Is phytophilous zooplankton community structure affected by nutrients and fathead minnows?

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Introduction

Two different stable states occur in shallow freshwater systems (Scheffer *et al.* 1993, Moss 1990). The clear-water state is characterized by low turbidity, and abundant macrophyte growth; the turbid state is characterized by abundant phytoplankton growth, and high turbidity (Scheffer *et al.* 1993). The clear-water state is most desirable for waterfowl populations. Hanson and Butler (1994) found that waterfowl use increased when a shallow lake was restored to the clear-water state. One component that has a stabilizing effect is submersed macrophyte beds and the associated invertebrate grazers. However, it is not fully understood how to maintain the clear water state, particularly when planktivorous fish are present.

The macrophyte beds and associated zooplankton may be thought of as a phytoplankton filter. Macrophytes provide habitat and refuge (when planktivorous fish are present) for these important filter feeders in order for them to maintain top-down control on the phytoplankton (Irvine *et al.* 1989), thus maintaining the clear water state. As long as zooplankton are present and the phytoplankton is edible, the clear-water state should be maintained. The most important factors in determining the stable state of the system are: 1) level of nutrient loading, 2) density of macrophytes, 3) density of phytoplankton grazers, and 4) density of planktivorous fish (Irvine *et al.* 1989). Zooplankton in the macrophyte beds ultimately determine the state of the system. Therefore, it is necessary to understand how these factors affect zooplankton density and community structure among the macrophytes. In this study, nutrients (inorganic N and P) and fathead minnows were added to separate enclosures to examine their effects on the zooplankton community.

The microcrustacean zooplankton community associated with the submersed macrophytes consists of two components, planktonic, filter-feeders and phytophilous (plant-loving) scrapers. Planktonic members include cladoceran species such as *Bosmina longirostris*, *Diaphanosoma birgei*, and *Ceriodaphnia dubia*, and calanoid and cyclopoid copepods. The scrapers include chydorid cladocerans such as, *Eurycercus longirostris*, *Pleuroxus denticulatus*, and *Chydorus* spp. Zooplankton associated with the submersed macrophytes can feed by one of two methods; thus they can control phytoplankton in two ways. First, the filter-feeders can feed on phytoplankton that moves into the macrophytes by water currents, or these filter feeders can migrate horizontally from the macrophyte bed into the open water column to filter feed at night (Timms and Moss 1984), while predation pressure from the visually feeding fish is low. Second, and probably less effective, the scrapers can feed on the phytoplankton that moves into the macrophyte bed and gets trapped on the epiphyton surface (Irvine *et al.* 1989).

Many factors affect zooplankton densities at differing macrophyte biomass. Macrophyte density itself will affect zooplankton density. If the macrophytes sampled are sparse, fish may be able to forage among them more easily and zooplankton density would be lower (Irvine *et al*. 1989, Lougheed and Chow-Fraser 1998). Epiphyton may also be a factor if the macrophytes are dense, as epiphyton may be shaded in dense macrophytes, resulting in less food available for the scrapers. Epiphyton quality is also important. Other factors may affect the species composition, such as phytoplankton biomass and the macrophyte species present. Phytoplankton can be a factor as food for filter-feeders.

Many methods have been used to sample invertebrates associated with submersed macrophytes. The sampling method used encloses a volume of water, macrophytes and associated fauna, which are then removed and processed. These methods effectively sample two niches occupied by microinvertebrates, the open water, and the macrophytes, from which the fauna are combined into one estimate of density. Thus the data obtained from such sampling can be treated in two ways: 1) the data can be standardized to macrophyte dry weight, i.e. number of individuals per unit dry weight of macrophyte, or 2) the data can be used as numbers of individuals per volumetric sample. Both these methods

were examined using multivariate analysis to determine which is most useful in the interpretation of community composition and structure.

The objectives of the study were: 1) to determine the effects of nutrient (N and P) addition and fathead minnow addition on the zooplankton species composition associated with the macrophytes, 2) to determine which environmental variables influence species composition among the macrophytes in each treatment, 3) to determine the best method of data standardization and analysis which most accurately represents the community sampled.

Methods

Study Site

The study was conducted in the Blind Channel at Delta Marsh, Manitoba, Canada (50º11'N, 98º12'W), one of the largest (22, 000 ha) freshwater marshes in North America, located on the south shore of Lake Manitoba, and connected to it by several channels. The vegetation in the marsh varies spatially with areas dominated by *Typha X glauca*, *Phragmites australis*, or open water with submerged macrophytes (*Ceratophyllum demersum, Potamogeton pectinatus, P. zosteriformis, Myriophyllum sibiricum*, and *Utricularia vulgaris*). Fathead minnows (*Pimephales promelas*) and brook sticklebacks (*Culaea inconstans*), both planktivorous minnows, are the most abundant fish in the spring. Adult fish come into the marsh in early spring to spawn, then migrate out of the marsh to the lake as water temperature rises and oxygen concentration decreases throughout the summer. The young of the year (YOY) remain in the marsh as they grow throughout the summer.

Experimental Design

The manipulations took place in 5 m by 5 m experimental enclosures which consisted of floating platforms (to accommodate fluctuations in water level) from which impermeable polyethylene curtains extended down through the water column and into the sediments about 20 cm, anchored with re-bar, sealing the inside water from the Blind Channel. The experiment examined two main factors: inorganic nutrient addition and fathead minnow addition. Three replicates of each treatment were assigned randomly to the enclosures using a latin square design. The treatment combinations were: 1) fish excluded, no nutrients (control), 2) nutrients added, fish excluded, and, 3) no nutrients, fatheads added.

The nutrients were nitrogen (N) as $NaNO_3$, and phosphorus (P) as $NaH_2PO_4 \cdot 2H_2O$, added to produce cumulative loadings of 23.4 g/m^2 N and 3.2 g/m^2 P. The pre-weighed nutrients were dissolved in 1L of carbon filtered water, mixed with water from the appropriate enclosure, and then sprinkled evenly over the enclosure. Nutrients were added three times a week during the treatment sampling period.

The enclosures were installed on May 27, 1997. Fathead minnows were added to the fish treatment enclosures on June 18. The density of fish added (5 fatheads/m^3 or 125/enclosure) was chosen to approximate estimates of fathead density in a study of eutrophic ponds in Michigan (Spencer and King 1984). The nutrient addition began on June 23. Sampling for invertebrates associated with the macrophytes was delayed until July 9 when the macrophytes had developed adequately to permit sampling.

Biotic Sampling

The zooplankton community associated with the submersed aquatic plants was sampled using the Downing box sampler (Downing 1986), a 'Plexiglas™ suitcase' (4 L), lowered into the water and closed around approximately the top 30 cm of macrophyte (Fig. 1). The liquid contents of the box were then poured through a 53 µm mesh net to collect the microinvertebrates. The residual macrophytes were placed in a large jar and shaken vigorously with carbon-filtered water to dislodge epiphyton from their surfaces. Epiphyton was separated from macrophyte tissue and macroinvertebrates by filtering through a 1 mm mesh sieve. The macrophyte tissue was sorted by species, dried at 105°C for 24 hours, then weighted to obtain dry weight for each macrophyte

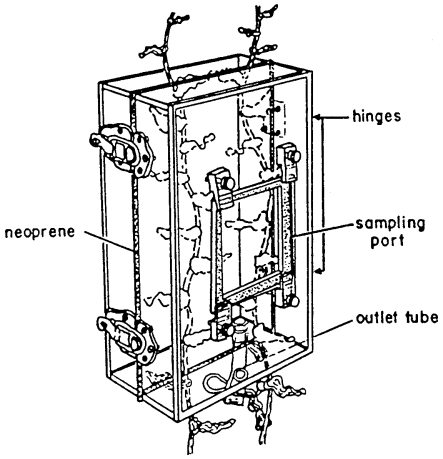

Figure 1. Downing box consists of clear Plexiglas™ (which is gently closed around a submersed macrophyte) enclosing a macrophyte and associated fauna and flora (Downing 1986).

species which were also pooled to obtain total dry weight. Epiphyton biomass was quantitatively estimated by determining the chlorophyll *a* concentration as described in McDougal *et al.* (1997). Phytoplankton biomass was determined from 3 samples per enclosure, collected in mid water column, and analyzed for chlorophyll *a* as for epiphyton.

Zooplankton were identified using Pennak (1989) and a reference collection (BJH). Cladoceran species (*Bosmina longirostris, Ceriodaphnia dubia, Diaphanosoma birgei, Simocephalus* sp., *Eurycercus longirostris, Chydorus* spp. and *Pleuroxus denticulatus*), copepods (nauplii, cyclopoid copepodites, cyclopoid adults, calanoid copepodites, calanoid adults) and ostracods were used in the analyses as 'species data'.

The Downing box data were treated in two ways. First, the density of invertebrates was calculated based on dry weight of macrophyte obtained in the sample (numbers of individuals per unit dry weight of macrophyte) as used in Downing (1986). Secondly, the density was calculated based on how many individuals were sampled in the Downing box (numbers of individuals per unit volume). There are problems with both methods. If the sample was mostly water, then numbers of individuals per dry weight of macrophyte would not be accurate, as the community sampled would be mostly planktonic species and standardizing to dry weight of macrophyte would not be appropriate. If numbers of individuals per unit dry weight of macrophyte was used, macrophyte biomass cannot be included in analyses as an independent variable as it was already used to standardize the data. If number of individuals per unit volume was used, a more accurate estimate of density may be obtained for planktonic species but would then be inaccurate for phytophilous species. However, macrophyte biomass can be used as an independent environmental variable. The greater the macrophyte biomass used in the sample, the higher the proportion of the sample is habitat for phytophilous species rather than for planktonic species. The hypothesis that the proportion of phytophilous individuals in the community was correlated positively with macrophyte biomass in the sample could then be tested. When number of individuals per unit volume was used, macrophyte biomass can also be partitioned according to the species of macrophyte, and thus species associations between zooplankton and species of macrophyte can be examined.

Fish were monitored daily using two minnow traps in each enclosure. Fish caught in fish treatment enclosures were counted and returned to the enclosure. Fish caught in all other enclosures were counted and removed from the enclosure. The mean daily fish catch was then calculated for each enclosure for each week. Only adult fish, most of which were fathead minnows, were large enough to be caught in the traps. In most enclosures there were many young-of-the-year (YOY) fatheads which could not be sampled quantitatively, but relative abundance was noted if they were present.

Data Analysis

Multivariate analysis was performed on log (x+1) species data, to normalize the data. The transformation x +1 was used because of the many zeroes in the data. Correspondence Analysis (CA) was performed on treatment mean data on each date in order to explore the species composition of zooplankton among treatments. Changes in species composition throughout the season were examined by connecting successive points on the biplots.

The effect of environmental variables on zooplankton species composition was also examined with the use of Canonical Correspondence Analysis (CCA). The CCA triplots include vectors for each environmental variable which increase in value along the vector from the origin. The importance of the factor is also proportional to the length of the vector (Ter Braak 1986). The factors which directly affect zooplankton were used in the CCA, which was performed using: 1) the Downing Box data (treatment means, LOG transformed) as numbers of individuals per unit volume, or 2) data standardized to macrophyte dry weight obtained in each sample (numbers of individuals per unit dry weight of macrophyte biomass). Environmental variables used with the volumetric data (numbers of individuals per Downing box sample) were adult fish density (mean number trapped/week), young of the year fish density (YOY), epiphyton biomass (µg Chl *a*/sample), phytoplankton biomass (µg Chl *a*/L), macrophyte biomass (dry weight/sample) and species of macrophyte (dry wt./sample for each species). Adult fish density, epiphyton biomass (µg Chl *a*/dry wt.) and phytoplankton biomass (µg Chl *a*/L) were used with the data expressed as numbers of individuals per unit dry weight of macrophyte. CA and CCA were performed using CANOCO version 3.10.

Total predation pressure from fish was likely high in the spring while adult fatheads were present, then declined as they died or were removed from the enclosures (controls and nutrient treatment), and increased again as young of the year fatheads exerted increased predation pressure from late July onward. YOY fish grew throughout the season and exerted increasing predation pressure on the zooplankton, but their numbers were not quantified. A simulated environmental variable was constructed to represent predation pressure from young of the year fatheads, estimated to increase exponentially through August. Data created for each

treatment on each date were log (x+1) transformed and used in the CCA. YOY and adult fish were added as separate environmental variables to the CCA, each with a unimodal distribution, satisfying the assumptions of the method (Ter Braak 1986).

Results

Species Composition

The first CA axis accounted for 41.3% of the variance in the data as numbers of individuals per unit dry weight of macrophyte biomass, and 39.2% of the variance in the data as numbers of individuals per unit volume. When the points were connected for each treatment between successive samplings, the pattern paralleled the first axis (Figs. 2, 3), thus representing the seasonal development of the zooplankton community. In early July, the community was composed mostly of filter-feeding species (*Bosmina longirostris*, *Simocephalus* sp. and calanoid copepods). By the end of the experiment, the zooplankton community was composed of phytophilous chydorid scrapers (*Pleuroxus denticulatus*, *Chydorus* spp. and *Eurycercus longirostris*) and ostracods.

The second CA axis accounted for 25% and 22.9% of the variation in the numbers of individuals per unit dry weight of macrophyte biomass data, and numbers of individuals per unit volume, respectively, and is important in separating the effects of experimental treatment on the species composition of the community. The species compositions in the two treatments and the control were similar in early July, then diverged from one another throughout the season (Figs. 2, 3). The fish treatment was most separated and showed a change in species composition to ostracods by the end of the experiment. In the nutrient treatment, there was a shift to species (*Pleuroxus denticulatus* and *Chydorus* spp.) that scrape epiphyton from macrophyte surfaces.

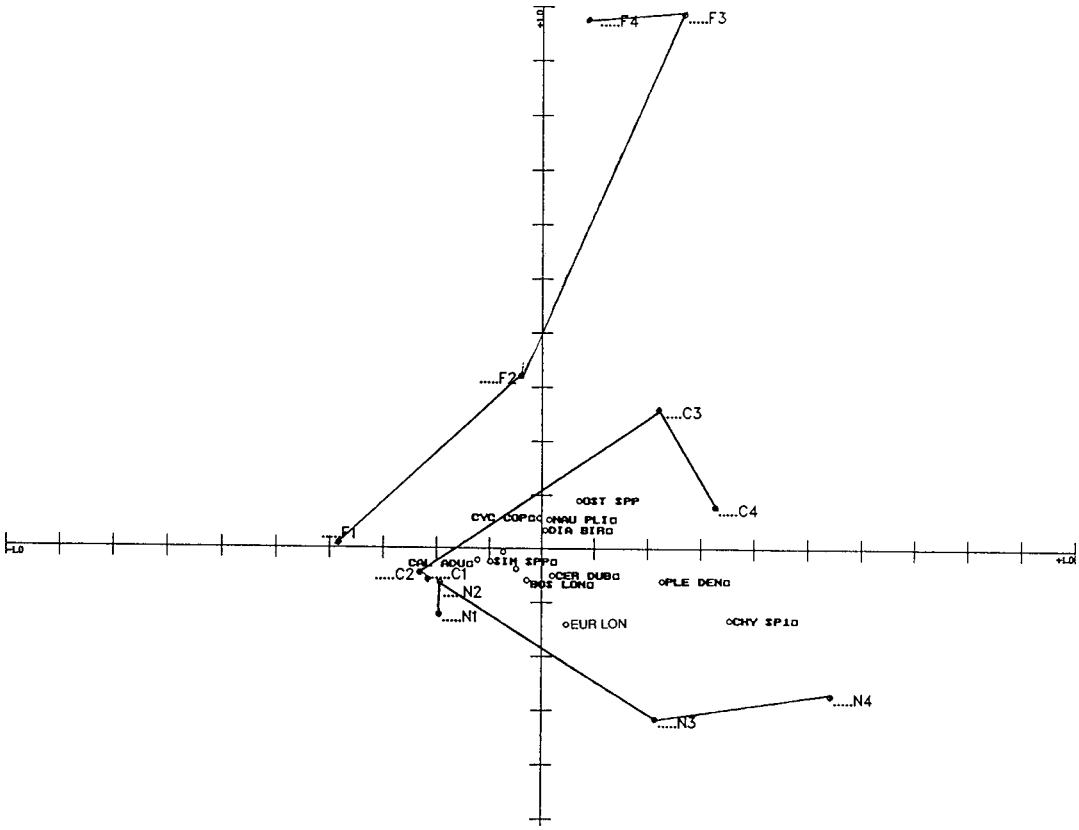

Figure 2. Correspondence Analysis biplot of numbers of individuals per unit macrophyte dry weight sampled with the Downing box. Labels for treatment mean sites (closed circles) are coded C - control, F - fish treatment, N - nutrient treatment, 1 - July 9, 2 - July 23, 3 - Aug. 6, and 4 - Aug. 20, 1997. Species (open circles) are identified as follows: BOS LON, *Bosmina longirostris*; CER DUB, *Ceriodaphnia dubia*; CHY SP1, *Chydorus* sp.; DIA BIR, *Diaphanosoma birgei*; EUR LON, *Eurycercus longirostris*; PLE DEN, *Pleuroxus denticulatus*; SIM SPP, *Simocephalus* spp.; NAU PLI, copepod nauplii; CYC COP, cyclopoid copepodites; CYC ADU, cyclopoid adults; CAL COP, calanoid copepodites; CAL ADU, calanoid adults; and OST SPP, ostracods.

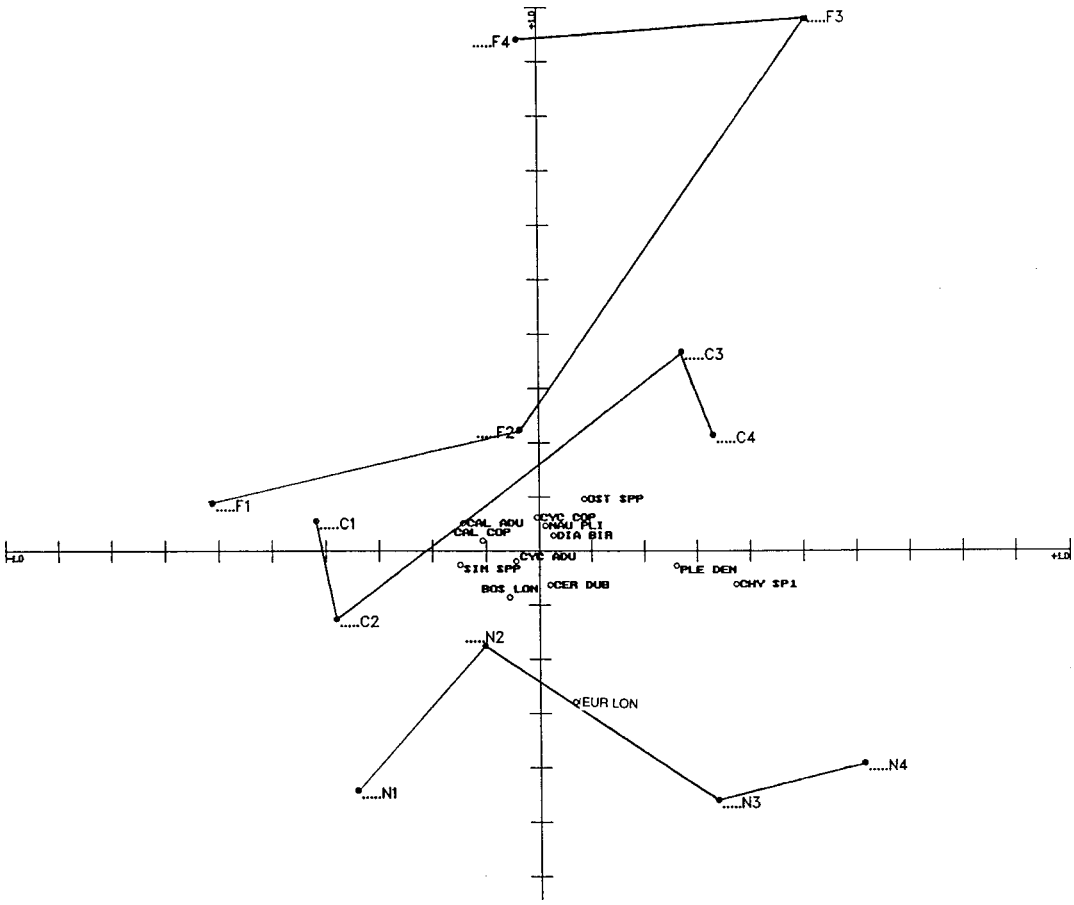

Figure 3. Correspondence Analysis biplot for numbers of individuals per Downing box sample of zooplankton. Labels for treatment sites, and zooplankton species are as labeled in Fig. 2.

Effect of environmental variables

CCA results (#/dry wt)

When data as numbers of individuals per unit dry weight of macrophyte were used in a CCA, the pattern of each treatment over the season was not as clear as in the CA (Fig. 4). The environmental data explained 41.5% ((sum of all canonical eigenvalues / sum of all unconstrained eigenvalues) x 100) of the variation in species composition. The effect of the epiphyton vector is confounded because the species and epiphyton data were standardized to macrophyte dry weight.

CCA results (#/unit volume)

When data as numbers of individuals per unit volume were used, macrophyte biomass can be added as an independent variable in the CCA. The environmental variables explained 54.7% of the variance in the species composition (figure not shown). Macrophyte biomass was highly correlated with the first axis (R= 0.783, Table 1). Macrophyte biomass increased throughout the season (Fig. 5), with a concurrent shift to phytophilous species.

When the YOY variable was added to the CCA (Fig. 5), the variance explained by the environmental variables increased to 72.4%. YOY predation pressure contributed to the shift to phytophilous species as this vector was correlated with the first CCA axis (R=0.914, Table 1).

Phytoplankton and epiphyton biomass were correlated with the second axis of the ordination (Fig. 4), separating the treatments. Phytoplankton biomass was highest in the fish treatments, and epiphyton biomass was highest in the nutrient treatment. There was a higher proportion of phytophilous cladocerans present in the nutrient treatment where epiphyton biomass was highest.

Dry weights of individual macrophyte species were also used as environmental variables to examine effects of macrophyte species on zooplankton species composition. *Ceratophyllum demersum* and *Potamogeton zosteriformis* were both present where higher proportions of phytophilous species occurred later in the season (Fig. 6). Planktonic species of zooplankton were in higher abundance where *P. pectinatus* biomass was higher earlier in the season.

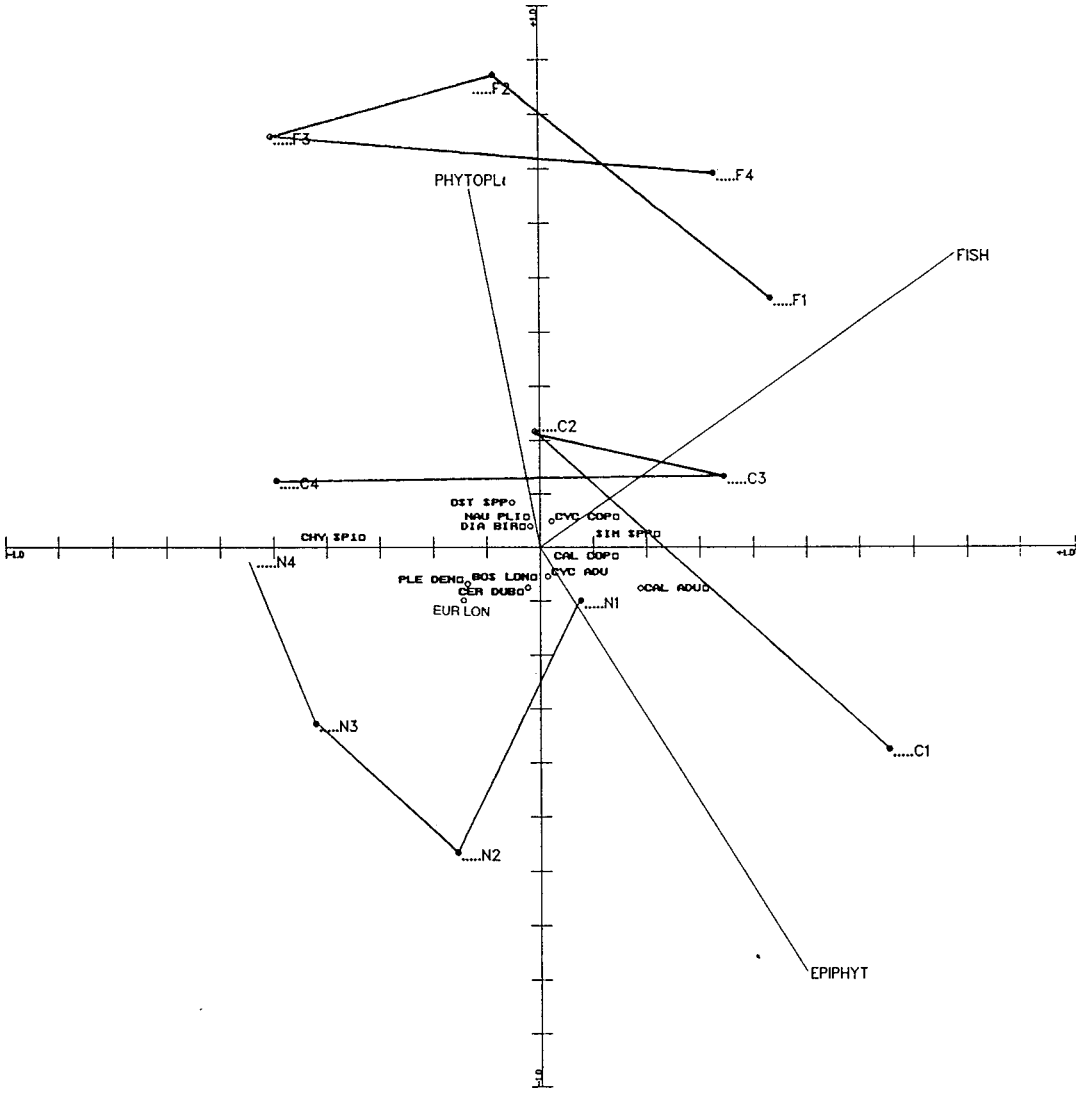

Figure 4. Canonical Correspondence Analysis triplot for numbers of individuals per unit macrophyte dry weight sampled with the Downing box. Labels for treatment mean sites and zooplankton species are labeled as in figure 2. Environmental variables are labeled as follows: FISH, mean daily number of adult fish trapped per treatment per week; EPIPHYT, mean epiphyton Chl a per unit macrophyte dry weight per treatment; and PHYTOPL, mean phytoplankton Chl *a* per treatment.

Table 1. Weighted correlation coefficients between the first two CCA axes for zooplankton community in submersed macrophytes (Fig. 5).

Variable	Axis 1	Axis 2
Macrophyte biomass	0.783	0.058
YOY Fish	0.914	-0.060
Adult Fish	-0.426	0.620
Epiphyton biomass	0.260	-0.322
Phytoplankton biomass	0.120	0.361

Discussion

Seasonal change in species composition

The most dramatic result found in this study was the change in species composition of the zooplankton community throughout the season. The proportion of phytophilous grazers (scrapers) in the community increased as the biomass of macrophytes increased throughout the season. There was more habitat available for these phytophilous species which graze epiphyton from the macrophyte surfaces. Lougheed and Chow-Fraser (1998) also found that macrophyte cover was important in determining the composition of the

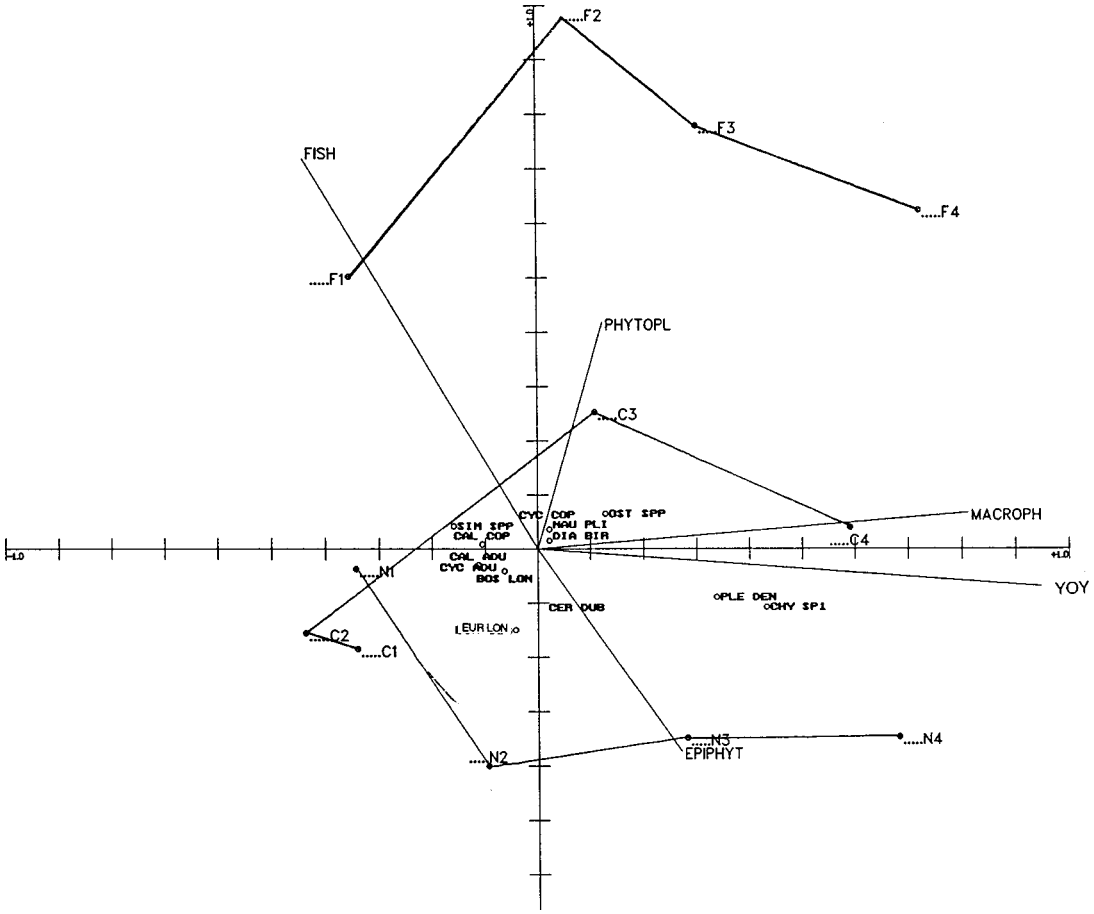

Figure 5. Canonical Correspondence Analysis triplot for numbers of individuals per Downing box sample. Labels for treatment mean sites and zooplankton species are as in figure 2. Environmental variables are labeled as follows: FISH, mean daily number of adult fish trapped per treatment per week; EPIPHYT, mean epiphyton Chl a per downing box sample per treatment; and PHYTOPL, mean phytoplankton Chl a per treatment; MACROPH, mean total macrophyte biomass (dry weight) per treatment; and YOY, estimated predation pressure from young of the year fathead minnows for each treatment.

zooplankton community in a hypereutrophic Great Lakes wetland.

Fish also had a substantial effect on the seasonal change in the community. Predation by fish led to a decline in proportion of planktonic filter-feeders throughout the season. The filter-feeding zooplankton, e.g. *Simocephalus*, were depredated first, as they were in the open water, and were easier prey than the scrapers which were closely associated with the macrophytes. The fish selectively fed on the larger cladocerans, in accordance with the size selection hypothesis (Brooks and Dodson 1965). Cyclopoid copepods declined later since they have been shown to exhibit evasive or escape behaviour in the presence of fish (Drenner *et al.* 1978).

The predation pressure exerted by YOY fish also contributed to the decline of filter-feeders throughout the season. YOY fish may also have been able to prey upon the smaller phytophilous species on the macrophytes, YOY fish are smaller than the adults and would be able to penetrate the macrophyte bed better than adult fish.

Effect of treatment

The treatments were separated on the second CCA ordination axis as the season progressed. The fish treatment had a higher proportion of ostracods at the end of the season, in part because fish probably do not prey on ostracods. However, the fish did eliminate the filter-feeding cladocerans. In the absence of these efficient filter feeders, phytoplankton biomass increased. Ostracods do not feed effectively on the phytoplankton, so phytoplankton was not controlled in the fish treatment, despite the abundance of ostracods. Thus the fish had a top-down effect on the food web, decreasing cladoceran zooplankton abundance and increasing phytoplankton

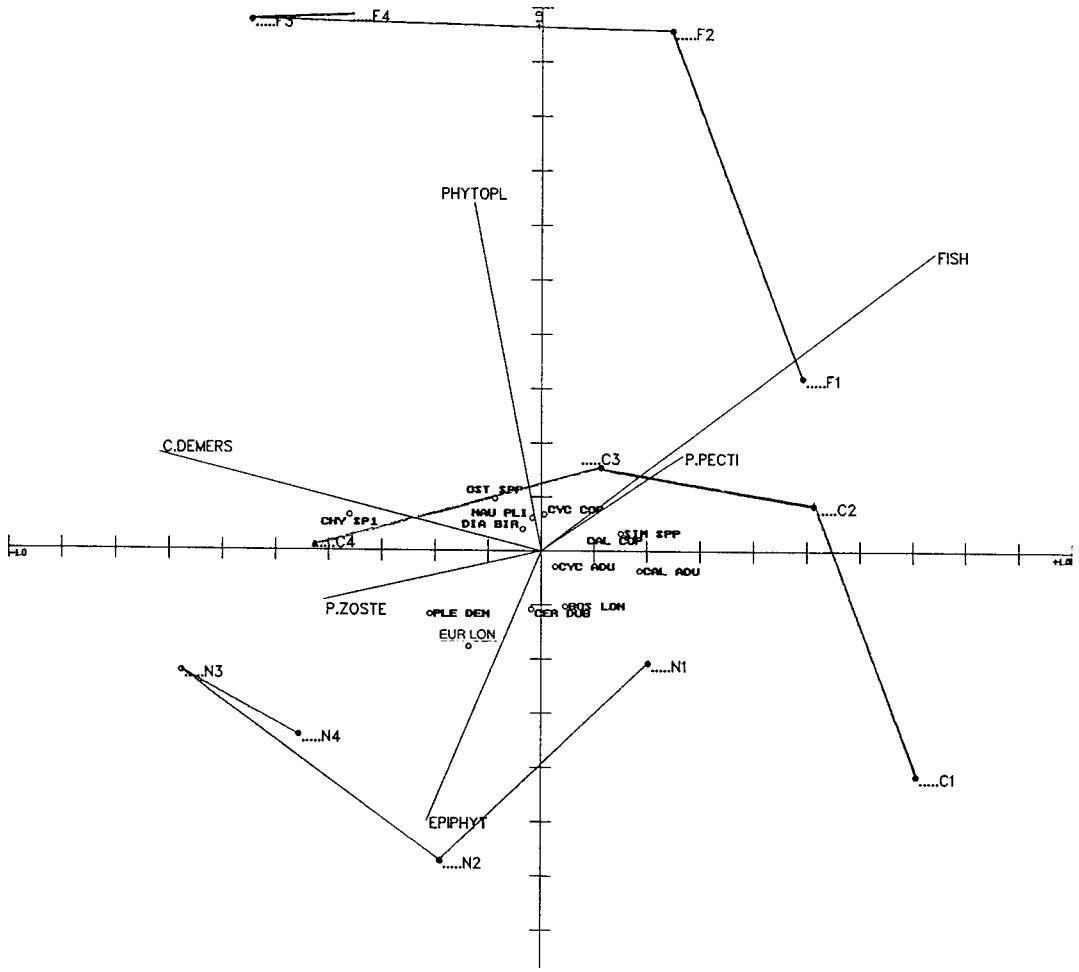

Figure 6. Canonical Correspondence Analysis triplot for numbers of individuals per Downing box sample. Labels for treatment mean sites and zooplankton species are as in figure 2. Environment variables are labeled as follows: FISH, mean daily number of adult fish trapped per treatment per week; EPIPHYT, mean epiphyton Chl *a* per Downing box sample per treatment; and PHYTOPL, mean phytoplankton Chl a per treatment; P.PECTI, mean dry weight of *Potamogeton pectinatus* per treatment; P.ZOSTE, mean dry weight of *Potamogeton zosteriformis* per treatment; and C.DEMERS, mean dry weight of *Ceratophyllum demersum* per treatment.

biomass via the trophic cascade (Carpenter *et al.* 1985).

The nutrient addition treatment was also separated from the controls on the second CCA ordination axis over time. The nutrient addition treatment had a higher proportion of phytophilous species than the control. The proportion of phytophilous cladocerans would be expected to be higher with abundant epiphyton available as food. Epiphyton biomass was found to be higher in the nutrient addition treatment. The epiphyton could have responded to nutrients directly or from nutrients obtained from the surfaces of leaky macrophytes (Brönmark 1989).

Filter-feeders were present where there was a higher biomass of *Potamogeton pectinatus.* This is expected as *P. pectinatus* has a simple structure, and therefore would offer less habitat for phytophilous species of zooplankton. *P. pectinatus* often occurred alone, and due to lower habitat complexity, samples with this macrophyte would contain a higher proportion of planktonic species. In comparison. *P. zosteriformis,* and especially *Ceratophyllum demersum,* have much greater structural complexity which favoured phytophilous species over planktonic species.

Data standardization

The Downing box was used to sample aquatic plants and associated microfauna, but depending upon the quantity of macrophytes in the sample, the accuracy of this method in estimating density of phytophilous fauna varies. If the macrophyte biomass was low, then it sampled more planktonic species, and if biomass was

high, more phytophilous species. Downing (1986) standardized the invertebrate density data by macrophyte dry weight. This is inappropriate when a small biomass of macrophyte is sampled, as planktonic individuals are represented per unit macrophyte dry weight. Numbers of individuals per unit macrophyte biomass more accurately represents phytophilous species density, but when a high macrophyte biomass is sampled this is not appropriate for truly planktonic species.

However, data in the form of numbers of individuals per unit volume is preferred since macrophyte biomass (an important determinant of microinvertebrate species composition) can be included in analyses to indicate whether the sample represented mostly planktonic habitat or phytophilous habitat. When macrophyte biomass is included as an environmental variable, more of the variation in the data is explained by environmental variables.

In summary, macrophyte biomass, predation from fish, and their interaction are important in determining the species composition of the zooplankton community throughout the season. Phytoplankton and epiphyton biomass are important in determining differences in species composition between treatments of fish and nutrient addition.

Acknowledgments

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