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A Species Diversity Study of the Benthic Population of Cedar Lake, Illinois

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A SPECIES DIVERSITY STUDY OF THE BENTHIC POPULATION OF CEDAR LAKE, ILLINOIS

by

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VITA

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INTRODUCTION

One of the basic characteristics of communities is species diversity (DeJong 1975). Diversity has been related to community stability, productivity, niche structure, and evolution (McIntosh 1967). Plant ecologists have long pursued the study of community structure, while animal ecologists have primarily been concerned with the study of populations (Elton 1949). More recently, animal ecologists have begun to explore the organization of animal communities, particularly the distribution of individuals among the species of a community (Preston 1948, Margalef 1958, Hairston 1959, MacArthur 1960, 1966, Lloyd and Ghelardi 1964, Ross 1972).

Diversity analysis has been widely applied to multispecies populations such as those found in aquatic environments. A number of works on marine and lotic ecosystems have utilized diversity indices to examine the complexities of benthic invertebrate associations (Sanders 1960, 1968, Milbrink et al 1974, Boesch 1973, Friberg et al 1977, Kinner et al 1974, Ransom et al 1974, Allan 1974).

It is logical that diversity analysis be applied to the investigation of lake benthic communities also. It is well known that the benthic population can supply a large amount of information about a lake, such as water quality, the long term effects of pollution, and the stability of physico-chemical conditions (Milbrink et al 1974, Sala et al 1977, Nichols 1976, Godfrey 1978).

In order to wholly understand the concept of diversity within a community, an analysis of the factors which determine, or contribute to, the diversity of the community is also in order.

Several physical features have been suggested as factors which influence benthic invertebrate diversity in aquatic environments. Animal-sediment association studies indicate that substrate type effects benthic diversity values. Sandy bottoms in marine ecosystems, particularly, have been found to be more diverse than mud bottoms (Driscoll and Brandon 1973, Sanders 1968, Young and Rhoads 1971). Oxygen levels and fluctuations in available oxygen have also been cited as affecting diversity, by limiting the distribution of organisms with restrictive oxygen demands (Petr 1968, Sala et al 1977). A third important determinant is the existence of aquatic macrophytes. The presence or absence of aquatic vegetation and the seasonal changes in macrophytic growth, most notably in cooler climates, results in corresponding changes in species diversity (Petr 1968, Odum 1971).

While recent literature has dealt extensively with the topic of diversity in marine and stream environments, few studies as of late explore the community organization of lake benthos. This dearth of recent literature regarding lake benthic communities prompted this study of benthic invertebrates in a freshwater environment. The specific goals of this study were established as follows:

1) sampling of benthic organisms along a depth gradient, with subsequent taxonomic classification of organisms;
2) analysis of community structure using diversity indices;

3) discussion of the factors which regulate species distribution and diversity in the benthos.

MATERIALS AND METHODS

The Site

This study was carried out on Cedar Lake, Lake County, Illinois. The site is a 285 acre, mesotrophic lake of glacial origin. Cedar Lake has a mean depth of 10.2 feet, and a maximum depth of 40 feet. The lake is essentially soft-bottomed; however, the substrate is not of uniform composition over the entire lake basin. The littoral zone is composed of a soft sand mixed with gravel. The very center of the lake, a deep hole of 35-40 feet, is silt mixed with a soft blue clay. The remaining areas that were sampled are composed of soft mud with a fairly stable water-substrate interface.

The littoral zone has a dense macrophytic growth, consisting mainly of *Ceratophyllum*, *Myriophyllum*, and several species of *Potamogeton*. By midsummer, this growth had extended all the way out to regions of 20 foot depths.

Sampling Procedures

I sampled for seventeen weeks during the summer of 1978, from early May until late September. Sampling stations were designated areas along two transects. The first transect originated at the region of maximum depth, which corresponds geographically with the center of the lake. This transect traveled north, covering a path approximately ten feet wide, to the southern edge of an island which is situated in the northeast section of the lake. The second transect had the same point of origin, was approximately ten feet in width, and ran diagonally to the southeast shore of the lake. The composition of benthic communities along these transects appeared to be similar, and were used interchangeably.

Benthic macroinvertebrates were collected by means of a 36 in.^{2} Ekman dredge. On each sampling date, three depths along one of the transects were randomly chosen as sampling sites. Three samples were taken at each site. A total of 154 samples were collected for use in this study. Water temperature and dissolved oxygen content (using a YSI Oxygen Meter) were measured at each sampling site.

Samples were processed in the laboratory by washing the sediment through a 500 micron copper screen. The remaining material was preserved with 70% alcohol and sorted in shallow, white-bottomed enamel pans. All organisms were then identified to the lowest taxonomic category possible; in many cases to genus, in most others to species.

Reference materials used in identification of the organisms were Johannsen (1969), Merritt and Cummins (1978), Usinger (1968), and Ward and Whipple (1918).

Community Diversity

Species diversity includes components of both "richness", i.e., numerical abudnance of species, and "evenness", the distribution of individuals among those species (Preston 1948, Hairston 1959, Pielou 1966, Whittaker 1972, DeJong 1975). A frequently used measure of the "richness" of a community is the Shannon-Weaver Information Function (Shannon-Weaver 1949), as adapted by Margalef (1958) as an index of community diversity. This index is:

$$H' = -\Sigma \text{ pi log pi} \quad (1)$$

where pi is the proportion of the i^{th} species in the population.

This index is more informative when combined with a diversity index for "evenness" (Whittaker 1972). A community would reach maximum diversity if each species contained the same number of individuals. If the distribution of individuals over those species present were equitable, the community would have total evenness. Pielou (1966, 1969) suggests that evenness be considered as a ratio of the observed diversity of a given community to its maximum possible diversity. On the basis of the Shannon-Weaver formula, evenness can be given as follows:

$$J' = H' / \log s$$

where log s is H'_{max} for a perfectly equitable community (Pielou, 1966, 1969).

To further define the communities under investigation, Whittaker's Beta diversity is utilized. Beta diversity (BD) is the extent of change in species composition between communities along an environmental gradient (McIntosh 1967, Whittaker 1972):

$$\text{Beta diversity (BD)} = Sc / \overline{S}$$

where Sc is the total number of species in a community, and $\overline{S}$ is the average number of species per individual sample in the composite community.

RESULTS

Community Organization

A total of]28 taxa of benthic macroinvertebrates from 154 grab samples were collected for this analysis. (See Table 1 for complete organism listing.) Following compilation of the sampling data, two separate communities were clearly delineated. The distinction was made on the basis of depth along the gradient, similarities in oxygen and temperature values, and taxonomic distribution. Graphical analysis of abundance versus depth (see Figure 1), indicated that the line of demarcation between the two existing communities was in the area of twenty foot depths. These two communities were subsequently labeled A and B.

Community A consists of all samples taken from 20 to 40 foot depths along either transect. The substrate was primarily a deep, fine mud. There was no aquatic vegetation present in this area. In the deepest part of the lake, a 40 feet deep "hole", approximately 12 feet in diameter, was comprised of a thick, blue clay sediment. The oxygen and temperature levels remained low throughout the sampling period (see Table 2, below). This area was identified as a Chaoborid community of low diversity.

TABLE 1: TAXONOMIC COMPOSITION LIST

SPECIES	COMMUNITY A	COMMUNITY B
Bryozoa		
Lophophorus sp.	0	1
Plumatella sp.	0	1
Mollusca (Gastropoda)		
Planobulidae		
Gyraulus sp.	0	537
Helisoma sp.	0	28
Helisoma campanulata	0	36
Helisoma trivolis	0	1
Planorbula sp.	6	419
Lymnadae		
Limnodritus sp.	0	1
Stagnicola caperata	0	5
Stagnicola palustris	0	3
Viviparus sp.	1	572
Physiidae		
Amnicola sp.	18	3233
Fossaria sp.	0	346
Physa gyrina	1	312
Somatogyrus sp.	1	23
Valvata sincera	0	23
Valvata trincarinata	7	1528
Mollusca (Bivalvia = Pelecypoda)		
Spaeriidae		
Sphaerium sp.	8	132
Pisidium		
Pisidium sp.	1	34
Musculidae		
Musculium sp.	2	38
Unionidae		
Utterbackia imbecilis	0	1
Annelida (Oligochaeta)		
Naididae	38	9
Annelida (Hirudinea)		
Glossiphoniidae		
Helobdella sp.	0	5
Helobdella fusea	0	1
Helobdella stagnalis	3	14
Placobdella sp.	0	5

TABLE 1 (CONTINUED)

SPECIES	COMMUNITY A	COMMUNITY B
Annelida (Hirudinea) (cont)		
Piscicolidae		
Illinobdella sp.	0	4
Illinobdella ablata	0	1
Illinobdella elongata	0	4
Erpobdellidae		
Erpobdella sp.	0	1
Erpobdella punctata	0	2
Arthropoda (Insecta)		
Baetidae		
Baetis sp. 1	0	14
Baetis sp. 2	0	112
Baetiscinae	0	32
Agrionidae		
Agrion sp.	0	1
Argiadae sp.	0	1
Lestesidae		
Archilestes grandis	0	2
Coenagrionidae		
Cinygmula sp.	0	2
Enallagma sp.	0	5
Libellulaidae		
Libellula sp.	0	1
Calopterygidae		
Hexaginia sp.	0	29
Haeterina sp.	0	6
Heliopsychidae		
Heliopsyche sp.	0	1
Hydroptilidae		
Stactiobiella sp.	0	3
Hydropsychidae		
Cheumatopsyche sp.	0	1
Leptoceridae		
Arthripsodes sp.	0	19
Leptocerus sp.	0	2
Oecetis sp.	0	20
Setodes sp.	0	1
Limnephilidae		
Limnophilus sp.	0	1
Molannidae sp.	0	2
Philopotamidae		
Wormaldia sp.	0	3
Chimarra sp.	0	1

TABLE 1 (CONTINUED)

SPECIES	COMMUNITY A	COMMUNITY B
Arthropoda (Insecta) (cont)		
Polycentropodidae		
Polycentropus sp.	0	31
Phylocentropus sp.	0	1
Psychomyiidae		
Psychomyia sp.	0	1
Rhyacophiloididae		
Rhyacophilia sp.	0	7
Pyralidae		
Parargyractic sp.	0	1
Chaoboridae		
Chaoborus albatus	183	5
Chaoborus asticopus	7	0
Chaoborus flavicans	8	0
Chaoborus punctipennis	227	5
Chironomidae		
Anatopynia sp.	0	3
Coelotanypus sp.	1	15
Pelopia (Tanypus) sp.	7	39
Pentaneura flavifrons	6	138
Procladius Adumbratus	72	143
Psectrotanypus sp.	0	4
Tanypus stellata	0	1
Diamesa sp.	1	5
Diamesa longimus	0	3
Prodiamesa sp.	0	4
Brillia par	1	0
Cricotopus sp.	0	6
Coryneura sp.	0	1
Metriocnemus sp.	0	1
Orthocladius sp.	0	1
Psectrocladius flava	0	10
Camptochironomus tentans	4	12
Chironomus sp.	0	7
Chironomus chironomus	1	0
Chironomus decorus	0	56
Chironomus fulvipilus	0	1
Chironomus militaris	7	19
Chironomus plumosus	84	24
Chironomus tentans	4	12
Cryptochironomus abortivus	0	76
Cryptochironomus nais	0	1
Cryptochironomus psectinella	1	1
Cryptochironomus psittacinus	0	93
Cryptochironomus sp.e.	0	1
Cryptochironomus stylifera	0	2

TABLE 1 (CONTINUED)

SPECIES	COMMUNITY A	COMMUNITY B
Arthropoda (Insecta) (cont)		
Dicrotendipes sp.	0	118
Endochironomus dimorphus	0	45
Endochironomus modestus	0	1
Endochironomus nigricans	0	20
Endochironomus quadripunctatus	0	1
Endochironomus sp.	0	4
Endochironomus tendens	2	7
Glyptotendipes sp.	0	6
Limnochironomus modestus	1	41
Microspectra dives	0	118
Microtendipes aberrans	0	1
Paralauterborniella sp.	0	7
Polypedilum flavus	0	132
Pseudochironomus richardsonii	14	352
Stenochironomus sp.	0	37
Stictochironomus flavicingula	0	16
Tanytarsus sp.	5	53
Tribelos sp.	0	15
Ceratopogonidae		
Culicodes sp.	0	1
Palpomyia pruinescens	0	17
Empididae		
Wiedemannia sp.	0	5
Arthropoda (Crustacea)		
Sidadae		
Sida crystillina	0	1
Daphniidae		
Alona	0	1
Ceriodaphnia	0	2
Latona setifera	0	4
Simnocephalus		
Simnocephalus serrulatus	0	1
Chydoridae		
Chydorus sp.	0	1
Arthropoda (Malacostraca)		
Asellidae		
Ascellus aquaticus	0	201
Ascellus militaris	0	32
Amphipodidae		
Hyalella azteca	0	1509
Gammarus sp.	0	4
Pontoporeia affinis	0	1

TABLE 1 (CONTINUED)

SPECIES	COMMUNITY A	COMMUNITY B
Arthropoda (Malacostraca) (cont)		
Palaemontidae		
Orconectes virilis	0	1
Arthropoda(Arachvia)		
Aranadae		
Aranea sp.	2	4

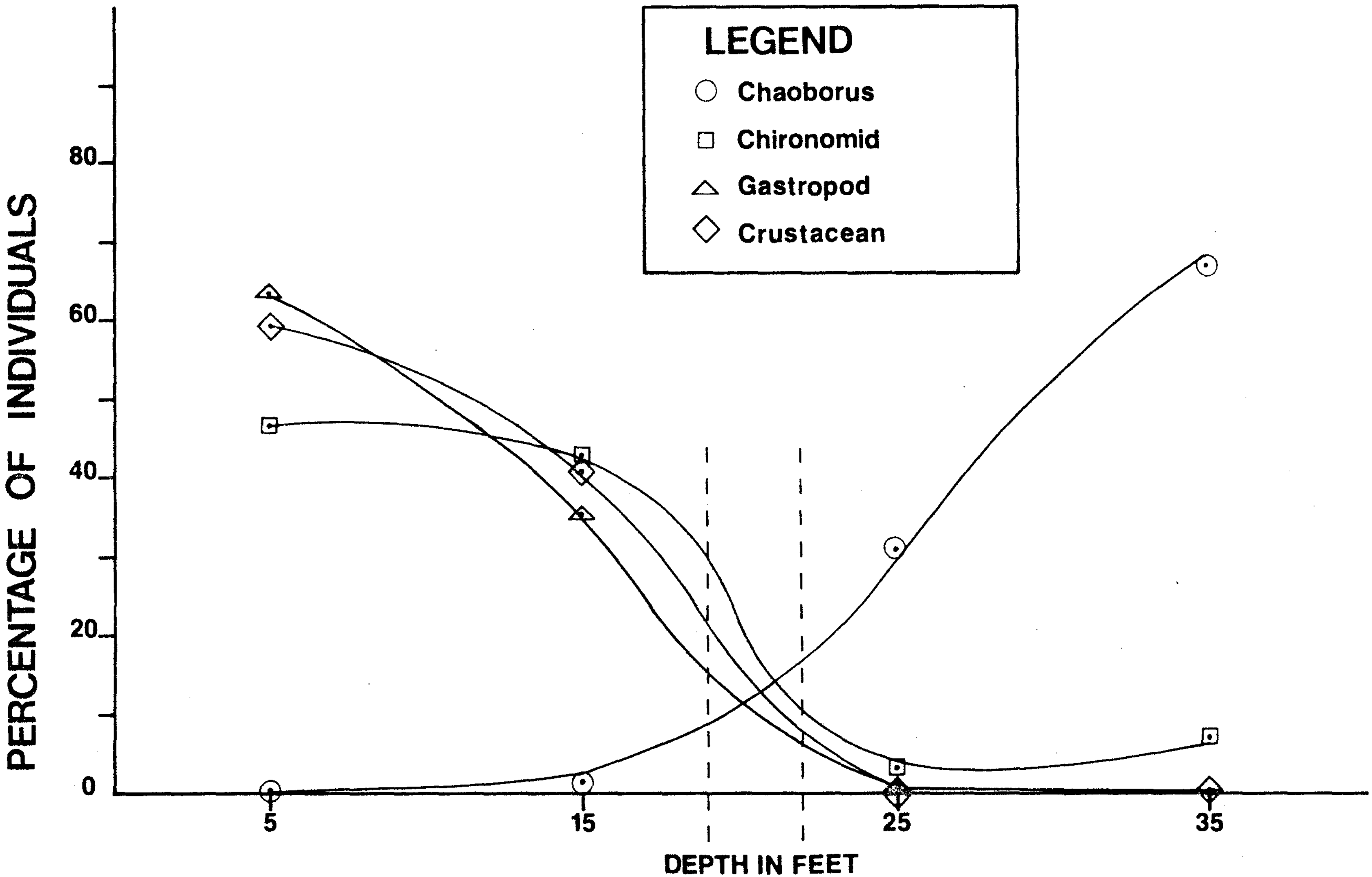

Fig.1 Relationship of dominant species of Community A and B to Depth along the gradient, showing ecotone between A and B at 19–21 feet.

TABLE 2: AVERAGE MONTHLY WATER TEMPERATURE (C°) AND OXYGEN CONTENT (PPM)

MONTH	TEMPERATURE C°		OXYGEN PPM	
	COMMUNITY A	COMMUNITY B	A	B
MAY	13.8	19.4	4.3	9.1
June	16.0	20.4	3.9	8.2
July	19.0	24.0	2.6	8.2
August*	15.5	24.6	1.3	7.6

*Data from first week in September included in August figures.

Community B is comprised of all samples from zero to twenty foot depths. The substrate changed along the gradient from sub-littoral to the littoral region. From the area of twenty foot depths shoreward along the gradient to depths of about five feet, the substrate was a soft, deep mud. From five foot depths into the shoreline (zero feet) the substrate became a sandy gravel containing rocks, shell fragments and other litter. Throughout the summer this community was marked by a heavy growth of macrophytes, extending from the shoreline out to depths of 20 feet at maximum growth. Prevalent in this region were *Myriophyllum*, *Ceratophyllum*, and several species of *Potamogeton*.

Community B is characterized as a Gastropod-Crustacean community.

Faunal Distribution

Of the 128 faunal groups collected, 2.9% were found in Community A but not in Community B; 84% were found in B, but not A; and 20% were present in both communities.

The dominant taxa of each community is given in Table 3. Dominance as used here refers to numerical abundance.

TABLE 3: RELATIVE PERCENTAGES OF TAXONOMIC GROUPS IN COMMUNITY A AND COMMUNITY B

TAXA	PERCENT COMMUNITY A	COMMUNITY B
Chaoborus	59.0	0.01
Chironomus	29.0	14.08
Other Diptera	00.0	0.02
Mollusca	06.4	65.06
Annelida	04.7	0.42
Crustacea	00.6	16.00
Arachnida	00.3	0.04
Trichoptera	00.0	0.98
Ephemeroptera	00.0	1.04
Odonata	00.0	0.33
Bryozoa	00.0	0.02
Empididae	00.0	0.07
Lepidoptera	00.0	0.04

As seen in Table 3, _Chaoborus_ dominated the bottom fauna of Community A. Chaoborids of four species were identified from Community A, representing 59% of all organisms collected from this community. Chaoborids have been found in great densities in deep waters of many temperate lakes (Juday 1908, Berg 1938). They are highly tolerant of low oxygen concentrations and can exist under anaerobic conditions for long periods of time (Juday 1908, Petr 1974). Sixty-eight percent of the _Chaoborus_ larva of Community A were collected in the deepest regions of the lake, at 30 to 40 foot depths, where the oxygen levels never exceeded 4.3 ppm.

The Chaoborid species present in Community B were _C. punctipennis_ and _C. albatus_, and these were never collected at depths of less than 15 feet. _Chaoborus_ in Community B comprised 0.1% of the total population.

The ubiquitous Chironomid larvae were the second most abundant organisms of the profundal zone. Chironomids of 15 species represented 29% of the fauna of Community A. The Chironomids most abundant in the deep mud of A were Chironomus plumosus, Chironomus tentans, and Procladius adumbratus. C. plumosus and C. tentans are members of the tribe Tendipedinni (or Chironomini) of the subfamily Tendipidinae. This is a group of burrowers and tube builders which utilize the soft and fine mud particles of the sediment to construct the tubes they inhabit. This group of midges, also known as bloodworms because of their distinctive reddish coloring, have specialized hemoglobin which acts on oxygen transport under very low O_2 conditions. This enables Chironomids to dwell in the deep, O_2 depleted waters of Community A.

P. adumbratus, also very numerous in Community A, is a member of the subfamily Pelopiinae (or Tanypodinae). P. adumbratus is a common predator of oligochaetes and other midge larvae in the profundal zone of northern lakes (Merrit and Cummins 1978, Usinger 1968).

Chironomids comprised 14.8% of the total benthic fauna collected in Community B, represented by 47 species. Among the most abundant were Dicrotendipes, Cryptochironomus abortivus, Polypedilum flavus, Cryptochironomus psittacinus, and Chironomus decorus. All of these organisms belong to a group of Tendipedinae that are known to breed in beds of aquatic vegetation and are commonly found in the benthos of water less than ten feet deep (Usinger 1968). These organisms were collected predominantly from the weed beds in depths of five to ten feet. P. adumbratus and P. flavifrons, also found in large numbers in Community B, are members of the subfamily Pelopiinae. P. adumbratus has been mentioned as a profundal species, but is also known to occur in the littoral zone. Apparently, P. adumbratus can utilize some crustaceans as a food source. Crustaceans are closely associated with aquatic vegetation, and it is here that P. adumbratus was found in Cedar Lake. P. flavifrons is a herbivore commonly inhabiting littoral waters with macrophytic growth.

An extremely large population of Pseudochironomus richardsonii was collected from the shallows of Community B, along with many Microspectra dives. M. dives, a member of the tribe Calospectrini (or Tanytarsini), and P. richardsonii, a Tendipedinae, are both collectors and gatherers of the littoral region. P. richardsonii probably lay eggs on rocks in the shallows, as large collections of this species were gathered in the particularly gravelly three to four foot depths of Community B.

Several other chironomid species were present in Community A in much smaller numbers. Several species of the genera Cryptochironomus and Endochironomus, some Stenochironomus, Stictochironomus, a few Tanypodinae, and a small number of Orthocladinae were identified.

Mollusks were the most abundant organism of Community B, and the third most abundant of Community A. Over 67% of the population of Community B were mollusks, represented by 17 species of Gastropods, and five species of Pelecypods.

Gastropods were present in very large numbers; it was not uncommon to collect 100 or more snails in a single grab sample from the sandy gravel bottom or weed beds of the shallows. The population numbers of snails fluctuated in Community B in accordance with the growth patterns of the submerged vegetation, suggesting that aquatic macrophytes have an important role in the ecology of freshwater Gastropods. Many snails are herbivores, cropping green plants as food or grazing on the algae that grow on stones and submerged vegetation (Macan 1963). *Potamogeton* and *Chara* are commonly used as sites for oviposition and as a habitat as well. Clinging to the leaves of plants as they grow may aid in avoiding predation by fish in the waters below.

Mollusks represented only a small proportion of the benthic fauna in Community A. Six percent of the population were Gastropods, and 0.4% were Pelecypods (mainly Spaeriids), for a total of eight species and only forty-five individuals.

Crustaceans were also abundant in Community B, represented mainly by amphipods (*Hyalella*) and ispods (*Asellus*). The crustacean population was closely associated with the weed beds in Cedar Lake. Like gastropods, their abundance was related to the littoral vegetation. It is known that *Asellus aquaticus*, the prevalent isopod collected here, lives among macrophytes, crawling on stems and leaves. They feed on vegetable matter. Particularly favored are diatoms, periphytic algae, and dead macrophytic tissue. Aquatic plants provide sites for oviposition for these organisms (Petr 1974).

Other crustaceans found here in small numbers were Ostracods, *Chydorus*, and *Ceriodaphnia*. These free swimming crustaceans were probably lifted from the water column as macrophytes were pulled in during a sampling grab.

Community A had a very small population of crustaceans, totaling

0.3% of the population. Only Ostracods were present.

Annelida is another group of animals that inhabits both A and B, although not in large numbers. Annelids comprised 4.7% of Community A. Those individuals in A were generally small oligochaetes. They were identified and listed simply as oligochaetes, but most of them belonged to the family Naididae, a group of mud burrowers.

In Community B, Annelida was represented mainly by Hirudinea (leeches). Common were Helobdella, and Placobdella (ectoparasites), and Erpobdella, a predaceous leech. Helobdella stagnalis, the most abundant species, is a predator of oligochaetes and Chironomid larvae (Learner and Potter, 1974). With Chironomids representing 14.8% of the organisms in Community B, Helobdella had plentiful food resources.

Leeches are common in lakes of the northern United States, and are usually denizens of the shallows. Since predacious species hide during the day and are active nocturnally, rocky bottoms and waters with submerged vegetation support the greatest numbers of these animals.

There were several groups of organisms in Community B that were never found to inhabit Community A. These were Tricopterans, Ephemeropterans, Odonata, Bryozoans, Empididae, and Lepidopterans.

Ephemeropterans (Mayflies) and Tricopterans (Caddisflies) were found in small numbers in the three to four foot depths of Community B. Mayflies tend to favor rock strewn bottoms for oviposition, and they feed upon aquatic vegetation. These two conditions clearly explain their presence in this sandy, rock-strewn region.

Caddisflies utilize sand, rocks, and plant material for the construction of their nets and cases. They feed upon micro-organisms which grow on decaying plant tissue. The greatest number of Trichopterans were collected in late summer when the submerged vegetation began to die off.

Also identified from the shallows were a few larvae of the order Odonata (Dragonflies), an occasional Empididae (Danceflies), and rarely, a Lepidoptera larva. The vegetation once again played an important role in the presence of these organisms: Odonata make use of plant material for both oviposition and as a food source, as do the Lepidopterans. Empididae often deposit their eggs on vegetation or rocks, and their larva are frequently found to rest on the rocky bottom or beneath plant silt.

Species Diversity

Values for diversity analysis are shown in Table 4. Of the two communities under investigation, Community B has the higher diversity (H' = 2.68), accompanied by the lower evenness factor (J' = 0.55), and larger species richness (s = 133). High population numbers in B contribute to the H' value, while the preponderance of mollusks (65%) in B is reflected in the relatively low evenness factor.

TABLE 4: DIVERSITY ANALYSIS VALUES

COMMUNITY	TOTAL SPECIES	$\overline{N}$/SAMPLE	H'	J'	BD
A	32	18	2.12	0.61	1.67
B	133	117	2.68	0.55	

For Community A, H' = 2.12, and J' = 0.61. The species list of Community A indicates a low species richness; only 32 species were collected from this region. The fact that the population is mainly distributed between Chaoborids and Chironomids, with very few rare species, results in an evenness factor which shows this higher degree of equitability. It appears that the relatively low number of species present is the main factor contributing to the lower H' value in Community A.

The Beta diversity index (BD) is a measurement of "between habitat" diversity, or the degree of change in species. An appropriate measure of beta diversity is: $BD = Sc / \overline{S}$, in which Sc is the number of species in a composite sample, and $\overline{S}$ the mean number of species in the alpha samples which comprise the composite. In order to determine the change in composition between Community A and Community B, the entire transect was considered as a composite sample. Sc was each species encountered along that transect counted once no matter how often a species appeared. $\overline{S}$ became the average number of species per individual alpha sample. The BD between Community A and Community B was 1.67.

This value is an indication of the turnover, or difference in species composition along the established gradient. Beta diversity is an expression of the ecological distance, or the degree to which communities differ from one another because of their separation along an environment gradient (Whittaker 1975).

The beta diversity index is a particularly useful tool when considered as a percentage of maximum possible turnover between communities.

Maximum, or complete turnover, between any two samples would result in no species in common between those two samples. Therefore, on the basis of $BD = Sc/\overline{S}$, the maximum beta value of two samples is $BD = 2$. Computing the ratio of species turnover occuring between two successive communities to the maximum possible turnover, we arrive at the following: a turnover of 67% between community A and Community B. This suggests that we are indeed dealing with two separate "assemblages", or communities of organisms.

DISCUSSION

Community Structure

The literature contains many discussions of the term "community" as used by ecologists (Hairston 1959, Sanders 1960, Byers 1963, Mills 1969, Ross 1972). The meaning of community used in this paper is a fairly general definition adapted from Sanders (1960): "A community is a group of species that show a high degree of association by tending to occur together." This association may be further understood to have a natural order or structure. To obtain an understanding of this structure, the distribution and numerical abundance of all species must be taken into consideration (Hairston 1959, Boesch 1973).

In order to demonstrate the distribution of organisms along the depth gradient, the four dominant groups of the benthos (representing 95% of all organisms collected) were plotted on a graph, using percent of organisms versus depth. This graph, shown as Figure 1, indicates the existence of two divergent communities: a shallow-water Gastropod-Crustacean dominated community and a deep water community dominated by *Chaoborus*.

Whittaker (1972) notes that "species distributions much more commonly overlap broadly than exclude one another", and that even "where these meet they occupy niches at least partly different." While there is a slight overlapping of populations along the depth continuum in Cedar Lake, the abrupt shift in the type and abundance of organisms at 19-21 foot depths suggests that at this point along the gradient a change occurs in some factor (or factors) which influence the distribution of benthic organisms. There is one very obvious physical characteristic which coincides precisely with this narrow band at approximately the twenty foot depths: the outer limits of the dense macrophyte bed. Except for the initial weeks of sampling in the spring, this growth of aquatic vegetation extended along the transects from the shoreline to the region of twenty foot depths during the entire sampling period. The outer boundary of the macrophyte bed, as it appears in Figure 1, suggests that this forms a physical transition zone, or ecotone, separating Community A from Community B.

Due to the natural overlap of organisms from each community it is common for an ecotone to have a greater variety and diversity than either of the adjoining communities. It may even support a community with characteristics not exhibited by either of the adjoining communities (Odum 1971). In order for this region of overlap to be a distinct community it must contain some habitats, and therefore some organisms that are not characteristic of the contiguous communities. In view of the very narrow range of this ecotone the presence of such additional habitats is not likely. Furthermore, the species distribution as shown in Figure 1 gives no indication that this zone contains any species that are not also found in either A or B or both. On the basis of these facts I have concluded that this zone is merely a junction between two diverse, adjacent communities, and not a distinct community in itself.

The use of various diversity measurements as described earlier allows a deeper understanding of the order of the "association" or "assemblage" organisms collected from points along the depth gradient in Cedar

Lake. That the species present in Community A differ from those in Community B is evident from even a cursory glance at the species composition list (Table 1). More importantly, a quantitative analysis of diversity indicates that the structural dynamics in the respective communities vary concurrently with the variation in species composition.

Whittaker's "beta" diversity index (BD) provides an additional dimension to the study of these communities. Rather than viewing each community as a distinct population zone, consider each community as a sample along a depth gradient. The extent of the difference in species composition along the gradient is calculable in terms of its beta, or between habitat, diversity. This measurement denotes an "ecological distance": the degree to which communities differ in species composition along an environmental gradient (Whittaker 1975). Relative to a maximum, or complete, turnover value of 2.00, a BD = 1.67 calculated for A and B is indicative of a 67% turnover in species composition between these two areas either side of the ecotone. The beta diversity index strongly supports the existence of two communities along this gradient (as indicated in Figure 1).

Factors Regulating Species Diversity

The habitat of a species within any environment is a complex interaction of physical and chemical characteristics. Whittaker (1972) notes, however, that it is possible to "abstract from the factor-gradients a few major directions of environmental variation", in order to analyze what effects those factors have upon species diversity. The literature indicates that there are three environmental variants most frequently cited as having a regulatory affect on the species diversity within, and between, aquatic environments. These are: sediment type (Driscoll and Brandon 1973, Sanders 1968, Young and Rhoads 1971); oxygen levels (Petr 1968, Sala et al 1977); and aquatic macrophytes (Petr 1968, Odum 1971).

Sediment type. Animal-sediment associations have been previously identified as having a definite influence upon the distribution of species in marine and tropical freshwater ecosystems. Diversity in sand has been found to be generally higher than diversity in mud-bottom communities. Boesch (1973) indicated that roughly one-half the difference between species richness of sand and mud bottoms was attributable to sediment variations. The presence of hard surfaces such as shells, shell fragments and small rocks and stones in the sand appears to increase diversity by increasing habitat potential. The utilization of stones and rocks by aquatic insects, most notably for oviposition and larval case-building, was discussed earlier. It is probable that the presence of such litter enhances the abundance of these organisms (Odonata, Ephemeropterans, Trichopterans), but it is not possible to determine from this study the degree of affect that substrate has on the relative diversity of the sand versus mud benthos. There is no indication in the distribution of organisms, the species composition along the gradient, or the diversity data that would point out sediment-assocations as a major factor in the distribution of benthic invertebrates in Cedar Lake.

Macrophytes. As might be expected, many of the inhabitants of Community B are herbivores. The major families which comprise the dominant Gastropod group (Physiidae, Lymnadae and Planorbulidae) are primary consumers, utilizing the available living macrophytes as their main food source (Ward and Whipple 1918). Trichopterans (Caddisflies) eat dead or decaying plant tissues, feeding off the plant debris in the benthos.

While dragonflies and damselflies are exclusively carniverous, the vegetation serves as an important function for them while food gathering. From the vantage point atop an emergent plant the nymphs of these groups can easily identify potential prey, using their hinged labium to snare their food as the unlucky creatures pass by them (Odum 1971).

Amphipods and isopods, the most abundant Crustacenas present in B, forage the decaying plant debris for their food. The isopods, along with some of the Mayfly larvae, the sprawling Odonata nymphs, Spaeriids and many of the pond snails, frequently rest on, or move along the bottom, hidden from the casual sight of predators beneath the plant debris (Merrit and Cummins 1978).

The zooplankton collected from this community consisted primarily of Cladocerans, particularly Daphnia and Sida. These, along with the ostracods, are considered the "less-buoyant" Crustaceans - weak swimmers which cling to the vegetation for support, or rest upon decaying plant material on the bottom (Odum 1971). These organisms were generally collected by carefully washing off the plant material hauled up in the dredge.

Many insects also utilize emergent vegetation as a site for oviposition. High upon a Potamogeton, the eggs are less likely to become dinner for another hungry animal. The Lepidopterans, Empididae, Odonata and many of the Gastropods are among those for whom the presence of plant life is an important part of their productive habits (Usinger 1968).

In Community A, all the organisms collected (except for a few rare Gastropods) are secondary consumers: 1) The hemoglobin carrying chironomid larvae, the so-called "blood-worms"; 2) The small "fingernail" clams of the Spaeriid family, and 3) The dominant Chaoborus, or "phantom larvae". The first two are benthic forms which burrow into the deep, fine mud, the last is actually a plankton form that migrates diurnally in search of food (smaller zooplankton) and returns to rest in the mud by day.

The eggs of both the Chaoborus and Chironomus are deposited on the surface of the water and sink to the bottom (Johannsen 1969). Berg (1938) noticed during studies with C. flavicans that the eggs were dropped near the shore, and that the larvae moved into the deeper water during the planktonic stage and later entered the mud of the deep waters. Only 10 Chaoborids (.02% of those collected) were gathered in grabs taken from Cedar Lake in waters less than 20 feet deep. If more Chaoborids were actually present in the shallow waters they most likely were lost due to the use of the Ekman dredge as a sampler. A finer mesh collecting apparatus, such as a plankton net, used in conjunction with very fine mesh sorting screen would be more appropriate for the collection of the small, early instars of Chaoborus.

While it has not been shown conclusively whether Chaoborus eggs are dropped inshore or in deep waters of the profundal zone, early laboratory studies show that attempts to induce the use of vegetation for oviposition were not successful (Berg 1938). Chaoborus consistently avoided the vegetation, always dropping their eggs directly upon the water surface.

What is notable in this comparison of Communities A and B is that unlike Community B, where vegetation is a major element in the life-cycle and physiological needs of all the organisms, the dominant organisms of Community A exist with no apparent need for aquatic macrophytes. From this it can be concluded that the presence of vegetation is one of the primary physical characteristics influencing the distribution of species type and abundance in Community B, and is the main reason for a higher H' diversity value (H' = 2.68) for Community B.

The presence of the macrophytes increases the living space and resource gradients within the community by satisfying a multitude of needs: as a resting place, a food source, a site for oviposition, even protection from predators. By expanding the resources available in Community B, the presence of the macrophytes enhances the species diversity of the benthic community.

Oxygen levels. Another environmental variant which regulated species diversity in Cedar Lake was oxygen concentration. Oxygen requirements are critical in determining which organisms can exist at a given point along a depth gradient. In Cedar Lake, oxygen levels may have affected the distribution of some of the dominant species. In Community A, O_2 levels were found to be increasingly low throughout the sampling season (see Table 2), due to the depth of the water column and summer stagnation. Chaoborus, the dominant organism found in Community A, has been found in great densities in the deep waters of many temperature lakes (Juday 1908, Petr 1974). Chaoborus larvae are remarkable in having four air sacs, two at each end of the body, which act as floats during diurnal migration and also provide a supply of reserve oxygen.

Also physiologically adapted to low oxygen levels are the Chironomids, which represent over 29% of the fauna in Community A. The ability of certain hemoglobin-carrying Chironomids (Tendipidae) to tolerate low oxygen levels was discussed previously. Aquatic oligochaetes collected from Community A, are known to tolerate anaerobic conditions for more than a month if exposed to some oxygen intermittently, since they cannot respire anaerobically for any appreciable period of time.

Other organisms are restricted to shallow, well oxygenated areas due to physiological requirements. Odonata (Dragonflies) and Ephemeroptera (Mayflies) have high respiratory demands, which limit them. Gastropods, the major organisms identified from Community B, are also intolerant of low oxygen levels. Although Gastropods are sometimes collected in deep areas of a lake, generally this is only during spring or winter turnover. At all other times, their oxygen needs dictate a shallower habitat.

Although macrophytes were discussed earlier, their influence is felt again in terms of the oxygen that they supply to the environment. As the weed beds flourished throughout the summer, it constantly supplied the Gastropod-Crustacean community with ample oxygen for metabolic utilization. No measure of community productivity was incorporated in the study, but it is probably safe to assume that the productivity of this region was high during the summer (eutrophic).

In Community A, however, this process had an adverse effect. The high productivity which the macrophytes helped to realize created a constant flux of organic matter from B into A. The resultant eutrophication hastened the depletion of oxygen from an already low-oxygen environment.

The lower (H' = 2.12) species diversity index of Community A may be largely attributable to the condition of physical stress created by critically low oxygen concentrations. This correlates with marine benthic diversity studies which suggest that as physical stress increases in an environment, diversity decreases (Sanders 1968). It may not be due to the low oxygen levels per se, but to the fact that the oxygen concentration fluctuates drastically throughout the year. An annual cycle of spring overturn, summer stagnation, fall overturn, winter stagnation, followed again by spring overturn, etc., creates wide fluctuations in the oxygen levels in Community A, exposing the animals to severe physiological stress, to which few organisms are capable of adapting. The population is thus restricted to those few species that can tolerate the unfavorable extremes produced by the fluctuations.

SUMMARY

Two distinct communities exist in the benthos of Ceder Lake along a depth gradient from the center of the lake to the shoreline. The first is a Chaoborid community, the second a Gastropod-Crustacean community.

Species distribution and diversity in Cedar Lake are primarily correlated to variations in the following environmental features:

1) The presence of aquatic macrophytes

2) Levels of oxygen concentration.

Diversity values were found to be higher in the Gastropod-Crustacean community due to the expansion of resources provided by the existence of the dense growth of aquatic macrophytes. Diversity may also be enhanced by the sandy sediments present in the sub-littoral region, but the data is not conclusive.

The lower species diversity of the Cahoborid community is related to the physical stress this region experiences from low relative oxygen levels throughout the sampling season.

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APPROVAL SHEET

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The final copies have been examined by the director of the thesis and the signature which appears below verifies the fact that any necessary changes have been incorporated and that the thesis is now given final approval by the Committee with reference to content and form.

The thesis is therefore accepted in partial fulfillment of the requirements for the degree of Master of Science.

April 20, 1981
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