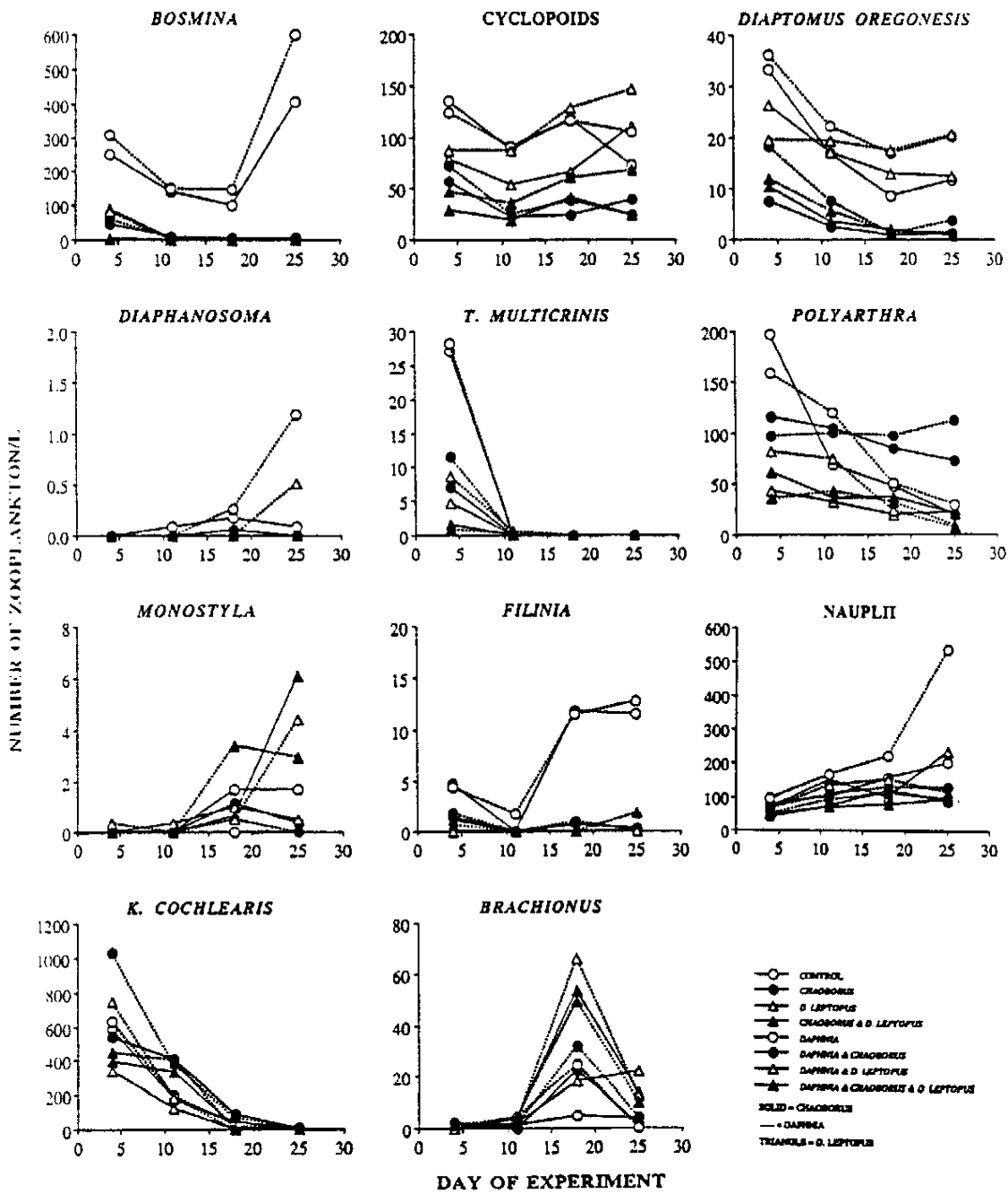


Figure 10: Mean density of small-bodied zooplankton in enclosures in 1991 Biotic Factors Experiment. Treatments were established in Morris Lake, adding *Daphnia pulex*, *Chaoborus americanus*, and *Diaptomus leptopus* to enclosures in a 3 x 3 factorial design. Each treatment consisted of 3 replicates. *Chaoborus* treatments are represented by solid symbols, *D. leptopus* treatment symbols are triangles, and *Daphnia* treatments are represented by symbols connected with broken lines. Day 0 indicates the day small-bodied zooplankton from Morris Lake were introduced into enclosures. First sampling was on day 4. Standard errors of the means are given in Table 6.



the final week and a half of the experiment, corresponding to a decrease in *D. leptopus* densities. The timing of the increase in rotifer density suggested that they were released from predatory pressure by *D. leptopus*, implying that the relationship between them and *D. leptopus* was negative, rather than positive, as suggested by statistical results.

Daphnia did not cause a decrease in population densities of any small-bodied zooplankton. Cyclopoid, *D. oregonensis*, and *D. birgei* densities were enhanced by the addition of *Daphnia* to enclosures. On the final day of the experiment, enclosures with *Daphnia* had significantly higher densities of *D. birgei* than controls (Table 7). There was no *Daphnia* effect for any of the 6 rotifer species present.

Several interactive effects between treatments were detected. For *B. longirostris* and *Filinia*, the effect of adding a second predator when one of either *Chaoborus* or *D. leptopus* was present did not have as much of an impact as adding a single predator when neither predator was present (Fig. 11). This significant interaction was because each predator is capable of reducing densities to near zero levels, thus the effect of adding an additional predator was negligible. A significant interaction between *Daphnia* and *Chaoborus* treatments was found for *D. birgei* (Table 6). In the absence of *Chaoborus*, *Daphnia* had a positive effect on *D. birgei* densities. However, in the presence of *Chaoborus*, *D. birgei* densities were reduced to 0/L, regardless of the presence or absence of *Daphnia* (Fig. 11). There was a significant interaction between *Daphnia*, *D. leptopus*, and *Chaoborus* treatments on population densities of *K. cochlearis*. When *Daphnia* were present and *Chaoborus* absent, addition of *D. leptopus* had little impact on *K. cochlearis* densities. The addition of *Chaoborus* to treatments with *D. leptopus* caused a dramatic decline in *K. cochlearis* densities. If *D. leptopus* were not present, population densities increased (Fig. 12).

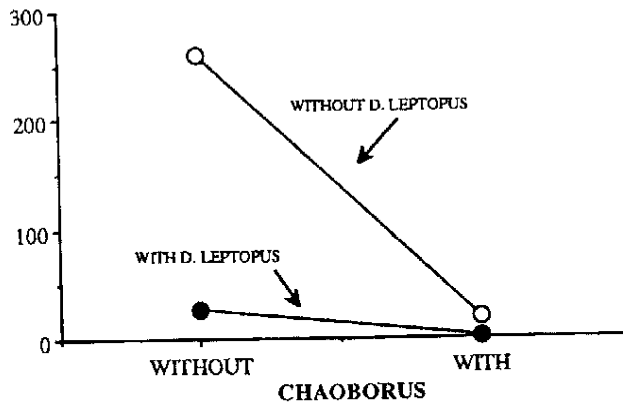
A pattern was apparent in the type of organism affected by each treatment

Table 7: Results of LSmeans comparison between densities in *Daphnia* verses Control enclosures and *Daphnia* & *D. leptopus* verses Control enclosures for the 1991 Biotic Factors Experiment. Significance values were determined using Bonferroni adjustments for a 2-way comparison ($P=0.05/2$). Significant values after adjustment ($P<0.025$) are in boldface.

Species	<i>Daphnia</i> vs. Control	<i>Daph</i> & <i>D. lep</i> vs. Control
<i>Bosmina longirostris</i>	0.238	<0.001
cyclopoids	0.305	0.065
<i>Diaptomus oregonensis</i>	0.666	0.266
<i>Diaphanosoma birgei</i>	0.003	0.078
<i>Keratella cochlearis</i>	0.726	0.098
<i>Polyarthra</i>	0.706	0.243
nauplii	0.071	0.135
<i>Filinia</i>	0.649	0.012
<i>Monostyla</i>	0.477	0.535
<i>Brachionus</i>	0.370	0.489

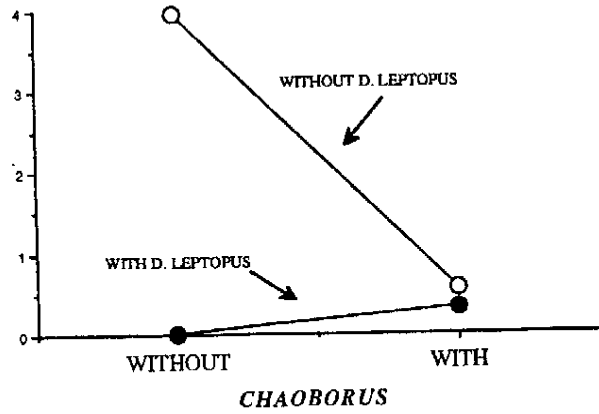
Figure 11: Mean zooplankton densities for zooplankton in 1991 Biotic Factors Experiment with significant 2-way interactions. Treatments were established in Morris Lake, adding *Daphnia pulex*, *Chaoborus americanus*, and *Diaptomus leptopus* to enclosures in a 3 x 3 factorial design. Figure is explicitly designed to portray statistical interactions. Non-parallel lines indicate a significant interaction between treatments. *Bosmina* had a significant *Chaoborus***D. leptopus* interaction, *Filinia* had a significant *Chaoborus***D. leptopus* interaction, and *Diaphanosoma* had a significant *Daphnia***Chaoborus* interaction.

BOSMINA



ZOOPLANKTON DENSITY (#/L)

FILINIA



DIAPHANOSOMA

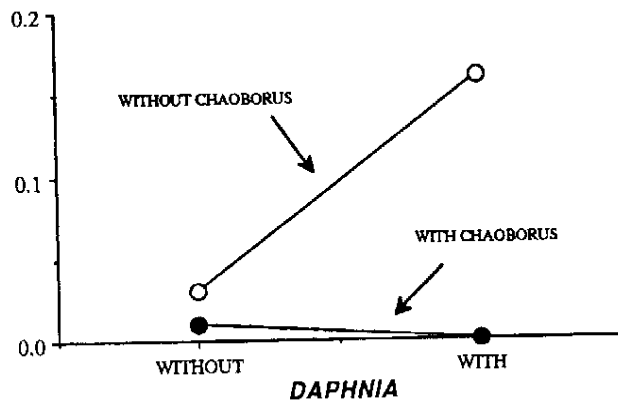
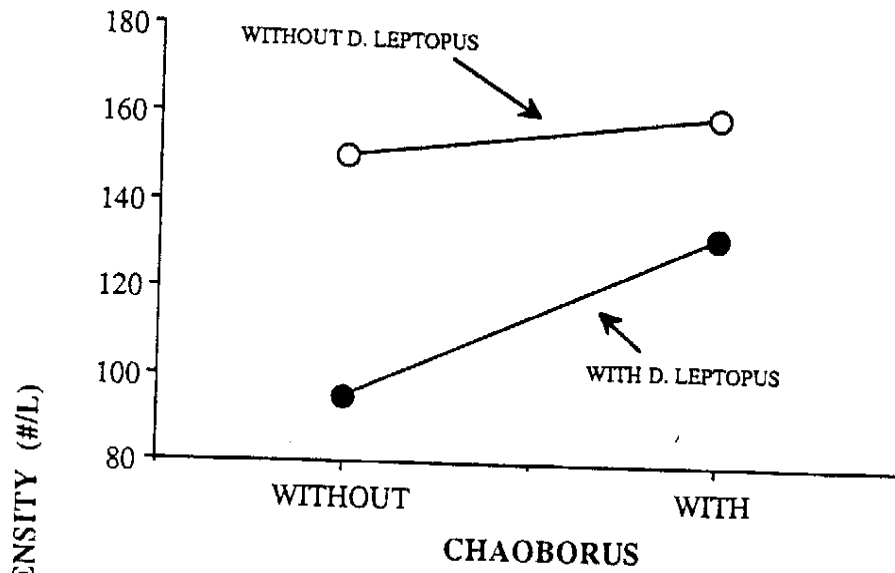
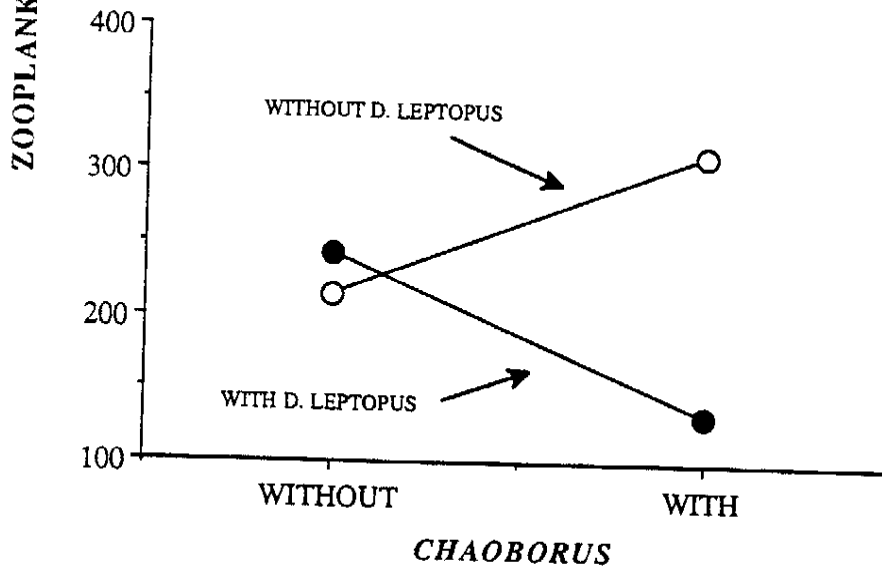


Figure 12: Mean zooplankton densities of *K. cochlearis* in 1991 Biotic Factors Experiment. Treatments were established in Morris Lake, adding *Daphnia pulex*, *Chaoborus americanus*, and *Diaptomus leptopus* to enclosures in a 3 x 3 factorial design. Figures are explicitly designed to portray statistical interactions. Non-parallel lines indicate a significant interaction between treatments. Figures depict a significant *Daphnia*Chaoborus*D. leptopus* interaction.

K. COCHLEARIS - WITHOUT DAPHNIA



K. COCHLEARIS - WITH DAPHNIA



(Table 6). In general, *Chaoborus* tended to impact cladocerans and copepod taxa. Only 3 of the 8 species affected were rotifers, one of which increased in *Chaoborus* treatments. The *D. leptopus* treatment primarily influenced rotifer populations, with only 2 of the 7 species affected being a cladoceran. *Daphnia* affected only crustaceans.

Total biomass of small-bodied zooplankton in each enclosure was estimated for the final day of the experiment. Individual zooplankton biomasses were estimated by either using published dry weights of individual species or calculated using published length-weight regressions (Table 8). At least 10 individuals were measured in control bags on day 18 of the experiment. At this point, most species densities in control bags had stabilized. The impact of each treatment organism (*Chaoborus*, *D. leptopus*, and *Daphnia*) on total zooplankton biomass (excluding treatment organisms) was estimated by comparing differences in total zooplankton biomass between treatments with and without that particular treatment organism. *Chaoborus* had the largest impact, reducing the mean total zooplankton biomass 82.5%, relative to *Chaoborus*-free enclosures (ANOVA; $P=0.0005$). Likewise, *D. leptopus* additions resulted in a 58.5% reduction in mean total biomass (ANOVA; $P=0.012$). There was a significant interaction between *Chaoborus* and *D. leptopus*; adding 2 predators failed to decrease the biomass more than adding only 1 of either predator. The addition of *Daphnia* to enclosures resulted in no significant change in biomass.

Phytoplankton and Chlorophyll *a* Results

Chlorophyll *a* analysis provided an indication of resource levels in enclosures during the 1990 and 1991 Biotic Factors Experiments. There was no significant difference in chlorophyll *a* concentration among treatments in the 1990 Biotic Factors Experiment (RM ANOVA: $P<0.05$). However, in the 1991 Biotic

Table 8: Dry masses of individual zooplankton used to convert zooplankton abundance to biomass for 1991 Biotic Factors Experiment.

Species	dry wt. ($\mu\text{g}/\text{individual}$)	
<i>Bosmina longirostris</i>	0.36	a
cyclopoids	0.29	a
<i>Diaptomus oregonesis</i>	2.29	a
<i>Diaphanosoma birgei</i>	0.56	a
nauplii	0.34	b
<i>Keratella cochlearis</i>	0.01	a
<i>Polyarthra</i>	0.02	a
<i>Trichocerca multicroinis</i>	0.08	c
<i>Filinia</i>	0.01	a
<i>Monostyla</i>	0.02	d
<i>Brachionus</i>	0.20	d

a - calculated from measured lengths in control bags on day 11 of 1991 Biotic Factors Experiment using regressions provided by Downing and Rigler (1984)

b - from Schindler and Novén, 1971

c - from Yan et al., 1991

d - from Bottrell et al., 1976

Factors Experiment, chlorophyll *a* was significantly higher in *Chaoborus* treatments and *D. leptopus* treatments (RM ANOVA: *Chaoborus* $P=0.0075$; *D. leptopus* $P=0.0439$) (Table 9). Chlorophyll *a* in *Daphnia* and *Daphnia* and *D. leptopus* treatments (the two treatments that maintained *Daphnia* populations throughout the experiment) was not significantly different from controls (LS Means comparison with Bonferroni adjustment: $P < 0.025$).

Phytoplankton composition was estimated from samples taken from enclosures during the Abiotic Conditions & Resources Experiment (Table 10). Tender Bog and Ed's Bog enclosures had high abundances of *Dinobryon divergens* and *Cryptomonas ovata*. Small species, such as *Merismopedia tenuissima*, *Ankistrodesmus braunii*, and *Crucigenia quadrata*, were dominant in Forest Service Bog enclosures. Morris Lake enclosures were dominated by *Anabaena wisconsiense*, *Peridinium wisconsiense*, and *Dinobryon divergens*.

DISCUSSION

Several factors apparently act simultaneously to prevent small-bodied zooplankton from successfully colonizing fishless lakes in this region. Although previous studies have focused primarily on the relative importance of competition or predation, results from this study suggest that abiotic factors are also important in determining zooplankton community structure in the absence of fish. Predation by two invertebrate predators, *C. americanus* and *D. leptopus*, was shown to impact zooplankton community composition and total biomass. Reduced densities of small-bodied zooplankton resulting from competition with *D. pulex* was not detected during either the 1990 or 1991 Biotic Factors Experiments.

The importance of abiotic factors to colonizing zooplankton was demonstrated in both the Abiotic Conditions & Resources Experiment and the pH-adjustment Experiment. Small-bodied zooplankton maintained lower densities when

Table 9: Mean concentration of chlorophyll *a* ($\mu\text{g/L}$) in enclosures in 1990 and 1991 Biotic Factors Experiments. Values in parenthesis represent 1 standard error of the mean. Results of RM ANOVA (with *Daphnia* and *Chaoborus* as the main effects in 1990 and *Daphnia*, *Chaoborus*, and *D.leptopus* as the main effects in 1991) are given in the last column.

Treatment	Mean	Significant Effects
1990 Biotic Factors Experiment		
Control	24.5 (0.6)	
<i>Daphnia</i>	24.0 (4.4)	none
<i>Chaoborus</i>	22.4 (3.1)	
<i>Daphnia&Chaoborus</i>	21.1 (1.5)	
1991 Biotic Factors Experiment		
Control	6.8 (0.8)	
<i>D. leptopus</i>	9.4 (0.4)	<i>D. leptopus</i>
<i>Chaoborus</i>	8.4 (0.1)	<i>Chaoborus</i>
<i>D. lept&Chaob</i>	11.0 (0.5)	
<i>Daphnia</i>	7.7 (0.5)	
<i>Daph&D. lept.</i>	10.0 (0.3)	
<i>Daph&Chaob</i>	8.0 (1.2)	
<i>Daph&Chaob&D. lept.</i>	13.2 (1.3)	

Table 10: Estimated relative abundance and length of phytoplankton from samples taken from enclosures during the Abiotic Conditions & Resources Experiment. '*' indicate relative abundance, with '****' being the most abundant and '' being the least abundant. A total of 8 '*'s were distributed throughout each lake.

LAKE	relative abundance	length (μm)
Ed's Bog		
<i>Cryptomonas ovata</i>	****	27
<i>Dinobryon divergens</i>	**	17
<i>Chrysophaerella longispina</i>	**	9
<i>Synura</i> sp.		10
<i>Oscillatoria wisconsiense</i>		
Tender Bog		
<i>Dinobryon divergens</i>	****	17
<i>Cryptomonas ovata</i>	***	27
<i>Dictyosphaerium</i> sp.	*	5
<i>Chrysochromulina</i> sp.		8
<i>Anabaena</i> sp.		
Forest Service Bog		
<i>Merismopedia tenuissima</i>	****	2
<i>Crucigenia quadrata</i>	*	4
<i>Ankistrodusmus braunii</i>	***	20
<i>Peridinium inconspicuum</i>		16
<i>Scenedesmus</i> sp.		
Morris Lake		
<i>Anabaena wisconsiense</i>	****	
<i>Peridinium wisconsiense</i>	**	50
<i>Dinobryon divergens</i>	**	17
<i>Glenodinium gymnodinium</i>		40
<i>Chrysochromulina</i> sp.		8

introduced to enclosures containing water and phytoplankton from fishless lakes than when introduced into similar enclosures containing water and phytoplankton from a lake abundant in fish (Table 11).

The Abiotic Conditions & Resources Experiment performed in 1991 provided evidence that non-zooplankton factors are important in determining the abundance and distribution of zooplankton species in fishless lakes. Of the 10 zooplankton groups introduced into enclosures containing only water and phytoplankton from the 3 treatment lakes, only 33% were able to attain population levels equivalent to those in Morris Lake, indicating that small-bodied individuals have a low probability of survival or reproduction in fishless lakes in this region.

The fishless lakes, Ed's Bog, Forest Service Bog, and Tender Bog are stained, acidic lakes with low oxygen levels. Rahel (1984) categorized the distribution of fish according to levels of pH and winter oxygen levels. The absence of fish at low pH and oxygen suggests that this environment may be incompatible with the physiology of other organisms. Zooplankton have been shown to experience depressed feeding rates when exposed to changes in pH or low oxygen levels (Kring and O'Brien 1976, Heisey and Porter 1977, LaBerge and Hann 1990), indicating that abiotic factors may be important in determining the distribution of zooplankton species. In a review of laboratory bioassays, Locke (1991) found differential abilities of zooplankton to withstand acidification stress. This may have important implications for the distribution of zooplankton species across pH gradients. For example, Sprules (1975) found that species diversity in the La Cloche Mountains was greatly reduced in acidic lakes, with only a few characteristic species common in the most acidic lakes. MacIsaac et al. (1987) found similar trends in species diversity of rotifer assemblages. In acidic lakes a few characteristic rotifer species dominated the rotifer fauna.

The increase in zooplankton density with the calcium carbonate addition of

Table 11: Summary of a posteriori comparisons between zooplankton densities in treatment lake enclosures and control lake enclosures (Morris Lake) on the last day of the Abiotic Conditions & Resources Experiment. 0 indicates that there was no significant difference between densities in treatment lake enclosures and control lake enclosures, '+' indicates that densities in treatment lake enclosures were higher than control lake enclosures, and '-' indicates that densities were lower in treatment lake enclosures. Three replicates were used for control and 4 for treatments. The bottom row gives the proportion of zooplankton that had significantly lower densities in treatment enclosures, relative to control enclosures.

	Ed's Bog	Forest Service Bog	Tender Bog
Crustacea			
<i>Bosmina longirostris</i>	0	-	0
<i>Daphanosoma</i>	0	0	0
<i>Diaptomus oregonensis</i>	-	-	-
cyclopoids	-	-	-
nauplii	-	-	-
Rotifera			
<i>Keratella cochlearis</i>	0	0	0
<i>Polycartha</i>	-	0	-
<i>Conochilus</i>	-	-	-
<i>Asplanchna</i>	-	-	-
<i>Trichocerca multicornis</i>	-	-	-
% spp. reduced	70	70	70

during the pH-adjustment experiment indicates that distribution of small-bodied zooplankton may be determined, in part, by pH. Four of the 5 taxa common to both the Abiotic Conditions & Resources and pH-adjustment Experiments increased their performance in at least one of the treatment lakes when pH was raised to approximately 7 (Table 12). However, there was considerable variation in the response to elevated pH. Some groups, such as cyclopoid copepods, did not respond to pH increase, while others, such as *B. longirostris*, attained a density in treatment lake enclosures 7-fold higher than in Morris Lake enclosures. Although this experiment does not show conclusively that pH is the only (or most important) factor in survivorship of small-bodied species, it does indicate that pH influences the abundance of some species.

It seems unlikely that pH was the only factor limiting the distribution of small-bodied zooplankton from fishless lakes in this region. Several species found in Morris Lake (pH = 7.18) were also common in Beaver Bog, an acidic lake containing a small population of *Umbra limi* (pH <5.0) (S. E. Arnott, personal observation), yet had a low "performance index" in fishless lakes during the Abiotic Conditions & Resources Experiment. These groups included *B. longirostris*, copepods, and the rotifer, *Polyarthra*; generally considered to be acid-tolerant taxa (MacIsaac et al. 1987, Locke 1991). Variation, both among lakes and among taxa, was observed in the response of small-bodied species introduced to pH-adjusted lake water. Although cyclopoids, calanoids, nauplii, and *K. cochlearis* had a higher "performance index" in at least one of the treatment lakes when pH was raised, values remained below 1, indicating higher population densities than in Morris Lake. This suggests that other factors are important in determining the distribution of zooplankton species of this region. In a survey of 146 lakes of various alkalinities, Tessier and Horwitz (1990) found a strong correlation between water hardness and zooplankton size structure, implicating calcium concentration as an important

Table 12: Summary of *a posteriori* comparisons between zooplankton densities in treatment lake enclosures and control lake enclosures (Morris Lake) on the last day of the pH-adjustment Experiment (n=4). 0 indicates that there was no significant difference between densities in treatment lake enclosures and control lake enclosures, '+' indicates that densities in treatment lake enclosures were higher than control lake enclosures, and '-' indicates that densities were lower in treatment lake enclosures. The bottom row gives the proportion of zooplankton that had significantly lower densities in treatment enclosures, relative to control enclosures.

	Ed's Bog	Forest Service Bog	Tender Bog
Crustacea			
<i>Bosmina longirostris</i>	0	0	0
<i>Diaphanosoma</i>	0	0	0
<i>Diaptomus oregonensis</i>	0	0	+
cyclopoids	-	-	-
nauplii	-	-	-
Rotifera			
<i>Keratella cochlearis</i>	0	0	0
<i>Polyarthra</i>	0	-	-
% of spp. reduced	29	43	43

determinant in community structure. Other potential influences include food quality, dissolved oxygen concentrations, temperature, and other unspecified water conditions.

Although not tested directly, several factors may have contributed to the low densities of small-bodied zooplankton in enclosures containing water and phytoplankton from fishless lakes. Food quantity is an important determinant of life history traits of zooplankton, affecting growth, fecundity, and survivorship (Lynch 1989, Porter et al. 1983). Likewise, food quality has been shown to influence growth and total performance (Sterner *In press*, Vanni and Lampert *In prep.*). Although phytoplankton composition varied among lakes (Table 10), Morris Lake algal composition was strikingly different from the fishless lakes during the Abiotic Conditions & Resources Experiment. In general, there was a greater richness, and dinoflagellates were more abundant in Morris Lake than in fishless lakes. The most abundant species was a filamentous cyanobacterium, *Anabaena wisconsinense*. Although there was a striking difference in phytoplankton composition between Morris Lake and treatment lakes, food quality was probably higher in treatment lakes than in Morris Lake based on the low densities of dinoflagellates, few species with thick gelatinous sheaths and an abundance of Cryptomonads in treatment lakes. Two of the most abundant phytoplankton found in the treatment lakes, *Cryptomonas* and *Ankistrodesmus*, are easily digested and rapidly assimilated (Schindler 1971). The size range of algae in treatment lakes fell within edible range (Knoechel and Holtby 1986). Morris Lake would actually be expected to have a lower food quality due to the high abundance of filamentous cyanobacteria and dinoflagellates (Porter 1973, Chow-Frazer and Sprules 1986). Therefore, it seems unlikely that food quality prevents small-bodied zooplankton from invading fishless lakes.

Despite the uncertainty over the specific factor (or factors) involved in maintaining low population densities in the Abiotic Conditions & Resources and pH-

adjustment Experiments, it is evident that abiotic factors reduce the success of invading species. In these experiments, invading species were a mixture of several life stages, ranging from juvenile to adult. Under natural conditions, invaders would disperse to nearby lakes in the form of resting eggs and subsequently hatch into juveniles. Thus it is possible that the performance of small-bodied species may be different if introduced as resting eggs. Because these experiments ran for several generations, introducing juveniles and adults into the treatment environment, they probably provided more opportunities for colonization than would colonization by resting eggs only.

Invertebrate predation plays an important role in preventing the invasion of small-bodied zooplankton into fishless lakes. In both 1990 and 1991, *Chaoborus* caused dramatic reductions in the populations of small-species zooplankton, both in number and biomass (Table 13 and 14). Crustaceans tended to be the most affected, consistent with lab experiments of Swift and Fedorenko (1975), Pastorok (1980, 1981), and Vinyard and Menger (1980). In field studies, *Chaoborus* have been shown to dramatically reduce densities of smaller zooplankton, such as rotifers (Neill and Peacock 1980, Neill 1985). This apparent discrepancy may be resolved by the fact that *Chaoborus* in my enclosures were stocked with a bias toward instars III and IV, due to the relative ease at which they could be sorted. *Chaoborus* have been shown to undergo an ontogenic shift in prey selection (Moore and Gilbert 1987). Early instars (I and II) were most successful at capturing and ingesting soft, small-bodied rotifers, while later instars are capable of handling larger, rigid zooplankton. In field studies involving primarily III and IV instar *C. americanus*, populations of crustaceans were notably depressed (von Ende and Dempsey 1981, Mackay et al. 1988, Vanni 1988). Experiments done by Neill and Peacock (1980) and Neill (1985) were conducted with *Chaoborus* and coexisting species. The crustaceans in Neill's experiments may have been morphologically or behaviorally

Table 13: Summary of RM ANOVA for 1990 Biotic Factors Experiment. *Daphnia* and *Chaoborus* were the main effects and time was the repeated measure. 0 indicates no significant effect of treatment on that particular species, '+' indicates a significant increase in density for that treatment, and '-' indicates a significant decrease in density for that treatment. The bottom row summarizes the total number of introduced species that decreased in abundance.

	<i>Daphnia</i> effect	<i>Chaoborus</i> effect
Crustacea		
<i>Bosmina longirostris</i>	0	-
<i>Diaphanosoma birgei</i>	0	-
<i>Ceriodaphnia quadrangula</i>	0	0
<i>Polyphemus pediculus</i>	0	0
cyclopoids	0	-
nauplii	0	-
Rotifera		
<i>Keratella tauricephala</i>	0	0
<i>Polysartha</i>	0	0
<i>Monosyla</i>	+	0
total # reduced	0	4

Table 14: Summary of RM ANOVA for 1991 Biotic Factors Experiment. *Daphnia*, *D. leptopus*, and *Chaoborus* were the main effects and time was the repeated measure. 0 indicates no significant effect of treatment on that particular species, '+' indicates a significant increase in density for that treatment, and '-' indicates a significant decrease in density for that treatment. The bottom row summarizes the total number of introduced species that decreased in abundance. Each treatment had 3 replicates.

	<i>Daphnia</i> effect	<i>Chaoborus</i> effect	<i>D. leptopus</i> effect
Crustacea			
<i>Bosmina longirostris</i>	0	-	-
cyclopoids	+	-	0
<i>Diaptomus oregonensis</i>	+	-	0
<i>Diaphanosoma birgei</i>	+	-	-
nauplii	0	.	0
Rotifera			
<i>Keratella cochlearis</i>	0	+	.
<i>Polyarthra</i>	0	0	-
<i>Trichocerca multicornis</i>	0	.	-
<i>Filinia</i>	0	-	-
<i>Monostyla</i>	0	0	+
<i>Brachionus</i>	0	0	+
total # reduced	0	7	6

adapted to *Chaoborus* predation and would, therefore, not be expected to show a strong response.

The spatial distribution of *Chaoborus* and small-bodied zooplankton probably overlapped more extensively in enclosures than in natural lake conditions. For example, *C. americanus* in fishless bog lakes exhibited a restricted vertical migration (von Ende and Dempsey 1981, S. E. Arnott and D. E. Schindler, personal observation). During the day, *Chaoborus* populations were concentrated between 2 and 4 meters, whereas at night they occupied the top 2 m. Other zooplankton, particularly *Daphnia* and calanoids remained concentrated in the upper meter of the lake. In enclosures, *Chaoborus* were evenly distributed throughout the water column and were not spatially separated from their potential prey at any time during the day. This probably caused the dramatic decline of *D. pulex* in enclosures stocked with *Chaoborus*. Although *D. pulex* and *C. americanus* were able to coexist in the lake, likely due to the migrational patterns of *Chaoborus*, *Daphnia* and *Chaoborus* were unable to coexist in enclosures. *Diaptomus leptopus*, in contrast with *Chaoborus*, tend to be concentrated in the upper 1 m of the water column of the lake at all times of the day. While enclosures were an accurate representation of spatial distributions between *D. leptopus* and small-bodied zooplankton, they may have intensified *Chaoborus-D. pulex* interactions.

Diaptomus leptopus had a large impact on both biomass and number of zooplankton. Although experiments in 1990 and 1991 indicated that *D. leptopus* could have substantial effects on community composition, there were conflicting results over which groups were most susceptible. In the 1990 Short-term Predation Experiment, crustacean densities were significantly reduced in *D. leptopus* treatments while rotifer densities were unaffected (Table 3). In contrast, most species affected in the 1991 Biotic Factors Experiment were rotifers, although *D. leptopus* did reduce population densities of *B. longirostris* (Table 14). The

differences in susceptibility of prey species may have resulted from different source lakes for small-bodied zooplankton used in each of the experiments. In the 1990 Short-term Predation Experiment, the prey source community (Beaver Bog) consisted of high crustacean densities, particularly *B. longirostris* and *D. parvula*, both significantly reduced by *D. leptopus*. Zooplankton used in the 1991 Biotic Factors Experiment (from Morris Lake) were principally rotifers and *B. longirostris*, which experienced significant density reductions in *D. leptopus* treatments. The differences in the species of zooplankton affected in the two experiments may, therefore, reflect density-dependent feeding patterns and not selectivity for particular prey species. In contrast Neill (1984) reported that removal of *D. leptopus* produced no population response in the zooplankton community. However, his results may have been confounded by increases in *Daphnia* populations (which suppressed rotifers) and high variation in controls. In addition, Neill's studies were done with zooplankton that coexist with *D. leptopus* and vulnerable species may have already been eliminated from the lake.

Daphnia treatments in both the 1990 and 1991 Biotic Factors experiments had no effect on most zooplankton species. The species that were significantly influenced by *Daphnia* increased in density relative to controls. Zooplankton positively influenced in the 1991 experiment were crustaceans, specifically cyclopoids, calanoids and *D. birgei*. In contrast, only one rotifer, *Monostyla* was affected by *Daphnia* in the 1990 experiment. This discrepancy was attributed to low population densities of small-bodied zooplankton in the 1990 experiment, preventing detection of some responses. Increases in some zooplankton species may have occurred through resource modification by *Daphnia*, resulting in resource enhancement for other species. Lynch (1978) presented a facilitation model depicting how one species modifies resources that directly benefits a second coexploiter.

The lack of evidence for competitive effects of *Daphnia* was supported by total algal biomass, measured as chlorophyll *a* for each of the enclosures. Total algal biomass was not significantly different among treatments for the 1990 Biotic Factors Experiment, suggesting that *Daphnia* were not having strong competitive effects related to resource depletion. In the 1991 Biotic Factors Experiment algal biomass in *Daphnia* and *Daphnia* & *D. leptopus* treatments (the two treatments that maintained *Daphnia* populations throughout the experiment) was not significantly different than in controls (LS Means comparison with Bonferroni adjustment: $P < 0.025$). Algal biomass was significantly higher in the presence of both *Chaoborus* and *D. leptopus* (RM ANOVA: *Chaoborus* $P=0.0075$; *D. leptopus* $P=0.0439$), probably due to the reduction in biomass of grazers caused by predation. Therefore, it seems unlikely that *Daphnia* in the established treatments were competing with small-bodied zooplankton through depression of resources.

It may be argued that competitive effects were not detected because experiments were conducted for short periods of time. Although they extended over several zooplankton generations, more time may have been required to detect competitive responses, which typically take longer to manifest themselves than responses to predation. In the 1991 Biotic Factors Experiment, *Daphnia* populations increased after day 18 of the experiment and may have reached high densities and outcompeted smaller zooplankton, given more time. However, this would not necessarily have influenced the conclusions of the experiments. When *Chaoborus* and *D. leptopus* were present, densities of small-bodied zooplankton were quickly reduced to such low numbers (in some cases to extinction) that competition with *Daphnia* may never have been realized. Given the length of time required for competitive effects to manifest themselves, the combined effects of low performance of small-bodied zooplankton and heavy predation may have eliminated all invading zooplankton. Also, some small species were able to maintain viable populations

when the phytoplankton community had been shaped by *Daphnia* grazing (as in the pH-adjustment experiment), suggesting that food availability was adequate. Thus grazing by *Daphnia* apparently does not modify food resources to the extent to prevent colonization.

In contrast to the absence of detectable competitive effects found in this study, other field studies have demonstrated that *Daphnia* can have a negative impact on small-bodied zooplankton. Neill (1984) showed a strong competitive effect of *Daphnia rosea* on rotifer populations. The removal of *D. rosea* resulted in a 250-fold increase of rotifers, particularly *Keratella*. In the presence of *Daphnia*, rotifers were only successfully recruited when substantial doses of fertilizer were added. Likewise, Vanni (1986) showed that the introduction of *Daphnia* into a community of small-bodied zooplankton can suppress some of the species, although none of them went extinct. These investigations provide strong evidence for the existence of competitive effects of *Daphnia* on small-bodied zooplankton.

However, this competitive relationship does not always occur. Frequently studies of competition between small and large zooplankton yield inconsistent results, varying from one experiment to the next (Sprules 1972, Lynch 1978, Smith and Cooper 1982). Several mechanisms have been proposed for this shift in competitive ability. Under high food levels, larger bodied zooplankton are better competitors. However, this relationship is reversed under steady low food concentrations (Tessier 1987, Tillmann and Lampert 1984, Stemberger and Gilbert 1985). Under conditions of fluctuating resources, characterized by periods of high resource concentration followed by extended periods of starvation, the competitive advantage is shifted back to larger species which have the ability to withstand longer periods of resource depression than small-bodied zooplankton (Threlkeld 1976, Goulden and Hornig 1980, MacIsaac and Gilbert 1991).

Vanni (1986) suggested that competition among zooplankton is greater in

more productive environments where *Daphnia* can attain high biomass, therefore exerting heavy grazing pressure on resources. The UNDERC lakes used in this experiment are highly oligotrophic bog lakes, and low food levels may restrict *Daphnia* population growth, preventing them from attaining high biomass, characteristic of more productive lakes. Under low food conditions, oscillations in herbivore and phytoplankton densities are reduced, thereby reducing the competitive advantage to larger herbivores (Romanovsky and Feniova 1985). Under these conditions, small species are expected to co-exist or even out-compete larger zooplankton. The abundance of large cladocerans may also be restricted in less productive lakes by low calcium levels (Tessier and Horwitz 1990). *Daphnia* may be unable to attain a biomass that would enable them to depress resource levels sufficiently to competitively exclude smaller species.

One could argue that densities used in the Biotic Factors Experiments were not high enough to detect competitive effects. However, Lynch (1979) and Smith and Cooper (1982) detected competitive effects of *Daphnia* on small-bodied zooplankton at a density of only 3 *Daphnia*/L. It therefore appears that the densities used in this experiment would be sufficient to detect a competitive response. Other factors, such as food quality may be important in suppressing the competitive advantage of *Daphnia* over small-bodied species.

Food quality in Morris Lake may have favored the growth of small-bodied species and suppressed the growth of *Daphnia* because Morris Lake enclosures contained high densities of *Anabaena wisconsinense* (Table 10). Lab studies have demonstrated that filamentous cyanobacteria can lead to reduced feeding rates and increased respiration rates for large cladocerans. Under these conditions, more selective species such as copepods, *B. longirostris*, *Polyarthra*, *Filinia*, and *Asplanchna* can still maintain high feeding rates (DeMott 1986, DeMott and Kerfoot 1982, Stemberger and Gilbert 1985). Larger species are more strongly affected,

surrendering the competitive advantage to small-bodied zooplankton (Webster and Peters 1978, Porter and McDonough 1984, Gliwicz and Lampert 1990). *Daphnia*, a less discriminatory species, experiences a reduced feeding rate and increased respiration rate due to increased rejection rates of algae that get trapped in the filtering apparatus (Webster and Peters 1978, Porter and McDonough 1984). *Anabaena wisconsinense* in Morris Lake enclosures attained densities of approximately 2×10^3 cells·cm⁻³, which was within the range of concentrations that affected *Daphnia* in experiments by Porter and McDonough (1984).

Interactions among factors tested may be important. Although small-bodied zooplankton were not completely eliminated from enclosures containing water and phytoplankton from fishless lakes, their numbers were reduced and this, in conjunction with high predation rates by both *C. americanus* and *D. leptopus*, may prevent their successful invasion into fishless lakes. Abiotic factors limiting growth and reproduction in zooplankton populations likely have important effects, including determining the outcome of biotic interactions. Production rates of zooplankton are important in determining the structure of a community where predation pressure is high. Yan et al. (1991) demonstrated that although predation rates were higher on *K. taurocephala* than on *B. longirostris*, *K. taurocephala* was able to coexist with *Chaoborus*, whereas *B. longirostris* was eliminated. This was because production rates of *K. taurocephala* exceeded *Chaoborus* predation rates, while production rates of *B. longirostris* were surpassed by predation rates. Therefore, abiotic and resource factors that affect production rates may be very important in determining community structure.

CONCLUSIONS

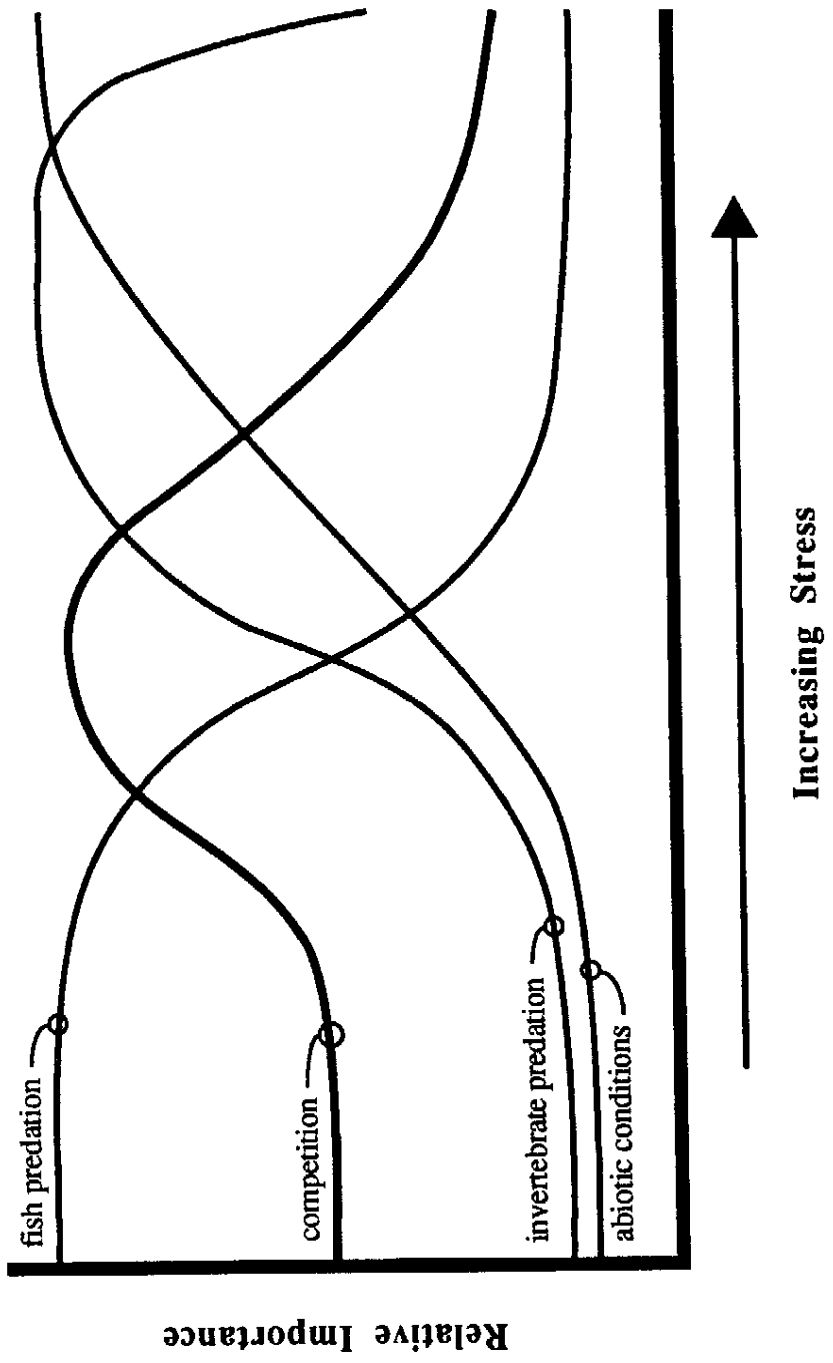
In summary, the combined influence of both predation, pH, and unspecified abiotic factors apparently leads to the absence of small zooplankton from fishless

lakes in this geographic region. Densities of invading species are initially low and individuals that are potentially capable of surviving and reproducing are quickly eliminated by predation, either from *Chaoborus* or *D. leptopus*. The combined influence of predation by *C. americanus* and *D. leptopus* had dramatic effects on community composition. Through niche partitioning the predators were able to coexist and have a substantial impact on a large size range of zooplankton species. *Chaoborus* tended to prey heavily on crustaceans, while *D. leptopus* primarily affected rotifer densities.

These results may be applicable to other regions where harsh environmental conditions could reduce the viability of certain species. Water quality (e.g. calcium levels, nutrient levels, light intensity, toxins) can have differential effects on zooplankton, altering the strength of biotic interactions and energy flow within a food web (*sensu* Paine 1980). Figure 13 provides a conceptual model of how these interactions may change along a stress gradient. As abiotic stress increases (e.g., pH becomes lower), the importance of predation by fish decreases as their population densities decline. At a critical stress level, fish are completely eliminated, and large invertebrate predators increase in abundance. Thus the importance of predation by invertebrates increases. Also, as fish decline, the abundance of large herbivores increases, and competitive interactions become more important. However, as environmental conditions become more harsh, large herbivores have reduced abundance and competition becomes relatively unimportant. Under these conditions, invertebrate predation and abiotic conditions become the main determinants of community structure. Ultimately, abiotic conditions exclude invertebrate predators, becoming the sole determining factor in community structure. Future studies should examine the effects of a variety of specific abiotic factors on biotic interactions within lakes.

Although not specifically tested, an interaction of unfavorable abiotic

Figure 13: Schematic representation of the relative importance of factors affecting community structure along a stress gradient. As stress increases (e.g., pH becomes lower), fish abundance decreases and large zooplankton abundance increases. Therefore the relative importance of competition and predation by invertebrates increases. Further increases in stress reduce the competitive ability of large herbivores. Ultimately, stress levels cause a reduction in invertebrate populations and abiotic conditions become the sole factor structuring the community.



conditions with predation by two invertebrate predators probably exists. In agreement with Dunson and Travis (1991) I see a need for more experiments which integrate the effects of both abiotic and biotic factors on community organization. Studies are needed in which the impact of biotic factors are tested along gradients of abiotic conditions. Although this has been incorporated into some recent models describing how local-scale processes such as competition and predation are modified by environmental stresses (Menge and Sutherland 1987, Menge and Olsen 1990), past studies concerned with community organization have tended to deal only with biotic processes (e.g., Hairston et al. 1960, Oksanen et al. 1981, Carpenter et al. 1985). Further study of abiotic and biotic factors is thus warranted. Lakes that represent gradients of acidity, fish predation, and invertebrate predation may be ideal systems for this approach due to the profusion of information that exists about the effects of acidity and predator-prey interactions in aquatic communities. However, very little work has been done on interactions between these factors (i.e., how abiotic factors may influence the outcome of biotic interactions). A synthesis of these two areas of interest is needed before community structure can be fully understood; this study is an initial step toward that goal.

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