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Scaling of nutrient inputs to submersed plant communities: temporal and spatial variations

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ABSTRACT: Experiments were designed to test the hypothesis that the response of a submersed plant community will differ with varying form, mode and timing of nutrient delivery. Two separate experiments were conducted in summer-fall 1993 and spring-summer 1994; each ran for a period of 12 wk. Dissolved and particulate forms of nutrient additions were made to 10 l microcosms containing a submersed vascular plant species (*Potamogeton perfoliatus* L.) formally abundant in brackish waters of the Chesapeake Bay, USA. Nutrients in the pulse treatments were added to each of 4 replicate chambers weekly in fall and bi-weekly in spring, while continuous inputs were administered via a peristaltic pump. Additions were made at a moderate loading rate of 38 µmol N $l^{-1}d^{-1}$ in both spring-summer and summer-fall experiments, and at a high loading rate of 5 times higher in spring-summer. Phosphorus was added to result in a 10:1 atomic N:P ratio. Results from the experiments involving moderate enrichment with dissolved nutrients indicate that water column concentrations remained low (1 to 2 µmol), while enrichment at the high levels exhibited an increase in concentrations over controls. Plant growth and biomass decreased with both moderate and high dissolved nutrient treatments, while morphological parameters also indicated plant stress. Algal concentrations, particularly epiphytes, increased with experimental treatment. Both plant and microalgal C:N ratios decreased with nutrient enrichment. In summer-fall, particulate organic nutrient (PON) enrichment at moderate levels resulted in a stimulation of plant growth in comparison to control. In spring-summer, PON enrichment resulted in initial stimulation of growth, followed by a decline. Total ecosystem production (P_a) and respiration (R_n) increased in experimental chambers. A nitrogen budget indicates a redirection of nutrients from plant biomass to algal biomass in the nutrient enriched systems. A seasonal comparison is made between the results from the summer-fall and spring-summer experiments. The relationship between water quality parameters in experimental chambers and established submersed plant habitat criteria is discussed.

KEY WORDS: Submersed aquatic vegetation · Mesocosms · Nutrient enrichment

INTRODUCTION

Over the last several decades, there have been numerous reports of declines in submerged aquatic vegetation (SAV) abundance worldwide (e.g. den Hartog & Polderman 1975, Orth & Moore 1983, Silberstein et al. 1986). Many of these losses have been attributed to eutrophication effects which cause the reduction of photosynthetically active radiation (PAR) by increases of suspended sediments and increased growth of microalgal communities (Phillips et al. 1978, Kemp et al. 1983, Twilley et al. 1985, Cambridge et al. 1986, Sand-Jensen & Borum 1991, Duarte 1995, Pedersen 1995). Although other mechanisms, such as inhibition of bicarbonate uptake (Sand-Jensen 1977) and nitrate toxicity (Burkholder et al. 1992, 1994), may also contribute to the overall stress to rooted macrophytes, the reduction of light availability seems to be the dominant factor (Sand-Jensen & Søndergaard 1981, Twilley et al. 1985, Duarte 1991, Sand-Jensen & Borum 1991).

Nutrients enter coastal habitats of submersed plants from several sources, in different chemical forms (e.g. dissolved vs particulate) and at varying frequencies of delivery. Important nutrient sources to estuaries include: runoff and direct groundwater flow from agri-

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cultural lands, sewage and industrial effluents, and atmospheric deposition. In addition, if concentration gradients are favorable, nutrients may be transported to shallow seagrass sites from adjacent deeper waters via tidal or wind-forced exchange (Sanford & Boicourt 1990). Predominant modes of input may be via periodic pulses (as with rainfall or runoff events and spring tidal exchanges) or more continual fluxes (e.g. direct groundwater flow, sewage discharge) depending on local conditions (Moore et al. 1995). Tidal exchanges may be more important in delivering nutrients as particulate organic matter, which are deposited on the sediment surface (e.g. Ward et al. 1984). Nutrients delivered in groundwater flow will be almost exclusively in dissolved inorganic forms. Hence, patterns of nutrient loading to submersed plant communities may vary markedly with local conditions. Such differences in the form and frequency of nutrient delivery may explain some of the observed spatial and temporal variability in SAV in large coastal ecosystems such as the Chesapeake Bay, USA (Stevenson & Confer 1978, Kemp et al. 1983, Orth & Moore 1983).

Seasonality in the growth cycle of the mesohaline submersed estuarine vascular plants, such as *Potamogeton perfoliatus* L., may render them particularly susceptible to nutrient loading cycles observed in the Chesapeake Bay. Bay water concentrations of nutrients are generally higher early in spring, decline moderately in summer and may become elevated again in fall (Kemp et al. 1983). During the spring, growth of *P. perfoliatus* begins from over-wintering tubers. As photosynthetic tissue develops, growth rate is maximal to allow the plant to reach the water surface and form a canopy (Stevenson & Confer 1978). As the plant biomass accumulation slows, healthy and low stressed plants send up sexual reproductive parts (Van Wijk 1989). As summer gives way to fall and temperatures and daylength decline, these macrophytes begin senescence, storing reserves in the below-ground tubers. Stressed plants (i.e. as a result of eutrophication) do not have the surplus energy necessary to produce reproductive tissues to store reserves for spring regrowth, as these materials are required for normal maintenance (Goldsborough & Kemp 1988). Thus, seasonal variability in nutrient concentrations in Bay waters may have differing effects on *P. perfoliatus* growth, reproduction and survival.

In the Chesapeake Bay, historically known for high productivity of commercially desirable finfish and shellfish, rooted macrophyte communities were an important food and refuge area (Lubbers et al. 1990). In recent years abundance of these plants has declined drastically (Orth & Moore 1992). Losses of SAV have been attributed to increased nutrient loading to Bay waters (Kemp et al. 1983). Concerns over reduction in these plant habitats and associated fisheries have led to the establishment of SAV habitat requirements considered important for plant community restoration (Batiuk et al. 1992, Dennison et al. 1993, Stevenson et al. 1993). Habitat criteria for waters of the Chesapeake Bay define maximum concentrations of suspended materials (solids and phytoplankton) and inorganic nutrients in the water column which still allow rooted macrophyte growth, reproduction, and survival of SAV. Although the habitat criteria are based on water column concentrations, many experiments defining the relationship between nutrient enrichment and SAV response have used loading rates as the basis for additions. A clear relationship between loading rates, water column nutrient concentrations, water exchange rates and SAV 'health' has not been established.

In this paper we examine the response of the submersed plant *Potamogeton perfoliatus* and its associated algal community to variations in the form and frequency of nutrient additions at moderate levels during initial plant growth (spring), continuing through the maximal growth period (summer), and ending with the plant senescence period (fall). Additionally, experiments involving higher nutrient loading rates were also conducted during spring-summer, bringing water column nutrient concentrations to those established as maximum acceptable levels for SAV growth and survival (Dennison et al. 1993, Stevenson et al. 1993).

METHODS

Experimental design. Two separate experiments were conducted in the greenhouse facilities at the University of Maryland's Horn Point Environmental Laboratories, Cambridge, Maryland, USA. The first, referred to as summer-fall experiments, were conducted from August 2 to November 3, 1993; the second, referred to as spring-summer, were conducted from May 2 to July 24, 1994. Plastic pots (15 cm diameter × 15.2 cm height) containing 15 cm of sediment with an organic content of 2.3% in summer-fall and 3.68% in spring-summer, collected from a vegetated area of the Choptank River, Maryland, were placed into clear acrylic microcosms (15.2 × 15.2 cm base × 61 cm height) containing 10 l of water. Microcosms (1 of each treatment) were randomly placed into large (1 m^3) tanks filled with flow-through Choptank River water to maintain microcosm temperature within 2°C of ambient river water temperature. Chambers received low nutrient Choptank River water (1 to 2 µM N d^{-1}) at a turnover rate of 7 d in summer-fall experiments and 3.5 d in spring-summer experiments.

Physical parameters were monitored throughout the experimental period and compared to the external environment (Choptank River). Salinity and temperature were monitored weekly using a refractometer (Reichert, Model 10419) and an immersion thermometer, respectively. PAR measurements were taken bi-weekly using a LiCor (Model 100-32) irradiance meter with a 4-pi sensor (Model 193 SA). Wall growth of periphytic material was cleaned weekly with all loose material remaining inside the chambers.

Nutrient loading and analysis. The experimental design consisted of 4 replicates of a control and of nutrient enrichment treatments. In summer-fall experiments treatments included 1 level of medium enrichment delivered in both a pulse and continuous inflow mode. In separate spring-summer experiments, 2 levels of enrichment (medium and high) were administered under pulse and continuous mode. Two forms of nutrients were included: dissolved inorganic nutrients (DIN; note that in this paper we use DIN to mean dissolved inorganic nutrients, not nitrogen) and particulate organic nutrients (PON). Pulse nutrient additions (DIN and PON) were injected weekly in summer-fall and bi-weekly in spring-summer experiments, while continuous inputs (DIN) were made using a peristaltic pump. PON was administered at medium loading rate in summer-fall and high loading rates only in spring-summer. Each of the medium enriched treatments received a loading rate of 38 $\mu M\ N\ l^{-1}\ d^{-1}$ (regardless of the mode of delivery), while high treatments received nutrients at a loading rate of 190 $\mu M\ N\ l^{-1}\ d^{-1}$. PO_4 was added in a 10:1 atomic ratio of nitrogen to phosphorus for all treatments.

The DIN additions were made using analytical grade ammonium nitrate (NH_4NO_3) and sodium phosphate (NaH_2PO_4). The PON addition was administered by using heat killed slurries of *Chlorella* spp. A culture of *Chlorella* spp. was centrifuged to remove excess water and stored in a dark, air tight tube at 2°C. A sample of the pellet was analyzed for nitrogen content and the results were used to adjust the loading rate of PON additions (to 38 $\mu mol\ N\ l^{-1}\ d^{-1}$). Appropriate portions of the pellet were dispersed into 40 ml of filtered river water (Whatman GF/F filter, 0.7 µm). The resultant solution was then heated to 40°C for a period of 4 min to kill but not lyse the algal cells (T. Kana pers. comm.).

Water column nutrient concentrations were measured on a weekly basis in all microcosms, and these data were calculated into 3 wk averages. Frozen samples were analyzed for NH_4, NO_3-NO_2, and PO_4 using a Techton AutoAnalyzer II within 30 d of original sampling date.

Plant measurement techniques. *Potamogeton perfoliatus* rhizome segments were obtained from a nearby system of experimental ponds (Twilley et al. 1985, Neundorfer & Kemp 1993). Twelve randomly selected rhizome-shoot segments were planted into the potted sediments to a depth of 2 cm and labeled. Pots were placed into acrylic chambers for a period of 15 d before initiation of nutrient treatments. Plants were measured weekly for stem elongation, leaf number and internodal length. Growth rates were computed utilizing the previous week's measurement and normalized to growth per day for the experimental period.

At the conclusion of each experiment, above-ground portions of the macrophytes were scraped free of epiphytic material, rinsed in de-ionized water, measured for total leaf area (LiCor Model 3100) and dried to a constant weight at 60°C. Ground plant material (Wiley mill with 20 mm screen) was analyzed for carbon and nitrogen content using a Perkin-Elmer CHN analyzer. Below-ground tissue was rinsed free of sediments and analyzed as for above-ground biomass and tissue nutrient concentrations.

Algal measurements. Epiphytic biomass on the macrophyte leaves was examined bi-weekly by chlorophyll *a* (chl *a*) analysis and by mass. Plant leaves (fourth leaf from top of the plant; n = 5) were taken from each chamber and epiphytic material scraped into filtered river water (1.2 µm). Resultant algal slurry was filtered onto pre-ashed, weighed filters, and stored at 0°C until analysis. Chl *a* was extracted in acetone and concentrations were determined using a Turner (Model 111) flourometer that had been calibrated against a Cary (Model 219) spectrophotometer (Strickland & Parsons 1972). All chl *a* values were corrected for degradation products. Scraped plant leaves were measured for leaf area on a LiCor Leaf Area Meter (Model 3100) and epiphyte concentrations normalized to leaf area. Nutrient content (C and N) for epiphytic material was determined from material collected, dried to a constant weight and analyzed in the same manner as macrophyte tissue.

Phytoplankton biomass was measured as chl *a*. Samples were collected onto a filter (Whatman GF/F) and stored at 0°C. Chlorophyll *a* analysis followed the same procedure as for epiphytic material described above. Carbon and nitrogen values for phytoplankton were calculated from chlorophyll *a* numbers using a carbon: chlorophyll ratio of 54 µg C:1 µg chl *a* (Salisbury & Ross 1985) and a C:N ratio of 6.6:1 (Redfield et al. 1963). Macroalgal components of each individual microcosm were processed in the same manner as the macrophyte biomass and analyzed for tissue nutrient concentration.

Representative sediments were characterized at the beginning and end of the treatment period for organic content, porewater nutrient concentration, and percent composition of carbon, hydrogen, and nitrogen. Samples were dried, combusted in a muffle furnace and percent organic material determined by difference.

Porewater nutrient concentrations (NH_4, NO_3-NO_2, and PO_4) were determined as described for water column nutrient analysis. Dried sediment samples were ground and percent compositions of C, H, and N were determined using a Perkin-Elmer CHN analyzer

Community metabolism. At the beginning, middle and end of the experimental period, apparent production (P_a) and night respiration (R_n) of the integrated experimental ecosystems were estimated from diel oxygen measurements using a polagraphic electrode (Model 2607, Orbisphere Laboratories, Geneva). During the night previous to the diel period of measurements, the mixing air stones were turned off. Measurements were made at a depth of 0.3 m, beginning at sunrise and continuing every 2 h until sunrise of the next morning. Production rates were calculated as the difference in oxygen concentrations during the daylight hours and the respiration as the differences during the dark hours. Rates were adjusted for diffusion (Fick's equation) after corrections for salinity and temperature based on coefficients from Pijanowski (1973) and McKellar (1975).

Statistical analysis. Data transformations were kept to a minimum and restricted to common area units for ease of comparison with previous studies. All data was tested for normality and homogeneity of variances in order to apply the appropriate statistical analyses. One-way ANOVA (analysis of variance) tests are reported at the $p < 0.05$ confidence interval unless stated otherwise.

RESULTS

Physical parameters

Temperature and salinity closely tracked conditions of the Choptank River estuary. In the summer-fall experiments, temperatures declined over the experimental period from a high in August of 28.6°C to a low of 21.1°C in late October and salinities ranged from 14.3 to 15.4‰. Diffuse downwelling PAR coefficients (K_d), calculated from surface and top of canopy measurements, remained relatively constant throughout the period in all chambers (K_d = 1.05), except in the continuous DIN treatments, in which they were considerably higher than in other treatments (K_d = 1.29).

In the spring-summer experiments, temperatures within experimental chambers increased as expected

Table 1. Water column nutrient concentrations (µM) during the experiments summarized over 3 wk time periods (mean ± SE, n = 4). Superscript letters show significant differences from indicated treatments as follows: [b]control, [c]DIN pulse medium, [d]DIN continuous medium, [e]DIN continuous high, [f]DIN pulse high, [g]PON pulse; $p < 0.05$, ANOVA

Treatment	Weeks 1 to 3		Weeks 4 to 6		Weeks 7 to 9		Weeks 10 to 12	
	DIN	PO_4	DIN	PO_4	DIN	PO_4	DIN	PO_4
A. Summer-fall								
Control	1.22 ±0.12	0.13 ±0.01	1.04 ±0.09	0.06 ±0.01	0.57 ±0.08	0.04 ±0.01	1.22 ±0.17	0.05 ±0.01
DIN pulse	1.12 ±0.11	0.13 ±0.08	1.35 ±0.17	0.12[bc] ±0.02	1.12 ±0.07	0.13 ±0.15	1.38 ±0.18	0.40[bc] ±0.20
DIN continuous	1.38 ±0.10	0.31[bcd] ±0.10	1.71 ±0.13	0.14[bc] ±0.02	1.06 ±0.08	0.69[bcd] ±0.23	1.63 ±0.17	0.80[bcd] ±0.24
PON pulse	0.98 ±0.15	0.05 ±0.09	1.01 ±0.09	0.07 ±0.01	0.98 ±0.09	0.05 ±0.01	1.27 ±0.22	0.66 ±0.02
B. Spring-summer								
Control	1.99 ±0.18	0.07 ±0.01	2.73 ±0.67	0.07 ±0.02	2.97 ±0.58	0.16 ±0.04	1.82 ±0.46	0.14 ±0.02
Medium DIN								
Pulse	6.96[bdg] ±0.50	1.81[bdg] ±0.13	7.23[bdg] ±0.97	1.62[bdg] ±0.13	6.06[bd] ±0.71	1.83[bdg] ±0.19	9.82[bd] ±1.09	1.75[bdg] ±0.14
Continuous	3.30[bg] ±0.17	0.98[bg] ±0.09	3.47[g] ±0.47	0.94[bg] ±0.13	3.73 ±0.55	0.57 ±0.57	3.13[b] ±0.46	0.48[bg] ±0.09
High DIN								
Pulse	33.93[bcdeg] ±2.58	5.05[bcdg] ±0.45	53.88[bcdeg] ±6.47	7.94[bcdg] ±0.98	77.06[bcdeg] ±5.39	13.85[bcdeg] ±1.04	47.48[bcdg] ±5.65	20.28[bcdeg] ±1.08
Continuous	15.76[bcdg] ±0.83	4.89[bcdg] ±0.46	18.17[bcdg] ±1.02	6.66[bcdg] ±0.94	25.34[bcdg] ±1.55	11.17[bcdg] ±0.66	49.92[bcdg] ±3.35	11.05[bcdg] ±0.74
PON pulse	1.56 ±0.14	0.09 ±0.02	2.45 ±0.17	0.15[b] ±0.06	6.10[bd] ±1.35	0.25 ±0.06	11.33[bd] ±1.02	0.18 ±0.02

during the treatment period from 19.3°C to a high of 27.9°C at the conclusion of the experiment. Salinities ranged from 7.1 to 13.6‰. Attenuation coefficients in the high DIN treatments (pulse K_d = 1.10 and continuous K_d = 1.08) were significantly elevated over other chambers (K_d = 1.06) during the final 3 wk time period. Ambient light was not considered limiting and ranged from 400 to 530 µE m^{-2} s^{-1} in the experimental chambers during both experiments.

Nutrient concentrations

Weekly measurements of nutrient concentrations within the experimental chambers are reported in Table 1. In the summer-fall experiments, nitrogen concentrations in all enriched treatments were comparable to concentrations found in the control chambers (Table 1A). Phosphate concentrations were elevated in both pulse and continuous DIN chambers beginning during Weeks 4 to 6 of the experiment compared to PON and controls. Nitrogen concentrations in the spring-summer experiments were slightly elevated above control levels in the medium enriched chambers (Table 1B), but still remained below 10 µM. Nutrient concentrations in high DIN treatments were significantly higher than those found in the other experimental treatments with total nitrogen values exceeding 50 µM. In the high nutrient PON pulse chambers nitrogen concentrations were elevated only during the final weeks of the experiment. Phosphate concentrations were generally high in the DIN treatments in comparison to the control and PON treatments.

Sediment porewater nutrient concentrations declined from initial values for all treatments in both summer-fall and spring-summer experiments (Table 2). Control chamber porewater concentrations were lower than those found in any of the enriched treatments. This enhancement of sediment porewater nutrients was most evident in the PON treatment, where concentrations at the end of the experimental period were much higher than controls.

Plant responses

Plant growth rates exhibited varying patterns in experimental treatments conducted in summer-fall (Fig 1A). Additions of DIN significantly increased plant growth rates over control and PON treatments during the first 3 wk. Growth in all chambers began to decline after the fourth week and continued to do so for the remainder of the experiment.

In the spring-summer experiments, plant growth rates were similar across all treatments during the initial 3 wk period (Fig. 1B, C). In the medium treatments, plant growth in chambers receiving pulse DIN nutrients declined more rapidly than in those receiving continuous inputs of nutrients. During the final weeks of the experimental period, both medium DIN enriched treatments exhibited significantly lower growth rates than in the control treatments. Plant growth rates in the high enrichment chambers followed the same pattern. However, growth declined more rapidly than in the medium enrichment chambers, especially in DIN pulse treatments, where all plants were dead at the end of the experiment. Plants in the PON pulse treatment had higher growth rates than all other chambers during Weeks 4 to 6, but dropped dramatically in the final 3 wk of the experiment. Positive growth was only found in the control microcosms for the entire time span of the experiment.

Other indicators of plant response suggest that the angiosperms in the enriched treatments were stressed. Above- and below-ground biomasses were significantly lower in DIN enriched systems during both experimental periods compared to controls (Table 3), resulting in reduced root:shoot ratios, which hampers the ability of the plants to reproduce vegetatively. The

Table 2. Porewater nutrient concentrations (µM) at the beginning and end of the experimental period for the summer-fall and spring-summer experiments (mean ± SE, n = 4). Superscript letters as in Table 1; $p < 0.05$, ANOVA

Treatment	Initial		Final	
	DIN	PO_4	DIN	PO_4
A. Summer-fall				
Control	108 ±2.8	10 ±1.4	47.8 ±2.7	2.6 ±0.4
DIN Pulse	105 ±2.5	9.2 ±1.3	62.8^{b} ±4.4	3.2 ±0.5
DIN Continuous	110 ±2.9	8.8 ±1.4	65.3^{b} ±3.5	3.7 ±0.8
PON Pulse	103 ±2.9	9.4 ±1.1	118^{bcd} ±10.6	4.8^{bd} ±0.7
B. Spring-summer				
Control	454 ±18.1	34.3 ± 2.3	279 ±16.3	18.5 ±1.9
Medium DIN				
Pulse	468 ±15.4	31.9 ±2.7	380 ±21.9	27.3^{b} ±1.8
Continuous	446 ±10.3	35.8 ±1.9	385 ±10.6	28.7^{b} ±1.2
High DIN				
Pulse	447 ±11.8	32.4 ±2.8	395 ±14.2	27.9^{b} ±2.0
Continuous	459 ±14.8	33.5 ±2.4	389 ±15.2	28.7^{b} ±1.6
PON pulse	451 ±12.9	33.9 ±2.1	422^{bcdf} ±29.1	29.7^{b} ±2.4

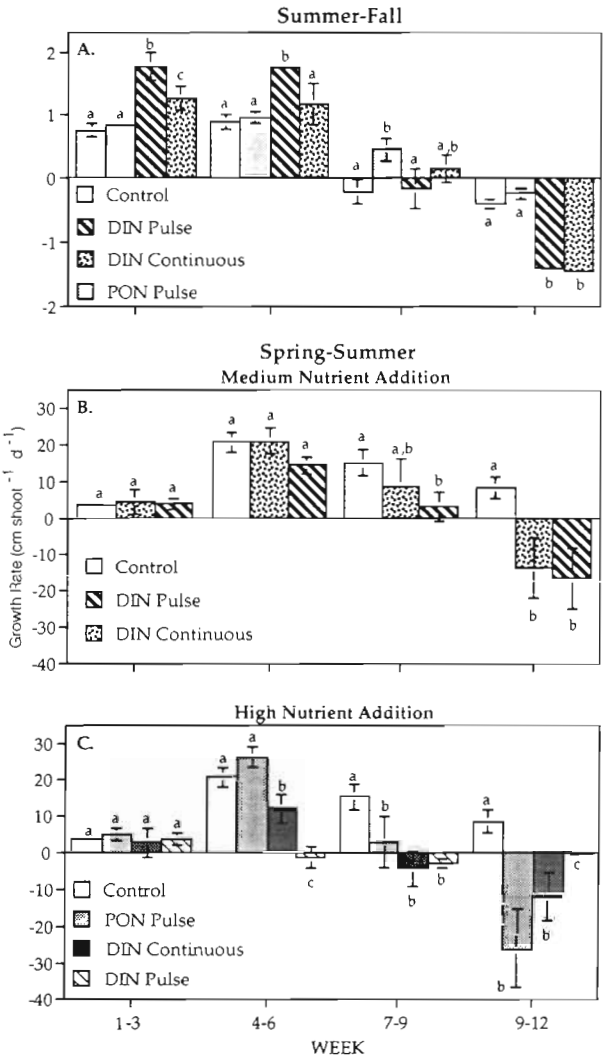

Fig. 1. *Potamogeton perfoliatus*. Growth response to medium and high nutrient treatments summarized over 3 wk periods for (A) summer-fall, (B) spring-summer medium, and (C) spring-summer high enrichment. Relative growth rate is expressed as means ± SE (n = 4) of shoot elongation. Treatment values within the same period sharing the same letter are not significantly different from each other

largest deviation from this parameter was found in the high DIN pulse chambers in spring-summer experiments; there was no below-ground tissue (Table 3B). Enrichment with medium PON resulted in elevated biomass; high levels of PON significantly decreased biomass in spring-summer. Plants in DIN enriched chambers in spring-summer experiments also had lower leaf densities; in summer-fall experiments, this phenomena only occurred in continuous chambers. Leaf 'thinning' has been attributed to plant stress as a result of reduced light conditions (Goldsborough & Kemp 1988).

Algal response

Microalgal responses (phytoplankton and epiphyte) to nutrient enrichment are depicted in Fig 2. In summer-fall experiments, phytoplankton levels in all treatments, except the DIN continuous, remained low and ranged from 0.5 to 14.3 µg l^{-1} (Fig. 2A). For the first 4 wk, levels in the DIN continuous chambers were relatively low, then exhibiting a steady increase to concentrations of over 170 µg l^{-1} at the end of the experimental period. Epiphytic chl *a* concentrations cm^{-2} leaf area was higher in both DIN treatments at the end of the summer-fall experiment when compared to controls, but followed different patterns with mode of nutrient addition (Fig. 2B); it increased earlier (Weeks 2 to 4) in DIN continuous treatments and reached an 'equilibrium' state by mid-experiment. Epiphytic chl *a* concentrations cm^{-2} leaf area in the PON treatments tracked controls.

In spring-summer experiments, phytoplankton chl *a* levels in medium enrichment treatments remained low and ranged from 0.5 to 9 µg l^{-1} throughout the experimental period (Fig. 2C). During the first 5 wk the values for the 2 high DIN treatments tracked those found in other treatments (Fig. 2E). By Week 7, chl *a* values were above 15 µg l^{-1} and increased steadily, particularly in the pulsed mode of nutrient addition. Epiphytic algae demonstrated a strong response to both medium (Fig. 2D) and high (Fig. 2F) nutrient additions at the onset. Levels in high enrichment chambers were significantly higher than medium treatments by Week 4, with pulse input chambers significantly higher than continuous (note: epiphyte values in high DIN pulse treatments were derived from material scraped from dead plant material). The PON pulse nutrient addition treatment stimulated growth of epiphytic algae during the sixth week of the experiment, and exhibited growth intermediate to medium and high enrichment chambers.

Macroalgal biomass increased (in comparison to controls) in all treatments with nutrient additions, but varied somewhat with level of nutrient addition (Table 4). The strongest positive relationship to nutrient additions was exhibited in summer-fall experiments within the DIN continuous chambers. In spring-summer experiments, the high DIN pulse chambers had significantly higher biomass when compared to both medium treatments and PON pulse chambers.

C:N ratios

Carbon to nitrogen ratios were calculated for the autotrophic components from percent concentrations within the tissues. Vascular plant C:N ratios were sig-

Table 3. *Potamogeton perfoliatus*. Morphological parameters in control and nutrient enriched treatments at experimental completion (mean) ± SE, n = 4). Superscript letters as in Table 1; $p < 0.05$, ANOVA

Treatment	Biomass (g dry wt m^{-2}) Above-ground	Below-ground	Mean shoot length (cm)	No. of leaves m^{-2}	C:N ratio
A. Summer-fall					
Control	34.3 ±9.2	111.6 ±12.2	7.05 ±0.85	8.559 ±2.241	19.99 ±0.37
DIN pulse	34.2 ±6.1	49.6^{bg} ±9.7	7.66 ±0.79	10.000^{d} ±1.324	10.97^{bdg} ±0.77
DIN continuous	10.9^{bc} ±5.2	21.2^{bcg} ±8.8	8.73^{g} ±0.91	4.880^{bcg} ±1.671	15.47^{bcg} ±0.67
PON pulse	54.6^{bcd} ±9.2	131.4 ±12.3	6.64 ±0.49	17.861^{bcd} ±3.843	19.65 ±1.58
B. Spring-summer					
Control	168.4 ±20.5	59.7 ±9.9	25.9 ±1.6	47.137 ±6.212	14.20 ±0.93
Medium DIN					
Pulse	37.5^{b} ±15.1	13.4^{bg} ±5.7	23.4 ±0.9	12.343^{b} ±6.158	10.09^{b} ±0.16
Continuous	86.5^{b} ±51.3	23.6^{b} ±14.2	28.6 ±5.3	13.900^{b} ±7.162	11.26^{bc} ±0.55
High DIN					
Pulse			No biomass		
Continuous	13.0^{bcdg} ±6.3	3.5^{bcdg} ±1.9	18.7^{bdg} ±3.6	4.421^{bdg} ±1.864	8.86^{d} ±0.34
PON pulse	46.7^{b} ±10.2	27.1^{b} ±6.7	24.3 ±2.4	23.767^{b} ±6.158	9.85^{bf} ±0.63

Table 4. Biomass organic content, and carbon to nitrogen (C:N) ratios of sediments and attached algae in mesocosms within treatments at the end of the experiment (means ± SE, n = 4). Superscript letters as in Table 1; $p < 0.05$, ANOVA. See text for phytoplankton C:N ratios and Fig. 3 for biomass values

Treatment	Sediment % Organic	C:N	Macroalgae Biomass (m^{-2})	C:N	Epiphytes Chl *a* conc. (µg cm^{-2})	C:N
A. Summer-fall						
Control	1.15 ±0.08	7.01 ±0.22			0.49 ±0.07	7.18 ±0.37
DIN pulse	1.63^{bd} ±0.07	7.54 ±0.48	64.7 ±23.3	20.17^{c} ±0.60	3.49^{bc} ±0.10	6.46 ±0.19
DIN continuous	2.63^{b} ±0.07	7.20 ±0.17	238.7^{cd} ±84.9	21.81^{c} ±0.68	3.81^{bcd} ±0.08	6.89 ±0.15
PON pulse	1.76^{bd} ±0.10	7.63 ±0.49	62.6 ±53.1	23.30 ±0.40	0.53 ±0.07	7.33 ±0.27
B. Spring-summer						
Control	3.33 ±0.13	9.23 ±0.74	4.2 ±2.1	24.58 ±0.59	0.51 ±0.32	9.70 ±0.93
Medium DIN						
Pulse	3.37 ±0.21	7.84^{b} ±0.36	23.3^{b} ±12.5	19.78^{b} ±0.95	4.50^{bde} ±0.25	8.40 ±0.40
Continuous	3.41 ±0.04	8.04^{b} ±0.20	13.8^{b} ±7.4	20.01^{b} ±0.74	2.38^{b} ±0.17	7.49^{bc} ±0.42
High DIN						
Pulse	3.53 ±0.25	9.33 ±0.65	29.7^{bcdeg} ±6.4	19.32^{b} ±0.47	5.49^{bcde} ±0.18	8.13 ±0.84
Continuous	3.27 ±0.04	9.46 ±0.66	32.9^{bcde} ±20.2	19.47^{b} ±0.83	4.69^{bdef} ±0.23	7.48^{bc} ±0.50
PON pulse	3.34 ±0.04	9.17 ±1.02	9.5^{f} ±4.2	20.85^{b} ±0.59	3.09^{bc} ±0.43	6.59^{bcd} ±0.22

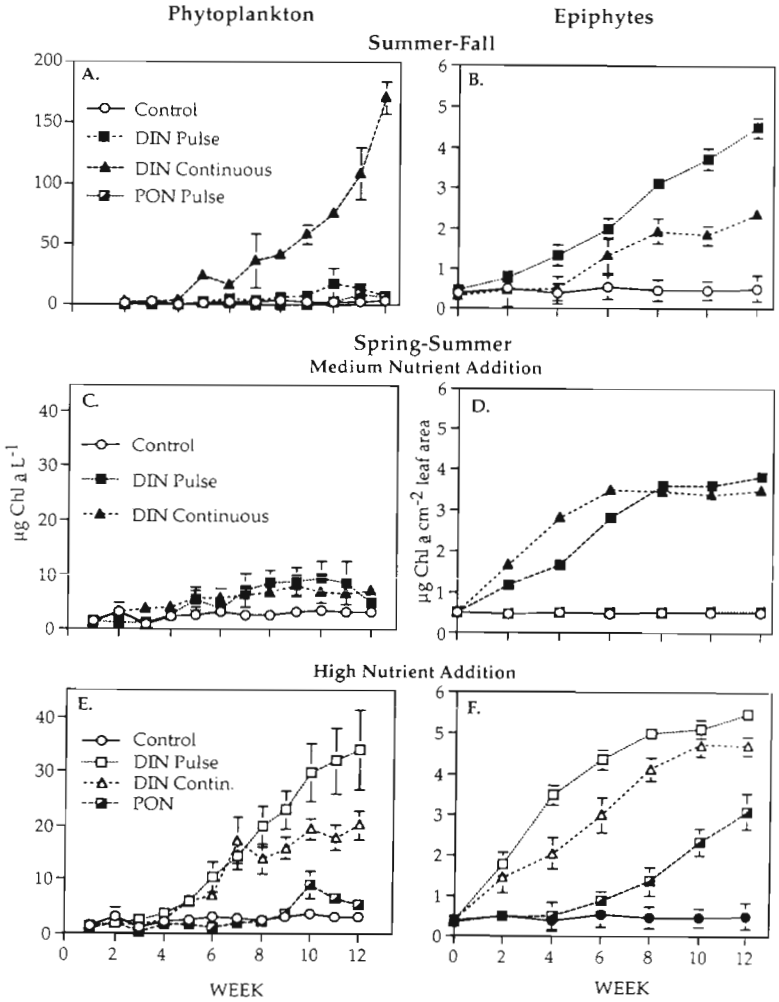

Fig. 2. Response of (A, C, E) phytoplankton and (B, D, F) epiphytic algae to medium (summer-fall) and medium and high (spring-summer) nutrient treatments. Response is plotted as mean (± SE, n = 4) chl *a*

nificantly lower than the control values in all DIN enrichment chambers (Table 3). (No ratio is reported for spring-summer DIN pulse high treatment due to lack of plant material for analysis). Under medium PON enrichment (summer-fall) C:N ratios were not significantly different from control (Table 3A), while high PON pulse treatments (spring) resulted in ratios intermediate between medium and high DIN enrichment chambers (Table 3B).

Spring-summer macroalgae C:N ratios were significantly lower in all enriched chambers in comparison to control chambers (Table 4). Epiphytic algae C:N ratios were significantly lower than the control values in the 2 continuously delivered nutrient additions and the PON pulse treatment in spring-summer experiments. Ratios for phytoplankton were calculated from literature values (see 'Methods: Algal treatments' section), resulting in a 6.7:1 ratio for all treatments.

Nitrogen budget

A nitrogen budget (based on biomass and percent nitrogen in tissues) was constructed for the experimental chambers to indicate the relative distribution of nitrogen within the autotrophic components of the SAV community (Fig. 3). In the control chambers, the majority of nitrogen is contained within the macrophytes, with all other algal components making up only 2% (summer-fall, Fig. 3A) to 8% (spring-summer, Fig 3B) of the total. In the summer-fall experiments, total nitrogen concentrations in medium PON treatments were higher than in the control treatment in both *Potamogeton perfoliatus* and algal components. However, the algal components contributed relatively more (22%) to total nitrogen biomass than in controls. In DIN chambers, the algal components were more important, comprising 40% in the DIN pulse and 80% in the DIN continuous nutrient treatments. A similar pattern was found in the DIN continuous medium chambers in the spring-summer experiments, where microalgae (especially epiphytic algae) dominated the nitrogen distribution. High levels of PON (spring-summer), resulted in a nitrogen distribution similar to medium DIN enrichment.

Community metabolism

Apparent production (P_a) and night respiration (R_n) is reported in Table 5. DIN nutrient enrichment increased production and respiration by the middle of the experimental period in both the summer-fall and spring-summer experiments. In summer-fall experiments, respiration values in continuous input chambers were significantly higher than pulse input chambers by the end of the experimental period. In spring-summer experiments, the medium DIN enrichment showed no difference in P_a and R_n with frequency of delivery. High DIN enrichment increased P_a and R_n values above those of medium and PON high treatments. PON enrichment at both medium and high levels increased P_a and R_n only by the end of the experimental period, suggesting a delay in the response of these parameters to treatment (e.g. Borum & Sand-Jensen 1996).

DISCUSSION

Response of submersed plant communities to nutrient enrichment has been reported and discussed in detail previously for a wide range of experimental studies using various plant species (Phillips et al. 1978, Kemp et al. 1983, Staver 1983, Borum 1985, Twilley et al. 1985, Cambridge et al. 1986, Neckles et al. 1993, Pedersen 1995, Short et al. 1995, Taylor et al. 1995, Pedersen & Borum 1996). Results from these experiments follow the same general pattern: decline in vascular plant growth and biomass and increase in algal abundance with nutrient enrichment. In turn, this causes a shift in dominant autotrophic component from vascular plant to algae (Duarte 1995, Short et al. 1995).

Results from the community metabolism monitoring underscored the shift in autotrophic dominance. A time series analysis indicated little change in apparent production (P_a) and respiration (R_n) in control chambers throughout both experimental periods, but an increase in both P_a and R_n in DIN enriched chambers. High total primary productivity has been found to be indicative of nutrient enriched systems in both fresh and saline waters (Borum 1985, Pringle 1987, Stevenson et al. 1991, Neckles et al. 1993). Others have also reported increases in respiration in eutrophic systems dominated by algae (Lee & Olsen 1985, McGlathery 1992); rates of oxygen production and consumption have been directly related to algal concentrations (Malone et al. 1986, Boynton et al. 1996). Thus, the increases in (P_a) and (R_n) further suggest a change in autotrophic dominance from vascular plant to algae.

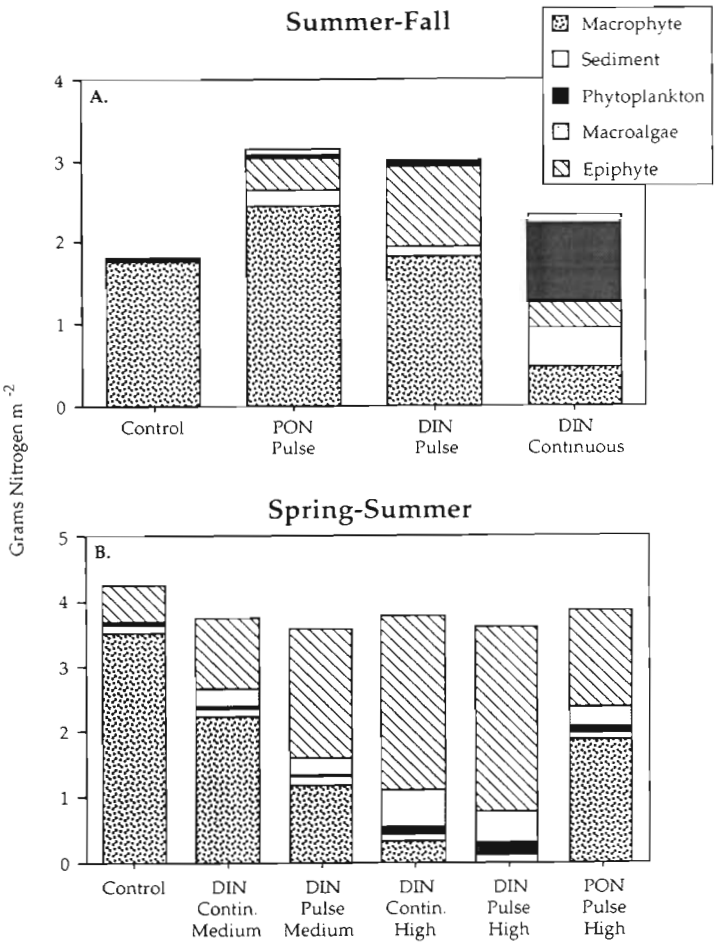

Fig. 3. Summary of the end of experiment distribution of nitrogen among autotrophic components within the experimental chambers during (A) summer-fall and (B) spring-summer. Values are derived from measures of biomass and percent nitrogen in autotrophic component tissues (Tables 2 & 3), with C:N for phytoplankton assumed to be 6.7:1 (Redfield et al. 1963, Salisbury & Ross 1985). For standard error estimates, see values associated with these data in the corresponding tables

In addition to the general pattern of vascular plant decline and a shift to an algal dominated community, we have also shown that variations in form, frequency and seasonal timing of nutrient delivery cause differing responses in the SAV community. Under these experimental conditions, DIN nutrient additions were more detrimental to macrophyte survival than inputs of PON. This trend was evident under both moderate and high nutrient loading rates in spring-summer experiments and under moderate enrichment in fall experiments. Here, we focus our discussion on a comparison of the results from medium DIN enrichment in summer-fall and spring-summer experiments in relation to season and to water retention time. We also discuss community response to moderate and high particulate organic enrichment. The implications of our results are related to established water quality criteria for submersed plant growth and survival (Dennison et al. 1993, Stevenson et al. 1993).

All indicators of SAV community decline [reduced plant growth (Fig. 1) and biomass (Table 3), algal accumulation (Fig. 2, Table 4), community metabolism (Table 5)] were more evident at an earlier stage in pulse enrichment in the spring-summer experiments. This trend is the reverse of the reported results for experiments conducted in the summer-fall at the medium loading rates, where a more rapid decline in SAV community structure occurred with continuous nutrient inputs. In summer-fall, the macrophyte and phytoplankton components in continuous treatments increased in biomass over pulse, whereas in spring-summer experiments epiphytic microalgae in pulse exhibited increased growth over continuous treatments (Table 6).

Table 5. Total ecosystem production (P_n) and respiration (R_n) (g O_2 m^{-2} d^{-1}) in experimental chambers at the beginning, middle and end of treatment period. Values are mean (±SE, n = 4). Superscript letters as in Table 1; $p < 0.05$, ANOVA

Treatment	Week 1		Week 6		Week 12	
	P_n	R_n	P_n	R_n	P_n	R_n
A. Summer-fall						
Control	1.00 ±0.10	−0.18 ±0.03	1.16 ±0.10	−0.25 ±0.07	0.79 ±0.03	−0.13 ±0.02
DIN pulse	1.16 ±0.12	−0.23 ±0.13	3.37^{bd} ±0.66	−0.99^{bg} ±0.22	1.13 ±0.32	−0.27^{bg} ±0.04
DIN continuous	1.16 ±0.09	−0.23 ±0.14	2.06^{b} ±0.50	−1.04^{bg} ±0.30	1.60^{bg} ±0.27	−0.84^{bcg} ±0.25
PON pulse	1.01 ±0.06	0.16 ±0.06	1.18 ±0.06	−0.16 ±0.06	0.98^{b} ±0.05	−0.17 ±0.04
B. Spring-summer						
Control	1.13 ±0.13	−0.21 ±0.06	1.46 ±0.10	−0.27 ±0.06	1.28 ±0.09	−0.23 ±0.08
Medium DIN						
Pulse	1.16 ±0.11	−0.25 ±0.09	3.53^{b} ±0.62	−1.43^{bge} ±0.19	2.98^{b} ±0.47	−1.26^{b} ±0.21
Continuous	1.15 ±0.10	−0.25 ±0.11	2.87^{h} ±0.43	−1.12^{b} ±0.15	3.13^{b} ±0.51	−1.45^{b} ±0.18
High DIN						
Pulse	1.19 ±0.06	−0.24 ±0.08	4.64^{bcdg} ±0.46	−2.03^{bcdg} ±0.26	3.11^{bg} ±0.29	−1.87^{bcdg} ±0.12
Continuous	1.18 ±0.08	−0.23 ±0.09	4.38^{bd} ±0.39	−1.82^{bcdg} ±0.27	3.68^{b} ±0.31	2.05^{bcdg} ±0.19
PON pulse	1.11 ±0.08	−0.22 ±0.05	1.55 ±0.09	−0.31 ±0.07	3.58^{b} ±0.14	−1.48^{b} ±0.15

Table 6. Comparison of experimental results for nutrients delivered in continuous and pulse mode in submerged aquatic vegetation (SAV) mesocosms from summer-fall and spring-summer experiments. Superscript letters as in Table 1; $p < 0.05$, ANOVA. Data cannot be compared statistically across seasons due to differences in experimental design

	Control	DIN continuous	DIN pulse
Plant biomass (g dry wt m^{-2})			
Above ground			
Spring-summer	168.4	86.4^{bc}	37.4^{bd}
Summer-fall	34.3	10.9^{b}	34.2
Below-ground			
Spring-summer	0.6	0.2^{b}	0.1^{b}
Summer-fall	0.9	0.2^{b}	0.2^{b}
Algae			
Epiphytes (µg chl *a* cm^{-2} leaf area)			
Spring-summer	0.9	2.4^{b}	4.3^{bd}
Summer-fall	0.9	3.5^{b}	3.9^{b}
Phytoplankton (µg chl *a* l^{-1})			
Spring-summer	3.2	7.1^{b}	4.9^{b}
Summer-fall	4.2	170.1^{bc}	8.2^{bd}
Macroalgae (g dry wt m^{-2})			
Spring-summer	0	10.6^{b}	10.6^{b}
Summer-fall	0	244.0^{bc}	63.7^{bd}

We suggest 2 possible explanations for these results. First, response differences may be related to seasonality of the plant growth cycle; *Potamogeton perfoliatus* exhibits a unimodal growth pattern, with rapid growth beginning in spring (May) and continuing through summer (August). In fall, as the plants begin their senescence period, above-ground growth slows while plants store energy reserves in below-ground tissues (Van Wijk 1989). Plants may be more susceptible to nutrient enrichment during their initial growth period and less responsive (at least in terms of above-ground growth) in fall during their die-back period (e.g. Moore et al. 1995). Additionally, epiphytic microalgae may be more responsive to temperature increases associated with spring-summer, than to declines in temperatures in fall. In similar mesocosm experiments, Neckles et al. (1993) reported increased epiphytic growth associated with the seagrass *Zostera marina* during summer months.

Secondly, we explain the seasonal differences between pulse and continuous inputs in relation to water retention time. In the summer-fall experiments, water retention time in the experimental chambers was 7 d, with nutrients added in pulse mode at the same time intervals. Rapid utilization of nutrients by the algal community quickly lowered the concentration within the pulse chambers and 'new' nutrients

were not re-introduced for a week. In continuous input chambers, nutrients were supplied and utilized constantly, allowing for increased microalgal growth. With a slow water exchange, phytoplankton (and other microalgae) may not be washed out of the chambers as rapidly as with short water retention time, enabling the phytoplankton to respond more effectively to nutrient enrichment (Malone et al. 1980). In the spring-summer experiments, turnover time was reduced to 3.5 d and nutrients were added at the new time interval. Since the population growth rate for microalgae corresponds closely to the same time frame (Day et al. 1989), we speculate that these conditions in the pulsed treatments result in higher concentrations of available nutrients, which would enhance algal growth, and explain the more rapid decline in vascular plants.

We find similar discrepancies in the response of submersed plant communities to nutrient enrichment reported in the literature. In studies where total nitrogen concentrations in the water column were low (2 to 5 µM), plant growth declined with increased algal accumulation (Twilley et al. 1985, Burkholder et al. 1992, Neundorfer & Kemp 1993). However, in 2 studies involving the seagrass species *Zostera marina*, in which nitrogen concentrations were higher (10 µM), there was little community response to enrichment (Neckels et al. 1993, Williams & Ruckelshaus 1993). Other studies with *Z. marina* reported a negative plant growth response to similar nutrient concentrations (Short et al. 1995, Taylor et al. 1995). Variability in water retention time may be one factor accounting for the discrepancies in submersed plant community responses reported in these studies. The studies involving longer retention (½ d to batch, e.g. no exchange) elicited a greater response to nutrient enrichment at lower concentrations (Twilley et al. 1985, Burkholder et al. 1992, Neundorfer & Kemp 1993, Short et al. 1995, Taylor et al. 1995), than those with rapid exchange rates (Neckels et al. 1993, Williams & Ruckelshaus 1993). Based on these reported results and those from our studies, we further speculate that coupling water retention time with delivery mode of nutrients may cause greater variability in SAV community response to enrichment.

Plant growth rate appeared to be stimulated by moderate additions of particulate organic nutrients in the third quarter of the summer-fall experimental period (Fig. 1A) and both above- and below-ground biomass were elevated at the end of the experiment (Table 3A). Other community parameters, such as epiphyte concentrations (Fig. 2B) and P_a and R_n (Table 5A), were similar to the control treatments, indicating less algal growth in PON enriched chambers than in DIN enriched chambers. These results suggest that vascular macrophytes in the medium PON treatments were less stressed than those in DIN enriched chambers. Two explanations exist which would account for lower stress in these plants. First, if algal mass was lower, then the light available to plants would be greater (Barko & Smart 1981, Sand-Jensen & Borum 1983, Dennison 1987), thereby enhancing plant growth. In the summer-fall study, chambers receiving medium PON enrichment had the same K_d as controls, while attenuation by epiphytic mass (Fig. 2B) was also similar to controls (approximately 10% in both treatments). In contrast, DIN enriched chambers had higher epiphyte concentrations and K_d than PON chambers. The second explanation for less stress in these plants is a greater sediment nutrient content. Dennison et al. (1987) reported sediment nutrient concentrations below 100 µM N were considered limiting in eelgrass *Zostera marina* beds, and sediment enrichment has been shown to stimulate rooted plant growth in some cases (Anderson & Kalff 1986, Duarte & Kalff 1988, Perez et al. 1991, Murray et al. 1992). Chambers enriched with PON had porewater nutrient concentrations above limiting concentrations (103 µM N; Table 2A). This elevation in sediment nutrients may have resulted from decomposition of added particulate algal material (Zimmerman & Montgomery 1984). We suggest that because sediment pore water nutrient concentrations were low, deposited PON were utilized by plant roots and not remineralized into the water column.

The results from the spring-summer high PON enrichment suggest a delayed response by the SAV community. Plant growth declined (Fig. 1C) and microalgae increased (Fig. 2E, F) later in the experimental period than in DIN enriched chambers, with levels comparable to medium dose chambers. We suggest that this reaction is a response to a delay in the enrichment of the water column. In contrast to the summer-fall experiments, sediment porewater nutrients in the spring-summer experiments were already nutrient enriched (Table 2B) (Dennison et al. 1987, Murray et al. 1992); the additional deposition of PON was remineralized and released into the water column. We attribute the lag in plant growth decline to enhancement of water column nutrients following remineralization and the consequential growth of microalgae, which in turn, limits light to the submersed plant (Borum 1985, Neundorfer & Kemp 1993). We also suggest that in naturally occurring submersed plant beds with organic rich sediments, deposition and decomposition of high concentrations of PON and fluxes of nutrients to the water column may enhance eutrophication through regeneration of DIN (Ward et al. 1984, Zimmerman & Montgomery 1984).

A comparison of the water quality data from these experiments and the levels established for SAV sur-

Table 7. Comparison of experimental results to established habitat criteria for SAV survival in Chesapeake Bay. Values are means of weekly measurements for the 12 wk experimental period. Dissolved inorganic nitrogen (DIN) and dissolved inorganic phosphate (DIP) values are in µM and chl *a* values are µg l^{-1}

Treatment	DIN		DIP		N:P		Chl *a*	
	Spring-summer	Summer-fall	Spring-summer	Summer-fall	Spring-summer	Summer-fall	Spring-summer	Summer-fall
Control	2.4	1.0	0.11	0.07	21.8	14.3	2.7	2.9
Medium DIN								
Continuous	3.4	1.5	0.75	0.49	4.5	3.1	5.5	49.4
Pulse	7.5	1.0	1.75	0.09	4.3	11.1	5.3	6.5
High DIN								
Continuous	27.3		8.4		3.2		10.4	
Pulse	53.1		11.8		3.2		14.9	
PON pulse	5.1	1.0	0.17	0.07	30.0	14.3	3.1	2.8
Habitat criteria[a]	10.7		0.33		32		15	

[a]After Dennison et al. (1993)

vival in the Chesapeake Bay (Batiuk et al 1992, Dennison et al 1993, Stevenson et al. 1993) indicates that only control chambers met the habitat criteria (Table 7). In high dose DIN treatments (spring-summer), nutrient and chl *a* concentrations (Fig. 2E, Table 1B) exceeded minimum levels early in the experiment and plants responsed almost immediately (e.g. declines in growth occurred after 3 wk). In all medium dose experiments, criteria levels for nitrogen (Table 1) were either below or exceeded minimum levels only at the experimental end. However, plant growth began to decline sooner in the experimental period (Fig. 1). At first glance it would seem that there is a discrepancy between plant decline in medium enrichment treatments and habitat criteria. However, a comparison of the phosphate concentrations indicates levels were exceeded immediately. Apparently, the SAV community is utilizing the N+P in a ratio higher than the added ratio of 10:1, resulting in excess phosphate. Thus, the results from these experiments support established habitat criteria and also emphasize the need for consideration of all parameters defined under the reported values for submersed plant survival.

It is difficult to compare results from mesocosm studies to field conditions. Naturally occurring submersed plant communities are subjected to a wide variety of differences in water quality, physical circulation and trophic complexity. However, few field studies report data collected from intensive sampling programs, which is needed to understand the relationship between water quality and SAV survival (Williams & Ruckelshaus 1993). Recently, studies conducted in various areas of the Chesapeake Bay have found that water quality conditions in and surrounding SAV beds vary daily, as well as seasonally, and that the established parameters are often exceeded (Moore et al. 1995). Mesocosm studies can provide guidelines for understanding the relationship between submersed plant growth and survival and nutrient enrichment under controlled conditions; however, extrapolation to natural communities should be made with caution.

Based on our results and on literature reports, we suggest that there may be a more complex relationship between nutrient enrichment and SAV growth and survival. This relationship seems to be dependent on variables associated with form, delivery frequency and loading rate of nutrients and on water retention time.

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