Snail-periphyton interactions in a prairie wetland

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Introduction

Wetland ecosystem function and dynamics are adversely affected through increasing use of pesticides, herbicides, and fertilizers (Perring and Mellanby 1977; Scorgie 1980; Murphy *et al*. 1981; Alho *et al.* 1988; Goldsborough 1991; Hann 1991). The effects of nutrients on various parts of aquatic ecosystems have been extensively studied through controlled experiments using treatments such as nitrogen and phosphorus additions (Cuker 1983; Moss 1983; Timms and Moss 1984; Osenberg 1989; Hough *et al*. 1989; Marks and Lowe 1989; Scheffer 1990; Winterbourn 1990; Hill *et al.* 1992; Rosemond *et al.* 1993; Daldorph and Thomas 1995; Hann 1995; McDougal *et al*. 1997). Generally, two different treatment effects were observed: (1) an increase in periphyton and associated grazers (Osenberg 1989; Winterbourn 1990; Rosemond *et al.* 1993), and (2) an increase in phytoplankton (Moss 1983; Scheffer 1990; Daldorph and Thomas 1991), metaphyton (McDougal *et al.* 1997) or floating macrophytes (Hough *et al*. 1989; Thomas and Daldorph 1994) with a subsequent decrease of submerged macrophytes and associated grazers (Thomas and Daldorph 1991; Daldorph and Thomas 1991; Daldorph and Thomas 1995).

A two stable state model has been described for shallow aquatic ecosystems, based on the effects of varying nutrient concentrations and turbidity in a water column (Timms and Moss 1984; Scheffer 1990). The alternative equilibria include: (1) a clear stable state dominated by submerged macrophytes and (2) a turbid state characterized by phytoplankton dominance. The transition from one state to the other has been suggested to occur in a step wise fashion (Scheffer 1990).

In addition to bottom-up (nutrient) control of wetland ecosystems, there is also top-down control. Many studies have shown grazers to strongly affect algae (Lamberti *et al.* 1989; Osenberg 1989; Daldorph and Thomas 1991; Hann 1991; Hill *et al.* 1992; Steinman 1992; Rosemond *et al*. 1993; Hann 1995; Kjeldson 1995; Hann and Goldsborough 1997). Benthic grazers such as snails have been found to both reduce periphyton biomass (Lamberti *et al.* 1989; Osenberg 1989; Daldorph and Thomas 1991; Hann 1991; Hill *et al.* 1992; Steinman 1992; Rosemond *et al.* 1993; Kjeldson 1995) and affect its species composition (Marks and Lowe 1989; DeNicola *et al.* 1990; Rosemond *et al.* 1993). If present, grazers could help push an aquatic ecosystem to either stable state depending on their effect on periphyton.

Portions of Delta Marsh exist in the stable clear-water state dominated by submerged macrophytes, while other parts of the marsh exhibit the alternative turbid state dominated by phytoplankton. Nutrient concentrations and extent of macrophyte development are important factors influencing the state of the system (Scheffer *et al.* 1993). Nutrient additions increase autotrophic growth (if nutrient limited), including phytoplankton. The increase in phytoplankton would increase turbidity in the water column, decreasing the amount of photosynthetically active radiation (PAR) reaching the sediments, ultimately resulting in phytoplankton dominance. Submersed macrophytes have been found to stabilize sediments and suppress algal growth (Timms and Moss 1984; Scheffer 1990). With their exclusion turbidity would increase, favoring proliferation of suspended phytoplankton, ultimately resulting in the turbid stable state dominated by phytoplankton.

The objectives of this study were to examine the treatment effects of nutrient addition and macrophyte exclusion on snail-periphyton interactions, and to assess any interactive effects between the two treatments. Based on the two stable state model, the following hypotheses were examined: (1) in response to nutrient addition, (i) in the clear state, all autotrophs will increase, including periphyton, with a subsequent increase in snails, or (ii) in the turbid state, phytoplankton will increase with a subsequent decrease in macrophytes, periphyton, and snails; and (2) in response to macrophyte exclusion, (i) in the clear state, autotrophs other than submerged macrophytes will increase, including periphyton, with a subsequent increase in snails, or (ii) in the turbid state, phytoplankton will increase with a subsequent decline in periphyton and snails.

Methods

Experimental Design

The study was conducted at the University Field Station, Delta Marsh, an extensive coastal prairie wetland on the southern shore of Lake Manitoba. Enclosures (5 m x 5 m) were located in the Blind Channel from June to August, 1996 (Fig. 1). The enclosures consisted of floating platforms from which were suspended impermeable polyethylene curtains. The bottom margins of the curtains which penetrated into the sediments at least 30 cm were weighted with iron rods, effectively isolating each enclosure from the surrounding marsh.

The experiment focussed on two manipulated variables in a modified factorial design. Each variable (macrophyte exclusion, nutrient addition) as well as their interaction (macrophyte exclusion and nutrient addition) in a combined treatment was represented in two replicate enclosures, and the control treatment (no manipulation) was found in three replicates (Fig 1). The experiment involved a one-week pre-treatment period for equilibration of the enclosures followed by a treatment period of ten weeks. The macrophyte exclusion treatment required placement of a permeable tarp (geotextile fabric) on the bottom of the enclosure to preclude macrophyte germination. Slits were cut in the geotextile to allow release of gases and emergence of biota from the sediments. The nutrient addition treatment consisted of adding nitrogen (as $NaNO_3$) and phosphorus

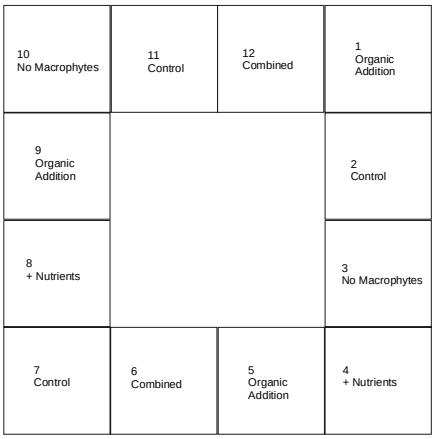

Figure 1. Arrangement of enclosure network constructed on the east end of the Blind Channel at Delta Marsh. The numbers correspond to the various controls and treatments (i.e. - 2, 7 and 11 - control; 3 and 10 - macrophyte exclusion; 4 and 8 - nutrient addition; 6 and 12 - macrophyte exclusion with nutrient addition; 1, 5 and 9 - used in a separate experiment.

(as $NaH_2PO_4.2H_2O$) in a ratio of 10N:1P, three times weekly. Nutrient additions were prepared in the laboratory by mixing a pre-weighed sample of inorganic solute in 1 L of carbon-filtered water. The mixture was diluted with approximately 10 L of water from the enclosure to which it would be added, then sprinkled evenly over the appropriate enclosure.

Study Biota

The pulmonate gastropods *Gyraulus* spp. (including mainly *G. circumstriatus* and some *G. deflectus*) were overwhelmingly most abundant in the enclosures, and consequently, the only snail analyzed in this study. However, *Physa gyrina*, *Lymnaea stagnalis*, *Stagnicola elodes*, and *Promenetus exacuous* were present in low numbers (identification was made using Clarke, 1978). The dominant submerged macrophytes in Blind Channel and the enclosures were *Potamogeton pectinatus, P. zosteriformis*, *Myriophyllum spicatum, Ceratophyllum demersum*, and *Utricularia vulgaris*. Fish present within the enclosures included: fathead minnows (*Pimephales promelas*), common shiners (*Luxilus cornutus*), brook sticklebacks (*Culaea inconstans*), emerald shiners (*Notropis atherinoides*), white suckers (*Catastomus commersoni*), carp (*Cyprinus carpio*) and yellow perch (*Perca flavescens*).

Water Chemistry and Environmental Variables

Water samples were collected twice weekly for analysis of soluble reactive phosphate, nitrate, and ammonia using colorimetric analytical methods described in Stainton *et al.* (1977), and pH using methods in APHA (1992). Dissolved oxygen concentrations were determined at 10 cm and 50 cm depths weekly, using a YSI Model 51B oxygen meter. Simultaneous temperature readings at corresponding depths were obtained so oxygen concentration could be transformed into percent oxygen saturation (Hutchinson 1957). Turbidity, measured in nephelometric turbidity units (NTUs), was determined on duplicate water samples collected weekly from each enclosure using a Hach 2100 turbidimeter. Irradiance (in µmoles/m^2/sec) was determined at 10 cm depth intervals biweekly using a Li-Cor light meter and underwater sensor.

Sampling Methods

Within each enclosure, polyethylene strips, 5 cm wide, were stapled along the north and east edges to obtain the greatest exposure to sunlight during the day. The strips draped inward from the enclosure curtains

and rested on the sediment, weighted down with a piece of re-bar placed within a stapled fold at the bottom of the strip. A strip from both edges was randomly sampled from each enclosure weekly over an eight-week period from 2 July 1996. From where each strip entered the water, 70 cm lengths were measured off and separated into 35 cm top and bottom portions, placed in separate plastic bags, and brought back to the lab to be analyzed. Snails from each strip were removed, counted, measured for width using calipers and grouped into 0.2 mm interval size classes and placed in separate vials containing 70% ethanol. Snails from the various 0.2 mm size class vials were dried (at 103°C) for 24 hrs and weighed. Snail biomass was then estimated by constructing a snail width-dry weight ordinary least squares (OLS) linear model.

Periphyton was sampled by cutting two 1 cm lengths (5 cm wide) from both the top and bottom portions of each strip using a template. Both 1 cm x 5 cm samples for each portion were placed into one vial, immediately frozen for a 24 hr period, then analyzed for periphyton biomass by measuring the chlorophyll *a* content in µg/cm^2 (detailed methods in McDougal *et al.* 1997). Data collected from top and bottom portions of strips were pooled for north and east separately.

Fish species and numbers were monitored daily by checking set minnow traps.

Statistical Analysis

Treatment effects were examined for July and August separately using SigmaStat. Monthly mean values for snail density and biomass were calculated for each replicate for each treatment. Data were log-transformed (natural log) prior to analysis. A two-way analysis of variance was used to test if treatment effects for macrophyte exclusion, nutrient addition and the interaction were significant (df = 8, $p < 0.05$).

Results

When plotted on a common log scatter plot of dry weight per individual on width, *Gyraulus* spp. demonstrated an OLS linear model of y = 2.45x + 2.24 with a r^2-value of 0.989 (N = 88) (Fig. 2).

Gyraulus demonstrated a unimodal size distribution on each sampling date throughout the study period (Fig. 3). Modal size increased, suggesting growth of a single cohort.

Macrophyte Exclusion Treatment Effects

Snail density increased initially in both the control and macrophyte exclusion treatments, then in the control, snail density leveled off, while in the macrophyte exclusion treatment, snail density decreased until the end of August (Fig. 4). The maximum snail density in the macrophyte exclusion treatment was slightly higher than that of the control; however, differences were not statistically significant in July or August.

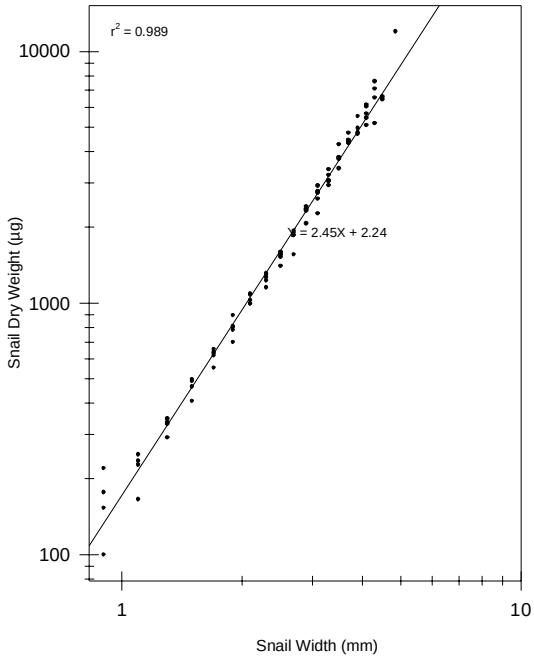

Figure 2. Snail width versus dry weight with its regression on a common log scale.

Snail biomass in the macrophyte exclusion treatment peaked at a mean value nearly twice that of the control. The biomass peak was followed by a decrease in the macrophyte exclusion treatment, whereas the control leveled off (Fig. 5). The differences in snail biomass between the macrophyte exclusion treatment and control were statistically significant in July ($p = 0.0370$), but not in August.

Periphyton biomass increased steadily in both the macrophyte exclusion treatment and control (Fig. 4), and there was no statistically significant difference in periphyton biomass between the macrophyte exclusion treatment and control in July or August.

Nutrient Addition Treatment Effects

In the nutrient addition treatment, by mid July, snail density increased to a mean value nearly twice that in the control (Fig. 4). Snail density then decreased in the nutrient addition treatment and leveled off at mean values similar to snail densities in the control. Snail densities were not significantly different between the nutrient addition treatment and control in July or August.

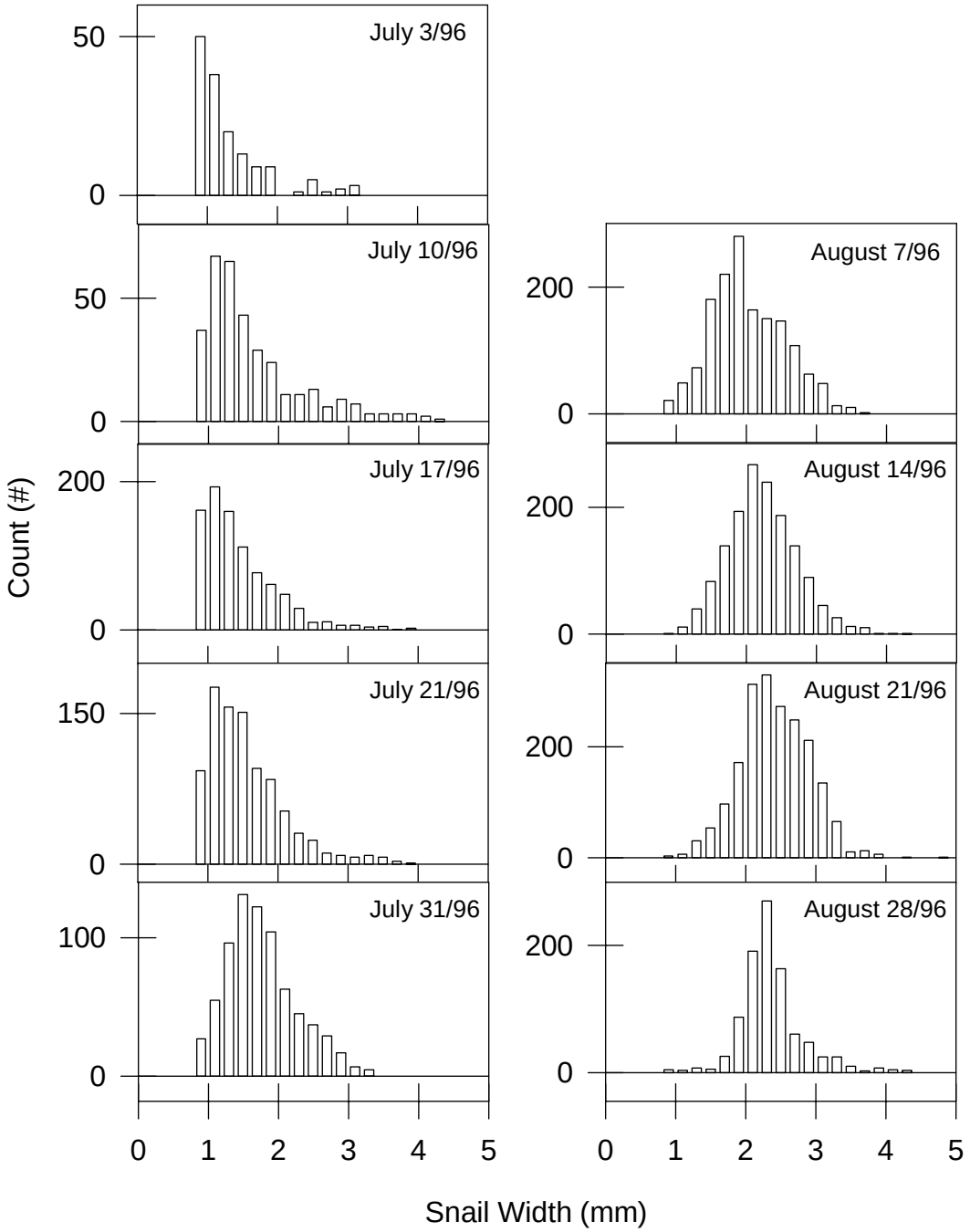

Figure 3. Histogram of snail counts within size classes for Downing box samples from July to August 1996.

Snail biomass in the nutrient addition treatment sharply increased until 22 July 1996, then stabilized throughout August, whereas snail biomass increased gradually in the control throughout the sampling period (Fig. 5). Differences in snail biomass between the nutrient addition treatment and control were statistically significant in July ($p = 0.0287$), but not in August.

Periphyton biomass generally increased throughout the sampling period in both the nutrient addition treatment and control (Fig. 4). During July, the increase of periphyton biomass in the nutrient addition treatment was significantly greater than the control ($p = 0.0076$); however, the difference was not statistically significant in August.

Combined Treatment Effects

In the combined treatment, snail density and biomass demonstrated dramatic changes, increasing sharply in July, then decreasing sharply and leveling off in August. These values were comparable to those observed in both the macrophyte exclusion and nutrient addition

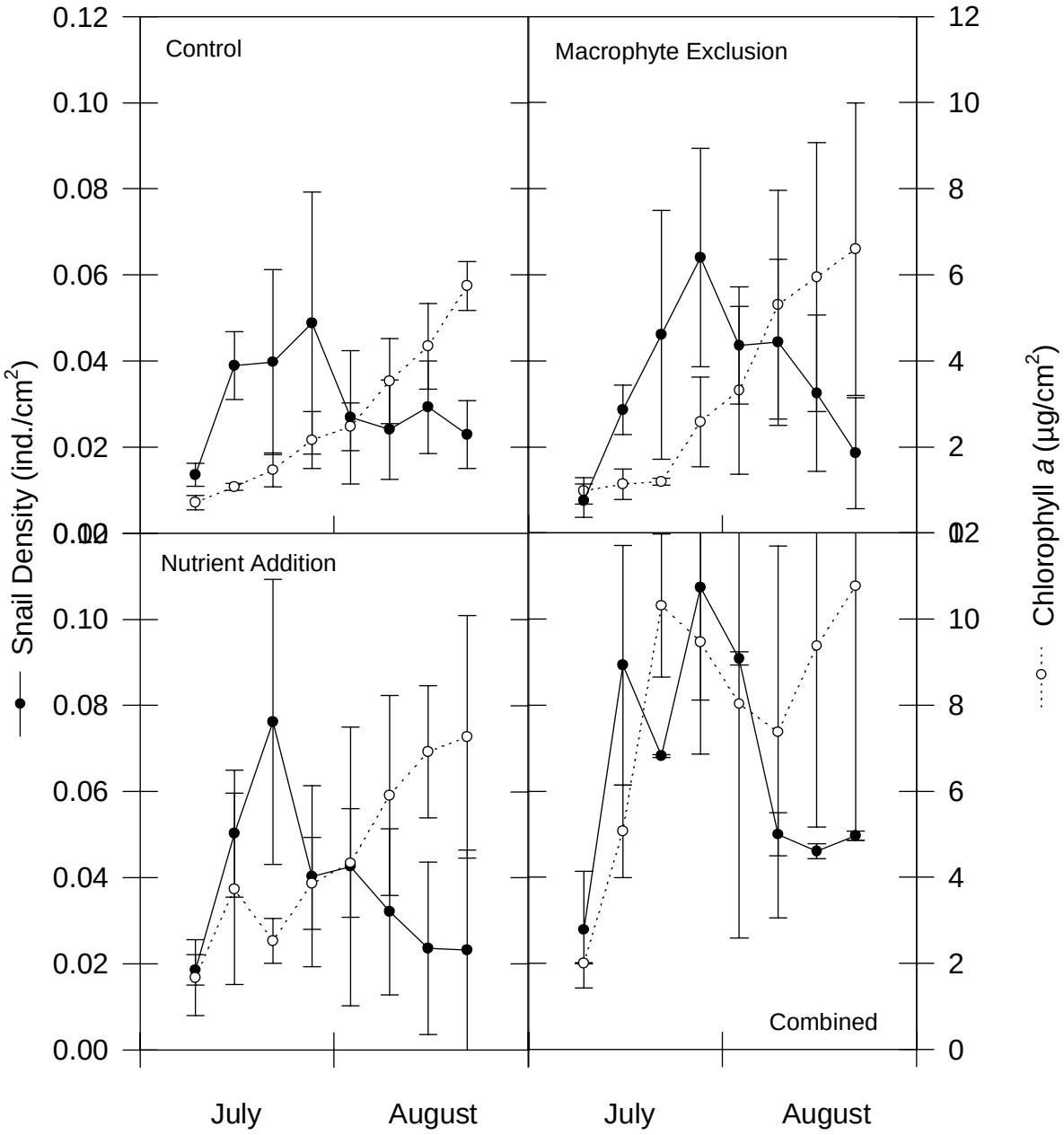

Figure 4. Snail density and periphyton biomass (as Chl a) means (± SE) found on strip substrata from July to August.

treatments (Fig. 4 and 5).

Periphyton biomass in the combined treatment increased sharply until mid July, then decreased, increasing again by the end of August (Fig. 4). In the macrophyte exclusion and nutrient addition treatments, periphyton biomass generally remained low in early July, then steadily increased throughout the rest of the sampling period (Fig. 4).

Inter-replicate variation

Among the three replicate control enclosures, snail densities in enclosures 2 and 7 demonstrated similar weekly mean values. Snail density in enclosure 11 was markedly higher than in the other two replicates, especially from mid-July to mid-August (Fig. 6). Snail biomass values in the control enclosures did not differ significantly among replicates throughout the sampling period, although snail biomass in enclosure 11 was consistently higher than in the other two replicates (Fig. 7). Periphyton biomass did not differ significantly among control replicate enclosures throughout July and August (Fig. 8).

There was substantial variation between the macrophyte exclusion treatment replicates. Snail density and biomass peaked in late July followed by a sharp

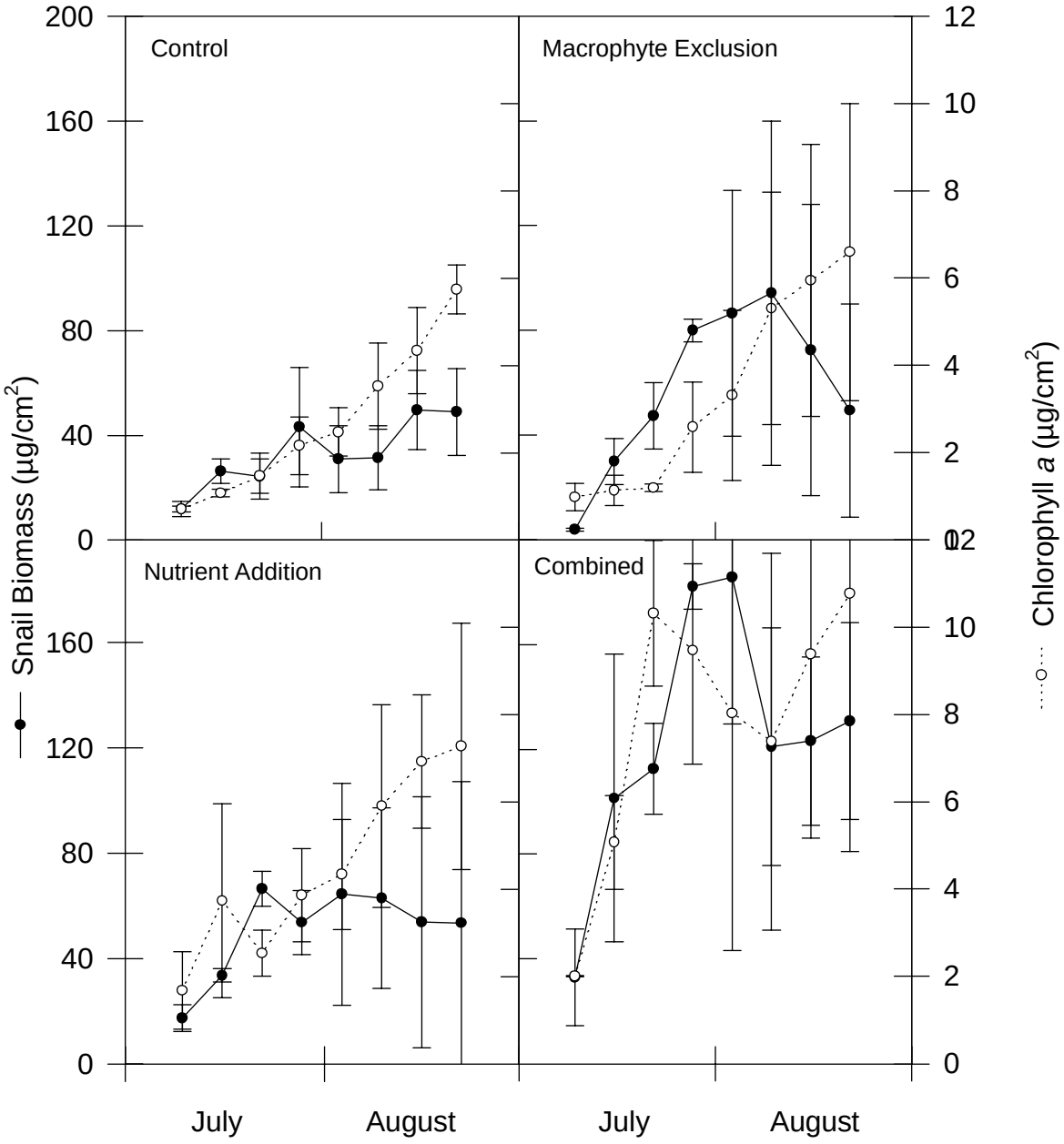

Figure 5. Snail biomass and periphyton biomass (as Chl a) means (± SE) found on strip substrata from July to August 1996.

decrease in enclosure 10, whereas the density peak showed a 2-week lag in enclosure 3 (Fig. 6). Periphyton biomass was significantly higher in enclosure 10 than in enclosure 3 from mid-July to the end of August (Fig. 8).

In the nutrient addition treatment replicates, snail density, snail biomass, and periphyton biomass were generally higher in enclosure 8 than in enclosure 4 from mid-July to the end of August (Fig. 6-8). Snail density and biomass in enclosure 4 decreased to 0 ind./cm^2 and 0 µg/cm^2, respectively, at the end of August. Turbidity was significantly higher in enclosure 4 than in enclosure 8 throughout the experiment (Fig. 9).

In the combined treatment, snail density was not significantly different between replicates throughout the summer (Fig. 6). Snail biomass and periphyton biomass demonstrated substantial variation among replicates in August (Fig. 7 and 8). During August, snail biomass and periphyton biomass in enclosure 6 decreased substantially, whereas in enclosure 12 both snail and periphyton biomass were significantly higher than in enclosure 6 (Fig. 7, 8).

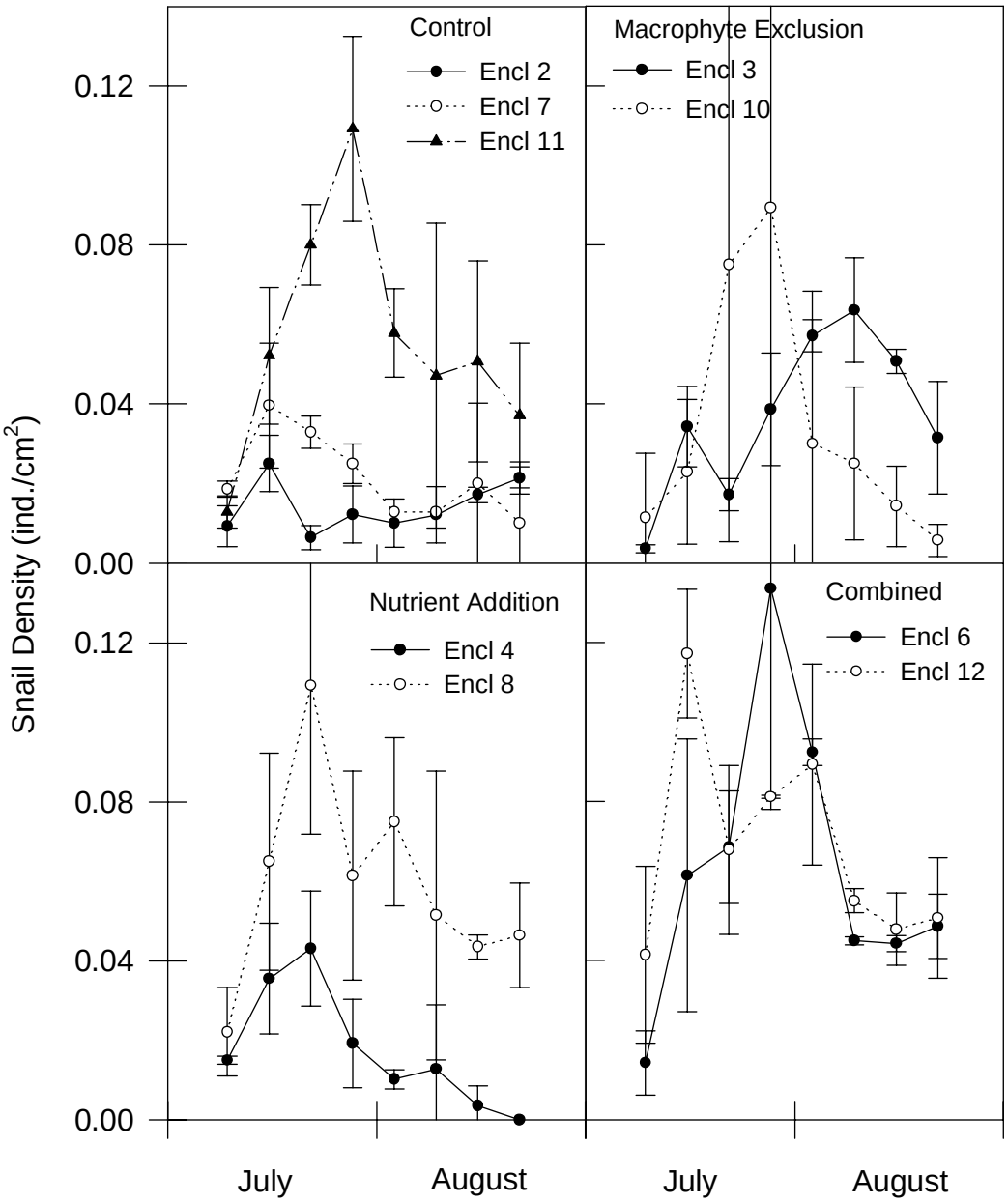

Figure 6. Treatment replicate means (± SD) of snail density found on strip substra from July to August 1996.

Discussion

Macrophyte Exclusion Treatment Effects

Eutrophication of shallow water bodies, due to such factors as anthropogenic influences, has been found to result in the dominance of phytoplankton (Moss 1983; Daldorph and Thomas 1991), floating macrophytes (e.g., *Lemna*) (Hough *et al*. 1989; Thomas and Daldorph 1994), or metaphyton (McDougal *et al*. 1997). Usually, this dominance is accompanied by an increase in turbidity of the water column (Timms and Moss 1984; Scheffer 1990) and the subsequent demise of submerged macrophytes (Moss 1983; Hough *et al.* 1989; Scheffer 1990; Daldorph and Thomas 1991; Thomas and Daldorph 1994; Daldorph and Thomas 1995). It has been speculated that this results from competitive inhibition of submerged macrophytes by phytoplankton (Moss 1983; Daldorph and Thomas 1991), floating macrophytes (Hough *et al.*, 1989; Thomas and Daldorph, 1994), or metaphyton (McDougal *et al*.

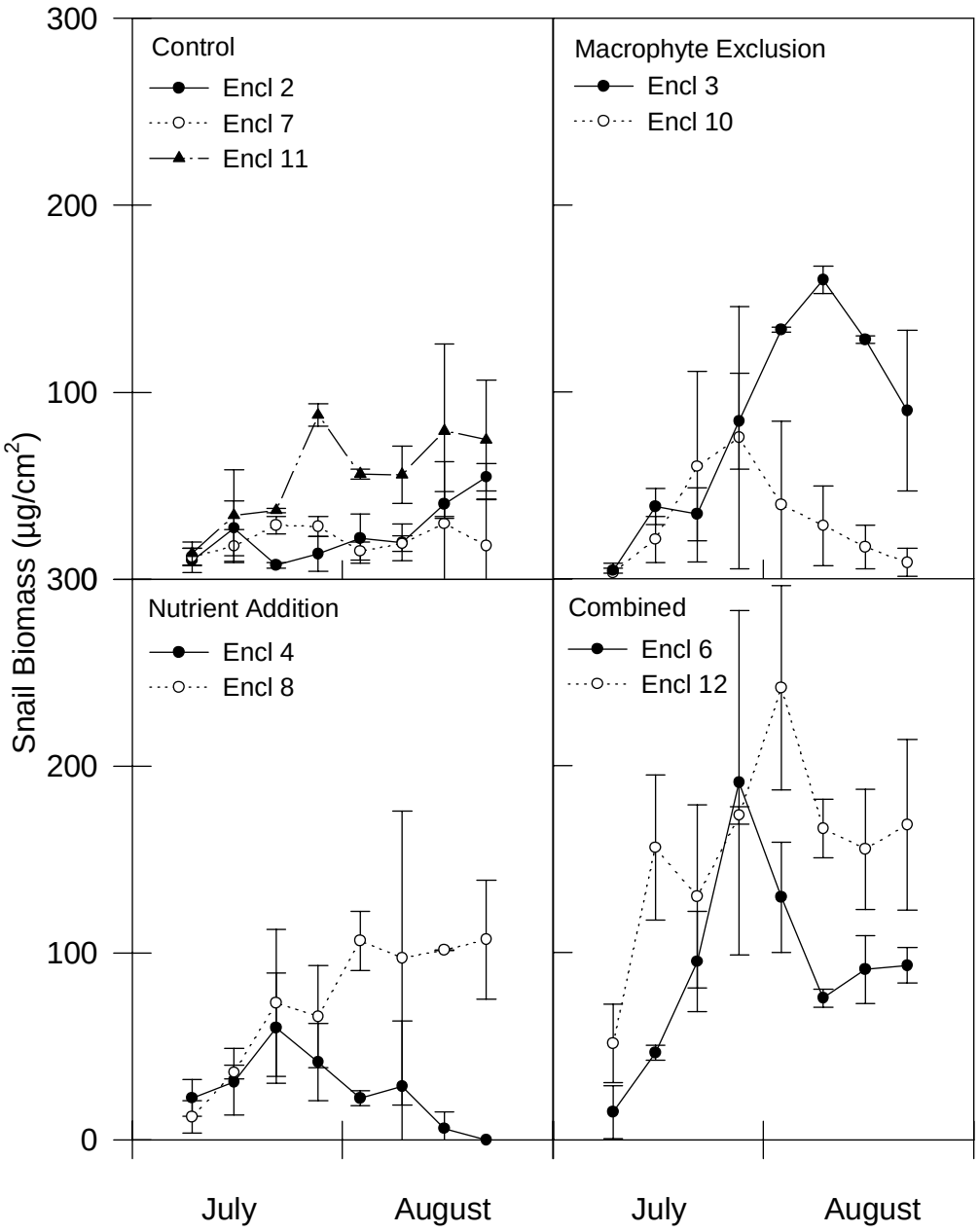

Figure 7. Treatment replicate means (± SD) of snail biomass found on strip substrata from July to August 1996.

1997). Ultimately, the water body would tend towards a turbid stable state dominated by suspended or floating autotrophs and devoid of submerged macrophytes.

With the demise of macrophytes, significant reductions in snail densities have been documented (Thomas and Daldorph 1991; Daldorph and Thomas 1991; Thomas and Daldorph 1994). Possible explanations for the decline include: (1) competitive inhibition of periphyton, the snails' food source, by phytoplankton or floating macrophytes (Thomas *et al.* 1985; Daldorph and Thomas 1991); (2) change towards a chemical environment unfavorable to snails because of hypoxic conditions and elevated levels of potentially toxic NH_3 due to decomposition of macrophytes (Thomas and Daldorph 1991); and (3) the loss of benefits derived from a mutualistic relationship between snails and macrophytes (Thomas 1982, 1987; Thomas *et al.* 1985).

Thomas and Daldorph (1991) attempted to assess the importance of macrophytes to snails through the mechanical removal of macrophytes. Macrophytes in their experiment were excluded to assess their relative importance in determining the resulting stable state of a water body. With the mechanical removal of

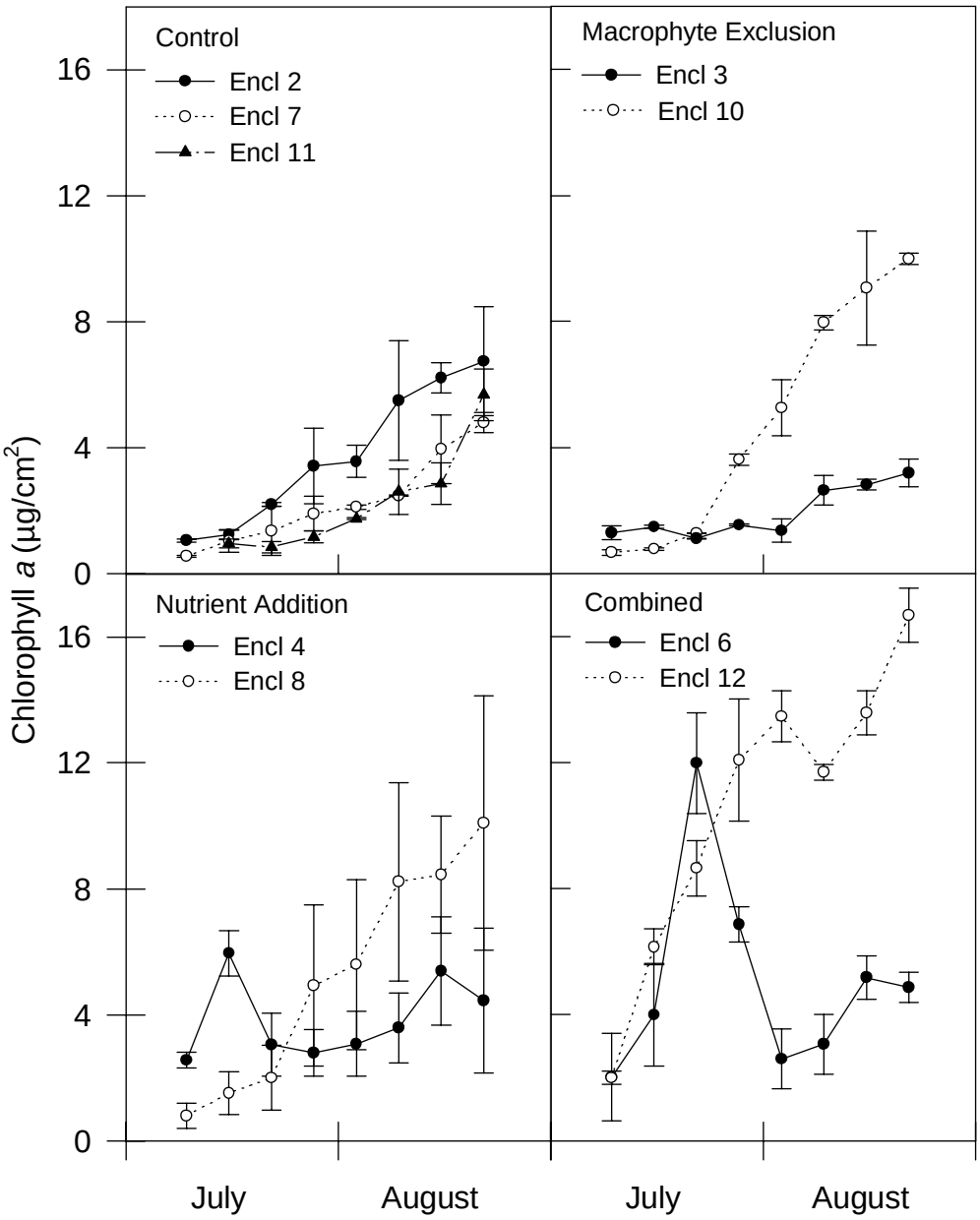

Figure 8. Treatment replicate means (± SD) of periphyton biomass (as Chl a) found on strip substrata from July to August 1996.

macrophytes, Thomas and Daldorph (1991) did not find the chemical environment of snails to be adversely affected while compensatory growth of periphyton on sediments and artificial plant decoys occurred. Consequently, they found significantly higher snail densities on artificial plants, concluding that the use of plant decoys reduced the effect of the treatment.

At Delta Marsh, similar results were found in response to macrophyte exclusion, including increased periphyton biomass and snail densities, and significantly higher snail biomass during July on artificial substrata. However, these positive treatment effects on snail density and biomass are contrary to those negative effects found in other studies (i.e. snails declined) where submerged macrophytes had declined due to phytoplankton or floating macrophyte dominance (Hough *et al.* 1989; Thomas and Daldorph 1991; Daldorph and Thomas 1991; Thomas and Daldorph 1994). These different results may depend on the method of macrophyte removal from the ecosystem.

With *in situ* decay of submerged macrophytes as a consequence of herbicide application (Murphy *et al.* 1981), macrophyte suppression (Boston and Perkins 1982) or shading by either phytoplankton (Thomas *et*

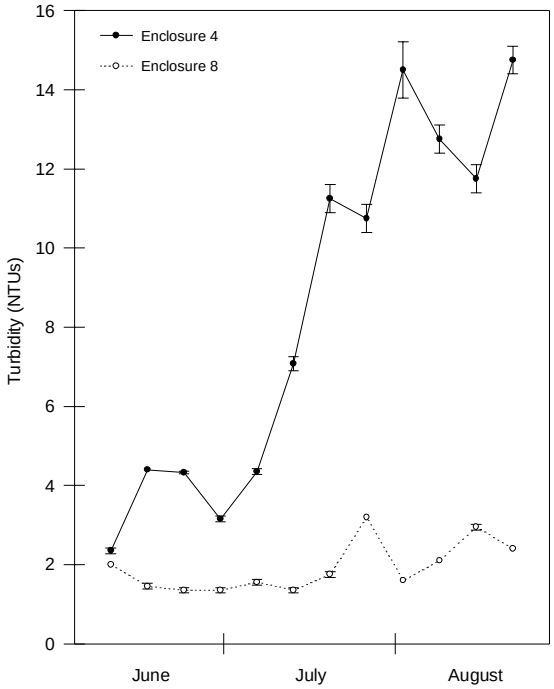

Figure 9. Turbidity mean values (± SD) for nutrient addition treatment replicates (enclosures 4 and 8) from June to August 1996.

al. 1985; Daldorph and Thomas 1991), floating macrophytes (Hough *et al.* 1989; Thomas and Daldorph 1994), or artificial black polyethylene cover (Thomas and Daldorph 1991), the aquatic environment has been shown to be drastically affected, resulting in lower oxygen concentrations (Murphy *et al.* 1981; Boston and Perkins 1982; Thomas and Daldorph 1991) and decreased periphyton biomass (Thomas *et al*. 1985, Thomas and Daldorph 1991). On the contrary, with the mechanical removal of macrophytes, the chemical environment of the snail did not drastically change (Thomas and Daldorph 1991), and with the prevention of macrophyte germination (this experiment), periphyton biomass increased. Therefore, it can be inferred that the major process causing snails to decline in response to a loss of submerged macrophytes is not the loss of benefits derived from a mutualistic relationship between snails and macrophytes, but the decrease in periphyton and the change in the snails' environment due to decomposition of macrophytes.

However, there were two confounding effects as a result of excluding macrophytes. The first was the loss of surface area made available by the presence of macrophytes. For instance, the control enclosures demonstrated an average macrophyte surface area of 1.67 m^2/m^2 of marsh bottom in mid-July and 1.12 m^2/m^2 of marsh bottom in mid-August (McDougal and Goldsborough, unpubl. data). The second confounding effect was an increase in nutrient availability in the absence of macrophytes which are thought to be competitively superior to phytoplankton with respect to nutrient uptake (Kantrud 1990; van Donk *et al.* 1990). Therefore, these confounding effects may have influenced the possible effects of macrophyte exclusion.

Nutrient Addition Treatment Effects

The increase in periphyton biomass in response to nutrient addition has been well documented (Cuker 1983; Osenberg 1989; Marks and Lowe 1989; Winterbourn 1990; Hill *et al.* 1992; Rosemond *et al.* 1993; Daldorph and Thomas 1995). Similarly, studies have demonstrated an increase in snail density and biomass, reflecting a positive response to increased food resources as periphyton biomass increases with nutrient addition (Osenberg 1989; Rosemond *et al*. 1993). In the nutrient addition enclosures during July, periphyton biomass increased in response to both early spring transparency and nutrient addition. Accordingly, in July both snail density and biomass increased above that in the control, due to an increased food supply in the form of algal (periphyton) biomass. However, in August, the nutrient addition treatment had no significant effect on either periphyton biomass or snail biomass. This suggests that algal biomass may be nutrient limited in Delta Marsh and that algal and snail biomass are positively correlated in this eutrophic wetland ecosystem.

Combined Treatment Effects

The positive nutrient addition treatment effects on periphyton biomass and snail density and biomass did not depend on the presence or absence of macrophytes. Similarly, the positive macrophyte exclusion treatment effects on the same three response variables did not depend on the level of nutrient addition. Both treatment responses appeared to occur as a result of increased nutrient availability to autotrophs. Thus, periphyton and snails may have become limited by factors other than nutrients and food (e.g., crowding effects, water temperature, water chemistry), respectively, and no significant interaction occurred.

Spatial and Temporal Variability

Spatial variability (among replicate treatment enclosures) in wetland ecosystems has been documented (Thomas and Daldorph 1994; Daldorph and Thomas 1995). In response to nutrient addition, they observed dominance of the floating plant *Lemna* in one replicate and phytoplankton in the other, and the demise of

macrophytes and decreased snail abundances in both.

The control treatment demonstrated relatively low variation among replicates, probably due to the observed stable clear water state dominated by submerged macrophytes. However, the nutrient addition treatment showed a divergence in periphyton biomass and snail density and biomass between replicates. This was most likely attributable to different early spring conditions in different parts of the Blind Channel. For instance, enclosure 4 was situated in slightly deeper water nearer mid-channel, whereas water depth was somewhat less in enclosure 8, nearer the channel margin. There was more turbulence mid-channel, possibly causing the higher spring turbidity found in enclosure 4. Reduced light penetration to the sediments subsequently delayed the germination of macrophyte seeds and turions. Therefore, phytoplankton was given the opportunity to use the nutrients provided. With growth of phytoplankton, turbidity increased substantially in enclosure 4, allowing phytoplankton to maintain its advantage over macrophytes and periphyton on sediments, curtains and the artificial strip substrata.

The resulting phytoplankton bloom consisted largely of blue-green algae. Blue-green algae can exist in high water temperatures, require low light energy for photosynthesis, fix nitrogen, control buoyancy, escape grazing pressures, survive at high pH and/or low CO_2 concentrations (Shapiro 1990).The bloom in enclosure 4 contributed to increasing turbidity values, attenuating PAR available to other autotrophs, including macrophytes and periphyton. Contrary to Thomas and Daldorph (1994), who noted the sudden demise of macrophytes as phytoplankton densities increased, macrophytes in enclosure 4 established themselves during late July. However, consistent with Osenberg (1989) and Thomas and Daldorph (1994), periphyton biomass initially increased in response to nutrient addition, then decreased and leveled off. As macrophytes established themselves, the amount of surface area available for colonization by periphyton and snails increased within the enclosure. Thus, snail numbers and biomass per unit surface area decreased on the artificial strip substrata as they colonized the newly available natural substrata, the macrophytes.

Conversely, enclosure 8 had considerably more transparent conditions, allowing noticeably earlier establishment of macrophytes, which have been found in previous studies to stabilize sediments and maintain low turbidity (Timms and Moss 1984; Scheffer 1990). This was accompanied by an initial increase in periphyton biomass and snail density and biomass, until late July when snail abundance and biomass leveled off.

During July, the initial response of treatment replicates was similar. However, during August the responses tended to diverge between replicates. Macrophytes, such as *P. pectinatus*, demonstrate a seasonal cycle with a period of rapid growth during June and July forming an extensive canopy, then senescence begins shortly after flowering and continues throughout August and September (Kantrud 1990). Also, decomposition of senescent macrophytes may be hastened due to cuticular damage by epiphyton (Howard-Williams *et al*. 1978). These and other factors, such as initial conditions (spatial variability), changes in light and nutrients under the developing canopy of macrophytes may have contributed to the temporal variability found among all treatment replicates.

Conclusions

During July, periphyton biomass and snail density and biomass increased in response to both macrophyte exclusion and nutrient addition. These positive bottom-up effects suggest that nutrient levels limited algae and food limited snails in the Blind Channel at Delta Marsh. Also, snails exhibited a stronger growth (biomass) response than a survival (density) response, to both treatments. During August, differential responses in periphyton biomass and snail density and biomass occurred due to different stable state conditions in separate enclosures.

Acknowledgments

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