Snail grazer-periphyton interactions: the effects of macrophyte removal, inorganic nutrient addition, and organic nutrient addition

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Introduction

The general interactions between periphytic algae and snail grazers have been well documented in various ecosystems (Cattaneo and Kalff 1986; Kairesalo and Koskimies 1987), including eutrophic ponds (Hann 1991; Swamikannu and Hoagland 1989). In a number of studies the grazing activity of snails has been shown to decrease the epiphyte biomass (Hann 1991; Cattaneo 1983; Cattaneo and Kalff 1986). Other studies have indicated a positive relationship between inorganic nutrient addition and algal biomass, as well as a negative relationship between herbivory and algal biomass (Rosemond *et al.* 1993; Cuker 1983), specifically snails and periphytic algae (Daldorph and Thomas 1991; Osenberg 1989). Also, Brönmark (1989) has suggested that low grazing pressure is coupled with high periphyton biomass, intermediate grazing pressure with a biomass decline but a productivity maximum, and high grazing pressure with a large decrease in both biomass and productivity of periphyton due to overgrazing. These studies conceptualize both the bottom-up and top-down models of a trophic system, and both must be utilized in order to fully understand the variety of pressures acting on grazer-periphyton interactions.

Although the effects of nutrient addition on algal biomass have been well documented, the relationship between macrophyte removal and periphyton biomass has not been studied in detail. It might be expected that the removal of macrophytes would decrease epiphyton biomass, but increase that of other forms of periphytic algae due to decreased competition for nutrients, increased availability of light at greater depths, and decreased abrasion between the macrophytes and periphyton. However, the effects of macrophyte removal on snail grazing activity must also be addressed to get a holistic view of the system. In fact, a mutualistic relationship between macrophytes and snails has been suggested with conclusive evidence by Thomas (1982, 1987) and Thomas *et al.* (1985) which helps to explain a preference of snails to feed on epiphytic algae found on macrophytes. This study will examine the periphyton-snail grazer relationship in ten enclosures, located in a channel of a eutrophic marsh, under various treatment conditions, such as inorganic nutrient addition, organic nutrient addition, and inorganic nutrient addition coupled with macrophyte removal.

Materials and Methods

Study Site

The Blind Channel is a long, shallow waterway within the Delta Marsh (98°19'W, 50°11'N), a large coastal wetland on the southern shore of Lake Manitoba. At mid-channel of the eastern portion of the Blind Channel, ten 5 m x 5 m enclosures were constructed as in Goldsborough (1991), and installed in May 1995. Woven polyethylene curtains, extending from above the water surface to approximately 30 cm into the sediments, isolated the 10 sections of the marsh for experimental treatments. Fish were removed as completely as possible from the enclosures using minnow traps.

Experimental Design

Submerged aquatic macrophytes were removed by regular clipping from four of the ten enclosures (Fig. 1), and inorganic nutrients were added three times per week to two of these beginning on 28 June, and continuing for 9 weeks. The inorganic nutrients consisted of nitrogen and phosphorus in a 10:1 molar ratio, respectively (Table 1a). Four other enclosures had organic nutrients added in two pulsed additions on 28 June and 21 July. The organic nutrient treatment was in the form of goose and duck feces, two with a high loading (7.2 kg/enclosure), and two with a lower loading (0.72 kg/enclosure). The chemical composition of the duck and goose feces is provided in Table 1b. The amount of organic nutrient added in the high loading rate was determined by calculating the weight of material needed to add a weight of phosphorus equivalent to the weight added in previous experiments in which inorganic phosphorus had been added. The remaining two enclosures served as controls and had no macrophytes removed, and no organic or inorganic nutrients were added. Further details of these experimental treatments are provided in Pettigrew and

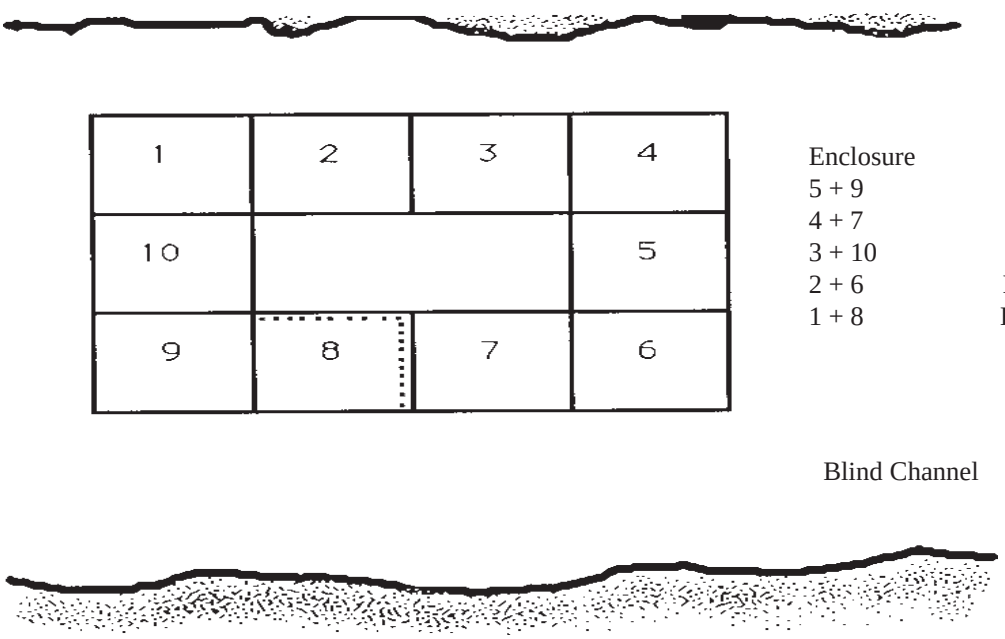

Figure 1. Diagrammatic representation of the 10 experimental enclosures located within the Blind Channel of Delta Marsh. Dots in enclosure 8 represent the position of the artificial substrata. All enclosures had substrata arranged similarly. The treatments consisted of two control enclosures, two enclosures with macrophytes removed and inorganic nutrients added (MR + N), two enclosures with macrophytes removed and no nutrients added (MR - N), two enclosures with a high concentration of organic nutrients added, and two enclosures with a low concentration of organic nutrients added.

Table 1a. Chemical composition of inorganic nutrients added to experimental treatment enclosures 4 and 7. Nutrients were added three times per week, for nine weeks, beginning on June 28/95.

Component	Amount /day	Amount /week	Amount /9 weeks
$NaH_2PO_4.2H_2O$	1.34 g	4.02 g	36.18 g
$NaNO_3$	9.71 g	29.13 g	262.17 g

Table 1b. Chemical composition of duck and goose feces added to enclosures 1, 2, 6, and 8. Enclosures 2 and 6 received 0.72 kg/enclosure, and enclosures 1 and 8 received 7.2 kg/enclosure. These amounts were added one week prior to the experiment (June 28/95) and between weeks 3 and 4 (July 21/95).

Component	Duck	Goose
Nitrate (mg/g)	<0.05	<0.05
Ammonium (mg/g)	2.82	2.58
Total organic N (mg/g)	1.54	3.14
Total nitrogen (mg/g)	4.36	5.72
Total phosphorus (mg/g)	14.40	14.00
Potassium (mg/g)	8.49	12.50
Sodium (mg/g)	3.17	2.84
Calcium (mg/g)	26.30	21.40
Magnesium (mg/g)	4.82	6.38
Sulfur (mg/g)	2.52	3.07
pH	6.8	6.9
Conductivity (µS/cm)	6.44	7.99
Moisture (%)	65.7	80.9

Hann 1996; Purcell and Goldsborough 1996; McDougal and Goldsborough 1996; Sandilands and Hann 1996).

Within each of the ten enclosures, twenty woven polyethylene strips (5 cm x 100 cm) were stapled to the wooden platform along the north and east sides (10 strips per side per enclosure) in order to receive maximum sunlight (Fig. 1). The strips were weighted on the lower ends with lead shot. Strips were colonized by periphyton during a 3-week period prior to sampling.

To estimate snail abundance and periphyton biomass, one strip from the north and east sides of each enclosure was sampled each week for 6 weeks beginning on 5 July and ending on 9 August. Each strip was gently rolled and placed individually into a small plastic bag, and returned to the lab where the top 30 cm of each strip was discarded. The artificial substratum was then divided into two 35 cm portions, and labeled top and bottom (Fig. 2). The numbers of snail grazers was

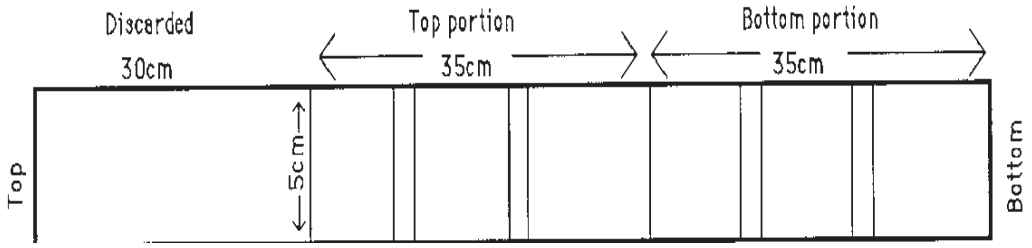

Figure 2. Diagrammatic representation of the artificial substrata located on the north and east sides of the 10 enclosures.

counted on one side of the strip by macro-inspection, magnifying glass, and dissecting microscope due to their variable size, and the variable thickness of periphyton on the strips. The snail species was identified as *Gyraulus circumstriatus* using Clark (1981), and the size of the individuals ranged from approximately 1.0 mm to 1.3 cm in diameter. Many similar individuals were found on the enclosure curtains, as well as on submerged aquatic macrophytes, where present.

After all of the grazers were counted and removed with forceps, two 1 cm x 5 cm sections were removed from the top and bottom of each strip (Fig. 2) and placed into separate vials. During the first two weeks of the experiment, the sections were first scraped (both sides) to remove periphyton which was then filtered through Whatman GF/C filter paper and the filters were frozen (method 1). These samples were analyzed for chlorophyll *a* content, as an estimate of periphyton biomass, according to methods in McDougal and Goldsborough (1995). During week 3, half of the strip sections were taken using method 1, and the remaining sections were taken using both method 1 and a second modified method 2 to permit comparison of the efficiency of periphyton biomass estimation via the two methods. In method 2, the periphyton was left intact on the strips (not scraped), and the entire strip section was frozen. Filtering of the scraped algae was therefore not required, and the chlorophyll *a* analysis procedure remained the same. For the remaining three weeks of the experiment, all of the sections were prepared using method 2. In all cases, the top sections from the north and east sides of each enclosure were combined in the same vial; bottom sections were treated identically. In subsequent analyses, the periphyton biomass estimates were averaged between replicate enclosures of the same treatment.

Results

Periphyton Biomass

Comparison of methods for estimating periphyton biomass indicated that there was a strong correlation between the two techniques (r = 0.80, Fig. 3). When the two outlying points were excluded, the correlation

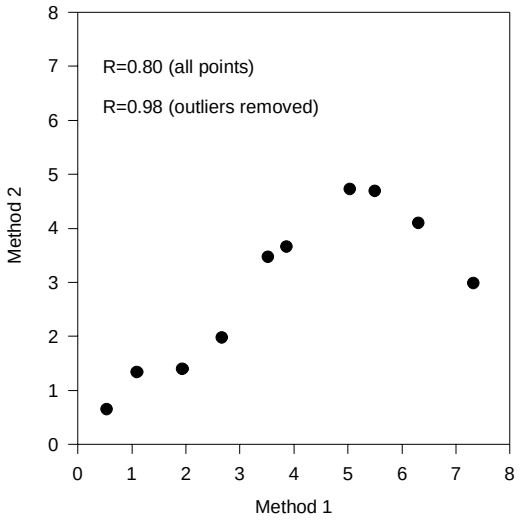

Figure 3. Comparison of methods for periphyton analysis on strips.

coefficient was 0.98. The two outliers represent biomass estimates in enclosure 4 (top and bottom subsamples) that were substantially higher using method 1 than method 2.

A comparison of periphyton biomass between the top and bottom portions of each strip showed that the bottom portions had more attached algal biomass (Fig. 4a-e). A much larger difference existed, especially in week 3, between replicate enclosures for macrophyte removal with inorganic nutrients added (Fig. 4b), and the high organic nutrient treatment (Fig. 4e).

Periphyton biomass varied slightly among treatments but not over the sampling period (Fig. 5, 6, Table 2). Both the macrophyte removal treatments (with and without nutrients added), as well as the high organic treatment, had intermediate to high periphyton biomass values, while the low organic treatment had comparatively low periphyton biomass, only slightly elevated above the control.

Snail Grazers

Comparison of the mean abundances of *Gyraulus* between top and bottom portions of each strip for the

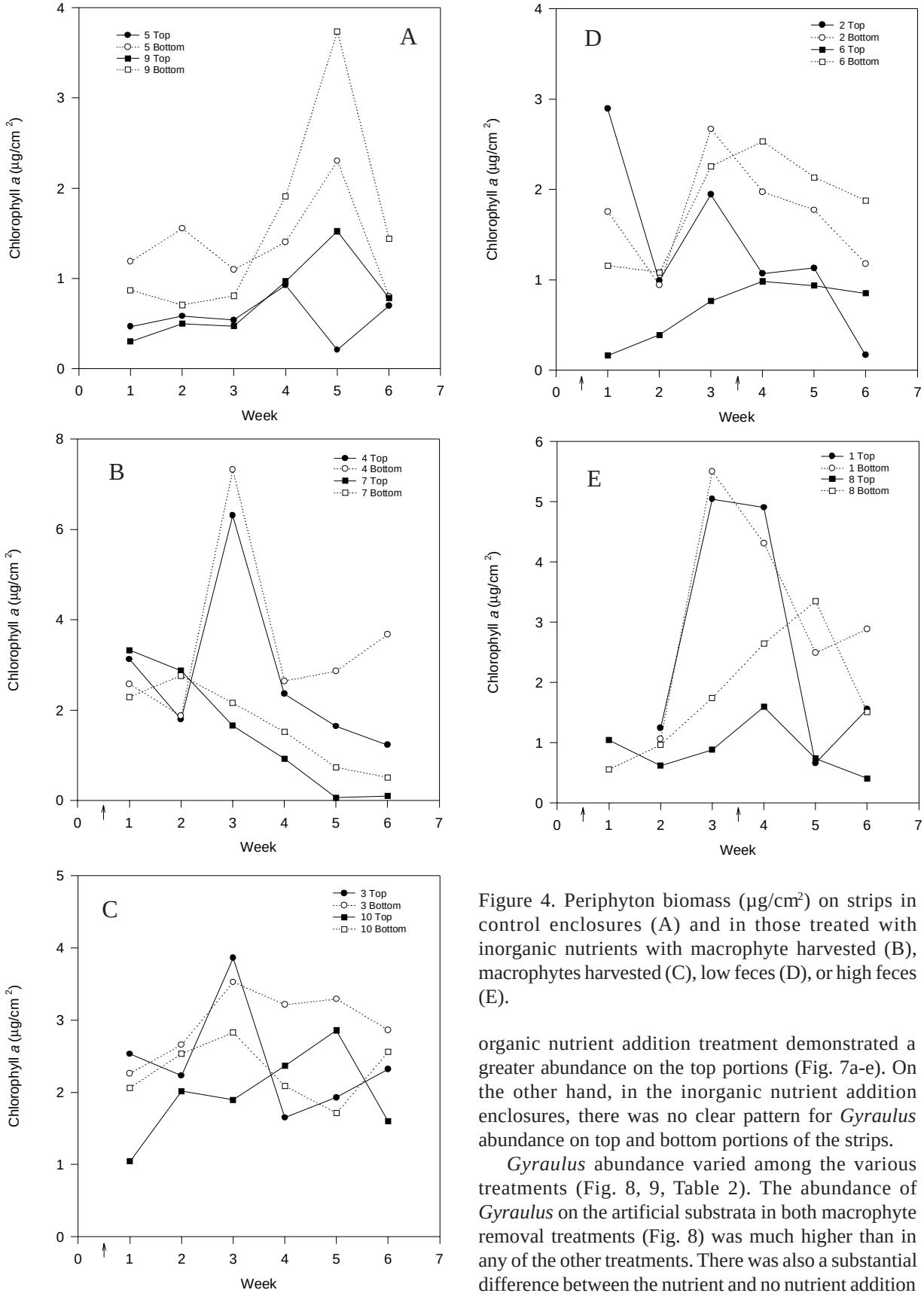

Figure 4. Periphyton biomass (µg/cm^2) on strips in control enclosures (A) and in those treated with inorganic nutrients with macrophyte harvested (B), macrophytes harvested (C), low feces (D), or high feces (E).

organic nutrient addition treatment demonstrated a greater abundance on the top portions (Fig. 7a-e). On the other hand, in the inorganic nutrient addition enclosures, there was no clear pattern for *Gyraulus* abundance on top and bottom portions of the strips.

Gyraulus abundance varied among the various treatments (Fig. 8, 9, Table 2). The abundance of *Gyraulus* on the artificial substrata in both macrophyte removal treatments (Fig. 8) was much higher than in any of the other treatments. There was also a substantial difference between the nutrient and no nutrient addition within the macrophyte removal treatment enclosures.

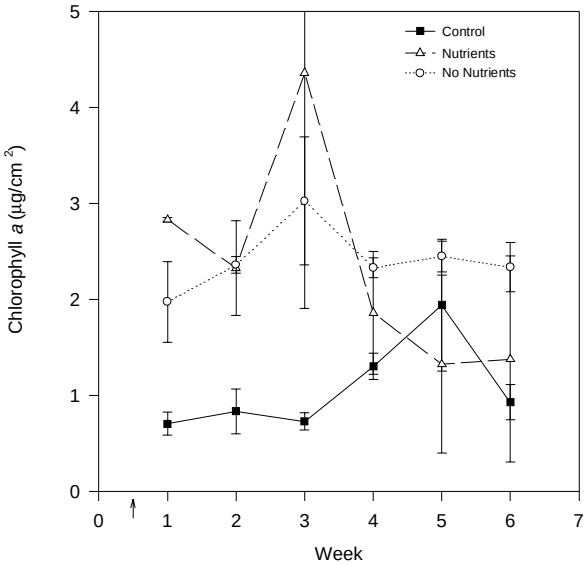

Figure 5. Periphyton biomass (µg/cm^2) on strips in control enclosures as compared to those from which macrophytes were harvested, with or without added inorganic nutrients.

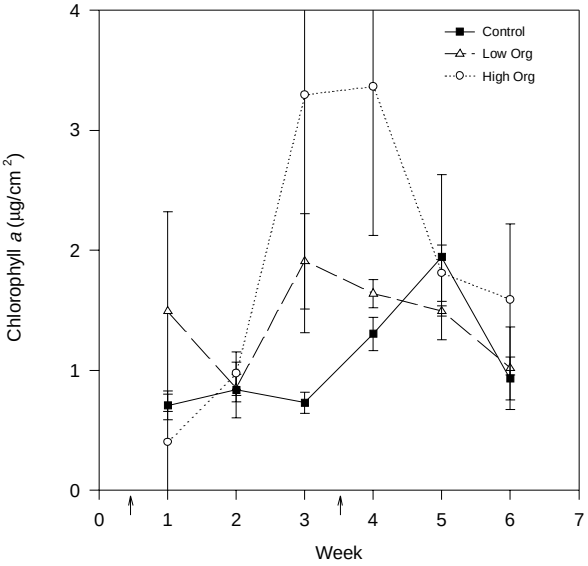

Figure 6. Periphyton biomass (µg/cm^2) on strips in control enclosures as compared to those enriched with low or high levels of waterfowl feces.

Table 2. *Gyraulus* abundance and mean algal biomass in ten experimental enclosures located within the Blind Channel of Delta Marsh. Samples were collected once per week, for 6 weeks, beginning on July 5/95.

		Week					
Treatment	Sample	1	2	3	4	5	6
Control (5+9)	*Gyraulus* (#/cm^2)	0.024	0.015	0.005	0.003	0.006	0.004
	Chlorophyll (µg/cm^2)	0.707	0.836	0.729	1.302	1.942	0.931
MR +N (4+7)	*Gyraulus* (#/cm^2)	0.096	0.159	0.266	0.321	0.216	0.081
	Chlorophyll (µg/cm^2)	2.830	2.325	4.360	1.862	1.325	1.379
MR - N (3+10)	*Gyraulus* (#/cm^2)	0.05	0.208	0.169	0.159	0.125	0.166
	Chlorophyll (µg/cm^2)	1.975	2.359	3.026	2.328	2.447	2.336
Low Org (2+6)	*Gyraulus* (#/cm^2)	0.039	0.051	0.049	0.088	0.048	0.037
	Chlorophyll (µg/cm^2)	1.491	0.850	1.908	1.638	1.492	1.017
High Org (1+8)	*Gyraulus* (#/cm^2)		0.069	0.04	0.036	0.031	0.054
	Chlorophyll (µg/cm^2)	0.799	0.971	3.293	3.364	1.809	1.589

Gyraulus abundance increased dramatically near the beginning of sampling with and without nutrients added, but appeared to stabilize in the treatment with no nutrients added. This contrasted with an increase then sharp and continual decrease found with the addition of nutrients (Fig. 8). Though not as substantial, the organic nutrient addition treatment (Fig. 9) showed a noticeable increase in *Gyraulus* abundance above the control, yet no specific trends could be distinguished between the high and low organic additions. Snails may have differed in their growth response in the various treatments, and this could have been detectable in terms of differential biomass changes. Technical difficulties with biomass determinations precluded any assessment of this aspect of the population response.

Periphyton-snail grazer interaction

From initially low densities of snails and periphyton biomass, by mid-summer the macrophyte removal with nutrient addition treatment showed the highest abundance of *Gyraulus circumstriatus* as well as the highest biomass of periphyton (Fig. 10). The periphyton biomass peaked at 4.36 µg/cm^2 in week 3, and this was followed by a peak in grazer abundance of 3,200 individuals/m^2 in week 4. The algal biomass dropped in

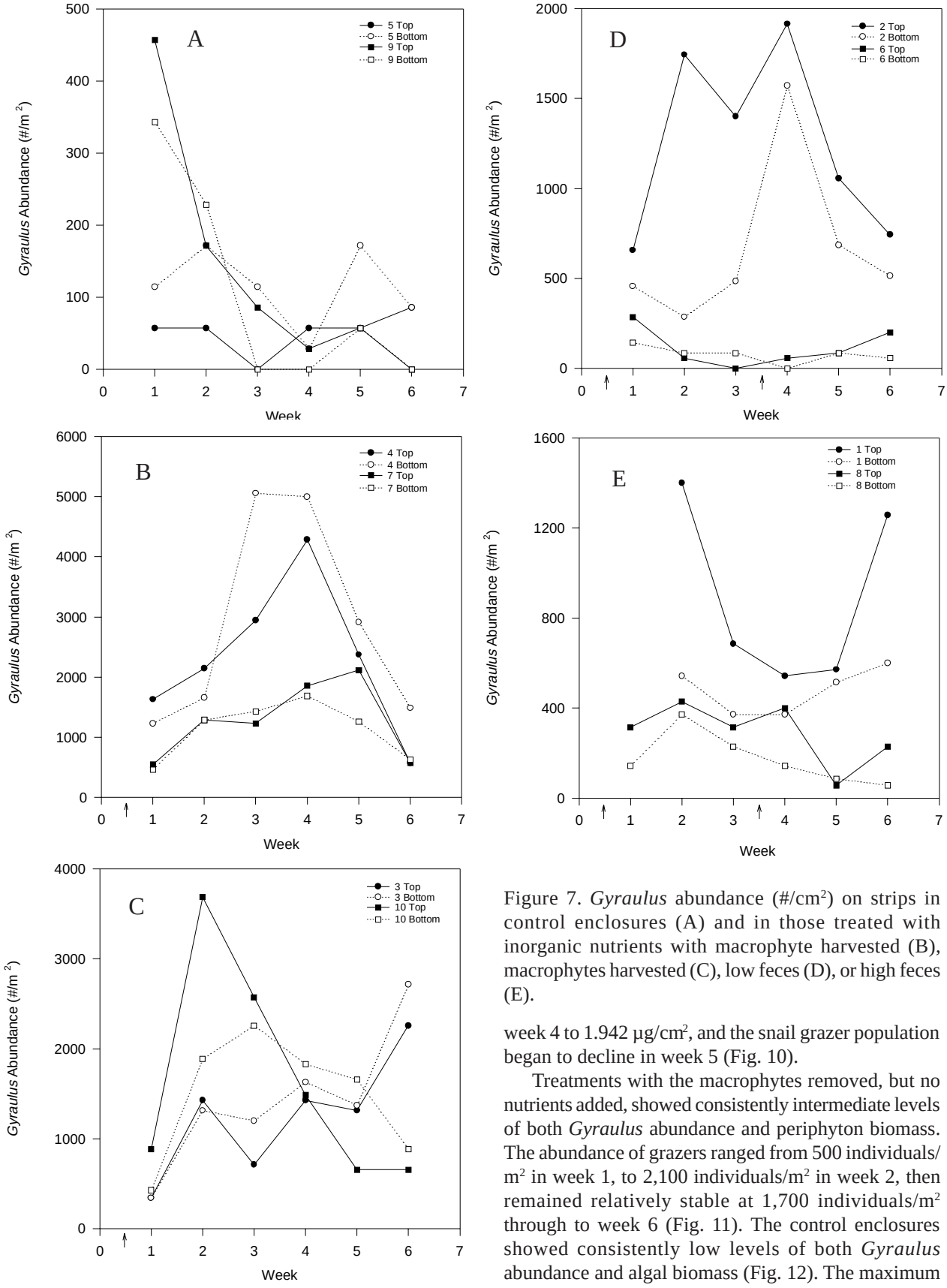

Figure 7. *Gyraulus* abundance (#/cm^2) on strips in control enclosures (A) and in those treated with inorganic nutrients with macrophyte harvested (B), macrophytes harvested (C), low feces (D), or high feces (E).

week 4 to 1.942 µg/cm^2, and the snail grazer population began to decline in week 5 (Fig. 10).

Treatments with the macrophytes removed, but no nutrients added, showed consistently intermediate levels of both *Gyraulus* abundance and periphyton biomass. The abundance of grazers ranged from 500 individuals/m^2 in week 1, to 2,100 individuals/m^2 in week 2, then remained relatively stable at 1,700 individuals/m^2 through to week 6 (Fig. 11). The control enclosures showed consistently low levels of both *Gyraulus* abundance and algal biomass (Fig. 12). The maximum number of grazers was 700/m^2 in week 2, and the

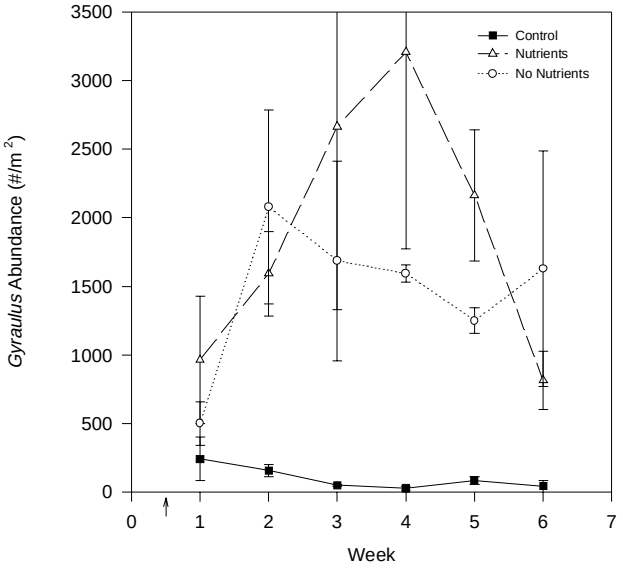

Figure 8. *Gyraulus* abundance (#/cm^2) on strips in control enclosures as compared to those from which macrophytes were harvested, with or without added inorganic nutrients.

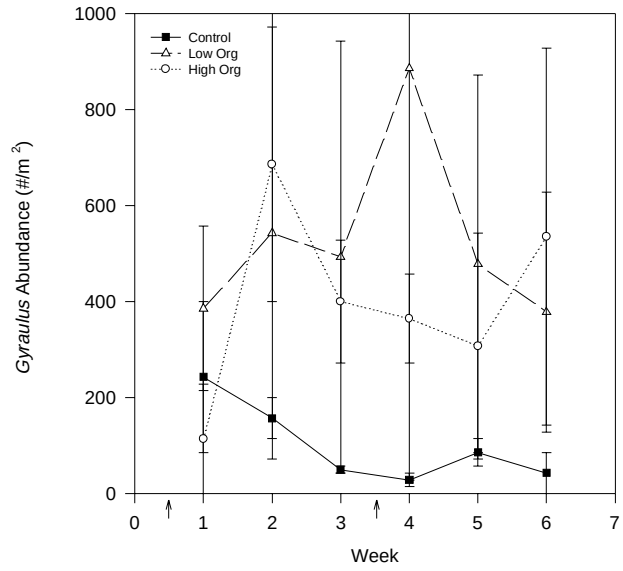

Figure 9. *Gyraulus* abundance (#/cm^2) on strips in control enclosures as compared to those enriched with low or high levels of waterfowl feces.

maximum chlorophyll a level was 1.81 µg/cm^2 in week 5.

The low organic treatment showed low levels of grazer abundance and algal biomass (Figs. 13, 14) although greater than the control on average (Fig.12). The chlorophyll *a* values range from 0.85 µg/cm^2 to 1.9 µg/cm^2. Enclosure 2 showed a mid-summer peak in

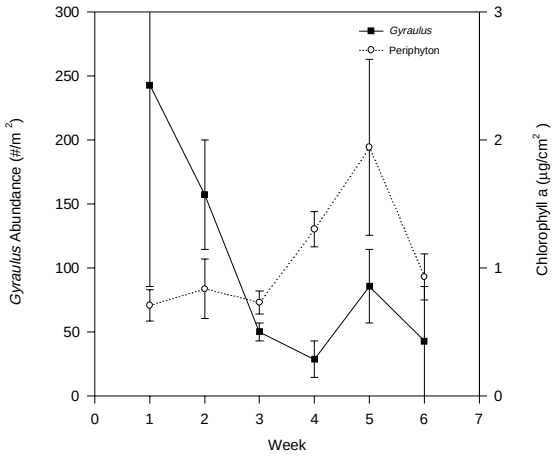

Figure 10. *Gyraulus* abundance (#/cm^2) versus periphyton biomass on strips in enclosures from which macrophytes were harvested and inorganic nutrients were added.

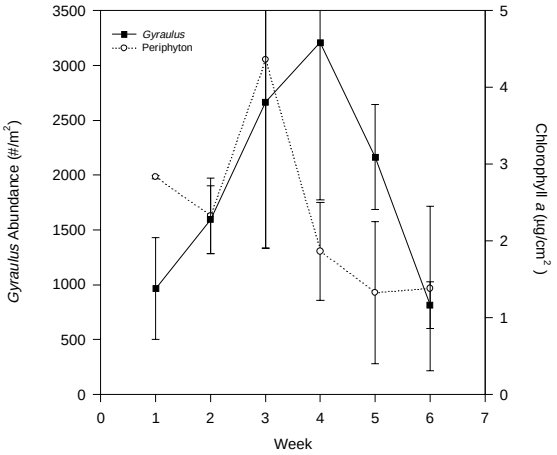

Figure 11. *Gyraulus* abundance (#/cm^2) versus periphyton biomass on strips in enclosures from which macrophytes were harvested.

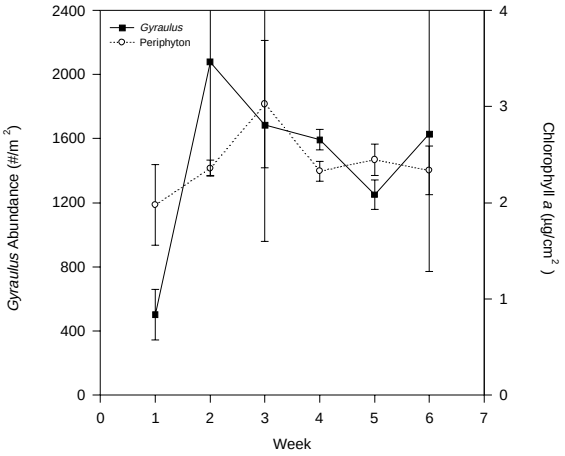

Figure 12. *Gyraulus* abundance (#/cm^2) versus periphyton biomass on strips in control enclosures.

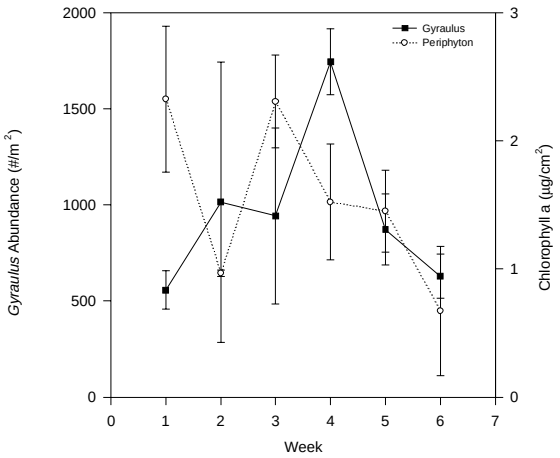

Figure 13. *Gyraulus* abundance (#/cm^2) versus periphyton biomass on strips in an enclosure (#2) enriched with a low level of waterfowl feces.

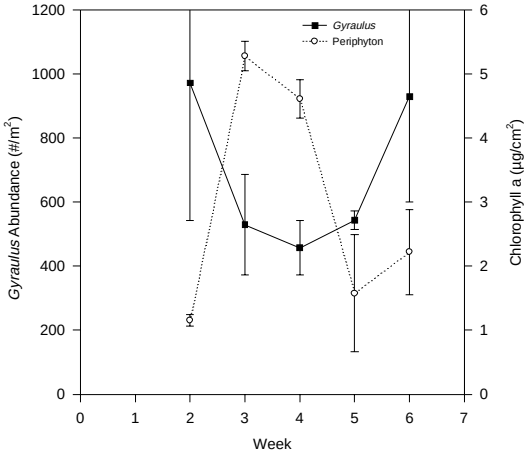

Figure 15. *Gyraulus* abundance (#/cm^2) versus periphyton biomass on strips in an enclosure (#1) enriched with a high level of waterfowl feces.

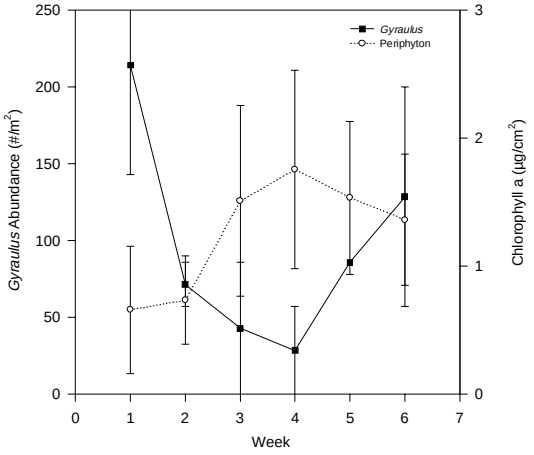

Figure 14. *Gyraulus* abundance (#/cm^2) versus periphyton biomass on strips in an enclosure (#6) enriched with a low level of waterfowl feces.

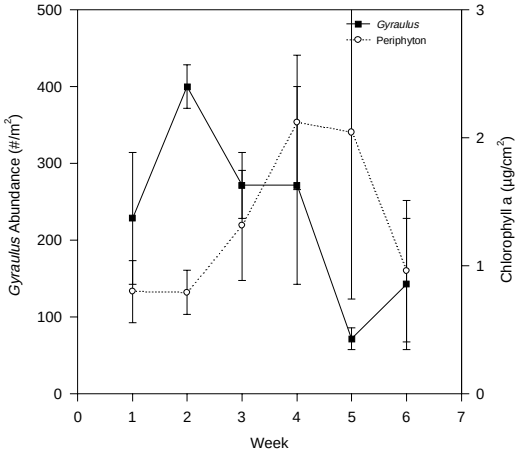

Figure 16. *Gyraulus* abundance (#/cm^2) versus periphyton biomass on strips in an enclosure (#8) enriched with a high level of waterfowl feces.

abundance of snails, coincident with a decline in periphyton biomass (Fig. 13). However, enclosure 6 (Fig. 14) showed a dramatic mid-summer decline in snails, with a concurrent increase in periphyton biomass, largely due to the presence of numerous fish (fathead minnows, brook stickleback) in this enclosure from the second week of the study (Pettigrew and Hann 1995).

In the enclosures with high organic nutrient loading, snail abundance was initially high, then declined and periphyton biomass increased. In August in enclosure 1 (Fig. 15), snail numbers were again elevated and periphyton biomass declined drastically. In contrast, in enclosure 8 (Fig. 16), snail abundance continued to decline as did periphyton biomass.

Discussion

Sand-Jenson (in Brönmark, 1989) suggested that large quantities of epiphytic algae could have a negative effect on the growth of the macrophyte. If this were true, the macrophyte may begin to senesce, reducing surfaces for epiphytes to attach. One might expect that epiphytic algae would then colonize other surfaces, or would decrease in biomass. Colonization of alternative substrata was stimulated in the macrophyte removal with nutrient addition treatment, where initially low levels of periphyton biomass on the artificial substrata rapidly increased, perhaps as a result of both the macrophyte removal and nutrient additions. The removal of the aquatic macrophytes may have increased periphyton

growth due to reduced competition for nutrient with epiphytes, decreased shading by the macrophytes, and decreased abrasion between the macrophytes and the periphytic algae. However, the increase in periphyton biomass with the addition of nutrients with macrophyte removal was short-lived. Elevated periphyton biomass appeared to stimulate an increase in grazer abundance, supporting Brönmark's (1989) hypothesis that high grazing pressure results in a collapse of both periphyton biomass and grazer populations. Enclosures with macrophytes removed but no nutrients added showed an intermediate, stable level of both algal biomass and snail grazer abundance, as predicted by Brönmark (1989).

In the organic nutrient experiment, the negative association between grazer abundance and periphyton biomass was again confirmed in all enclosures. Top-down control by snail grazing appears to regulate the amount of periphyton biomass and intense grazing can destabilize both components of the system and lead to their decline as observed in the macrophyte removal experiment.

The lower periphyton biomass on the top (versus bottom) portions of each strip may have been caused by occasional exposure of the top portion of the strips to desiccation due to fluctuating water levels. Also, lower periphyton biomass on the top portion of each strip correlated with a greater abundance of *Gyraulus* (in the organic loading treatments), supporting the hypothesis of a negative relationship between snail abundance and periphyton biomass (Daldorph and Thomas 1991; Osenberg 1989). In the macrophyte removal and inorganic nutrient addition enclosures, there was no apparent pattern in top versus bottom distribution of *Gyraulus* which might be a consequence of the removal of macrophytes from within these enclosures. For example, the snails would not have their usual macrophyte substrata to colonize and might distribute themselves more randomly along the strips due to the artificial conditions.

The relatively low abundance of snail grazers on the artificial substrata in both the high and low organic treatments may result from the presence of macrophytes in the enclosures. The large number of macrophytes within the enclosures represent an extremely large surface area for the snails to colonize and graze, and therefore may reduce the abundance of snails occurring on the artificial substrata. As well, epiphytic algae may outcompete the periphytic algae on the artificial substrata due to mutualistic interactions with the macrophyte. Therefore, *Gyraulus* may have chosen to graze preferentially on the epiphytic algae (on macrophytes) rather than the periphytic algae (on artificial substrata). If true, then a marked increase *Gyraulus* abundance may have occurred in these treatment enclosures but was masked by the presence of macrophytes.

In the macrophyte removal treatments, however, a stronger relationship was evident between periphyton biomass and grazer abundance on the artificial substrata. It appears that Brönmark's (1989) hypothesis regarding the interactions between snail grazers and periphyton, is best demonstrated in experiments with macrophytes removed. Further studies to compare grazer abundance and periphyton biomass on artificial substrata to that on macrophytes would help to determine the influence of macrophytes in this regard. If the presence of macrophytes obscures grazer responses to increased periphyton levels, as it appears to have done in this experiment, the use of artificial substrata in the presence of macrophytes to quantify grazer-periphyton interactions would give inaccurate results. Therefore, removing macrophytes in grazer-periphyton experiments would demonstrate direct responses of snail grazers to changes in periphyton biomass, and therefore yield more accurate results than experiments in which macrophytes are present.

Summary

Snail grazer abundance increased in response to both macrophyte removal (with or with out nutrient addition) and organic nutrient addition (with macrophytes). The removal of aquatic macrophytes from experimental enclosures, located in Blind Channel in the eutrophic Delta Marsh (Manitoba), had a particularly dramatic effect on periphyton and snail abundance on artificial substrata. Periphyton biomass on artificial substrata may have increased in the absence of macrophytes as a consequence of decreased competition for nutrients, decreased abrasion, and increased light availability. Increased snail abundance on the artificial substrata appeared to have occurred primarily due to selection of the artificial substrata for grazing of periphyton in the absence of the macrophytes. The increase also appeared to be accentuated by the addition of inorganic nutrients. When present, the macrophytes provided a preferred substratum for both periphyton and snail grazers due to their large surface area, as well as mutualistic biotic interactions between both periphyton and macrophytes, and snails and macrophytes. In enclosures with organic nutrient additions, in the presence of macrophytes, periphyton biomass increased, concurrent with a substantial increase in snail grazers.

Acknowledgments

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