1958). Temperatures above 33°C are lethal, as are dissolved oxygen concentrations of 0.7 ppm at 20°C (Sprague 1963).

Hyaella has been found associated with mud, sand, and gravel substrates, but usually in association with rooted vegetation (Wienert 1950, Cooper 1965). Wienert (1950) indicated that it preferred Chara to Pomatogeton, but Biette (1965) found the opposite to be true in a northern Manitoba lake.

In this study, Hyaella was found in every lake, but was collected in substantial numbers only in East Blue Lake (Table 6). In Beautiful Lake, Lake 239 and Lake 240, Hyaella were seldom found below 4 m, but in East Blue Lake the distribution at the mean depth of occurrence extended to 30 m (Figure 19).

Pisidium

The ecology of the genus Pisidium is not well known. They live in burrows in mud, paralleling the surface, and are believed to feed on bacterial plates attached to sediment particles. Thut (1969) and Jonasson (1972) suggest that the animals have a life-span of more than one year, with young being released in late summer or early fall, and adults dying in mid-summer.

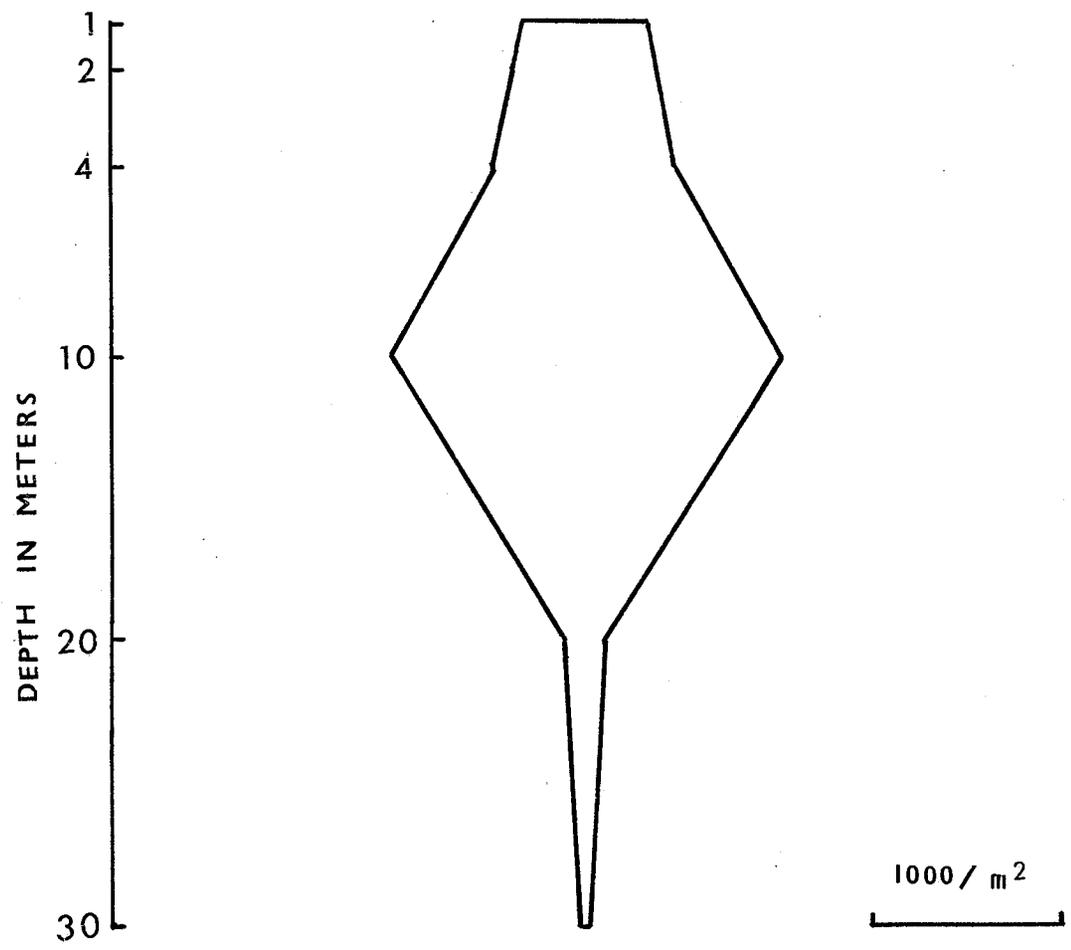
Three species of the genus were identified. Pisidium conventus was the only species found in Lakes 239 and 240, P. conventus, P. casertanum, and P. variable in East Blue, and only P. variable in Beautiful Lake.

P. conventus was the only species having high enough densities to dominate the benthos in any part of a lake, and this occurred in Lake 239. The species was distributed between 10 and 20 m and made up 39% of the benthic standing crop at those depths. Throughout the year the animals were evenly distributed between the two depths except in mid-summer when a few individuals were collected at 1 and 2 m (Table 7).

Diversity in Lakes

Diversity indices were calculated as a measure

Figure 19. Bathymetric distribution of Hyaella
azteca in East Blue Lake.



of the complexity of interaction within the biological systems studied. The indices for each sampling period with mean and standard deviation are given in Table 8.

East Blue Lake

The diversity values in this lake were lower overall than in the other three lakes. From the shore to 20 m, the seasonal means per depth sampled ranged from 1.90 to 2.54, with the low values having relatively high standard deviations (Table 8).

At 30 m, the diversity was lowest, ranging from 1.1 to 1.4. An unexplained decline occurred at all depths below 2 m in mid-winter.

Lake 239

The sampling stations from shore to thermocline had high diversity values, ranging from 1.0 to 3.8, with means of 2.56 to 3.04. Below the thermocline, the values dropped to 1.2 to 2.1, with means of 1.57 (10 m), 1.64 (20 m), and 1.51 (30 m).

Lake 240

The littoral stations to the thermocline had high diversities, 1.6 to 3.8, with seasonal means of 2.73 to 3.14. At 10 m the diversity remained high

Table 8. Temporal and spatial distribution of
diversity indices in (a) East Blue Lake; (b) Lake 239;
(c) Beautiful Lake; (d) Lake 240.

EAST BLUE LAKE

| Date | 7/70 | 8/70 | 9/70 | 2/71 | 5/71 | 6/71 | 7/71 | Mean Div. | S.D. |
|--------------|------|------|------|------|------|------|------|--------------|------|
| Depth (m) | | | | | | | | | |
| 1 | 2.3 | 0 | 2.1 | 3.0 | 2.8 | 2.3 | 0.8 | 1.90 | 1.09 |
| 2 | 2.5 | 2.1 | 0.4 | 3.0 | 2.6 | 2.9 | 1.0 | 2.07 | 0.99 |
| 4 | 2.3 | 1.0 | 1.8 | 1.1 | 3.0 | 1.5 | 1.9 | 1.80 | 0.68 |
| 10 | 2.8 | 3.0 | 2.4 | 1.9 | 2.8 | 2.6 | 2.3 | 2.54 | 0.37 |
| 20 | 2.6 | 2.7 | 2.7 | 1.2 | 2.4 | 2.6 | 2.4 | 2.37 | 0.53 |
| 30 | 1.3 | 1.3 | 1.3 | 0 | 1.4 | 1.1 | 1.4 | 1.11 | 0.50 |

LAKE 239

| | | | | | | | | | |
|----|-----|-----|-----|-----|-----|-----|-----|------|------|
| 1 | 2.7 | 3.8 | 2.4 | 3.6 | 3.5 | 3.8 | 1.5 | 3.04 | 0.87 |
| 2 | 1.5 | 2.3 | 3.6 | 3.0 | 3.3 | 3.2 | 1.0 | 2.55 | 0.99 |
| 4 | 2.2 | 3.4 | 3.1 | 1.6 | 2.9 | 3.3 | 2.7 | 2.74 | 0.64 |
| 10 | 1.2 | 1.7 | 1.1 | 1.3 | 1.8 | 1.8 | 2.1 | 1.57 | 0.37 |
| 20 | 1.4 | 1.2 | 1.7 | 2.1 | 1.8 | 1.4 | 1.9 | 1.64 | 0.32 |
| 30 | 2.1 | 1.2 | 1.4 | 1.4 | 1.2 | 1.5 | 1.8 | 1.51 | 0.33 |

BEAUTIFUL LAKE

| | | | | | | | | | |
|----|-----|-----|-----|-----|-----|-----|-----|------|------|
| 1 | 1.0 | 3.5 | 0.9 | 3.0 | 3.3 | 2.8 | 1.6 | 2.30 | 1.10 |
| 2 | 0 | 2.2 | 0 | 2.9 | 0 | 0 | 0 | 0.77 | 1.30 |
| 4 | 0 | 1.9 | 0 | 0.8 | 1.0 | 1.6 | 0 | 0.76 | 0.80 |
| 10 | 2.8 | 1.0 | 1.5 | 1.8 | 2.5 | 2.7 | 1.2 | 1.93 | 0.74 |
| 18 | 2.5 | 1.0 | 1.5 | 1.4 | 2.4 | 2.8 | 0 | 1.66 | 0.99 |

LAKE 240

| | | | | | | | | | |
|----|-----|-----|-----|-----|-----|-----|-----|------|------|
| 1 | 3.1 | 3.8 | 3.2 | 3.4 | 3.6 | 2.9 | 1.9 | 3.33 | 0.33 |
| 2 | 3.3 | 2.9 | 3.0 | 2.9 | 3.3 | 2.1 | 1.6 | 2.72 | 0.64 |
| 4 | 2.6 | 3.8 | 2.9 | 3.1 | 3.2 | 2.7 | 2.9 | 3.02 | 0.40 |
| 10 | 2.4 | 2.2 | 1.6 | 1.9 | 2.3 | 2.2 | 1.4 | 2.00 | 0.38 |
| 13 | 1.7 | 0 | 2.1 | 1.5 | 1.7 | 1.0 | 0 | 1.14 | 0.85 |

(seasonal average 2.00), but at maximum depth they dropped to a low of 1.13.

Beautiful Lake

The area sheltered by reeds (1 m) had a wide range of diversities, 0.9 to 3.5, with a mean of 2.3. In the exposed areas (2 m and 4 m), the diversities were low, 0 to 2.9, with means of 0.728 and 0.757 respectively. The indices increased at and below thermocline to seasonal means of 1.92 and 1.79. It was difficult to assess patterns in diversity indices through depth and time in this lake because the rooted aquatic vegetation zones offered protection from wind and supported high diversities.

The data show that the highest diversity indices found were recorded in the epilimnia of the lakes studied; however, at certain times of the year the lowest values also were recorded there.

The lowest average diversity indices were recorded at the maximum depths sampled. The exception to this was Beautiful Lake.

The mean diversities for each lake were plotted with the coefficients of variation of the physical and chemical parameters. These results are shown in

Figure 20 (High value = instability; low values = stable).

The mean coefficient of variation was used as a measure of the temporal variability in the area, and was interpreted as a measure of seasonal "stability" of the habitat.

"Stability" was lowest in the top four meters sampled in East Blue, Lake 239, and Lake 240. Generally, the mean coefficient of variation showed a trend of decreasing with depth, and this was interpreted as increasing environmental "stability". In Beautiful Lake, the trend was reversed.

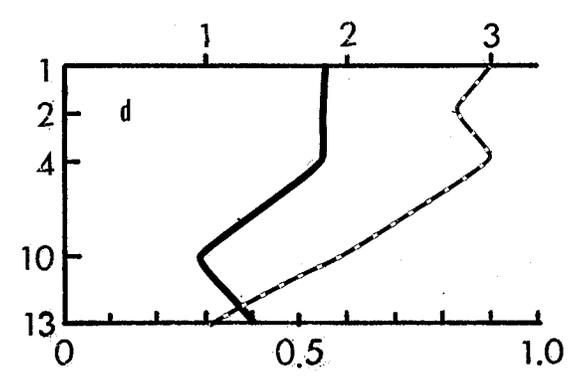
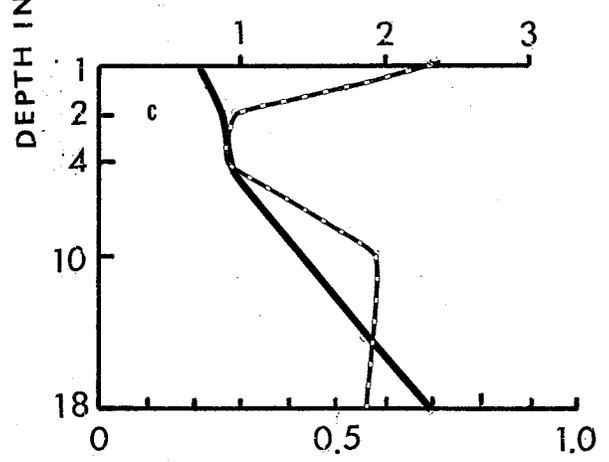
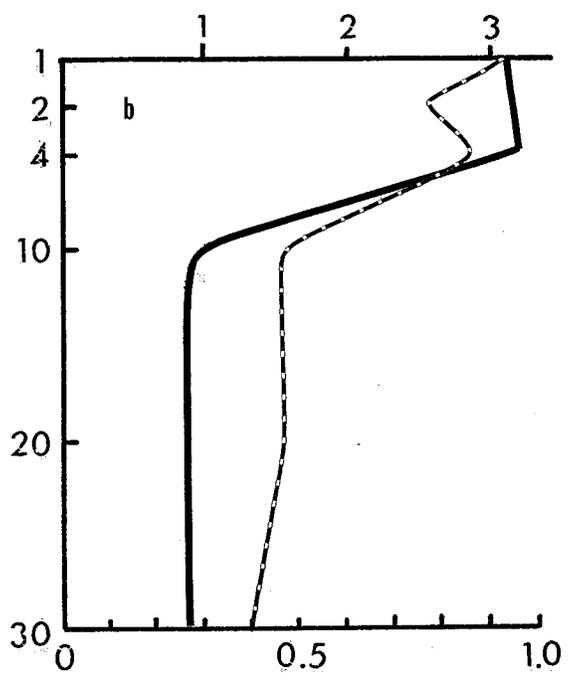
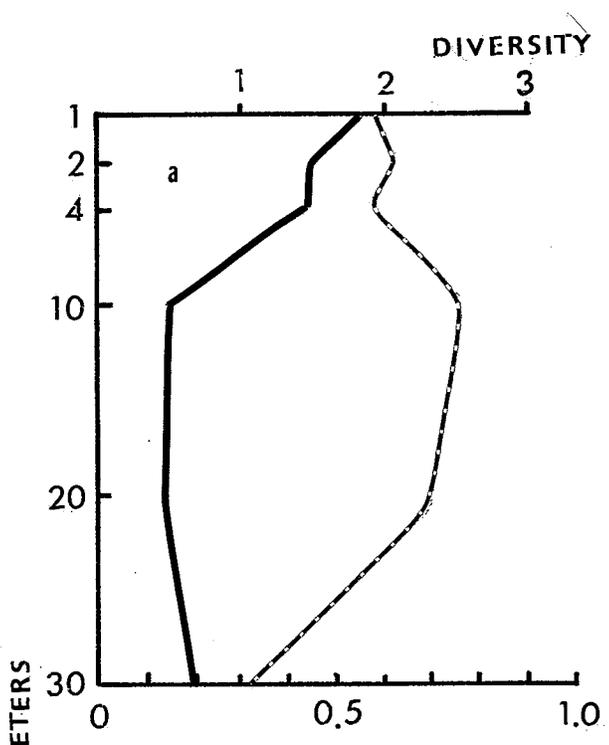
The mean diversity values in these lakes appeared to be negatively correlated to the trends shown by the "stability" curves in Lakes 239, 240, and Beautiful Lake below 1 m. In East Blue Lake, however, no correlation was found. At 1 to 4 m, where the stability was lowest, the diversity values were also low, and at 10 and 20 m, where the recorded stability was highest, the mean diversities were lowest.

Faunal Assemblages in Lakes

i. Assemblages within lakes

For each lake, all the samples were used in

Figure 20. Bathymetric distribution of the coefficient of variation of the physico-chemical parameters (solid line) and the mean diversity values (broken line) in (a) East Blue Lake; (b) Lake 239; (c) Beautiful Lake; (d) Lake 240.



COEFF. OF VARIATION

the mutual information analysis; the results of the analysis at the species level are summarized in four dendograms (Appendix IV). The assemblages are plotted on depth and time axes for each lake (Figure 21). The results are presented in terms of the faunal composition of each assemblages in Appendix IV.

The number of assemblages described with time and depth differed among lakes. Between four and five were found in three of the lakes, but only two in Beautiful Lake, which had only a littoral and profundal assemblage.

In all four lakes, the first major division in the dendograms was between the faunas down to approximately thermocline depth, and those below the thermocline. Further divisions then occurred, subdividing each group into the individual assemblages (Appendix IV). Within the littoral stations of each lake the various assemblages were similar in species composition, usually varying only in the dominant species. This I interpret as indicating a temporal shift in dominance created by the reduction in numbers of certain chironomids, perhaps due to emergence. Samples in the hypolimnetic zone showed close similarity to each other, as shown by the low levels of fusion. In the littoral stations the opposite was true. The fact

Figure 21. Temporal and spatial distribution of assemblages composed of species in (a) East Blue Lake; (b) Lake 239; (c) Beautiful Lake; (d) Lake 240. Legend to the assemblages is in Appendix IV. (Broken lines have been drawn around areas being occupied by similar assemblages, to emphasize distribution.)

that the fusions were so close below the thermocline and so far apart above it I interpreted as indicating the greater environmental homogeneity in the hypolimnion as compared to the heterogeneity of the littoral zone. This resulted in the higher littoral diversity previously mentioned. Part of this greater diversity was due to the physical heterogeneity of the substrate, and part due to unpredictable temporal changes from weather conditions.

The results clearly indicate that in each lake the faunal assemblages were spatially stratified along a depth gradient, with minimal temporal variations.

East Blue Lake

Five distinct assemblages were recognized in East Blue Lake (Figure 21a). At 1 m, the assemblage I was dominated by Chironomus sp. 1, Paratanytarsus sp. 2, and Dicrotendipes sp. 1. This group maintained its identity throughout the year, showing a winter extension to 2 m.

For most of the study, at 2 and 4 m there were two species of Tanytarsus, sp. 4 and sp. 5, which were dominant. These remained prominent at the summer thermocline level, though they were numerically dominated by the amphipod Hyalella azteca. Below the

thermocline, two assemblages were found: one (IV) at 20 m dominated by three species of Tanytarsus and two of the profundal Chironomus, and the other (V) at 30 m by the two species of Chironomus, sp. 5 and sp. 7. In winter, the Chironomus assemblage appeared to extend its distribution into the shallower water.

Lake 239

Four assemblages characterized Lake 239 (Figure 21), the two littoral ones being stratified both temporally and spatially, while the two hypolimnetic ones were strictly spatially stratified.

The Parantanytarsus sp. and Tanytarsus sp. and sp. 1 assemblage (I) were found mainly at 1 and 2 m from August to May, with a winter extension to 4 m. The Pisidium conventus, Tanytarsus sp. 1 assemblage (II) occupied the region of the summer thermocline, with extensions to 1 m during July of both years. These two littoral assemblages were species rich, the dominant forms making up only 20 to 30% of the total numbers of organisms found. The remainder were other members of the Chironomini, as well as Ephemeroptera, Tricoptera, and Ceratopogonidae.

Below the thermocline, a species-poor fauna was found. A Pisidium conventus - Pontoporeia affinis

complex (III) dominated the 10 m and 20 m sampling points; these species accounted for nearly 90% of the total numbers present, the remainder being Procladius spp. and oligochaetes. At 30 m, Pisidium and Pontoporeia disappeared, and two species of Chironomus replaced them.

Lake 240

In Lake 240, five assemblages were identified (Figure 21). A Parantanytarsus sp. - Hyalella azteca group occupied the 1 m station from September to July. This same area, plus some of the 2 m region, were occupied during the rest of the year by a species of Tanytarsus which became dominant, accounting for nearly 50% of the total fauna. The summer thermocline station (4 m) was occupied by a Tanytarsus spp. - Paratanytarsus sp. - Heterotrissocladus sp. assemblage (III), with little temporal variation. Below the thermocline, two distinct assemblages were evident. One, temporally of short duration and occurring almost exclusively at 10 m, was a Phaenopsectra spp. assemblage (IV), dominated by two species of Phaenopsectra which accounted for more than 55% of the numbers present. This assemblage corresponded to the period when the individuals of the second instar began to be collected (July, August),

and adults were seen to emerge in May. At 13.3 m or maximum depth a Chaoborus punctipinnis - Chaoborus flavicans assemblage V was evident, these two species comprising 70% of the total fauna; the remainder at this depth was shared by Chironomus sp. 6 and Procladius spp., the only truly benthic species that occurred here in significant numbers.

Beautiful Lake

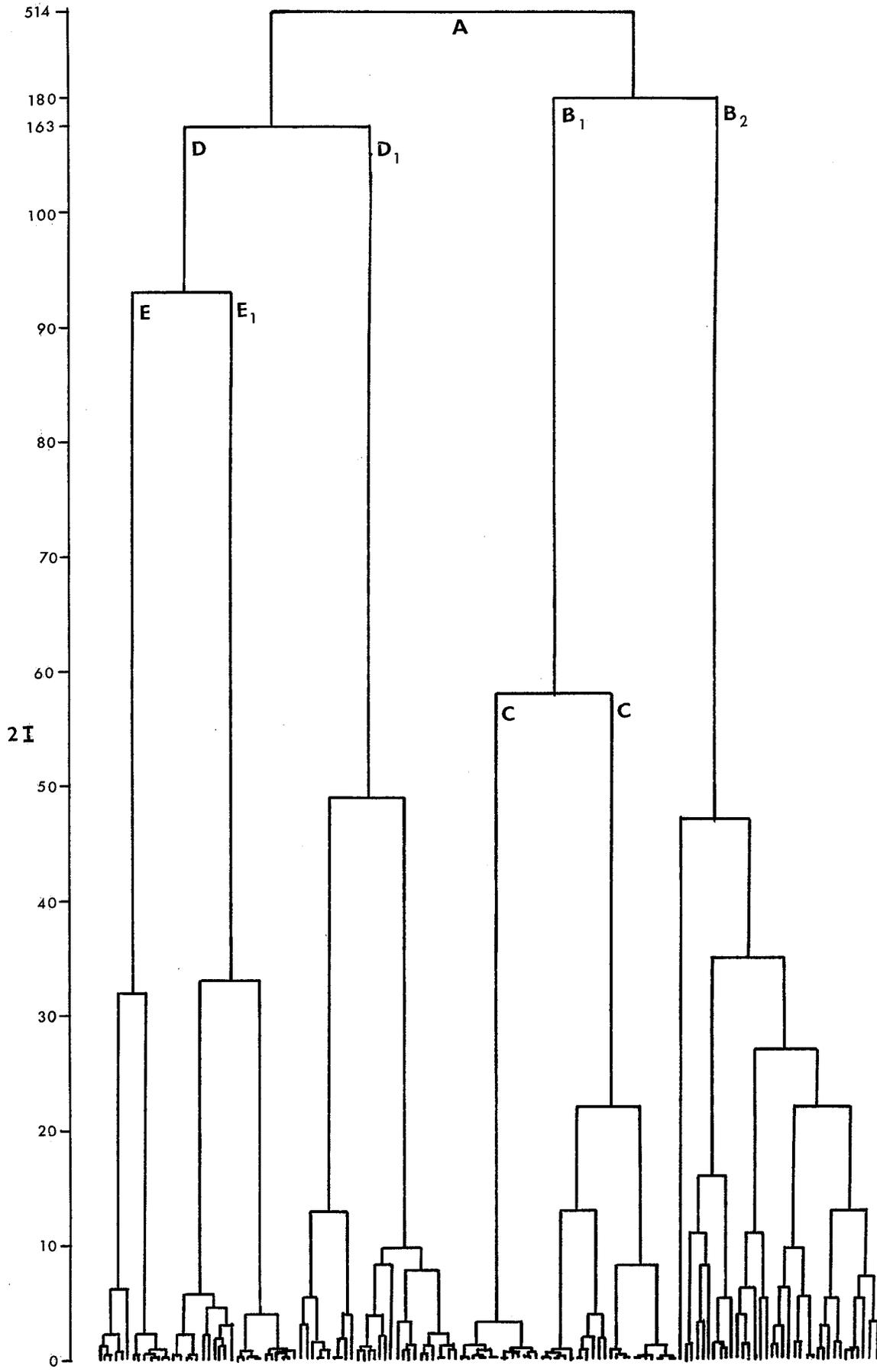
Beautiful Lake contained the least complex faunal spatial patterns, with only two assemblages, each characteristic of a different depth zone (Figure 21). The first (I), a Parantanytarsus sp. 3 - Tanytarsus complex, extended to 4 m, while a Chironomus sp. 2 - Chironomus sp. 3 was found at 10 m and deeper.

ii. Species assemblages among lakes

The mutual information analysis was run using all the samples from all four lakes, using the species level of identification. It was hoped that such an analysis would allow the comparison of the distribution of faunal assemblages among the lakes.

The mutual information analysis results (Figure 22) indicated a major fusion (A) separating the two geographical areas as a first division.

Figure 22. Hierarchical classification of among-lakes samples identified at the species level, with key fusions indicated.



Within the Laurentian Shield, there were two major fusions. The first separated the samples from below the thermocline (B_1) from those above it (B_2), excepting a group of five samples from the littoral zone of Lake 239, which were characterized by the presence of Pisidium conventus and Pontoporeia affinis. Within the hypolimnetic group of samples, the next lower fusion (C) mainly separated the profundal fauna of the two lakes. Above the thermocline, no major fusion between lakes was evident, indicating close affinity between the littoral faunas of Lakes 239 and 240.

Within the Agassiz escarpment, the highest fusion separated all the East Blue samples shallower than 20 m (D_1) from all other samples (D). The next lower fusion separated the East Blue (E) profundal samples from the Beautiful Lake data (E_1), thus forming the three major groups:

- (E) East Blue profundal
- (E_1) Beautiful Lake
- (D_1) East Blue littoral and sub-littoral

The East Blue profundal was separated into samples from 20 m and samples from 30 m. Beautiful Lake was separated into the littoral fauna and profundal fauna, identical to the specific breakdown by lake previously discussed.

iii. Assemblages among lakes using genera

The among lakes analysis at the species level yielded some information, but the similarity of species faunal assemblages among lakes was low except for the littoral zone of the Laurentian Shield lakes.

It was obvious from the untreated data that most species present were lake-specific, although most genera were common to all. Therefore, if common relationships among lakes are desired, the mutual information analysis at the generic level might be most appropriate. Such an analysis is reasonable, and even advantageous, because it lessens the identification error generated by the shaky state of chironomid larval taxonomy, as well as allowing comparisons of the results with most of the literature published to date.

The dendrogram based on the generic level data (Figure 23) can be interpreted as follows:

The analysis suppressed among lakes variation, while emphasizing distribution through depth. The highest fusion created two groups, one predominantly of littoral samples (A), and one of profundal (A_1) samples. The profundal group contained eleven samples occurring at the 2 and 3 m depths in East Blue Lake.

This seemingly misplaced group fused with the profundal faunas of East Blue because its dominant form was a littoral species of Chironomus (Chironomus sp. 1) occurring solely in East Blue; since Chironomus is characteristic of profundal zones, the shallow water samples fused with these groups. The second part of this major fusion, the littoral groups, also contained a seemingly misplaced group of 17 samples mainly from 10 and 20 m in East Blue and 10 and 18 m in Beautiful Lake. These occurred in the littoral groups because of the predominance of Tanytarsus in the profundal zones of these lakes.

The highest major fusion can be interpreted with few exceptions as a Tanytarsus - Chironomus split (Table 9 and Figures 23 and 24). The break appears to occur at the thermocline, but in fact the inclusion of 17 samples from the area below the thermocline in the littoral grouping indicates that in some lakes, primarily East Blue, Beautiful, and to a lesser extent Lake 239, some taxa were collected from the shallow water zone to below the thermocline.

The next lower fusions (B) in the mutual information analysis separated mainly the fauna of the profundal stations into the two geological areas studied. Within the littoral zones, most of the

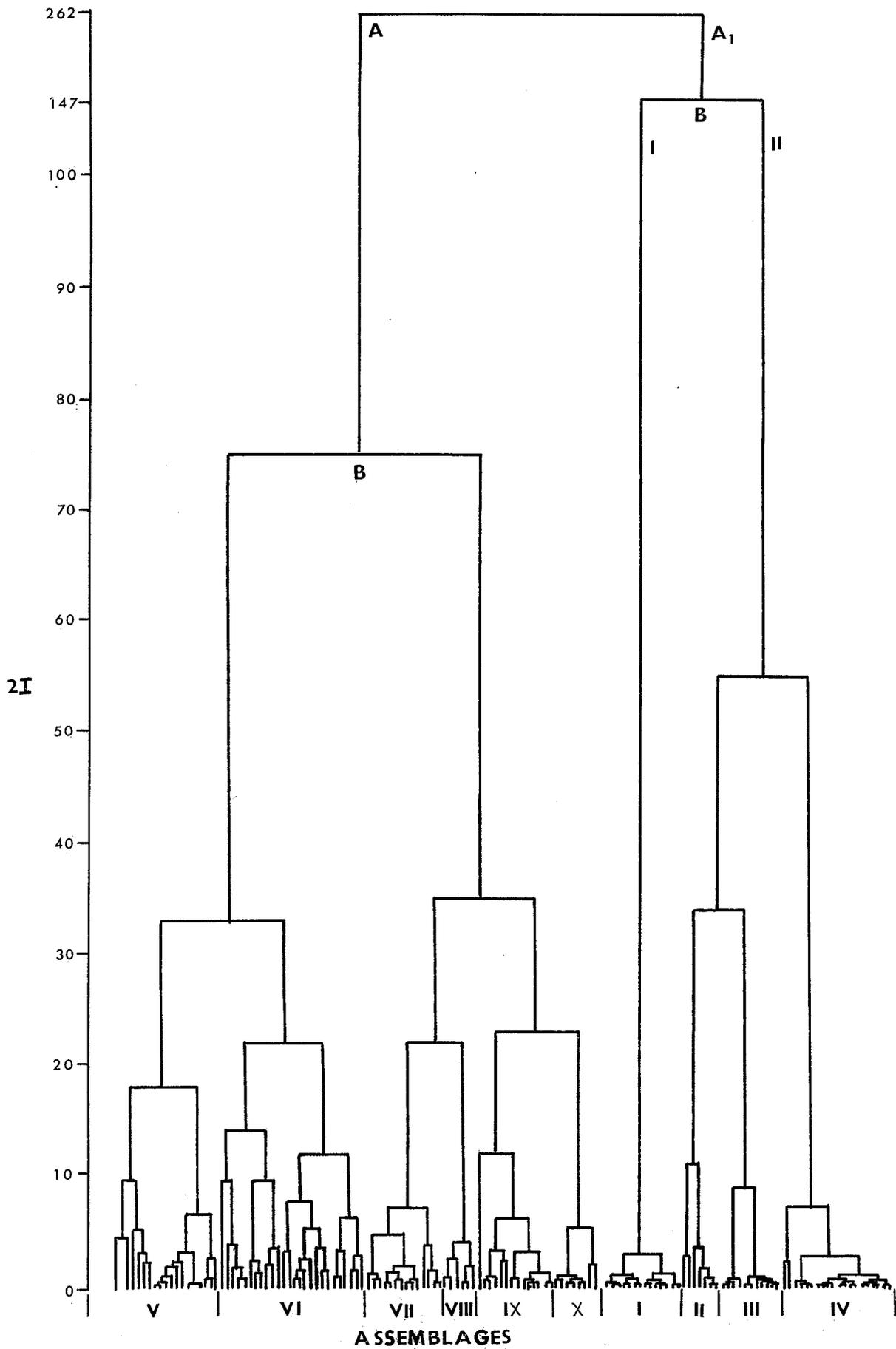
assemblages (except for the Chironomus sp. 1, Paratanytarsus - Dicrotendipes (II), and the Tanytarsus - Pseudochironomus (VIII) assemblages) were similar between the two geological areas. The fact that it is only the second fusion which separates the geological areas indicates how pronounced the littoral - profundal break in faunal types is, in most lakes.

The final results of the mutual information analysis at the generic level were ten faunal assemblages (Table 9) which were distributed spatially and temporally among the lakes as illustrated in Figure 24.

Interactions of the Biological Components and the Physical Environment

To define the environmental space occupied by the benthic organisms, the discriminant analysis method was used. This method was executed on data from a number of genera which were dominant components of faunal assemblages, and then the same analysis was carried out on the assemblages themselves. This dual analysis is valuable in evaluating the relative usefulness of using either taxa or assemblages as indicators of environmental conditions.

Figure 23. Hierarchical classification of among-lakes samples identified at the generic level, with key fusions and assemblages indicated.



i. Dominant genera and the environment

The following dominant taxa were used:

Tanytarsus spp., Paratanytarsus spp., Hyalella azteca,
Pisidium conventus, Chaoborus spp., Phaenopsectra spp.,
Chironomus spp. (hypolimnion group), Chironomus sp. 1,
and Pontoporeia affinis.

A summary of untransformed means for each of the 13 variables used in the analysis is presented in Table 10. The test of significance of among-genera differences yielded $\chi^2_{m(g-1)} = 104$ df = 593, which is highly significant. This test is biased because of the heterogeneity of variances of the groups in the discriminant space. However, if the overall test for the groups is highly significant and the discriminant functions are ecologically interpretable, it is reasonable to assume that the vectors described may represent the variables which best separate the groups in the discriminant space.

A summary of the contribution by each discriminant function needed to account for 95% of the among-genera variance is presented in Table 11.

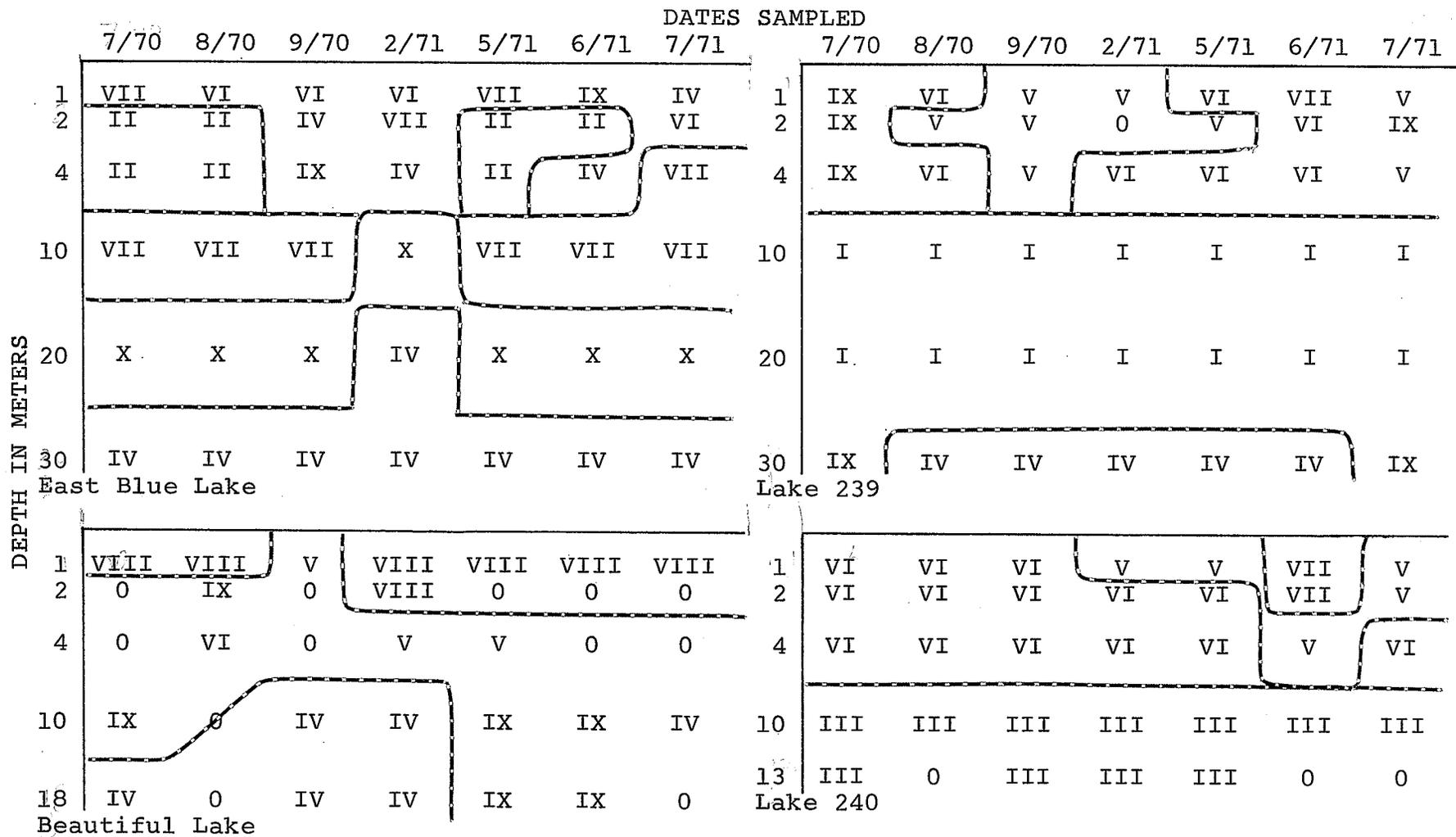
The relative contribution of each of the original parameters to each discriminant function can be interpreted from the discriminant function

Table 9. The genera numerically dominating the assemblages and their relative contributions.

TABLE 9

| Assemblage Number | Taxa | % Composition |
|----------------------|----------------------------|---------------|
| I | <u>Pontoporeia affinis</u> | 50.6 |
| | <u>Pisidium conventus</u> | 38.4 |
| | <u>Tanytarsus</u> | 7.4 |
| II | <u>Chironomus</u> sp. 1 | 33.6 |
| | <u>Paratanytarsus</u> | 18.7 |
| | <u>Dicrotendipes</u> | 15.5 |
| III | <u>Chaoborus</u> | 37.0 |
| | <u>Phaenopsectra</u> | 25.8 |
| | <u>Chironomus</u> | 7.3 |
| IV | <u>Chironomus</u> | 88.8 |
| V | <u>Paratanytarsus</u> | 32.8 |
| | <u>Tanytarsus</u> | 10.5 |
| | <u>Procladius</u> | 13.2 |
| VI | <u>Tanytarsus</u> | 33.8 |
| | <u>Paratanytarsus</u> | 12.3 |
| | <u>Pagastiella</u> | 8.9 |
| VII | <u>Hyalella azteca</u> | 22.5 |
| | <u>Procladius</u> | 19.4 |
| | <u>Tanytarsus</u> | 15.8 |
| | <u>Polypedilum</u> | 8.6 |
| VIII | <u>Tanytarsus</u> | 39.3 |
| | <u>Pseudochironomus</u> | 11.0 |
| IX | <u>Chironomus</u> | 22.4 |
| | <u>Cryptocladopelma</u> | 18.0 |
| | <u>Tanytarsus</u> | 12.4 |
| X | <u>Tanytarsus</u> | 64.4 |
| | <u>Chironomus</u> | 26.9 |

Figure 24. Temporal and spatial distribution of assemblages composed of genera in (a) East Blue Lake; (b) Lake 239; (c) Beautiful Lake; (d) Lake 240. Legend to the assemblages is in Table 4. (Broken lines have been drawn around areas being occupied by similar assemblages to emphasize distribution.)



coefficients (Table 11), and the interpretations of the discriminant functions are summarized at the bottom of Table 11.

The means plus and minus one standard deviation, approximately 68% of the individuals, for each genus and each of the four discriminant functions, were calculated and are shown in Figure 25.

Discriminant function IV was difficult to interpret. Although it was primarily loaded on calcium, other variables such as sediment loss on ignition, pH, presence of rooted vegetation, dissolved oxygen, alkalinity, and magnesium hardness all appeared to contribute significantly to the discriminant function. Because of the large number of interacting variables, and the fact that this function contributed only 5.13% of the among-genera variance, it will not be discussed further.

Discriminant function I accounted for 68% of the among-genera variance, and was controlled by the concentration of magnesium relative to the calcium ions, and by the organic content of the sediment. Discriminant function I primarily separated the deep-water genera from the littoral types (Figure 25). The result was that no among-lakes separation occurred.

Table 10. Summary of physical and chemical data used in the multiple discriminant analysis. Untransformed mean values for each taxon are shown.

TABLE 10

| Taxon. | Code | pH | D.O. ppm | Alk. ppm | Fe ppm | Mg ppm | Ca ppm | Temp. °C | CO ₂ mg/l | L.O.I. % | $\bar{\theta}$ | S.C. θ | C.P. P/A | Veg. P/A |
|----------------------------|------|-----|-------------|-------------|-----------|-----------|-----------|-------------|-------------------------|-------------|----------------|---------------|-------------|-------------|
| <u>Tanytarsus</u> | 1 | 7.1 | 8.9 | 74.3 | 0.7 | 46.2 | 41.9 | 10.3 | 13.9 | 14.4 | 1.9 | 1.7 | 0.8 | 0.27 |
| <u>Paratanytarsus</u> | 2 | 6.8 | 9.9 | 17.1 | 0.5 | 29.0 | 30.1 | 12.6 | 6.5 | 5.0 | 1.9 | 1.6 | 1.0 | 0.38 |
| <u>Hyalella azteca</u> | 3 | 7.1 | 10.0 | 114.7 | 0.3 | 53.0 | 47.4 | 15.7 | 21.5 | 9.0 | 1.8 | 1.9 | 1.0 | 0.70 |
| <u>Pisidium conventus</u> | 4 | 6.1 | 7.5 | 7.1 | 2.0 | 2.0 | 13.4 | 7.2 | 13.3 | 25.3 | 1.8 | 1.3 | 0.1 | 0.06 |
| <u>Chaoborus</u> | 5 | 5.8 | 4.8 | 8.6 | 3.8 | 8.6 | 8.6 | 5.8 | 33.1 | 31.4 | 3.0 | 1.8 | 0 | 0 |
| <u>Phaenopsectra</u> | 6 | 5.8 | 5.0 | 8.6 | 3.8 | 8.6 | 8.6 | 6.7 | 32.7 | 24.5 | 3.1 | 1.8 | 0 | 0 |
| <u>Chironomus</u> Spp | 7 | 7.1 | 5.2 | 119.4 | 1.2 | 50.0 | 90.8 | 5.9 | 22.4 | 38.4 | 2.9 | 1.9 | 0.2 | 0 |
| <u>Chironomus</u> Sp 1 | 8 | 8.1 | 10.2 | 192.4 | 0.1 | 104.9 | 88.4 | 12.2 | 3.5 | 10.3 | 2.8 | 2.2 | 1.0 | 1.0 |
| <u>Pontoporeia affinis</u> | 9 | 5.8 | 6.6 | 7.1 | 2.5 | 1.3 | 8.6 | 4.8 | 27.0 | 26.8 | 2.1 | 1.4 | 0 | 0 |

Figure 25. The mean plus and minus one standard deviation for each genus in terms of the four discriminant functions. The legend to the number code is present in Table 10.

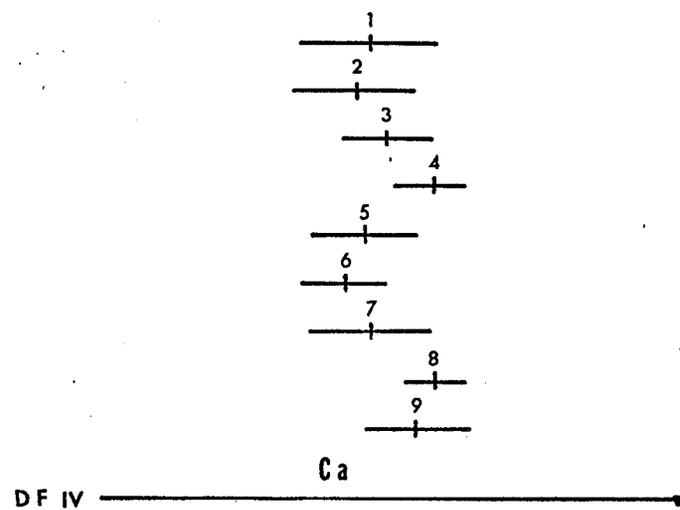
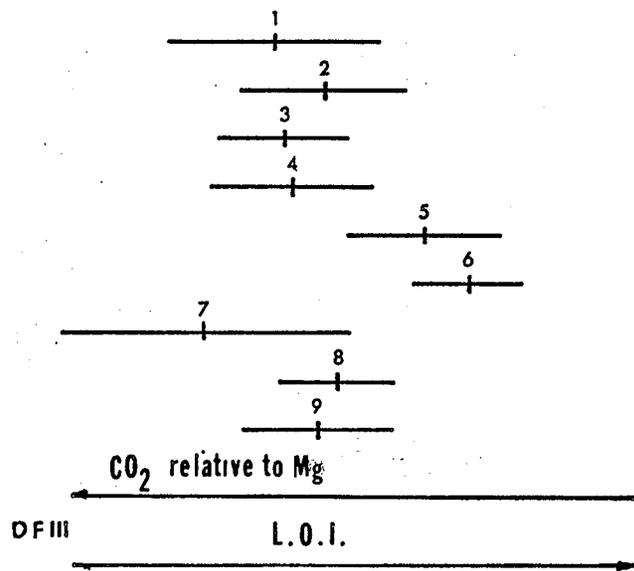
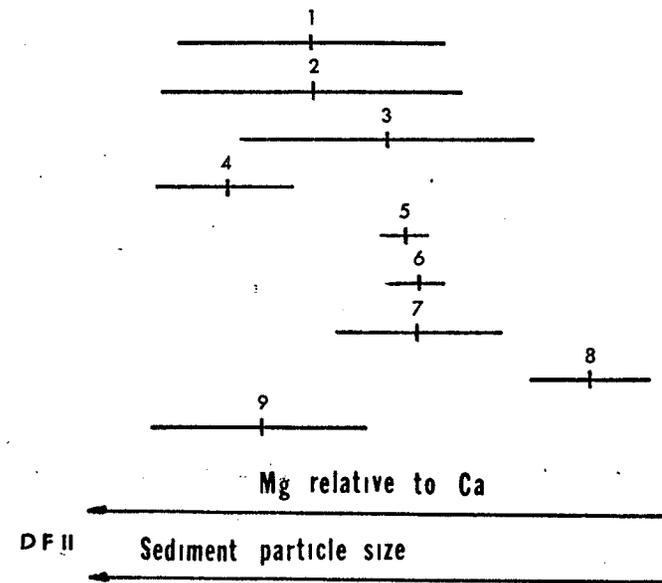
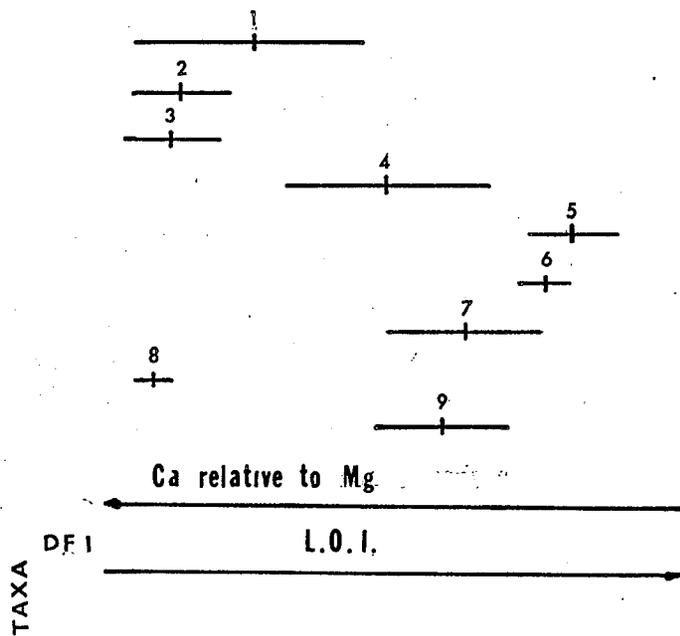


Table 11. Discriminant function coefficients of the among-taxa analysis showing the relative contribution of each of the original parameters to the discriminant function.

TABLE 11

| Disc. Function | I | II | III | IV |
|-------------------------|--------|--------|--------|--------|
| % Contr. to Variance | 68.02 | 13.93 | 8.71 | 5.13 |
| | 68.02 | 81.95 | 90.66 | 95.79 |
| pH | -0.018 | 0.014 | 0.175 | -0.268 |
| D.O. | -0.162 | -0.120 | 0.102 | 0.228 |
| Alk. | -0.049 | 0.320 | -0.281 | -0.264 |
| Fe | 0.186 | -0.014 | 0.336 | 0.018 |
| Mg | 0.465 | 0.484 | 0.459 | -0.204 |
| Ca | -0.683 | -0.547 | -0.242 | 0.749 |
| Temp. °C | -0.010 | -0.034 | 0.141 | 0.073 |
| CO ₂ | 0.068 | -0.078 | 0.476 | 0.127 |
| L.O.I. | 0.450 | -0.048 | -0.436 | 0.305 |
| \bar{x} | 0.066 | 0.462 | 0.186 | -0.022 |
| S.C. | 0.170 | 0.101 | 0.094 | -0.165 |
| C.P. | 0.040 | -0.014 | -0.079 | -0.045 |
| Veg. | -0.109 | 0.358 | 0.109 | 0.246 |

I Ca relative to Mg and organic content of sediment.

II Magnesium relative to calcium, mean sediment particle size.

III Magnesium and CO₂ relative to organic content of sediment.

IV Calcium concentration.

The loss on ignition of the sediment was a good depth indicator in all lakes, the significance of Mg relative to Ca is not clear. This function thus became a good within-lake discriminator over all four lakes, separating Paratanytarsus, Chironomus sp. 1, and Hyaella azteca from the deep-water types, Chironomus spp., Phaenopsectra, and Chaoborus. Tanytarsus and Pisidium straddled the two groups because of their widespread depth distributions.

Discriminant function II accounted for 14% of the among-genera variance, and was primarily loaded on the concentration of magnesium relative to calcium ions, and the mean particle size of the sediment. Discriminant function II was very similar to discriminant function I, except for the loading on sediment particle size instead of loss on ignition. Mean sediment particle size often decreases with depth, but this was not the case in parts of East Blue, Lakes 239 and 240. Because of this, the interaction of the three coefficients became a good discriminator of genera occurring primarily in one lake and having a limited within-lake distribution, e.g. Chironomus sp. 1 (East Blue), Chaoborus and Phaenopsectra (Lake 240), and Pisidium and Pontoporeia in Lake 239. Discriminant function II, although efficient in separating the above genera which are

lake characteristic, was of limited value because of the difficulty in interpreting the coefficients ecologically.

Discriminant function III contributed only 8.71% of the among-genera variance, and was expressed as magnesium and total CO₂ relative to the organic content of the sediment. Discriminant function III was probably the most ecologically interpretable function. This function separated the genera characteristic of reduced conditions and some exclusive to hardwater lakes, from genera found in well-aerated hypolimnia. It thus separated out Chironomus spp., Phaenopsectra, and Chaoborus from the other taxa.

It was clear that all three functions were depth related functions.

Although discriminant functions I and II provided the maximum separation (nearly 82% of the among-genera variance), they were not the most useful functions for ecological interpretation because sediment particle size was an attribute which did not appear to follow predictable patterns in the lakes sampled.

The most ecologically interpretable separation among genera was provided by discriminant functions I and III. These latter results showed Chaoborus and Phaenopsectra occupying a high CO₂ and low oxygen hypolimnion typical of eutrophic conditions. Chironomus spp. also occupied the profundal stations, but tended to be more widespread both in terms of depth and CO₂ concentration tolerance, clearly reflecting its ubiquitous distribution. The position of Pontoporeia affinis and Pisidium conventus on the two functions indicated their shallower, more mesotrophic distribution.

- ii. The distribution of the assemblages in a multi-dimensional space

The ten faunal assemblages identified in Table 9 were used in this analysis. Each temporal occurrence of the assemblage in a lake was associated with fourteen physical and chemical determinations.

The untransformed means of the fourteen variables for each assemblage are summarized in Table 12. The test of significance of among-assemblages differences yield χ^2 $m(g-1) = 126$ $df = 642.761$, which is highly significant.

The discriminant functions, the relative contribution of each coefficient, and the ecological

interpretation of the functions are summarized in Table 13. The means plus and minus one standard deviation, for each assemblage and each discriminant function, are shown in Figure 26.

Six functions accounted for 96.91% of the among-assemblages variance. The first three discriminant functions accounted for nearly 75% of the among-assemblages variance, while discriminant functions IV, V, and VI combined only accounted for 13% of the among-assemblages variance. Because of the latter three functions' low contribution to the total variance, they will not be discussed further.

Discriminant function I accounted for 39.29% of the among-assemblages variance, and the vector was dominated by alkalinity and CO_2 relative to magnesium ions.)

The first discriminant function separated high CO_2 , low magnesium, and low alkalinity assemblages from high alkalinity, high magnesium, and relatively low CO_2 . Ecologically the function had a dual role. First, based on alkalinity and hardness, it separated the assemblages that were unique to each lake (7, 8, and 10); secondly, based on the CO_2 and alkalinity relationship, it separated the assemblages characteristic

Table 12. Summary of physical data used in the multiple discriminant analysis. Untransformed mean values for each assemblage are shown.

TABLE 12

| Biotic Characteristics of Assemblage | Assemblage | pH | D.O. ppm | Alk. ppm | H ₂ S ppm | Fe ppm | Mg ppm | Ca ppm | Temp. °C | CO ₂ mg/l | L.O.I. % | $\bar{\theta}$ | S.C.θ | C.P. P/A | Veg. P/A |
|---|------------|------|----------|----------|----------------------|--------|--------|--------|----------|----------------------|----------|----------------|-------|----------|----------|
| <u>Pontoporeia affinis</u> <u>Pisidium conventus</u> | 1 | 5.82 | 7.3 | 6.5 | 0 | 2.3 | 2.5 | 8.6 | 4.9 | 24.7 | 26.8 | 1.8 | 1.3 | 0 | 0 |
| <u>Chironomus</u> Sp 1 <u>Paratanytarsus</u> <u>Dicrotendipes</u> | 2 | 8.14 | 7.1 | 182.3 | 0 | 0.2 | 100.1 | 83.1 | 15.2 | 3.1 | 12.6 | 1.9 | 2.7 | 0.4 | 0 |
| <u>Chaoborus</u> <u>Phaenopsectra</u> | 3 | 5.77 | 4.7 | 8.0 | 0 | 3.8 | 9.3 | 8.6 | 6.6 | 33.0 | 29.4 | 3.0 | 1.8 | 0 | 0 |
| <u>Chironomus</u> <u>Paratanytarsus</u> <u>Tanytarsus</u> | 4 | 7.43 | 4.0 | 118.2 | 0.02 | 0.6 | 100.0 | 60.8 | 6.9 | 11.1 | 37.0 | 3.0 | 2.1 | 0.1 | 0.1 |
| <u>Tanytarsus</u> <u>Paratanytarsus</u> | 5 | 6.86 | 8.7 | 28.8 | 0 | 0.2 | 24.6 | 26.2 | 14.1 | 3.2 | 5.5 | 1.9 | 1.5 | 1.0 | 0.4 |
| <u>Tanytarsus</u> <u>Paratanytarsus</u> | 6 | 6.74 | 9.4 | 32.2 | 0 | 0.8 | 15.8 | 21.6 | 14.8 | 7.2 | 5.0 | 2.0 | 1.4 | 1.0 | 0.3 |
| <u>Hyalella azteca</u> <u>Tanytarsus</u> | 7 | 8.1 | 10.2 | 72.3 | 0 | 0.1 | 76.9 | 74.0 | 13.6 | 1.4 | 12.6 | 1.9 | 2.1 | 1.0 | 0.6 |
| <u>Tanytarsus</u> <u>Pseudochironomus</u> | 8 | 8.2 | 7.9 | 130.4 | 0 | 0.1 | 114.6 | 93.0 | 11.9 | 2.0 | 2.9 | 1.3 | 2.3 | 0.9 | 1.0 |
| <u>Chironomus</u> <u>Cryptocladopelma</u> <u>Tanytarsus</u> | 9 | 7.4 | 6.4 | 91.6 | 0 | 0.5 | 57.4 | 52.6 | 12.6 | 8.6 | 25.8 | 2.4 | 1.9 | 0.6 | 0.4 |
| <u>Tanytarsus</u> <u>Chironomus</u> | 10 | 8.2 | 9.1 | 153.2 | 0 | 0.1 | 124.4 | 78.4 | 6.0 | 2.3 | 30.3 | 2.2 | 2.2 | 1.0 | 0 |

Table 13. Discriminant function coefficients of the among-assemblages analysis showing the relative contribution of each of the original parameters to the discriminant function.

TABLE 13

| Disc. Function | I | II | III | IV | V | VI |
|----------------------------|--------|--------|--------|--------|--------|--------|
| % contribution to variance | 39.29 | 29.33 | 16.20 | 6.15 | 4.10 | 2.84 |
| pH | 0.325 | 0.568 | 0.620 | -0.440 | 0.475 | 0.252 |
| Diss. oxygen | 0.043 | -0.019 | -0.173 | 0.012 | 0.119 | 0.321 |
| T. Alk. | -0.581 | -0.388 | -0.017 | -0.081 | -0.530 | -0.182 |
| H ₂ S | -0.047 | -0.012 | 0.038 | -0.067 | -0.019 | -0.006 |
| Iron | 0.174 | 0.077 | -0.161 | 0.261 | -0.011 | -0.162 |
| Mg | 0.417 | 0.175 | 0.119 | 0.741 | -0.141 | -0.503 |
| Calcium | -0.110 | -0.251 | -0.537 | 0.067 | 0.485 | 0.181 |
| Temperat. | 0.076 | -0.030 | -0.070 | 0.143 | 0.064 | 0.390 |
| CO ₂ | 0.466 | 0.358 | 0.095 | 0.094 | 0.420 | 0.279 |
| L.O.I. | 0.231 | 0.322 | 0.077 | -0.352 | 0.171 | 0.134 |
| Mean Part. Size | -0.037 | 0.043 | 0.336 | 0.031 | -0.067 | 0.470 |
| Sorting Coeffic. | 0.008 | 0.055 | 0.181 | 0.057 | -0.056 | -0.012 |
| Compensation Point | -0.236 | 0.434 | -0.259 | 0.101 | 0.001 | 0.130 |
| Veg. | 0.056 | 0.018 | 0.151 | 0.081 | 0.079 | 0.052 |

I Alk. rel. to Mg and CO₂

II pH and Compensation Pt.

III pH rel. to Ca

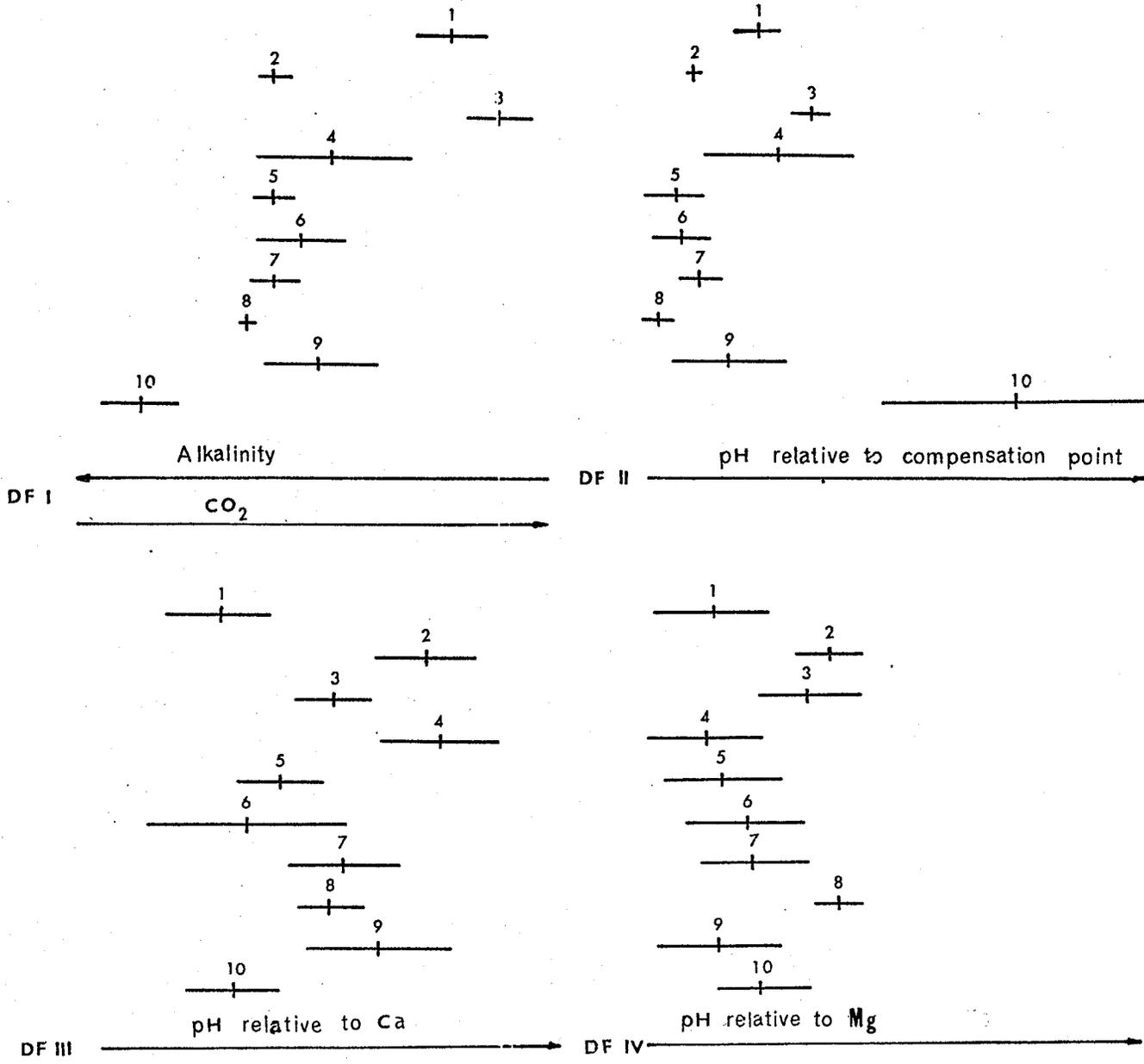
IV pH rel. to Mg

V Alk. rel. to pH, Ca and CO₂

VI Mg rel. to mean particle size

Figure 26. The mean plus and minus one standard deviation for each assemblage in terms of the four main discriminant functions. The legend to the number code is presented in Table 9.

ASSEMBLAGES



of oxygen-poor zones (1, 3) from those in O₂-rich zones (8, 10) (Figure 26).

Discriminant function II, contributing 29.33% of the among-assemblages variance, was based primarily on pH and compensation point. Within each lake the pH decreased with depth, while the compensation point was a depth-light penetration characteristic which separated each lake into two distinct zones, the trophogenic and tropholytic.

Ecologically, function II was interpreted as a depth-trophic (food) relationship. The assemblages occurring primarily above the compensation point (1, 2, 5, 6, 7, 8, and 9) were found in high pH areas relative to the rest of the lake, and presumably relied on epiphytic production for food, or preyed on other organisms. Those found below the compensation point presumably depended on organic fallout from the water column for food, or bacterial production at or in the sediment. In areas of high oxygen depletion (or high CO₂) and below the compensation point, such as that of assemblage 3 in Lake 240, it is interesting to see the predominance of highly motile groups such as Chaoborus, which exhibit diurnal movements to prey on zooplankton in the water column.

Discriminant function III contributed 16.20% of the among-assemblages variance, and was primarily influenced by the increase of pH relative to the calcium ion.

This relationship was difficult to interpret ecologically. The results were the separation of the very deep assemblages among lakes, where we have seen a decrease in pH relative to Ca (4, 9, 3), and the littoral assemblages characteristic only of the Duck Mountain lakes (2, 8), from littoral assemblages common among lakes (5, 6, 7) and mid-depth assemblages characteristic of deeper and more oligotrophic lakes (1, 10).

Two discriminant functions, I and II, appeared to be composed of the environmental factors which best separated the assemblages spatially, and which were also ecologically interpretable.

Discriminant function I was primarily a lake-type function, separating assemblages found in high-alkalinity areas and relatively low CO₂ concentrations (e.g. Tanytarsus - Chironomus, and Tanytarsus assemblages) from those found in low-alkalinity areas with relatively high CO₂ concentrations (e.g. Chaoborus - Phaenopsectra and the P. affinis - P. conventus assemblages) for that

lake. Discriminant function II was a depth-trophic function, separating assemblages in the trophogenic zone from those in the tropholytic zone. Taking both functions into account, it can be summarized that in these four lakes the Tanytarsus - Chironomus assemblage was found solely in the tropholytic zone of high-alkalinity, low CO₂ lakes, while the Chaoborus - Phaenopsectra and P. affinis - P. conventus assemblages were found only in the tropholytic zone of low-alkalinity lakes. The Chironomus spp. assemblage was primarily tropholytic, common to the lakes having zones of low oxygen tension. The Chironomus - Cryptocladopelma - Tanytarsus assemblage seemed to straddle the trophogenic-tropholytic boundary of most lakes, where the CO₂ content was low. The Paratanytarsus - Chironomus sp., the Paratanytarsus - Tanytarsus, the Tanytarsus - Paratanytarsus, and the H. azteca - Tanytarsus assemblages occupied similar trophogenic zones where the calcium to magnesium hardness ratio was slightly higher and the CO₂ was low. The Tanytarsus spp. assemblage was restricted to the trophogenic zone of the alkaline lakes.

DISCUSSION

The results of this benthic investigation indicated that in each lake the benthic faunal composition changed with water depth. Generally the faunal diversity and total numbers decreased through depth, but the littoral zone stations displayed greater temporal oscillations in diversity than profundal stations. Faunal assemblages of the littoral zones of all four lakes were similar in taxonomic composition, with small temporal variations, but those of the profundal zones differed from lake to lake. The physical and chemical data collected indicated that the littoral zone of each lake had the greatest temporal variations, whereas the profundal zones had the least, Beautiful Lake being the exception.

When an attempt was made to identify the environmental variables which best separated the benthic fauna, it was found that depth-related variables were most important, and were usually coupled with other ecologically interpretable variables, usually those related to trophic conditions in the lakes. The genera appeared to be separated along a depth-related gradient described by the mean sediment particle size and loss on ignition of the sediment. The taxa occupying the profundal zone could be further subdivided

by variation in CO₂ concentration, and stations specific taxa were separated along such geologically influenced variables as the concentration of calcium relative to magnesium ion.

The faunal assemblages were separated along variables which were ecologically more interpretable than those separating genera. These were compensation level, rooted vegetation, and factors such as CO₂ related to oxygen depletion in the hypolimnion.

Diversity in Lakes

In the context of this study, similarity or dissimilarity in diversity are not to be interpreted as indicating commonness of species at different points, or even similarity of faunal assemblages. Rather, as described by Margalef (1968), "... regard it as an expression of the richness and variety of species, and, in consequence, of the information-carrying capacity in an assemblage", or as a measure of the complexity of the food web at a point in space and time.

Wilhm (1967, 1968) proposed the use of diversity indices as indices of faunal assemblages, and championed their use as water quality indicators.

Others (Sanders 1968, Bechtel and Copeland 1970, Boesch 1972) used diversity indices as environmental indicators in marine studies, and often relied on the accepted relationships among diversity, stability, and maturity to interpret the results.

Before similar uses can be made in lacustrine macro-zoobenthic studies the inherent diversity patterns in lakes must be identified and their ability to reflect environmental stability and maturity verified.

In each lake the overall trend was one of decreasing diversity with depth (Tables 5 and 8). The littoral zone was usually occupied by many species (Table 3), usually small in size, which appeared to occur in large numbers for short periods of time. These species were present in the fourth instar for considerable portions of the year, which may be interpreted as indicating more than one generation per year; they also occupied a relatively high mean temperature zone (Table 2). From observation of gut contents made during the identification process and from the literature available, it appeared that the species present probably relied primarily on epiphytic growth and other invertebrates for food. The above characteristics have often been attributed to non-equilibrium species occupying ecosystems of low maturity

(MacArthur 1960, Levinton 1970). The littoral zone was the most heterogeneous area of the lakes (Table 4), with large spatial variations in sediment particle size and temporal changes in physical-chemical parameters (Table 3). Important variables such as temperature and percent cover of rooted aquatic plants fluctuated considerably over the seasons in a predictable manner (Table 2). Although other variables changed considerably over time, they were not all on a predictable seasonal basis (Appendix II).

The profundal regions of the lakes studied were occupied by a fauna of organisms of larger size than those in the littoral zone fauna. These animals typically can be expected to depend on bacteria and organic material which filtered down the water column for food. Some have been described in the literature as having life cycles of one year or more, and occupying a lower mean temperature zone. The hypolimnion in these lakes represented a region physically much more stable on the average within a year than the littoral zone (Table 4), but exceptions to this are found in oxygen-related parameters. The variables which exhibited larger fluctuations in the hypolimnion than the epilimnion also had a strong seasonal component, primarily centered on the spring

and fall overturns (Appendix II). The sediment appeared to be both spatially and temporally homogeneous. Reflecting the environmental stability, the profundal fauna displayed little change through time either in numbers (Figure 7) or diversity (Table 8). Exceptions were Beautiful Lake in August of 1970 and July of 1971 when summer mixing took place. Immediately following these overturns, sharp decreases in numbers of organisms and diversity occurred. Similar phenomena were evident in Lake 240 at the times of low oxygen concentration.

The value of using diversity indices in environmental studies rests on the premises expressed by Margalef (1963) and others, that environments which are temporally more stable possess the characteristics of evolutionally mature systems and support a more diverse flora and fauna.

In this study, no such relationships among diversity of zoobenthic, maturity as indicated by the zoobenthic taxa present, and stability were evident. The littoral zones, while being utilized by the most diverse faunas, had the greatest fluctuations in diversity values through time. These areas also had the lowest seasonal habitat stability of the portions of lakes studied. The highest mean seasonal diversity

at the maximum depths sampled was found in Beautiful Lake, which also had the lowest hypolimnetic seasonal habitat stability. Diversity values in fact tended to be negatively correlated with the seasonal habitat stability of the areas studied. Also, the species occupying the littoral zone had more opportunistic characteristics than the equilibrium species which would be expected in a mature system. The hypolimnetic region, on the other hand, was inhabited by few species having relatively low fluctuations in numbers or diversity through time, and these species bore the characteristics of equilibrium species as defined by MacArthur (1960) and Levinton (1970). If any maturity-diversity relationship exists in this study, it has the characteristics of the low maturity-high diversity concept postulated by Pielou (1966).

From the results obtained from these four lakes, one cannot help but question the value of using diversity indices as the ultimate means of evaluating an ecosystem. First of all, if the diversity index obtained is to be reliable, each organism must be identified and counted. Considerable information is gained in this process, but much is lost when the results are consolidated into an index whose meaning is not really clear. Furthermore, with lacustrine

benthos, this index is dependent on where in the lake the sample is taken, and on the time of year. It can vary greatly in shallow waters and in some deeper waters (e.g. Beautiful Lake) because of climatic conditions.

The only reliable information gained from diversity indices is a measure of the complexity of a sample of a faunal assemblage at one place and time. The value of the index itself is in reducing the original biological data into a single constant which can be used to detect temporal or spatial changes in the structure of faunal assemblages.

Faunal Classifications in Lakes

Attempts were made to assess the similarity of the faunas among the lakes.

These results indicated that each lake, even in as close proximity as Lakes 239 and 240, retained its identity at the species level of identification. This phenomenon may be misleading because the species of chironomids, especially immature specimens, are poorly known; species usually are separated on minor morphological differences which in fact could result from responses of the same species to different environments. The only areas of faunal assemblages common among lakes were the littoral zones. In these,

some degree of similarity was evident between near shore samples of Lakes 239 and 240, and two samples from Beautiful Lake displayed close affinity to the East Blue Lake littoral samples. The greatest difference was seen between lakes in the Pre-Cambrian Shield as compared to the Agassiz Escarpment lakes.

Because of the apparent lake specificity of the assemblages composed of species, their value in comparing lakes of different geographic regions appeared to be minimal. Their usefulness could conceivably be increased if and when the taxonomic problems with the North American Diptera are solved and if, upon solution, it is found that aquatic larvae can be identified as true biological species. Until this degree of taxonomic proficiency is attained, the use of genera should be encouraged for such comparisons.

The results of the analysis at the generic level yielded results which were relatively easy to interpret. Ten faunal assemblages were described (Table 9), and most were found in narrow depth zones in the littoral region of several lakes. Some profundal assemblages were characteristic of individual lakes (Figure 24a, b, c, d). Individual lakes could not be identified by their littoral assemblages because

of the similarity between lakes of similar geographic areas.

From the space-time distribution of the assemblages of each lake (Figure 24) and from the species distribution in each lake (Table 6), a gradient in species distribution similar to those found in phytosociological studies found in Whittaker 1967 became evident. Had samples in this been taken at closer intervals along each gradient, it would probably have been possible to show unimodal densities of species overlapping along these gradients. Within the limitations of the data available, a similar approach can still be used to illustrate this using the dominant genera in each lake. The percentage of the total numbers collected at each depth was calculated for each major taxon. The results were plotted by uniting the values obtained along the various depths, assuming a smooth change in numbers between points (Figure 27 and 28). The top curves indicated by arrows in Figures 27 and 28 correspond to the dominant taxa that caused the assemblages in Table 9 to be identified.

From these plots, some distribution patterns appeared to be more similar among lakes than others, the main ones being Tanytarsus, Paratanytarsus, Hyalella azteca, and Chironomus spp. From the distribution of

the above taxa, and the space-time distribution of the assemblages in each lake, it became apparent that the four taxa were the primary contributors to assemblages which were common in the lakes and appeared to be primarily depth distributed.

Other taxa such as Chironomus sp. 1, P. affinis, P. conventus, Phaenopsectra, and Chaoborus were lake specific in their abundance, and fitted among the distribution of the main taxa discussed above; these were the main contributors in causing lake specific assemblages to be identified. The results in Figures 27 and 28 graphically illustrate where the assemblages shown in Table 9 were distributed in each of the four lakes.

A depth related taxonomic continuum would appear to exist, as all the taxa used overlap considerably. This phenomenon has been used in the past as an argument against creating benthic assemblages (Brinkhurst 1974). However, if relative abundance of each taxon at each depth sampled had been used in this case, peaks of dominance of groups of one to three taxa, distributed unimodally through depth, as in Figures 27 and 28, would have become evident.

From the above results, a simplified sequence of assemblages among and within the four lakes was

Figure 27. Distribution of each major taxon shown as a percentage of the total numbers collected at each depth of (a) East Blue Lake and (b) Beautiful Lake. Arrows indicate areas which would appear as assemblages in this study.

Tanytarsus 
Paratanytarsus 
Chironomus sp.1 
Hyalella azteca 
Chironomus spp. 

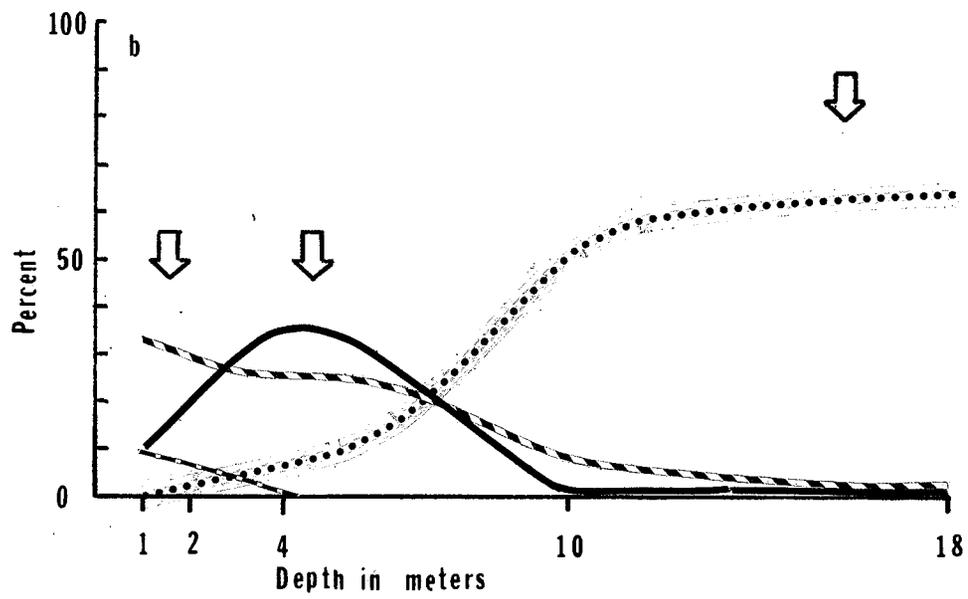
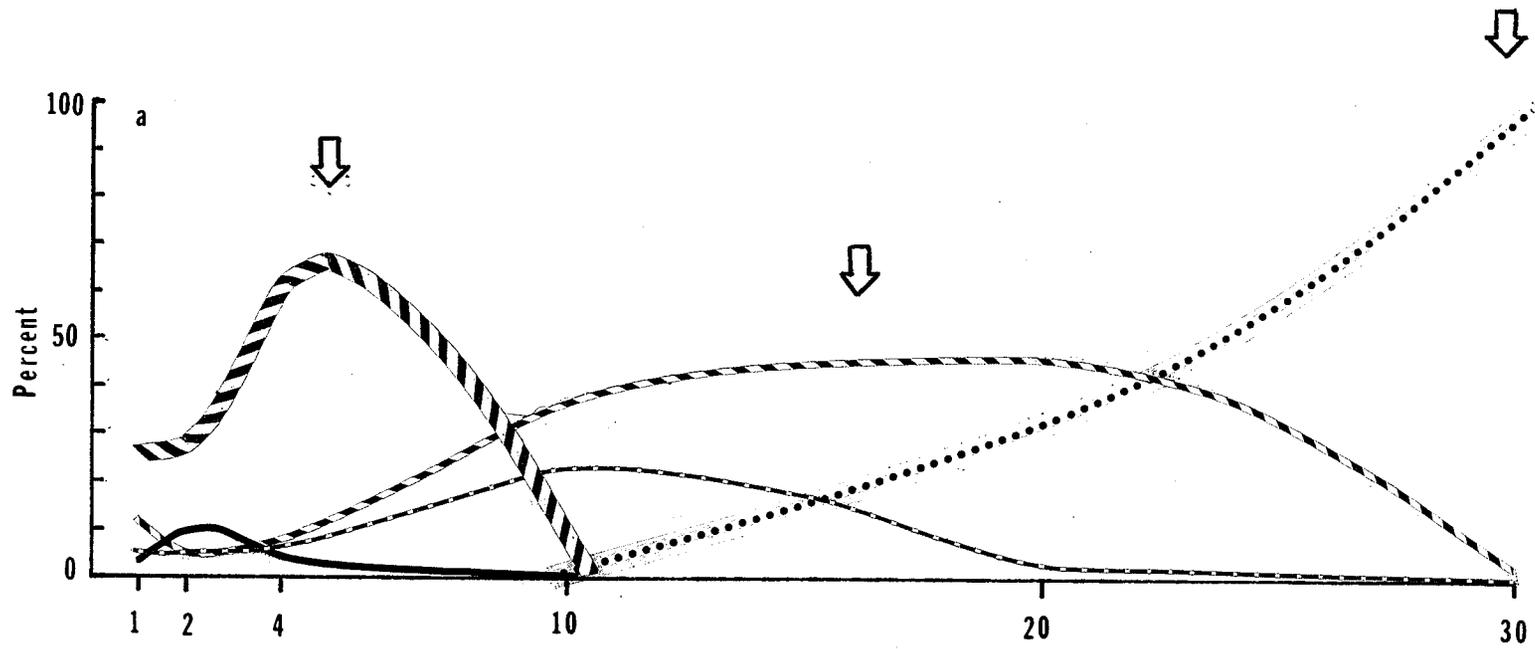
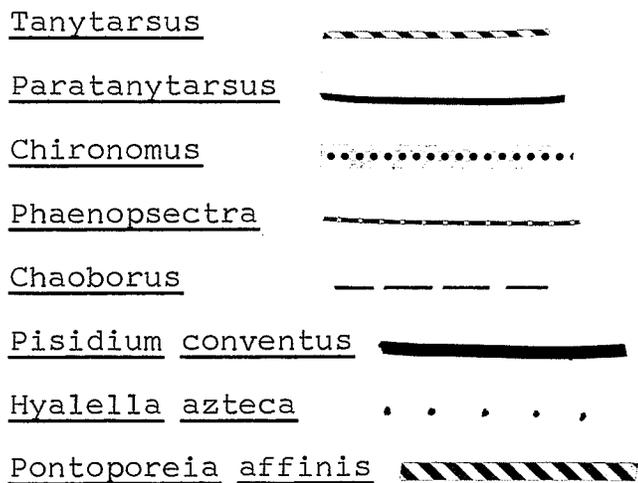
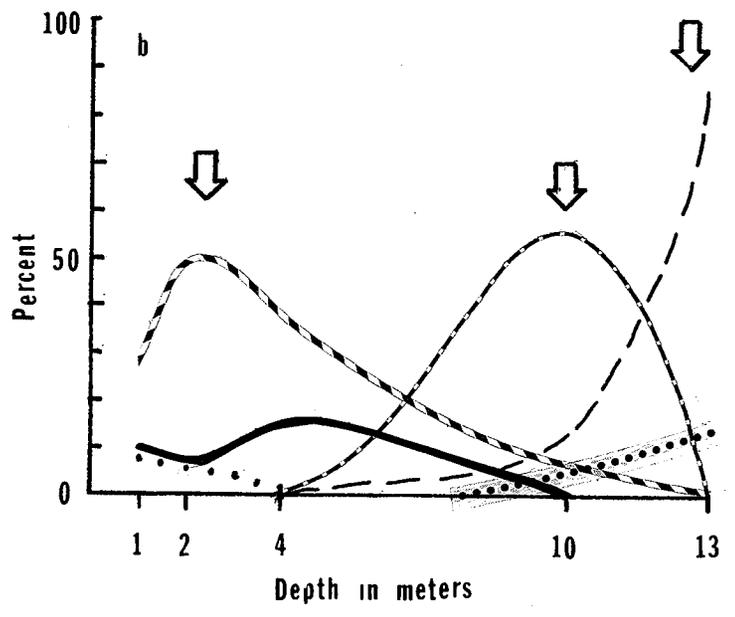
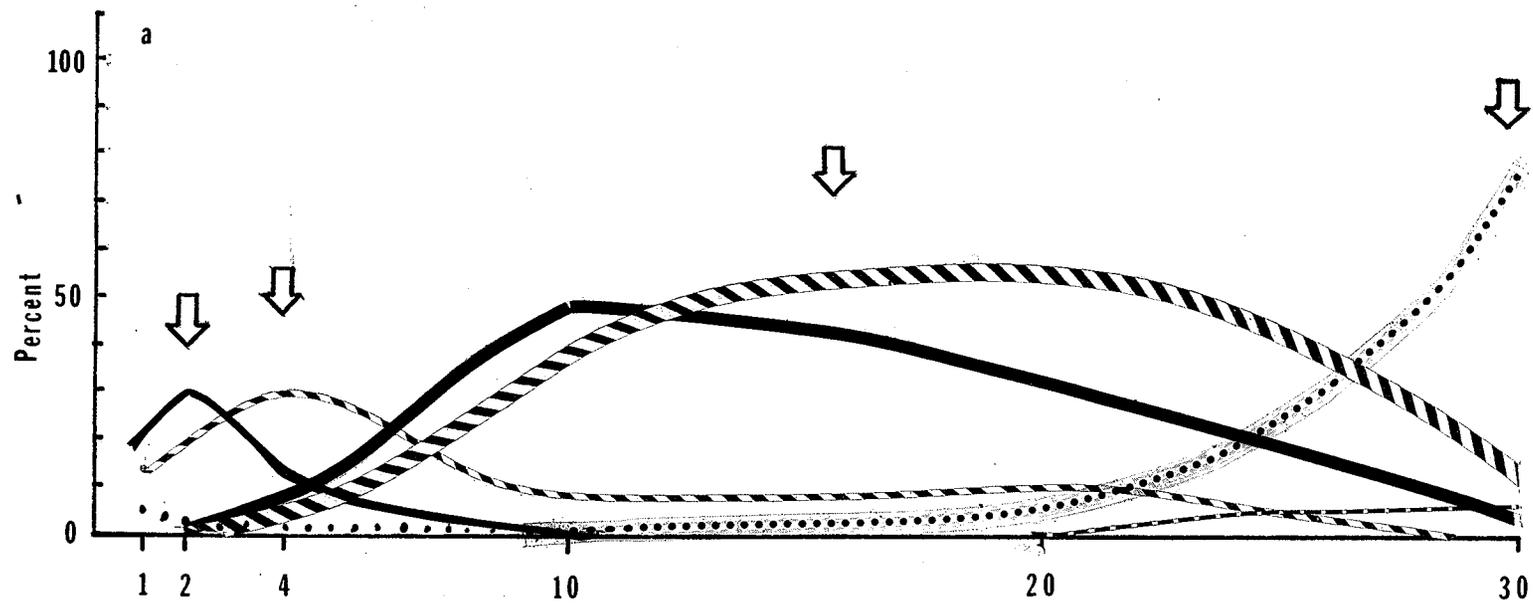


Figure 28. Distribution of each major taxon shown as a percentage of the total numbers collected at each depth of (a) Lake 239 and (b) Lake 240. Arrows indicate areas which would appear as assemblages in this study.





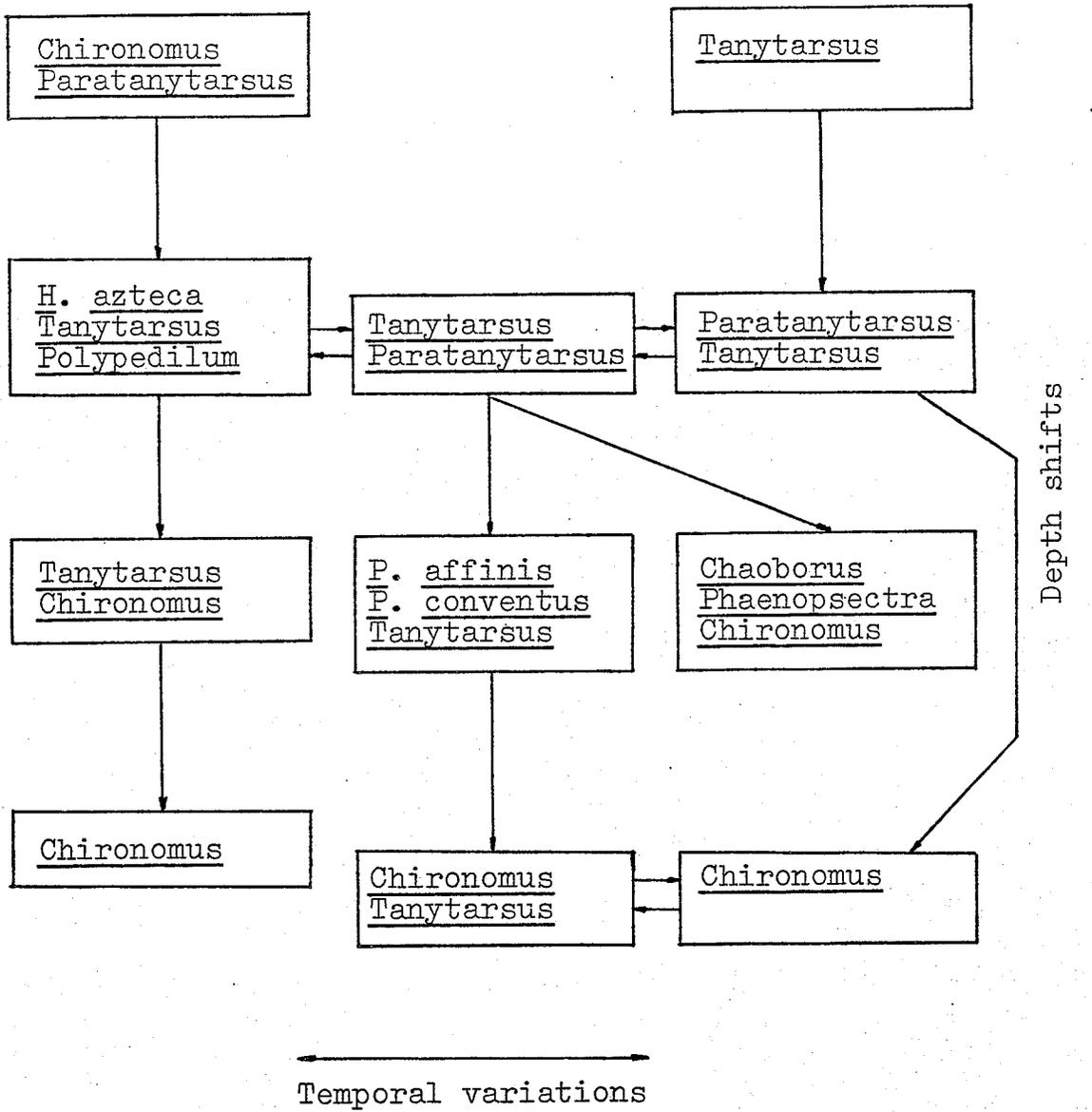
created (Figure 29). In this figure, joined vertical sequences indicate changes in assemblage through depth. Joined horizontal sequences indicate temporal changes in assemblage, presumably caused by life history patterns or physical disturbances.

Certain benthic faunal assemblages appeared to be common above the thermocline in all the lakes studied, while below the thermocline lake specific assemblages could be found. In every lake there was a predominance of Tanytarsini, Tanytarsus and/or Paratanytarsus in the littoral zone, accompanied by a mixture of Chironomini. At depths below the Tanytarsini group, variations among lakes became evident, some having the Pontoporeia - Pisidium assemblage, others having the Chaoborus - Phaenopsectra assemblage, and still others having a pure Chironomus complex.

In each lake a depth gradient of Paratanytarsus, Tanytarsus, Chironomus occurred. Within each step in this sequence variations occurred, which either characterized the lake or reflected temporal variations, the latter principally in the littoral zone.

Examples of lake specific variations were the P. affinis - P. conventus - Tanytarsus assemblage in

Figure 29. Simplified spatial and temporal
distribution of faunal assemblages in the lakes
studied.



Lake 239, the Chaoborus - Phaenopsectra - Chironomus assemblage in Lake 240, and the H. azteca - Tanytarsus - Polypedilum (Tripodura) in East Blue Lake. These characteristic groupings were usually found below the thermocline, but not at maximum depth. I had expected that they would be found at maximum depth, or the zone where maximum O₂ depletion should occur. The finding of these "lake indicator" assemblages below the thermocline but above maximum depth leads me to speculate that factors other than, or interacting with, minimum dissolved oxygen concentration (the variable widely accepted in the literature) may determine the distribution of these characteristic faunas.

Temporal variations were exemplified by Paratanytarsus - Tanytarsus groups shifting to Tanytarsus - Paratanytarsus, a characteristic shared by three of the lakes, and the Paratanytarsus - Chironomus group shifting to either H. azteca - Tanytarsus or Paratanytarsus - Tanytarsus groups in East Blue Lake.

Ecological Variables and the Benthic Distribution

When the ecological interpretation of the discriminant functions obtained in the analysis among

assemblages and among genera is considered, the advantage of using assemblages over organisms becomes evident. For example, the first two discriminant functions among genera could not be ecologically interpreted, even though they represented 82% of the among-genera variance. In the among-assemblages analysis, on the other hand, the first two discriminant functions, which accounted for 68% of the among-assemblages variance, are more easily interpreted.

From the original data and the compilation of the assemblages, it was noted that at least one of the three most numerous genera, Paratanytarsus, Chironomus, and Tanytarsus, was present in 99% of the samples collected. It seemed logical to assume that all the assemblages identified existed at least partially within the physical environment occupied by the three genera.

To illustrate the relationship between the taxa and the assemblages, the discriminant scores for each sample containing one or more of the three taxa were plotted in a space defined by functions I and III of the among-genera analysis (Figure 30). Functions I and III were chosen because they were easier to interpret ecologically than function II. From these plots, one can see that Chironomus can occur under a

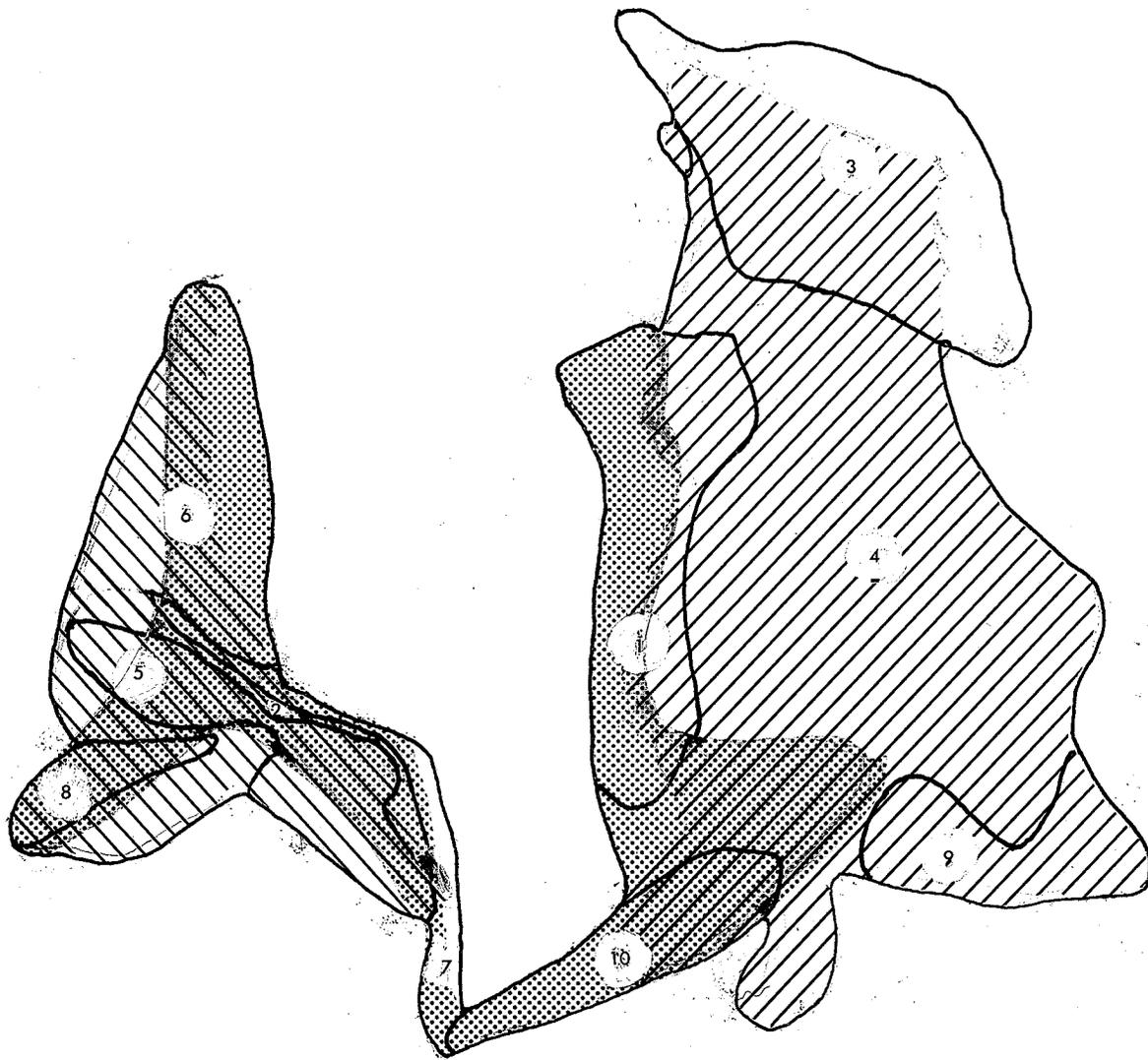
variety of conditions, from very anoxic to well-aerated, exploiting a variety of particle sizes and organic contents of sediments, and—as a whole—found in deeper portions of lakes. Tanytarsus, another widespread genus, is found in all lake types, but tends to be missing from sediment containing more than 30% organic material, or areas that during the year show prolonged periods of oxygen depletion. Paratanytarsus overlaps the Tanytarsus distribution in the shallow zones of lakes, but extends its range into shallower waters having considerable standing vegetation.

The distribution of the assemblages as represented by their temporal and spatial distribution were plotted on the space enclosed by discriminant functions I and III of the among-genera analysis (Figure 30). The assemblages clustering around the Chironomus distribution are the ones previously described as tropholytic, and those around the Paratanytarsus and Paratanytarsus - Tanytarsus overlap zone are trophogenic.

Within the shallow water distribution, two assemblages, the Tanytarsus - Paratanytarsus and the Paratanytarsus - Tanytarsus dominate the physical space. The two occupy very similar physical space, and the presence of one or the other assemblage is

Figure 30. Distribution of each assemblage
(Table 9) on the discriminant space occupied
by Tanytarsus, Paratanytarsus, and Chironomus.





Ca relative to Mg

Mg ions

L.O.I. & CO₂

DF I

L.O.I.

DF III

probably a temporal phenomenon reflecting the differences in life cycle patterns of the two genera. These two should not be distinguished as true assemblages, but rather expressions of the same assemblage reflecting the emergence of one or the other of the dominant genera. The H. azteca - Tanytarsus assemblage is typically found at the deepest edge of the Paratanytarsus range, and at the edge of the vegetated zones, deeper than the Chironomus sp. 1 - Paratanytarsus assemblage found in East Blue Lake. The Tanytarsus assemblage, found only in the 1 m station of Beautiful Lake, occurred in shallow, hard water, with very low organic material in the sediment. Thus, within the trophogenic zone of the four lakes several assemblages are found, all reflecting variations in Tanytarsus or Paratanytarsus densities. These variations seem to reflect normal temporal density changes due to emergence, seasonal peaks in macrophytic growth which may affect the densities of Hyaella, and the effects of storms which may disturb the habitat.

The transition between the trophogenic and tropholytic zones can take two forms. One, as in East Blue Lake, is a gradual change from the Hyaella - Tanytarsus assemblage to the Tanytarsus - Chironomus assemblage, and then to a Chironomus spp. assemblage.

In the lakes having a lower oxygen concentration (or higher total CO₂) at the transition zone, a Chironomus - Cryptocladopelma - Tanytarsus assemblage may be present, though only for short periods of time and disappearing as the oxygen drops below 25% saturation. Lakes typically having a low oxygen concentration in the hypolimnion for the greater part of the year, and where the bottom of the thermocline and compensation point coincide closely, also show a marked decrease in the diversity of the zoobenthos at this depth zone. In these lakes, the genera Chironomus and Tanytarsus do not overlap to form a common assemblage. Rather, an assemblage dominated by completely different groups exists, as in Lake 239 (the P. affinis - P. conventus assemblage) and in Lake 240 (the Chaoborus - Phaenopsectra assemblage). In Lake 239, the P. affinis - Pisidium assemblage yields to a Chironomus spp. assemblage with increased depth and increase in CO₂ or decrease in oxygen concentration. In the profundal zone of Lake 240, the Phaenopsectra - Chaoborus assemblage is the dominant one, as the lake's hypolimnion has the highest CO₂ concentration and temperature level of the four lakes studied.

In Figure 30, the P. affinis - P. conventus assemblage straddles the environmental space where

Tanytarsus and Chironomus meet and overlap in areas of lower oxygen concentration than the trophogenic zones. Where the physical environment changes gradually from shore to maximum depth, and the breaks between the trophogenic and tropholytic zones are gradual, as in East Blue Lake, there is a gradual shift in dominance from Tanytarsus to Chironomus. Where the changes in the physical environment are seemingly compressed between the trophogenic and tropholytic zones as in Lake 240, Tanytarsus gives way to Chironomus and Phaenopsectra. Lake 239, which appears to have a condition intermediate between the two lakes, has a zone where Tanytarsus and Chironomus are found in low numbers, but is inhabited by high densities of the amphipod Pontoporeia affinis and the mollusk Pisidium conventus. This type of distribution leads one to speculate that perhaps at the regions of overlap the habitat is marginal for both genera. Whether the limitations are trophic or physical is not known. It may be that Chironomus and Tanytarsus are in direct competition for a common resource, and may inhibit each other's success and allow other groups to become dominant. This would not be the case if only the two species were in competition, as most competition models suggest that one species will out-compete the other. But in a complex situation where many species involved,

one or two unrelated taxa, might out-compete the first two.

Overall, the plots indicate the futility of using individual taxa as indicator organisms because of their ability to survive in small numbers outside their optimum environment. Faunal assemblages, on the other hand, take into account the biological interactions of the taxa present as measured by the similarity in the species composition and their relative abundance. As a result, the groups formed, and here identified as faunal assemblages, represent associations which are more likely to be limited in their distribution by the physical environment; thus, the results of a multivariate analysis such as discriminant function analysis based on environmental variables should be easier to interpret ecologically.

The Bottom Faunistic Lake Type System and its
Application to the Four Lakes in Central Canada

In 1920, Thienemann proposed that two main types of bottom faunistic lakes existed in northern Europe, the Tanytarsus lake and the Chironomus lake. More detailed divisions were proposed by Lenz (1925) and Lundbeck (1926), and these concluded that the bottom fauna found reflected the trophic characteristics

of lakes. An oligotrophic lake would be an Orthocladius or a Tanytarsus lake; a mesotrophic lake would be a Stictochironomus or Sergentia lake; and a eutrophic lake would be a primarily Chironomus lake.

Brundin (1958) extended the lake classification to the southern hemisphere. A rigorous review of lake typology is presented in Brinkhurst (1974). To my knowlege, no such attempts have been made in North America, and particularly central Canada. Based on the data discussed in previous sections, and information available in the literature, it became obvious that central Canadian lakes could not be fitted into any of the existing lake typology schemes.

In the areas of this study, the macrobenthic organisms which numerically dominate the profundal assemblages cannot be used as indicators of the trophic state of a lake, but may be useful as indicators of combinations of physical factors such as oxygen, temperature, substrate types, and pH standards in portions of lakes.

Evidence was sought that others had found some of the organisms which dominated the faunal assemblages described in this study. For this region, few studies were available, and even fewer provided

enough information to allow an estimation of the depth distribution of benthic organisms in lakes, or to relate the benthic distribution to physical characteristics of the lakes, particularly in the shallow water regions. However, where information was available, comparisons were made.

Based on the literature available and on the results from this study, a scheme was created, not with the objective of typifying lakes, but rather to present environmental conditions under which certain types of invertebrates may be dominant in parts of lakes.

These groups of benthic organisms inhabiting soft sediments can be arbitrarily broken into three basic components in the four lakes studied: the littoral groups, the transition groups between the trophogenic and tropholytic zones, and the profundal groups. In most cases, with the possible exception of the profundal groups, the assemblage identified can be part of a distribution gradient of the dominant taxa; for example, very shallow sampling in a lake may result in classifying the benthic fauna as a Tanytarsus - Paratanytarsus assemblage, while sampling deeper might reveal a Tanytarsus - Chironomus grouping, and just below the summer compensation point

one may find a Chironomus - Tanytarsus grouping. Obviously one is sampling along a taxa distribution gradient, but the fact that one taxon is dominant over the other in space should reflect the physical conditions present at that point in space.

The littoral groups

Tanytarsus - Parantanytarsus, other Chironomini, other orders of insects, and amphipods—These occur in the littoral zones of most lakes with waters above pH 5.5 and varying substrates.

The transition groups

Tanytarsus - Chironomus—This is a group present at about the compensation point in lakes with pH above 7, and organic content of sediment near 20%. It represents an intermediate form between littoral and profundal zones, and was identified in East Blue Lake only.

Chironomus - Tanytarsus and Chironomus - Cryptocladopelma - Tanytarsus—These are two assemblages found below the compensation point, in areas where there is little oxygen depletion during the summer, where the pH is above 6, and the organic content of the sediment between 20 and 30%.

The profundal groups

Pontoporeia affinis - Pisidium conventus—This is characteristic of the tropholytic zone of glaciated

lakes with low summer temperature, high oxygen content, and high organic content of the sediment. Lakes in which this assemblage was found were Lakes 239, 465, and Hillock Lake (Hamilton 1971) in western Ontario, Lake Winnipeg in the deeper North Basin (personal observations) and Lake Athapapuskow, and Twin Lake (Slack 1967).

Chironomus—This is a common assemblage in most lakes which have zones below the trophogenic zone with considerable oxygen depletion during the summer, but seldom, or only briefly, exhibiting complete anoxia. This zone typically has high CO_2 , low O_2 , very high organic content of the sediment, and the animals can withstand reduced pH.

Phaenopsectra coracina, often with Chaoborus—This is a common assemblage in zones of Shield-bordering lakes which suffer severe oxygen depletion during the summer. So far, the areas where these assemblages appear to occur, as estimated from this work and other reports are: Lake 240; Lakes 241 and 122 (Hamilton 1971): Falcon Lake and Twin Lake (Slack 1967) in the deeper stations. All reports of this assemblage are from areas where pH is 7 or lower, and organic contents are high.

Chaoborus—When found in the sediment of stratified lakes, this appears to indicate zones of acute

oxygen shortages, often being reported from meromictic lakes, e.g. Lake 120 in western Ontario (P. Campbell, personal communication) and West Blue Lake, Duck Mountains (F. Ward, personal communication).

The literature of this area suggests that shallow lakes which do not stratify often have taxa which are also present in anoxic regions of lakes, as well as littoral types. For example, Lake 303 in western Ontario has a benthic fauna dominated by Chaoborus and various Chironomini and Tanytarsini (Hamilton 1971), and a similar situation appears in Twin Lake in eastern Manitoba described by Slack (1967).

CONCLUSIONS

On the basis of this study and the literature available, the following conclusions relating to the original objectives (Page 7) were reached.

- (1) The standing crop as well as numbers of species collected typically decreased with depth.
- (2) The littoral zones hosted several species of Tanytarsini, Chironomini, and other orders of insects as well as the amphipod Hyaella azteca.

- (3) With the exception of East Blue Lake, the Tanytarsini decreased in numbers with depth, and were replaced by members of the genus Chironomus, Phaenopsectra, P. affinis, P. conventus, and Chaoborus.
- (4) Within each lake, the benthic community showed greater differences in taxonomic composition between samples collected in the littoral and profundal zones, than among samples collected at different depths within each zone.
- (5) Among the lakes sampled, greater differences in taxonomic composition were found among samples collected among the profundal zones than among littoral zone samples.
- (6) Benthic faunal assemblages were identified, some lake specific and others common to the soft bottom of all the lakes studied. The littoral community was composed mainly of one assemblage dominated by Tanytarsus and Paratanytarsus. Variations of the above assemblage were found, these often reflecting the life cycles of the dominant taxa. Where rooted vegetation was abundant, Hyalella azteca and/or Chironomus sp. 1 were conspicuous in the assemblage. In the profundal zones, lake specific assemblages were typically found; these were P. affinis - P. conventus, Phaenopsectra - Chaoborus, and the most common one made up mainly of Chironomus. Between the littoral

and profundal zones, assemblages intermediate between Chironomus and Tanytarsus were commonly found.

(7) Diversities, as determined by the Shannon-Weaver function, typically decreased with depth. The highest diversities were encountered in the sampling areas having the greater seasonal variation in the physical variables measured.

(8) The areas in which the highest diversities were recorded also had the greatest temporal variation in diversity values.

(9) There appeared to be little correlation between diversity of the benthic fauna and stability or maturity of the habitat.

(10) Because of the temporal and spatial variation in diversity values encountered, and because of the lack of correlation between diversity, stability, and maturity, diversity indices were found to have limited predictive value in lacustrine benthic ecology.

(11) Of the organisms which have been typically used as lake type indicators, three were collected in the lakes studied.

Heterotrissocladus, usually associated with very oligotrophic conditions, was collected in very low numbers in Lakes 239 and 240.

Tanytarsus, usually considered an indicator of oligotrophic conditions, was found in all the lakes

studied, but the depth to which its range extended changed from lake to lake.

Chironomus, usually considered an indicator of eutrophic conditions, was found in the profundal zones of all four lakes.

These distributions precluded the use of the above taxa as a lake type indicator.

(12) Benthos diversities, indicator organisms, or faunal assemblages should not be used as lake type indicators. Faunal assemblages, however, give an indication of the structure of the benthic community and its environment, yet require less rigorous sampling since their identification is based on 2 or 3 of the most abundant members of the benthic fauna.

(13) When attempts were made to relate individual zoobenthic faunal assemblages to the physical environment that they occupied, it was found that lake-specific assemblages tended to separate mainly along variables which were geologic zone specific to geologic areas, e.g. alkalinity. Assemblage distributions within lakes were associated with depth related variables such as the decline of pH with depth, or variables such as compensation depth and CO_2 which reflected biotic activity.

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APPENDIX I

Distribution of taxa by lake

| | | East Blue | Beautiful | Lake 239 | Lake 240 |
|-------------------------------|------|--------------|-----------|-------------|-------------|
| <u>Chaoborus flavicans</u> | | | | | x |
| <u>Chaoborus punctipinnis</u> | | x | x | x | x |
| <u>Pseudochironomus</u> | sp | x | | | |
| <u>Pseudochironomus</u> | sp 1 | x | | | |
| <u>Micropsectra</u> | sp | | | x | x |
| <u>Paratanytarsus</u> | sp | | | x | x |
| <u>Paratanytarsus</u> | sp 1 | | | x | |
| <u>Paratanytarsus</u> | sp 2 | x | | | |
| <u>Paratanytarsus</u> | sp 3 | x | x | | |
| <u>Dicrotendipes</u> | sp | | | x | x |
| <u>Dicrotendipes</u> | sp 1 | x | | | |
| <u>Dicrotendipes</u> | sp 2 | | x | | |
| <u>Dicrotendipes</u> | sp 3 | | x | | |
| <u>Ablabesmyia</u> | sp | | x | | |
| <u>Ablabesmyia</u> | sp 1 | x | | | |
| <u>Ablabesmyia</u> | sp 2 | | | x | x |
| <u>Cryptocladopelma</u> | sp | | | x | x |
| <u>Cryptocladopelma</u> | sp 1 | | | x | x |
| <u>Cryptocladopelma</u> | sp 2 | x | x | | |
| <u>Paralauterborniella</u> | spp | | | x | x |
| * <u>Pagastiella</u> | | x | x | x | x |
| <u>Cryptochironomus</u> | sp | x | | | |
| <u>Cryptochironomus</u> | sp 1 | | | x | x |
| <u>Cryptochironomus</u> | sp 2 | | x | | |
| <u>Phaenopsectra</u> | sp | | | | x |
| <u>Phaenopsectra</u> | sp 1 | | | x | x |
| <u>Heterotanytarsus</u> | sp | | | x | x |
| <u>Heterotanytarsus</u> | sp 1 | | | | x |
| <u>Microtendipes</u> | sp | | | x | x |
| <u>Paratendipes</u> | sp | x | | | |
| <u>Paratendipes</u> | sp 1 | x | | | |

| | | East Blue | Beautiful | Lake 239 | Lake 240 |
|----------------------------------|-------|--------------|-----------|-------------|-------------|
| <u>Stictochironomus</u> | sp | | | x | |
| <u>Stictochironomus</u> | sp 1 | | | | x |
| <u>Monodiamesa</u> | | | | | x |
| <u>Protanypus</u> | | | | x | |
| <u>Einfeldia</u> | sp | x | | | |
| <u>Einfeldia</u> | sp 1 | | x | | |
| * <u>Orthocladus</u> | spp | | x | | |
| <u>Cricotopus</u> | sp | | | x | x |
| <u>Cricotopus</u> | sp 1 | x | | | |
| <u>Cricotopus</u> | sp 2 | x | | | |
| * <u>Heterotrissocladus</u> | spp | | | x | x |
| <u>Tanytarsus</u> | sp | | | x | x |
| <u>Tanytarsus</u> | sp 1 | | | x | x |
| <u>Tanytarsus</u> | sp 3 | | x | | |
| <u>Tanytarsus</u> | sp 4 | x | | | |
| <u>Tanytarsus</u> | sp 5 | x | | | |
| <u>Tanytarsus</u> | sp 7 | x | | | |
| <u>Tanytarsus</u> | sp 8 | | x | | |
| <u>Chironomus</u> | sp | x | | | |
| <u>Chironomus</u> | sp 1 | x | | | |
| <u>Chironomus</u> | sp 2 | | x | | |
| <u>Chironomus</u> | sp 3 | | x | | |
| <u>Chironomus</u> | sp 4 | | | x | |
| <u>Chironomus</u> | sp 5 | x | | | |
| <u>Chironomus</u> | sp 6 | | | x | x |
| <u>Chironomus</u> | sp 7 | x | | | |
| * <u>Procladius</u> | spp 1 | x | x | x | x |
| <u>Polypedilum</u> (nubeculosum) | | | | x | x |
| <u>Polypedilum</u> (Tripodura) | sp | | | x | x |

| | | East Blue | Beautiful | Lake 239 | Lake 240 |
|----------------------------|------|--------------|-----------|-------------|-------------|
| <u>Polypedilum</u> | sp 1 | x | x | | |
| <u>Polypedilum</u> | sp 2 | x | | | |
| <u>Pentapedilum</u> | sp | | | x | x |
| <u>Psectrocladius</u> | sp | x | | | |
| <u>Psectrocladius</u> | sp 1 | x | x | | |
| <u>Hyaella azteca</u> | | x | x | x | x |
| <u>Pontoporeia affinis</u> | | | | x | x |
| <u>Mysis relicta</u> | | | | x | |
| <u>Elmiidae</u> | sp | | | x | x |
| <u>Pisidium conventus</u> | | x | | x | x |
| <u>Pisidium variable</u> | | x | | | |
| <u>Pisidium casertanum</u> | | x | x | | |
| <u>Helisoma</u> | sp | | | | x |
| <u>Leptophlebia</u> | sp | | | | x |
| <u>Hexagenia limbata</u> | | x | | x | x |
| <u>Ephemera gluttulata</u> | | | | | x |
| <u>Ephemera varia</u> | | x | | x | |
| <u>Caenis</u> | sp | | x | | |
| <u>Athripsodes</u> | sp | | x | x | x |
| <u>Bezzia/Palpomyia</u> | sp | | | x | x |
| <u>Bezzia/Palpomyia</u> | sp 1 | x | x | | |
| * <u>Halobdella</u> | spp | x | x | | |
| <u>Hydracarina</u> | sp A | x | x | x | x |
| <u>Hydracarina</u> | sp B | | | x | x |
| <u>Hydracarina</u> | sp C | | | x | x |
| <u>Hydracarina</u> | sp D | | | | x |
| <u>Hydracarina</u> | sp E | | | | x |
| <u>Oligochaeta</u> | | x | x | x | x |

APPENDIX II

Synthesis of Chemical Results

Annual temperature cycles

East Blue Lake

At East Blue Lake, temperature profiles were measured at station #6 (30 m). Results are in Figure 5d, while Table 1 shows additional temperature readings collected at individual sampling stations.

Thermal stratification was already well established at the time of the first sampling on July 2, 1970. The epilimnion, showing little temperature variation, extended to 8 m. From 8 m to 15 m, the temperature dropped an average of $2^{\circ}\text{C}/\text{m}$, while in the hypolimnion the drop was from 7°C to about 5°C between 15 and 30 m (Figure 5d).

Fall turnover was completed by October 8. The lake was beginning to freeze between the last week of October and the first week of November, 1970. A patch of open water remained until early December.

In February, 1971, the lake was covered with 45.7 cm of ice and approximately 15 cm of snow. No true thermal stratification was evident, although the

water warmed slightly with depth. The apparent lack of inverse thermal stratification in winter was probably due to the degree of exposure of the lake; the prevailing north-south winds of late fall caused continuous mixing of the water, and its cooling below 4°C.

The ice left the lake early in May, 1971, and by May 19 the lake was beginning to stratify. By July a good thermocline had been formed at the same depth as in the previous summer.

Typically, the water temperatures immediately above the sediment at depths 1 m, 2 m, and 4 m were considerably warmer than those shown in the temperature curves, except in winter (Table 1). Jonasson (1972) observed a similar phenomenon in Lake Esrom, and attributed this difference to the sheltering effect of the forest.

The transparency of the water showed a predictable cycle with minima at times of turnover and a maximum in winter. Although the winter maximum of 16 m was double the spring minimum of 8 m, little light penetrated because of snow cover on the ice. In both years, Secchi readings stabilized at 10 m by July and remained so until September.

Table 1. Temperature - oxygen levels at 2 m depths
in the littoral zone, and Secchi depths in mid-lake.

Table 1

East Blue
Lake

| Dates | 7/70 | 8/70 | 9/70 | 2/71 | 5/71 | 6/71 | 7/71 | |
|---------------------|------|------|------|------|------|------|------|--------------------------------|
| Temp. °C | 16 | 22 | 18 | 1 | 9 | 12 | 16 | Measured at 2 m |
| Oxygen | 11 | 7 | 9 | 10 | 11 | 11 | 12 | |
| Secchi in metres | 9.0 | 10.0 | 10.0 | 16.0 | 8.0 | 10.0 | 10.0 | Measured at deepest station |

Beautiful
Lake

| Dates | 7/70 | 8/70 | 9/70 | 2/71 | 5/71 | 6/71 | 7/71 | |
|---------------------|------|------|------|------|------|------|------|--------------------------------|
| Temp. °C | 15 | 22 | 18 | 1 | 14 | 16 | 14 | Measured at 2 m |
| Oxygen | 8 | 6 | 7 | 9 | 10 | 8 | 8 | |
| Secchi in metres | 1.8 | 2.0 | 2.0 | 4.2 | 2.5 | 2.5 | 2.0 | Measured at deepest station |

Lake 239

| Dates | 7/70 | 8/70 | 9/70 | 2/71 | 5/71 | 6/61 | 7/71 | |
|---------------------|------|------|------|------|------|------|------|--------------------------------|
| Temp. °C | 22 | 23 | 18 | 1 | 10 | 21 | 20 | Measured at 2 m |
| Oxygen | 8 | 8.5 | 9 | 12 | 10 | 9 | 8 | |
| Secchi in metres | 3.8 | 4.5 | 5.0 | 4.5 | 4.0 | 4.0 | 4.0 | Measured at deepest station |

Lake 240

| Dates | 7/70 | 8/70 | 9/70 | 2/71 | 5/71 | 6/61 | 7/71 | |
|---------------------|------|------|------|------|------|------|------|--------------------------------|
| Temp. °C | 23 | 24 | 22 | 1 | 11 | 22 | 21 | Measured at 2 m |
| Oxygen | 10 | 10 | 9 | 12 | 11 | 10 | 9 | |
| Secchi in metres | 4.0 | 3.5 | 4.0 | 4.5 | 3.5 | 4.0 | 4.5 | Measured at deepest station |

Beautiful Lake

The temperature profiles in the summer and fall of 1970 indicated a main thermocline at 10 m, with secondary ones at 4 m present in July and August. Some mixing may have occurred sometime between July and August, as hypolimnetic temperatures rose 4°C during that period.

On October 6, 1970, ice was already present along the edge, and temperatures collected at three points in the water column (Figure 5c) showed the beginnings of inverse thermal stratification. By October 15 a 3.5 cm ice cover was present on all the lake except for a small section south of the island (Figure 5c).

In February, 1971, the lake had a 75 cm ice cover near the shore and 50 cm at maximum depth, with 10 to 12 cm of snow over the ice. The water column exhibited inverse thermal stratification, especially at the 16 - 18 m depth. This was likely due to early freezing of the surface water coupled with the peculiar morphometry of the basin.

In spring of 1971, the lake stratified before the first sampling trip, and retained this stratification until a four-day storm in the first week of July caused it to overturn again.

As expected, temperatures at sediment level in the top 4 m (Table 1) were higher than those of the temperature profile.

The Secchi transparencies indicated maximum turbidities in July of both years (Table 1). In 1971 this was clearly a period of turnover, and in 1970 a time when the lake appeared to be turning over. The maximum transparency was, as expected, in winter, though it was also high (2.5 m) in the spring. This latter fact, together with dissolved oxygen and temperature curves discussed later, indicate that the lake did not overturn at all in the spring.

Lakes 239 and 240

The lakes were well stratified on July 9, 1970, and retained their stratification until at least the fourth week in September.

In February the lakes were covered with approximately 46 cm of ice and some snow, and the water columns were beginning to show inverse thermal stratification (Figure 5a, b).

The lakes had not yet begun their summer stratification by May 5, 1971, having 2.5°C difference between top and bottom, though the surfaces were

warming considerably. By June the thermoclines were well established at approximately 4 m, the same depth as in the previous year. The beginning of the thermocline was slightly deeper in Lake 239 than in Lake 240, perhaps partly due to the geographic orientation of the two lakes in relation to the prevailing winds. Because the basins are relatively small and sheltered from winds by forest and granitic bluffs, the formation of a shallow thermocline was possible in the spring.

The littoral zone showed slightly higher temperatures than the temperature profiles at 2 m. Temperature profile data for 1971 in Lakes 239 and 240 were provided by R. Schmidt, Fisheries Research Board of Canada.

The Secchi transparencies remained constant throughout the year, with the exception of winter (Table 1). On the average, Lake 240 was slightly clearer than Lake 239.

Dissolved oxygen, hydrogen sulphide, and iron

Selected results of these and subsequently discussed chemical analyses are summarized in Table 2.

Table 2. Water chemistry of the four lakes collected
at the sediment surface.

Table 2

| Lake | Depth | Date | D.O. ppm | pH | Alk. ppm | H ₂ S ppm | Fe ppm | Hard.T. ppm | Ca ppm | Temp. °C | Veg. P/A | CO ₂ mg/l |
|-----------|-------|------|-------------|-----|-------------|-------------------------|-----------|----------------|-----------|-------------|-------------|-------------------------|
| East Blue | 2 m | 7/70 | 11 | 8.0 | 113 | 0 | 0.1 | 103 | 86 | 16 | P | 2.7 |
| | 2 m | 8/70 | 7 | 7.5 | 296 | 0 | 0 | 86 | 86 | 22 | P | 21.9 |
| | 2 m | 9/70 | 9 | 8.5 | 153 | 0 | 0 | 86 | 68 | 18 | P | 1.8 |
| | 2 m | 2/71 | 10 | 7.5 | 152 | 0 | 0 | 120 | 103 | 1 | P | 11.3 |
| | 2 m | 5/71 | 11 | 8.2 | 169 | 0 | 0 | 103 | 103 | 9 | P | 3.0 |
| | 2 m | 6/71 | 11 | 8.2 | 141 | 0 | 0 | 103 | 86 | 12 | P | 2.6 |
| | 2 m | 7/71 | 12 | 8.5 | 141 | 0 | 0 | 86 | 86 | 16 | P | 1.7 |
| | 10 m | 7/70 | 11 | 8.0 | 155 | 0 | 0.1 | 120 | 68 | 10 | A | 3.7 |
| | 10 m | 8/70 | 9 | 8.2 | 155 | 0 | 0.1 | 103 | 86 | 14 | A | 2.8 |
| | 10 m | 9/70 | 9 | 8.5 | 172 | 0 | 0.1 | 103 | 86 | 15 | A | 2.1 |
| | 10 m | 2/71 | 9 | 8.5 | 155 | 0 | 0 | 120 | 85 | 1.5 | A | 1.9 |
| | 10 m | 5/71 | 11 | 8.2 | 141 | 0 | 0 | 137 | 86 | 6 | A | 2.5 |
| | 10 m | 6/71 | 11 | 8.5 | 141 | 0 | 0.1 | 86 | 68 | 9 | A | 1.7 |
| | 10 m | 7/71 | 11 | 8.5 | 155 | 0 | 0.1 | 120 | 68 | 13 | A | 3.9 |
| | 20 m | 7/70 | 11 | 8.0 | 169 | 0 | 0.1 | 137 | 68 | 7 | A | 4.1 |
| | 20 m | 8/70 | 7 | 8.2 | 169 | 0 | 0.1 | 137 | 68 | 7 | A | 3.0 |
| | 20 m | 9/70 | 6 | 8.0 | 169 | 0 | 0.1 | 137 | 68 | 6 | A | 4.1 |
| | 20 m | 2/71 | 6 | 8.2 | 169 | 0 | 0 | 120 | 86 | 1.8 | A | 3.0 |
| | 20 m | 5/71 | 6 | 8.2 | 169 | 0 | 0 | 120 | 86 | 6 | A | 3.0 |
| | 20 m | 6/71 | 9 | 8.2 | 155 | 0 | 0.1 | 120 | 68 | 7 | A | 2.8 |
| | 20 m | 7/71 | 6 | 8.0 | 169 | 0 | 0.1 | 137 | 68 | 7 | A | 4.1 |
| | 30 m | 7/70 | 11 | 8.0 | 169 | 0 | 0.1 | 137 | 68 | 5 | A | 4.1 |
| | 30 m | 8/70 | 6 | 8.0 | 169 | 0 | 0.2 | 137 | 68 | 6 | A | 4.1 |
| | 30 m | 9/70 | 3 | 7.8 | 173 | 0 | 0.2 | 137 | 68 | 5 | A | 6.6 |
| | 30 m | 2/71 | | | | | | Not Sampled | | | | |
| | 30 m | 5/71 | 3 | 7.8 | 169 | 0 | 0 | 137 | 68 | 6 | A | 6.4 |
| | 30 m | 6/71 | 9 | 7.5 | 155 | 0 | 0.1 | 120 | 68 | 6 | A | 11.5 |
| | 30 m | 7/71 | 6 | 8.0 | 169 | 0 | 0 | 137 | 68 | 6 | A | 4.1 |

Table 2 (Cont'd)

| Lake | Depth | Date | D.O. ppm | pH | Alk. ppm | H ₂ S ppm | Fe ppm | Hard.T. ppm | Ca ppm | Temp. °C | Veg. P/A | CO ₂ mg/l |
|----------|-------|------|-------------|-----|-------------|-------------------------|-----------|----------------|-----------|-------------|-------------|-------------------------|
| Lake 239 | 2 m | 7/70 | 8 | 6.8 | 0 | 0 | 0.8 | 0 | 0 | 22 | P | 0 |
| | 2 m | 8/70 | 8.5 | 6.2 | 0 | 0 | 0.5 | 0 | 0 | 23 | P | 0 |
| | 2 m | 9/70 | 9 | 7.0 | 0 | 0 | 0.4 | 0 | 0 | 18 | P | 0 |
| | 2 m | 2/71 | 12 | 6.2 | <14 | 0 | 0 | 17.1 | 0 | 1 | A | 10.5 |
| | 2 m | 5/71 | 10 | 6.5 | <14 | 0 | 0.3 | 17.1 | 0 | 10 | A | 5.2 |
| | 2 m | 6/71 | 9 | 6.8 | 0 | 0 | 2.0 | 0 | 0 | 21 | A | 0 |
| | 2 m | 7/71 | 8 | 7.0 | 0 | 0 | 0 | 0 | 0 | 20 | P | 0 |
| | 10 m | 7/70 | 8 | 6.0 | 0 | 0 | 2.0 | 0 | 0 | 7 | A | 0 |
| | 10 m | 8/70 | 7 | 5.8 | 14 | 0 | 4.5 | 0 | 0 | 7 | A | 3.4 |
| | 10 m | 9/70 | 5 | 5.8 | <14 | 0 | 5.0 | 0 | 0 | 5 | A | 26.6 |
| | 10 m | 2/71 | 9 | 6.0 | 0 | 0 | 1.5 | 17.1 | 0 | 2 | A | 0 |
| | 10 m | 5/71 | 10 | 5.8 | 14 | 0 | 5.0 | 0 | 0 | 5 | A | 26.6 |
| | 10 m | 6/71 | 8 | 5.8 | 14 | 0 | 0.3 | 0 | 0 | 6 | A | 26.6 |
| | 10 m | 7/71 | 7 | 6.0 | <14 | 0 | 0 | 0 | 0 | 6 | A | 16.5 |
| | 20 m | 7/70 | 8 | 5.8 | <14 | 0 | 3.0 | 0 | 0 | 6 | A | 26.6 |
| | 20 m | 8/70 | 7 | 5.8 | <14 | 0 | 3.0 | 0 | 0 | 5 | A | 26.6 |
| | 20 m | 9/70 | 6 | 5.8 | 14 | 0 | 5.0 | 8.6 | 8.6 | 4 | A | 26.6 |
| | 20 m | 2/71 | 8 | 6.0 | <14 | 0 | 2.0 | 17.1 | 8.6 | 3 | A | 16.5 |
| | 20 m | 5/71 | 6 | 5.8 | 14 | 0 | 0.8 | 8.6 | 8.6 | 4 | A | 26.6 |
| | 20 m | 6/71 | 6 | 5.8 | <14 | 0 | 0.5 | 0 | 0 | 4 | A | 26.6 |
| | 20 m | 7/71 | 7 | 5.8 | <14 | 0 | 0 | 0 | 0 | 4 | A | 26.6 |
| | 30 m | 7/70 | 5 | 6.2 | 14 | 0 | 4.5 | 0 | 0 | 6 | A | 10.5 |
| | 30 m | 8/70 | 4 | 5.8 | 14 | 0 | 1.5 | 0 | 0 | 6 | A | 26.6 |
| | 30 m | 9/70 | 2.5 | 5.8 | 14 | 0 | 6.0 | 8.6 | 8.6 | 4 | A | 26.6 |
| | 30 m | 2/71 | 2 | 6.2 | 14 | 0 | 2.2 | 17.1 | 8.6 | 3 | A | 10.5 |
| | 30 m | 5/71 | 6 | 6.0 | 14 | 0 | 0.8 | 8.6 | 8.6 | 4 | A | 16.5 |
| | 30 m | 6/71 | 5 | 5.8 | 14 | 0 | 0.3 | 8.6 | 8.6 | 4 | A | 26.6 |
| | 30 m | 7/71 | 4 | 5.8 | 14 | 0 | 0 | 8.6 | 8.6 | 4 | A | 26.6 |

Table 2 (Cont'd)

| Lake | Depth | Date | D.O. ppm | pH | Alk. ppm | H ₂ S ppm | Fe ppm | Hard.T. ppm | Ca ppm | Temp. °C | Veg. P/A | CO ₂ mg/l |
|-----------|-------|------|-------------|-------|-------------|-------------------------|-----------|----------------|-----------|-------------|-------------|-------------------------|
| Beautiful | 2 m | 7/70 | 8 | 8.0 | 141 | 0 | 0.2 | 120 | 69 | 15 | P | 3.4 |
| | 2 m | 8/70 | 6 | 8.5 | 162 | 0 | 0.1 | 86 | 69 | 22 | P | 1.9 |
| | 2 m | 9/70 | 7 | 8.5 | 162 | 0 | 0.2 | 120 | 86 | 18 | P | 1.9 |
| | 2 m | 2/71 | 9 | 7.8 | 99 | 0 | 0 | 137 | 137 | 1 | P | 3.8 |
| | 2 m | 5/71 | 10 | 8.2 | 127 | 0 | 0.5 | 95 | 69 | 14 | P | 2.3 |
| | 2 m | 6/71 | 8 | 8.2 | 141 | 0 | 0 | 123 | 86 | 16 | P | 2.5 |
| | 2 m | 7/71 | 8 | 8.2 | 141 | 0 | 0 | 96 | 86 | 14 | P | 2.5 |
| | 10 m | 7/70 | 8 | 8.0 | 155 | 0 | 0.1 | 86 | 86 | 6 | A | 3.7 |
| | 10 m | 8/70 | 1.5 | 7.8 | 141 | 0.4 | 0.1 | 103 | 86 | 16 | A | 5.4 |
| | 10 m | 9/70 | 0 | 8.0 | 157 | 0.5 | 0.5 | 120 | 86 | 17 | A | 3.8 |
| | 10 m | 2/71 | 8.0 | 8.0 | 127 | 0 | 0 | 154 | 154 | 2 | A | 3.0 |
| | 10 m | 5/71 | 5.0 | 8.0 | 141 | 0 | 0.5 | 120 | 86 | 10 | A | 3.4 |
| | 10 m | 6/71 | 7.5 | 8.2 | 141 | 0 | 0.1 | 86 | 86 | 12 | A | 2.5 |
| | 10 m | 7/71 | 7.8 | 8.0 | 148 | 0 | 0 | 120 | 68 | 14 | A | 3.6 |
| | 18 m | 7/70 | 0 | 8.0 | 155 | 0.1 | 0.1 | 86 | 86 | 6 | A | 3.7 |
| | 18 m | 8/70 | 0 | 6.8 | 211 | 1.0 | 0.1 | 120 | 86 | 8 | A | 80.2 |
| | 18 m | 9/70 | 0 | 7.3 | 176 | 1.5 | 1.0 | 120 | 86 | 9 | A | 20.8 |
| | 18 m | 2/71 | 2.0 | 7.8 | 155 | 0 | 0 | 120 | 103 | 4 | A | 5.9 |
| | 18 m | 5/71 | 1.0 | 7.5 | 183 | 0 | 0.2 | 120 | 103 | 4 | A | 13.5 |
| | 18 m | 6/71 | 0 | 7.5 | 155.1 | 0 | 0.1 | 120 | 69 | 4 | A | 11.5 |
| 18 m | 7/71 | 7.4 | 7.8 | 155.1 | 0 | 0.1 | 120 | 69 | 15 | A | 5.9 | |

Table 2 (Cont'd)

| Lake | Depth | Date | D.O. ppm | pH | Alk. ppm | H ₂ S ppm | Fe ppm | Hard.T. ppm | Ca ppm | Temp. °C | Veg. P/A | CO ₂ mg/l |
|----------|-------|------|-------------|-----|-------------|-------------------------|-----------|----------------|-----------|-------------|-------------|-------------------------|
| Lake 240 | 2 m | 7/70 | 10 | 6.8 | 0 | 0 | 0.5 | 8.6 | 8.6 | 23 | P | 0 |
| | 2 m | 8/70 | 10 | 6.5 | 0 | 0 | 1.2 | 8.6 | 8.6 | 24 | P | 0 |
| | 2 m | 9/70 | 9 | 6.8 | 0 | 0 | 3.8 | 8.6 | 8.6 | 22 | P | 0 |
| | 2 m | 2/71 | 12 | 6.0 | <14 | 0 | 0.3 | 8.6 | 8.6 | 1 | A | 16.5 |
| | 2 m | 5/71 | 11 | 6.8 | <14 | 0 | 0.3 | 8.6 | 8.6 | 11 | A | 2.7 |
| | 2 m | 6/71 | 10 | 6.8 | <14 | 0 | 0.2 | 8.6 | 8.6 | 22 | P | 2.7 |
| | 2 m | 7/71 | 9 | 6.2 | 0 | 0 | 0 | 8.6 | 8.6 | 21 | P | 0 |
| | 10 m | 7/70 | 6 | 5.8 | 0 | 0 | 3.8 | 8.6 | 8.6 | 9 | A | 0 |
| | 10 m | 8/70 | 3 | 5.5 | 14 | 0 | 4.2 | 8.6 | 8.6 | 11 | A | 104.3 |
| | 10 m | 9/70 | 1 | 5.5 | 14 | 0 | 3.2 | 0 | 8.6 | 9 | A | 104.3 |
| | 10 m | 2/71 | 9 | 6.5 | <14 | 0 | 5.4 | 17.1 | 8.6 | 3 | A | 5.2 |
| | 10 m | 5/71 | 8 | 5.5 | <14 | 0 | 3.0 | 17.1 | 8.6 | 5 | A | 52.0 |
| | 10 m | 6/71 | 7 | 5.5 | 14 | 0 | 4.0 | 8.6 | 8.6 | 7 | A | 104.3 |
| | 10 m | 7/71 | 4 | 5.5 | 14 | 0 | 3.0 | 8.6 | 8.6 | 6 | A | 104.3 |
| | 13 m | 7/70 | 2 | 5.8 | 0 | 0 | 4.0 | 8.6 | 8.6 | 8 | A | 0 |
| | 13 m | 8/70 | 1 | 6.0 | 14 | 0 | 6.0 | 8.6 | 8.6 | 8 | A | 33.3 |
| | 13 m | 9/70 | 0 | 5.8 | 0 | 0 | 2.5 | 8.6 | 8.6 | 7 | A | 0 |
| | 13 m | 2/71 | 6 | 6.5 | 7 | 0 | 6.5 | 17.1 | 8.6 | 3 | A | 5.2 |
| | 13 m | 5/71 | 6 | 5.5 | 7 | 0 | 3.0 | 8.6 | 8.6 | 4 | A | 51.8 |
| | 13 m | 6/71 | 6 | 5.5 | 14 | 0 | 4.5 | 8.6 | 8.6 | 6 | A | 104.3 |
| | 13 m | 7/71 | 4 | 5.5 | 14 | 0 | 0.6 | 8.6 | 8.6 | 6 | A | 104.3 |

East Blue Lake

At no time during the study was oxygen limiting in this lake (Figure 6a). The lowest levels were obtained at 30 m in August and September, 1970, when values were 3 ppm or 25% saturation. Oxygen levels did not follow the temperature curves and, except for this slight depletion, were characteristic of an oligotrophic condition.

Hydrogen sulphide was never detected anywhere in the study transect.

Iron was detectable in small amounts, 0.10 to 0.25, almost throughout the year at the stations below 4 m.

Beautiful Lake

In both 1970 and 1971, oxygen was limiting in the hypolimnion. The oxygen curves closely followed the temperature curves (Figure 6c), with the anoxic zone even extending above the thermocline during a period of relative calm in September, 1970. Measurable amounts of oxygen in the hypolimnion (15% saturation, Table 1b) in late fall indicated that the lake had turned over then. Oxygen declined to zero in the hypolimnion during the spring and early summer, but became abundant again in July, 1971.

Hydrogen sulphide followed the oxygen depletion cycle in the hypolimnion, reaching measurable amounts at zero oxygen concentration (Table 2).

Iron was present at all depths and at most of the sampling times (Table 2). At 10 m and 18 m the iron concentration rose steadily as the oxygen concentration dropped, reaching high values at 10 m in August and September of 1970 and May of 1971. During this same period, iron concentration dropped in the hypolimnion while the H_2S concentration levels rose, thus showing the sequences ascribed by Mortimer (1941, 1942) and Einsele (1937) to very eutrophic lakes. As the oxygen level dropped, ferrous iron was liberated by the sediment, thereby increasing levels in the water during the early part of the summer.

Lake 239

At no time during this study were anoxic conditions encountered in Lake 239. Oxygen concentrations in the epilimnion were high (Table 2), and low utilization by the low macrophyte standing crop resulted in close to 100% saturation at all times. Hypolimnetic oxygen levels declined somewhat as the summer progressed, reaching 1.5 - 2.0 ppm in September. Winter concentration was high throughout the water

Column, except at 30 m where a sharp decline to 0.5 - 1.0 ppm or 5 - 10% saturation occurred.

No H₂S was detectable.

Lake 240

Although Lake 240 was reported anoxic below 10 m in the fall of 1969 (Schindler 1971), this was not observed at sampling times in 1970 or 1971. At stations above 4 m, dissolved oxygen was quite high, though still lower than in Lake 239 (Table 2). This latter was probably due to a more limited wind-induced circulation in the sheltered bay of Lake 240. Below the epilimnion, oxygen decreased steadily through the summer, dropping sharply from 8 m downwards. Lows of 2.5 ppm were measured at maximum depth in August and September. By February, oxygen depletion to 2.0 ppm at maximum depth was again evident. During the vernal turnover in May, the water column was well saturated with oxygen as in Lake 239, but by June depletion was already occurring.

Iron followed the same patterns as in Lake 239, though with higher absolute values, and H₂S was never detected.

Alkalinity and CO₂

East Blue Lake

Alkalinity increased slightly with depth from 141 - 153 ppm at the surface to 169 ppm at 30 m where no seasonal variation was observed. Variation above the thermocline was unpredictable, presumably reflecting the photosynthetic activity of the extensive Chara beds.

CO₂ increased in the epilimnion during winter, possibly as a respiration product.

Beautiful Lake

Alkalinity ranged from 49 to 211 mg/l during the sampling period, with minima in the littoral station in winter. An increase with depth was observed during the anoxic periods of August and September, 1970.

CO₂ closely followed the oxygen curves, increasing to highs in the hypolimnion of 4009 mg/l and 1038 mg/l during August and September.

Lakes 239 and 240

The alkalinity in these lakes was extremely low, and methods used allowed only measurements of <14 ppm and 14 ppm. Therefore, no seasonal variation could be interpreted. No spatial variation through

depth was detected in Lake 239. In Lake 240 values less than 14 ppm were found in the epilimnion and values of 14 ppm were detected during summer stagnation in the hypolimnion.

In both lakes CO_2 content increased with depth, and inversely to the oxygen concentration. CO_2 minima in the hypolimnion were obtained in February (Table 2). The CO_2 values for these two lakes are greatly inflated due to the extremely low alkalinity and pH values, and at best they represent trends.

pH

East Blue Lake

pH maxima of 8.0 to 8.5 were found in the littoral zone, and minima of 7.5 to 8.0 at 30 m. The lowest values were 7.5 in the littoral zone in mid-winter. At this time, they were comparable to 30 m values.

Beautiful Lake

pH fluctuations corresponded to those described for East Blue Lake, but a greater range was displayed (8.5 to 6.8).

Lakes 239 and 240

Both lakes are slightly acid, pH 5.75 to 7.0 in Lake 239 and 5.50 to 6.75 in Lake 240. In the littoral zone pH minima were evident in winter (Table 2). However, in the hypolimnion, yearly maxima were measured in winter, reflecting low CO₂ content.

Total hardness and calcium

East Blue and Beautiful Lakes

These lakes are rich in cations from the dissolution of limestone. Hardness ranged from 154 to 308 ppm, with East Blue having slightly higher values. Ca⁺⁺ expressed as CaCO₃ generally decreased in concentration from the littoral zone to deeper stations in East Blue, but remained fairly constant in Beautiful Lake.

Maxima at all stations were recorded in winter.

Lakes 239 and 240

Total hardness and calcium levels were very low in both lakes and, because of the analytical techniques employed, Ca can only be stated as being below 20 ppm at all times (Table 2). Total hardness was below 20 ppm most of the year.

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APPENDIX III

A Key to Chironomid

Key to species present in the study

The identification of the Chironomid larvae to the generic level was carried out using the identification keys referred to in the text. Below the generic level a key was formulated, based on morphological characteristics, to consistently separate types sharing similar characteristics. The results of this key are referred to as "species" in the text.

These species would be more accurately referred to as "morphological types" because within some of these types more than one "true" species may be found.

This working key is included in the following pages.

TANYPODINAE

Ablabesmyia

1. a) Eyes anterior to lingua, head less than 1.5x width
Ablabesmyia Sp
b) Not as above (2)
2. a) Eyes dark and well defined, lateral teeth of lingua not sharply pointed
Ablabesmyia Sp 2
b) Eyes light coloured, lateral teeth of lingua pointed
Ablabesmyia SSp 1

CHIRONOMINAE

CHIRONOMINI

CHIRONOMUS

1. a) Venter of head capsule dark (2)
b) Venter light coloured (4)
2. a) First 4 mandibular teeth black, dorsal eye spot anterior to ventral and usually lunate in shape
(3)
b) First 3 mandibular teeth black, dorsal and ventral eyespot in the same plane, both eyespots not lunate
Chironomus Sp 5
3. a) Tip of second lateral tooth of labial plate curving apically, 3rd lateral tooth definitively pointed
Chironomus Sp 6
b) Not as above
Chironomus Sp 4

DICROTENDIPES

1. a) Central tooth of labial plate sharply notched dorsolaterally, anterior margin of paralabial plates sharply crenulated
Dicrotendipes Sp 3
- b) Central tooth of labial plate usually rounded, anterior margin of paralabial plates slightly crenulated
(2)
2. a) Second to fifth lateral teeth of labial plate pointed, all teeth black
Dicrotendipes Sp 2
- b) Not as above
(3)
3. a) Central tooth of labial plate lighter than others, all labial and mandibular teeth rounded.
Dicrotendipes Sp 1
- b) All teeth of labial plate brown
Dicrotendipes Sp

PHAENOPSECTRA

- a) Second antenna segment as large or larger than remaining apical segments combined; first lateral teeth of labial plate rounded
Phaenopsectra Sp
- b) Second antenna segment smaller than remaining apical segments combined; first lateral teeth of labial plate pointed.
Phaenopsectra Sp 1

PSEUDOCHIRONOMUS

- a) Teeth of labial plate truncate; apical tooth on mandible distinct
Pseudochironomus Sp
- b) Teeth of labial plate pointed; apical tooth on mandible reduced or missing
Pseudochironomus Sp 1

POLYPEDILUM

1. a) Lauterborn organ curled; median and second lateral teeth of labial plate at least three times as long as first laterals
Polypedilum (Tripodura) Sp
- b) Not as above
(2)

APPENDIX IV

Composition of specific assemblages by lake.

APPENDIX I

| Lake | Assemblage Number | | | % Composition |
|-------------------|-------------------|-------------------------|-----------------------|---------------|
| East Blue | I | <u>Tanytarsus</u> | sp 5 | 15.0 |
| | | <u>Tanytarsus</u> | sp 4 | 10.3 |
| | | <u>Chironomus</u> | sp 1 | 11.2 |
| | | <u>Hyalella azteca</u> | | 11.4 |
| | II | <u>Chironomus</u> | sp 1 | 53.6 |
| | | <u>Paratanytarsus</u> | sp 2 | 12.2 |
| | | <u>Dicrotendipes</u> | sp 1 | 10.8 |
| | III | <u>Hyalella azteca</u> | | 22.9 |
| | | <u>Tanytarsus</u> | sp 4 | 11.1 |
| | | <u>Tanytarsus</u> | sp 5 | 8.7 |
| | | <u>Procladius</u> | spp 2 | 25.3 |
| | IV | <u>Tanytarsus</u> | sp 7 | 26.2 |
| | | <u>Tanytarsus</u> | sp 5 | 20.3 |
| | | <u>Tanytarsus</u> | sp 4 | 16.1 |
| | | <u>Chironomus</u> | sp 7 | 18.2 |
| | | <u>Chironomus</u> | sp 5 | 10.1 |
| | V | <u>Chironomus</u> | sp 5 | 58.1 |
| | | <u>Chironomus</u> | sp 7 | 37.4 |
| | Beautiful | I | <u>Paratanytarsus</u> | sp 3 |
| <u>Tanytarsus</u> | | | sp 3 | 12.8 |
| <u>Tanytarsus</u> | | | sp 8 | 10.2 |
| II | | <u>Chironomus</u> | sp 3 | 35.8 |
| | | <u>Chironomus</u> | sp 2 | 26.9 |
| | | <u>Cryptocladopelma</u> | sp 2 | 10.2 |
| Lake 239 | I | <u>Paratanytarsus</u> | sp | 17.8 |
| | | <u>Paratanytarsus</u> | sp 1 | 9.2 |
| | | <u>Tanytarsus</u> | sp | 12.1 |
| | | <u>Tanytarsus</u> | sp 1 | 9.0 |
| | | <u>Procladius</u> | spp 1 | 11.3 |
| | | <u>Pagastiella</u> | | 7.4 |

APPENDIX I (Cont'd)

| Lake | Assemblage Number | Taxa | % Composition |
|----------|-------------------------------|----------------------------|------------------|
| Lake 239 | II | <u>Pisidium conventus</u> | 10.7 |
| | | <u>Tanytarsus</u> | sp 9.2 |
| | | <u>Tanytarsus</u> | sp 1 7.7 |
| | III | <u>Pontoporeia affinis</u> | 50.0 |
| | | <u>Pisidium conventus</u> | 39.0 |
| | IV | <u>Chironomus</u> | sp 4 49.1 |
| | | <u>Chironomus</u> | sp 6 34.6 |
| Lake 240 | I | <u>Hyalella azteca</u> | 19.7 |
| | | <u>Paratanytarsus</u> | sp 13.2 |
| | | <u>Procladius</u> | spp 1 10.3 |
| | | <u>Elmiidae</u> | 9.2 |
| | | <u>Tanytarsus</u> | sp 8.5 |
| | II | <u>Tanytarsus</u> | sp 29.1 |
| | | <u>Tanytarsus</u> | sp 1 19.5 |
| | | <u>Paratanytarsus</u> | sp 10.8 |
| | III | <u>Paratanytarsus</u> | sp 17.6 |
| | | <u>Tanytarsus</u> | sp 13.6 |
| | | <u>Tanytarsus</u> | sp 1 12.2 |
| | | <u>Heterotrissocladus</u> | spp 11.3 |
| | IV | <u>Phaenopsectra</u> | sp 1 46.8 |
| | | <u>Phaenopsectra</u> | sp 8.8 |
| | | <u>Chironomus</u> | sp 6 20.6 |
| V | <u>Chaoborus punctipinnis</u> | 54.3 | |
| | <u>Chaoborus flavicans</u> | 26.1 | |

