AN INVESTIGATION OF SOME ASPECTS OF THE INTRA-LAKE DISTRIBUTION OF CHYDORUS SPHAERICUS (CLADOCERA:CHYDORIDAE)

By

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ABSTRACT

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Chydorus sphaericus was associated in very high densities with the macrophyte *Myriophyllum heterophyllum*, and very low densities with *Scirpus subterminalis*. Standardizing *Chydorus* numbers by surface areas (calculated from marl-free dry weights using regressions I determined) of the plants showed that the differential distribution is not simply an artifact of variation in surface area between macrophyte species. Tests using plastic plants indicated that the *Scirpus* shape is favored over the *Myriophyllum* shape. The effect of new surface area (which *Myriophyllum* continually generates while *Scirpus* does not) was tested by comparing cleaned plants to naturally marled controls; little effect was seen. Finally, observations of relatively predator-free aquaria indicated that predation may play a secondary role to that of the macrophyte itself. The alternatives of variation in food resources, chemical exudates, and predation as potential causes of the observed distribution are discussed.

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INTRODUCTION

The Chydoridae are nearly microscopic crustaceans inhabiting the littoral and benthic regions of lakes, ponds, and sluggish streams worldwide. It is a large family, consisting of a total of about 185 species ranging in length as adults from about 0.28 to 6.0 mm, with most species smaller than 1.5 mm. In general, they are adapted for moving over and feeding on submerged surfaces, such as macrophytes and rocks, or in softer sediments. Fryer (1963, 1968) and Smirnov (1966, 1968, 1971 a & b) suggest that various species are adapted to their modes of life with remarkably subtle morphological adaptations.

The earliest taxonomic work is attributed to O. F. Müller, who named, among others, *Chydorus sphaericus* in 1785 (Smirnov, 1971b). Yet even in this field, there is much ongoing research, both in description of species (Frey 1965, Megard 1967, Flössner and Frey 1970, Flössner and Kraus 1977) and in allocation of species to genera (Fryer 1968, Smirnov 1971b, Frey 1976).

Most ecological work with chydorids has been descriptive in nature, for example, species lists of various locales (e.g., Smyly 1958, Smirnov 1963, Anderson et al. 1977). In contrast, there have recently been attempts to make broad generalizations about distribution and control of diversity and abundance (DeCosta 1964, Straškraba 1965, Whiteside and Harmsworth 1967, Harmsworth and Whiteside 1968, Whiteside 1970). Also, paleolimnologists have begun to make use of techniques pioneered by Frey (1958) based on the fact that chydorid carapaces are preserved very nicely in lake sediments (Megard 1964; Goulden 1964, 1966; Whiteside 1970). Unfortunately, interpretation has been hampered by the lack of detailed ecological information on individual species (Frey 1969).

In the last 15 years, some workers have begun to tackle the problems of quantitative sampling, producing studies of two general types. In the first of these, one or more lakes in a region have been examined in the attempt to define assemblages of species associated with fairly broad habitat subdivisions, i.e., limnetic, benthic, or plant surfaces (Flössner 1964, Pennak 1966, Quade 1969, Lang 1970). Others have examined population trends and dynamics (Goulden 1971; Keen 1973, 1976; Whiteside 1974).

There has been very little published on the affinity of chydorids for various macrophytes, although some authors, such as Quade (1969), do report applicable data. However, Quade's data are such that, while they indicate dominant species on each plant, comparisons between macrophyte species are not easily made. This is because his results are expressed as proportions of total chydorid fauna collected on all plants of a given species with no attempt to standardize for the amount of plant material collected. I have chosen to explore this aspect of the ecology of the chydorids more closely.

In a preliminary study on Lawrence Lake, Barry County, Michigan, I developed a method for sampling individual macrophytes (see General Methods) and obtained data on the distribution of many chydorid species (Appendix A). Many species were found in greatest density (numbers per gram plant tissue) on _Myriophyllum_ _heterophyllum_, some seemed to prefer other macrophytes, and most were present only in low numbers, if at all, on Scirpus subterminalis or the lily pads Nuphar variegeta and Nymphaea odorata. Chydorus sphaericus was chosen for more detailed study because it is the most abundant in the lake (see also Keen 1973, 1976) and has the most consistent distribution among the macrophytes over the entire summer.

Chydorus sphaericus (O. F. Müller, 1785) is the most widely distributed chydorid in the world (Smirnov 1971b). It is a small crustacean (adult size about 0.5 mm maximum), with wide tolerance limits in terms of oxygen concentration, temperature, and pH (Fryer 1968). The morphology of C. sphaericus has been detailed by Fryer (1968) who showed that it is capable of utilizing a variety of substrates provided that they are not perfectly smooth and provide purchase for the first pair of legs. It is not found in the benthos of Lawrence Lake (personal observation), nor in the plankton, although it may be found in the limnetic zone of some lakes under conditions of blue green algal blooms which supply a substrate (Fryer 1968). In 1976, I found it in very low densities on Scirpus subterminalis Torr., a plant that accounts for 70-80% of the total macrophyte biomass in Lawrence Lake (Rich et al. 1971). In contrast, the highest densities of Chydorus were always supported by Myriophyllum heterophyllum Michx. (similar findings were reported by Flössner 1964, Pennak 1966), a minor constituent of the macrophyte assemblage of the lake (Rich et al. 1971). Myriophyllum and Scirpus are also very dissimilar stucturally; the former is very complex, with whorls of finely divided leaves extending from the stem, while the latter is grass-like in appearance.

In this study, I examine various aspects of the distributional dichotomy of Chydorus sphaericus between these two very different plants. I begin with a simple physical explanation and proceed to more complex biological alternatives.

STUDY SITE

Lawrence Lake (Figure 1) is a small (4.9 ha), oligotrophic, marl lake 2.1 km east of Hickory Corners in southern Barry County, Michigan. For the most part, the littoral zone is composed of a shallow marl bench gradually sloping to about 1.5 m depth, after which the bottom falls sharply to about 7 m. The maximum depth is 12.6 m. The dominant macrophyte over much of the littoral zone is Scirpus subterminalis (Rich et al. 1971).

Studies of many facets of the limnology and biology of this lake are available, including the history (Rich 1970), general limnology (Wetzel et al. 1972, Wetzel 1975), macrophytes (Wetzel 1969, Rich et al. 1971, Wetzel and Manny 1972, Hough and Wetzel 1975), periphyton (Allen 1971, Wetzel and Allen 1972), fish communities (Werner et al. 1977, Hall and Werner 1977), and previous work on the Chydoridae (Keen 1973, 1976).

The study area (Figure 2) was located in the southwestern corner of the natural lake basin, next to an abandoned marl excavation site (Rich 1970). In contrast to most of the littoral zone, the bottom here slopes gradually to a depth of about 4 meters and supports a variety of macrophytes (see maps in Rich et al. 1971). The Scirpus bed extends from about 1 to 3 m depth in a C-shape around the western part of the area. The Myriophyllum bed was in 2.5 to 4 m of water, with a small band of Najas flexilis (Willd.) Rostk. & Schmidt separating it from

Figure 1. Bathymetric map of Lawrence Lake, Michigan.

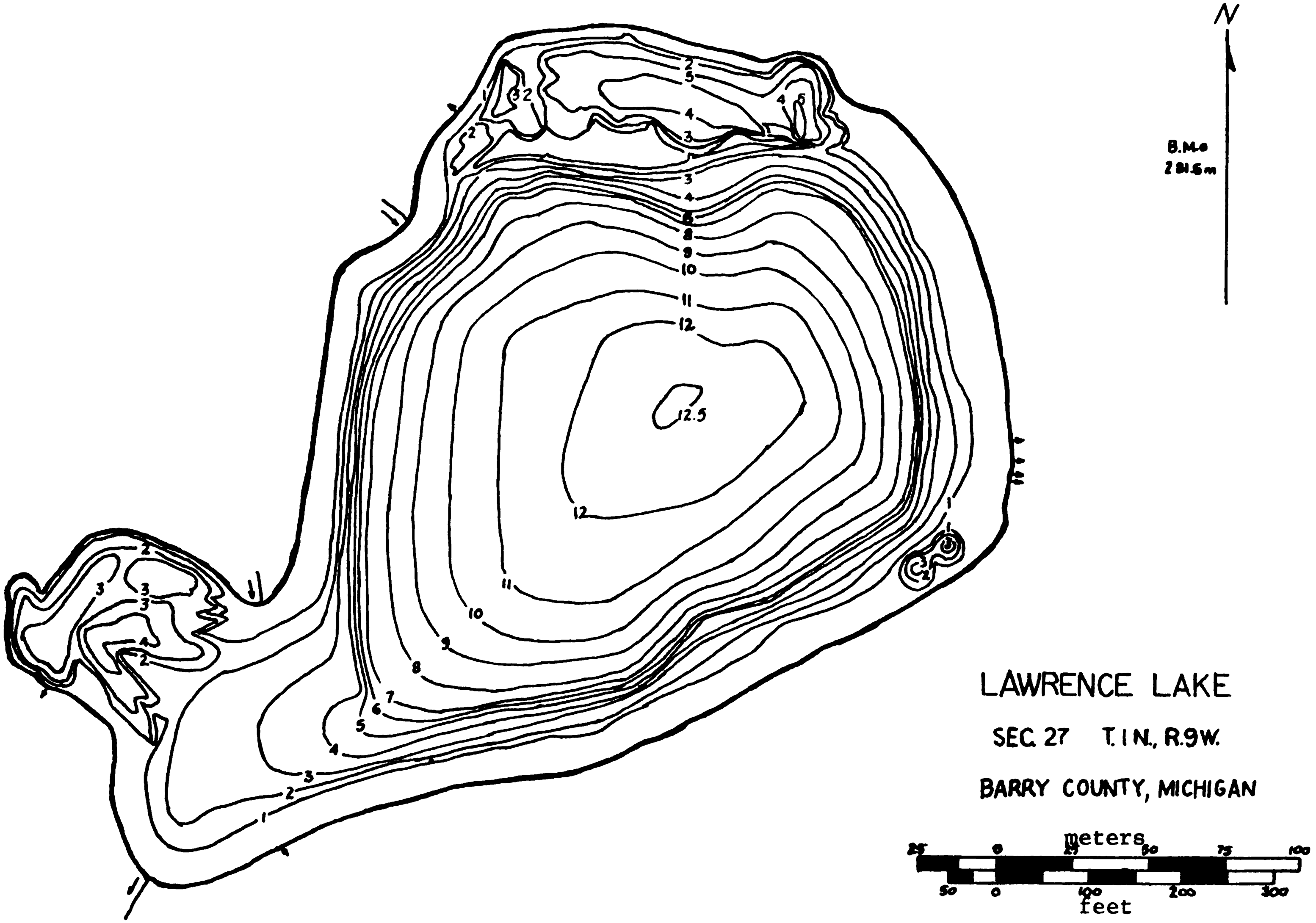

Figure 1.

contour intervals in meters

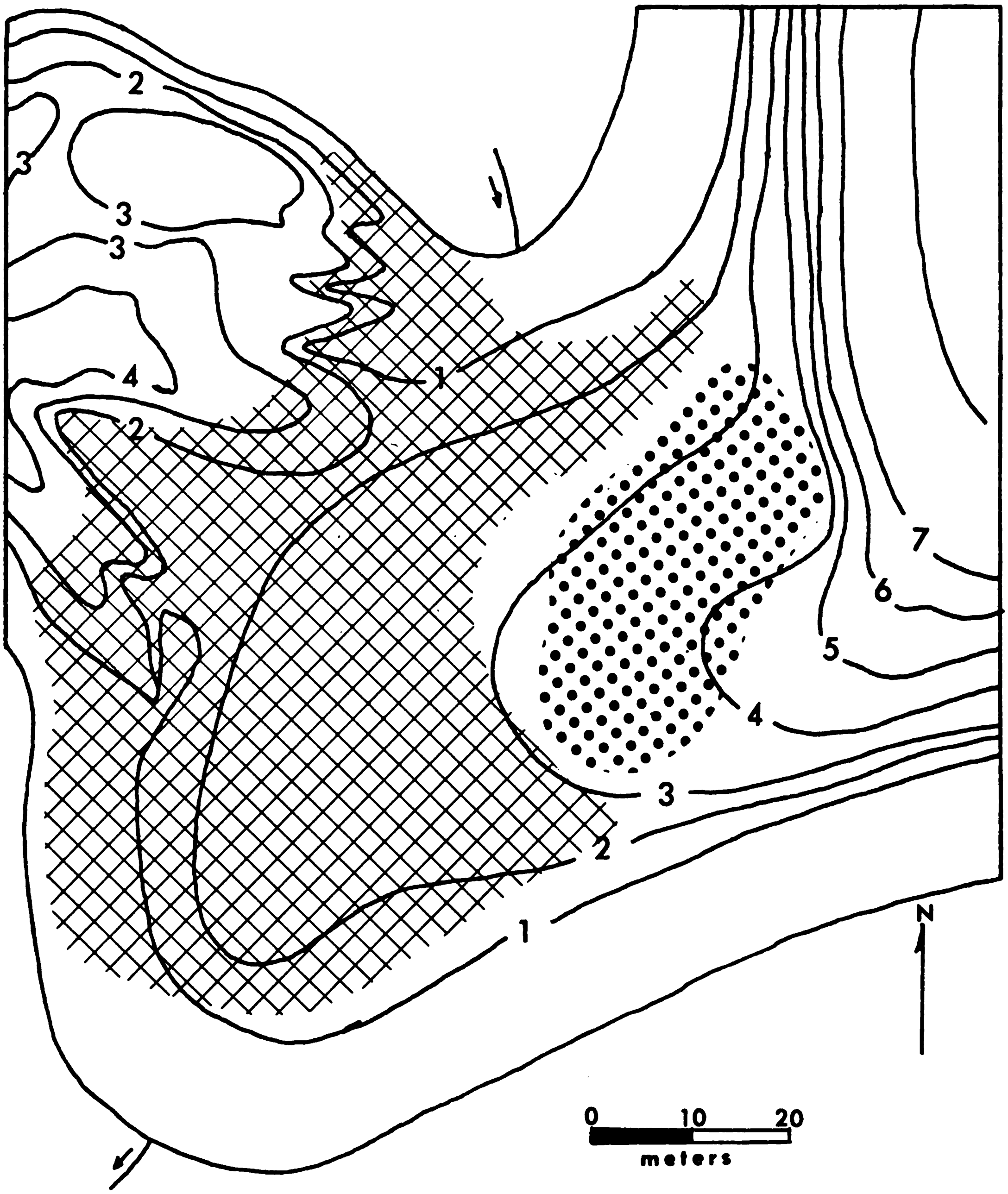

Figure 2. Bathymetric map of the southwestern corner of Lawrence Lake. Crosshatching indicates the approximate distribution of *Scirpus*, while stippling indicates the approximate distribution of *Myriophyllum*. Contour intervals in meters.

the *Scirpus*. Sampling (see next section) was restricted to plants 2.5 to 3.5 m deep. The bottom was composed of a soft mixture of marl (mostly $CaCO_3$) and organic sediments.

GENERAL METHODS

Individual plants (or bunches of leaves in the case of Scirpus) were collected while diving with SCUBA. A 143 µ mesh plankton net with a one quart collecting jar attached was submerged and held near the base of the plant. The plant stem was gently pinched to break it and the plankton net was raised around the plant. This method excludes animals in the sediments from the sample. The contents of the net (i.e., the plant and associated fauna) were washed into the collecting jar and transported to the laboratory.

The contents of each jar were emptied into a sieve made with 143 µ Nitex screening, and the plant was washed thoroughly with a stream of water. The sieve was then submersed in carbonated water for several minutes to anesthetize the animals; samples were preserved in 4% sucrose formalin (Haney and Hall 1973).

The washed plants were rinsed with 0.2 N HCl to remove carbonate deposits (Wetzel 1960) and oven dried at 100-105°C for at least 24 hours. Dry weights were determined with a microbeam balance to the nearest 10 µg. Macrophytes were identified using Fassett (1957).

Preserved animal samples were placed in 90 mm disposable petri dishes with a grid etched on the underside and examined at 12-50 X with a dissecting microscope. The entire sample was examined for Chydorus sphaericus, and often all chydorids and invertebrate predators were noted. Chydorids were classified to species level if possible (to genus in the case of small *Alona* and *Alonella* spp.), and predators to various levels using Edmondson (1959), Pennak (1953), and Smirnov (1971b).

In several field experiments (see Substrate Morphology, The Effect of New Surface), samples of experimental and control plants were collected for analysis of periphyton. These samples were preserved with Lugol's iodine, but unfortunately most of them later developed what appeared to be bacterial blooms, and had to be discarded.

EXPERIMENTS, WITH RATIONALE, TECHNIQUES, RESULTS, AND INTERPRETATION

Surface Area

The simplest way to explain the observation that more *Chydorus sphaericus* are found on some macrophyte species than others is that it is a surface area phenomenon. That is, the animals are evenly distributed over the available surfaces, and it is the difference in surface area between plants that produces the effect. If this is so, when the numbers of animals found on each plant are standardized by the surface area of the plant, there should be no significant differences in density of animals between plant species. Other studies (Pennak 1966, Lang 1970, Whiteside 1974, and others) have recognized this possibility, but because of the difficulties associated with determination of plant surface areas (cf. Wohlschlag 1950, Mrachek 1966) these investigators have preferred to develop sampling methods that standardize the area of lake bottom sampled or restricted their studies to a single macrophyte species.

In this study, regression lines relating marl-free dry weight (an easily obtained quantity) to an estimate of each plant's surface area were developed. The method used for estimating surface area was that of Harrod and Hall (1962). Between 20 and 40 plants of each species were collected while diving or with a grappling hook. Each plant was rinsed in 0.2 N HCl to remove marl, rinsed in water, and dipped in acetone. After allowing the acetone to evaporate, surface dry weights (i.e., weight of plant with dry surface, but with hydrated cells) were obtained. The plant was then immediately dipped in a 50% solution of the surfactant Teepol 610^R (Shell Chemical Corp., N. Y.), shaken for 20 sec to remove the excess, and weighed again for a Teepol wet weight. The difference between the Teepol wet weight and the acetone dry weight is the weight of Teepol covering the plant, which is proportional to the surface area of the plant. The Teepol was rinsed from the plant which was then oven dried (100-105°C for 24 hr) and finally weighed for a marl-free dry weight. (The plastic plants used in a later experiment were similarly treated, except that they were air dried rather than dipped in acetone or oven dried.)

The amount of surface area covered by a given weight of Teepol varies depending on a number of factors, including the microstructure of the surface (i.e., presence of hairs, grooves, etc. that can trap liquid). It was assumed in this study that such differences were negligable, and a single proportionality constant relating weight of Teepol to surface area was determined. Leaves of the lily pad <u>Nuphar</u> <u>variegeta</u> Engelm., which could be cut into easily measured pieces were used. These were treated as above, producing a mean value of 23 g Teepol / m^2 surface area ($\sigma^2 = 1.5$). (Pieces of acetate stock were used to determine the proportionality constant for the plastic plants of 16 g Teepol / m^2 surface area ($\sigma^2 = 9.4$).) Multiplication of these proportionality constants by the weight of Teepol covering a plant gives an estimate of the total surface area of the plant.

Regression equations of the relationship between marl-free dry weight and surface area were calculated for several species of macrophyte, and are presented in Table 1. It can be seen that in spite of the complex technique and the many weighings and estimations involved, these relationships are strongly linear. The observed results are strong enough to show that determination of marl-free dry weight and appropriate conversion to surface area produces accurate estimates of the latter, at least in a relative sense, and that comparison of numbers using these relationships are valid.

Using these regression lines, the density of _Chydorus_ _sphaericus_ was determined for several macrophytes on a number of sampling dates. These results are presented in Table 2.

While it is apparent that the rank order of the various macrophytes is relatively constant (with the exception of the single night sample and the fall sample), the comparison of most interest in this study is between _Myriophyllum_ and _Scripus_, and statistical treatment is limited to these. Depending on the number of samples, the densities in Table 2 were compared using the Mann-Whitney U-Test of means (Sokal and Rohlf 1969), or Fisher's Exact Probability Test applied to population medians (Bradley 1968). In all cases the density of _Chydorus sphaericus_ was greater on _Myriophyllum_ than on _Scirpus_. It should be mentioned that although Fisher's Exact Test gave fairly large probabilities for the observed differences not being real, this value ($p = 0.17$) is the lowest obtainable with the small number of samples (2) involved. Also, all 1977 sampling dates were combined and a Mann-Whitney U-Test (one-tailed) was performed on the pooled data. The result is that for the entire season _Myriophyllum_ plants supported a higher density of _Chydorus_ than did the _Scirpus_ with $\alpha < 0.001$.

I conclude that through the summer and into the fall, in Lawrence

Table 1. Surface area (Y) to marl-free dry weight (X) regressions for several macrophytes.

Plant Species	Regression Equation	F Value	Significance	Correlation
Myriophyllum heterophyllum	$Y = 1956.23 (X) - 8.90$	161	<<0.001	0.95
Najas flexilis	$Y = 1163.29 (X) - 4.65$	330	<<<0.001	0.95
Potamogeton pectinatus	$Y = 1456.52 (X) + 5.41$	308	<<<0.001	0.97
Potamogeton praelongus	$Y = 1051.51 (X) + 110.03$	54.8	<<0.001	0.87
Scirpus subterminalis	$Y = 1452.86 (X) + 8.38$	549	<<<0.001	0.98

Table 2. Mean density (# / m^2) of *Chydorus sphaericus* on various macrophytes.

Date @	1 9 7 6			1 9 7 7										
Plant	9J	29J	26A	2J	19J	2A	12A	15A	19A	22A*	23A	30A	6S	29S
Myriophyllum	3836	2505	2316	2468	3300	3096	1511	1888	813	852	1378	456	376	136
Scirpus	318	38	0	46	594	682	0	0	112	13	123	57	167	23
Najas	782	395	166	622	-	-	-	-	-	437	-	-	-	272
P. pectinatus	184	118	47	64	-	-	-	-	-	643	-	-	-	62
P. praelongus	242	242	116	163	-	-	-	-	-	25	-	-	-	45
Significance of *Myrio-Scirp* Comparison	$0.10^{\S}$	$0.10^{\S}$	$0.10^{\S}$	$0.05^{\S}$	0.17^{Ψ}	0.17^{Ψ}	0.17^{Ψ}	0.17^{Ψ}	0.17^{Ψ}	0.17^{Ψ}	0.17^{Ψ}	0.17^{Ψ}	0.17^{Ψ}	0.17^{Ψ}

@ J = July; A = August; S = September.
* 22A sample taken at night (2230-2400 hrs); all others taken during daylight (0930-1230 hrs).
§ = Mann-Whitney U-Test of means.
Ψ = Fisher's Exact Probability Test of medians.

Lake, the density of Chydorus sphaericus is greater on Myriophyllum plants than on Scirpus. The remainder of this study consists of a number of attempts to explain the causes of this differential distribution.

Substrate Morphology

Quade (1969) has reported some success in correlating an assemblage of particular species of chydorids with a particular plant form (e.g., fine-leaved submersed, floating leaved, etc.). Fryer (1968) elucidated the functional morphology of a number of species of chydorids and showed that individual species are adapted to various microhabitats to different degress. For example, he showed that Alonella exigua and especially Graptoleberis testudinaria were particularly adept to clinging to the underside of horizontally oriented surfaces. While he described C. sphaericus as a generalist, I felt that the differences in density of this animal on different macrophytes might be most easily explained as being due to differential ability to cling to and feed from substrates of various geometrical configurations. Specifically, the surfaces of Scirpus plants are essentially entirely vertical in orientation, while the finely-divided leaves of Myriophyllum extend horizontally from the vertical stem.

Accordingly, an in situ experiment was devised to test this hypothesis indirectly, assuming that the density differences reflect differences in suitability between various substrates. In order to test only for differences in the shape of the substrate, artificial plants were used. It was assumed that differences in predatory regime, chemical attractants or repellants, etc., would be negligable if the same materials were used for construction of all artificial plants and the entire experiment were set up in a small, uniform area. Food supply, however, presents a potentially confounding variable. Studies on orientation of glass slides (Castenholz 1961; reviews in Cooke 1956, Slàdečkovà 1962, Wetzel 1964; and Wetzel, personal communication) have shown that horizontally oriented surfaces support up to six times as much material as vertically oriented ones, including much detritus and unattached material. Presumably this relationship holds for different kinds of natural surfaces as well, but no one seems to have studied this. Since detritus is one food source for chydorids (see General Discussion) this would seem to favor higher densities of *Chydorus* on *Myriophyllum* plants, with their many horizontal leaves. Thus, in this experiment, higher densities of *Chydorus* on *Myriophyllum*-type than on *Scirpus*-type plants could be due to either the orientation of the surface itself or to secondary effects on food supply.

Plastic aquarium plants (Penn-Plax, Inc., Gardencity, N. J.), consisting of *Myriophyllum*-like leaf whorls on plastic tubing were used to simulate this substrate. By cutting off the leaflets, *Najas*-like plastic plants were made. Finally, by cutting some of the plastic tubing into thin strips, a simulated *Scirpus* plant was made.

Four individual plastic plants of each type were randomly placed in a 3 X 4 grid (approximately 0.5 m between each plant) in a uniform *Chara* spp.- *Najas* bed at 3.5 m depth in the study area. The plants were anchored with small pieces of brick, and small labelled pieces of styrofoam were attached with thread to the tops to provide the proper vertical orientation and for identification. The experiment was set up on 1 July, 1977. Allowing time for colonization of the surfaces, two of each type were randomly selected and sampled on 19 July and again on 2 August. Concurrent duplicate samples of real *Myriophyllum*, *Najas*, and *Scirpus* were taken for comparison.

If substrate morphology (in the sense of leaf shape and orientation) is an important determinant of the distribution of *Chydorus*, then the ranking of densities of these animals on the plastic plants should be similar to that on the analogous real plants. An expected ranking was generated from the results of analysis of the real plants, and was compared to the observed ranking of the plastic plants using Spearman's Rank Correlation Coefficient (Siegel 1956). Equality or inequality signs within rankings were determined by comparison of medians using Fisher's Exact Test (Bradley 1968). Results are presented in Table 3.

There is no statistically significant correlation between the rank orders of real and plastic plants, i.e., the animals are treating the real and plastic substrates differently. Since plastic *Scirpus* plants supported a higher density of *Chydorus* than plastic *Myriophyllum*, it seems reasonable to conclude that the shape of a natural *Myriophyllum* plant is not the feature responsible for the regularly observed chydorid density. These results are also contrary to the expected result if quantity of food were a major force in determining *Chydorus* distribution, since the total amount of detritus was greater on the *Myriophyllum*-type plastic plant (personal observation). An alternative explanation might be that there exist qualitative differences in the periphyton associated with different experimental and control substrates. I had hoped to analyze samples in this regard, but difficulties with preservation techniques (see General Methods) made this impossible. The following section, while it suffers from the same

Table 3. Comparison of real and artificial substrates using Spearman's Rank Correlation Coefficient (r_s).

Date	Substrate	Mean Density (#/m^2) of *Chydorus*	Ranking	r_s	Probability of Correlation
19 July 77	*Myriophyllum*(M)	3300	M > S ≈ N	0.5	0.33
	Najas (N)	320			
	Scirpus (S)	594			
	Plastic "M"	380	"S" > "N" ≈ "M"		
	Plastic "N"	580			
	Plastic "S"	2975			
2 Aug. 77	*Myriophyllum*(M)	3096	M > S ≈ N	0.32	< 0.33
	Najas (N)	361			
	Scirpus (S)	682			
	Plastic "M"	363	"S" > "N" > "M"		
	Plastic "N"	904			
	Plastic "S"	3448			

shortcoming, deals with one aspect of the quality of food resources.

The Effect of New Surface

One of the qualities of a surface that is important to colonizing bacteria and algae has to do with the age or condition of the surface with regard to previous colonizers. When using artificial substrates, the time of exposure is tailored to the objectives of the study in order to allow for a succession of periphytic organisms up to a mature assemblage that is similar to naturally occurring ones. This same process occurs on new growth of natural plants.

It is possible that herbivorous animals like *Chydorus sphaericus* prefer particular stages in the succession. The results of the previous section seem to refute this; although the several different plastic plants were of equal ages, and presumably supported similar periphyton assemblages, there did exist significantly different *Chydorus* densities between them. However, although the ages of the plastic plants were equal, the stages of development of the periphyton may have differed, owing to dissimilar colonization rates of surfaces that differ in orientation. The unfortunate lack of periphyton samples for analysis precludes a definitive statement on this point.

When the substrates to be compared are living organisms of different species, further complications are introduced into any consideration of the qualities of the attached flora. For example, during regular sampling, it was noticed that, due to their different life habits, *Myriophyllum* and *Scirpus* present surfaces of very different natures to periphytic organisms. *Scirpus*, at the depths involved in this study, is a perennial plant. Much of the total surface is heavily encrusted with a marl-epiphyte complex (Wetzel 1975); new growth is not extensive and seems to be complete by early to mid-July, after which the new shoots also become increasingly encrusted (Keen 1976). In contrast, *Myriophyllum* is an annual, and continuously grows at its apices through the summer. Older (deeper) portions of the plant develop an increasingly heavy marl-epiphyte complex.

The possible significance of this difference is indicated in an observation made by Lang (1970): he found that on *Myriophyllum* plants in Lake West Okoboji, Iowa, the density of *C. sphaericus* (and most other chydorids) was greatest on the top 10 cm and decreased rapidly on the lower sections.

An experiment was set up to test the direct or indirect role of new surface on the distribution of *C. sphaericus* in Lawrence Lake. Two uniform areas in each plant bed (*Myriophyllum* and *Scirpus*) 0.25 m^2 in extent (0.5 m square) were selected and marked. One area of each bed was designated the control with no manipulation. In the other (experimental) area, the surfaces of all plants were manually cleaned of their marl-epiphyte coatings, care being taken not to injure the plants. This was much more easily and completely accomplished with the *Scirpus* plants, but even the more delicate and complex experimental *Myriophyllum* plants were markedly cleaner than the controls. The experiment was set up on 9 August, 1977; duplicate samples of control and experimental plants of both species were taken on 12, 15, 19, 23, and 30 August and 6 September.

If the amount of new surface alone is an important factor in controlling the distribution of *Chydorus*, the expected ranking of plant species by density of animals would reflect the proportion of new or clean surface on the plant:

Experimental _Myriophyllum_ (ME) ≈ Experimental _Scirpus_ (SE)
> Control _Myriophyllum_ (MC) > Control _Scirpus_ (SC). (1)

Another possibility makes use of information from the previous section, where plastic _Scirpus_ plants supported higher densities of _Chydorus_ than did plastic _Myriophyllum_. Then, if both the amount of new surface and the substrate morphology are important, the expected ranks, by density of _Chydorus_ would be:

$$SE > ME > MC > SC. \tag{2}$$

As time passed and the marl-epiphyte complex built back up, it was expected that the observed ranking would revert back to:

$$MC \simeq ME > SC \simeq SE. \tag{3}$$

Results are presented in Table 4. Signs of inequality were obtained using Fisher's Exact Test for differences between medians, and the correlation between the observed and expected rank orders was tested using Spearman's Rank Correlation Coefficient (Siegel 1956).

The results show little correlation between the observed and the first two expected rankings, and a very rapid (within 6 days) attainment of high correlation with the third, indicating that the state of the marl-epiphyte complex does not account for the distribution of _Chydorus_. In general, any _Myriophyllum_ plant always supported a greater density of _Chydorus_ than any _Scirpus_ plant. It was not until three weeks after the start of the experiment that the experimental _Myriophyllum_ plants

Table 4. Analysis of observed and expected (1,2,3) rank orders of macrophytes by density (#/m^2) of *Chydorus sphaericus*, using Spearman's Rank Correlation Coefficient. Critical value (n=4;α=.05)=1.

Date	Plant*	Mean Density	Observed Rank Order	r_{s1}	r_{s2}	r_{s3}
12 Aug.	ME	794	MC > ME > SE ≃ SC	0.06	-0.11	0.94
	MC	1511				
	SE	56				
	SC	0				
15 Aug.	ME	635	MC ≃ ME > SE ≃ SC	0.24	0	1.0
	MC	1888				
	SE	120				
	SC	0				
19 Aug.	ME	731	MC ≃ ME > SC > SE	-0.06	-0.32	0.94
	MC	813				
	SE	0				
	SC	112				
23 Aug.	ME	1277	MC ≃ ME > SC ≃ SE	0.24	0	1.0
	MC	1378				
	SE	97				
	SC	123				
30 Aug.	ME	695	ME > MC > SC ≃ SE	0.39	0.11	0.94
	MC	456				
	SE	27				
	SC	57				
6 Sept.	ME	428	ME > MC > SC ≃ SE	0.39	0.11	0.94
	MC	367				
	SE	107				
	SC	167				

* ME = Experimental *Myriophyllum*; MC = Control *Myriophyllum*; SE = Experimental *Scirpus*; SC = Control *Scirpus*.

supported a higher density than the controls (Fisher's Exact Probabilty = 0.21), even though by then the plants were very similar in appearance and presumably in the assemblage of bacteria and algae they supported. The differences between the controls and experimental *Scirpus* plants were expected to be the most drastic, yet only once were there any significant differences (19 August, $p = 0.17$), and then the controls ranked ahead of the experimental plants.

Thus, cleaning the marl-epiphyte complex from the surface of these plants had little effect on the density of *Chydorus* other than a slight reduction. It seems, not surprisingly, that the plants act as more than just inert surfaces, and are somehow involved in determining the distribution of *Chydorus* through some biological means. Unlike those in the previous section, this experiment does not control for equivalence of food organisms, chemical exudates, or predation pressure. The roles of food and chemical excretions by the macrophytes or their associated algae in determining the distribution of *Chydorus* may be complimentary rather than antagonistic (see General Discussion). Although such information is essential to a complete understanding of the situation, it is not included in the present study.

Alternatively, it is possible that the results of the present experiment are not due to differences in food quality (or chemical excretions) at all, but instead are imposed upon the chydorid population by predators. That is, predators of various sorts may be feeding on *Chydorus* more heavily in *Scirpus* than in *Myriophyllum* beds, and are unaffected by the amount of marl present. Before further analysis of the role of food can be justified, some basic elucidation of the relative importance of predation is necessary. The next section details some observations relevant to this topic.

Aquaria Observations

In an effort to get first-level information about the importance of predation relative to food and/or chemical effects, relatively predator-free laboratory situations were set up for observation. Five replicate, large (29 gal; 74 cm X 30.5 cm X 40.5 cm) aquaria were erected in the laboratory facility at the Experimental Ponds site at the Kellogg Biological Station. The first three aquaria were filled with water obtained from Lawrence Lake, while the last two were filled with water from an on-site reservoir. All the water was filtered through a 74 μ sieve to remove invertebrates. The aquaria were continuously, lightly aerated, and exposed to a 14 hour light-10 hour dark cycle.

Myriophyllum and *Scirpus* plants were collected from Lawrence Lake. No attempt was made to keep the animals associated with these plants; in fact, it was hoped that as many as possible would remove themselves during collection. The plants were not handled vigorously however, since as much natural algae and bacteria as possible were desired to inoculate the aquaria, helping to insure food conditions as natural as possible.

Although there were varying numbers of potential invertebrate predators (hydras, some *Chaetogaster* spp.) and potential competitors (other chydorids, notably *Camptocercus rectirostris* Schoedler, *Graptoleberis testudinaria* Fischer, and small *Alona* spp.; copepods; snails) in the aquaria, the numbers were small relative to nature in most cases. The one aquarium that had large numbers of hydras (#2) produced results not notably different from the others (see below).

Therefore, the effect of animals other than Chydorus sphaericus was considered negligable.

Six Myriophyllum and six Scirpus plants were anchored in each aquarium with small pieces of brick. The aquaria were then left undisturbed for 1 to 3 weeks to allow the plants to adjust and the food organisms to recover and build up their populations. Next 600-1,000 C. sphaericus were seperated from laboratory cultures and added to the aquaria. Allowing 2-4 days for the animals to adjust, the plants were then examined through the side of the aquarium using a dissecting microscope at 6X, and the number of Chydorus seen on each plant were recorded. These observations were repeated 3-5 days after initial observations.

Tests with a very small aquarium, in which the entire volume was visible with the microscope, indicated that 46-51% of the Chydorus actually on a plant were seen with this method, with little difference in visibility between the macrophyte species used. While generally only 7 - 15% of the total number of Chydorus in a aquarium were seen, this was usually more than 95 individuals, which I consider an adequate sample size. The major exceptions were the second observations of aquarium #4 (95 individuals, approximately 2% of total Chydorus) and #5 (79 individuals, approximately 34% of total Chydorus), but these too are acceptable samples. Thus, this technique provides results that are considered representative samples.

At the termination of each setup, the plants were removed and the aquarium drained through a 143 μ sieve. The plants were rinsed as before, with all Chydorus collected on the sieve. The animals so collected were anesthetized, preserved, and enumerated as before (see

General Methods). Plants were also treated as before, so that all observations of Chydorus could be expressed as numbers per square meter of plant surface. Winter buds produced in the last aquaria were not included because they were not included in the plants used to establish the dry weight - surface area regressions, and because Chydorus were never seen on them.

These animals are motile, and those added were capable of sampling all environments within the aquarium in the time before observations were begun. Thus, we may regard the relative density of Chydorus observed on each plant as a measure of the relative amount of time spent on that plant by an average individual. Further, we may use the average density as a measure of the relative attractiveness of a macrophyte to an average chydorid. The nature of this attraction is unknown, but, as discussed previously, is probably either the food associated with each plant or some chemical attractant (or repellant).

The densities of Chydorus on each species of macrophyte were compared using the Mann-Whitney U-Test (one-tailed)(Sokal and Rohlf 1969). Means for each plant species on each day of observation were compared, as were the overall means for each plant species across all aquaria, summed separately over the first and second observations. The means and results of comparisons are presented in Table 5.

Of the total of ten comparisons (two observations in each of five aquaria), only two yielded means that were not significantly different between macrophyte species at the 0.10 level. The overall comparisons were highly significantly different ($\alpha < 0.005$). Thus, just as in the lake, Myriophyllum plants in the relatively predator-free aquaria harbor greater densities of Chydorus than do Scirpus plants. However,

Table 5. Comparison of mean densities (# / m^2) of <u>Chydorus sphaericus</u> on <u>Myriophyllum</u> (M) and <u>Scirpus</u> (S) plants in relatively predator-free aquaria, using the Mann-Whitney U-Test.

Aquar. #	Plant	1st Observation density	1st Observation U-value	1st Observation signif.	2nd Observation density	2nd Observation U-value	2nd Observation signif.
1	M	845	36	0.005	1813	36	0.005
	S	201			186		
2	M	1368	27	0.10	1675	29	0.05
	S	883			1120		
3	M	177	29	0.05	330	31	0.025
	S	58			92		
4	M	184	16	n.s.	362	21	n.s.
	S	224			209		
5	M	787	29	0.05	431	31	0.025
	S	363			185		
All	M	688	601.5	0.005	941	670.5	0.005
	S	349	t_s=2.78		359	t_s=3.56	

the fact that two of the laboratory comparisons were not significantly different (at the 0.1 level), plus the fact that the magnitude of the differences between macrophytes are lower (Mann-Whitney U-Test, $0.005 > \alpha > 0.001$) in the lab than in the natural setting (see Tables 2 and 5) suggest that predation may have a greater effect in the field.

Another analysis of the data was performed, producing further insight. By comparing the <u>changes</u> in density of <u>Chydorus</u> within plant species between the two observations in each aquarium, to the change in population size in the entire aquarium, one can get some idea of how the attractiveness of a macrophyte changes as the population grows.

The chydorid population in each aquarium has a growth rate (or in the case of #5, a decline rate). Assuming this growth to be exponential, we can calculate, for each aquarium : (next page)

$r = (\ln N_t - \ln N_0) / t$, where:

r = population growth rate (number X individual^{-1} X day^{-1}),

N_0 = initial population size (number of chydorids added),

N_t = final population size, and

t = number of days between addition of chydorids and termination of aquarium.

Similarly, a rate of change of density of Chydorus on each plant species in each aquarium can be calculated. For Myriophyllum:

$r_m = (\ln NM_t - \ln NM_0) / t'$, where:

r_m = rate of change of density of Chydorus on Myriophyllum,

NM_0 = average density of Chydorus on Myriophyllum plants on first observation date,

NM_t = average density of Chydorus on Myriophyllum plants on second observation date, and

t' = number of days between observations.

An analogous rate of density change (r_s) can be calculated for Scirpus.

Note that, due to the fact that individuals can move around, it is impossible to calculate a population growth rate for animals associated with a particular macrophyte. Rather, by using density of Chydorus as a measure of attraction to a plant species, the rate of change of attractiveness of a plant is calculated. If either r_m or r_s is greater than r for an aquarium, this indicates that the average chydorid is spending a greater proportion of its time on Myriophyllum or Scirpus as the population as a whole changes in size. Notice also that, since the aquarium itself contributes to the total substrate surface area available to the animals, there is no inherent reason why r_m and r_s should be directly or inversely related.

The various growth rates for each aquarium are presented in Table 6 (see Appendix B for the data used in these computations). Aquarium #4 was omitted because the mean chydorid densities were not significantly different between plants (see Table 5), although this aquarium otherwise does not seem exceptional. Notice that $r_m > r$ in 2 of 4 comparisons, $r_s > r$ only once, and $r_m > r_s$ three times. Thus there is a trend for Myriophyllum to be incresingly preferred over Scirpus, under conditions of both population growth and decline. One possible explanation of these trends is that bacterial growth rates are greater on Myriophyllum than on Scirpus, producing a generally greater source of food on the former. This possibility is examined in more detail in the General Discussion.

Table 6. Rates of population increase (r) and rates of increase of density of Chydorus sphaericus on Myriophyllum (r_m) and on Scirpus (r_s) plants in several aquaria.

Aquarium	r	r_m	r_s
1	0.189	0.191	-0.019
2	0.269	0.050	0.059
3	0.015	0.125	0.092
5	-0.134	-0.123	-0.135

In any event, the conclusion that can be drawn from these aquaria studies is that the general dichotomy of distribution of Chydorus between these macrophytes occurs under relatively-free laboratory conditions as well as in the lake. This supports the contention that the animals are responding primarily to some food (or chemical) difference. However, the more equivocal nature of the lab results indicates that predation may have an additional effect in the lake.

GENERAL DISCUSSION

This study was undertaken in an attempt to delineate the factors responsible for the observed distribution pattern of *Chydorus sphaericus* within Lawrence Lake. It has shown that uneven distribution between macrophytes cannot be explained simply by variation in surface area between macrophyte species, nor does the gross morphology of the substrate seem to be directly involved. However, there is a suggestion from the latter experiments that variation in food quality may be important. This could be because different surface orientations support different kinds of periphytic communities (Cooke 1956, Castenholz 1961, Slàdečkovà 1962, Wetzel 1964).

Further experiments with artificially cleaned natural surfaces suggested that a dominant role in determining *Chydorus* distributions is played by the macrophyte itself, either directly through excretions or indirectly through qualitative differences in periphyton or through differences in predatory regime between plant beds. Experiments with relatively predator-free aquaria supported this viewpoint: distribution of *Chydorus* within aquaria was similar to that in the lake, but the dichotomy between *Myriophyllum* and *Scirpus* was not so consistant, suggesting that predation may enhance the distributional trends in the lake. A discussion of information related to this idea and possible mechanisms for the action of these three factors follows.

Chydorus feeds by scraping small particles off of submerged surfaces; it cannot filter feed (Fryer 1968, Smirnov 1971b). The nature of the food is not well known, but it includes attached algae and detritus. It is most likely that the nutritional value of the latter is due to its bacterial flora; Saunders (1969) states that detritus is more refractory to digestion by zooplankton than are bacteria. Conversely, the bacteria associated with a detrital particle varies, depending on the particle's source, condition, and so on (Wetzel 1975). A large amount of detritus does not necessarily represent a good food source for *Chydorus* if the material is highly refractory. This may explain the rather anomalous results of the Substrate Morphology experiments, i.e., the fact that although the plastic "*Myriophyllum*" plants had much more detritus than plastic "*Scirpus*", the former had fewer *Chydorus* (per square meter) than the latter.

Bacteria do not necessarily need to be ingested with a detrital particle to be useful to *Chydorus*: Smirnov (1971b) cultured these animals very successfully on bacteria alone. In a lake, many macrophytes and algae excrete organic compounds (Wetzel 1969, Fogg 1971, Wetzel and Manny 1972, Hough and Wetzel 1975) that can be used by attached algae and especially bacteria for growth (Wright and Hobie 1966, Allen 1969, Wetzel and Allen 1972). While it seems that excretion rates and epiphyte assemblages differ between emergent, floating leaved, and submerged macrophytes (Allen 1971, Wetzel 1975), there is little comparative data within these groups. Hough and Wetzel (1975) reported that *Scirpus subterminalis* has lower excretion rates for several organic compounds than does *Najas flexilis* (which supports the second highest density of *Chydorus* after *Myriophyllum* - see Table 2). It is also suggestive that *Myriophyllum* appears to be especially leaky with regard to some inorganics, notably potassium (Wetzel, personal communication). It is possible, then, that Myriophyllum plants support a better epiphytic flora than do Scirpus plants, and so the former represent better feeding sites for Chydorus. It must be stressed that much of this is circumstantial and requires more information on excretion of dissolved organics by various macrophytes as well as the epiphytic flora's response.

Furthermore, the suitability of different food sources for the growth and reproduction of Chydorus must be assessed before this scheme can be adequately evaluated. In this regard, one might make use of the fact that some Cladocera have been shown to respond to varying food levels through egg production (Green 1956, Hall 1964, Kerfoot 1975). Chydorids are limited in their response in that they can carry a maximum of two eggs (except Eurycercus lamellatus). Even so, egg ratios (# eggs / mature female) were calculated for the Chydorus in each plant bed during July, 1977 (the period of population steady state) and late August (the period of decline) (Table 7).

Table 7. Egg ratios (E = #eggs / mature female) for Chydorus sphaericus in two plant beds during July and August, 1977.

Plant Bed	Time Period	Total Indiv. Examined	# Mature Females	Total # Eggs	E
Myriophyllum	late July	100	67	72	1.08
	late Aug.	104	72	70	0.97
Scirpus	late July	22	14	14	1.0
	late Aug.	14	10	4	0.4

Comparison of these results shows that the only noticeable difference is a lowered value in August in Scirpus. This indicates that variation in food supply among the two plant beds may be responsible for the observed density differences in August. However, it does not explain the existance of difference in density of Chydorus in July, nor the population decline in both plant beds concurrently. It should be pointed out that visiblity-selective predation (Zaret 1972) of egg bearing females could also produce these differences in egg ratios if the predatory regime differs between plant beds.

Future studies to further explore this problem might include the following. First, macrophytes of several species could be grown in single species stands under predator-free conditions in laboratory and/or field situations and the response of the Chydorus populations (as well as the food organisms) determined. This would provide stronger evidence on the question of macrophyte-food source effects. Alternatively, one could take samples of periphyton concurrently with the animal samples, and analyze the epiphyte composition and biomass. Statistical treatment of these results could produce associations between the animals and specific food resources. Laboratory populations could be cultured on different foods based on these results to quantify more precisely the benefits accruing to selective feeders. Finally, a series of field studies using radioactive tracers could provide much insight into natural production rates of bacteria and epiphytes associated with particular macrophytes , and into utilization of these food organisms by the chydorids. All such experiments would be most meaningful, at least initially, in the absence of predators.

The effect of dissolved organic substances on aquatic animals are only slightly known (Beauchamp 1952 (in Zaret 1972), Katona 1973, Griffiths and Frost 1976, Poulet and Marsot 1978), but it is apparent that they are potentially very important in a variety of ways. In the present context, if Myriophyllum has higher excretion rates than Scirpus (as already discussed), Chydorus might simply be reacting positively to this. A similar phenomenon has recently been reported for a marine harpacticoid copepod (Hicks 1977). However, the presence in Lawrence Lake of large amounts of monocarbonates that strongly adsorb organic compounds and remove them from the water (Wetzel and Allen 1972) makes such a scheme unlikely. Furthermore, even if it were possible, it is unlikely that the dissolved material itself has any direct value to the animals (Saunders 1969, Seepers 1977). Rather, it would seem that the ultimate attraction would be the food with which such dissolved organics would be associated.

As has already been stated, the aquaria studies performed in this study suggested a subordinate role for predation in producing the observed distribution of Chydorus. That food and predation could act in a complimentary fashion is suggested by several sets of results reported above, that could be explained by either alternative. While there is some limited evidence that predation by invertebrates (Goulden 1971) or vertebrates (Keen unpublished manuscript) may regulate population sizes of chydorids within a lake, there are no data directly pertinant to the question at hand. The following discussion of the potentiality of differing predation regimes between plant beds is culled from very limited data from this and other studies on a variety of topics by other investigators working in Lawrence Lake.

Potential invertebrate predators of C. sphaericus include tanypodine midges, some caddisflies, odonates, hydras, and oligochaete worms of the genus Chaetogaster (Roback 1969, Goulden 1971, personal observation). In many cases, these predators were recorded during analysis of samples in the present study. These data were used to prepare graphs of population density of Chydorus and density of all invertebrate predators in each plant bed over the summer of 1977 (Figure 3). It can be seen that, in August, there were more predators in Scirpus than in Myriophyllum ($\alpha = 0.05$, Mann-Whitney U-Test). This coincides with the period of maximum decline of the Chydorus population, and may be a contributing factor to the distribution of the chydorids. It is by no means the complete story, however, since the decline of Chydorus in Myriophyllum is still unexplained.

Furthermore, in the present study, of the many (∿100) tanypods examined, only two had Chydorus in their guts. Rarer predators also contained few Chydorus. Finally, the single night sample taken showed relatively higher densities of Chydorus in Scirpus and lower in Myriophyllum than normal, while typical values were obtained the next day (see Table 2). This suggests that the normal daytime pattern was established after visual predators (fish) began to feed. Keen (unpublished manuscript) attributes the population declines he observed in Lawrence Lake chydorids to fish predation.

Potential vertebrate predators of Chydorus include many small fish of various species (Costa and Cummins 1972, L. Wilsmann and E. Werner personal communication). In Lawrence Lake, the primary predators are small (<50 mm) bluegills (Lepomis macrochirus) and shiners of the genus Notropis (L. Wilsmann personal communication). Werner et al. (1977) found the shiners to be limited to the shallow Scirpus bench, which

Figure 3. Density (# / m^2 plant surface area) of *Chydorus sphaericus* and invertebrate predators in two plant beds during the summer of 1977. Symbols represent individual observations and lines connect means.

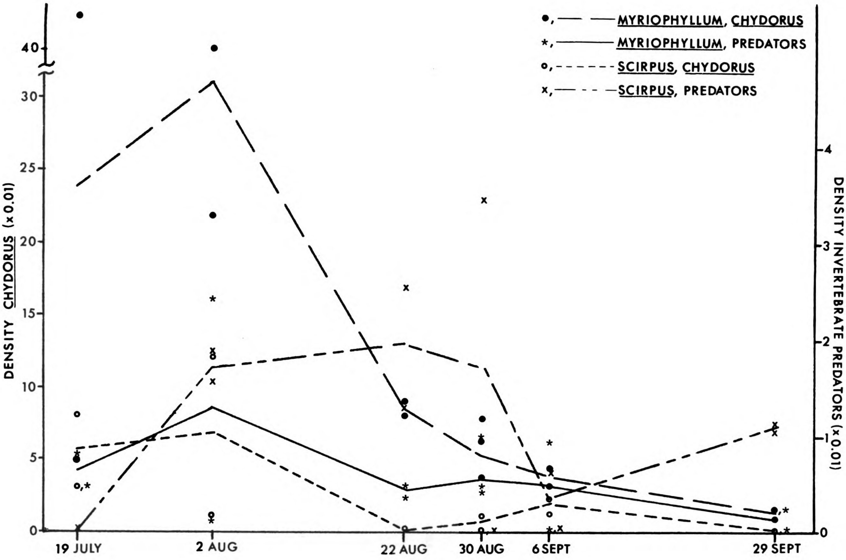
●, — — MYRIOPHYLLUM, CHYDORUS
*, ——— MYRIOPHYLLUM, PREDATORS
o, - - - - - SCIRPUS, CHYDORUS
x, — - - — SCIRPUS, PREDATORS
DENSITY CHYDORUS (x 0.01)
DENSITY INVERTEBRATE PREDATORS (x 0.01)
40
30
25
20
15
10
5
0
4
3
2
1
0
19 JULY
2 AUG
22 AUG
30 AUG
6 SEPT
29 SEPT

FIGURE 3.

excludes them from the present study area, and the bluegill to be the dominant species in the deeper littoral. Hall and Werner (1977) explored the distribution of the bluegills further and found that, in late June, the small (<50 mm) ones are in dense *Scirpus* and *Chara* beds at several meters depth. By late July, these fish are getting larger and moving into the water stratum above the *Scirpus* beds, which would include the more open *Myriophyllum* areas. Finally, R. G. Werner (1967) noted that the bluegill fry in Crane Lake, Iowa, return to the littoral zone in early August. This pattern has also been noted in Lawrence Lake (Hall and Werner 1977, L. Wilsmann personal communication). Thus, these small fish are almost constantly found in the *Scirpus* beds while larger bluegills, which would eat fewer of the small *Chydorus*, are associated more with the *Myriophyllum* beds.

Evidence that bluegill predation is actually different between plant beds is indirect. Use can be made of evidence that the small bluegills feed selectively on larger *Chydorus* (from comparison of the size distribution of *Chydorus* in fish guts with that in concurrent resource samples - data and samples supplied by L. Wilsmann). Whether these fish are actively seeking only larger *Chydorus* and neglecting the smaller ones or just cannot see the smaller prey as well is not known. In either case, the effect is the same: the proportion of small *Chydorus* in the guts is noticably smaller than the proportionof the same sized individuals in the resources, and the maximum size of *Chydorus* in the guts is larger than the maximum found in the resource samples.

If predation by smaller bluegills is significantly more severe in *Scirpus* beds than in *Myriophyllum*, we would expect to see differences in the size distribution of *Chydorus* in the two locations, with a greater proportion of large individuals in the latter. Cumulative size-frequency distributions of the Chydorus in both plant beds in July and late August are presented in Figure 4. The largest difference occurred in late August, when there was a reduction of juveniles in the Scirpus beds, but even this difference is not significant (χ^2 test).

Thus, there is no evidence that predation is strongly involved in producing the observed distribution of Chydorus among macrophytes. This is not unexpected because the results previously discussed (Aquaria Observations) would lead one to expect that any such effects would be subtle and difficult to detect. Conclusive studies need to be designed specifically for this question and should include a more refined analysis of the distribution and feeding ecology of the various potential predators coupled with continual monitoring of the chydorids. Specifically, one must determine the distribution of the predators more precisely, including movements on a diel and seasonal basis. Next, data on the rates of predation by the various predators would be required, also including diel and seasonal patterns and (especially for fish) the effect of foraging in different plant beds, i.e., can bluegills feed as effectively from a Myriophyllum plant as from a Scirpus plant? Finally, these predation rates, combined with the density of predators in various places at various times, must be compared to data on the distribution and growth rates of the Chydorus population, to see if the predators could be responsible for the decline of the chydorids. In addition, there might also be indirect effects to account for, such as fish eating invertebrate predators and thereby decreasing overall predation pressure on the chydorids.

In conclusion, the most probable primary reason for the different

Figure 4. Cumulative size-frequency distributions of *Chydorus sphaericus* in *Myriophyllum* (——) and *Scirpus* (- - -) beds. A. For the period 19 July - 2 August. B. For the period 19 August - 6 September. Sizes to the left of the heavy vertical lines are juveniles.

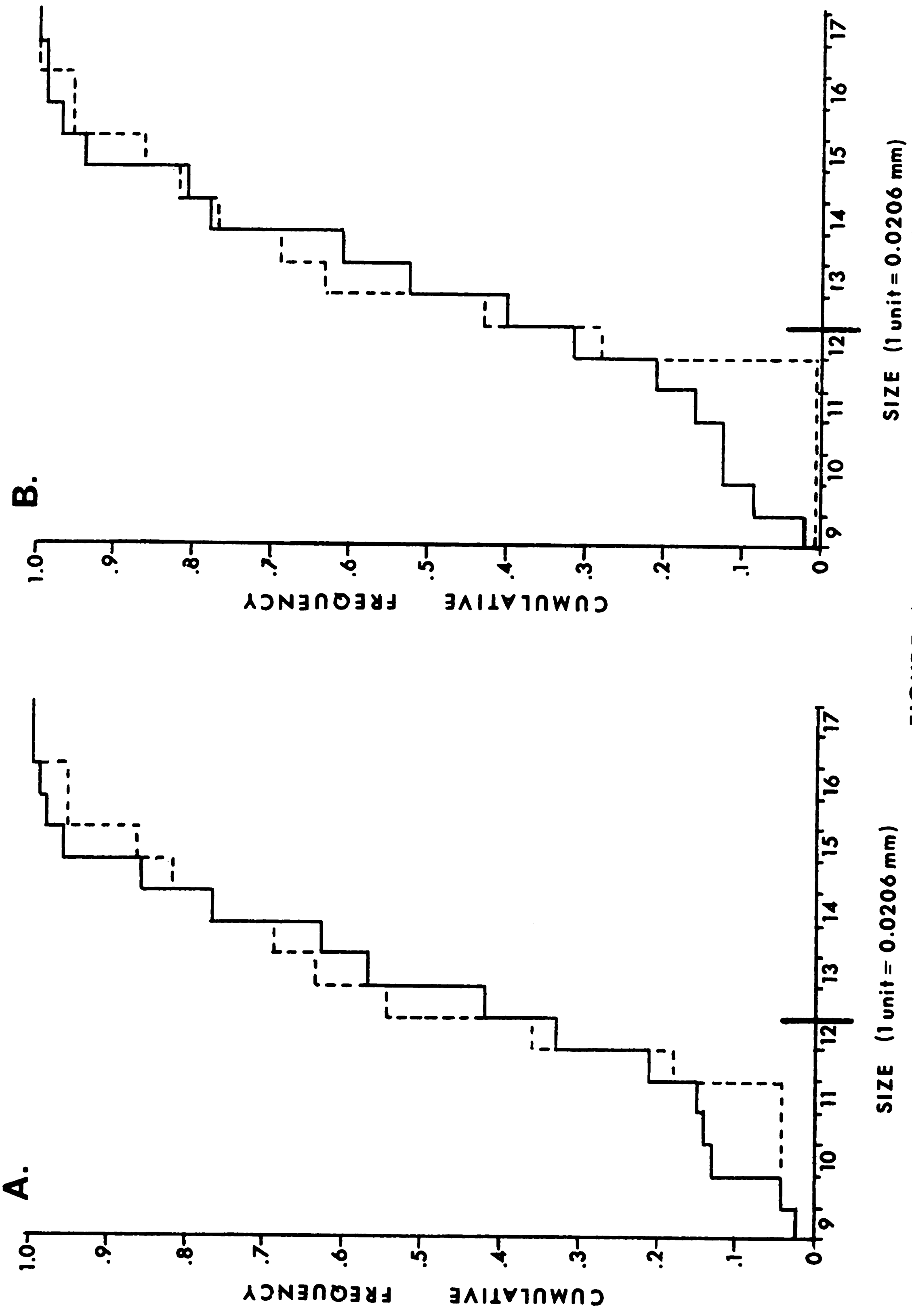
A.
B.
CUMULATIVE FREQUENCY
0
.1
.2
.3
.4
.5
.6
.7
.8
.9
1.0
9
10
11
12
13
14
15
16
17
SIZE (1 unit = 0.0206 mm)

FIGURE 4.

densities of Chydorus sphaericus between plant beds in Lawrence Lake is that it is a response to different food resources. Predation of various types may enhance these effects. The significance of this study is that it is the first of its kind undertaken with the Chydoridae and that it has shown that a full understanding of the intra- (and possibly inter-) lake distribution of these animals will require much more study of a variety of related organisms as well: the macrophytes and the condition of their associated bacteria and algae, and the distribution and feeding ecology of potential predators. Since chydorids are a basic link in many aquatic food webs, and since they are a part of a process that recycles detritus directly back into the consumer components of such webs (Smirnov 1971b), knowledge such as that gained in this study and future offshoots is potentially important for a more complete understanding (and perhaps management) of carbon flow in lakes.

Finally, studies of the ecology of individual chydorid species will provide a basis for explorations of the coexistence of related species. While it may not seem unusual to have 185 different species of chydorids inhabiting the littoral regions of the world, it is remarkable that Keen (1976) found 21 species in Lawrence Lake and not infrequently I found 10 or more species on individual macrophytes. Presumably the complexity of the structure of the littoral, with a number of macrophyte and inanimate substrates, provides many opportunities for specialization, while the diversity and abundance of food resources could also provide additional means for avoiding competition. It may also be that these populations seldom escape predatory or climatic constraints long enough to allow competitive exclusion (Hutchinson 1961). The solutions to these and similar questions must await the development of more basic ecological information on the members of the Chydoridae, which will require increasingly creative and sophisticated approaches.

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APPENDICES

APPENDIX A

DISTRIBUTION OF CHYDORIDS IN LAWRENCE LAKE,MICHIGAN, SUMMER 1976.

Table A-1. Mean proportions of the eleven most abundant chydorids of species i associated with macrophyte species j $(\bar{x}_{ij} / \sum_{j} \bar{x}_{ij}$, where $\bar{x}_{ij}$ = mean number of animals of species i / g plant species j).

Key to Animal Species

A = *Eurycercus lamellatus*
B = *Camptocercus rectirostris*
C = *Acroperus harpae*
D = *Graptoleberis testudinaria*
E = small *Alona* spp.
F = *Alona affinis*
G = *Pleuroxus procurvus*
H = *Pleuroxus denticulatus*
K = *Chydorus sphaericus*
L = *Alonella nana*
M = *Alonella exigua/excisa*

Key to Plant Species (number samples)

1 = *Myriophyllum heterophyllum* (n=3)
2 = *Najas flexilis* (n=2)
3 = *Potamogeton pectinatus* (n=2)
4 = *Scirpus subterminalis* (n=2)
5 = *Potamogeton praelongus* (n=3)
6 = *Nymphaea odorata* (n=2)
7 = *Nuphar variegeta* (n=2)

* = Actual total number of animals of species i collected on that date.

Table A-1.

Animal Species (i)

	9 July	A	B	C	D	E	F	G	H	K	L	M
Plant Species (j)	1	.64	.89	.19	.35	.22	.19	.06	.65	.79		.29
	2	.15		.35	.12	.10	.23		.21	.10	.69	
	3			.34	.17	.60	.43	.42	.05	.03	.16	.35
	4	.15	.06	.09	.18	.03	.13			.05	.14	
	5	.04	.04	.02	.17	.05	.02	.41	.08	.03	.01	.34
	6	.02	.01	.01								
	7			.01	.01	.01		.11	.02			.01
	*	130	27	926	76	403	14	39	36	1792	18	49

	22 July	A	B	C	D	E	F	G	H	K	L	M
Plant Species (j)	1	.73	.59	.29	.71	.05	.59		.55	.83	.41	.08
	2	.13	.26	.26	.05	.18	.41	.24	.36	.08		.25
	3	.03	.06	.28	.08	.56		.25	.10	.03	.20	.21
	4		.02	.01	.04	.09				.01		
	5	.10	.03	.12	.07	.11		.35		.05	.39	.45
	6	.01	.02	.03	.05			.02				
	7		.01	.01				.14			.01	
	*	21	26	180	43	120	10	79	14	521	4	70

	26 Aug.	A	B	C	D	E	F	G	H	K	L	M
Plant Species (j)	1	1.0	.61	.52	.37	.04	1.0	.05	1.0	.91		.15
	2		.10	.08		.16		.10		.04		.21
	3			.28	.13	.69		.55		.01		
	4		.20		.50	.07						
	5		.07	.05		.01		.10		.03		.62
	6			.01				.01				
	7		.02	.06		.03		.19				.02
	*	3	25	181	6	54	1	35	9	445	0	36

APPENDIX B

DATA FOR COMPUTATION OF r, r_m, AND r_s.

Table B-1. Relevant data necessary for computation of growth rates of population sizes and densities of *Chydorus sphaericus* on *Myriophyllum* (M) and *Scirpus* (S) plants in several aquaria.

Aquarium #	Total *Chydorus* Begin	Total *Chydorus* End	Total Time(d)	Densities (#/m^2) Plant	Obs 1	Obs 2	Days Between Observations
1	1000	3772	7	M	845	1813	4
				S	201	186	
2	1000	5028	6	M	1368	1675	4
				S	883	1120	
3	600	705	11	M	177	330	5
				S	58	92	
4	1000	4719	12	M	184	362	5
				S	224	209	
5	1000	230	11	M	787	431	5
				S	363	185	