Enclosure affects trophic structure of a freshwater prairie wetland

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Introduction

Freshwater prairie wetlands support complex food webs comprising primary producers (algae and macrophytes), primary consumers (planktonic and benthic invertebrates, and fish), secondary consumers (fish and mammals), and decomposers (fungi and bacteria). One approach to understanding this complexity is through experimental manipulation of an enclosed subset of the natural system, wherein conditions can be controlled and the consequent effects of stimulation or inhibition of one or more ecosystem component on other interacting trophic levels can be examined. However, it must be recognized that the enclosure of the wetland can lead to physical, chemical and biological conditions that differ from those of the unenclosed ecosystem. Such "enclosure effects", where substantial, confound the extrapolation of experimental results to the whole system. Consequently, examination of the nature and magnitude of enclosure effects is a necessary component of any investigation using *in situ* enclosures.

As part of ongoing studies of ecosystem structure and function in Delta Marsh, we compared primary and secondary production in three adjoining areas of the Blind Channel over a three month period: 1) in a fish-less 5m x 5m enclosure; 2) in a largely enclosed area that afforded similar physical isolation as the enclosure but which did not exclude fish; and 3) in the surrounding marsh. We made the following predictions about the consequences of enclosure:

1. The exclusion of planktivorous fish will permit herbivorous invertebrate (zooplankton) abundance to increase in the absence of vertebrate predation.
2. Abundant zooplanktonic herbivores will exert strong grazing pressure on phytoplankton, reducing its biomass. Abundant phytophilous invertebrates (grazers associated with macrophytes) will exert strong grazing pressure on periphytic algae, reducing its biomass and productivity.
3. Elimination of water flow by the enclosure will lead to reduced turbidity, increased subsurface irradiance, and increased macrophyte biomass.
4. Enclosure will lead to increased pH and lower alkalinity as a consequence of depletion of carbonate supply during photosynthesis by abundant macrophytes.

Methods

This experiment was conducted as a corollary to nutrient enrichment experiments conducted in 1994 (Hann 1995, McDougal and Goldsborough 1995). Ten enclosures, enclosing a marsh surface area of 25 m^2 and a water volume of about 20,000 L, were deployed in Blind Channel near its confluence with the Field Station's canoe launching channel in water of about 80 cm depth. The rectangular arrangement of enclosures provided a 5 m x 10 m area in the middle which was protected by the enclosures, to a degree, from wind but which was connected to the surrounding marsh (Fig. 1). Previous experiments using similar enclosures has shown that the water column becomes noticeably clearer within a few weeks due to protection of the water column and elimination of horizontal water flow. Consequently,

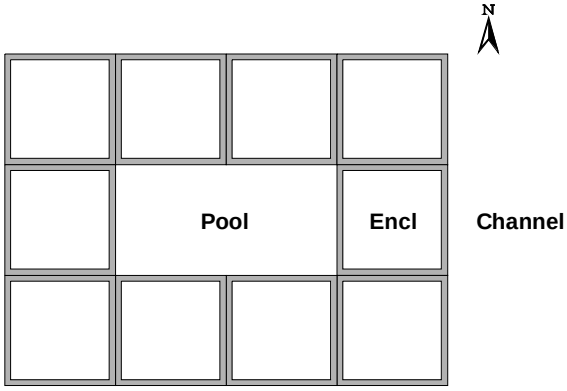

Figure 1. Schematic diagram of the enclosures deployed in Blind Channel during the summer of 1995. Water chemistry, algal biomass and productivity, and cladoceran abundance were sampled at biweekly intervals in an unmanipulated enclosure, in a sheltered area between enclosures ("pool") and in the surrounding marsh.

we expected that the physical and chemical properties of this central area (designated the "pool") would be similar to those of the enclosures but that its biological features, notably the presence of fish which were actively excluded from the enclosures, would more closely resemble the surrounding marsh. Therefore, we expected there to be differences in algae and invertebrates in the enclosure, the pool and the marsh reflecting these physical, chemical and biological differences.

Surface water samples were collected at weekly intervals from a randomly selected site in one unmanipulated enclosure, the pool, and the Blind Channel. They were analyzed for turbidity, pH, alkalinity, nitrate and soluble reactive phosphorus (SRP) following methods of APHA (1992). Phytoplankton biomass (chlorophyll *a* concentration) was measured spectrophotometrically by filtering a known water volume through a glass fiber filter and extracting algal pigments on the filter using 90% methanol. Absorbance readings of the extract were used to calculate chlorophyll using the formulae of Marker *et al.* (1980). Extruded acrylic rods, scored at pre-determined intervals to facilitate subsampling, were deployed at each site on 26 May to provide a substratum for periphytic algae. They were collected at approximately two-week intervals. Two rod samples were analyzed for periphyton biomass using the same method as for phytoplankton. Periphyton photosynthesis was measured by inoculating two rod samples with $NaH^{14}CO_3$ (37 kBq/mL), and incubated them at 25°C for four hours at a saturating irradiance of about 500 µmoles/m^2/s. The samples were subsequently fumed with concentrated HCl to liberate residual inorganic 14C and transferred to vials of scintillation cocktail (Beckman ReadySafe). Radioactivity of the vials was determined by liquid scintillation counting, and photosynthetic rate was calculated with measurements of available carbon determined from pH and alkalinity data.

Submersed macrophyte dry weight (g/m^2) was measured at the end of the experiment in late August. A 0.48 m^2 diameter plastic cylinder was lowered into the water column at three randomly selected positions within each site, delimiting a subset of the macrophyte assemblage. All macrophytes were harvested at the sediment/water interface using long-handled shears and transported to the laboratory where they were sorted by species, dried at 105°C and weighed.

Methods of sampling and analyzing invertebrate (zooplankton) abundance are described by Hann (1995).

Differences in fish abundance between the three sites were assessed using standard Gee minnow traps deployed just below the water surface (Kiers and Hann 1996). Traps were checked daily and fish were enumerated and identified to species, where possible. Results were expressed in fish caught per trap-day.

Results

Physical, chemical and biological differences between the pool and the marsh were generally minor but both areas were noticeably different from the enclosure. The enclosure water cleared within two weeks of isolation and remained so throughout the rest of the experiment whereas the other areas remained turbid (Fig. 2). Alkalinity in the enclosure was lower than in the pool and marsh (Fig. 3) whereas its pH was consistently higher (Fig. 4).

Phytoplankton chlorophyll (Fig. 5), and periphyton chlorophyll (Fig. 6) and photosynthesis (Fig. 7) were generally higher in the pool and marsh as compared to the enclosure, often by large margins. There was no difference in the biomass of submersed macrophytes among the three areas (Fig. 8). However, composition

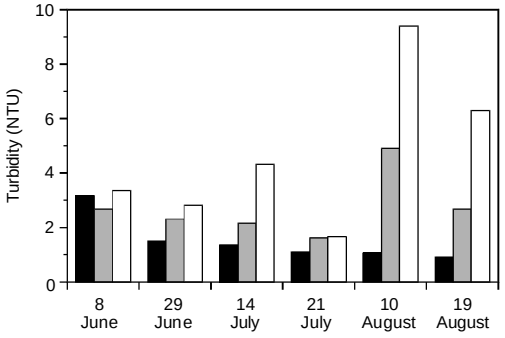

Figure 2. Differences in turbidity (NTU) in an unmanipulated enclosure (black bars) as compared to a sheltered area between enclosures (gray bars) and the surrounding marsh (white bars).

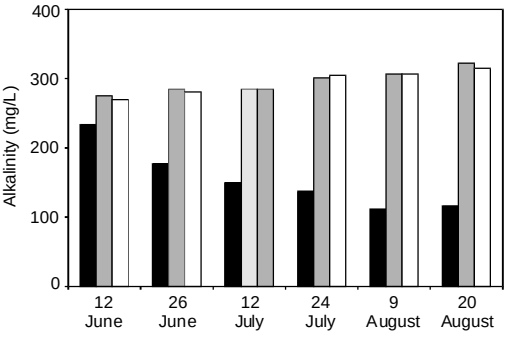

Figure 3. Differences in titratable alkalinity (mg/L) in an unmanipulated enclosure (black bars) as compared to a sheltered area between enclosures (gray bars) and the surrounding marsh (white bars).

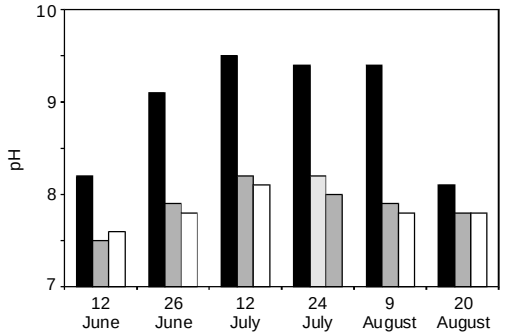

Figure 4. Differences in pH in an unmanipulated enclosure (black bars) as compared to a sheltered area between enclosures (gray bars) and the surrounding marsh (white bars).

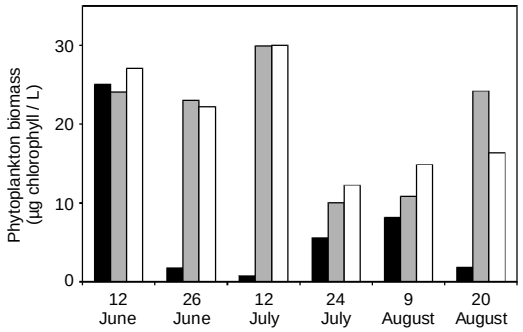

Figure 5. Differences in phytoplankton chlorophyll (µg/L) in an unmanipulated enclosure (black bars) as compared to a sheltered area between enclosures (gray bars) and the surrounding marsh (white bars).

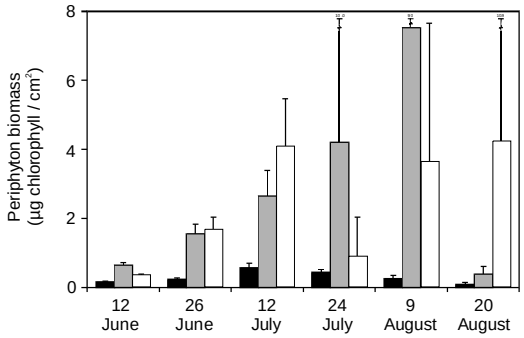

Figure 6. Differences in periphyton chlorophyll (µg/cm^2) on artificial substrata in an unmanipulated enclosure (black bars) as compared to a sheltered area between enclosures (gray bars) and the surrounding marsh (white bars).

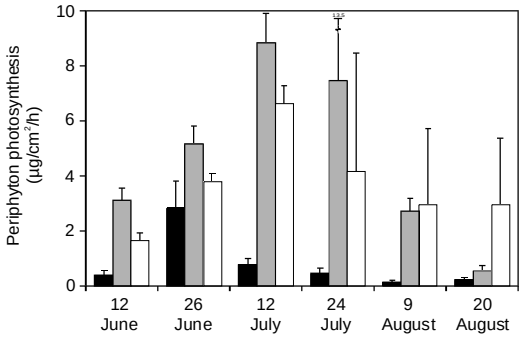

Figure 7. Differences in periphyton photosynthetic rate (µgC/cm^2/h) on artificial substrata in an unmanipulated enclosure (black bars) as compared to a sheltered area between enclosures (gray bars) and the surrounding marsh (white bars).

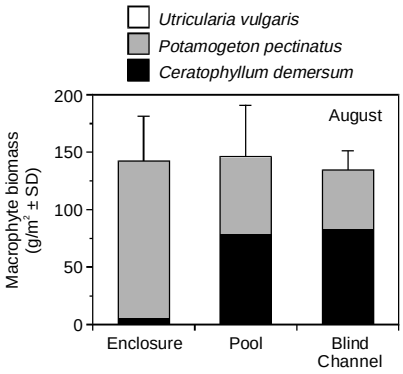

Figure 8. Dry weight of submersed macrophytes (g/m^2), sampled at peak biomass in late August, in an unmanipulated enclosure (black bars) as compared to a sheltered area between enclosures (gray bars) and the surrounding marsh (white bars). The contributions of the three major species, as a proportion of the total, are shown.

of the macrophyte assemblage differed, being comprised largely of *Potamogeton pectinatus* in the enclosure but equal proportions of *P. pectinatus* and *Ceratophyllum demersum* in the pool and marsh. *Utricularia vulgaris* was present at all sites but was only collected in pool samples where it contributed < 1% of total biomass.

Planktonic cladocerans, cyclopoid copepods, calanoid copepods and rotifers were markedly more abundant in the enclosure than in the unenclosed areas (Fig. 9). Fish were equally abundant in traps deployed in the pool and the surrounding marsh but they were absent from traps in the enclosure (Fig. 10). Yellow perch (*Perca flavescens*) was the most commonly caught species in the marsh whereas fathead minnows (*Pimephales promelas*) were abundant in the pool.

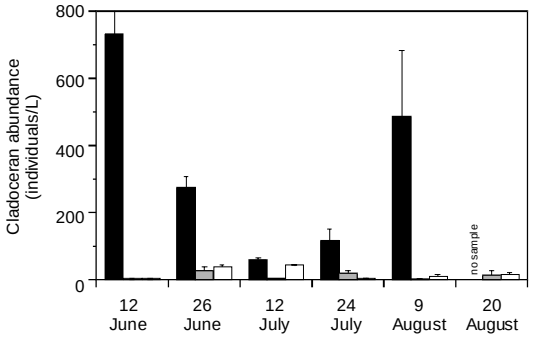

Figure 9. Differences in cladoceran abundance (individuals/L) in an unmanipulated enclosure (black bars) as compared to a sheltered area between enclosures (gray bars) and the surrounding marsh (white bars).

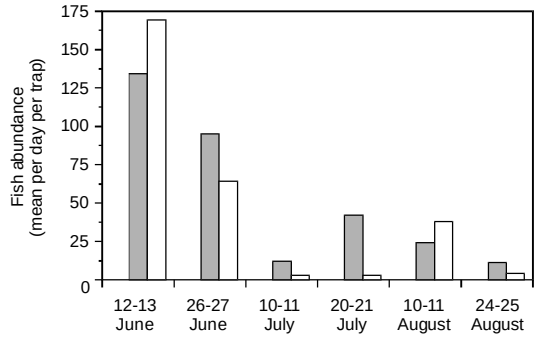

Figure 10. Differences in fish abundance (catch/trap/day) in a sheltered area between enclosures (gray bars) and the surrounding marsh (white bars). Fish were absent from the enclosure.

Discussion

Logistical limitations prevented us from having replicates of the pool and marsh "treatments"; consequently, marked differences in water chemistry, algal production, and invertebrate abundance between the enclosure, pool, and marsh should be treated cautiously. Nevertheless, the consistency with which differences between sites were maintained between sampling times, combined with close agreement with results from studies in previous years, leads us to believe these trends are real. If so, they support three of our four hypotheses. Our hypotheses regarding a change in macrophyte biomass with enclosure was not supported but changes in species composition, possibly reflecting interspecific differences in ecological preferences between the respective sites, did occur.

It is arguable that the severity of chemical and physical effects of enclosure should be greatest in small enclosures where the ratio of wall surface area to enclosed water volume is high, such as in 0.48 m^2 enclosures used in previous manipulative experiments in Delta Marsh (Goldsborough *et al*. 1986). This study shows that enclosure effects also occur in much larger 25 m^2 enclosures due, in part, to chemical isolation afforded by enclosure walls and exacerbated by the consequences of excluding a fundamental ecosystem component, such as planktivorous fish. Fish present in the pool and the marsh consumed invertebrates, reducing their numbers in these areas sufficiently that grazing pressure on phytoplankton and periphyton was reduced, causing them to flourish. Conversely, invertebrates free from predation in the fishless enclosure grazed heavily on algae, reducing its abundance. Such ecological cascade effects likely persist regardless of enclosure dimensions. For example, enclosure effects were obvious in fishless 5-7 hectare areas (cells) of Delta Marsh that were monitored over a 10-year period during the Marsh Ecology Research Program (Murkin *et al*. 1984). Floating mats of metaphytic algae occurred abundantly in all cells but they were rare in the marsh as a whole (Hosseini and van der Valk 1989). As in our enclosures, the reduction in predation on zooplankton due to the absence of fish could have increased herbivory on small, easily digested algae, thereby reducing competition with the filamentous green algae that, by virtue of their large size, escaped grazing. These algae then flourished on nutrients hypothesized to be liberated from the flooded wetland soil, forming conspicuous mats.

We draw two conclusions from these data: 1) top-down control mechanisms are important in freshwater wetlands, but the role of fish in the ecosystem, as regulators of invertebrate populations, grazing pressure, and ultimately primary producer production, needs further clarification, and 2) results from manipulative enclosure experiments should only be extrapolated to the natural wetland with due recognition of potential enclosure effects.

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