Effect of fish and submersed macrophytes on the abundance of zooplankton in a prairie wetland

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Introduction

Presence or absence of fish has been examined as an indicator for assessing habitat quality for waterfowl (Mallory et al. 1994). Fish can have a profound influence on the food web dynamics via the trophic cascade (Carpenter et al. 1985). This top-down control in the aquatic food web can affect waterfowl which feed in wetlands. Planktivorous fish such as fathead minnows and brook stickleback feed mainly on zooplankton which in turn feed on phytoplankton. Schriver et al. (1995) found that with increasing fish density, the zooplankton community changed from large-bodied cladocerans to small cladocerans, as predicted by the size-efficiency hypothesis (Brooks and Dodson 1965). At high fish density, Schriver et al. (1995) also found a shift to cyclopoid copepods. This change in the zooplankton community (both cladocerans and copepods) results in decreased grazing pressure on the primary producers which may then respond by increasing in biomass due to decreased grazing.

Macrophytes provide a structurally complex habitat for many organisms. Macrophytes act as a refuge for many invertebrates in wetlands and are thus another indicator of habitat quality for waterfowl (Mallory *et al.* 1994). Water lilies were found to provide a refuge for large-bodied zooplankton from planktivorous fish (Timms and Moss 1984). The amount of submersed macrophytes in the habitat may also affect when the shift in the cladoceran community, from large to small cladocerans, occurs as fish numbers increase (Schriver *et al.* 1995).

The zooplankton community is composed of planktonic and phytophilous components. The planktonic component includes those species found in the water column that filter-feed, e.g. *Daphnia* sp., *Bosmina longirostris, Diaphanosoma* sp., *Ceriodaphnia dubia*, calanoid and cyclopoid copepods (cyclopoid copepods are not filter-feeders but are present in the water column). The phytophilous component includes the cladocerans that feed on the epiphyton associated with submersed macrophytes, e.g., *Chydorus* sp. *Simocephalus serrulatus, S. vetulus*, and *Eurycercus longirostris*. The objectives of this study were: (1) to examine the effects of planktivorous fish on the zooplankton community, and to test the hypothesis that planktonic zooplankton density will be lower when planktivorous fish are present than when fish are absent, and (2) to determine if submersed macrophytes provide a refuge for phytophilous zooplankton against predation from fish, and to test the hypothesis that in the presence of planktivorous fish, phytophilous zooplankton density will remain higher within the refuge provided by the macrophytes.

Methods

Study Site

The study was conducted in Blind Channel, Delta Marsh. Water depth is shallow (~1m) allowing the growth of submersed macrophytes, including primarily *Potamogeton (P. zosteriformis, P. pectinatus)* and *Ceratophyllum demersum*. The planktivorous fish *Pimephales promelas* (fathead minnow) and *Culaea inconstans* (brook stickleback) are commonly found in Delta Marsh and were present in the enclosures in 1996.

Experimental Design

The effect of fish on zooplankton abundance was examined by comparison of control enclosures when fish were absent (1995) or present (1996). Experimental enclosures (5 m x 5 m) consisted of floating platforms from which impermeable polyethylene curtains extended down through the water column and into the sediments approximately 10 cm. The bottoms of the curtains were weighted with iron bars, sealing the inside water from the Blind Channel.

The experimental design in 1995 involved a set of enclosures from which all the fish were removed, irrespective of treatment. Four enclosures received a nutrient addition treatment, two enclosures received a macrophyte removal treatment, and two controls which had no fish, no nutrient addition and no macrophytes removed. In 1996, nutrient addition and macrophyte exclusion treatments were applied, but fish removal/ exclusion was unsuccessful. Thus the controls received no nutrients, no macrophyte removal when fish were present. Comparison of macrophyte removal/exclusion treatments between 1995 (no fish) and 1996 (fish present) was not possible since removal of macrophytes in 1995 was not successful.

Invertebrate Sampling

The planktonic component of the zooplankton community was sampled quantitatively using a water column sampler (described in Hann and Goldsborough 1997). Samples were taken weekly (June through August) using a clear acrylic cylinder (5.5 cm in diameter, 4 L volume), filtered through a 53 µm mesh net, and preserved with 1 mL of formalin. The phytophilous component was sampled semiquantitatively with funnel traps (described in Hann and Goldsborough 1997) which were set on top of submersed macrophytes overnight. Funnel trap samples were filtered through a 53 µm mesh net and preserved as above. Zooplankton present among the macrophytes are trapped when moving vertically. Cladocerans and copepods in all samples were identified using Pennak (1989). Total numbers of cladocerans and copepods (nauplii, cyclopoid copepodites, cyclopoid adults, calanoid copepodites, and calanoid adults) were determined from subsamples.

Macrophytes and associated invertebrates were sampled weekly using a Downing Box sampler (Downing 1986). The microinvertebrates obtained by this sampling technique represent both planktonic members filtering among the macrophytes, and phytophilous members which were found grazing directly on the macrophyte surface. The microinvertebrate samples were obtained by filtering the 6 L volume of the box through a 53 μ m mesh net, and the contents were preserved. The macrophyte tissue was dried at 105°C for 24 hours to obtain dry weight.

Phytoplankton was sampled (McDougal and Goldsborough 1996) weekly and quantitative estimates of biomass (performed by R. McDougal) were obtained by analysis of chlorophyll a concentration (methods in McDougal *et al.* 1997).

Results

1995

A rapid increase in cladoceran density was documented in all enclosures when fish were absent (no fish, Fig. 1). Planktonic cladocerans increased rapidly from 50 ind./L to 650 ind./L after the enclosures were in place and fish excluded (late June). By early July

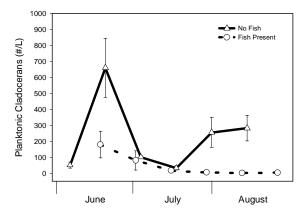


Figure 1. Planktonic cladoceran density $(\pm SE)$ in 1995 (no fish) and 1996 (fish present).

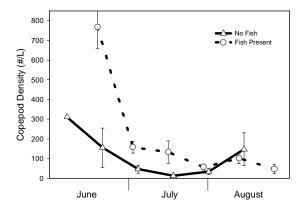


Figure 2. Planktonic copepod density (\pm SE) in 1995 (no fish) and 1996 (fish present).

density had dropped to ~100 ind./L (Fig. 1). Cladoceran density then increased from ~50 ind./L to ~ 275 ind./L by August (Fig. 1). Copepods in the water column declined from ~300 ind./L in early June to close to zero in mid-July (Fig. 2). Copepod density then increased in August to ~175 ind./L. Phytoplankton biomass (as Chl a) reached a maximum level in early June (20 mg/L) and peaked again in early August at ~13 mg/L (Fig. 3).

In the absence of fish, phytophilous cladocerans generally increased throughout the summer to reach a peak of $50,000/m^2$ in August (Fig. 4). Copepod density decreased throughout June and July from ~55,000 ind./m² of wetland bottom to ~5000 ind./m² by early August. Density increased in early August to 40,000 ind./m² and decreased to a final density of ~30,000 ind./m² in late August (Fig. 5).

1996

In 1996, when fish were present, planktonic cladocerans did not increase rapidly after enclosure installation (as they had in 1995) and numbers declined after the enclosures were in place (Fig. 1). Cladoceran

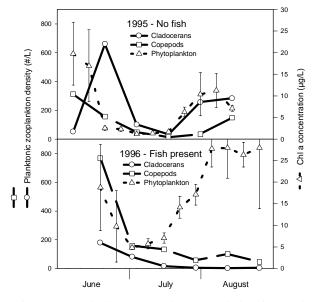


Figure 3. Cladoceran and copepod density and phytoplankton biomass (as Chl a, \pm SE) as an estimate of available food in 1995 (no fish) and 1996 (fish present).

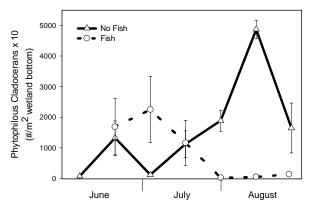


Figure 4. Phytophilous cladoceran density (\pm SE) in 1995 (no fish) and 1996 (fish present).

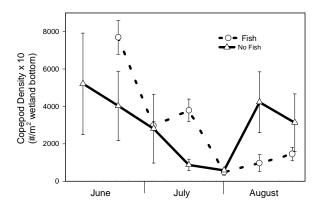


Figure 5. Phytophilous copepod density (\pm SE) in 1995 (no fish) and 1996 (fish present).

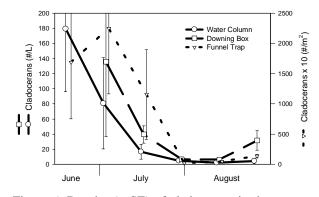


Figure 6. Density $(\pm$ SE) of cladocerans in the water column (planktonic), Downing Box (planktonic/phytophilous), and funnel traps (phytophilous) in 1996 (fish present).

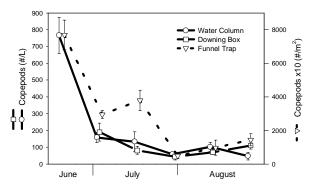


Figure 7. Density (\pm SE) of copepods in the water column (planktonic), Downing Box (planktonic/phytophilous), and funnel traps (phytophilous) in 1996 (fish present).

density remained low for the rest of the summer (< 5 ind./L, Fig. 1), even though there was an abundance of phytoplankton available as food in late summer (Fig. 3). Phytoplankton biomass (as Chl *a* concentration) reached a maximum of ~28 mg/L in August, while the density of zooplankton remained low (Fig. 3).

When fish were present, phytophilous cladocerans declined to low density by August (Fig. 2). The density of phytophilous copepods generally declined throughout the summer from almost 80,000 ind./m2 to ~5000 ind./m² by early August (Fig. 5). During August density increased to about 15,000 ind./m².

Cladoceran density declined first in the water column (planktonic), then in the Downing Box samples (planktonic/phytophilous), and finally in the funnel traps (phytophilous) when fish were present (Fig. 6). Copepod density also declined first in the water column, then in the Downing Box, and lastly in the funnel traps (Fig. 7).

Discussion

Enclosure Effect

The rapid increase after installation of the enclosures is the result of release from predation by fish, and because the cladocerans reproduced parthenogenetically, they responded to this absence of fish by quickly increasing in number. This enclosure effect has occurred previously in enclosure experiments in Delta Marsh (Hann and Goldsborough 1997; Pettigrew 1996) This high density of filter-feeding cladocerans did not persist as much of the food was removed due to intense grazing from the high density of zooplankton. Densities declined rapidly as a result of the decrease in available food. This enclosure effect did not occur in the presence of fish, probably because there was intense predation pressure exerted on the zooplankton from the planktivorous fish.

Fish Effect

In the presence of fish, the cladocerans showed no enclosure effect, and density declined rapidly to a low level that was maintained throughout the study. Numbers were kept low even though there was much more phytoplankton available as food in 1996 than in 1995, during the period of late summer increase in seasonal density of cladocerans. It is likely that this decline in zooplankton density was due to predation from fish and probably not from lack of phytoplankton as food. The lower abundance of phytoplankton when fish were absent than when fish were present supports the idea of top-down control on phytoplankton cascading from the planktivore level (Carpenter et al. 1985). This top-down control has been demonstrated in lakes (McQueen et al. 1986; Carpenter et al. 1987) and would be expected to occur in shallow water systems also (Hanson and Butler 1994). This is likely to happen in Delta Marsh due to the presence of fathead minnows which feed primarily on cladocerans and copepods which can contribute ~73% of food volume (Held and Peterka 1974). The composition of the phytoplankton community was not investigated, thus it cannot be determined if the phytoplankton was available and/or edible to the zooplankton in 1996. In 1996, phytoplankton biomass could have been high because of inedibility by zooplankton, and therefore not subject to grazing pressure. One such group of phytoplankton that is unavailable/inedible are the cyanobacteria, but there was no indication of the characteristic colour of a cyanobacterial bloom in the enclosures.

Fish also seemed to have an effect on the phytophilous cladocerans and copepods in 1996. Density was very low throughout August, whereas

density had been high the previous year with no fish. This suggests that the fish prevented the increase in seasonal abundance late in the season. The epiphyton composition is not known for either year, and thus differences in density could be due to inedibility of epiphyton, upon which the phytophilous cladocerans feed, in 1996.

The Refuge

A time lag occurred in the decline in densities of cladocerans and copepods among different habitats. Cladoceran numbers declined first in the water column, then in the Downing Box, and lastly in the funnel traps. This is consistent with the idea that macrophytes provide zooplankton with a refuge from fish predation. Diehl (1992) demonstrated this time lag between open water and among the macrophytes when macroinvertebrates were preyed upon by fish. The fish probably have reduced foraging ability among the macrophytes because they feed visually. Potamogeton and Ceratophyllum are structurally complex, providing a physical and visual obstacle to foraging. Fish would therefore be expected to forage in the open water first until that food supply is used up, and then move into the least dense macrophytes to forage. This time lag in declining densities of zooplankton between open water and macrophytes may also be an artifact of enclosure. The fish may be forced to forage in the macrophytes after feeding in the open water. If the fish were not enclosed, they may forage in another part of the marsh in the open water instead of being forced to feed among the macrophytes. Timms and Moss (1984) found that cladocerans associated with plants were not affected by the presence of fish when macrophytes were present, and that these cladocerans were able to migrate to the open water at night to control phytoplankton. This did not happen in our study, as phytoplankton biomass was high in 1996. Schriver et al. (1995) discussed the interaction between two factors that influence predation on zooplankton, macrophyte density and fish abundance. When there are few macrophytes, zooplankton can be controlled with relatively few fish, whereas if macrophytes are dense, more fish are required to control zooplankton. Thus cladocerans associated with plants may be able to control phytoplankton only when the macrophytes are dense and/or when fish abundance is low (Timms and Moss 1984). In 1996, the fish could have been abundant enough to control the phytophilous zooplankton at the macrophyte density present at the time. It is not known how dense macrophyte beds must be in order to provide protection at different densities of planktivorous fish. Predation of zooplankton only in the water column may then occur if the density of planktivores is low and macrophyte density is high. Based on these statements, it is likely that fish density was relatively high in 1996, since zooplankton declined in both the water column and among the macrophytes.

Acknowledgments

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