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Influence of freshwater macrophytes on the littoral ecosystem structure and function of a young Colorado reservoir

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Abstract

The presence of rooted macrophytes, mostly the milfoil *Myriophyllum sibiricum*, was manipulated in enclosures in the littoral zone of a Colorado reservoir. The presence of macrophytes significantly increased the abundance of major invertebrate taxa by 70–1725% and increased the emission of methane 127%. The increase in abundance of most invertebrates was probably due to the habitat and surfaces provided by milfoil as stable isotope analyses indicated that milfoil was an insignificant carbon source for all of the invertebrate taxa, except for the milfoil midge *Cricotopus myriophylli*. *Cricotopus* is known to specialize on milfoil (other members of the genus specialize on *Hydrilla* or are generalists), had an isotopic signature that indicated a diet of milfoil, and was about 15 times more abundant when milfoil was present than when it was absent. Milfoil had no detectable effect on the total particulate phosphorus (TPP), soluble reactive phosphorus (SRP), total dissolved phosphorus (TDP), dissolved organic phosphorus (DOP), and Chl a of water within the enclosures. However, enclosures containing milfoil had higher concentrations of SRP in the pore water of surface sediments than enclosures that had milfoil removed. SRP in pore water dropped below 2 μg/L at >2 cm sediment depth and DOP increased progressively from nearly zero at the surface to about 150 μg/L at 15 cm depth, regardless of vegetation. Thus, milfoil had significant effects on many, but not all, measures of littoral ecosystem structure and function that were monitored.

Keywords: *Cricotopus myriophylli*; Ecosystem function; Littoral zone; Macrophyte; Milfoil; *Myriophyllum sibiricum*

1. Introduction

Rooted macrophytes serve as a living link between the sediment, water, and (sometimes) atmosphere in wetlands, lakes, and rivers. The most notable function that plants serve is primary production. However, macrophytes are also involved in ecosystem processes such as biomineralization, transpiration, sedimentation, elemental cycling, materials transformations, and release of biogenic trace gases into the atmosphere (Carpenter and Lodge, 1986). Recent studies also suggest that macrophytes play a central role in shallow lakes which can have two possible stable equilibria: a clear-water state that is dominated by aquatic macrophytes and a turbid-water state that is dominated by phytoplankton (Scheffer et al., 1993; Moss et al., 1994; Jeppesen et al., 1998). Macrophytes maintain the clear-water state by a variety of mechanisms (e.g., stabilizing sediments, promoting zooplankton populations) whose relative importance is probably variable (Ozimek et al., 1990; Scheffer et al., 1993; Jeppesen et al., 1998; Vermaat et al., 2000; Madsen et al., 2001).

Macrophytes affect the distribution and abundance of animals by providing habitat and food. Direct herbivory on living biomass is probably as important for macrophytes as for terrestrial plants (Lodge, 1991; Newman, 1991; Cronin et al., 1998; Lodge et al., 1998). Herbivores show preferences for certain macrophyte species (Bolser et al., 1998; Cronin, 1998; Cronin et al., 1998, 1999, 2002) and specific macrophyte taxa tend to support specific animal assemblages (McGaha, 1952; Gaevskaya, 1969; Lodge, 1985; Humphries, 1996). Macrophyte tissue that is not consumed by herbivores enters the detrital food web upon senescence. Macrophyte structure also provides refugia and surfaces for biofilms (Shelford, 1918; Carpenter and Lodge, 1986).

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Rooted macrophytes serve as a direct living link between the sediment, water, and in the case of floating or emergent plants, the atmosphere. They can therefore affect the emission of biogenic trace gases from sediments and enhance oxygen penetration into the sediment (Pedersen et al., 1998). Plant-mediated factors that can increase methane flux include an increased supply of substrates that support methanogenic bacteria in the rhizosphere (i.e., increased methanogenesis) and gas transport via aerenchema and internal winds (i.e., increased transport) (Segers, 1998; Garnet et al., 2005). Other factors tend to reduce methane fluxes such as oxygenating the rhizosphere and increasing the redox potential of sediments (i.e., reduced methanogenesis) or providing oxygen and surfaces to methanotrophs (Gerard and Chanton, 1993; Segers, 1998). On balance, macrophytes generally increase the flux of methane from sediments to the atmosphere (Smith et al., 2000).

The purpose of the study reported here was to understand how macrophytes affect the structure and function of the littoral zone, measuring many ecosystem attributes simultaneously. In situ manipulation of macrophytes was conducted in the littoral zone of an oligotrophic reservoir. We used the 'ecosystem ecology' (sensu Schindler, 1996) approach in this study, documenting the importance of macrophytes to both community structure and ecosystem function. Specifically, we monitored the effects of vegetation on the abundance of phytoplankton (i.e., Chl a) and invertebrates, water total particulate phosphorus (TPP), soluble reactive phosphorus (SRP), total dissolved phosphorus (TDP), and dissolved organic phosphorus (DOP), sediment TPP, SRP, TDP, and DOP, and methane emissions.

2. Site description and methods

Aurora reservoir, which was completed in 1990, is used for municipal water storage and non-motorized recreation and is located on the plains of Aurora, Colorado (39°37′N, 104°41′W). Because it receives mostly mountain snowmelt, the water is more transparent and has a lower nutrient loading than most reservoirs on the plains of Colorado. Secchi depths of 7 m are common in the reservoir. The substrate in the littoral zone is organic muck (1–10 cm) over clay, the latter which was terrestrial soil inundated by the reservoir. Aurora reservoir supports a high biomass of macrophytes, consisting mostly of northern watermilfoil (*Myriophyllum sibiricum* Komarov), cattail (*Typha latifolia* L.), great bulrush (*Scirpus lacustris* L.), water crowfoot (*Ranunculus trichophyllus* Chaix), coontail (*Ceratophyllum demersum* L.), and bushy knotweed (*Polygonum ramosissimum* Michx.).

Northern watermilfoil *M. sibiricum* (hereafter milfoil) accounted for >95% of plant biomass where the enclosures were placed. Thus, any treatment effect attributed to macrophytes was likely due to milfoil. Four cylindrical enclosures, which each had a diameter of 4 m and a height of 1.8 m, were made of opaque sheets of black rubber attached to a stainless steel base extending 2–10 cm into the sediment. Each enclosure was divided into four equal quadrants using sheets of black rubber. The outside wall and dividing walls of the enclosure extended to the surface where they were attached to floating PVC pipe. Therefore, there was little exchange of materials in and out of the enclosures, including water, organisms, and nutrients. Two of the quadrants were de-vegetated (i.e., treatment plots) and two were natural (i.e., control plots). Non-vegetated plots were created by cutting the shoots of plants with hedge clippers and by gently pulling up plants with shallow roots. Care was taken to minimize disturbance to the sediment while removing vegetation. To control for some of the unavoidable disturbance that occurred, plants in the vegetated plots were handled, but not removed. Regrowth was removed every 1–2 weeks during the 7-week manipulation. A third treatment consisted of sampling that was conducted in unmanipulated areas located 1 m outside the enclosures.

Sampling was done on August 26–29, 1997 at the end of the 7-week treatment within each of the quadrants and outside of the enclosures where there was no experimental disturbance. At this time, macrophyte biomass was near the seasonal peak and had not begun to senesce. Data were analyzed with two-way ANOVA, with three different 'treatments' (i.e., non-vegetated plots, vegetated plots, and plots outside the enclosures) blocked by location within the reservoir. A third factor, 'sediment depth', was added to the ANOVA models to analyze data on sediment and pore water properties. Regression analyses were performed for each measured variable versus macrophyte biomass within the enclosures (data from outside the enclosures were not used for regressions). Bonferroni corrections were made for each ANOVA model, and differences among means were determined using the least significant difference test.

Organisms above the sediment were sampled with a 0.25 m^2 net bag (mesh size of 500 μm) extending from the water surface to the sediment surface. Vegetation within the bag was cut at the sediment surface, and all the contents were placed into plastic bags. Upon returning to the lab, the vegetation was rinsed into a 128 μm sieve with a stream of freshwater to remove animals and weighed. The animals were preserved in ethanol (final target ethanol concentration was 70%), sorted, identified to the lowest practicable taxonomic unit, and counted. Sampling was done during daylight, when horizontally migrating zooplankton outside the enclosure would have been expected to be in macrophyte beds (Lauridsen et al., 1998).

Sediments in the quadrants were cored to 15 cm depth (8 cm diameter) and sieved for animals (smallest mesh size of 128 μm), which were preserved in ethanol, sorted, identified, and counted. Each sediment core was subsampled at 0–2, 2–5, 5–8, and 8–11 cm. These subsamples were centrifuged at 1000 × *g* for 20 min, after which the pore water was decanted and filtered and immediately analyzed for SRP and TDP (DOP was calculated as the difference between TDP and SRP). The remaining sediment was dried and analyzed for organic carbon by combustion. TPP was determined for each dried subsample.

Because a large, but non-significant increase of sediment SRP in the presence of macrophytes occurred in 1997, the plant manipulations were repeated during the growing season of 1998 at the same locations, except the enclosure walls were removed. The stainless steel bases remained in place to locate the

sampling sites. The sediments were cored and analyzed for SRP to determine if 1997 results were anomalous.

Water samples were taken shortly before organisms were sampled in order to prevent that sampling disturbance from affecting water quality. Water samples were transported to the lab on ice and assayed for chlorophyll a, TSS, SRP, TDP, TPP, and DOP concentrations using standard methods (Murphy and Riley, 1962; Solorzano and Sharp, 1980; Lewis et al., 1984).

Separate samples of each abundant taxon and organic carbon source were made within the enclosures for stable isotope analyses. Animals were prepared for analyses shortly after collection, so it is possible that gut contents contributed to the isotopic signatures. Whole bodies of small insects, amphipods, and cladocerans were analyzed, whereas a representative subsample of dried, crushed large insects was used. For crayfish, only the tail muscle tissue was analyzed. The snail was acid treated prior to analysis. Macrophyte tissue was not acid treated as no visible marl was observed. TSS was collected on 2 μm glass filters. Stable isotopes of N and C were measured using elemental analysis and isotope ratio mass spectrometry (EA-IRMS) at the lab of Carol Kendall, USGS.

Methane was captured within each quadrant in 40 cm × 40 cm × 30 cm chambers constructed with stainless steel sides and a Plexiglas top. Chambers with no headspace were placed on the sediment surface to measure the flux of methane across the sediment–water interface, and were floated at the water surface to measure the flux across the air–water interface. Syringes equipped with stopcocks allowed water (60 mL) or air (10 mL) samples to be collected from the chambers. Within each replicate, sediment and floating chambers were simultaneously deployed to avoid temporal variation in methane fluxes from confounding the interpretation of results. Duplicate samples were taken every half hour for a total of 2.5 h of monitoring, placed on ice, and analyzed by gas chromatography within 6 h.

Rate of increase in methane concentration over time was used to calculate flux. In a few cases, the concentration of methane increased with a spike followed by the more typical gradual increase in concentration. This spike was interpreted as ebullition. Because ebullition was rare, unpredictable, possibly associated with disturbance, and not controlled for, the methane flux in these instances was determined by averaging the pre- and post-ebullition slopes of methane increase (i.e., the

Table 1
The effects of rooted macrophytes on the community structure, water and sediment properties, and emissions of methane

Variable	Outside enclosures	With plants	Without plants	%Increase with vegetation
Community				
Milfoil (g DM/m^2)	12.6 ± 3.6 ab (N = 5)	23.6 ± 8.0 a (N = 10)	0.7 ± 0.4 b (N = 10)	3271
Gastropods (#/m^2)	50 ± 16 ab (N = 5)	73 ± 24.8 a (N = 10)	4 ± 3 b (N = 10)	1725
Chironomids (#/m^2) [mostly *Cricotopus myriophylli*]	182 ± 50 ab (N = 5)	331 ± 148 a (N = 10)	20 ± 11 b (N = 10)	1555
Trichopterans (#/m^2)	88 ± 38 ab (N = 5)	122 ± 47 a (N = 10)	11 ± 6 b (N = 10)	1009
Ephemeropterans (#/m^2)	11.2 ± 3.6 a (N = 5)	16.3 ± 5.3 a (N = 10)	2.1 ± 0.5 b (N = 10)	676
Amphipods (#/m^2)	508 ± 156 a (N = 5)	752 ± 228 a (N = 10)	110 ± 49 b (N = 10)	584
Ostracods	1782 ± 124 a (N = 5)	656 ± 83 b (N = 10)	114 ± 13 c (N = 10)	475
Daphnids (#/m^2)	510 ± 19 a (N = 5)	514 ± 45 a (N = 10)	110 ± 10 b (N = 10)	367
Odonates (#/m^2)	19 ± 6 a (N = 5)	37 ± 9 a (N = 10)	10 ± 6 a (N = 10)	270
Oligochaetes (#/m^2)	34 ± 13 a (N = 5)	27 ± 9 a (N = 10)	12 ± 8 a (N = 10)	125
Copepods (#/m^2)	57 ± 24 a (N = 5)	34 ± 8 a (N = 10)	20 ± 7 a (N = 10)	70
Water properties				
TSS (μg/L)	2.88 ± 0.83 a (N = 5)	4.62 ± 0.59 a (N = 10)	4.04 ± 0.36 a (N = 10)	14
TPP (μg/L)	4.6 ± 0.3 a (N = 5)	5.2 ± 0.5 a (N = 10)	4.7 ± 0.1 a (N = 10)	11
SRP (μg/L)	0.35 ± 0.04 a (N = 5)	0.38 ± 0.02 a (N = 10)	0.32 ± 0.02 a (N = 10)	19
TDP (μg/L)	5.7 ± 0.5 a (N = 5)	5.5 ± 0.2 a (N = 10)	7.3 ± 1.8 a (N = 10)	−25
DOP (μg/L)	5.4 ± 0.5 a (N = 5)	5.1 ± 0.2 a (N = 10)	7.0 ± 1.9 a (N = 10)	−27
Chl a (μg/L)	5.4 ± 0.3 a (N = 5)	5.3 ± 0.3 a (N = 10)	5.1 ± 0.3 a (N = 10)	4
Surface sediment properties				
% Water	44 ± 5 a (N = 5)	52 ± 4 a (N = 10)	53 ± 4 a (N = 10)	−2
% AFDM	4.8 ± 0.8 a (N = 5)	6.5 ± 0.9 a (N = 10)	6.2 ± 0.7 a (N = 10)	5
TPP (μg/g sediment)	0.45 ± 0.05 a (N = 5)	0.51 ± 0.03 a (N = 10)	0.47 ± 0.02 a (N = 10)	9
TDP(μg/L pore water)	88 ± 56 a (N = 5)	149 ± 57 a (N = 10)	32 ± 4 a (N = 10)	366
SRP (μg/L pore water) 1997	84 ± 83 a (N = 5)	181 ± 89 a (N = 10)	12 ± 5 a (N = 10)	1408
SRP (μg/L pore water) 1998		236 ± 94 a (N = 10)	33 ± 8 b (N = 10)	615
Methane (μmol/m^2/day)				
Emissions to atmosphere	–	0.59 ± 0.10 a (N = 8)	0.26 ± 0.08 b (N = 8)	127
Flux from sediments	–	1.07 ± 0.31 a (N = 8)	1.35 ± 0.62 a (N = 8)	−21

Applying a Bonferroni adjustment for the 3-treatments resulted in a P-value of 0.017 being considered statistically significant. Lower case letters following the means (±1 S.E.) represent statistical groups that do not differ at $\alpha = 0.05$ using least significant difference tests. The last column indicates the percent increase between the 'with plant' column and the 'without plant' column [(with plant − without plant)/without plant × 100]. The flux of methane is based on area of littoral bottom, not leaf area.

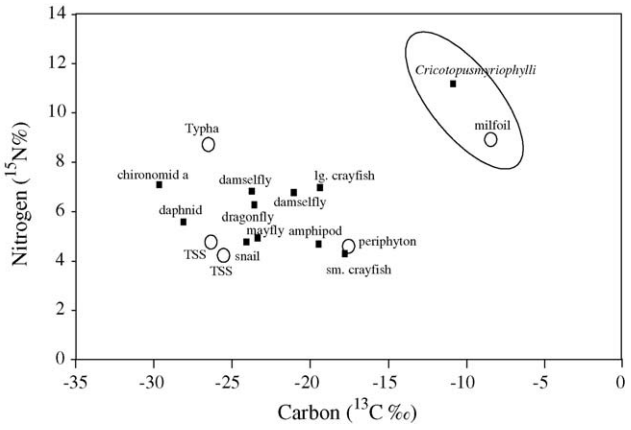

Fig. 1. Stable isotopic composition of carbon sources (○) and animals (■) collected from the shallow littoral zone of Aurora reservoir, Colorado.

ebullition event was removed from the regression). Fluxes of methane from vegetated versus non-vegetated quadrants were compared with paired-sample *t*-tests (paired by adjacent quadrants).

Lacunar gas from milfoil was sampled in situ by capturing the bubbles that escaped from cut stems with an inverted vial. Each gas sample was obtained from multiple plants, as individual plants did not provide enough gas for analysis.

3. Results

For 7 of the 10 most abundant animal taxa, there were significantly more animals in the vegetated than in the non-vegetated quadrants. The number of epiphytic organisms (e.g., *Cricotopus myriophylli*, gastropods, trichopterans, ephemeropterans, amphipods, and odonates) generally showed a greater increase with vegetation than did organisms associated with the water column (e.g., ostracods, daphnids, and copepods) or the sediment (e.g., oligochaetes; animals were extremely rare in sediment cores and were therefore excluded from analyses). Benthic animals were generally more abundant within the enclosures than outside of them (Table 1).

Milfoil had an isotopic signature very different from those of other carbon sources and was particularly heavy in ^{13}C. The milfoil signature closely matched the one of *C. myriophylli*

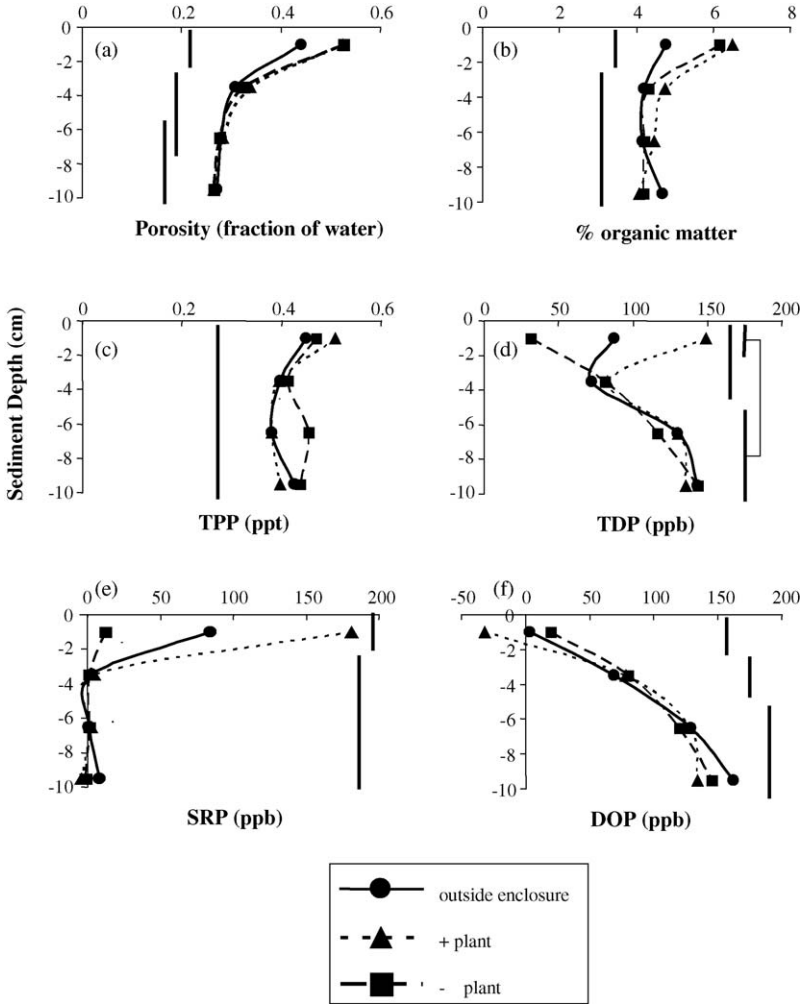

Fig. 2. Depth profiles of sediment and pore water variables outside of the enclosures (●) and vegetated (▲) and weeded (■) plots. Verticle bars adjacent to the depth profiles represent groups of means that do not differ statistically with sediment depth at $\alpha = 0.05$.

Table 2
Regressions between animal taxa and the dry mass of *Myriophyllum sibiricum* for samples collected within the enclosures

Variable	R^2	Slope	S.E.	*y*-Intercept	S.E.	*P*-value
Animal taxa						
Gastropods	0.57	2.32	0.48	2.580	2.835	<0.001
Chironomids	0.78	15.35	1.90	−3.007	11.280	<0.001
Trichopterans	0.64	4.50	0.79	2.92	4.71	<0.001
Ephemeropterans	0.66	2.12	0.36	2.72	2.13	<0.001
Amphipods	0.79	25.71	3.16	29.372	18.801	<0.001
Ostracods	0.72	29.58	4.36	5.95	25.89	<0.001
Daphnids	0.74	14.38	1.98	34.110	11.785	<0.001
Odonates	0.15	0.48	0.26	4.190	1.575	0.088
Oligochaetes	0.36	0.79	0.25	2.45	1.48	0.005
Copepods	0.01	0.14	0.27	6.219	1.607	0.608

The number of individuals per m^2 represents the area of benthos extended to the water surface (i.e., it is not per area of plant surface area). *P*-values, R^2, slope + S.E., and intercept + S.E. are provided. Statistics for water properties, surface sediment properties, and methane emissions are not shown because they were not significantly correlated with plant biomass.

(Fig. 1). The isotopic signatures of benthic herbivorous amphipods and small crayfish matched those of periphyton, whereas daphnids, snails, and mayflies best matched the isotopic signature of TSS. None of the animals appeared to use *Typha* as an appreciable carbon source. However, *Typha* was not located within the enclosures.

Macrophyte removal had no detectable influence on the water quality parameters. SRP of surface pore water was 1408% higher in vegetated enclosures than enclosures that had vegetation removed, which resulted in a 366% increase in TDP (Table 1, Fig. 2). The data were highly variable, resulting in non-significant *P*-values. A significant increase in SRP occurred the following year when vegetated plots had 615% more SRP in shallow pore water than did plots that had vegetation removed. The submersed clay soils below 2 cm apparently were unaffected by vegetation, had extremely low SRP, and increasing TDP concentrations between 2 and 11 cm (Fig. 2).

The presence of macrophytes did not significantly affect the flux of methane from the sediments to the water column (Table 1). However, the emission of methane into the atmosphere was 127% higher in vegetated than in vegetation removal plots. There was no significant correlation between milfoil biomass and methane fluxes from the sediments ($P = 0.788$, $R^2 = 0.01$) or air ($P = 0.195$, $R^2 = 0.12$). The concentration of methane in the two composite samples of lacunar gases were 4.1 and 2.7 ppm, which was higher than the 1.8 ppm for the ambient air.

4. Discussion

There was a positive relationship of most secondary producers with macrophyte biomass (Tables 1 and 2), but this increase in secondary producer numbers was not the result of increased food provided directly by the macrophytes, with the notable exception of the milfoil midge *C. myriophylli*. The isotopic composition of *M. sibiricum* ($\delta^{13}C = -8.52‰$) was very different from other carbon sources in the reservoir which made it easy to follow through the food web. Even though the enclosures forced animals to be in close proximity to milfoil, which should have increased the chance of milfoil carbon being incorporated into the food web, stable isotope data showed that only the milfoil midge known to specialize on *Myriophyllum* spp. (MacRae et al., 1990; Newman, 2004) obtained its carbon from milfoil, while none of the other common animals used milfoil carbon (Fig. 2). Similarly, *Myriophyllum spicatum* from a lake in Oklahoma had a distinct isotopic signature of about −10‰, although there was no evidence that any of the carbon from *M. spicatum* got transferred up the food web (Toetz, 1997). The likely reasons that animals were more abundant in our vegetated plots despite little of the *M. sibiricum* providing food are (1) the plants provided habitat for the animals and (2) the macrophytes provided surfaces that biofilms can colonize. These biofilms increase the availability of periphyton and probably TSS, which were carbon sources for most of the remaining animals. In this study, the indirect effects of macrophytes on feeding of most invertebrates were thus more important than the direct effects, except for the specialist *C. myriophylli*.

We attempted to minimize artifacts with our experiment by using large enclosures. Despite this effort, some artifacts were associated with the enclosures (see Vermaat et al., 1990 for discussion of enclosure artifacts). For example, periphyton grew on the surface of the enclosure walls, water exchange was greatly hindered, and large predators (e.g., fish) were excluded. Also, surface sediments within the enclosures tended to have greater water and organic contents than did surface sediments outside of the enclosures (Fig. 2a and b). These trends were likely the result of fine organic particles settling on the sediments rather than being exported by currents. Deeper sediments below 2 cm were not significantly impacted by the enclosures, but these deeper layers are they clayey soils that were flooded by the creation of the reservoir.

Whereas water column nutrients were not significantly affected by vegetation removal, SRP in surface sediments was higher in vegetated than in the vegetation removal plots. This SRP represented the majority of the TDP, indicating that the amount of DOP was minimal in the surface sediments of all treatments (Fig. 2). Even though surface pore water SRP was higher in the presence of macrophytes than in their absence, within the plant beds SRP was not significantly correlated with plant biomass. In contrast, phosphorus in deeper pore water largely outside the influence of the macrophyte rhizosphere did not differ among treatments and was mainly in the organic form. Pore waters under the influence of the rhizosphere had most of the soluble phosphorus in the inorganic form.

The mechanisms responsible for this pattern of pore water SRP were not addressed in this study, and it is possible that the decrease in pore water SRP with macrophyte removal was an artifact of our treatment. Despite our efforts to minimize and control for disturbance to the sediments while removing vegetation, SRP in surface sediments could have been lost to the water column (Holdren and Armstrong, 1980), without

sufficient time for recovery during the 7-week experiment, in which periodic macrophyte removal took place. Additionally, the weeding process could have increased the redox potential of the surface sediments, leading to reduced levels of SRP (Carlton and Wetzel, 1988; James et al., 1995).

The youth of the reservoir, low nutrient loading, and minimal organic matter in the clayey sediments probably explain why the measured rates of methane emissions were three orders of magnitude less than they are in older eutrophic systems (Chanton et al., 1992; Smith and Lewis, 1992; Segers, 1998; Smith et al., 2000). The macrophytes did not significantly affect the flux of methane from the sediment into the water column, but the plants did enhance the emission of the trace gas into the atmosphere as expected from previous studies (Chanton et al., 1992; Smith and Lewis, 1992). This is probably because the lacunar space of the plants provided an easier pathway for methane to reach the atmosphere, compared to traveling through the water column. The gas bubbles that escaped from milfoil when the tips were cut contained elevated concentrations of methane, indicating that plants could serve as a conduit for methane to travel from methanogenic sediments to the water column and atmosphere.

This study demonstrates that macrophytes (mostly milfoil in our system) had a significant impact on the structure and function of the littoral zone ecosystem. Macrophytes provided habitat and food for animals in the water column, enhanced the emission of methane to the atmosphere, and probably altered the phosphorus cycle in the sediments.

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References

Bolser, R.C., Hay, M.E., Lindquist, N., Fenical, W., Wilson, D., 1998. Chemical defenses of freshwater macrophytes against crayfish herbivory. J. Chem. Ecol. 24, 1639–1658.

Carlton, R.G., Wetzel, R.G., 1988. Phosphorous flux from lake sediments: effect of epipelic algal oxygen production. Limnol. Oceanogr. 33, 562–570.

Carpenter, S.R., Lodge, D.M., 1986. Effects of submersed macrophytes on ecosystem processes. Aquat. Bot. 26, 341–370.

Chanton, J.P., Martens, C.S., Kelley, C.A., Crill, P.M., Showers, W.J., 1992. Methane transport mechanisms and isotopic fractionation in emergent macrophytes of Alaskan tundra lakes. J. Geophys. Res. 97, 16681–16688.

Cronin, G., 1998. Influence of macrophyte structure, nutritive value, and chemistry on the feeding choices of a generalist crayfish. In: Jeppesen, E., Søndergaard, Ma., Søndergaard, Mo., Christoffersen, K. (Eds.), The Structuring Role of Submerged Macrophytes in Lakes, vol. 131. Springer-Verlag, pp. 307–317.

Cronin, G., Lodge, D.M., Hay, M.E., Miller, M., Hill, A.M., Horvath, T., Bolser, R.C., Lindquist, N., Wahl, M., 2002. Crayfish feeding preferences for freshwater macrophytes: the influence of plant structure and chemistry. J. Crustacean Biol. 22, 708–718.

Cronin, G., Schlacher, T., Lodge, D.M., Siska, E.L., 1999. Intraspecific variation in feeding preference and performance of *Galerucella nymphaeae* (Chrysomelidae: Coleoptera) on aquatic macrophytes. J. N. Am. Benthol. Soc. 18, 391–405.

Cronin, G., Wissing, K.D., Lodge, D.M., 1998. Comparative feeding selectivity of herbivorous insects on water lilies: aquatic vs. semi-terrestrial insects and submersed vs. floating leaves. Freshwater Biol. 39, 243–257.

Gaevskaya, N.S., 1969. The role of higher plants in the nutrition of the animals of freshwater basins. In: D.G.M. Muller (translator), K.H. Mann (Ed.), 3 vols, 629 pp.

Garnet, K.N., Megonigal, J.P., Litchfield, C., Taylor Jr., G.E., 2005. Physiological control of leaf methane emission from wetland plants. Aquat. Bot. 81, 141–155.

Gerard, G., Chanton, J., 1993. Quantification of methane oxidation in the rhizosphere of emergent aquatic macrophytes: defining upper limits. Biogeochemistry 23, 79–97.

Holdren Jr., G.C., Armstrong, D.E., 1980. Factors affecting phosphorus release from intact lake sediment cores. Environ. Sci. Tech. 14, 79–87.

Humphries, P., 1996. Aquatic macrophytes, macroinvertebrate associations and water levels in a lowland Tasmanian river. Hydrobiologia 321, 219–233.

James, W.F., Barko, J.W., Eakin, H.L., 1995. Internal phosphorus loading in Lake Pepin, upper Mississippi River. J. Freshwater Ecol. 10, 269–276.

Jeppesen, E., Søndergaard, M., Søndergaard, M., Christoffersen, K. (Eds.), 1998. The Structuring Role of Submerged Macrophytes in Lakes. Ecological Series, vol. 131. Springer-Verlag, 423 pp.

Lauridsen, T.L., Jeppesen, E., Søndergaard, M., Lodge, D.M., 1998. Horizontal migration of zooplankton: predator-mediated use of macrophyte habitat. In: Jeppesen, E., Søndergaard, M., Søndergaard, M., Christoffersen, K. (Eds.), The Structuring Role of Submerged Macrophytes in Lakes. Ecological Series, vol. 131. Springer-Verlag, pp. 233–239.

Lewis Jr., W.M., Saunders III, J.F., Crumpacker Sr., D.W., Brendecke, C.M., 1984. Eutrophication and Land Use. Springer-Verlag, NY.

Lodge, D.M., 1985. Freshwater macrophyte-gastropod associations: observations and experiments on macrophyte choice by gastropods. Freshwater Biol. 15, 695–708.

Lodge, D.M., 1991. Herbivory on freshwater macrophytes. Aquat. Bot. 41, 195–224.

Lodge, D.M., Cronin, G., van Donk, E., Froelich, A.J., 1998. Impact of herbivory on plant standing crop: comparisons among biomes, between vascular and nonvascular plants, and among freshwater herbivore taxa. In: Jeppesen, E., Søndergaard, M., Søndergaard, M., Christoffersen, K. (Eds.), The Structuring Role of Submerged Macrophytes in Lakes. Ecological Series, vol. 131. Springer-Verlag, pp. 149–174.

MacRae, I.V., Winchester, N.N., Ring, R.A., 1990. Feeding activity and host preference of the milfoil midge, *Cricotopus myriophylli* Oliver (Diptera: Chironomidae). J. Aquat. Plant Manage. 28, 89–92.

Madsen, J.D., Chambers, P.A., James, W.F., Koch, E.W., Westlake, D.F., 2001. The interaction between water movement, sediment dynamics and submersed macrophtes. Hydrobiologia 444, 71–84.

McGaha, Y.J., 1952. The limnological relations of insects to certain flowering plants. T. Am. Microsc. Soc. 71, 355–381.

Moss, B., McGowan, S., Carvalho, L., 1994. Determinations of phytoplankton crops by top-down and bottom-up mechanisms in a group of English lakes, the West Midland meres. Limnol. Oceanogr. 39, 1020–1029.

Murphy, J., Riley, J.P., 1962. A modified single solution method for the determination of phosphate in natural waters. Anal. Chim. Acta 27, 31–36.

Newman, R.M., 1991. Herbivory and detritivory on freshwater macrophytes by invertebrates: a review. J. N. Am. Benthol. Soc. 10, 89–114.

Newman, R.M., 2004. Biological control of Eurasian watermilfoil by aquatic insects: basic insights from an applied problem. Arch. Hydrobiol. 159, 145–184.

Ozimek, T., van Donk, E., Gulati, R.D., 1990. Can macrophytes be useful in biomanipulations of lakes? The Lake Zwemlust example. Hydrobiologia 200/201, 399–409.

Pedersen, O., Borum, J., Duarte, C.M., Fortes, M.D., 1998. Oxygen dynamics in the rhizosphere of *Cymodocea rotundata*. Mar. Ecol. Prog. Ser. 169, 283–288.

Scheffer, M., Hosper, S.H., Meijer, M.L., Moss, B., Jeppesen, E., 1993. Alternative equilibria in shallow lakes. Trends Ecol. Evol. 8, 275–279.

Schindler, D.W., 1996. Ecosystems and ecotoxicology: a personal perspective. In: Newman, M.C., Jagoe, C.H. (Eds.), Ecotoxicology: A Hierarchical Treatment. CRC Lewis, NY, New York, USA, pp. 371–398.

Segers, R., 1998. Methane production and methane consumption: a review of processes underlying wetland methane fluxes. Biogeochemistry 41, 23–51.

Shelford, V.W., 1918. Conditions of existence. In: Ward, H.B., Whipple, G.C. (Eds.), Freshwater Biology. Wiley, New York, pp. 21–60.

Smith, L.K., Lewis Jr., W.M., 1992. Seasonality of methane emissions from five lakes and associated wetlands of the Colorado Rockies. Global Biogeochem. Cycles 6, 323–358.

Smith, L.K., Lewis Jr., W.M., Chanton, J.P., Cronin, G., Hamilton, S.K., 2000. Methane emissions from the Orinoco River Floodplain, Venezuela. Biogeochemistry 51, 113–140.

Solorzano, L., Sharp, J., 1980. Determination of total dissolved phosphorus and particulate phosphorus in natural waters. Limnol. Oceanogr. 25, 754–758.

Toetz, D., 1997. Does Eurasian watermilfoil, *Myriophyllum spicatum*, contribute to the diet of animals in a turbid reservoir? J. Freshwater Ecol. 12, 545–551.

Vermaat, J.E., Hootsmans, M.J.M., Van Dijk, G.M., 1990. Ecosystem development in different types of littoral enclosures. Hydrobiologia 200/201, 391–398.

Vermaat, J.E., Santamaria, L., Roos, P.J., 2000. Water flow across and sediment trapping in submerged macrophyte beds of contrasting growth form. Arch. Hydrobiol. 148, 549–562.