

# Aquatic Invertebrate Assemblages in Shallow Prairie Lakes: Fish and Environmental Influences

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## ABSTRACT

We sampled zooplankton and benthic macroinvertebrate assemblages in 30 shallow natural lakes to determine the effects of the environment (i.e., habitat and fish abundance) on invertebrates. Zooplankters were identified to genus, and up to 120 individuals per genus were measured. Macroinvertebrates were identified to order, class, or family. Fish communities were also sampled. Relative abundances of zooplankton and macroinvertebrates were low at increased chlorophyll *a* concentrations, although mean zooplankton length increased with total phosphorus, possibly because of an increased proportion of microzooplankton (rotifers and copepod nauplii) at higher phosphorus levels. Canonical correspondence analysis revealed that zooplankton and macroinvertebrate abundance was influenced by submersed vegetation coverage, whereas zooplankton abundance and size structure were also related to productivity (i.e., chlorophyll *a* and total phosphorus). However, relative abundance of fish species or fish feeding guilds was not strongly correlated with zooplankton or macroinvertebrate abundance or zooplankton size structure. Physical habitat (e.g., vegetation coverage) may exert substantial influences on invertebrate assemblages in these lakes, possibly providing a refuge from fish predation.

## INTRODUCTION

Aquatic invertebrate assemblages in lentic systems may be influenced by nutrients, physical lake habitat, and fish abundance. For zooplankton, productivity measures (e.g., chlorophyll *a* and phosphorus) have been linked to biomass, although relationships to size structure have been mixed (Pace 1986, Lougheed and Chow-Fraser 1998). In addition, eutrophication can alter zooplankton community structure through bioreplacement by species better suited for more eutrophic conditions (Attayde and Bozelli 1998). Macrophyte coverage may also alter zooplankton assemblages in lentic waters. Increased macrophytes were related to increased cladocerans and decreased rotifers (Hansen and Jeppesen 1992), perhaps because rotifers were out-competed by other taxa in vegetated areas (Lougheed and Chow-Fraser 1998).

Benthic macroinvertebrates are also influenced by the environment. Benthic macroinvertebrate species composition may be influenced by lake size, water hardness, phosphorus, and macrophyte coverage (Allen et al. 1999, De Szalay and Resh 2000, Heino 2000). However, chlorophyll *a* concentrations were not related to benthic macroinvertebrate biomass in moderately productive Canadian lakes (Dinsmore et al. 1999). Macrophyte coverage and habitat structure may be more important than water chemistry in structuring macroinvertebrate assemblages (Heino 2000). Macroinvertebrates, which are an important food source for many of the fishes in Nebraska lakes (e.g., Wilkens et al. 2002), were more abundant in open-water habitats than vegetated habitats (Gilinsky 1984, Olson et al. 1995, De Szalay and Resh 2000).

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Table 1. Water chemistry and habitat characteristics of 30 Nebraska Sandhill lakes sampled in 1998 and 1999. N=number of lakes where the species was collected. Relative abundance is mean number of fish per hour of electrofishing for largemouth bass and the mean number of fish per modified fyke net night for all other species. SE=standard error.

Variable	Mean (SE)	Median	Range
<b>Habitat</b>			
Lake area (ha)	133 (32)	74	15-907
Shoreline development index	1.9 (0.1)	1.8	1.2-2.9
Secchi depth (cm)	123 (13)	102	14-258
Total dissolved solids ( $\mu\text{S cm}^{-1}$ )	208 (18)	182	107-559
Total alkalinity ( $\text{mg L}^{-1}$ )	148 (15)	121	85-447
Chlorophyll <i>a</i> ( $\text{mg m}^{-3}$ )	6.5 (1.5)	2.7	0.7-29.5
Total phosphorus ( $\text{mg L}^{-1}$ )	0.42 (0.08)	0.26	0.03-1.79
Mean lake depth (m)	1.8 (0.1)	1.7	1.0-3.0
Maximum lake depth (m)	2.9 (0.1)	2.8	1.5-4.3
Emergent vegetation (%)	10 (1)	8	0-28
Submersed vegetation (%)	43 (6)	38	0-97
<b>Fish relative abundance</b>			
Black bullhead (N=25)	54 (27)	4	1-565
Black crappie (N=12)	6 (2)	3	0.2-23
Bluegill (N=22)	41 (13)	16	0.1-233
Golden shiner (N=7)	7 (3)	3	0.1-22
Green sunfish (N=6)	246 (241)	5	0.2-1,449
Largemouth bass (N=22)	89 (17)	52	1-311
Northern pike (N=16)	1 (0.2)	1	0.2-3
Pumpkinseed (N=7)	4 (1)	3	0.6-8
Yellow perch (N=29)	23 (6)	14	0.1-143

Fish predation on invertebrates may be one of the most important elements in determining community structure. In both field and experimental conditions, benthic macroinvertebrate or zooplankton abundance was reduced when fish were present (Threlkeld 1979, Post and Cucin 1984, Svensson et al. 1999, Zimmer et al. 2000). Zimmer et al. (2000) found that prairie wetlands with fathead minnows (*Pimephales promelas*) had reduced invertebrates. In a mesocosm experiment, enclosures with zooplanktivorous fish had lower macrozooplankton (e.g., cladocerans) compared to enclosures with fish (Christoffersen et al. 1993). However, benthic macroinvertebrate (primarily chironomids) density was not reduced in the presence of fish in a small reservoir (Thorp and Bergey 1981). Species composition may be affected by fish predation as many fishes selectively prey on certain taxa. Gilinsky (1984) found that the effects of bluegill (*Lepomis macrochirus*) presence on species of Chironomidae were

mixed, with some species increasing in abundance and others decreasing. In addition, Crowder and Cooper (1982) found that the presence of bluegills reduced total benthic biomass because the bluegills primarily preyed upon larger macroinvertebrates (i.e., odonates and amphipods). However, Diel (1992) suggested that fish and macroinvertebrates could coexist in vegetated habitats. In his study, Eurasian perch (*Perca flaviatilis*) foraging efficiency on macroinvertebrates was reduced in vegetation, allowing the invertebrates to remain in relatively high abundance.

The objective of our study was to determine the relations between the environment and predators on the aquatic invertebrate assemblages in shallow natural lakes with moderate to high vegetation coverage. We specifically wanted to determine the most important variables in structuring these communities and to determine if zooplankton and macroinvertebrate structure were affected by similar mechanisms.

## METHODS

**Study Sites.** Thirty natural lakes in the Nebraska Sandhill region in north central Nebraska were sampled (Table 1). These lakes were relatively alkaline (total alkalinity from 85 to 447 mg L<sup>-1</sup>) and shallow (mean depth, 1.0 to 3.0 m). Mean submersed vegetation coverage was 43% (range, 0 to 97%), and vegetation was dispersed throughout these shallow lakes. The lakes varied in size from 15 to 907 ha, but only six lakes were larger than 200 ha. All lakes had relatively undisturbed watersheds. Ranching was the most common land practice surrounding these lakes, and nine lakes were within national wildlife refuges. Many of the lakes were privately owned or difficult to access by the public and thus had lightly exploited fish communities.

The fish communities in these lakes were relatively simple (Table 1). Common species were yellow perch (*Perca flavescens*; 29 lakes), black bullhead (*Ameiurus melas*; 25 lakes), bluegill (22 lakes), largemouth bass (*Micropterus salmoides*; 22 lakes), northern pike (*Esox lucius*; 16 lakes), and black crappie (*Pomoxis nigromaculatus*; 12 lakes). The common carp (*Cyprinus carpio*) was found in nine lakes, while green sunfish (*L. cyanellus*), pumpkinseed (*L. gibbosus*), and golden shiner (*Notemigonus crysoleucas*) were found in fewer than 10 of the 30 lakes (Paukert and Willis 2000).

**Sampling.** We sampled zooplankton and macroinvertebrate assemblages during 2-26 July 1998 and 1-24 July 1999 at four random locations in each of the 30 lakes. Fifteen of the lakes were sampled once each in 1998; the others were sampled once in 1999. Zooplankton was collected during the daytime as two replicates at each of the four sites using a 2-m long tube sampler (Rabeni 1996); samples were filtered through a 65- $\mu$ m mesh net. Benthic macroinvertebrates were sampled at the same time and sites using an 231-cm<sup>2</sup> Ekman grab sampler. Three samples of macroinvertebrates were collected at each site and hand-sieved through a 583- $\mu$ m mesh in the field. Zooplankters were identified to genus and enumerated in the laboratory and a maximum of 120 individuals of each genus was measured. Macroinvertebrates were identified to either order, class, or family and enumerated. Average chlorophyll *a* was estimated from duplicate samples at each of the four sites using a 2-m long vertical tube sampler. Samples were filtered through glass fiber filters in the field and extracted in the laboratory by methods described by Lind (1985). From the same four sampling locations, total alkalinity and total phosphorus were estimated using Hach kits, and total dissolved solids (TDS) were recorded 0.5 m below the surface using an electronic meter. Secchi disk transparency was measured at four locations in each lake during midday. Topographical maps and aerial photos were used to calculate the shoreline development index (SDI; Ling 1985).

Vegetation was quantified for all 30 lakes in July 1999 at five to seven evenly spaced transects across each lake. At 50- to 200-m intervals (depending on lake size)

along each transect, vegetation was classified as either emergent or submersed within a 1-m<sup>2</sup> grid beside the boat (Paukert et al. 2002a). Mean and maximum lake depths were calculated using measurements (nearest 0.1 m) taken at each of the vegetation sites.

Fish were sampled in May or June of the same year that invertebrate sampling was conducted. Largemouth bass and common carp were sampled using nighttime electrofishing; the remaining species were collected using modified fyke nets (Paukert et al. 2002b). Relative abundance was indexed as the mean number of all sizes of fish collected per hour of electrofishing for largemouth bass and common carp or per modified fyke net for all other species (Table 1). To determine an index of abundance for benthic invertivores and zooplanktivores, fish species were classified by feeding guild from the literature, typically from research on these same lakes. All sizes of northern pike and largemouth bass were classified as piscivorous (Paukert et al. 2003), whereas the majority of the other species were classified as benthic invertivores- bluegill (Olson et al. 2003), yellow perch (Wilkens et al. 2002), pumpkinseed (Liao et al. 1995), green sunfish (Sadzikowski and Wallace 1976), and golden shiner (Hall et al. 1979). All sizes of black crappie were considered zooplanktivores (Ellison 1984), and the black bullhead was considered half benthic invertivore and half zooplanktivore (Repsys et al. 1976) as all sizes consumed both diet items similarly. We then determined an index of relative abundance of each feeding guild by summing individual relative abundance indices for each species in these feeding guilds.

*Statistical analysis.* We used correlation analysis to determine the relationships between zooplankton populations (abundance and mean length), macroinvertebrate abundance, and zooplankton mean length with chlorophyll *a* and total phosphorus. We examined the overall relationships among environmental variables and zooplankton and macroinvertebrate assemblages with canonical correspondence analysis (CCA) using the software program CANOCO (ter Braak and Smilauer 1998). This is a direct gradient analysis technique in which the species are directly related to the measured environmental variables (i.e., the ordination is constrained so that the axes are linear combinations of the environmental variables used in the analysis). The advantages of this technique are that CCA is sufficiently robust to handle nonlinear and unimodal species gradients and to handle skewed species distributions when there is noise in the environmental data and when environmental variables are highly correlated (Palmer 1993).

We first conducted separate CCAs using 1) zooplankton taxon abundance, 2) zooplankton taxon mean length, and 3) benthic macroinvertebrate abundance as the species variables. All of the above analyses used the same environmental variables (lake area, SDI, Secchi disk transparency, TDS, total alkalinity, chlorophyll *a*, total phosphorus, mean and maximum lake depth, emergent vegetation coverage, and submersed vegetation coverage). In addition, we included an index of zooplanktivore relative abundance for the zooplankton CCAs and a benthic invertivore index of relative abundance for the macroinvertebrate CCA. In addition to the previous tests, we conducted a CCA using the same taxon data but relative abundance for each fish species as the environmental variable. These tests would determine the effect of individual fish species on the zooplankton and macroinvertebrate structure in these lakes. In all analyses, the species data were square-root transformed to dampen the effects of dominant species, and rare species were down weighted (ter Braak and Smilauer 1998). To assess the significance of the CCA axes, we ran 999 Monte Carlo permutations to determine if the eigenvalues from the axes were greater than what would occur by chance. If the axes were significant ( $P < 0.05$ ), then this would suggest that there was a significant relationship between the invertebrate communities and the environmental variables.

## RESULTS

Eight genera of zooplankton (including copepod nauplii) constituted >97% of the total zooplankton abundance (Table 2). Copepod nauplii were found in all 30 lakes, but made up 13% of the total number of zooplankton collected. *Keratella* spp. were found in 29 lakes and made up the majority (26.8%) of the zooplankton. *Daphnia* spp. only made up 8% of the total number of zooplankton, although it was collected in 22 of the 30 lakes.

Gastropods dominated the macroinvertebrate assemblage, with a mean of 3,636 per m<sup>2</sup> in the 26 lakes where they were collected (Table 2). Chironomids were collected in all 30 lakes and made up almost 19% of all macroinvertebrates enumerated. Amphipods were exclusively *Hyalella* spp., whereas oligochaetes were from the family Tubificidae. Odonates only made up 0.1% of the macroinvertebrates by number but were typically larger in size than other macroinvertebrates and likely would have made up a larger proportion if macroinvertebrates were summarized by weight.

Table 2. Summary of dominant invertebrates collected in 30 Nebraska Sandhill lakes, July 1998 and 1999. N=number of lakes where the taxon was collected. Abundance is expressed as number L<sup>-1</sup> for zooplankton and number m<sup>-2</sup> for macroinvertebrates. The percent of total is the percent of invertebrates (zooplankton or macroinvertebrates separately) collected in all 30 lakes.

	N	Abundance		Percent of total
		Mean	Range	
<b>Zooplankton</b>				
<b>Cladocerans</b>				
<i>Bosmina</i> spp.	27	101	1-630	18.9
<i>Ceriodaphnia</i> spp.	15	39	1-84	4.1
<i>Chydorus</i> spp.	27	102	1-752	19.1
<i>Daphnia</i> spp.	22	52	1-196	7.9
<b>Copepods</b>				
<i>Cyclops</i> spp.	29	33	3-346	6.5
<i>Diaptomus</i> spp.	17	10	1-44	1.2
Nauplii	30	63	10-311	13.1
<b>Rotifers</b>				
<i>Keratella</i> spp.	29	133	12-346	26.8
<b>Macroinvertebrates</b>				
Order Odonata	9	10	4-18	0.1
Order Amphipoda	15	96	4-416	1.1
Class Oligochaeta	19	576	11-2,076	8.0
Class Hirudinea	14	86	4-898	0.9
Class Pelecypoda	15	51	4-162	0.6
Class Gastropoda	26	3,636	11-54,112	68.9
Family Ceratopogonidae	20	89	4-1,518	1.3
Family Chironomidae	30	863	14-2,891	18.9

Abundance of all zooplankton or macroinvertebrates was typically lower with higher chlorophyll *a* concentrations. When chlorophyll *a* concentrations were above 15 mg m<sup>-3</sup>, zooplankton and macroinvertebrate abundances were low (Fig. 1). Relationships were similar when using total phosphorus as the productivity variable; however, chlorophyll *a* concentrations were correlated with total phosphorus ( $r=0.55$ ,  $N=28$ ,  $P=0.003$ ). Overall zooplankton mean length was related to total phosphorus ( $r=0.62$ ,  $N=29$ ,  $P=0.0004$ ) and chlorophyll *a* ( $r=0.39$ ,  $N=29$ ,  $P=0.04$ ). High levels of productivity were related to larger mean length of zooplankton, which may be related to zooplankton taxa composition as the proportion of copepod nauplii (mean length across all lakes: 0.18 mm) to total zooplankton tended to decrease with total phosphorus ( $r=-0.34$ ,  $N=29$ ,  $P=0.07$ ).

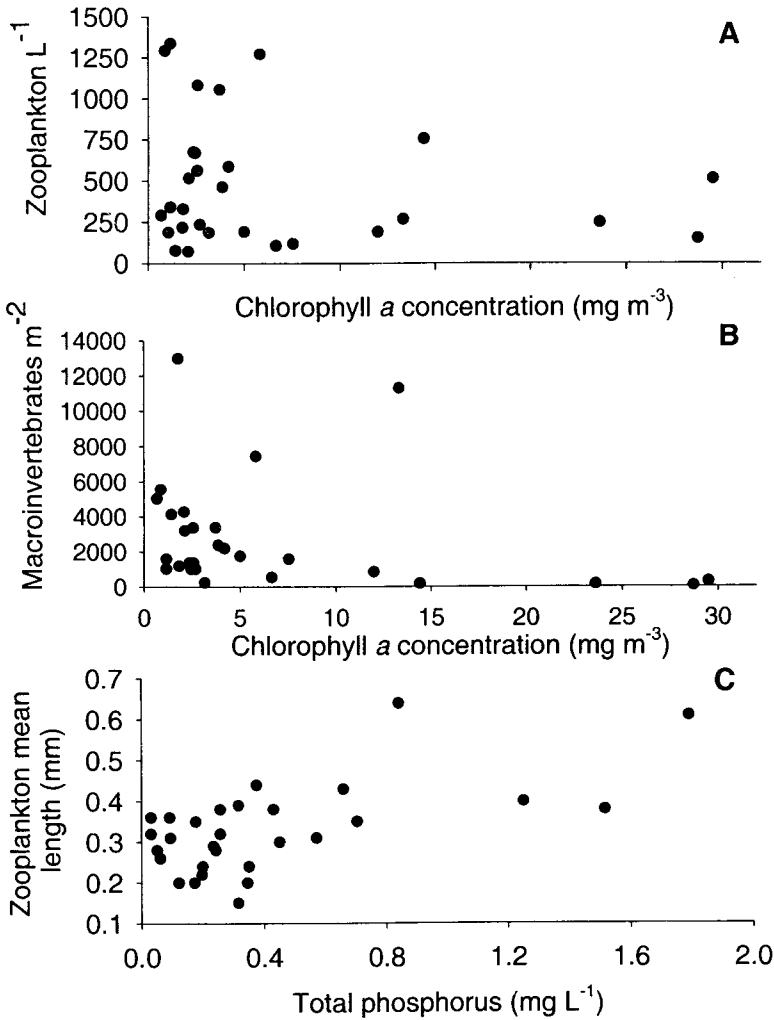


Figure 1. Relationship between chlorophyll *a* concentrations and zooplankton (A) and macroinvertebrate (B) abundance, and total phosphorus and zooplankton mean length (C) in 30 Nebraska Sandhill lakes sampled in summer, 1998 and 1999.

The first two axes of the zooplankton abundance CCA explained 65.8% of the variation in the relationship between zooplankton taxa and environmental variables (Table 3). All axes were significant ( $P=0.005$ ), suggesting that the axes explain a significant amount of variation in the relationship between the environmental variables and the taxa. Based on high (i.e.,  $|r| \geq 0.45$ ) correlation coefficients with the ordination axes, the first ordination axis was primarily a gradient of submersed vegetation and total phosphorus, whereas the second axis was a gradient of lake area, shoreline development index (SDI), total alkalinity, chlorophyll *a* concentration, and also submersed vegetation coverage (Fig. 2). *Ceriodaphnia* spp. were strongly related to lakes with increased submersed vegetation, whereas *Daphnia* spp. and *Chydorus* spp. abundance were associated with lakes with relatively high total phosphorus and chlorophyll *a* concentrations. Larger, more alkaline lakes with more irregular shorelines had high *Keratella* spp. abundance. In addition, *Diaptomus* spp. was associated with the larger lakes. Surprisingly, the relative abundance of zooplanktivorous fishes was not related to either CCA axis, suggesting that the relative abundance of these fishes did not have a substantial effect on zooplankton taxon abundance (Table 3).

Table 3. Correlation coefficients between environmental variables and the first two canonical correspondence analysis axes.

Variable	Zooplankton abundance		Zooplankton mean length		Macroinvertebrate abundance	
	Axis 1	Axis 2	Axis 1	Axis 2	Axis 1	Axis 2
Lake area	0.07	0.64	-0.38	-0.11	0.18	0.20
SDI	-0.15	0.53	-0.18	-0.59	0.35	0.47
Secchi depth	-0.33	-0.18	-0.02	0.30	-0.20	-0.60
TDS	0.06	0.39	-0.62	-0.24	0.11	-0.14
Total alkalinity	-0.08	0.62	-0.44	-0.51	-0.21	0.18
Chlorophyll <i>a</i>	0.21	-0.46	0.28	0.35	-0.06	0.25
Total phosphorus	0.48	-0.09	-0.16	0.44	0.41	-0.35
Mean lake depth	0.40	0.08	-0.31	-0.17	0.44	-0.12
Maximum lake depth	0.40	0.07	-0.22	-0.22	0.38	-0.07
Emergent vegetation	0.31	-0.14	-0.35	0.01	0.45	0.30
Submersed vegetation	-0.57	-0.52	0.51	0.14	-0.49	-0.31
Invertivore CPE					0.27	-0.03
Zooplanktivore CPE	-0.09	-0.02	-0.01	-0.05		
Eigenvalue	0.116	0.078	0.074	0.033	0.303	0.125
Variance of species-environment relationship explained	39.2	26.6	55.3	25.1	54.2	22.4

The first two axes of the macroinvertebrate abundance CCA explained 76.6% of the taxa and environment relationship (Table 3), and the axes explained significantly more variation in the species and environment relationships than what would occur by chance ( $P=0.007$ ). Variables that were highly correlated ( $|r| \geq 0.45$ ) with CCA axis one were submersed vegetation coverage and emergent vegetation coverage, whereas variables that were correlated with axis two were shoreline development index and Secchi depth (Fig. 2). Gastropod and amphipod abundance were most strongly related to submersed vegetation coverage and Secchi depth, whereas chironomids were associated with higher SDI, lower Secchi depth, and emergent vegetation coverage. Other macroinvertebrate taxa were not strongly related to either environmental axis. Relative abundances of fishes classified as invertivores were not strongly related to either CCA axis, suggesting that they did not have a substantial effect on macroinvertebrate abundance in these lakes (Table 3).

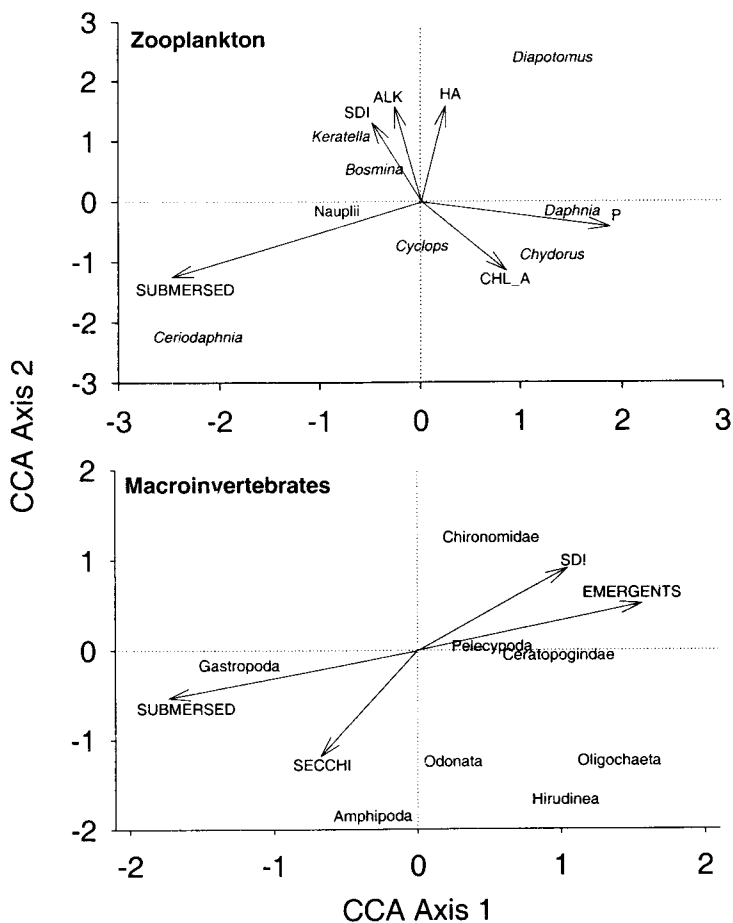


Figure 2. Canonical correspondence analysis (CCA) ordinations of zooplankton genera (top) and macroinvertebrate taxa (bottom) abundance and environmental variables in 30 Nebraska Sandhill lakes sampled in summer 1998 and 1999. Only environmental variables that were highly correlated ( $|r| \geq 0.45$ ) with ordination axis 1 or 2 are shown.



Mean length of zooplankton taxa was somewhat related to the environment (Fig. 3); however, the axes were only marginally significant ( $P=0.089$ ). The CCA axis one explained 55% of the taxa-environment relationship and was primarily an index of submersed vegetation and TDS, whereas axis two, which explained 25% of the taxa and environment relationship, was primarily an index of alkalinity and SDI (Fig. 3; Table 3). Rotifer (i.e., *Keratella* spp.) mean length was higher in alkaline lakes with more irregular shorelines and higher TDS. Larger *Daphnia* spp. mean length was somewhat related to lower alkalinity lakes with less irregular shorelines, whereas larger *Chydorus* spp. mean length was associated somewhat with increased submersed vegetation coverage. As with the zooplankton abundance CCA, the relative abundance of zooplanktivorous fish was not related to either CCA axis one or two.

There were no significant relationships among fish species abundance and zooplankton abundance or size structure or macroinvertebrate abundance. The CCAs with the fish species as the environmental variables revealed no relationships between zooplankton abundance ( $P=0.116$ ), macroinvertebrate abundance ( $P=0.700$ ), or zooplankton mean length ( $P=0.414$ ) and the environmental variables (i.e., fish species relative abundance). Relative abundance of fish species or fish feeding guild did not appear to strongly influence invertebrate abundance or zooplankton size structure and abundance in these lakes.

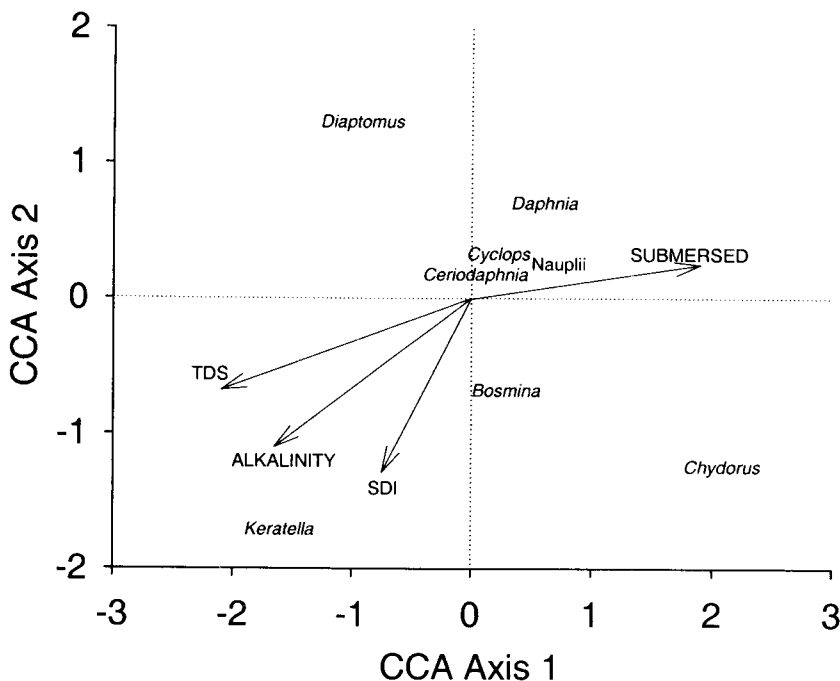


Figure 3. Canonical correspondence analysis (CCA) ordinations of zooplankton genera mean length and environmental variables in 30 Nebraska Sandhill lakes sampled in summer 1998 and 1999. Only environmental variables that were highly correlated ( $|r| \geq 0.45$ ) with ordination axis 1 or 2 are shown.

#### DISCUSSION

Aquatic invertebrates were influenced primarily by vegetation coverage and measures of productivity in these shallow, natural lakes. Increased productivity measures (i.e., chlorophyll *a* and total phosphorus) were associated with low abundances of benthic

macroinvertebrates and zooplankton. The literature on the effects of productivity on aquatic invertebrates is mixed. Zooplankton abundance or biomass has increased with increased productivity (Pace 1986, Attayde and Bozelli 1998), while low chlorophyll *a* values in vegetated habitats were attributed to grazing zooplankton (Karabin et al. 1997, Lougheed and Chow-Fraser 1998). Our inverse relationship between chlorophyll *a* and zooplankton abundance may be attributable to increased zooplankton grazing, which may reduce phytoplankton biomass (Perez-Fuentetaja et al. 2000). We found that mean length of zooplankton was positively related to productivity, which contrasts with other studies (Bays and Chrisman 1983, Pace 1986). Bays and Chrisman (1983) found that more eutrophic lakes had increased biomass of microzooplankton, whereas Pace (1986) did not document any relationships between trophic state and zooplankton size structure. Our increased size structure with productivity may be related to taxon differences in these lakes. Microzooplankton (i.e., rotifers and nauplii) abundance decreased with lake productivity and the cladoceran *Chydorus* spp. increased with lake productivity, which is similar to Bays and Crisman (1983) but contradicts findings by Pace (1986) in Quebec lakes. Macroinvertebrate abundance and biomass typically are not strongly related to productivity (Rasmussen 1988, Johnson and Weiderholm 1989, Dinsmore et al. 1999, Heino 2000), which is somewhat similar to our study.

Our ordinations suggest that vegetation coverage, lake productivity, and physical features of the lake were most influential in structuring aquatic invertebrate populations. *Ceriodaphnia* spp. were strongly associated with lakes having increased submersed vegetation coverage, whereas *Chydorus* spp., *Daphnia* spp., and *Diaptomus* spp. were found in lakes with more open water and higher productivity. *Daphnia* spp. and *Chydorus* spp. are considered open-water zooplankton (Pennak 1989). However, *Ceriodaphnia* spp., which are also considered an open-water zooplankters (Pennak 1989), were associated with submersed vegetation. *Ceriodaphnia* spp. replaced *Daphnia* spp. in macrophyte beds in natural lakes in England (Stansfield et al. 1997), which may have occurred in our study as these two taxa ordinated nearly opposite of one another. Although *Diaptomus* spp. were not related to aquatic vegetation coverage in wetlands (Zimmer et al. 2000) and were typically in lower abundance in more alkaline waters (Attayde and Bozelli 1998), our study suggested that they were found in larger, somewhat more alkaline lakes with lakes with lower submersed vegetation. Increased size structure of *Daphnia* spp. was associated with increased submersed vegetation coverage, although abundance of these zooplankters was typically higher in open water habitats. Measures of productivity (i.e., chlorophyll *a* and total phosphorus) were not strongly related to individual zooplankton taxon size structure. Similarly, Pace (1986) suggested that lake trophic status was not related to *Daphnia* spp. or *Keratella* spp. mean length.

Increased amphipod and gastropod abundances were associated with submersed vegetation coverage, whereas increased chironomids were associated with emergent vegetation coverage, although emergent vegetation coverage only ranged up to 28% of the lake surface. Chironomids are typically associated with open-water habitats (Gilinsky 1984, Olson et al. 1995) and were negatively associated with submersed vegetation coverage in our study, suggesting increased use of open-water habitats. Not surprisingly, amphipod and gastropod abundances have been associated with clear lakes with submersed vegetation (Pennak 1989, Lewis and Magnuson 2000). Physical habitats (e.g., vegetation) appeared to have more influence on macroinvertebrate abundance than water chemistry in our study, which was similar to Finland lakes (Heino 2000).

Fish abundance did not appear to affect aquatic invertebrate abundance or zooplankton size structure in our summer samples in these 30 shallow lakes. When fish are present, most research demonstrates that invertebrates typically have been reduced.

After yellow perch were introduced into a Canadian lake, benthic macroinvertebrate abundance was reduced (Post and Cucin 1984), whereas littoral macroinvertebrates increased after fish were removed in a eutrophic lake (Svennsson et al. 1999). Zooplankton abundance and size structure have also been reduced when fish are present (Threlkeld 1979, Zimmer et al. 2000) or with increased planktivorous fish abundance (Mills et al. 1987). Our study suggests that fish density did not significantly alter macroinvertebrate abundance or zooplankton abundance or size structure, which is consistent with Thorp and Bergey (1981). However, the effects of fish predation on invertebrates may be at a finer scale than the invertebrate classification that we utilized. Gilinsky (1984) suggested that the effects of bluegill on chironomids were dependent on the chironomid species. Crowder and Cooper (1982) suggested that total benthic macroinvertebrate biomass was reduced with bluegill predation, but this was related to the fish selectively feeding on larger invertebrates (e.g., amphipods and odonates). Foraging efficiency of fish on invertebrates is reduced with the increased structural complexity of vegetation (e.g., Diel 1992, Manatunge et al. 2000), thus minimizing the effects of fish on invertebrate abundance and size structure. This could explain why our study of productive, vegetated lakes did not show an effect of fish abundance on aquatic invertebrates. However, broadening the study to include fishless lakes would provide further insight to the effects of fish on invertebrate communities in these shallow, natural lakes.

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