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Effect of *Vallisneria americana* (L.) on community structure and ecosystem function in lake mesocosms

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Abstract

Submerged aquatic vegetation is known as a key structural component and regulator in ecosystems. In this mesocosm study, we examine community- and system-level responses to the presence of *Vallisneria americana* (L), a deep-rooted macrophyte. Phytoplankton, bacteria and filamentous algal biomasses were significantly lowered in the presence of *V. americana*. In addition, mesocosms with macrophytes had significantly reduced porewater phosphate and iron, water column dissolved organic carbon and total suspended solids, but elevated sediment redox. All mesocosms were net autotrophic (gross primary production/respiration >1). Compared to the macrophyte treatments, the control mesocosms had lower diel net primary production (NPP) midway through the experiment (d 16), but at the end of the experiment (d 36), the controls had the higher values, presumably due to increased filamentous algae. NPP and NPP/R were constant in the macrophyte treatments, whereas NPP/R increased significantly from middle to end of the experiment in the controls. We show that community and system-level responses to the presence of *V. americana* have significant consequences on system structure and function.

Introduction

It is well known that submerged vegetation provides habitat for animals, acts as a nutrient filter and stabilizes sediments of aquatic systems (e.g. Thayer et al., 1975; Kikuchi & Peres, 1977; Ward et al., 1984; Kemp et al., 1984; Carpenter & Lodge, 1986). However, submerged macrophyte effects on ecosystems and the resulting system responses (e.g. changes in trophic structure or nutrient status) are less well-studied. The presence of submerged macrophytes may have a significant effect on the trophic structure of a system because of interactions of macrophytes with fish and zooplankton (Jeppesen et al., 1998). For example, zooplankton may use macrophytes as a refuge against predation from fish. The structuring impact on the zooplankton may cascade to lower trophic levels and the chemical environment (Jeppesen et al., 1998). In addition, direct and indirect effects of the macrophytes on nutrient cycling can cause system-level alterations (Carpenter & Lodge, 1986; Barko et al., 1991; Jeppesen et al., 1998).

Submerged macrophytes rely primarily on sediment nutrient pools for assimilation (Carpenter & Adams, 1977; Carignan & Kalff, 1980; Carpenter & Lodge, 1986; Smith & Adams, 1986; Chambers et al., 1989; Barko et al., 1991) and as a result, sediment porewater pools are frequently depleted and replen-

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ished throughout the growing season to meet plant demand (Barko & Smart, 1980; Andersen & Olsen, 1994). Furthermore, because exchange of nutrients between the benthos and overlying water can fuel the growth of phytoplankton and filamentous algae, submerged macrophytes regulate ecosystem structure through their role in benthic exchange with the overlying water (Howard-Williams, 1981; Rissgård et al., 1996; Søndergaard & Moss, 1998). Since some species decrease the flux of nutrients from the sediment to the water column and also promote zooplankton production, it is hypothesized that in lake systems, the presence of submerged vegetation may be responsible for a clear-water phase and in the absence of macrophytes, a high phytoplankton turbid-water state may occur due to phytoplankton blooms (Scheffer et al., 1993; Scheffer & Jeppesen, 1998). Some deep-rooted macrophyte species indirectly modify subsurface processes by releasing oxygen into the root zone (Wium-Andersen & Andersen, 1972; Tessenow & Baynes, 1975). Oxygen release into root zones with low organic content results in lowered porewater phosphorus and higher retention of solid-phase phosphorus (Jaynes & Carpenter, 1986; Christensen & Andersen, 1996; Wigand et al., 1997). Therefore, in phosphorus-poor systems with sediment of low organic content, less PO_4 exchange with the overlying water is predicted in aquatic grassbeds because of oxygenation of the root zone (Jaynes & Carpenter, 1986; Carpenter & Lodge, 1986; Andersen & Olsen, 1994; Riisgård et al., 1996) and direct phosphorus sequestration into plant tissues (Carpenter & Adams, 1977; Smith & Adams, 1986). However, in systems with organically enriched sediments, the reducing nature of the sediment consumes oxygen which minimizes the root oxygenation effect on phosphorus retention.

In this study, we examined community- and system-level responses to the presence of *V. americana*, a deep-rooted macrophyte with ribbon-like leaves arising from clusters at the base of the plant. At the community level, we quantified snail, epiphytes, phytoplankton, bacteria and macroalgae, and at the system level we characterized light availability, nutrients, sediment biogeochemistry and community metabolism in mesocosms with and without *V. americana*. From our results, we describe the effect of submerged macrophytes on system structure and function at the community and system level.

Methods

The experiments were conducted over 36 days (beginning on June 26, 1995) at the Louis Calder Center, Armonk, NY, U.S.A. Mesocosms (90 l; ht=100 cm; l,w=30 cm) were filled with well water (dissolved inorganic nitrogen <50 μg l^{-1}; total dissolved phosphorus <10 μg l^{-1}) and later enriched with Calder Lake water (10% by volume) to provide a seed community of bacteria, phytoplankton and zooplankton in the water column. Mesocosms were gently aerated (except during diel experiments; see below) and their volumes maintained periodically with well and lake (9:1 ratio) water. They were maintained in an aquatic greenhouse receiving natural daylight (about 15 h L: 9 h D). Each mesocosm also received 10 snails (*Physa gyrina*) that were marked with opaque paint for identification. Snail survivorship was estimated based on % recovery at the end of the study. The snails had a mean length of 5.8 mm and a mean weight of 0.26 g. At the end of the experiment, the surviving adult snails were remeasured for growth (length and weight), and in addition, we counted the juvenile snail density in each mesocosm.

The macrophyte treatment and control group were replicated four times each for a total of eight mesocosms. In each mesocosm, there were four (2 l; 14 cm in d) pots of pond sediment (29.8% organic matter). For the macrophyte treatments, two over-wintering buds of *Vallisneria americana* (from F&J Seed Service, Woodstock, IL, U.S.A.) were planted in each of the four sediment-filled pots four weeks prior to the beginning of the experiment. Macrophytes averaged about 40 cm in length, about halfway to the water surface, at the beginning of the study. At the end of the 36 day experiment, *V. americana* biomass was measured.

Epiphyte biomass was measured at the midpoint (d 16) and end (d 36) of the experiment on green, flat polypropylene strips (width and length similar to *Vallisneria* leaves) placed in the mesocosms at the start of the study and used to simulate macrophyte leaves standing erect. Each strip had a total above-sediment surface area of approximately 30 cm^2. Strips were removed from each mesocosm and placed in centrifuge tubes containing neutral (with $MgCO_3$) 90% acetone for chlorophyll extraction overnight. Extracts were centrifuged and chlorophyll *a* (chl *a*) concentration was measured using a Shimadzu UV-160 spectrophotometer and corrected for phaeophytin a (Lorenzen 1967). Epiphyte biomass was expressed as μg chl *a* cm^{-2}.

Weekly measurements of dissolved inorganic phosphorus (DIP) and inorganic nitrogen (NH_4, NO_3), chl *a*, total suspended solids (TSS) and dissolved organic carbon (DOC) were measured by sampling the water of each tank and filtering it through a GF/F filter. Samples were analyzed for dissolved inorganic (=soluble reactive) phosphorus (DIP) by using the antimony-ascorbate-molybdate method (A.P.H.A., 1985; Bran+Luebbe Analyzing Technologies, 1986a), NH_4–N using phenol-hypochlorite and NO_3 after reduction to NO_2 in a Cd-Cu column, via reaction with sulfanilamide-NNED (A.P.H.A., 1985; Bran-Luebbe Analyzing Technologies, 1986b, 1987a). Dissolved organic carbon (DOC) was measured following removal of inorganic-C via acid sparging, then digested with acid persulfate and high-energy UV. The resultant CO_2 was dialyzed and reacted with buffered phenolphthalein and measured at 550 nm (Goulden & Brooksbank, 1975; Bran+Luebbe Analyzing Technologies, 1989). Total dissolved P (TDP) was digested in-line using acid persulfate (Eisenreich et al., 1975) and analyzed for DIP as described above. All procedures were modified for automated analysis and run on a TrAAcs 800 automated analyzer (Bran+Luebbe Inc., Buffalo Grove, IL, U.S.A.).

Weekly bacteria samples were collected by pump sampler, preserved with 2% glutaraldehyde immediately during filtration (1 ml sample + 9 ml deionized water), stained with DAPI, and filtered onto Irgalan black, polycarbonate filters (25 mm, 0.2 μm pore size) (Porter & Feig, 1980). Samples were stored frozen (-15 °C) until enumeration. Bacterial counts were made at 1000$\times$ magnification using a Nikon Labophot epifluorescence microscope with a UV-2A filter set (excitation 330 nm; barrier 430 nm). A minimum of 10 grids and 300 cells were counted per sample.

Diel measurements (every 3 h) of nutrients (NH_4–N, NO_3–N, PO_4–P), temperature, dissolved oxygen and pH were taken at the midpoint (d 16) and end (d 36) of the experiment. Nutrients were measured using automated wet chemistry (Alpkem, 1986). Community metabolism was estimated by measuring changes in dissolved oxygen using a YSI Model 57 meter with a hand-held probe at 15 cm depth. Gross primary production (GPP), net primary production (NPP) and respiration rates (*R*) were estimated using standard methods (Odum & Hoskin, 1958). NPP is the calculated mass of oxygen produced by the mesocosm community in the daytime. *R* is the calculated mass of oxygen consumed during the night-time and GPP is the sum of NPP and *R*.

In the calculations of NPP, *R* and GPP, no adjustment for atmospheric diffusion of oxygen was used because oxygen diffusion was found to be negligible (as tested in the first diel study). Atmospheric diffusion of oxygen was estimated by covering half of the mesocosms with plastic sheeting (an effective barrier to diffusion) and comparing % saturation and production data from the covered vs. uncovered treatments. Because there was no significant difference in oxygen diffusion between covered and uncovered mesocosms, we assumed diffusion to be negligible and the second diel metabolism study was conducted without plastic covering on any of the tanks.

Light, leaf elongation and bacterial productivity were also quantified at the middle and at the end of the experiment. Light was measured with a LICOR spherical bulb and data logger. Leaf elongation was measured by marking the leaves with a needle and piece of thread just above the meristem and recording the increase in length after approximately one week. Bacterial production was estimated as the rate of incorporation of tritiated thymidine into DNA (Findlay et al., 1984). Briefly, 10 ml of water were incubated for 1 h with 40 μCi of ^{3}H-thymidine (specific activity of 80 μCi per nmole). After the incubation, cells were collected and washed with cold 5% TCA on a polycarbonate filter and frozen. DNA was extracted and productivity is reported as DPM of ^{3}H-thymidine incorporated into the DNA fraction per l per h. In addition, zooplankton densities and filamentous algal cover were quantified at the end of the experiment. Zooplankton were filtered from water samples (2 l) through a 35 μm sieve and preserved in buffered formalin (to 2%) until they were enumerated. Only total zooplankton composed of *Daphnia*, *Chydorus*, copepod nauplii, ostracods, adult cyclopoid and calanoid copepods, and *Alona*-like organisms were included in statistical analyses. Five individual observers estimated the total percent cover of filamentous algae for each mesocosm at the end of the experiment and the separate observations were averaged for each tank.

Sediment redox status in the light and dark on the last day of the experiment at a depth of 5 cm was measured with a platinum microprobe and a calomel electrode as a reference. In addition, the sediment was sampled with a cut-off 60 ml (diameter = 25 mm) syringe, deoxygenated with argon gas and centrifuged for determination of porewater NH_4–N, PO_4–P and Fe. The separated porewater was sampled by syringe and placed in HCL-acidified vials for later analysis. NH_4–N and PO_4–P were measured as described above using

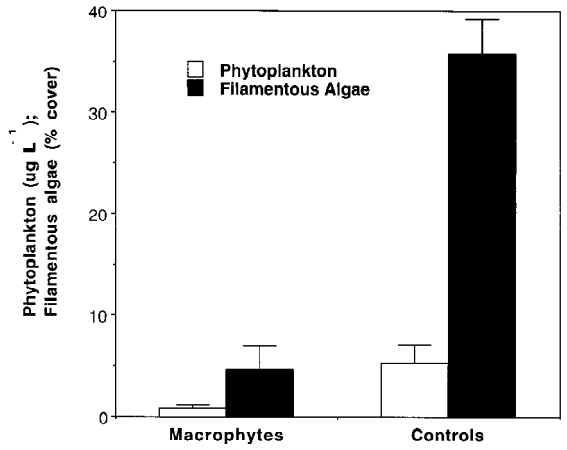

Figure 1. Average weekely phytoplankton biomass and end-experiment (d 36) filamentous algal (for macrophytes and controls: mean±se, n=4; Levels in the presence of macrophytes were signicantly lowered, $p<0.05$).

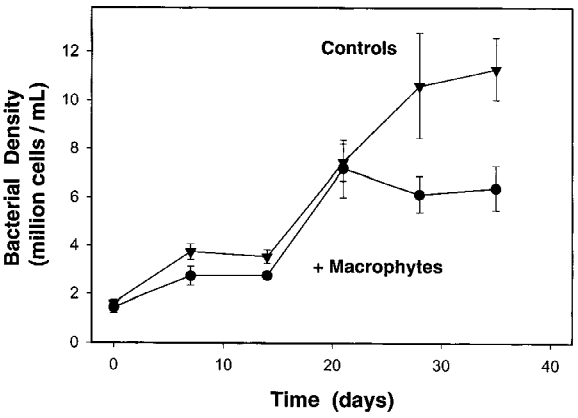

Figure 2. Mean of weekly bacterial densities in mesocosms as influenced by macrophytes (mean±se, n=4).

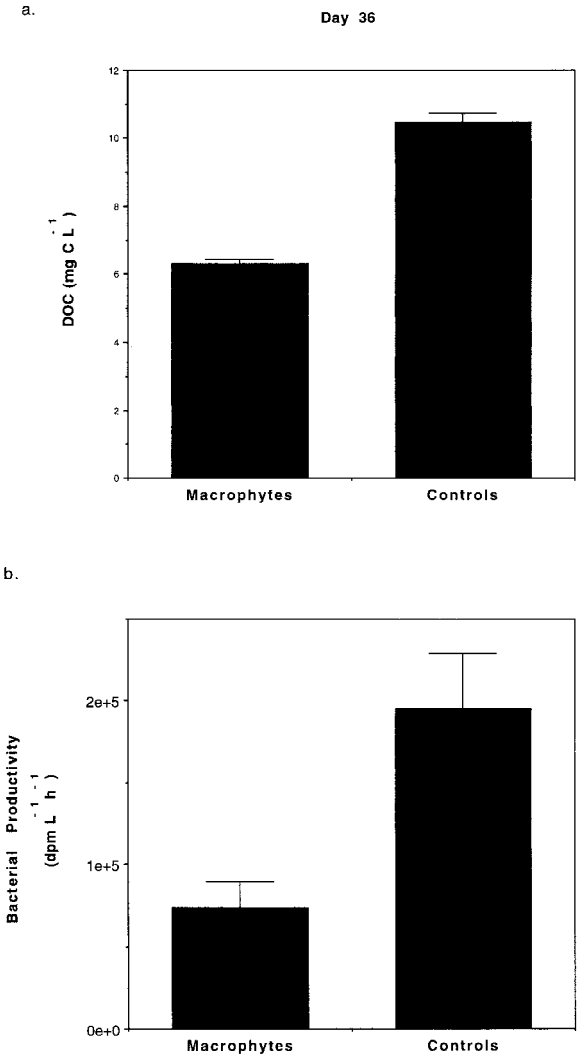

Figure 3. End-experiment (d 36) (a) DOC in the water column and (b) bacterial productivity in the mesocosms (for macrophytes and controls, mean±se, n=4; Levels in the presence of macrophytes were signicantly lowered, $p<0.05$).

Alpkem methodologies and Fe using plasma emission (Leventhal, 1990).

Student t-tests were used to determine differences between treatment and control means. Effects were judged to be significant if the probability (p) of a type I error (alpha) was <0.05.

Results

Effects on community structure

In the Macrophyte treatments, biomass of *V. americana* was 80.5±5.3 gdw m^{-2} and leaf elongation 1.4±0.09 cm d^{-1}. Average weekly phytoplankton and end-experiment filamentous algal biomasses were significantly lower in the presence of *V. americana* (Figure 1). Algal epiphyte levels were significantly lower in the macrophyte treatment at mid-experiment (d 16), but at the end of the experiment did not differ from the controls (Table 1).

Along with the low phytoplankton biomass and filamentous algal cover, the mesocosms with submerged macrophytes had significantly lower average weekly DOC (3.77±0.51 vs. 6.75±1.21 mgC l^{-1}) and bacterial densities (6.62±0.77 vs. 11.30±1.27 millions ml^{-1}). At the end of the third week (d 21), bacterial densities diverged between groups, becoming signific-

Table 1. Measurements of mid- and end-experiment epiphytes, TSS, zooplankton, adult and juvenile snails, (for macrophytes and controls, n=4, mean±se)

	Macrophytes	Controls	Significance
Mid-Epiphytes (μg chl *a* cm^{-2})	0.015±0.004	0.024±0.002	*
End-Epiphytes (μg chl *a* cm^{-2})	0.027±0.007	0.033±0.008	ns
TSS (mg l^{-1})	2.39±0.39	7.32±1.2	*
Zooplankton (# l^{-1})	34.5±8.4	15.8±0.9	ns
Adult snail survivorship (#)	3.8±1.6	0.75±0.3	ns
Adult snail length (mm)	2.1±0.43	2.5±0.46	ns
Adult snail weight (g)	0.03±0.007	0.04±0.008	ns
Juvenile snails (#)	12.0±4.73	12.5±4.03	ns

*$p<0.05$.

antly lower in the presence of submerged vegetation (Figure 2). By the end of the experiment (d 36), DOC and bacterial productivity were significantly lowered in the mesocosms with macrophytes (Figure 3a, b).

Invertebrate responses to the presence of submerged macrophytes were not significant. Final zooplankton densities, adult snail survivorship and growth, and juvenile snail densities showed no statistical differences between the macrophyte treatment and the controls (Table 1).

Effects on chemical and physical variables

In systems with *V. americana*, TSS levels were less than half that in the controls (Table 1). Midway through the experiment, light attenuation did not differ between the macrophyte treatments and controls. However at the end, light attenuation (1.3±0.2 vs. 2.3±0.4 m^{-1}) was significantly lower in the macrophyte treatment.

Mesocosms with submerged macrophytes had significantly greater sediment redox potential in the dark than the controls (Figure 4a). Daytime redox status did not differ between the macrophyte treatments and the controls (Macrophytes: 283±25 mV; Controls: 241±4 mV). Sediment porewater Fe and PO_4–P were significantly lower in the presence of submerged macrophytes (Figure 4b, c). Water column DIP levels did not vary significantly in weekly analyses, but ammonium levels were significantly lower in the macrophyte treatments (Table 2). There was no significant difference in nitrate levels between the macrophyte treatments and the controls.

Table 2. Mean of weekly measurements (n=4 per treatment; mean±se) of pelagic nutrients

	Macrophytes	Controls	Significance
DIP (μg l^{-1})	4.1±1.5	3.8±1.0	ns
NH_4–N (μg l^{-1})	181.4±23.9	228.4±30.56	*
NO_3–N (μg l^{-1})	3.8±0.7	2.7±1.2	ns

*$p<0.05$.

Diel metabolism studies

Temperature (26±1 °C) between the macrophyte treatments and controls did not vary significantly in either diel study. During the first diel study (d 16), the macrophyte treatments had significantly higher average pH (8.9±0.04) than the controls (8.0±0.04). However, the pH levels had increased significantly in both groups by the second diel experiment (d 36) but did not significantly vary (Macrophytes: 9.4±0.02; Controls: 9.2±0.11). Although DIP levels were not significantly different between treatments in the once-per-week observations that were sampled during daylight hours (Table 2), for both treatments night-time PO_4–P in the overlying water was significantly elevated between 2400 and 0300 h and was lower in the macrophyte treatments than the controls (Figure 5). The lower PO_4–P measured in the dark hours in the mesocosms with macrophytes coincides with the significantly greater redox potential associated with the sediments (Figure 4a). There was no significant difference in the dissolved nitrogen levels between the treatments during the diel studies.

In the controls, the diel oxygen curves displayed greater amplitudinal differences between the midpoint (d 16) and end (d 36) of the experiment (Figure 6a)

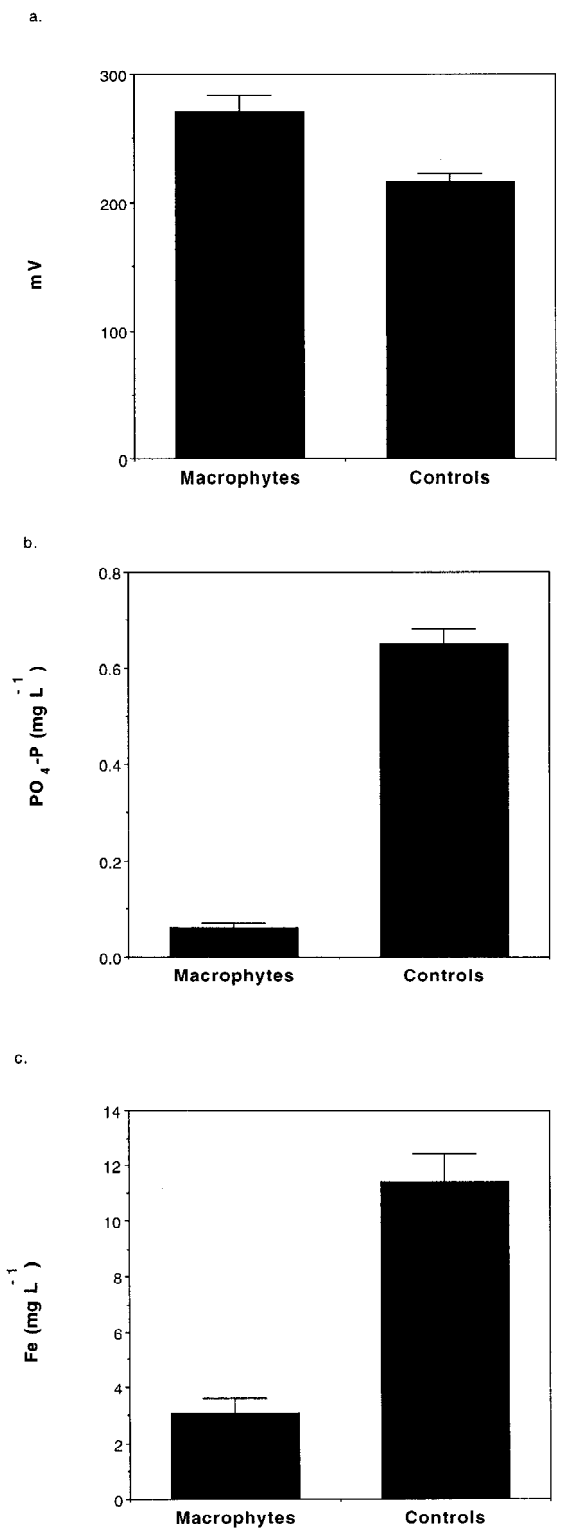

Figure 4. End-experiment (d 36) biogeochemical measurements of (a) redox status in the dark, (b) porewater phosphate, (c) porewater iron (for macrophytes and controls, mean±se, n=4; Levels in the presence of macrophytes were significantly altered, $p<0.05$).

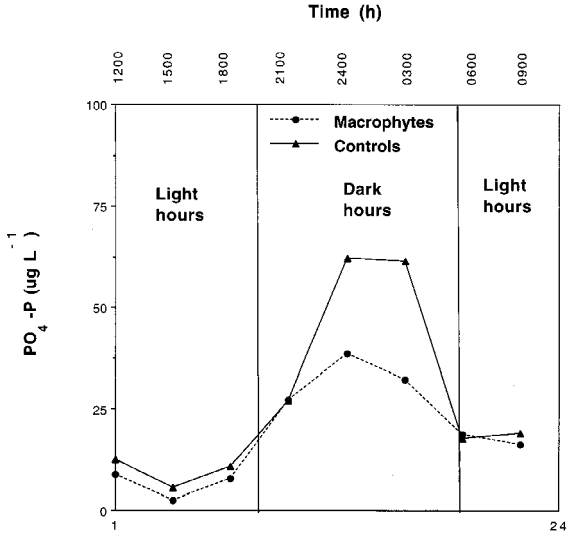

Figure 5. Phosphate measured over a 24 h period in the water column of the macrophyte and control mesocosms at the end (d 36) of the experiment. Approximate light and dark hours are shown.

than did the curves in the macrophyte treatments (Figure 6b). Extensive filamentous algal mats were observed in the controls along with increased metabolic activity at the end of the study. All mesocosms were net autotrophic (GPP/R >1). Compared with the macrophyte treatments, the controls had lower NPP (16.1±4.48 vs. 45.0±3.59 mg O_2 m^{-2} d^{-1}) midway through the experiment, but by the second diel, the controls had much higher values (72.5±5.7 vs. 49.2±3.61 mg O_2 m^{-2} d^{-1}) (Figure 7a), coinciding with increased biomass of filamentous algae later in the study. NPP and NPP/R were constant (d 16 vs. d 36) in the macrophyte treatments, whereas NPP/R increased significantly from the middle to end of the experiment in the controls (Figure 7b).

Discussion

Although this mesocosm study may not reflect the effects of changing variables in the context of other major controls of ecosystem processes, we were able to examine submerged macrophyte effects on some community and system-level processes and propose possible mechanisms for the plant effects. However, we recognize the difficulty in extrapolating measurements from small-scale mesocosm experiments to larger scales in which key controls of ecosystem processes may be different (Carpenter, 1998).

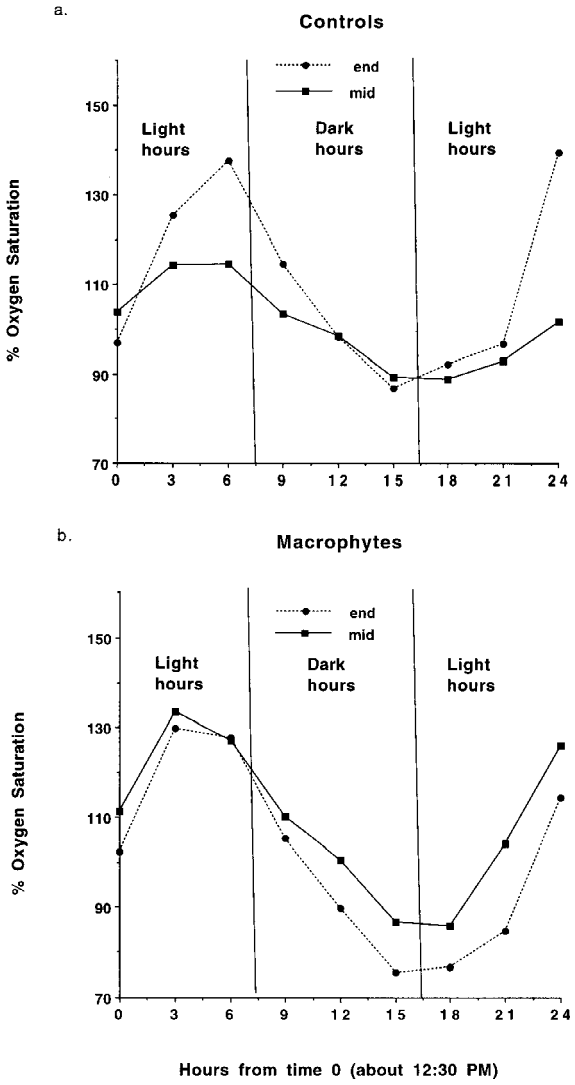

Figure 6. Percent oxygen saturation for diel cycles at the midpoint (d 16) and end (d 36) of the experiment for the (a) controls and (b) macrophyte treatments. Approximate light and dark hours are shown.

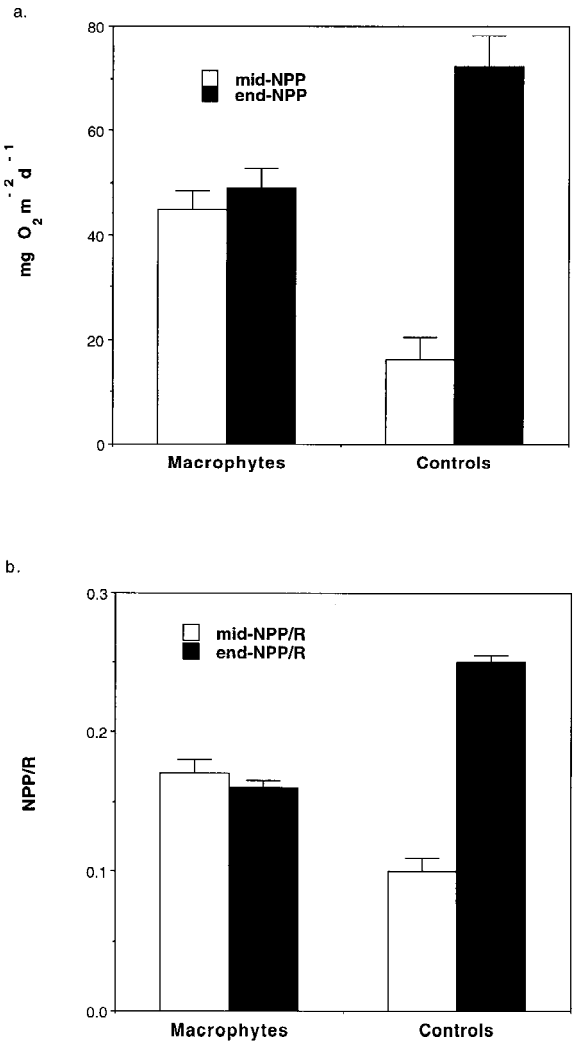

Figure 7. Mid (d 16) and end (d 36) (a) net primary production (NPP) and (b) NPP/Respiration (NPP/R) (for macrophyte and controls, mean±se, n=4).

In the study, modifications of sediment chemistry by the deep-rooted *V. americana* may have lowered the availability of nutrients to the overlying water, and subsequently, changed the water column community structure as shown by the reduced phytoplankton and filamentous algae levels in the macrophyte treatments. *V. americana* significantly lowered sediment porewater iron and PO_4–P, most likely due to metal and nutrient retention in the sediment and phosphorus sequestration into plant biomass (Jaynes & Carpenter, 1977; Carpenter & Adams, 1977; Christensen & Andersen, 1996; Christensen et al., 1997; Wigand et al., 1997). In the macrophyte mesocosms during dark hours, the coincident measurements of higher sediment redox potential and lower dissolved phosphorus in the overlying water as compared with the controls suggests that the plants may have reduced the availability of phosphorus for exchange with the overlying water at night. Furthermore, these results suggest that in the absence of *V. americana*, increased exchange of nutrients with the overlying water fueled the growth of filamentous algae and phytoplankton.

Elevated bacterial production and greater DOC supply were also measured in the absence of *V. americana*. We suggest that the excess phytoplankton and

filamentous algae in the control mesocosms indirectly provided a labile DOC source for bacterial production. In contrast to our results with *V. americana*, in very dense macrophyte beds especially of canopy-forming species, anoxic conditions and large pH swings often promote phosphorus release from sediments (Pokorny et al., 1984; Stephen et al., 1997). Therefore, submerged macrophyte effects on structure and function of systems may in part depend upon differential species effects on sediment chemistry, plant density and grassbed morphology (e.g. canopy-forming versus understory grassbeds).

The modification of sediment chemistry by submerged vegetation may be even more important in oligotrophic systems where plants such as isoetids (e.g. *Lobelia dortmanna*) have an evergreen growth strategy and low biomass turnover throughout the year (Moeller, 1978; Sand-Jensen & Søndergaard, 1978). In contrast, in systems where the plants senesce following summer growth or have high biomass turnover during the growing season, there would be a pulse of nutrients following plant degradation which could stimulate the growth of filamentous algae, DOC, phytoplankton and bacterioplankton (Carpenter, 1980; Lodge et al., 1988; Wehr et al., 1999). In other systems where submerged macrophyte biomass mostly declines in the fall, low nutrient exchange from the sediments during peak macrophyte growth in the summer may decouple the availability of nutrients to non-rooted producers in the overlying water in summer when conditions are otherwise most favorable for primary production. In addition, senescing macrophytes have a lower turnover rate than filamentous algae and phytoplankton (Carpenter & Lodge, 1986; Rissgård et al., 1996). In the absence of submerged macrophytes, decomposing filamentous algae provide major inputs of nitrogen and phosphorus to the sediment and overlying water during the growing season, fueling phytoplankton blooms (Howard-Williams, 1981; Rissgård et al., 1996).

In addition to the primary mechanisms of nutrient sequestration and reduced exchange of nutrients with the overlying water in the mesocosms with macrophytes, we suggest two possible alternative explanations for the reduced phytoplankton and filamentous algal populations in the presence of *V. americana*. One alternative explanation, or at least a possible contributing factor for the low phytoplankton levels in the presence of submerged macrophytes, could be grazing pressure by the elevated zooplankton densities in the mesocosms with macrophytes as has been shown in other studies (e.g. Timms & Moss, 1984). However, zooplankton densities in the mesocosms with submerged macrophytes were variable, and although there was a trend (p=0.07) of increased densities in the presence of macrophytes, there was no significant difference from the controls. A second alternative explanation may be the release of allelopathic compounds by macrophytes which inhibit non-rooted producers (Phillips et al., 1978; Wium-Andersen, 1987). However, *V. americana* is found in oligotrophic to eutrophic systems where the phytoplankton range is quite variable, which suggests that allelopathic compounds are not likely the major cause of the lower phytoplankton levels in the mesocosms with submerged vegetation.

Submerged macrophytes provide many functions in ecosystems, but their effect on above-ground community structure is not well studied and may be critical in maintaining species composition among systems (Jeppesen et al., 1998). Because non-rooted producers (i.e. phytoplankton and filamentous algae) are limited by nutrients in oligotrophic and phosphorus-poor systems, benthic-pelagic nutrient exchange is key to dictating the species composition and stability of plant communities in these systems. Our results suggest that some species of submerged macrophytes may be strong regulators of benthic-pelagic nutrient exchange in mesotrophic and oligotrophic systems. If submerged macrophytes are displaced in an ecosystem (e.g. due to eutrophication), the entire system may shift into an alternate equilibrium (i.e. a high phytoplankton state) quite unlike the clear-water rooted macrophyte system (Scheffer et al., 1993; Riisgård et al., 1996; Scheffer & Jeppesen, 1998). Under turbid water conditions phytoplankton and filamentous algae tend to be dominant. Because of the change in the dominant producers in the perturbed ecosystem there may be key interactions with the biotic and abiotic environment that are also altered which result in system-level changes (e.g. alterations in trophic structure and nutrient status). Along with the loss of submerged macrophytes in a turbid water system is the loss of other organisms (some zooplankton, crustaceans and juvenile fish) that rely on macrophytes for habitat and as a refuge.

Submerged vegetation is often light-limited in systems dominated by phytoplankton and filamentous algae due to shading effects. Therefore, to promote a clear-water state not only do nutrients in the overlying water need to be reduced, but the phytoplankton and filamentous algae need to be reduced. Water manage-

ment agencies have to consider both the stressor (i.e. elevated nutrients) and the plant community structure of the resulting system to restore perturbed aquatic systems (Scheffer et al., 1993; Scheffer & Jeppesen, 1998). It is because of these alternative equilibrium states that researchers and managers use biomanipulation to restore disturbed aquatic grassbeds (Scheffer et al., 1993). Two mechanisms reported to maintain or restore grassbeds are grazing of phytoplankton by a successful zooplankton population (Timms & Moss, 1984) and the lowering of the water surface to increase light penetration to submerged macrophytes (Blindow, 1992).

Conclusions

In the absence of *V. americana*, there were high levels of phytoplankton and filamentous algae and large changes in productivity and pH from the start to the end of the experiment. In contrast, in the presence of *V. americana*, we did not observe large fluctuations in the structure or function of the system.

Sustained vigor of aquatic communities is typically dependent upon the balance between nutrient losses, gains and availability which in sum are determined by species composition (Barko et al., 1991). *V. americana* clearly can alter benthic-pelagic coupling and nutrient availability both indirectly (modifying sediment redox status) and directly (nutrient sequestration). Often these biotic-abiotic couplings are difficult to unravel in the field because they are masked by other interactions and overlooked. Many studies examine environmental effects on plants, but to understand ecosystem processes it is also necessary to study the effect of plants on the function and structure of systems (Carpenter & Lodge, 1986). In order to describe function and community structure in ecosystems, it is necessary to identify key biotic-abiotic interactions as well as trophic cascades that define the system.

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