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Microcrustacean Communites Along A
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# MICROCRUSTACEAN COMMUNITIES ALONG A HORIZONTAL HABITAT GRADIENT

By

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# ABSTRACT

# MICROCRUSTACEAN COMMUNITIES ALONG A HORIZONTAL HABITAT GRADIENT

By

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I explored the microcrustacean community from nearshore to offshore in Lower Crooked Lake (Barry Co., Michigan) in relation to macrophytes and associated changes of food resources and predators. A nearshore guild of microcrustaceans (*Sida crystallina*, *Simocephalus exspinosus*) primarily lived among the submersed macrophytes, an intermediate guild (*Bosmina freyi*, *Ceriodaphnia reticulata*) lived among the floating-leaved macrophytes, and an open-water guild (*Daphnia retrocurva*, *Diaphanosoma brachyurum*, *Chydorus spp.*) lived mostly in areas free of macrophytes. Some species changed their distribution along this habitat gradient on a diel or seasonal basis (e.g., *Bosmina*, *Ceriodaphnia*). Planktonic food resources changed from heterotrophic forms nearshore to more autotrophic forms offshore. Invertebrate sit-and-wait predators dominated nearshore, while cruising predators were more common in the open water.

A reciprocal transplant experiment revealed that the nearshore and intermediate guilds survive equally well when fed lilypad or open-water food resources, whereas the open-water guild performed poorly when fed lilypad resources. Hence, the food gradient may contribute to microcrustacean species segregation along this habitat gradient.

I examined the importance of macrophytes and two types of predators (fish and damselfly larvae) in determining microcrustacean community structure. I exposed a mixed lilypad and open-water zooplankton community to all combinations of these three factors using small (60 L) enclosures. Invertebrate predators did not significantly influence microcrustacean population dynamics. A second experiment looked at the effects of macrophytes and fish predators in larger (2500 L) enclosures. Macrophytes had a positive effect on the nearshore guild and, additionally, protected them from fish predation. The intermediate guild was negatively affected by macrophytes, but responded to fish in a species-specific manner in the absence of macrophytes. Hence, fish and macrophytes interacted to affect nearshore and intermediate guilds. Fish predation effects were also species-specific in the open-water guild. *Diaphanosoma* was positively impacted by fish, whereas *Daphnia* was greatly reduced by fish predation. Macrophytes had a negative impact on the open water guild and did not interact with fish.

I dedicate this dissertation to my grandmother, Mary Jane MacKenzie, and Laura Eckels
for their love of exploring, awe of nature, and never ending belief in me.

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# TABLE OF CONTENTS

# LIST OF TABLES

CHAPTER 2

# LIST OF FIGURES

## CHAPTER 1

## CHAPTER 2

# INTRODUCTION

Deep lakes in temperate regions stratify during the summer, forming distinct vertical habitats for organisms living in the pelagic zone. Vertical habitat selection by zooplankton has been well studied and is influenced by a variety of biotic (e.g., food resources, predators) and abiotic (e.g., oxygen, temperature, light) factors (Stich and Lampert 1981, Kerfoot 1985, Lampert 1989, Neill 1990, Wright and Shapiro 1990, Leibold 1991, Tessier and Welser 1991, Williamson *et al.* 1996). Shallow lakes, on the other hand, are usually vertically well mixed with respect to chemistry, predators, and food resources for zooplankton. Shallow lakes can, however, have well developed littoral zones with the density and growth forms of macrophytes changing from nearshore to offshore with increasing depth. This zonation of vegetation is believed to create horizontal gradients in the physico-chemical conditions which in turn should influence the amount and types of sestonic food available for zooplankton and other suspension-feeding animals. This zonation can also influence the presence of different types of predators (e.g., sit-and-wait versus cruising). Hence, suspension-feeding invertebrates should also exhibit horizontal zonation in lakes, although this has received little study (Smyly 1952).

In this dissertation, I focus on microcrustaceans which are active swimmers capable of choosing between habitats (Siebeck 1964, Szlauer 1973, Meyers 1980). Many microcrustaceans are suspension feeders, meaning that they forage on particles in the water column (i.e., phytoplankton, bacteria, protozoa, detritus). However, there is some evidence that species may differ in ability to forage on particular types or size classes of particles (DeMott 1989). This can lead to spatial partitioning of species if habitats differ in resource types. Habitat selection by microcrustaceans may also be driven by differential mortality rates in the different vegetative zones (Davies 1985, Jakobsen and Johnsen 1987, Gliwicz and Rykowska 1992). This may be due to the types or density of predators present or the amount of habitat complexity which can decrease predator foraging efficiency (Gilinsky 1984, Dionne and Folt 1991, Persson 1991).

The purpose of this study is to document the horizontal distribution of microcrustaceans and to explore likely ecological factors causing differences of habitat use among species. I first took a descriptive approach, examining the abundance of different microcrustacean species from nearshore (i.e., littoral) to open water offshore (i.e., limnetic) in Lower Crooked Lake (Barry Co., MI) and comparing this with the distribution of the same species in a nearby pond. The macrophyte zones in the pond are greatly compressed compared with the lake so there is a potential for easier movement between the habitats than in the lake where much greater distances separate vegetation types. In this descriptive study, I specifically explore how the macrophyte zonation relates to the physico-chemical environment, food quantity and quality, and predators. While the descriptive approach revealed how the factors covaried along the horizontal gradient in a lake, I employed an experimental approach to more directly quantify the importance of food availability, macrophyte structure, and predators in determining the distributions of microcrustaceans along this horizontal habitat gradient. Microcrustaceans include a wide variety of taxa and feeding guilds, however, I restricted my attention largely to the suspension-feeding cladoceran taxa (primarily the Daphniidae, Sididae, Bosminidae families). An appendix provides descriptive information on more benthic cladocerans (Chydoridae, Macrothricidae) and copepods.

## DISSERTATION OVERVIEW

Chapter One examines the daytime and nighttime horizontal distribution of cladoceran microcrustaceans in a lake and pond over a two-year period. I focus on seven common genera of cladoceran Crustacea (i.e., *Simocephalus, Sida, Bosmina, Daphnia, Diaphanosoma, Chydorus, Ceriodaphnia*) which potentially share similar sestonic food resources. I describe the distribution of macrophyte communities, predators, and food resources and the physico-chemical characteristics (i.e., temperature, light, oxygen, pH, conductivity, particulate organic matter) of the lake in relation to the microcrustacean distributions.

Three distinct microcrustacean assemblages were found in both Lower Crooked Lake and the pond. Nearshore, the community was dominated by *Simocephalus* and *Sida*, while the intermediate zone of the lake and pond was dominated by *Bosmina*, and the open water zones were dominated by *Daphnia* and *Diaphanosoma*. Some genera, such as

*Ceriodaphnia*, were most abundant offshore in the summer and changed to being more abundant nearshore in the fall. *Chydorus* distributions, on the other hand, differed between the pond and the lake. They were evenly distributed horizontally throughout the pond, but were primarily found in the open water zone of the lake. I observed a strong seasonal component to the distribution pattern which may be due to a combination of environmental factors.

A reciprocal transplant experiment which examined the effects of littoral versus limnetic seston on littoral and limnetic microcrustaceans is also presented in Chapter One. Food resources varied along the horizontal habitat gradient with more planktonic algae being available in the limnetic compared to the littoral zone. Not surprisingly, limnetic microcrustaceans (e.g., *Daphnia*) performed very poorly when fed littoral compared to limnetic seston, suggesting that resource quantity restricts their use of nearshore habitats. On the other hand, littoral species did unexpectedly well with either type of food suggesting that other factors, such as vegetative structure and predation, play a more important role in determining their habitat selection.

Another factor which may be important in determining habitat selection is the type of predation experienced by microcrustaceans in the different zones. I document in Chapter One a horizontal gradient of predator types: the most common macroinvertebrate predators were damselfly larvae (*Enallagma*, Odonata, Insecta*)* found in the watermilfoil zone, phantom midge larvae (*Chaoborus*, Diptera, Insecta) found in the lilypad zone, and *Leptodora* (Cladocera, Crustacea) found in the open water zone of the lake. Predation by bluegill sunfish *(Lepomis*, Centrarchidae*)* also occurs throughout this gradient and should be an important influence on the horizontal distribution of microcrustaceans.

Chapter Two presents the results from experimental approaches to explore the influence of predators and macrophytes on a mixed littoral and limnetic microcrustacean community. I first employed a short-term experiment to examine the interactive effects of macrophytes, sit-and-wait insect predators (damselfly larvae), and cruising predators (bluegill sunfish). Macrophytes and bluegill had substantial effects on the microcrustacean populations, so a longer experiment was conducted to better quantify the interaction of these two factors on the mixed microcrustacean community. This second experiment was long enough to allow the microcrustaceans to have several generations of response to the treatments. Both experiments indicated that macrophytes were beneficial for nearshore genera, while having a negative impact on offshore species. Surprisingly, macrophytes also negatively impacted the microcrustaceans from the intermediate vegetation zones. Fish negatively affected one open water genus (i.e., *Daphnia*), but positively affected another genus (i.e., *Diaphanosoma*). These two genera normally do not greatly overlap in the lake seasonally, with *Diaphanosoma* dominating in the summer and *Daphnia* dominating in the fall. The seasonal shift observed in these genera may be driven, in part, by changes in feeding intensities of bluegills from summer to fall. Genera inhabiting the intermediate vegetation zone (i.e., *Bosmina*, *Ceriodaphnia*) were positively affected by fish in the absence of macrophytes, while being negatively or unaffected by fish in the presence of macrophytes. In contrast, the nearshore genera (i.e., *Sida*, *Simocephalus*) showed the opposite response with fish predation negatively impacting them in the absence of macrophytes but not in the presence of macrophytes. Hence, the three distinct horizontal assemblages of microcrustaceans had unique responses to the combination of macrophytes and fish predation.

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# CHAPTER 1

# ENVIRONMENTAL GRADIENTS AND THE HORIZONTAL DISTRIBUTION OF MICROCRUSTACEANS IN LAKES

# ABSTRACT

1. The assemblage of suspension-feeding microcrustaceans in lakes changes along a habitat gradient from nearshore to offshore. I explored this gradient of microcrustaceans in relation to differences in macrophytes and the associated changes in water chemistry, food resources, and types of predators.

2. There was a large shift in the composition of sestonic food with a gradient of more heterotrophic seston nearshore to more autotrophic seston offshore. Sit-and-wait predators (e.g., *Enallagma spp.*) dominated nearshore and cruising predators (e.g., *Leptodora kindtii*) were more common offshore.

3. Some microcrustacean species were littoral or limnetic specialists, while others changed their distribution along this horizontal habitat gradient on a diel or seasonal basis. Distribution patterns were similar in a lake and pond which differed in extent of macrophyte habitat.

4. A reciprocal transplant experiment revealed that littoral specialists could survive equally well when fed littoral or limnetic seston, while limnetic specialists performed poorly when fed littoral seston. Food resources may be important in determining where some microcrustacean species live along this horizontal habitat gradient.

# INTRODUCTION

Spatial partitioning of shared resources is an important means of coexistence of species, and is believed to involve tradeoffs in the ability of different species to perform under different environmental conditions. A variety of both biotic and abiotic factors have been implicated in determining the boundaries of species distributions (Connell, 1961; Schoener, 1974; Soluk & Collins, 1988). One well-documented spatial pattern is the vertical partitioning of zooplankton in the pelagic zone of freshwater lakes. Different species typically segregate at different depths in the water column (Tappa, 1965; Threlkeld, 1980; Leibold & Tessier, 1991), corresponding to distinct combinations of biotic and abiotic characteristics. Biotic factors important to this vertical segregation include resources and predators (Kerfoot, 1985; Leibold, 1991; Williamson, *et al.*, 1996). Abiotic factors such as dissolved oxygen, temperature, and light can also influence the vertical distribution of species (Lampert, 1989; Wright & Shapiro, 1990; Tessier & Welser, 1991).

Although far less studied, zooplankton and related microcrustaceans are typically segregated horizontally as well as vertically in lakes. The type and abundance of macrophyte vegetation changes from nearshore to offshore with increasing depth of a lake (Hutchinson, 1975; Wetzel, 1983) and can form distinct habitats for microcrustaceans (Smyly, 1957; Rybak, Rybak & Tarwid., 1964; Shiel, 1976; Havens, 1991; Schriver, *et al.*, 1995). For example, some microcrustaceans prefer or avoid certain species of macrophytes because of the growth form of the macrophytes (Quade, 1969; Cyr & Downing, 1988; Beklioglu & Moss, 1996) or due to the release of inhibitory chemicals by the vegetation (Pennak, 1973). The type of structure provided by the macrophytes, physico-chemical properties of the water, food resources, and predators should change concurrent with changes in macrophyte composition and are expected to influence the distribution of microcrustaceans along the horizontal vegetative gradient. However, few studies have examined horizontal gradients of microcrustaceans from nearshore to offshore (but see Smyly, 1952, 1955; Gliwicz & Rybak, 1976; Beaver & Havens 1996).

Gliwicz & Rybak (1976) hypothesized that there may be tradeoffs between the competitive abilities of different species of zooplankton and their tolerance for changing physico-chemical conditions which influence their distribution within a lake. While macrophytes do affect temperature, oxygen, light, and pH (Straskraba, 1965; Kairesalo, 1980; Meyers, 1980; Carpenter & Lodge, 1986), these abiotic factors are not often measured concurrently in the littoral and limnetic zone of lakes (but see Rybak & Sikorska, 1976). Further, there is little information on the tolerance of microcrustaceans for abiotic variation typical of the littoral to limnetic gradient, nor any tests of hypotheses of shifts in competitive abilities.

Biotic factors are also likely to vary with macrophytes along a gradient from littoral to limnetic. Microcrustacean food resources can differ quantitatively and qualitatively between vegetative habitats. Phytoplankton abundance can be greatly reduced in the presence of macrophytes due to shading effects and release of allelopathic compounds by macrophytes (Hasler & Jones, 1949; Hogetsu, Okanishi, & Sugawara, 1960). Kairesalo

(1980) found that different species of phytoplankton were dominant in the littoral compared to the limnetic zone, suggesting foods of potentially varying nutritional levels for the herbivorous microcrustaceans grazing on them. It is unknown if these different phytoplankton communities affect the microcrustaceans which feed on them.

The types of predators foraging on microcrustaceans (e.g., sit-and-wait versus cruising; invertebrate versus vertebrate) might also be expected to vary along a vegetative habitat gradient. Different predators can affect microcrustacean assemblages through size and habitat specific foraging behaviors (Cryer & Townsend, 1988; Hanazato & Yasuno, 1989; Hambright & Hall, 1992). Predators dependent on mechanical cues (e.g., *Chaoborus*) are less likely to be affected by physical structure, but may be less likely to detect and capture attached prey. Fish can detect and capture both attached and more mobile prey, but perform best in well lit habitats with low physical structure (Dionne & Folt, 1991). In contrast, visually oriented insects such as damselfly larvae typically use the physical structure provided by the macrophytes as perch sites. Few studies have examined the horizontal distribution of multiple predator types in both the littoral and the limnetic zones concurrently.

This study compares the horizontal distributions of the common species of cladocerans in a lake with a large basin and extensive stands of vegetation to those in a nearby pond with a much smaller basin having greatly compressed vegetation zones relative to the lake. The pond has much reduced distances which microcrustaceans would have to travel to change habitats. I explore how the cladoceran distributions correspond to ecological factors such as macrophyte structure, abiotic characteristics of the habitats, food resources, and types of predators. While many studies have examined the impacts of predators on microcrustaceans, few have studied the effects of different natural food resources. To this end, I performed a reciprocal transplant experiment to test whether microcrustacean species respond to the difference in food resources between the littoral and limnetic zones.

## METHODS

### *Study site*

Lower Crooked Lake is a shallow (4 m maximum depth, 106 ha) mesotrophic lake (annual mean total phosphorus: 14 $\mu g\ l^{-1}$) located in southwest Michigan (Barry Co.). A winding shoreline with numerous shallow bays (Shoreline development, Ds=5.1; Marsh & Borton, 1974) allows the development of an extensive littoral zone. A much smaller adjacent pond (2.5 m maximum depth, 9 ha, Ds=1.6) was also studied. The lake and pond both contain a centrarchid-dominated fish community typical of warmwater lakes in southern Michigan (Werner *et al.,* 1977; personal observation).

Macrophyte species composition and growth forms changed in a similar way from nearshore to offshore in both Lower Crooked Lake and the pond (Fig. 1). Submersed macrophytes with short, bushy growth forms such as *Myriophyllum*, *Ceratophyllum*, and *Utricularia* were dominant along the shoreline (zone 1). Dense stands of *Nymphaea* and *Nuphar* with floating-leaved, slender-stemmed growth forms became dominant as the water became deeper (zone 2). Further from shore, the floating-leaved vegetation

Figure 1. Overhead and cross-sectional view of Lower Crooked Lake and an adjacent pond in southwest Michigan (Barry Co., Lux Arbor Preserve). Zone 1 is dominated by macrophytes with bushy growth forms (e.g., *Myriophyllum*, *Ceratophyllum*), Zone 2 by densely packed floating-leaved growth forms (e.g., *Nymphaea*, *Nuphar*), Zone 3 by sparse floating-leaved growth forms (e.g., *Polygonum*, *Potamogeton*), and Zone 4 is open water.

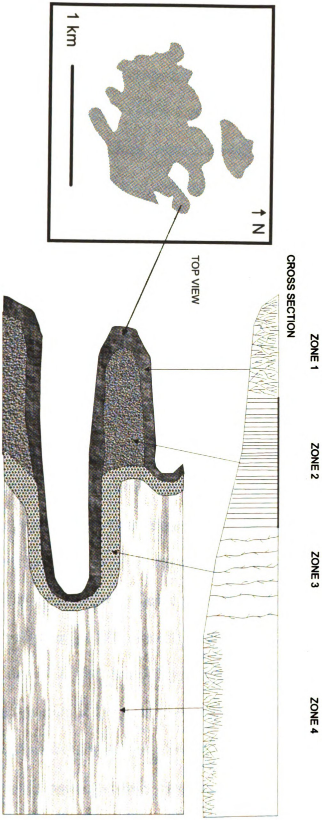

Figure 1

dominated by *Polygonum* and *Potamogeton* became more sparse (zone 3) and gradually transitioned into a water column free of macrophytes (zone 4). The zones were three to ten times as wide in the lake relative to the pond. For example, zone 1 was about 6 m wide in the lake, while being only about 2 m wide in the pond. Zone 2 was approximately 40 to 50 m minimum width in the lake and only about 4 to 5 m wide in the pond. Zone 3 was about 10 to 12 m wide in the lake compared to only 4 m wide in the pond. Each of these four vegetation zones was sampled to determine the physical and chemical characteristics of the water, as well as the distribution of microcrustaceans and their resources and predators.

### *Field Sampling and Analysis*

Stands of macrophytes are at annual peak densities during the summer, and begin to decline in density during the fall. Physico-chemical characteristics of Lower Crooked Lake were measured in 6 sites per zone in the summer (26 July) and fall (8 October) of 1993 in order to examine how these characteristics differed with seasonal changes in macrophyte densities. All measurements were performed during the mid-morning (1000-1300 hours). Dissolved oxygen (polarographic sensor) and temperature were measured at 1 m depth intervals using a YSI model 57 meter. Light was measured at 0 and 1 m depth using a Li-Cor model LI-185B flat quantum photometer and expressed as percent of surface light transmission at 1 m depth for comparative purposes. Water samples were collected in 1-l plastic bottles at approximately 0.5 m depth for determination of pH, specific conductance, and chlorophyll-*a* by *in vivo* fluorescence (Heaney, 1978).

Liter samples of water were collected from two sites per zone on 29 August 1994 for quantification of phytoplankton taxa. Samples were preserved with acid Lugol's solution and condensed by settling prior to microscopic enumeration of cells and colonies.

Quantitative samples of macroinvertebrate predators of microcrustaceans were collected using standardized sweeps with an aquatic net (650 µm mesh) through the water column. Each sweep consisted of an approximately 0.5 m horizontal movement at the surface, mid-depth, and bottom of lake down to a maximum depth of 1.5 m. Three sweeps were collected from six different sites per zone in the lake and two sweeps from four sites per zone in the pond. All samples were preserved in 95% ethyl alcohol for later counting. The most abundant macroinvertebrate predators were damselfly larvae (Coenagrionidae) which hatch from eggs in late summer, complete development in fall and spring, and emerge as adults in late spring or early summer in Michigan (McPeek, 1989). Samples were collected from Lower Crooked Lake during the summer (28 July) and fall (5 October 1993) in order to capture them at the minimum and maximum densities and from the pond on 25 August 1992 (summer). Similar distribution patterns were found in Lower Crooked Lake in the fall of 1992 (17 October), but I present only the 1993 data (see Appendix A).

Microcrustaceans living in the nearshore, thickly vegetated areas (zone 1) were collected using a clear, plexiglass tube (1.25 m long, 6.5 cm diameter). A valve attached to the top of the tube was closed off once the sediments were reached, effectively trapping the water and animals in it. Microcrustaceans living in less densely vegetated areas (zones 2-4) were collected using a collapsible tube sampler with a trap door and net attached to the bottom (Knoechel & Campbell, 1992). All samples encompassed the entire water column and the depths were estimated to the closest 25 cm. Samples were condensed through 80 μm mesh nets and preserved in sugar formalin solution for later analysis.

The capture efficiency of the two sampling methods was measured by collecting microcrustaceans from zone 2 using both methods. Zone 2 was the only area shallow enough to use the plexiglass sampler, while having sparse enough vegetation to allow the use of the Knoechel-Campbell sampler. There were no significant differences in capture efficiency for the five species commonly found in zone 2 (Hotelling's Trace F=1.82; d.f.=5, 2; p=0.391).

Microcrustaceans were collected over a two year period during mid-day in Lower Crooked Lake in the summer (7 August 1992; 23 July 1993), fall (18 October 1992; 4 October 1993), winter (17 February 1994) and spring (19 April 1994) to examine seasonal changes in horizontal distributions. Nighttime samples were also collected to measure diel changes in distributions in summer, fall, and spring (1993-1994). During 1992, two samples were collected from three different sites per vegetation zone. In 1993 and 1994, there were three samples collected from four different sites per vegetation zone, with the exception of the winter collection which had three samples collected (through ice cover) from three sites per zones 1, 2, 4 and at one site in zone 3. In order to compare horizontal distributions over different spatial scales, the summer and fall daytime samples from the lake were compared to those in an adjacent pond which had much smaller distances between vegetative zones. Two samples were collected from 3 sites per vegetation zone of the pond in both seasons (3 August, 8 October 1992). Densities of the seven most abundant cladoceran species are reported for all samples. Planktonic invertebrate predators (e.g., *Chaoborus*, *Leptodora*) were rarely captured during the day, therefore all values reported are from the nighttime samples.

### *Transplant Experiment*

The presence of macrophytes can influence the abundance and species composition of food resources. I conducted an *in situ* reciprocal transplant experiment in Lower Crooked Lake to assess the relative value of open water versus littoral food resources to both open water and littoral zone microcrustacean species. Microcrustaceans from the littoral (zone 2) and limnetic (zone 4) areas of the lake were incubated in 60-l polyethylene enclosures (2 m deep, 20 cm diameter) filled with water and food resources from zone 2 and zone 4, separately. There were four replicates of each treatment (source of animals x resource incubation location) for a total of 16 enclosures. The enclosures were placed in the zone from which the water and food resources originated (8 in zone 2 and 8 in zone 4). The water was filtered through a 130 μm mesh net to remove most macro-zooplankton, without reducing the grazeable resources. No submersed plants were included in the enclosures. Animals were stocked at natural densities in each enclosure and left for one week (16 - 23 August 1993). In order to simulate natural light conditions, the tops of the tubular enclosures in zone 2 were covered with lilypads, which were replaced throughout the week as they dried out.

Animals were collected from either zone 2 or zone 4 using an 80 μm mesh plankton net (30 cm diameter). The contents from one 2 m tow was added to each 60-l enclosure. Preliminary comparisons between a quantitative Knoechel-Campbell sampler and the 80 μm mesh plankton net allowed me to mimic natural densities of the attached and planktonic forms of microcrustaceans in the littoral and limnetic zones. Two samples from each zone were randomly collected at the beginning of the experiment to estimate initial zooplankton stocking densities. At the end of 7 days, animals from the entire enclosure were harvested using a 130 μm mesh net and preserved in sugar formalin for later counting.

Population growth rates (r) were calculated for each of the seven common microcrustacean species using the following equation:

$$r = [\ln(N_{t2}) - \ln(N_{t1})]/ 7 \text{ days}$$

where $N_{t1}$ = initial stocking density, $N_{t2}$ = final density at the end of the experiment. Multivariate analysis of variance was used to test for effects of the incubation location (i.e., the type of food the animals were fed) on the population growth rates, analyzing data for the nearshore (i.e., *Sida*, *Simocephalus*) and open-water (i.e., *Daphnia*, *Diaphanosoma*, *Chydorus*) guilds separately. A third analysis examined the intermediate guild (*Bosmina*, *Ceriodaphnia*) which inhabited both zones. In addition to testing for incubation location, this third analysis tested for effects of the source population from which animals were collected (zone 2 versus zone 4) and the interaction between incubation location and source population.

# RESULTS

## *Environmental Gradient*

Lower Crooked Lake was well mixed with uniform temperatures throughout the water column only in zone 4, and the strongest temperature gradient in zone 2 (Figs. 2 and 3). Beneath the lilypads, in zone 2, temperatures dropped almost 2°C from the surface waters to the bottom in both summer and fall indicating a weak stratification in this environment of low wind mixing and light penetration. Consequently, dissolved oxygen reached anoxic levels (<1 mg/L) near the bottom of this zone during the summer (Figs. 2 and 3).

Percent transmission of light was highest in the more open water (zones 3 and 4) and lowest in the heavily vegetated zones 1 and 2 in the summer (Figs. 2 and 3). Light transmission remained low in zone 2 in the fall while increasing in zone 1.

The pH was lower in the thickly vegetated areas (zones 1 and 2) in both summer and fall (Figs. 2 and 3). Specific conductance was higher in zones 1-3 during summer in the presence of macrophytes and lowest in the open water. In the fall, however, values were similar in all zones.

In summer, sestonic chlorophyll-*a* was lowest in zones 2 and 3 and highest in zones 1 and 4 (Fig. 2), while in fall, chlorophyll-*a* was more uniform across the four zones. The high summer chlorophyll-*a* in zone 1 may have been due to epiphytes disturbed from the dense submerged vegetation. Surprisingly, summer chlorophyll-*a* was also low in zone 3 where light levels were high.

Figure 2. Physical and chemical characteristics (mean ± S.E.) of the four vegetative habitat zones of Lower Crooked Lake in July 1993. Dissolved oxygen (mg/l) = dark squares, temperature (°C) = pentagons, light (% transmission at 1 m) = diamonds, chlorophyll-*a* = light squares, pH = circles, and specific conductivity (μmhos/cm at 25°C) = triangles. Dashed lines represent the mean total depth (m) per zone. Vegetative zones are the same as in Figure 1.

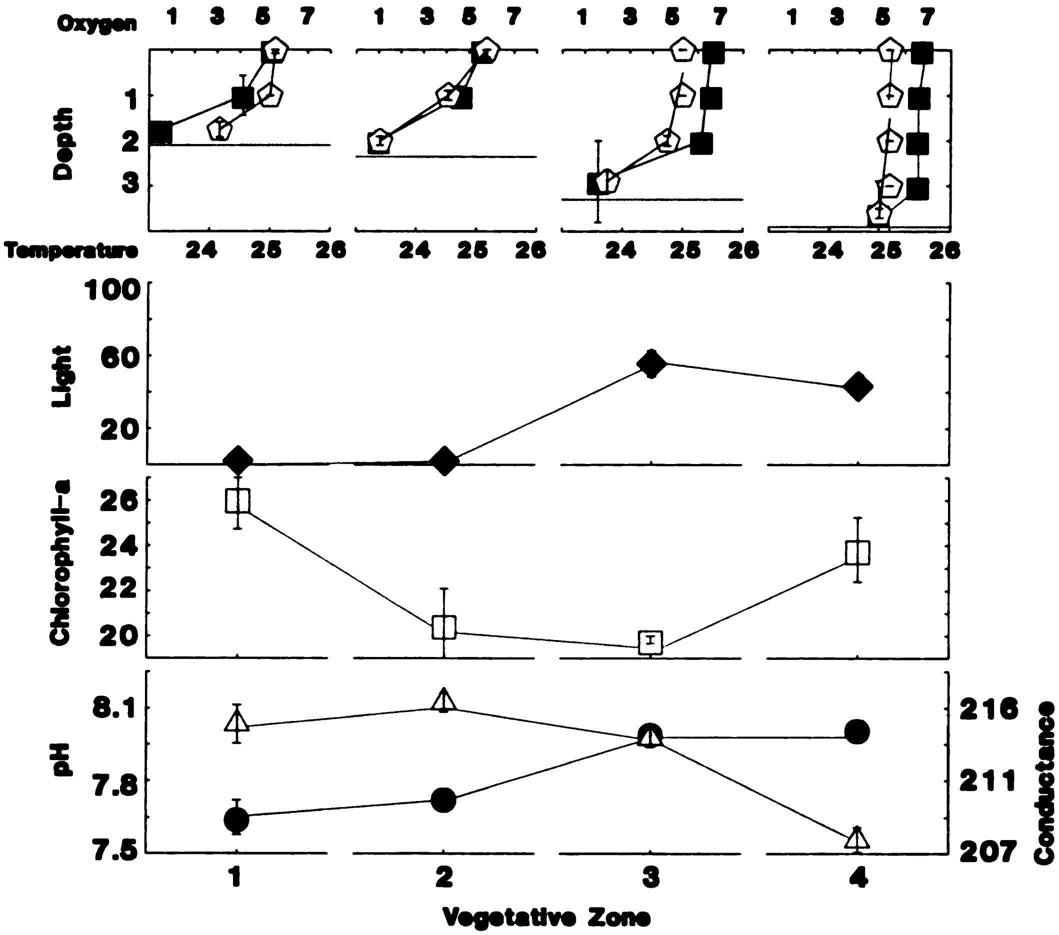
Oxygen
1 3 5 7
1 3 5 7
1 3 5 7
1 3 5 7
Depth
1
2
3
Temperature
24 25 26
24 25 26
24 25 26
24 25 26
Light
100
60
20
Chlorophyll-a
26
24
22
20
pH
8.1
7.8
7.5
Conductance
216
211
207
1
2
3
4
Vegetative Zone

Figure 2

Figure 3. Physical and chemical characteristics (mean ± S.E.) of the four vegetative zones of Lower Crooked Lake in October 1993. Symbols are the same as in Figure 2. Dashed lines represent the mean total depth (m) per zone. Vegetative zones are the same as in Figure 1.

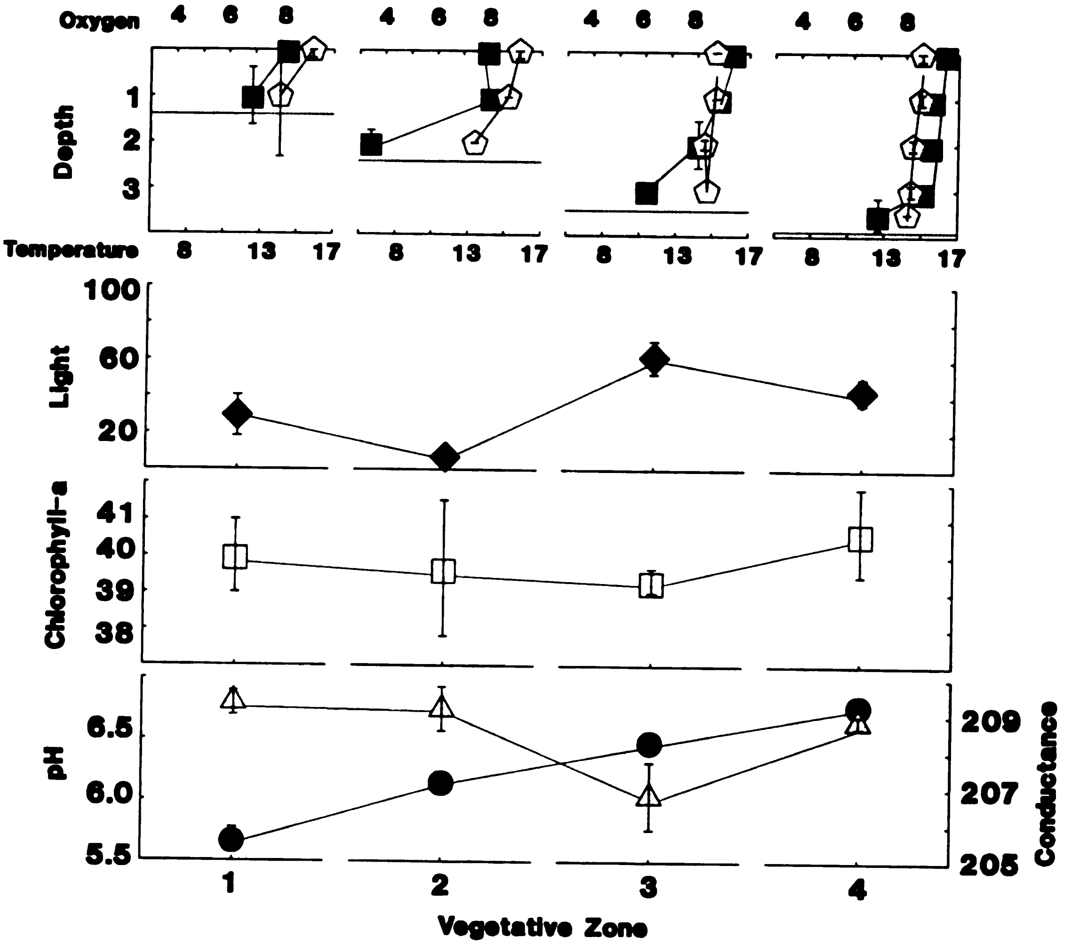
Oxygen
4
6
8
Depth
1
2
3
Temperature
8
13
17
100
Light
60
20
Chlorophyll-a
41
40
39
38
pH
6.5
6.0
5.5
Conductance
209
207
205
1
2
3
4
Vegetative Zone

Figure 3

The phytoplankton community changed across the four zones, but did not mirror the chlorophyll-*a* pattern. Edible algae, such as small flagellates (*Trachylomonas*, *Mallomonas*, *Cryptomonas*, *Phacus*) and small greens (*Scenedesmus*, *Crucigenia*, single celled greens), were most abundant in zones 3 and 4 (Fig. 4). Ciliates were most abundant in zones 1 and 2, while pennate diatoms, which are usually attached to substrates, were most abundant in zone 1 and 4 (Fig. 4). Large colonial forms (*Anabaena*, *Microcystis*, *Anacystis*, *Merismopedia*, *Oscillatoria*) and dinoflagellates did not differ greatly between zones.

Invertebrate predators exhibited a striking partitioning along the horizontal gradient in both the lake and the pond (Figs. 5 and 6). The dominant macroinvertebrates included sit-and-wait predators, such as damselfly larvae (*Enallagma*), which were most abundant in zones 1 and 2 in both the lake and pond, and the phantom midge larvae (*Chaoborus*), which primarily inhabited zone 2 in the lake. Another invertebrate predator, *Leptodora kindtii*, was most abundant in zones 3 and 4 of the lake. Like fish, *Leptodora* is a visual cruising predator. Other invertebrate predators were present in low numbers in zones 1 and 2, including dragonfly larvae (Libellulidae), damselfly larvae (*Lestes spp.*), and water mites (Hydracarina; Appendix A). The dominant vertebrate predator was the bluegill sunfish (*Lepomis macrochirus*), which was observed in all four vegetative zones.

### *Microcrustacean Pattern*

During the summer, cladoceran populations showed distinct changes in abundance along the horizontal gradient in Lower Crooked Lake (Fig. 7). *Sida crystallina* and

Figure 4. Distribution of the three most common algal resource groups (mean ± S.E.) in Lower Crooked Lake. Vegetative zones are the same as in Figure 1. Diatoms are pennate forms and are usually attached to substrates.

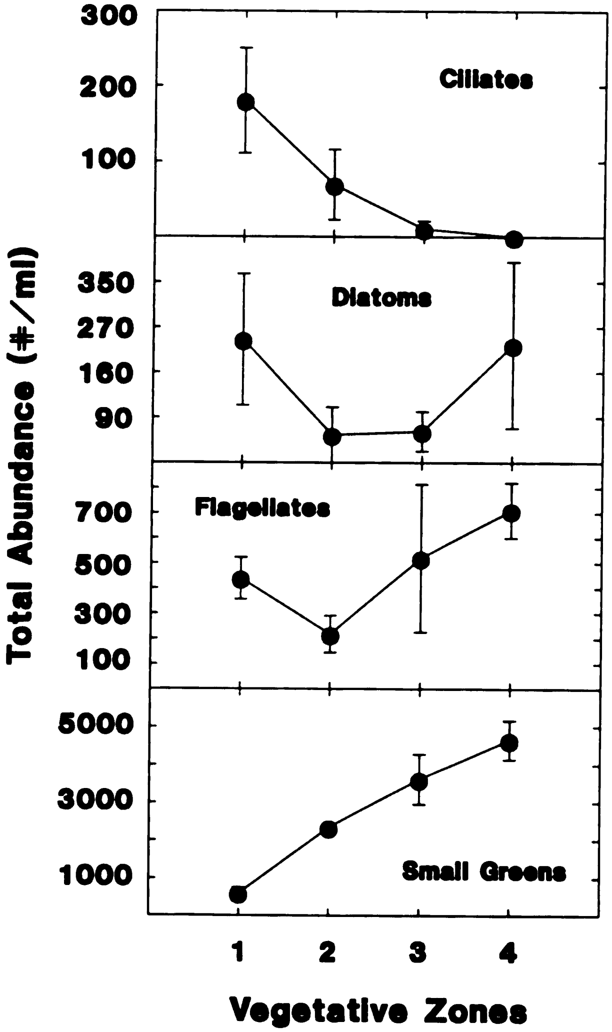
Total Abundance (#/ml)
Ciliates
300
200
100
Diatoms
350
270
160
90
Flagellates
700
500
300
100
Small Greens
5000
3000
1000
1
2
3
4
Vegetative Zones

Figure 4

Figure 5. Distribution of the common invertebrate predators in Lower Crooked Lake in the summer and fall of 1993 (mean ± S.E.). *Leptodora* (numbers/l) = circles, *Chaoborus* (numbers/l) = squares, *Enallagma* (catch/unit effort) = triangles. Vegetative zones are the same as in Figure 1.

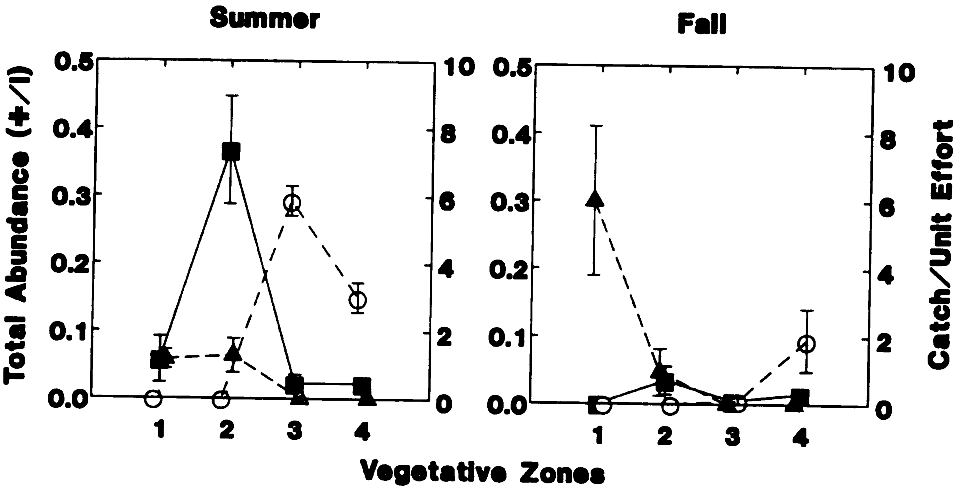
Summer
Fall
Total Abundance (#/l)
0.5
0.4
0.3
0.2
0.1
0.0
10
8
6
4
2
0
Catch/Unit Effort
1
2
3
4
Vegetative Zones

Figure 5

Figure 6. Distribution of *Enallagma* (catch/unit effort) in the pond in the summer of 1992 (mean ± S.E.). Vegetative zones are the same as in Figure 1.

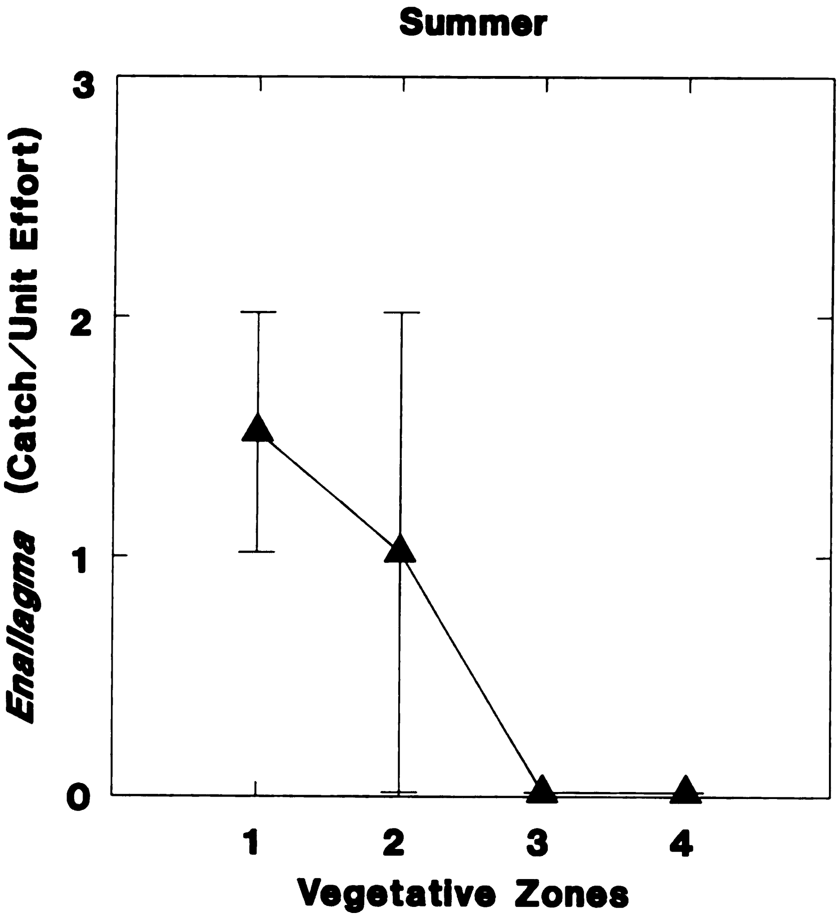
Summer
Enallagma (Catch/Unit Effort)
0
1
2
3
1
2
3
4
Vegetative Zones

Figure 6

Figure 7. Distribution of microcrustaceans (mean ± S.E.) in Lower Crooked Lake in the summer of 1992 (lighter shading) and 1993 (darker shading). Vegetative zones are the same as in Figure 1.

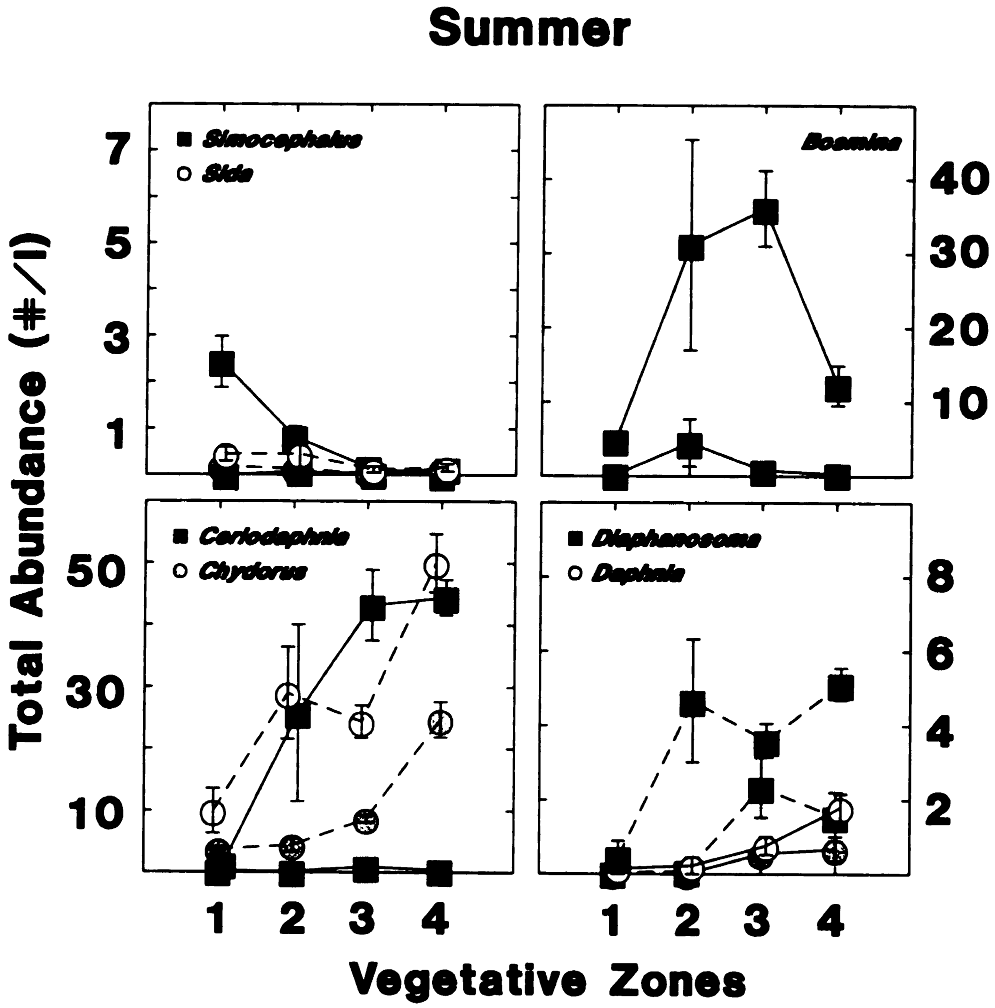
Summer
Total Abundance (#/l)
7
5
3
1
■ Simocephalus
○ Sida
Bosmina
40
30
20
10
50
30
10
■ Ceriodaphnia
○ Chydorus
■ Diaphanosoma
○ Daphnia
8
6
4
2
1
2
3
4
1
2
3
4
Vegetative Zones

Figure 7

*Simocephalus exspinosus* (Pennak, 1989) are most common in the littoral, occurring primarily in zone 1 and secondarily in zone 2. *Daphnia retrocurva*, *D. dubia* (Brooks, 1957), *Chydorus spp.*, and *Ceriodaphnia reticulata* (Pennak, 1989) are most abundant in the open water (primarily zone 4 and secondarily zone 3). *Diaphanosoma brachyurum* (Korinek, 1981) utilized all areas except zone 1. *Bosmina freyi* (De Melo & Herbert, 1994) was primarily found in zone 2 (lilypads) and transitional zone 3.

Despite large seasonal and interannual differences in abundance of cladocerans in the lake, the general distribution patterns of the species remained largely unchanged (Fig. 8). *Sida* was most abundant in late fall in the lake, while *Simocephalus* was abundant during both summer and fall, but both always occurred most frequently in zone 1. *Daphnia* was primarily a fall form in the lake, with *D. retrocurva* as the most abundant species and *D. dubia* present at lower densities. As in the summer, both species were found primarily in zone 4 during the fall. *Diaphanosoma* was predominately a summer form in the lake, and, although rare in the fall, it maintained a largely open water distribution (zones 3 and 4). *Chydorus* was less abundant in the fall, although it maintained the same distribution pattern for open lake in the fall as in the summer, with some differences among years. In the fall, *Bosmina* was most abundant in zones 2 and 3 in the lake, similar to the summer distribution. *Ceriodaphnia* was the only species to show marked seasonal changes in habitat preferences. Its distribution changed from a summer limnetic form to a fall littoral form (zones 1 and 2).

In the lake all species were absent or in very low abundances during the winter and spring with the exception of *Bosmina*, *Chydorus*, and *Daphnia ambigua*. *Daphnia*

Figure 8. Distribution of microcrustaceans (mean ± S.E.) in Lower Crooked Lake in the fall of 1992 (lighter shading) and 1993 (darker shading). Vegetative zones are the same as in Figure 1.

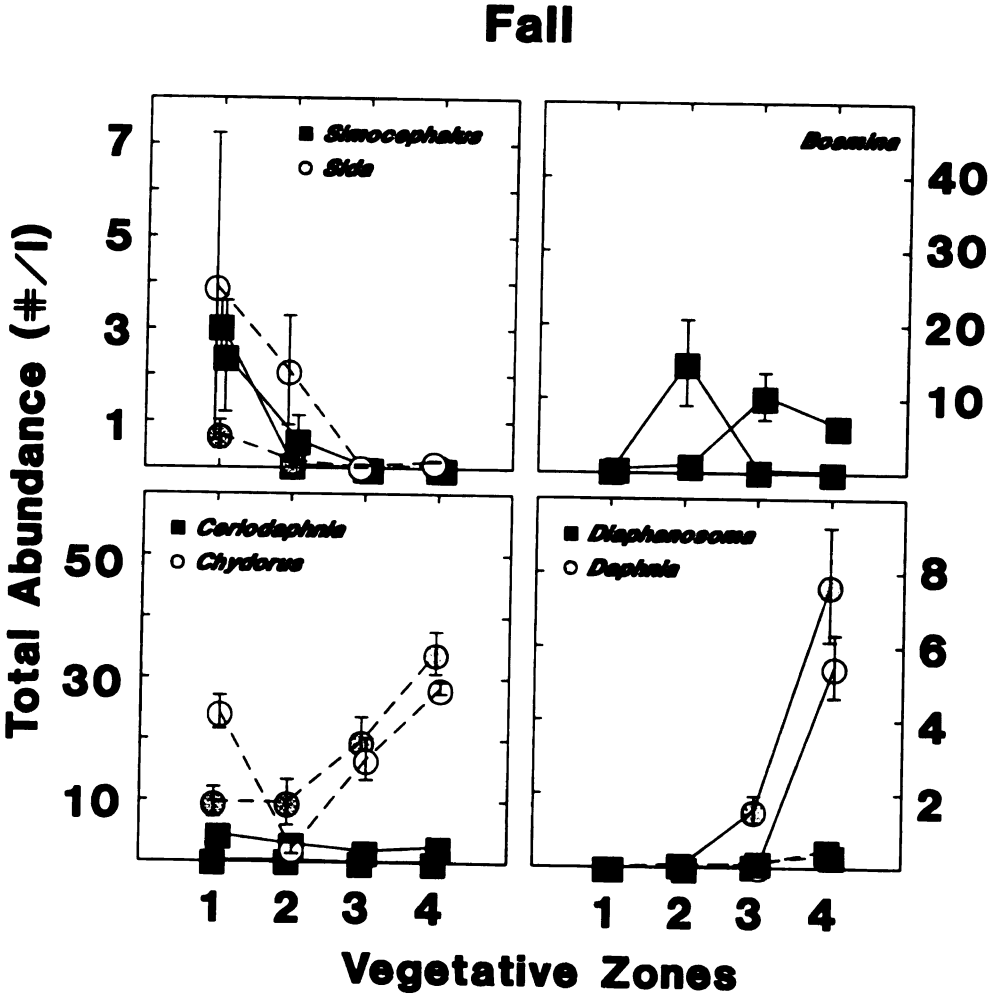
Fall
Total Abundance (#/l)
7
5
3
1
■ Simocephalus
○ Sida
Bosmina
40
30
20
10
50
30
10
■ Ceriodaphnia
○ Chydorus
■ Diaphanosoma
○ Daphnia
8
6
4
2
1 2 3 4
1 2 3 4
Vegetative Zones

Figure 8

*ambigua* was present in the spring at very low densities and was evenly spread between zones 2, 3, and 4. *Bosmina* was present in low densities in both winter and spring and was evenly spread across all four zones. *Chydorus* was present at greatly reduced abundances in both winter and spring and was found primarily in zone 1 during the winter, while it showed a more even distribution between all four zones in the spring.

In the lake, nocturnal distributions of all species were similar to the daytime distributions, with the exception of *Ceriodaphnia* during the summer (Fig. 9) when they apparently moved inshore to zone 2 at night and offshore to zone 3 during the day. There was no difference in the diel distributions of this species in the fall and spring; they remained inshore in zones 1 and 2 both day and night.

Even though the habitats in the pond were greatly compressed in size compared to the lake, microcrustacean distributions were very similar in both bodies of water with only two exceptions. In both summer and fall, *Chydorus* was more broadly distributed in the pond than it was in the lake and *Bosmina* was most abundant in the more open zones (3 and 4) in the pond compared to being most abundant in zone 2 as in the lake (Fig. 10). Interestingly, *Ceriodaphnia* showed the same pattern of shifting preference seasonally from the limnetic zones in the summer to the littoral zones in the fall that was observed in the lake.

Other microcrustaceans, which are not a focus of this chapter, also showed a distinct horizontal distribution in both the lake and the pond and are reported in Appendix B. For example, cyclopoid copepods were primarily in zones 1 and 2, while calanoid copepods were more broadly distributed throughout most of the year in both the lake and the pond.

Figure 9. Diel distributions of microcrustaceans (mean ± S.E.) in Lower Crooked Lake in the summer of 1993. Light symbols = daytime, dark symbols = nighttime. Vegetative zones are the same as in Figure 1.

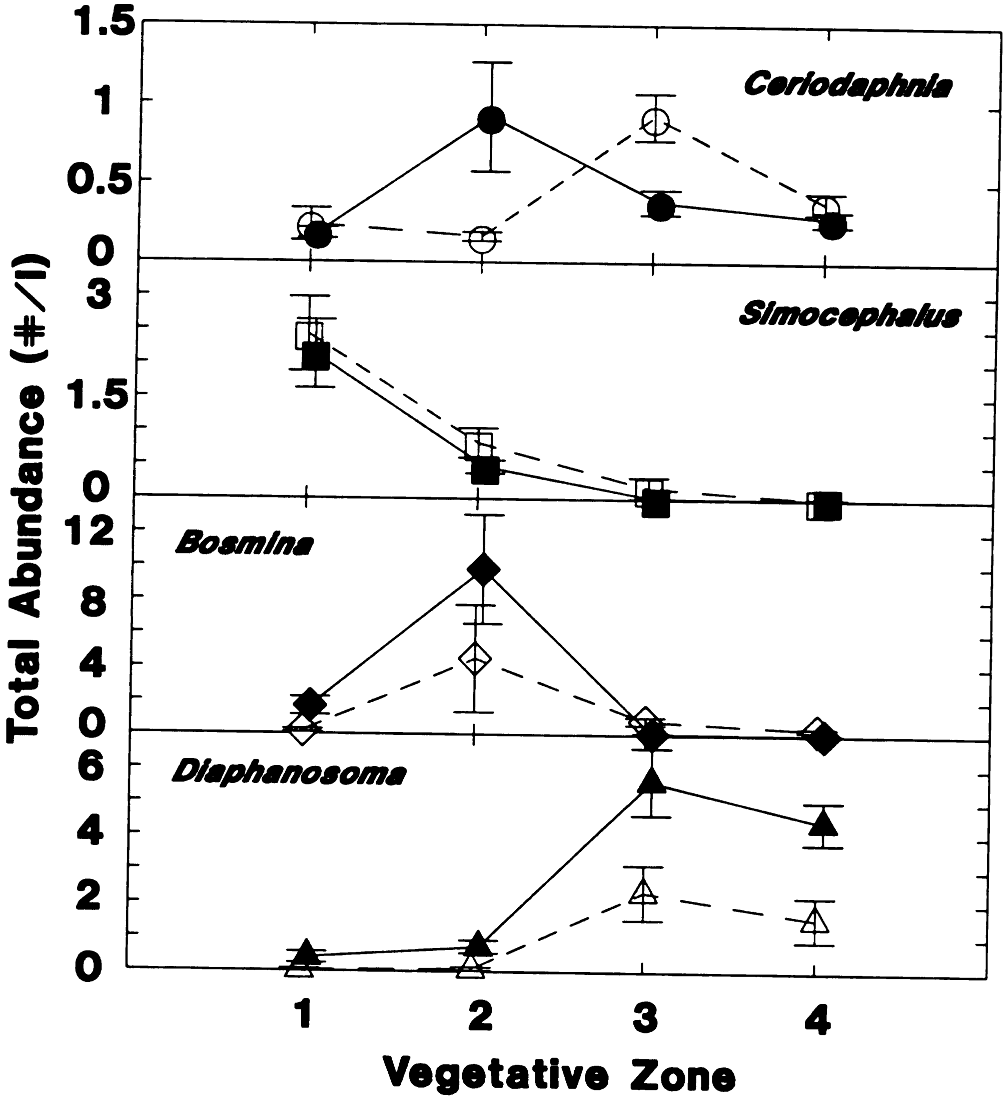
1.5
1
0.5
0
3
1.5
0
12
8
4
0
6
4
2
0
Ceriodaphnia
Simocephalus
Bosmina
Diaphanosoma
Total Abundance (#/l)
1
2
3
4
Vegetative Zone

Figure 9

Figure 10. Distribution of microcrustaceans (mean ± S.E.) in the pond in the summer and fall of 1992. Vegetative zones are the same as in Figure 1.

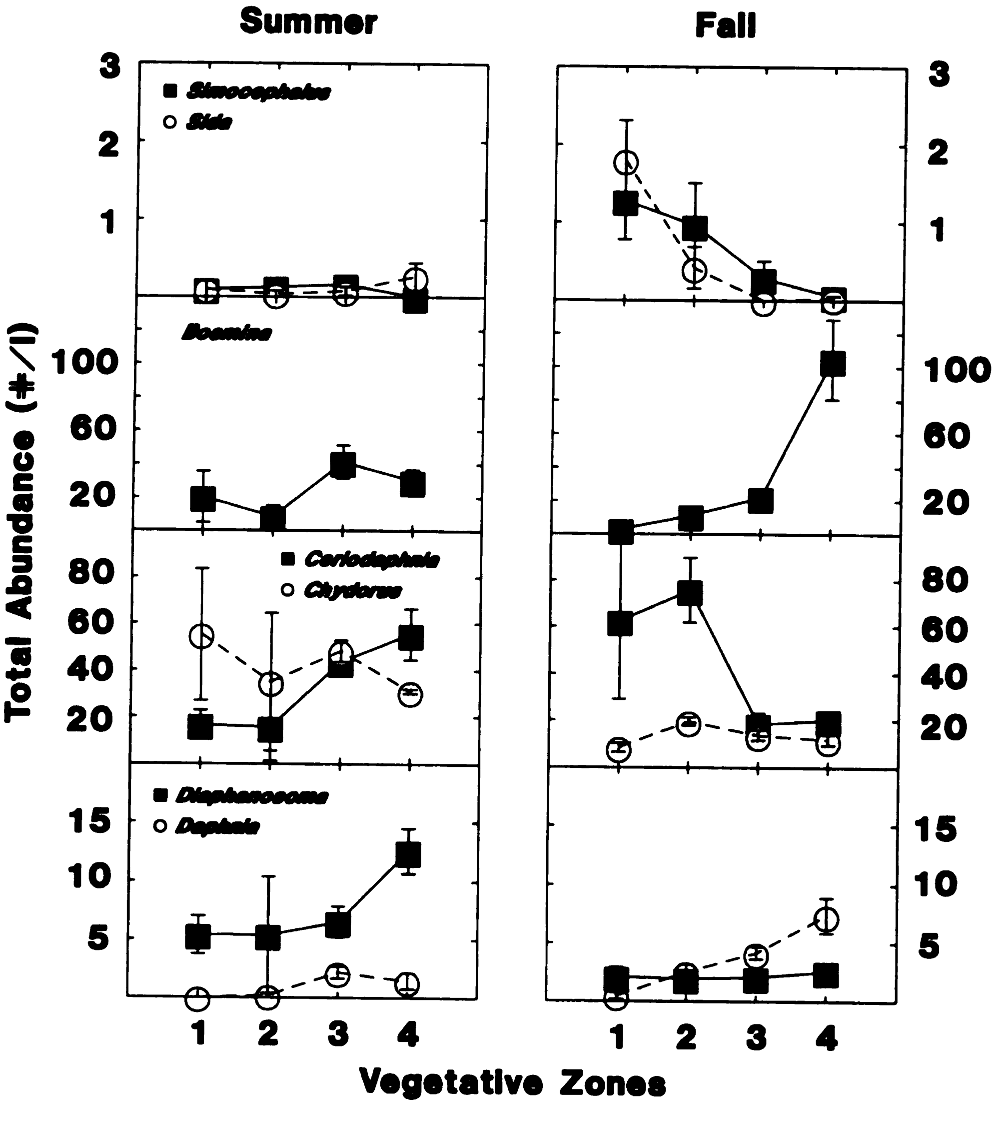
Summer
Fall
Total Abundance (#/l)
■ *Simocephalus*
○ *Sida*
*Bosmina*
■ *Ceriodaphnia*
○ *Chydorus*
■ *Diaphanosoma*
○ *Daphnia*
3
2
1
100
60
20
80
60
40
20
15
10
5
1
2
3
4
Vegetative Zones

Figure 10

Many benthic genera of cladocerans were occasionally collected with my sampling techniques. In the lake, some genera were most common in either the littoral (e.g., *Kurzia*, *Camptocercus*, *Alona*, *Pleuroxus*) or the limnetic zones (e.g., *Streblocercus*), while others occurred across most vegetative zones (e.g., *Alona* and *Ilyocryptus*). Some, like *Ceriodaphnia*, changed habitat preferences seasonally: *Graptoleberis* and *Acroperus* were dominant in the littoral in the fall, but in the limnetic zone in the summer. In the pond, however, many genera were more broadly distributed than in the lake (e.g., *Alona*, *Camptocercus*, *Pleuroxus*, *Acroperus*).

### *Transplant Experiment*

To examine differential responses of the species to littoral versus limnetic seston resources, I first grouped the species into three categories: those which are most abundant in the littoral zones (i.e., *Simocephalus*, *Sida*), the open-water zones (i.e., *Chydorus*, *Daphnia retrocurva*, *Diaphanosoma*), and the intermediate, transitional lilypad zone (i.e., *Bosmina*, *Ceriodaphnia*). *Diaphanosoma* was included in the open-water zone category because they typically were more abundant there, especially when at low densities and in the pond. A multivariate analysis of variance was then used to test each group for the effect of location ("resource") on population-specific growth rates.

Littoral and limnetic specialist species differed in response to the resource treatments. Littoral species (*Simocephalus* and *Sida*) did equally well when placed in either littoral or limnetic zones (Wilk's $\lambda$ F=0.468; d.f.=2, 5; p=0.651). Populations of both species increased in both resource treatments with *Simocephalus* increasing more than *Sida* (Fig.

11). In contrast, open water species generally did better in the limnetic zone. While *Chydorus* populations did only slightly better in the limnetic treatment, *Daphnia* and *Diaphanosoma* performed more poorly in the littoral compared to the limnetic treatment (Wilk's $\lambda$ F=7.952; d.f.=3, 4; p=0.037) (Fig. 11). It is important to note that in this experimental design I cannot directly compare the absolute performance of littoral to limnetic species in a given resource treatment since total densities of animals from the different zones were not similar.

Species which are most abundant in the intermediate lilypad zones (but present in both zone 2 and 4 in high numbers) did not show a significant resource effect (Wilk's $\lambda$ F=1.403; d.f.=2, 11; p=0.287) nor an interaction effect between the source where the animals were collected and the resource (Wilk's $\lambda$ F=0.124; d.f.=2,11; p=0.885). However, there was a significant effect of the source where the animals were collected; *Bosmina* from the limnetic zone performed much better than the ones taken from the littoral zone (Fig. 11). On the other hand, *Ceriodaphnia* collected from the littoral zone performed better than those collected from the limnetic zone (Fig. 11). The reasons for the varied response of the animals from the different source populations is unclear, but may have been due to differences in stocking density, or clonal or demographic structure of the populations at the time.

Figure 11. Population growth rates (r) of animals (mean ± S.E.) in the reciprocal transplant experiment. For *Bosmina* and *Ceriodaphnia*, the sources of the animals are portrayed with limnetic zone=light symbols and littoral zone=dark symbols.

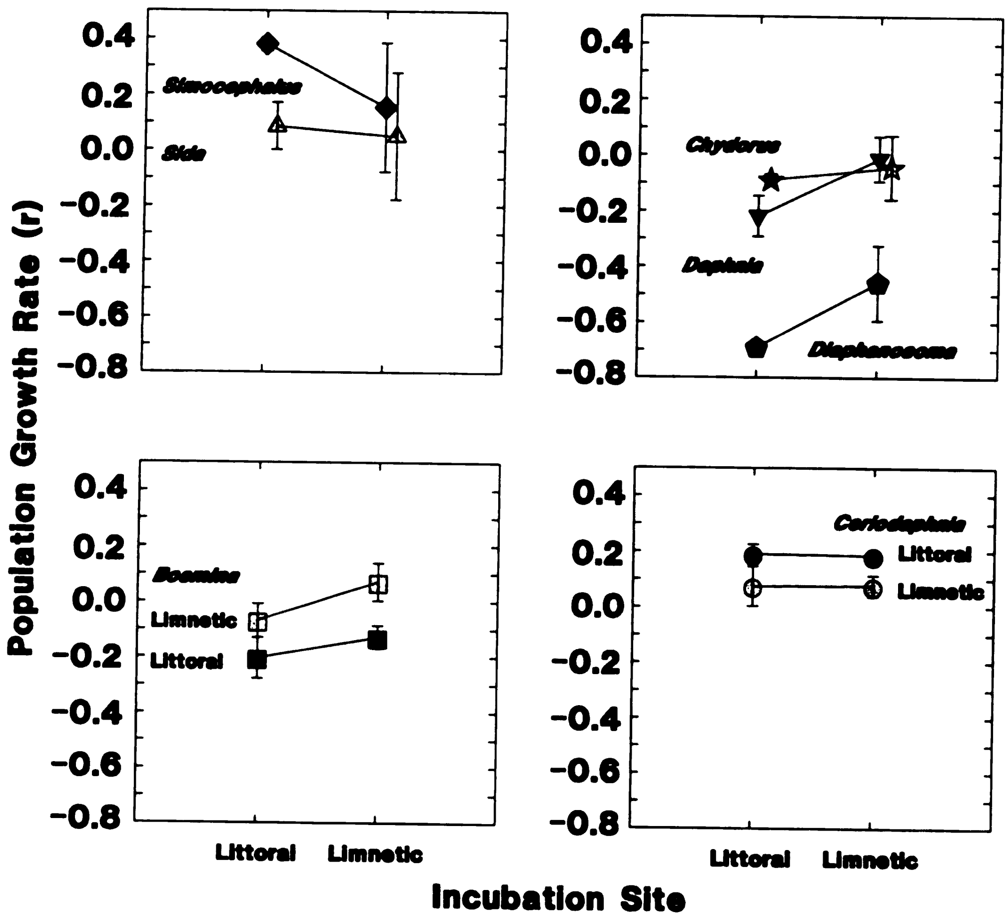
Population Growth Rate (r)
0.4
0.2
0.0
-0.2
-0.4
-0.6
-0.8
Simocephalus
Sida
Chydorus
Daphnia
Diaphanosoma
Bosmina
Limnetic
Littoral
Ceriodaphnia
Littoral
Limnetic
Littoral
Limnetic
Littoral
Limnetic
Incubation Site

Figure 11

# DISCUSSION

The suspension-feeding microcrustaceans displayed distinct distributions along a nearshore to offshore gradient in both the lake and pond. The physical environment changes across the lake basin with changes in depth or shelter from wave action (e.g., bays and coves), which influences the forms of macrophytes growing along this horizontal gradient. The macrophytes, in turn, modify the environment by reducing light levels (e.g., *Nymphaea*) and adding structural complexity which reduces turbulent mixing (Losee, 1991). Low light and turbulence can lead to a decline in the abundance of phytoplankton available for suspension grazers. Low light and high structural complexity can also reduce the foraging efficiencies of visual, cruising predators (e.g., fish; Crowder & Cooper, 1982; Diehl, 1988; Dionne & Folt 1991). Macrophytes may also provide microcrustaceans with a refuge from fish predation by reducing the dissolved oxygen content of the water (Davis, 1975). The macrophytes provide perches for invertebrate predators and attachment sites for some microcrustaceans; damselfly larvae were most abundant in zone 1 (milfoil beds), as were *Simocephalus* and *Sida*, two species of microcrustaceans which have special adaptations to attach to macrophytes. I found that these factors (e.g., physical parameters, resources, predators, and structure) varied in a distinct fashion along the nearshore-offshore gradient and were associated with a consistent spatial partitioning of microcrustaceans.

Similar horizontal distributions of microcrustaceans were observed in the nearby pond where the distance across vegetative zones was smaller and horizontal movement between patches easier. The variance in the abundance of a given species at different sites within each vegetative zone was low relative to the differences in abundance between the different zones. Thus, the behavioral and the ecological mechanisms underlying such patterns was related to macrophyte zonal structure, irrespective of the physical extent of each vegetative zone. This pattern is striking, considering that many species of microcrustaceans move horizontally dielly (Kairesalo, 1980; Timms & Moss 1984; Davies, 1985). The one exception to the similarity of distributions between the lake and pond was *Chydorus*, which was more evenly distributed in all zones in the pond while being a limnetic specialist in the lake. I cannot, however, rule out the presence of different species of *Chydorus* in the pond than the lake, or within the different zones of the pond.

Since many microcrustaceans are active swimmers, can cover large distances, and can recognize a wide variety of visual and chemical cues (Siebeck, 1964 & 1980; Meyers, 1980; Fairchild, 1981; Watt & Young 1994), there is potential for active, individual habitat choice. Risk assessment by prey species often plays a major role in their habitat selection if a less risky habitat is available (Mittelbach & Chesson, 1987; Soluk & Collins 1988; Lima & Dill 1990). Some microcrustaceans have been reported to migrate to the littoral during the day to hide among macrophytes from fish predators and out to the limnetic zones at night to forage on higher concentrations of algae (Timms & Moss, 1984; Davies, 1985). However, other microcrustaceans avoid the littoral zones either because of allelopathic chemicals released by the macrophytes (Pennak, 1973; Dorgelo & Heykoop, 1985; Lauridsen & Lodge, 1996) or due to high rates of mortality imposed by young-of-year fish, which are also using the macrophyte zones as refuges from their predators (Cryer, Peirson & Townsend, 1986; Whiteside, 1988; Taleb, Reyes-Marchant & Lair, 1994). These two factors may contribute to the lack of diel horizontal migration by most species in my study. The only species I found which migrated horizontally on a diel basis was *Ceriodaphnia*, which showed the opposite migration pattern to that previously described for other species, moving out into the open water during the day and into the vegetation at night. Again, this could be related to potentially high rates of mortality caused by young-of-year fish congregating in the vegetation and feeding primarily during the day. On the other hand, the movement of *Ceriodaphnia* into the littoral at night resulted in an overlap with peak densities of *Chaoborus*. There is a potential for fish and invertebrate predators to interact in their impact on microcrustacean communities, however, these relationships have not been well studied along a habitat gradient.

An alternative to behavioral preferences for a specific habitat is that different population dynamics among various habitats may be the underlying mechanism of habitat partitioning. In multi-species assemblages where competition is intense, species often become more restricted in habitat (Rosenzweig, 1991). The microcrustaceans studied here may only be able to compete successfully in a specific vegetative zone of the lake based on the available food resources found in each zone. For example, the limnetic specialist *D. retrocurva* performed poorly in enclosures containing seston from the littoral zone. Phytoplankton resources were lower in the littoral habitats in the summer, with the exception of the zone dominated by submerged macrophytes. Vuille (1991) also found that the littoral zone of a eutrophic lake in Switzerland often had a greater fraction of large inedible algae than in the open water. Microcrustaceans which are limnetic specialists may need a higher quantity of resources than is available in the littoral zone and are thereby restricted to the limnetic zones of lakes. However, food resources do not provide an explanation for the distribution of littoral species. I found that littoral species performed well when fed seston from the limnetic zone, suggesting that their distribution is potentially limited by something other than resources.

The contrasting responses of littoral and limnetic species to resource conditions in the transplant experiment cannot be explained by phylogenetic similarity. While the Bosminidae were represented by a single species that occupied the lilypad vegetation, members of the Sididae and the Daphniidae were present in both the nearshore and offshore zones. *Sida* (nearshore) and *Diaphanosoma* (offshore) are both members of the Sididae, yet had completely different responses to the resource conditions in the two habitats. Similarly, *Simocephalus* (nearshore) and *Daphnia* (offshore) are both Daphniidae, yet differed in their response to the resource types. So, while species of microcrustaceans appeared to have specific habitat choices, higher taxonomic status was not a good predictor of horizontal distribution nor response to resource manipulation.

Differences in food quality may contribute to resource partitioning in microcrustaceans. Some species can selectively feed on flagellates (e.g., *Bosmina*), while others are more efficient at capturing and consuming bacteria (e.g., *Ceriodaphnia* and *Diaphanosoma*; DeMott, 1989). The more heterotrophic environment in the littoral zone potentially has a higher abundance of bacteria, which could be a large part of the diet for species able to capture them efficiently. Even though all phytoplankton groups were reduced beneath the lilypads, *Bosmina* and *Ceriodaphnia* may thrive in this marginal habitat if they can utilize microbial food sources (e.g., protozoans, bacteria) more efficiently than other species to supplement the low numbers of small edible algae. It is important to note that in my experiment I did not test the seston resources in zones 1 and 3 to see how the microcrustaceans used them. I also measured only the chlorophyll-*a* content of the seston. How efficiently the different species can utilize non-algal food resources such as bacteria, protozoans (e.g., ciliates) and detritus may contribute to how the species partition the use of the vegetative habitats. My results documenting a relationship between food types and microcrustacean species distributions suggest that this would be a fruitful avenue of research.

The two intermediate species, *Ceriodaphnia* and *Bosmina*, did equally well whether raised in the littoral or limnetic habitats. However, the source of these species had a significant effect on the population growth rates, albeit in opposite ways. The littoral *Ceriodaphnia* population performed better than the limnetic population, while the limnetic *Bosmina* population performed better than littoral population in both incubation sites. Intraspecific density-dependent effects were not a general explanation in this case since *Ceriodaphnia* was stocked at almost twice the density in the littoral enclosures than in the limnetic enclosures. Interspecific competition, on the other hand, could be an important explanation. The two intermediate species were incubated with different densities of different specialist species in the limnetic versus littoral resource treatments. Unlike *Ceriodaphnia*, *Bosmina* may be influenced by intraspecific density-dependent effects. The littoral animals were stocked at almost four times the density of the limnetic animals and could not maintain population growth rates similar to those of the limnetic animals. However, despite this difference in stocking density of littoral and limnetic populations, the response to the resource treatments was identical, suggesting that the intermediate guild perceived no striking food differences between littoral and limnetic habitats.

While I did not directly test for competition, the seasonal changes in distribution which I observed for *Bosmina* and *Daphnia ambigua* can be viewed as indirect evidence that competition occurs. During the winter and spring when the macrophyte zones were undeveloped and the abundances of other species were very low or zero, *Bosmina* and *D. ambigua* were much more broadly distributed across the lake. However, as the macrophyte beds developed and other species repopulated the vegetative zones, *Bosmina* became confined primarily to the lilypad zone and *D. ambigua* was driven out of the system completely. I also observed that *Ceriodaphnia* was more common in the littoral zones during the fall when the limnetic specialist, *D. retrocurva*, was at its peak. It is likely that *Ceriodaphnia* is not moving from the limnetic to the littoral seasonally, but rather, that the limnetic populations decline with increased interspecific competition, while the littoral populations stay the same or only slightly decrease.

Chemical differences observed between the vegetative zones did not seem to be any greater in amplitude than those experienced by pelagic zooplankton in deep lakes. Individuals undergoing diel vertical migration undergo much greater temperature, dissolved oxygen, light, and pH extremes (Hutchinson, 1957 & 1967) than those which would be experienced by species migrating between the vegetative zones. However, dissolved oxygen was not measured at night and with increased respiration by macrophytes, these zones can become stressful for some species (Meyers, 1980).

In summary, the pattern of horizontal distributions of microcrustaceans which I observed was similar between the pond and lake regardless of the distance between habitat types. This distribution was strongly related to the macrophyte growth forms, which in turn influenced the amount and type of sestonic food available. Both descriptive and experimental results suggest that food was an important influence on the habitat choice of limnetic species. Moreover, food resources varied between the vegetative zones and whether they are utilized differentially by the different species of microcrustaceans needs further study. Finally, my results document a clear sequence of different invertebrate predators (*Enallagma*, *Chaoborus*, *Leptodora*) along the macrophyte gradient. Since there was no evidence that resources limited the distribution of most of the nearshore and intermediate zone species, it is likely that changes in the predator regime may be important in determining their habitat use.

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# CHAPTER 2

# THE ROLE OF PREDATION AND MACROPHYTES IN STRUCTURING MICROCRUSTACEAN COMMUNITIES

# ABSTRACT

The distribution of microcrustaceans in a Michigan lake and pond changes along a horizontal gradient from nearshore to offshore. These changes are associated with a gradient in the dominant types of macrophytes (e.g., submersed, floating-leaved). The macrophytes influence the physico-chemical environment as well as the food resources available and the types of predators present.

I examined the interaction of macrophytes (or habitat complexity) and invertebrate versus vertebrate predation in determining microcrustacean community structure and habitat selection along this habitat gradient. I exposed a mixed littoral and limnetic assemblage of microcrustaceans to macrophytes (*Myriophyllum, Nymphaea*), damselfly larvae (*Enallagma*) and bluegill sunfish (*Lepomis*) using a block factorial design. The damselfly predators did not substantially influence the microcrustacean population dynamics. In order to better quantify the effects of macrophytes and fish predators, a second factorial experiment was conducted over a longer time period to allow more generations of the microcrustaceans to respond. In both experiments, the macrophytes had a strong positive effect on microcrustacean species dominating the nearshore, submersed macrophyte areas (i.e., *Simocephalus*, *Sida*) and a strong negative impact on limnetic species (i.e., *Daphnia*, *Diaphanosoma*, *Chydorus*). Surprisingly, the taxa commonly found under lilypads (i.e., *Bosmina*, *Ceriodaphnia*) were also negatively affected by macrophytes. Fish predation differentially affected the limnetic species with the taxa more abundant during the summer (i.e., *Diaphanosoma*) positively affected by fish, while those dominant in the fall (i.e., *Daphnia*) greatly reduced by fish predation. The genera typically living among the nearshore, submersed macrophytes were negatively affected by fish in the absence of macrophytes but not in the presence of macrophytes. In contrast, the species living under the lilypads were unaffected or positively affected by fish in the absence of macrophytes but not in their presence. Hence, the distinctive assemblages of microcrustaceans occurring along the horizontal gradient each had a unique response to the combination of macrophytes and fish predation.

Key words: predation; habitat complexity; habitat partitioning; refuge; littoral; limnetic; microcrustaceans; fish, damselfly; macrophyte

## INTRODUCTION

Predation has been found to structure prey communities in both terrestrial and aquatic systems (Morin 1983, Fagan and Hurd 1994, Morin *et al.* 1996). Both vertebrate and invertebrate predators are known to structure zooplankton communities with vertebrates (e.g., fish; Hanazato and Yasuno 1989, Irvine *et al.* 1989, Wright and Shapiro 1990, Hambright and Hall 1992) selecting large-bodied prey and most invertebrates (e.g., *Chaoborus*, *Asplanchna*, *Lestes*; Hanazato and Yasuno 1989, Lair 1990, Havel *et al.* 1993) generally selecting small-bodied prey (with some exceptions, e.g., *Notonecta*).

Despite the fact that they commonly co-occur, few studies have looked at the interaction of vertebrate and invertebrate predators (see Gonzalez and Tessier, in press). Co-occurring predators may spatially partition their habitats vertically, whether on a large scale in lakes (e.g., *Chaoborus* and fish; Dawidowicz *et al.* 1990, Kvam and Kleiven 1995) or on a smaller scale of individual rocks in streams (e.g., fish and stoneflies; Soluk and Collins 1988). Predators also partition habitats along a horizontal gradient in lakes (e.g., Winfield and Townsend 1988, Persson 1993). However, little is known about how multiple predators interact to influence prey species along such gradients.

Predators can influence the habitat use of prey species in two distinct ways. First, predator presence may change the prey's behavior so as to reduce mortality risk (Werner *et al.* 1983, Neill 1990, Loose and Dawidowicz 1994). Second, habitat specific predation may deplete prey in particular habitats (Jakobsen and Johnsen 1987, Gliwicz and Rykowska 1992, Taleb *et al.* 1994).

Habitat complexity (i.e., the density or heterogeneity of physical structure) can influence prey communities by decreasing predator foraging efficiency. For example, piscivorous and planktivorous fish have decreased swimming speeds and capture rates of prey in dense macrophytes (Crowder and Cooper 1982, Anderson 1984, Cook and Streams 1984, Persson 1991). Growth form of macrophytes can also influence the ability of prey to hide (Dionne and Folt 1991); macrophytes which have finely dissected leaves and bushy growth forms (e.g., *Myriophyllum*) can decrease detection of prey more than plants with fewer, large whole leaves (e.g., *Polygonum*). Although plants such as *Nymphaea* provide less structure to hide behind, they may reduce the foraging efficiency of visual predators by greatly decreasing the light levels in the water column beneath their floating leaves.

Because vegetation generally adds to habitat complexity, it can reduce predation rates for microcrustaceans and serve as a refuge for horizontally migrating prey species (Timms and Moss 1984; Davies 1985). However, macrophytes are also known to repel zooplankton due to allelopathy (Pennak 1973; Lauridsen and Lodge 1996). Also, some invertebrate predators (e.g., damselfly larvae; *Hydra*) can use vegetation structure for perches to forage in the upper water column. Additionally, I found that macrophytes are associated with reduced levels of phytoplanktonic food important to limnetic species of microcrustaceans (Chapter 1). The low food availability, risk from invertebrate predation, and possibly the repellant nature of macrophytes may not, at times, outweigh the risk of mortality from planktivorous fish, causing zooplankton to hide in the macrophytes rather than being eaten (Lauridsen and Lodge 1996).

Young-of-year fish may also use the vegetation as refuge from predation by piscivores (Mittelbach 1981, 1984; Werner *et al.* 1983). If fish densities are high among the macrophytes, these areas no longer act as refuges for microcrustaceans and can be sites of high planktivory (Whiteside 1988). On the other hand, if the densities of fish are high in the open water zone of a lake, zooplankton densities can be higher in the littoral than the limnetic zone (Cryer and Townsend 1988). This may be due to behavioral changes such as diel horizontal migration or simply due to the large mortality imposed on the limnetic relative to littoral populations of zooplankton. Clearly, there is a complex relationship between vegetation and the amount of fish predation which contributes to the role of macrophyte zones as refuges for microcrustaceans.

In Chapter 1, it was shown that microcrustacean communities change along a horizontal (littoral to limnetic) environmental gradient in a lake and a pond. With increasing water depth, different types of macrophyte growth forms establish distinct vegetation zones of differing habitat complexity and light levels. The various types of macrophytes can lead to changes in the physical or chemical environment of microcrustaceans, sestonic food resources, and types of predators which can, in turn, influence the distributions of microcrustaceans along this habitat gradient. Specifically, I found three groups of microcrustaceans (i.e., nearshore specialists, offshore specialists, and taxa living in the intermediate lilypad zone; Chapter 1) which will be referred to as habitat guilds throughout this chapter. This study employs an experimental approach to examine the interaction of habitat complexity (i.e., presence of macrophytes) and vertebrate (i.e., bluegill sunfish) versus invertebrate (i.e., damselfly larvae) predators in structuring microcrustacean communities along a horizontal gradient in a lake. In a short term experiment, I examine whether the habitat guilds respond differentially to macrophytes and predators. Given that guild responses did indeed differ in the short term experiment, a second experiment explored whether fish and macrophytes can interact to structure assemblages of microcrustaceans similar to those found in nature.

## METHODS

### *Study site*

Lower Crooked Lake (Barry Co., MI) is a shallow (4 m maximum depth, 106 ha) mesotrophic (mean annual total phosphorus: 14 μg/L) lake with an extensive littoral zone. A winding shoreline with numerous bays allows the development of dense macrophyte beds. Submersed macrophytes with short, bushy growth forms such as *Myriophyllum*, *Ceratophyllum*, and *Utricularia* dominate along the shoreline. Dense stands of water lilies (*Nymphaea* and *Nuphar*) begin at 3 to 4 meters offshore and continue for tens of meters. Beyond the lilypads, there is a sparse zone of submersed and floating-leaved macrophytes such as *Potamogeton* and *Polygonum* which transitions into a water column free of macrophytes.

Three distinct guilds of suspension-feeding microcrustaceans are found in Lower Crooked Lake (see Chapter 1). In the nearshore, submersed macrophyte zone, the community is dominated by *Simocephalus exspinosus* and *Sida crystallina*. The intermediate, floating-leaved macrophyte zone is dominated by *Bosmina freyi* and the open water zone is dominated by *Chydorus spp., Daphnia retrocurva,* and *Diaphanosoma brachyurum*. Some species, such as *Ceriodaphnia reticulata*, occur more frequently in the open water or transitional zone during the summer, but switch to being more common in the floating-leaved macrophyte zone in the fall.

The type of macroinvertebrate predators which feeds on microcrustaceans also changes along this vegetative habitat gradient with damselfly larvae (*Enallagma spp.*) dominant in the submersed macrophyte zone, phantom midge larvae (*Chaoborus spp.*) found primarily in the floating-leaved macrophyte zone, and *Leptodora kindtii* common in the open water zone.

The lake contains a centrarchid fish community typical of warmwater lakes in southern Michigan (Werner *et al.* 1977, personal observation). Planktivores, such as

*Lepomis spp.*, were observed in all three vegetative zones, although foraging efficiency is expected to differ with the types and density of vegetation (Dionne and Folt 1991).

### *Macrophyte and Two Predator Experiment*

In order to test the hypothesis that the three microcrustacean habitat guilds are differentially affected by macrophyte structure and predator type, a mixed littoral and limnetic assemblage of microcrustaceans was exposed to the absence or presence of macrophytes (*Myriophyllum* and *Nymphaea*), sit-and-wait predators (*Enallagma*), and cruising fish predators (*Lepomis*) in a 2 x 2 x 2 randomized-block factorial design (Fig. 1). Experimental treatments were replicated three times for a total of 24 enclosures. Each enclosure was a 60 L polyethylene tube (2 m deep, 20 cm diameter) filled with limnetic water and seston from which most microcrustaceans had been removed using a 130 µm mesh net. The experiment was conducted in mid-September 1993 when the macrophyte vegetation was still dense and large littoral macroinvertebrates (damselflies) were becoming more abundant (the larvae grow from eggs laid earlier in the summer). While the microcrustaceans were collected from Lower Crooked Lake, the enclosures for experimental studies were placed in an adjacent pond which had similar macrophyte and microcrustacean communities but less boat traffic (see Chapter 1).

Macrophyte treatments contained three bundles with 3-10 stems each of *Myriophyllum* (0.5-1 m in length) such that the bundles were approximately the same dry mass (ca. 15-28 g). The bundles were weighted with stainless steel washers to simulate natural positioning on the bottom and in the water column. Two small clipped *Nymphaea* leaves were added to the macrophyte treatments to simulate shading conditions. All

Figure 1. Schematic showing the treatments imposed in the short-term, 2 x 2 x 2 block factorial design experiment. A mixed littoral and limnetic microcrustacean community was exposed to the presence and absence of macrophytes crossed with the presence or absence of the two predators (1 bluegill sunfish and/or 16 damselfly larvae).

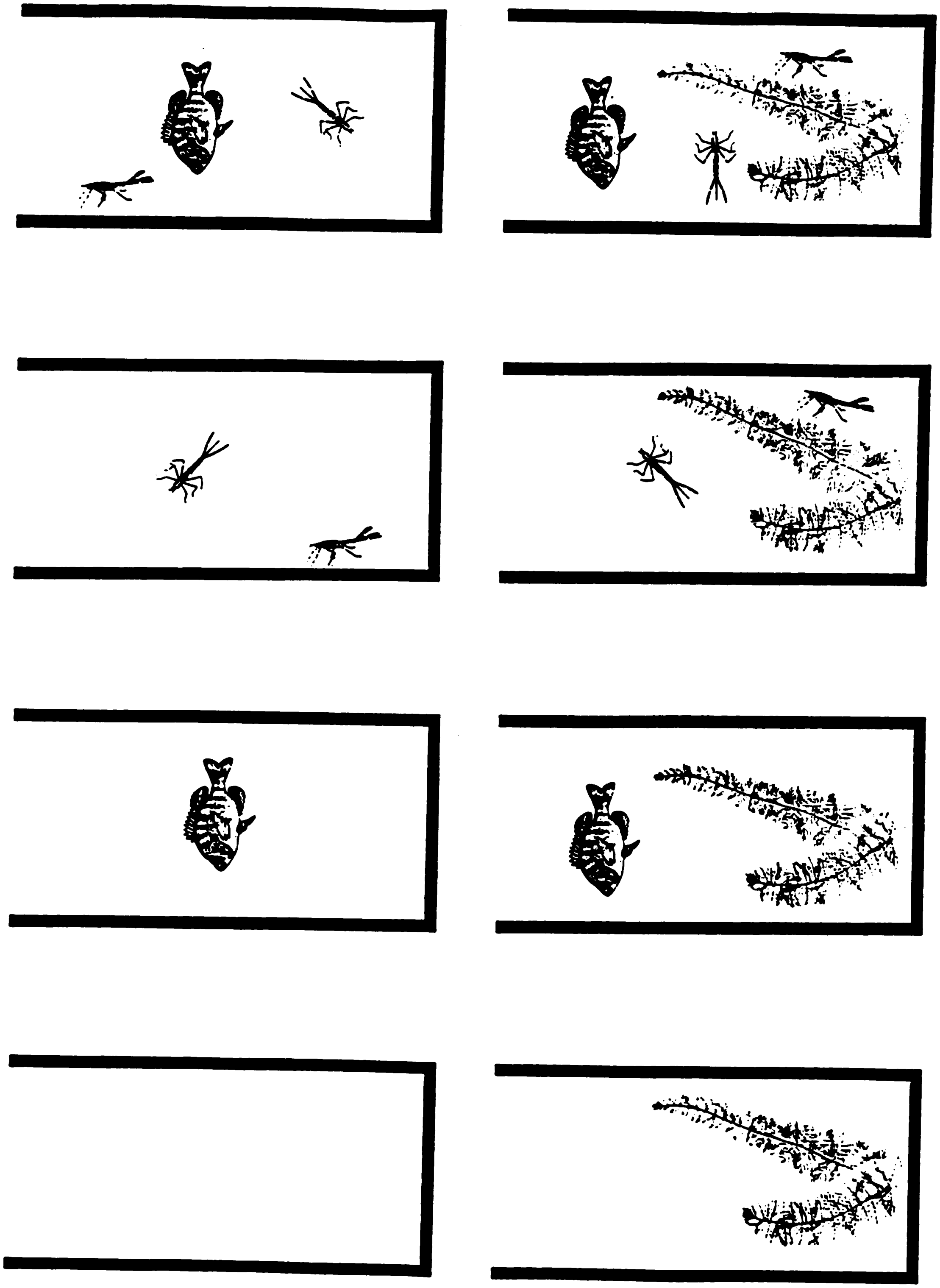

Figure 1

macrophyte material was thoroughly rinsed to remove attached invertebrates. Replicate bundles of rinsed macrophytes were treated with carbonated water and examined under a microscope to determine the efficiency of rinsing in removing microcrustaceans and their predators. Rinsing of the macrophytes was very effective with none of the microcrustaceans under study and only a few early instar damselfly larvae remaining. The very small numbers of damselflies recorded from the macrophyte-only treatments at the end of the experiment also attest to the success of rinsing macrophytes in the removal of animals. Damselfly treatments received 16 *Enallagma* larvae (13 mm ± 0.8 S.E. total length) to mimic the density of damselflies typically observed per square meter of lake bottom in local lakes (Chapter 1, McPeek 1989). Fish treatments consisted of one young-of-year *Lepomis spp.* (ca. 25-30 mm standard length). The stocking density of one fish per enclosure was high compared to most lakes (about twenty times higher than the average juvenile bluegill densities found in the littoral of nearby Lawrence Lake, $32/m^2$ versus $1.6/m^2$, respectively; Mittelbach 1988), so only very small bluegill were used.

I stocked microcrustaceans at natural densities (Chapter 1) into each enclosure. Animals were collected using an 80 µm mesh zooplankton net (30 cm diameter). Twenty-six containers each received the contents of one 2 m vertical tow from the littoral and one 2.5 m vertical tow from the limnetic zone. These containers of animals were then randomly assigned to each enclosure except for two which were preserved to determine initial stocking densities. At the end of seven days, all microcrustaceans were collected and preserved in sugar formalin for later counting. In order to quantify the changing densities of species within the enclosures over time, the population growth rate (r) was calculated for the five most common microcrustacean genera using the following equation:

$$r = [\ln(N_1)-\ln(N_0)]/7 \text{ days},$$

where $N_1$ = final densities and $N_0$ = initial stocking densities.

Multivariate analysis of variance (MANOVA) was used to test for effects of treatments on the population growth rates of the microcrustaceans found nearshore in the submersed macrophytes (*Simocephalus*, *Sida*), and the species characteristic of the intermediate, floating-leaved zones (*Bosmina*, *Ceriodaphnia*). The response of the open water species (*Daphnia*) was analyzed using univariate analysis of variance (ANOVA). *Diaphanosoma* (also an open water species) did not survive in any enclosures in numbers sufficient for inclusion in the analysis. *Chydorus* were present but not included in the analysis of this short-term experiment due to the large amounts of detritus found in the final samples and the resulting difficulty involved in counting them. The fish in one replicate of the fish-by-damselfly-by-macrophyte treatment did not survive and so this replicate was not included in the analyses. Since fish are potential predators on damselflies, damselfly larvae were collected and counted at the end of the experiment. A T-test was utilized to compare the mean survivorship of damselfly larvae in treatments with and without fish.

### *Macrophyte and Fish Predator Experiment*

Since fish and macrophytes were important factors influencing the microcrustacean habitat guilds in the first short-term experiment, I conducted an additional manipulation of just these two factors over a longer time period that would allow several generations of response by the microcrustaceans. There were three replicates of each treatment arranged in a 2 x 2 randomized-block factorial design for a total of 12 enclosures (Fig. 2). Each polyethylene enclosure (2.5 m deep, 1.1 m diameter) contained 2500 L of limnetic water and seston from which zooplankton had been removed using a 130 μm mesh net. The experiment was conducted over a four week period in July 1994 when the vegetative zones were well developed and young-of-year fish were achieving appreciable size and abundance. As in the first experiment, the microcrustaceans were collected from Lower Crooked Lake and the enclosures for the experiment were placed in an adjacent pond.

Figure 2. Schematic showing the treatments imposed in the longer-term, 2 x 2 block factorial design experiment. A mixed littoral and limnetic microcrustacean community was exposed to the presence and absence of macrophytes crossed with the presence or absence of bluegill sunfish (2).

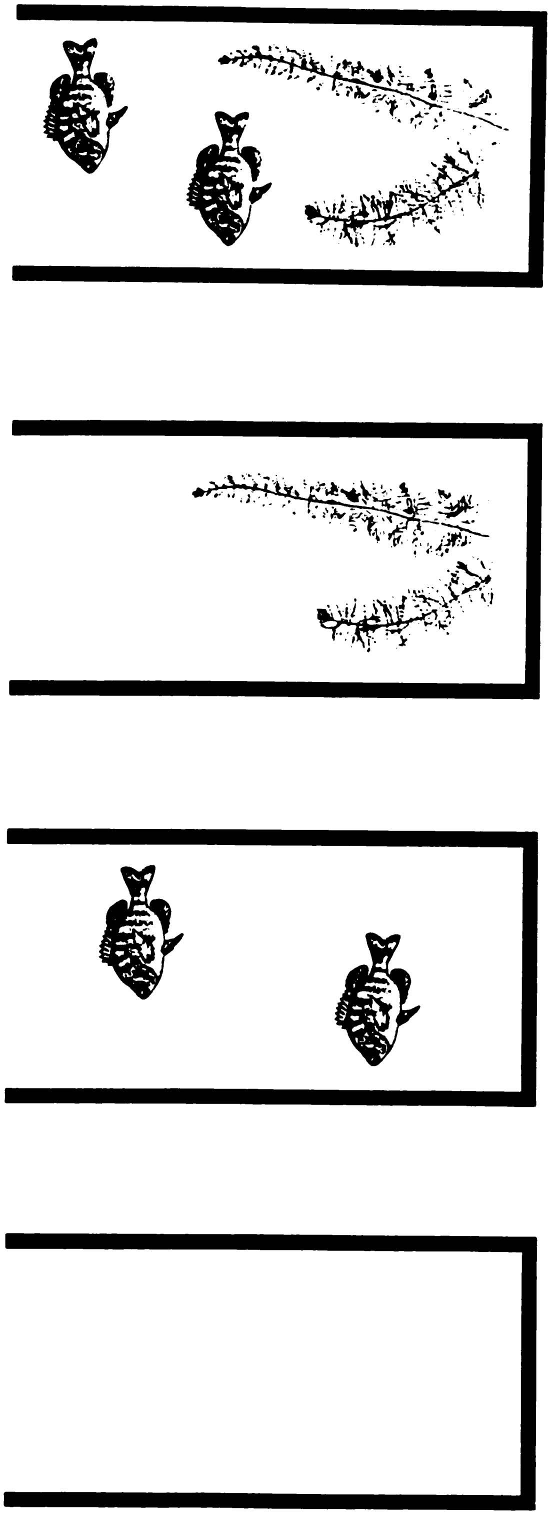

Figure 2

Macrophyte treatments consisted of bundles with 10-15 stems each of *Myriophyllum* (0.5-1 m long) which were weighted with stainless steel washers. Each enclosure received six bundles with the washers attached directly to the base so they sank to the bottom, and three bundles that had 1 m of fishing line between the washer and the base of the bundle to allow more of the water column to be filled with plants and, thereby, simulate natural conditions more closely. *Nymphaea* leaves were added to the surface of the macrophyte treatments to simulate natural shading in the littoral zone. Dried lily leaves were replaced with fresh ones, as necessary, throughout the course of the experiment. All macrophytes were thoroughly rinsed, as in the first experiment, to remove any attached invertebrates prior to placement in the enclosures. Predator treatments consisted of two young-of-year *Lepomis spp.* (25-30 mm standard length) added to each enclosure. A stocking density of two fish per enclosure for this experiment closely mimicked the average densities in the littoral of nearby Lawrence Lake ($2/m^2$ versus $1.6/m^2$, respectively; Mittelbach 1988). Microcrustaceans were given 24 hours to acclimate to the enclosures before fish were added.

A mixed littoral and limnetic microcrustacean community was stocked into the enclosures at natural densities (see Chapter 1). Animals were collected from the limnetic zone by taking two 2.5 m vertical tows using a 150 μm mesh zooplankton net (50 cm diameter). Littoral animals were collected by combining three 1.5 m vertical tows using an 80 μm mesh zooplankton net (30 cm diameter) and one 1.5 m vertical tow using a 500 μm mesh zooplankton net (42 cm diameter). Fourteen containers each received the combined limnetic assemblage and the combined littoral assemblage. The animals in each container were randomly assigned to an enclosure except for two containers which were preserved to estimate initial stocking densities.

The physico-chemical characteristics of the lake water differ between the vegetative and open water zones (see Chapter 1). Water chemistry parameters were measured to determine whether the enclosures mimicked the natural zonation patterns observed previously in the lake and whether the control enclosures mimicked the open water of the pond at the time of the experiment. Dissolved oxygen and temperature were measured using a YSI model 57 meter and polarographic sensor at 1 m depth in weeks 3 and 4 of the experiment. Light was measured at 1 m depth using a Li-Cor model LI-185B flat quantum photometer (week 4 only). Water samples were collected in 1 L plastic bottles at approximately 0.5 m depth and taken back to the laboratory for determination of pH (week 3 only).

In order to estimate the phytoplankton food resources available for the suspension feeding microcrustaceans, water samples were collected from 0.5 m below the surface during weeks 3 and 4. To measure particulate organic matter, water was filtered through Gelman A/E glass fiber filters and the ash-free dry weight was calculated after drying overnight at 55°C and placing in a muffle furnace for 50 minutes at 450°C. *In vivo* chlorophyll-*a* fluorescence was measured using a Turner fluorometer model 110 (Heaney 1978). In addition, chlorophyll-*a* was measured during week 3 using an ethanol extraction procedure (Welschmeyer 1994) and a Sequoia-Turner fluorometer model 450 equipped with narrow band filters. This measurement was then used to convert the *in vivo* chlorophyll-*a* measurements to μg/L.

Microcrustacean densities were sampled weekly using a collapsible tube sampler with a trap door and a net attached to the bottom (Knoechel and Campbell 1992) after thoroughly mixing the water in the enclosures to dislodge attached forms. The animals were preserved in sugar formalin solution for later counting.

I employed a hierarchical approach to the statistical testing for treatment effects on the microcrustacean assemblages. First, the response of the entire assemblage structure to macrophyte and fish treatments was tested after ordination of the data set. Since significant effects were found in this first analysis, I then tested the responses of each habitat guild spearately. Again, all three guilds showed significant responses so I then examined each species in separate analyses. In all three levels of statistical analysis, I treated data from different collection dates as repeated measures on the same experimental unit (enclosure). Considering the relatively few number of enclosures (12), it was important to reduce the number of sampling dates examined in order to achieve sufficient power. Since the densities of the seven species did not show any divergence in response to treatment until the second week of the experiment, I used only data from the last three weeks of the experiment in statistical analyses (except where noted).

I used a 2-dimensional, multidimensional scaling (MDS) to ordinate the densities of all seven species on the last three collection dates, in order to test for overall assemblage responses to the treatments. The MDS was performed on the Pearson correlation matrix of the log-transformed densities in order to standardize the variance and adjust for differences in density of small versus large species. Pearson correlation of the original variables to each of the 2 MDS dimensions was employed to aid in interpretation of the MDS ordination. Repeated measures ANOVAs were then performed on the first two dimensions of the MDS to see if treatment or time interactions significantly influenced the microcrustacean assemblage patterns.

Based on the MDS procedure, it was evident that microcrustacean assemblages as a whole diverged in response to the treatments, but this divergence varied with time. To examine how the three guilds performed with respect to the treatments, I performed repeated measures MANOVAs on the population growth rates (r) of the nearshore specialists (*Simocephalus*, *Sida*), the open-water species (*Chydorus*, *Diaphanosoma*), and the intermediate zone species (*Bosmina*, *Ceriodaphnia*). *Daphnia* was analyzed separately from the other open-water species because after the first two weeks of the experiment its densities were effectively zero and population growth rates could not be calculated. The following equation was used to calculate population growth rates:

$$r = [\ln(N_i)-\ln(N)_o]/t,$$

where $N_i$ = density from the weekly samples, $N_0$ = initial stocking density, and t = number of days from stocking. Finally, I conducted repeated measures ANOVAs on the species level in order to examine how the individual species within each guild performed in the different treatments. The Greenhouse-Geisser adjustment of p values was used in all repeated measures analyses to compensate for what amounted to only slight violations of the sphericity assumption.

Statistical analyses of both experiments were conducted using SYSTAT (MANOVA, repeated measures ANOVA, MDS; Wilkinson *et al.* 1992) and SAS (doubly-multivariate repeated measures design; SAS Institute Inc. 1989). Blocking had no significant effects in either experiment and was excluded from the final statistical models.

## RESULTS

### *Macrophyte and Two Predator Experiment*

The presence of fish in the damselfly treatment did not significantly affect the survivorship of the damselflies compared to those in the non-fish treatments ($t = 0.479$, $p= 0.643$; Fig. 3). This was true both in the presence and absence of macrophytes.
The short-term responses of the microcrustacean assemblages to fish and macrophytes were strong and varied with the type of guild present, while predation by damselfly larvae did not significantly affect any of the assemblages of microcrustaceans both in the presence and absence of fish predators. Microcrustaceans which dominate in the nearshore, submersed macrophyte zone (*Simocephalus*, *Sida*) were positively affected by

Figure 3. Mean number of damselfly larvae surviving to the end of the short-term experiment (± 1 S.E.). Note that 16 larvae were originally added to each enclosure. Circles = no predators, squares = damselfly predators, triangles = fish, stars = damselflies and fish.

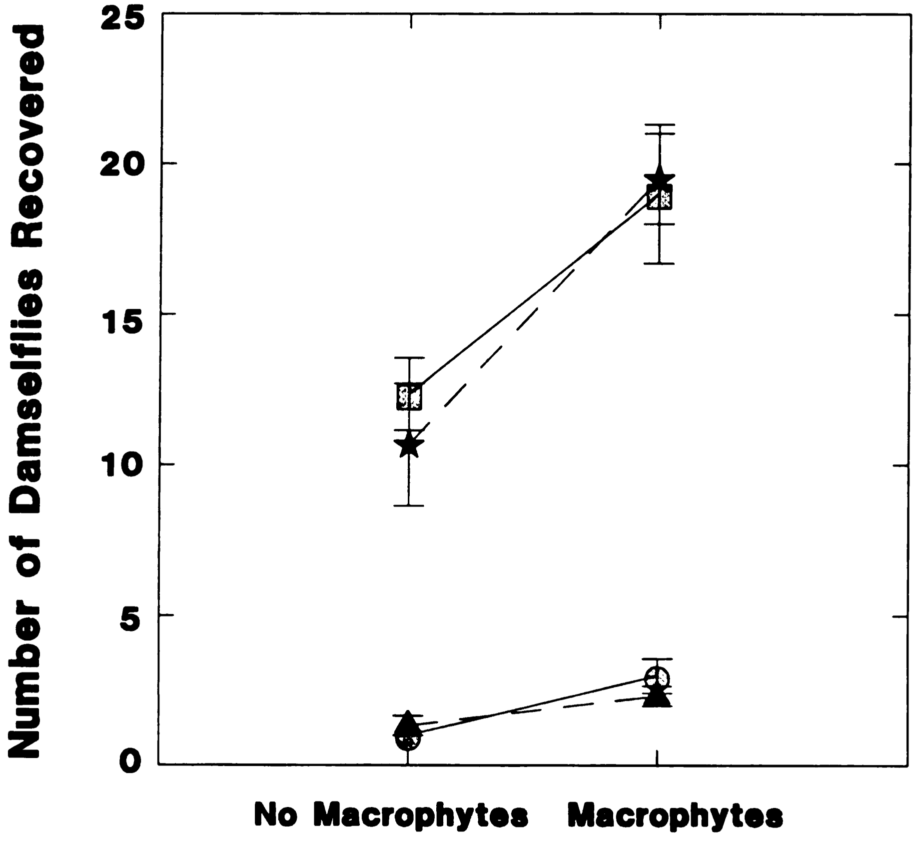
25
20
15
10
5
0
Number of Damselflies Recovered
No Macrophytes
Macrophytes

Figure 3

the presence of macrophytes in the enclosures (Wilk's λ F=10.539; d.f.=2,14; p=0.002, Fig. 4). There was no overall fish effect nor fish-by-macrophyte interaction observed for the nearshore guild. However, *Sida* strongly affected the MANOVA results and the response of *Simocephalus* is less clear cut with the fish tending to negate the positive effects of the macrophytes.

Species which dominate in the intermediate, floating-leaved macrophytes showed significant fish-by-plant interactions (Wilk's λ F=6.827; d.f.=2,14; p=0.009), with both species being significantly affected by fish, but only in the absence of macrophytes. However, the two species in this habitat guild responded to fish in opposite ways. In the absence of macrophytes, *Bosmina* tended to be positively affected by fish, while *Ceriodaphnia* tended to be negatively affected by fish (Fig. 5). Microcrustaceans from the open water, represented here by *Daphnia*, were negatively impacted by both fish (F=4.383, d.f.=1, p=0.054) and macrophytes (F=4.264, d.f.=1, p=0.057, Fig. 6). Unlike the intermediate guild, there is no evidence of an interaction effect despite the strong effects of both fish and macrophytes.

### *Macrophyte and Fish Predator Experiment*

The long-term macrophyte manipulation mimicked natural conditions found in the littoral and limnetic zones of the lake with regard to light and water chemistry. The enclosures without macrophytes had similar dissolved oxygen, pH, and light to that observed in the open water of the pond (Fig. 7). In enclosures with macrophytes,

Figure 4. Mean population growth rate (± 1 S.E.) for the nearshore guild (i.e., *Sida, Simocephalus*) in the short term experiment. Circles = no predators, squares = damselfly larvae, triangles = fish, stars = damselfly larvae and fish.

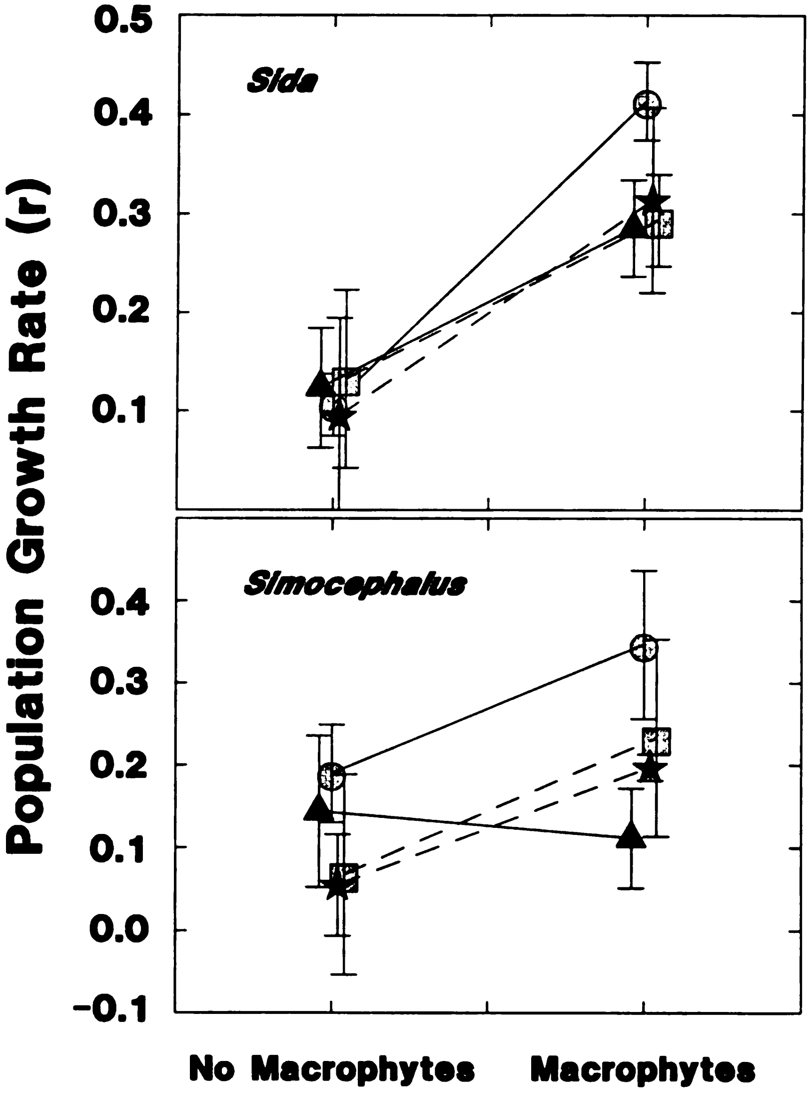
Population Growth Rate (r)
0.5
0.4
0.3
0.2
0.1
*Sida*
*Simocephalus*
0.4
0.3
0.2
0.1
0.0
-0.1
No Macrophytes
Macrophytes

Figure 4

Figure 5. Mean population growth rate (± 1 S.E.) for the intermediate guild (*Bosmina*, *Ceriodaphnia*) in the short term experiment. Circles = no predators, squares = damselfly larvae, triangles = fish, stars = damselfly larvae and fish.

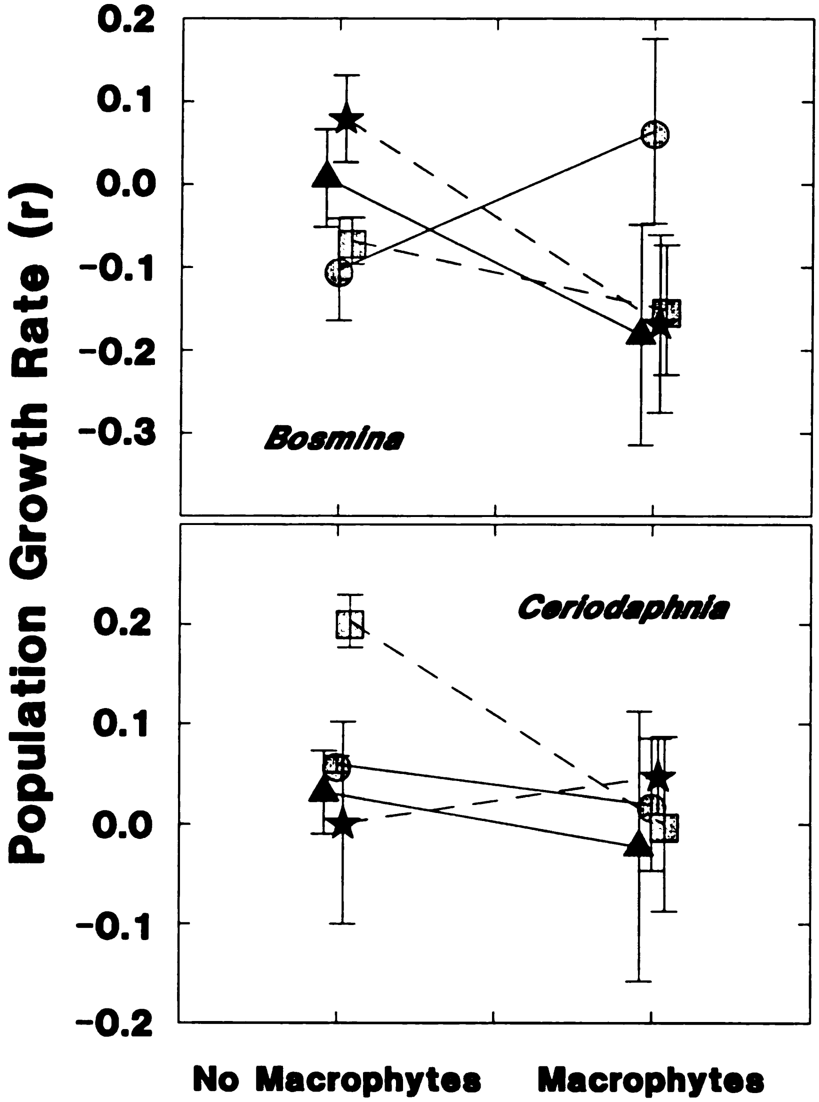
Population Growth Rate (r)
0.2
0.1
0.0
-0.1
-0.2
-0.3
Bosmina
0.2
0.1
0.0
-0.1
-0.2
Ceriodaphnia
No Macrophytes
Macrophytes

Figure 5

Figure 6. Mean population growth rate (± 1 S.E.) for *Daphnia* for the short term experiment. Circles = no predators, squares = damselfly larvae, triangles = fish, stars = damselfly larvae and fish.

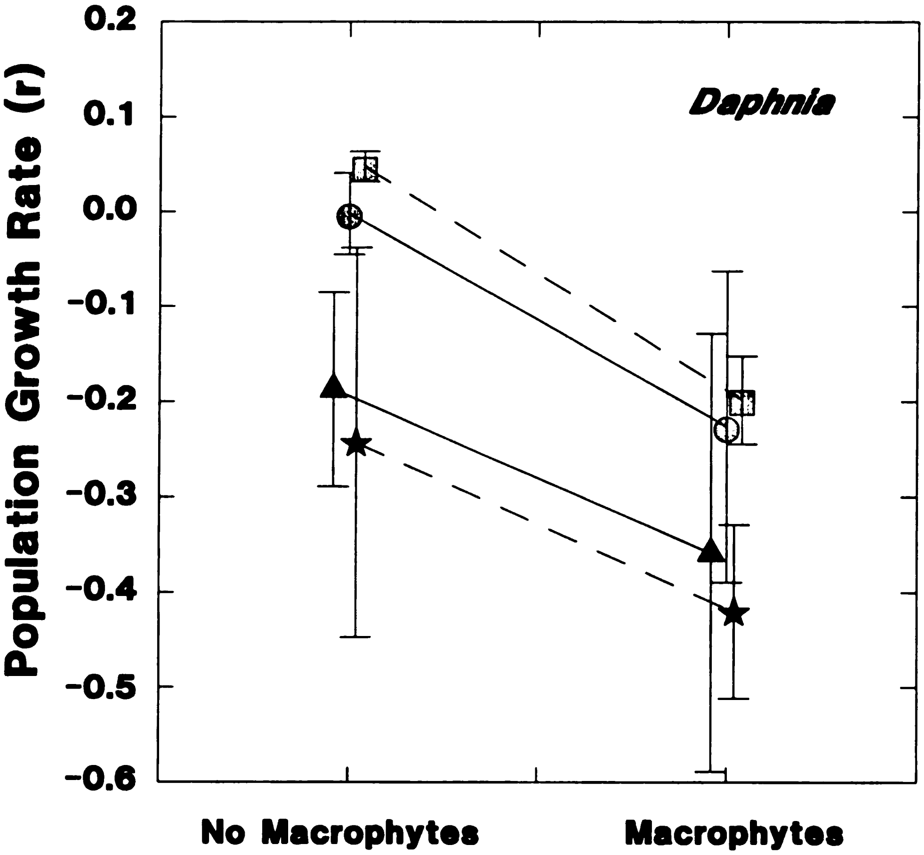
Daphnia
Population Growth Rate (r)
0.2
0.1
0.0
-0.1
-0.2
-0.3
-0.4
-0.5
-0.6
No Macrophytes
Macrophytes

Figure 6

dissolved oxygen and pH were reduced compared to enclosures without macrophytes (Fig. 7) in similar magnitude to differences in these parameters previously observed between the littoral and limnetic region of the lake (see Chapter 1). Macrophytes also lowered light levels at 1 m depth by about 75% compared to the non-macrophyte enclosures (Fig. 7). However, this amount of shading was not as extreme as the 96% reduction observed in the lilypad zone of the lake compared to the open water zone (see Chapter 1). This is probably an artifact of the enclosures being placed in the middle of the pond which allowed more diffuse light from the water surrounding the enclosures to enter the bags compared to the littoral zone which has extensive areas of similar shading.

The experimental manipulation also mimicked the differences in food resources found in the different zones in the lake. The presence of macrophytes reduced the food available for microcrustaceans in the enclosures (59% reduction in chlorophyll-*a* compared to the non-macrophyte enclosures; Fig. 8), even more so than in the lake itself (14% reduction in the lilypad zone compared to the open water zone; Chapter 1). Particulate organic matter was reduced by 49% in the macrophyte compared to non-macrophyte enclosures (Fig. 8). The enclosures without macrophytes had similar chlorophyll-*a* and particulate organic matter to that found in the open water of the pond (Fig. 8).

The MDS ordination captured 95% of the variance in assemblage differences among enclosures during the last three weeks, in a two dimensional representation. The first dimension was strongly correlated with the densities of many of the dominant members of the intermediate and open water guilds (i.e., *Bosmina*, *Ceriodaphnia*, *Daphnia*; Table

Figure 7. Mean percent saturation of dissolved oxygen, light intensity at 1 m depth (μEinsteins/$cm^2$/s), and pH (± 1 S.E.) for the long term experiment. Light bars = week 3, dark bars = week 4, Macro = macrophyte treatments, F*M = fish and macrophyte treatments. In comparison, the open water zone of the pond had 89 (week 3) and 76 (week 4) percent saturation of dissolved oxygen, a light intensity at 1 m depth of 45 μEinsteins/$cm^2$/s, and a pH of 8.4.

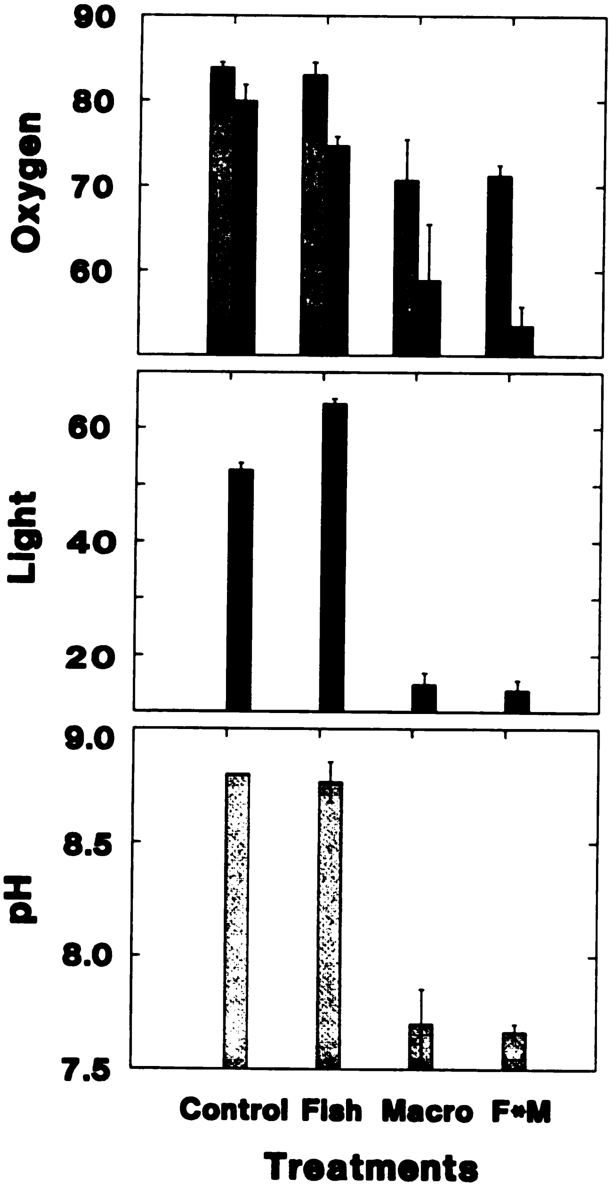
90
80
70
60
Oxygen
60
40
20
Light
9.0
8.5
8.0
7.5
pH
Control
Fish
Macro
F*M
Treatments

Figure 7

Figure 8. Mean chlorophyll-*a* (µg/L, ± 1 S.E.) and particulate organic matter (mg/L ash-free dry weight, ± 1 S.E.) for the long term experiment. Light bars = week 3, dark bars = week 4, Macro = macrophyte treatments, F*M = fish and macrophyte treatments. For comparison, the open water zone of the pond had chlorophyll-*a* levels of 6.5 (week 3) and 10.9 (week 4) µg/L and particulate organic matter of 2.9 (week 3) and 3.9 (week 4) mg/L ash-free dry weight.

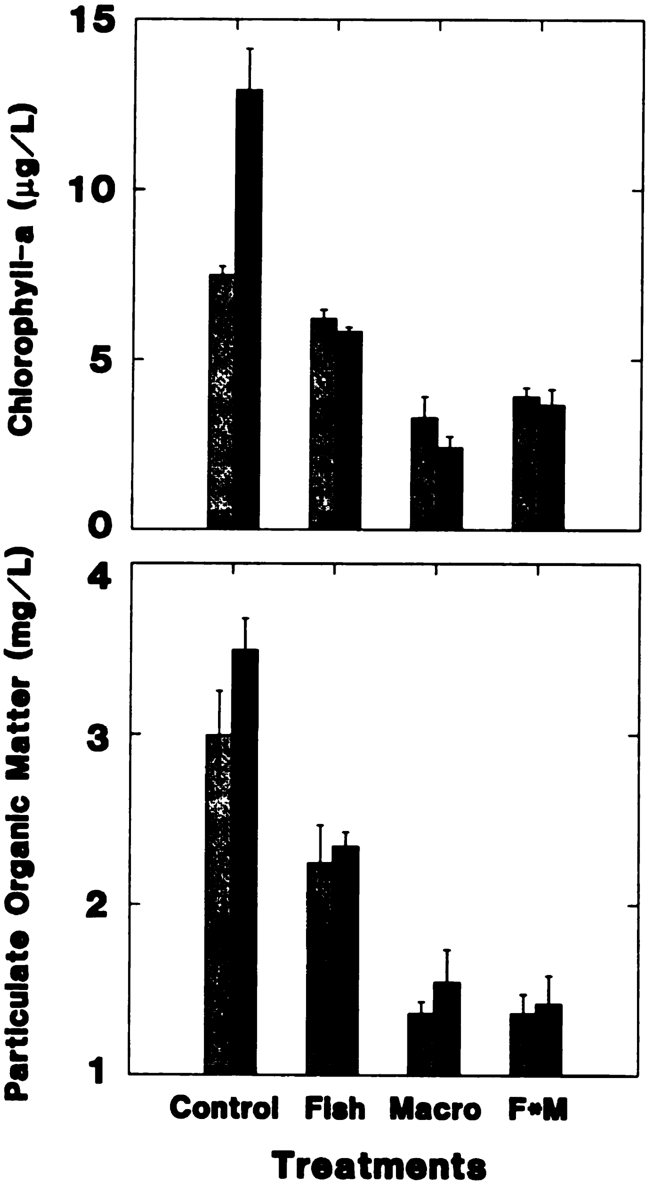
15
10
5
0
Chlorophyll-a (µg/L)
4
3
2
1
Particulate Organic Matter (mg/L)
Control
Fish
Macro
F*M
Treatments

Figure 8

1). This first component of assemblage structure was affected by fish and the fish-by-macrophyte interaction (Table 2). The second dimension of the MDS was strongly, positively correlated with the attached forms of microcrustaceans (i.e., *Simocephalus*, *Sida*) while being negatively correlated with the small-bodied, free-swimming forms (i.e., *Bosmina*, *Chydorus*; Table 1). This second dimension was affected significantly only by macrophytes. Based on the results of the MDS analysis, the treatments did cause an overall change in assemblage structure and did appear to influence the species and guild assemblages differentially. There was also a clear effect of time in the response of the assemblages to the treatments.

Repeated measures (M)ANOVAs were next employed to test whether guilds responded differentially to the treatments. The nearshore guild (*Simocephalus*, *Sida*) was positively affected by the presence of macrophytes (Table 3; Fig. 9). However, there was also a fish-by-macrophyte interaction caused by fish having a negative effect in the absence of macrophytes but no effect in the presence of macrophytes (Table 3; Fig. 9). There were effects of time, but no time-by-treatment interactions (Table 3). Hence, the interpretation of the between-enclosure results (macrophytes and fish-by-macrophytes treatments) is not confounded by the within-enclosure temporal population dynamics. *Simocephalus* weighed heavily in the MANOVA compared to *Sida*, with *Simocephalus* exhibiting a significant fish, macrophyte, and fish-by-macrophyte interaction, while *Sida* was only significantly affected by macrophytes (Table 4).

The intermediate, floating-leaved vegetation guild (*Bosmina*, *Ceriodaphnia*) was negatively impacted by the presence of macrophytes, but was not affected by fish nor a

Figure 9. Mean population growth rates (± 1 S.E.) for the nearshore guild (i.e., *Sida*, *Simocephalus*) for the last 3 weeks of the long term experiment. Macro = macrophyte treatments, F*M = fish and macrophyte treatments.

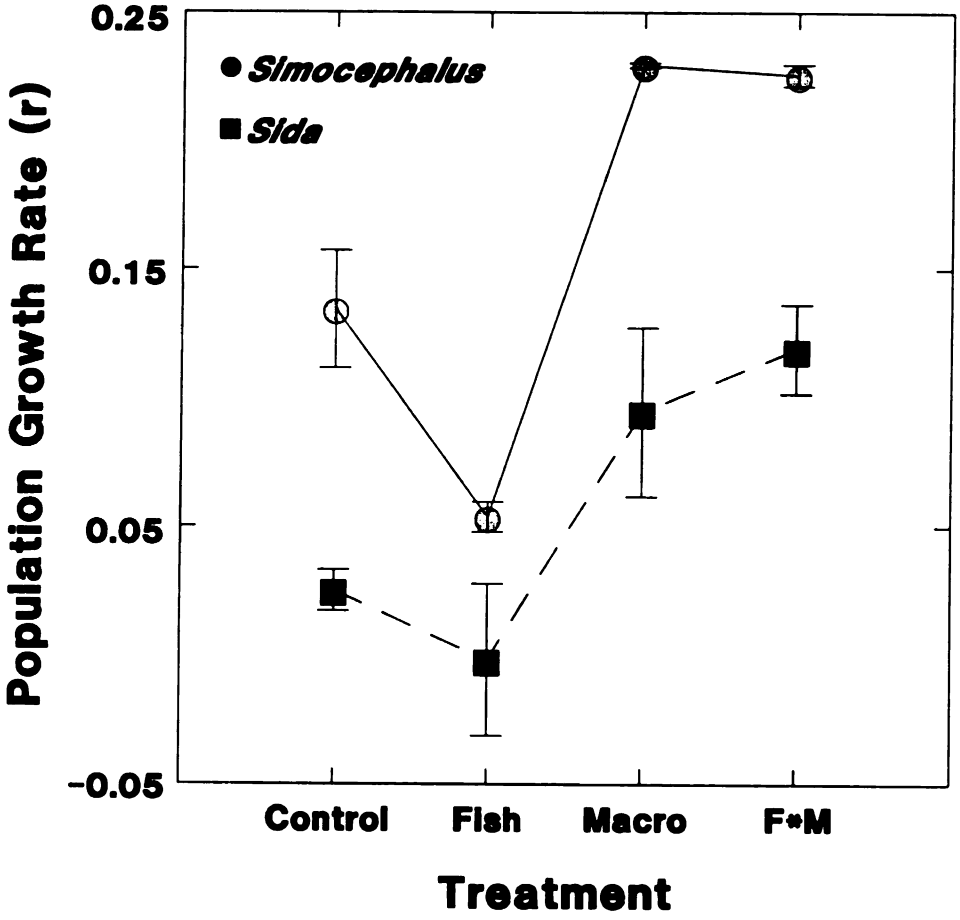
● Simocephalus
■ Sida
Population Growth Rate (r)
0.25
0.15
0.05
-0.05
Control
Fish
Macro
F*M
Treatment

Figure 9

Table 1. Results of the Pearson correlation of the first two dimensions of the multidimensional scaling procedure with the density of each microcrustacean species in the last three weeks of the experiment. Dashed lines indicate non-significant values, while the values given are significant at the $\alpha \leq 0.05$ level.

| **Species** | **Dimension 1** | **Dimension 2** |
|---|---|---|
| *Sida* | --- | 0.39 |
| *Simocephalus* | --- | 0.54 |
| *Bosmina* | -0.33 | -0.79 |
| *Ceriodaphnia* | -0.87 | --- |
| *Chydorus* | --- | -0.38 |
| *Diaphanosoma* | --- | --- |
| *Daphnia* | -0.50 | --- |

Table 2. Results of the repeated measures ANOVA for the first two dimensions of the multidimensional scaling procedure with the main effects of fish and macrophytes and their interaction for the last three weeks of the experiment.

| | **Dimension 1** | | **Dimension 2** | |
|---|---|---|---|---|
| Source | MS | F | MS | F |
| **Between Subjects** | | | | |
| Fish | 0.45 | 7.75* | 0.61 | 0.96 |
| Macrophytes | 0.18 | 3.10 | 3.48 | 5.51* |
| Fish*Macrophytes | 0.75 | 12.95** | 0.63 | 1.00 |
| Error | 0.06 | | 0.63 | |
| **Within Subjects** | | | | |
| Time | 5.81 | 58.46*** | 0.40 | 2.04 |
| Time*Fish | 2.15 | 21.63*** | 0.18 | 0.94 |
| Time*Macrophytes | 0.62 | 6.28** | 0.04 | 0.18 |
| Time*Fish*Macrophytes | 0.27 | 2.70 | 0.38 | 1.96 |
| Error | 0.10 | | 0.20 | |

Table 3. Results of the repeated measures MANOVAs for the three microcrustacean guilds with main effects of fish and macrophytes and their interaction for the last three weeks of the experiment. Nearshore guild = *Simocephalus* and *Sida*, intermediate guild = *Bosmina* and *Ceriodaphnia*, open water guild = *Diaphanosoma* and *Chydorus*.

| | **Nearshore** | | **Intermediate** | | **Open Water** | |
|---|---|---|---|---|---|---|
| Source | d.f. | Wilk's F | d.f. | Wilk's F | d.f. | Wilk's F |
| **Between Subjects** | | | | | | |
| Fish | 1, 8 | 3.32 | 1, 8 | 0.26 | 1, 8 | 2.48 |
| Macrophytes | 1, 8 | 91.83**** | 1, 8 | 12.26** | 1, 8 | 31.92*** |
| Fish*Macrophytes | 1, 8 | 7.21* | 1, 8 | 1.89 | 1, 8 | 0.84 |
| **Within Subjects** | | | | | | |
| Time | 4, 5 | 8.15* | 4, 5 | 61.24*** | 4, 5 | 10.85** |
| Time*Fish | 4, 5 | 1.61 | 4, 5 | 10.95** | 4, 5 | 5.72* |
| Time*Macrophytes | 4, 5 | 0.97 | 4, 5 | 8.74* | 4, 5 | 4.84 |
| Time*Fish*Macrophytes | 4, 5 | 1.12 | 4, 5 | 7.74* | 4, 5 | 2.39 |

fish-by-macrophyte interaction (Table 3, Fig. 10). However, the guild and individual species each displayed transient effects of fish (i.e., time-by-fish interaction; Table 3 and 4) during the experiment; the general pattern was that fish benefitted each species (Fig. 11). This guild also showed time-by-macrophyte and time-by-fish-by-macrophyte interactions (Table 3) which the species did not display individually (Table 4). In general, this guild displayed complex dynamics in response to both fish and macrophytes but overall the macrophytes negatively impacted and fish benefitted or had no effect its on population growth rates (Table 4).

The open water guild (*Diaphanosoma*, *Chydorus*) also performed very poorly in the presence of macrophytes (Table 4, Fig. 12). This guild as a whole had only a weak time-by-treatment (fish) interaction caused by fish being beneficial to population growth rates. Each individual species also showed significant negative macrophyte effects (Table 4), but only *Diaphanosoma* was significantly (positively) affected by fish (Fig. 12). *Diaphanosoma* also showed a significant time-by-fish interaction, declining in all non-fish treatments through time while increasing in the fish enclosures (Fig. 11, Table 4). Hence, fish provided a positive influence on their rates of population growth but only after some initial time delay. In addition, *Diaphanosoma* showed a weak time-by-macrophyte interaction but with no consistent trend evident. *Daphnia* could not be included in the analyses with the other two open water forms since it performed so poorly in all enclosures that it was no longer present after week 2. Looking only at the first two weeks, however, *Daphnia* performed even more poorly in the presence of fish and showed a significant time and time by fish interaction (Table 4, Fig. 13).

Figure 10. Mean population growth rates (± 1 S.E.) for intermediate guild (i.e., *Ceriodaphnia*, *Bosmina*) for the last 3 weeks of the long term experiment. Macro = macrophyte treatments, F*M = fish and macrophyte treatments.

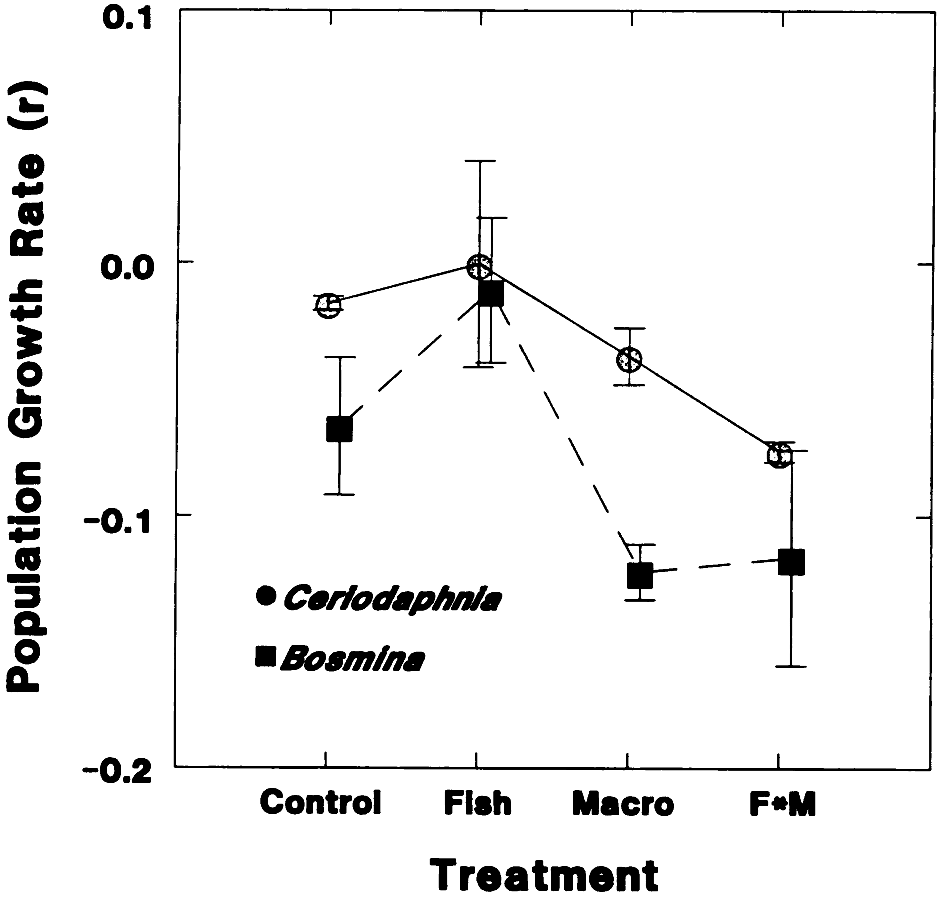
Population Growth Rate (r)
0.1
0.0
-0.1
-0.2
Control
Fish
Macro
F*M
Treatment
● Ceriodaphnia
■ Bosmina

Figure 10

Figure 11. Mean population densities (± 1 S.E.) for representative species over the course of the long term experiment. Circles = controls, triangles = fish, squares = macrophytes, stars = fish and macrophyte treatments.

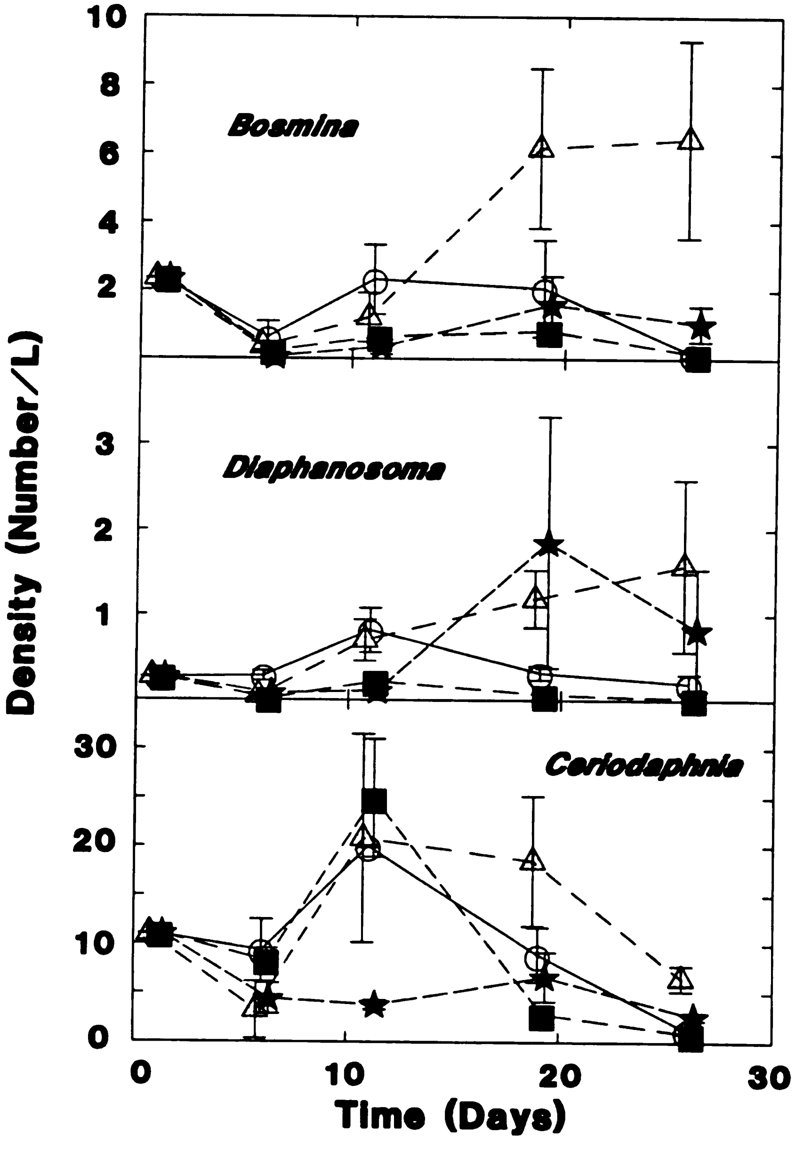
Bosmina
Diaphanosoma
Ceriodaphnia
Density (Number/L)
Time (Days)
10
8
6
4
2
3
2
1
30
20
10
0
0
10
20
30

Figure 11

Table 4. Results of the repeated measures ANOVAs for the individual species with main effects of fish and macrophytes and their interaction for the last three weeks of the experiment.

**Nearshore Guild**

| | ***Simocephalus*** | | ***Sida*** | |
|---|---|---|---|---|
| Source | MS | F | MS | F |
| **Between Subjects** | | | | |
| Fish | 0.02 | 12.36** | 0.00 | 0.00 |
| Macrophytes | 0.16 | 123.42*** | 0.08 | 15.63** |
| Fish*Macrophytes | 0.01 | 10.18** | 0.01 | 1.14 |
| Error | 0.00 | | 0.01 | |
| **Within Subjects** | | | | |
| Time | 0.08 | 22.85*** | 0.01 | 2.13 |
| Time*Fish | 0.01 | 2.55 | 0.01 | 2.11 |
| Time*Macrophytes | 0.00 | 0.69 | 0.01 | 2.14 |
| Time*Fish*Macrophytes | 0.01 | 2.25 | 0.01 | 2.94 |
| Error | 0.00 | | 0.01 | |

**Intermediate Guild**

| | ***Bosmina*** | | ***Ceriodaphnia*** | |
|---|---|---|---|---|
| Source | MS | F | MS | F |
| **Between Subjects** | | | | |
| Fish | 0.01 | 1.01 | 0.00 | 0.27 |
| Macrophytes | 0.06 | 7.63* | 0.02 | 4.99* |
| Fish*Macrophytes | 0.01 | 0.66 | 0.01 | 1.57 |
| Error | 0.01 | | 0.00 | |
| **Within Subjects** | | | | |
| Time | 0.04 | 9.21** | 0.02 | 5.37* |
| Time*Fish | 0.04 | 8.59** | 0.04 | 9.59** |
| Time*Macrophytes | 0.01 | 2.00 | 0.00 | 0.29 |
| Time*Fish*Macrophytes | 0.00 | 0.15 | 0.00 | 1.21 |
| Error | 0.00 | | 0.00 | |

Table 4 (cont'd).

| | **Open Water Guild** | | | | | |
|---|---|---|---|---|---|---|
| | ***Chydorus*** | | ***Diaphanosoma*** | | ***Daphnia*** | |
| Source | MS | F | MS | F | MS | F |
| **Between Subjects** | | | | | | |
| Fish | 0.00 | 0.66 | 0.04 | 5.04* | 0.17 | 31.00*** |
| Macrophytes | 0.05 | 17.43** | 0.10 | 13.58** | 0.00 | 0.59 |
| Fish*Macrophytes | 0.00 | 0.99 | 0.00 | 0.16 | 0.01 | 1.29 |
| Error | 0.00 | | 0.01 | | 0.01 | |
| **Within Subjects** | | | | | | |
| Time | 0.01 | 3.90 | 0.01 | 1.96 | 0.96 | 96.20*** |
| Time*Fish | 0.00 | 1.78 | 0.03 | 11.48** | 0.06 | 5.74* |
| Time*Macrophytes | 0.00 | 1.90 | 0.01 | 4.00* | 0.00 | 0.11 |
| Time*Fish*Macrophytes | 0.00 | 0.45 | 0.01 | 2.67 | 0.00 | 0.00 |
| Error | 0.00 | | 0.00 | | 0.01 | |

# DISCUSSION

The two experiments I conducted consider different time scales of response by the cladoceran assemblages to the predator and macrophyte treatments, yet lead to similar conclusions. Macrophytes and fish predators are both important factors influencing the composition of microcrustacean assemblages, but different taxa respond in fundamentally different ways to the interaction of these two factors. Further, guilds of microcrustaceans categorized by their habitat use also had distinct patterns of response to fish and macrophytes, suggesting that these two factors contribute to the horizontal partitioning of habitats by microcrustaceans in lakes.

The presence of macrophytes benefitted the two-species guild of nearshore specialists (i.e., *Simocephalus*, *Sida*) irrespective of whether fish were present or absent. In the long-term experiments, macrophytes also provide a refuge from fish predation for this guild; in the absence of macrophyte structure fish decimated the populations of nearshore taxa, but with macrophytes present, fish predation was essentially unimportant. Hence, this guild can be considered a true vegetation specialist, performing better in the presence of macrophytes even in the absence of predators, and requiring macrophytes in the presence of an effective, visually-feeding, fish predator.

Figure 12. Mean population growth rates (± 1 S.E.) for open water guild (i.e., *Diaphanosoma, Chydorus*) for the last 3 weeks of the long term experiment. Macro = macrophyte treatments, F*M = fish and macrophyte treatments.

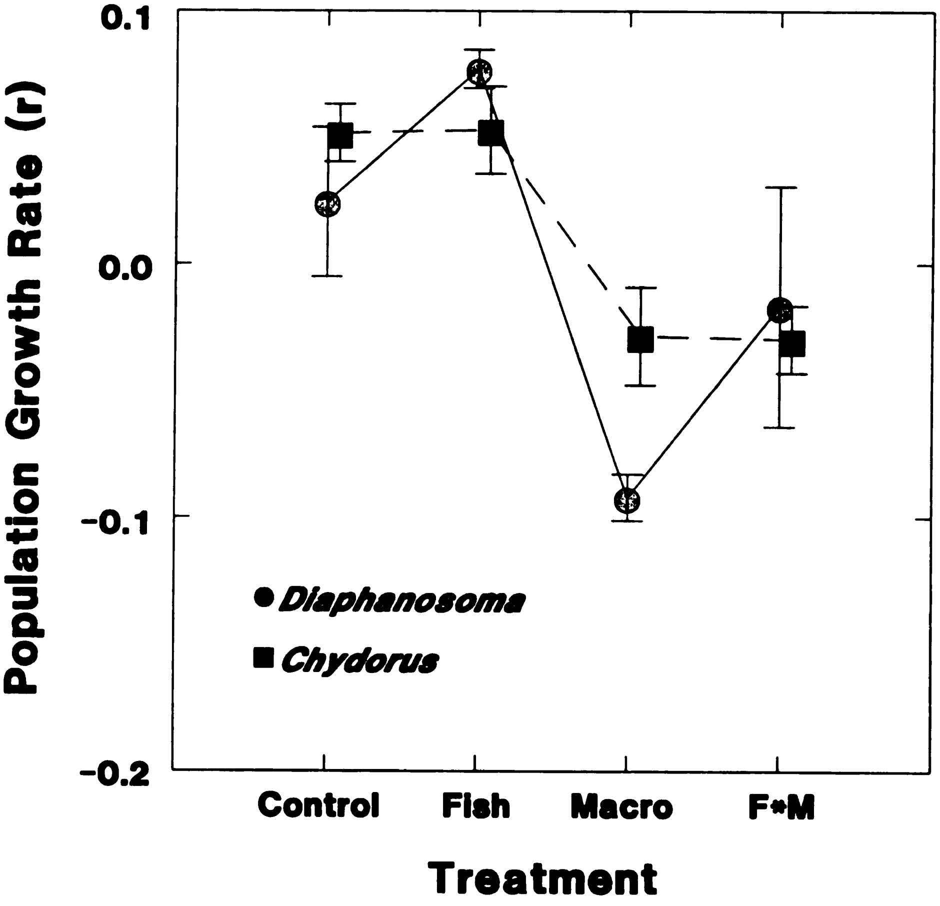
0.1
0.0
-0.1
-0.2
Population Growth Rate (r)
● Diaphanosoma
■ Chydorus
Control
Fish
Macro
F*M
Treatment

Figure 12

Figure 13. Mean population growth rates (± 1 S.E.) of *Daphnia* for the first 2 weeks of the long term experiment (after which the populations crashed and growth rates could not be calculated). Macro = macrophyte treatments, F*M = fish and macrophyte treatments.

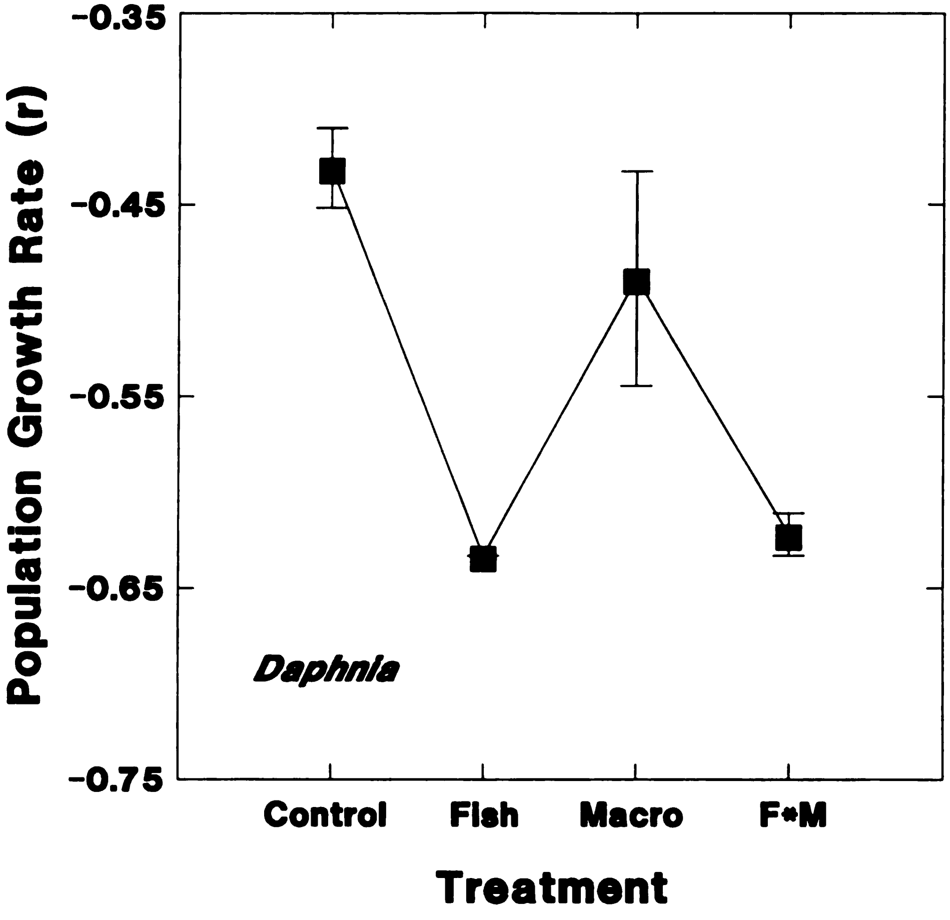
-0.35
-0.45
-0.55
-0.65
-0.75
Population Growth Rate (r)
Daphnia
Control
Fish
Macro
F*M
Treatment

Figure 13

In contrast to the nearshore guild, the guild of species that typically dominate in the lily pad and transitional vegetative zones of lakes (i.e., *Bosmina*, *Ceriodaphnia*) did not preform as well in the presence of macrophytes in the long term experiment. Even more surprising was the observation that this intermediate-zone guild was not strongly affected by fish predation. In fact, the only effects of fish were as time interactions that acted to enhance the population growth rates of this guild. Since this fish benefit was particularly strong in the absence of macrophytes (time-by-fish-by-macrophyte effect), it suggests that the benefits may be due to fish reducing the abundance of other taxa of microcrustaceans (i.e., the nearshore guild). This supports the previous evidence of competition which was observed with the constriction of habitat utilized by this guild on seasonal basis (Chapter 1). The presence of fish may also indirectly benefit cladocerans via nutrient regeneration which can, in turn, increase algal growth providing more food for the cladocerans to consume (Vanni *et al.* 1997).

The open-water guild (i.e., *Daphnia, Diaphanosoma*, *Chydorus*) was also negatively impacted by the presence of macrophytes. The species within the open water guild responded in very different ways to fish predation; the smaller-bodied, typically dominant summer species (i.e., *Diaphanosoma*) was positively affected, while the larger-bodied, dominant fall species (i.e., *Daphnia*) was strongly negatively impacted by fish. The differential response to fish within this guild may contribute to the patterns of seasonal succession observed.

The positive effect of macrophytes on the nearshore guild (*Simocephalus*, *Sida*) may be related to their ability to attach to macrophytes while filter-feeding. This attachment behavior can reduce their chances of being found and eaten by fish (Beklioglu and Moss

1996), but on the other hand, may increase their chances of being found by invertebrate predators such as damselflies, which can significantly deplete their populations (Johnson, *et al.* 1987). The results of this study confirm that the presence of macrophytes does negate the negative effect of fish on these taxa, but whether this is due to the attaching behavior of the microcrustaceans or to the reduced foraging efficiency of fish with increased habitat complexity is unknown. The use of macrophytes by the nearshore guild as attachment sites may also benefit them by providing resting sites while they filter feed. Due to the shape of their body (e.g., more robust carapace, smaller antennae than other cladocerans, reduction of abdominal spines), swimming by these species is considered to be much more energetically costly than for open-water species (Thomas 1963, Fryer, 1991).

All three habitat guilds are composed of suspension-feeding cladocerans and while there could be some resource partitioning by food type, there is potential for diet overlap and, hence, strong exploitative competition. The negative effect of macrophytes on the open water and intermediate guilds may be influenced by the reduction in phytoplankton resources in the presence of macrophytes, as suggested in Chapter 1 and by Kairesalo (1980). In addition, macrophytes may negatively influence these two guilds via the release of allelopathic chemicals (as observed by Pennak 1973, Lauridsen and Lodge 1996). However, my experimental design does not allow me to tease apart the relative contribution of each of these factors and their potential role in determining the habitat selection of this guild.

To date, the literature concerning habitat selection of microcrustaceans has demonstrated both beneficial and negative impacts by macrophytes. Cladoceran biomass

can be positively related to the density of macrophytes in shallow lakes (Schriver *et al.* 1995). Macrophytes, at times, serve as a refuge for zooplankton against predation by decreasing fish foraging effciency with increasing structure and decreasing light levels (Crowder and Cooper 1982, Diehl 1988, Dionne and Folt 1991) or by reducing low oxygen levels below those tolerated by fish (Davis 1975). Timms and Moss (1984) found that microcrustacean species migrate into the littoral during the day to avoid fish predation. However, in Lower Crooked Lake, I observed diel horizontal migration in only one species (i.e., *Ceriodaphnia*) and it migrated in the opposite direction, moving to the open water during the day (Chapter 1). Even though macrophyte beds may provide more hiding places, microcrustacean biomass can decrease earlier in the summer in the littoral compared to the limnetic zone due to fish predation (Vuille 1991). Juvenile fish often use the macrophyte zones as a refuge from their predators and can, in turn, change the macrophyte zones to population sinks rather than refuges for microcrustaceans when fish fry densities are high (Fairchild 1982, Boikava 1986, Whiteside 1988, Gliwicz and Rykowska 1992). As the density of fish in the limnetic zone fluctuates from year to year, it can affect the habitat selection of microcrustaceans. Cryer and Townsend (1988) found that in years of low fish density, free-swimming microcrustaceans favored the limnetic zone, while in years of high fish density they favored the littoral. Finally, artificial macrophytes, when first added to a lake, can act as refuges and allow higher densities of *Daphnia* and *Ceriodaphnia* to exist, but in the long term (3 years) population densities and size structure became similar in and out of the refuges (Irvine *et al.* 1990). It is still unclear how general or predictable microcrustacean responses to differences in the density of fish predators and the amount of habitat complexity may be and how this will affect predictions concerning where species will choose to live or be able to survive.

I had expected that damselfly larvae would prove to be effective predators on at least the nearshore guild of microcrustaceans, but found no strong evidence for this effect in the short-term experiment. This was probably not a result of using too few larvae per enclosure, as they were stocked in the range of natural densities found in the area (McPeek 1990), and other studies have shown no significant effect of low versus high densities of damselflies on their prey populations in experimental enclosures (Johnson, *et al.* 1987). Based on previous feeding trials with various species of damselfly larvae, the *Enallagma* used in this experiment were of sufficient size to capture even the larger-bodied *Simocephalus* and *Sida* (Johnson 1973, McPeek 1989, Havel *et al.* 1993). However, the experiment was run in the early fall when damselflies were still fairly small and their foraging rates may have been too low to have had much impact on microcrustacean populations. It is also possible that the short duration of this experiment did not allow the damselflies to thoroughly explore or utilize the perch sites available higher up in the water column of the macrophyte treatments. Sarnelle (1997) found that results from longer-term, large enclosure experiments can more closely match the ecology or dynamics observed in lakes compared to those results from short-term, small enclosure experiments. Longer term experiments may be needed to examine the potential impacts of damselflies on microcrustacean communities.

Invertebrate and vertebrate predation can change prey behavior in different ways. Watt and Young (1994) found that some zooplankters tend to migrate horizontally in the presence of invertebrate predators while migrating vertically in the presence of fish. My study only looked at the effects of one of the major invertebrate predators and how it interacted with the fish predators to affect the prey communities. Other common invertebrate predators (e.g., *Chaoborus* and *Leptodora*) have very different distributions in the lake and very different modes of foraging. They could be important in determining habitat selection by the prey and may interact with the fish predators in very different ways.

Both short- and long-term experiments lead to similar conclusions about the differential impact of macrophytes on habitat guilds. However, fish effects were not consistent between experiments. Apparent discrepancies between my short- and long-term experiments in terms of fish effects include 1) fish predation was not important for the nearshore guild in the short-term, but was in the long-term experiment, and 2) fish predation was only important as a time interaction (transient effect) on the intermediate guild in the long-term experiment, but it was important as an interaction effect (fish-by-macrophyte) in the short-term. A likely explanation for both of these discrepancies is depletion of preferred prey (e.g., *Simocephalus*, *Daphnia*) in the long-term, but not the short-term experiment. In the short-term experiment, the fish fed primarily on the swimming prey (e.g., *Daphnia* and *Ceriodaphnia*), even to the extent that there was no impact on the density of damselflies. This behavior was probably driven by the relative abundance of *Daphnia* in the short-term experiment compared to the long-term experiment, where fish effects were strongest on the attached (nearshore guild) species. These results suggest caution in inferring long-term effects of predation from short-term experiments in general. Foraging behaviors are apt to change with alternative prey and selective predation can have indirect effects through changes in competitive interactions.

The presence of macrophytes and fish predators interacted to affect the three microcrustacean assemblages in different ways and strongly influenced the structure of microcrustacean communities. These factors may contribute to the habitat selection observed along a horizontal gradient from nearshore to offshore. The density of fish predators and macrophytes may play an important role in habitat selection by microcrustaceans. Differences in food quantity or quality caused by the presence or absence of macrophytes may also contribute to determining microcrustacean distributions. More work examining the role of other major invertebrate predators is needed to see how they interact with macrophytes to impact the prey communities.

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# APPENDICES

# APPENDIX A

APPENDIX A. Abundance (catch per unit effort) of the macroinvertebrates (mean ± S.E.). All samples were collected using three standardized sweeps with a 650 μm mesh net. Zones refer to the different vegetative habitats found from nearshore to offshore as described in Chapter 1, Figure 1.

**Lux Arbor Pond 6 – Summer (25 August 1992)**

| **Taxon** | **Zone 1 (n=4)** | **Zone 2 (n=4)** | **Zone 3 (n=4)** | **Zone 4 (n=4)** |
|---|---|---|---|---|
| Odonata | | | | |
| Coenagrionidae | 1.5 (0.5) | 1.0 (1.0) | 0 | 0 |
| Libellulidae | 0.3 (0.3) | 0.3 (0.3) | 0.3 (0.3) | 0 |
| Diptera | | | | |
| Chironomidae | 1.5 (0.6) | 3.0 (1.3) | 1.8 (0.9) | 0 |
| Ceratopogonidae | 0.8 (0.5) | 0.8 (0.5) | 0 | 0 |
| Trichoptera | 0.3 (0.3) | 0.5 (0.3) | 0 | 0 |
| Ephemeroptera | 0.5 (0.5) | 0.5 (0.3) | 0.3 (0.3) | 0 |
| Coleoptera | | | | |
| Haliplidae | 0.5 (0.3) | 0 | 0.5 (0.5) | 0 |

**Lower Crooked Lake – Fall (17 October 1992)**

| **Taxa** | **Zone 1 (n=2)** | **Zone 2 (n=2)** | **Zone 3 (n=6)** | **Zone 4 (n=6)** |
|---|---|---|---|---|
| Odonata | | | | |
| Coenagrionidae | 1.5 (0.5) | 1.0 (0.0) | 0 | 0 |
| Diptera | | | | |
| Chironomidae | 0.5 (0.5) | 0 | 0 | 0 |
| Ceratopogonidae | 0 | 0.5 (0.5) | 0 | 0 |
| Trichoptera | 0 | 1.5 (1.5) | 0 | 0 |

APPENDIX A. (continued).

**Lux Arbor Pond 7 – Fall (23 & 28 September 1992)**

| **Taxa** | **Zone 1 (n=6)** | **Zone 2 (n=6)** | **Zone 3 (n=4)** | **Zone 4 (n=4)** |
|---|---|---|---|---|
| Odonata | | | | |
| Coenagrionidae | 12.7 (2.1) | 6.2 (1.2) | 4.3 (1.0) | 0.3 (0.3) |
| Lestidae | 1.0 (0.4) | 0 | 0 | 0 |
| Libellulidae | 2.2 (0.5) | 0.8 (0.2) | 0 | 0.3 (0.3) |
| Diptera | | | | |
| Chironomidae | 0.2 (0.2) | 0.3 (0.2) | 0 | 0.5 (0.3) |
| Ceratopogonidae | 0 | 0.2 (0.2) | 0 | 0 |
| Trichoptera | 0.8 (0.3) | 0.7 (0.5) | 1.8 (1.8) | 5.0 (4.4) |
| Ephemeroptera | 6.5 (1.3) | 3.2 (0.9) | 5.5 (2.8) | 0.5 (0.5) |
| Hemiptera | | | | |
| Notonectidae | 0.2 (0.2) | 0 | 0 | 0 |
| Pleidae | 0.3 (0.2) | 0 | 0 | 0 |

**Middle Crooked Lake – Fall (1 October 1992)**

| **Taxa** | **Zone 1 (n=4)** | **Zone 2 (n=6)** | **Zone 3 (n=8)** |
|---|---|---|---|
| Odonata | | | |
| Coenagrionidae | 2.8 (1.8) | 0.8 (0.3) | 0.3 (0.2) |
| Lestidae | 0.5 (0.3) | 0 | 0 |
| Diptera | | | |
| Chironomidae | 0.5 (0.3) | 0.7 (0.5) | 1.0 (0.6) |
| Ceratopogonidae | 0.3 (0.3) | 0.3 (0.2) | 0.3 (0.3) |
| Trichoptera | 0 | 0.2 (0.2) | 0 |
| Ephemeroptera | 4.8 (2.4) | 0.3 (0.2) | 0.1 (0.1) |
| Coleoptera | | | |
| Haliplidae | 0.5 (0.5) | 0 | 0 |
| Hemiptera | | | |
| Pleidae | 0.3 (0.3) | 0 | 0 |

# APPENDIX B

APPENDIX B. Abundance of the adult microcrustaceans (numbers per liter; mean ±S.E.) not focused on in this study (i.e., benthic and neustonic Cladocerans and non-Cladocerans). Zones refer to the different vegetative habitats found from nearshore to offshore as described in Chapter 1, Figure 1.

**Lux Arbor Pond 6 – Summer (3 August 1992)**

| **Taxa** | **Zone 1 (n=3)** | **Zone 2 (n=2)** | **Zone 3 (n=4)** | **Zone 4 (n=4)** |
|---|---|---|---|---|
| **Cladocera** | | | | |
| Chydoridae | | | | |
| *Acroperus* | 0.2 (0.2) | 0.1 (0.0) | 0.1 (0.1) | 0.1 (0.1) |
| *Alona* | 5.0 (2.7) | 2.7 (2.1) | 2.10 (1.1) | 0.5 (0.4) |
| *Camptocercus* | 0.3 (0.3) | 0.4 (0.3) | 0.1 (0.1) | 0 |
| *Graptoleberis* | 0.2 (0.1) | 0 | 0 | 0 |
| *Kurzia* | 0.3 (0.3) | 0 | 0 | 0 |
| *Pleuroxus* | 0.3 (0.3) | 0.6 (0.5) | 0.5 (0.3) | 0 |
| Daphniidae | | | | |
| *Scapholeberis* | 0.1 (0.1) | 0 | 0 | 0 |
| Macrothricidae | | | | |
| *Illyocryptus* | 0.6 (0.4) | 0.4 (0.1) | 0.1 (0.0) | 0 |
| *Streblocerus* | 0.3 (0.1) | 0 | 0.1 (0.0) | 0 |
| Sididae | | | | |
| *Latona* | 0.1 (0.1) | 0 | 0 | 0 |
| *Latonopsis* | 0 | 0 | 0.1 (0.1) | 0 |
| **Copepoda** | | | | |
| Calanoida | 9.6 (6.8) | 2.7 (2.1) | 10.1 (3.3) | 9.4 (2.7) |
| Cyclopoida | 133.6 (38.5) | 31.8 (12.8) | 28.6 (5.0) | 30.1 (4.2) |
| Harpacticoida | 4.8 (3.0) | 0.4 (0.0) | 0.1 (0.0) | 0 |
| **Amphipoda** | 0.4 (0.2) | 0.1 (0.1) | 0 | 0 |
| **Ostracoda** | 6.4 (2.6) | 3.5 (2.4) | 2.6 (1.5) | 0.7 (0.4) |

APPENDIX B (continued).

**Lux Arbor Pond 6 -- Fall (8 October 1992)**

| **Taxa** | **Zone 1 (n=4)** | **Zone 2 (n=4)** | **Zone 3 (n=4)** | **Zone 4 (n=4)** |
|---|---|---|---|---|
| **Cladocera** | | | | |
| Chydoridae | | | | |
| *Alona* | 0.8 (0.6) | 6.5 (3.6) | 0.2 (0.1) | 0.3 (0.2) |
| *Camptocercus* | 2.0 (0.6) | 0.8 (0.5) | 0.2 (0.1) | 0.2 (0.1) |
| *Eurycercus* | 0 | 0.1 (0.1) | 0 | 0 |
| *Graptoleberis* | 0.3 (0.1) | 0.6 (0.3) | 0 | 0 |
| *Kurzia* | 0.1 (0.1) | 0.1 (0.1) | 0 | 0 |
| *Pleuroxus* | 0.7 (0.6) | 0.9 (0.3) | 0.2 (0.1) | 0.2 (0.2) |
| Macrothricidae | | | | |
| *Illyocrpytus* | 0 | 0.1 (0.1) | 0 | 0.1 (0.0) |
| Polyphemidae | | | | |
| *Polyphemus* | 0.2 (0.1) | 0 | 0 | 0 |
| Sididae | | | | |
| *Latona* | 0.1 (0.1) | 0 | 0 | 0 |
| **Copepoda** | | | | |
| Calanoida | 0.9 (0.2) | 2.3 (0.2) | 0.8 (0.8) | 0 |
| Cyclopoida | 98.6 (32.1) | 91.9 (17.5) | 14.3 (14.3) | 0 |
| Harpacticoida | 1.1 (0.9) | 0.6 (0.4) | 0 | 0 |
| **Ostracoda** | 2.1 (1.3) | 2.8 (1.1) | 0.1 (0.0) | 0.1 (0.0) |

APPENDIX B (continued).

**Lower Crooked Lake – Summer (7 August 1992)**

| **Taxa** | **Zone 1 (n=2)** | **Zone 2 (n=4)** | **Zone 3 (n=6)** | **Zone 4 (n=4)** |
|---|---|---|---|---|
| **Cladocera** | | | | |
| Chydoridae | | | | |
| *Acroperus* | 0 | 0 | 0 | 1.4 (0.7) |
| *Alona* | 0.2 (0.2) | 3.2 (1.5) | 0.6 (0.2) | 0 |
| *Camptocercus* | 0 | 0.5 (0.3) | 0.2 (0.0) | 0.1 (0.0) |
| *Graptoleberis* | 0 | 0.2 (0.1) | 0.2 (0.1) | 0.4 (0.2) |
| *Kurzia* | 0 | 0.2 (0.1) | 0 | 0 |
| *Pleuroxus* | 0 | 0.2 (0.2) | 0.2 (0.1) | 0 |
| Daphniidae | | | | |
| *Scapholeberis* | 0 | 1.9 (0.9) | 0 | 0 |
| Macrothricidae | | | | |
| *Illyocrpytus* | 0 | 0.8 (0.3) | 0.1 (0.1) | 0 |
| *Streblocerus* | 0 | 0 | 0.2 (0.1) | 0 |
| **Copepoda** | | | | |
| Calanoida | 1.4 (0.5) | 5.1 (2.5) | 8.0 (1.7) | 8.7 (1.4) |
| Cyclopoida | 26.4 (2.3) | 43.3 (7.3) | 25.1 (4.1) | 13.5 (1.5) |
| Harpacticoida | 2.1 (0.9) | 3.6 (2.8) | 0.7 (0.4) | 0 |
| **Amphipoda** | 0 | 0.1 (0.1) | 0 | 0 |
| **Ostracoda** | 4.1 (2.3) | 6.6 (2.2) | 2.5 (1.2) | 0.5 (0.3) |

APPENDIX B (continued).

**Lower Crooked Lake – Fall (18 October 1992)**

| **Taxa** | **Zone 1 (n=2)** | **Zone 2 (n=4)** | **Zone 3 (n=6)** | **Zone 4 (n=4)** |
|---|---|---|---|---|
| **Cladocera** | | | | |
| Chydoridae | | | | |
| *Acroperus* | 0.3 (0.3) | 0 | 0 | 0 |
| *Alona* | 7.2 (3.0) | 0.7 (0.5) | 0.1 (0.0) | 0 |
| *Camptocercus* | 21.7 (10.2) | 3.6 (0.3) | 0 | 0 |
| *Graptoleberis* | 0.6 (0.0) | 0.4 (0.3) | 0 | 0 |
| *Kurzia* | 8.4 (1.8) | 0.1 (0.1) | 0 | 0 |
| *Pleuroxus* | 2.1 (0.9) | 0.3 (0.2) | 0 | 0 |
| Macrothricidae | | | | |
| *Illyocrpytus* | 0.3 (0.3) | 0 | 0 | 0 |
| **Copepoda** | | | | |
| Calanoida | 0 | 0 | 3.5 (0.9) | 6.3 (0.7) |
| Cyclopoida | 57.2 (12.1) | 16.2 (4.5) | 10.7 (1.9) | 16.1 (1.0) |
| **Amphipoda** | 0.6 (0.6) | 0 | 0 | 0 |
| **Ostracoda** | 5.7 (3.9) | 2.8 (1.5) | 0 | 0 |