

Feedback effects in a coastal canopy-forming submersed plant bed

Renee K. Gruber* and W. Michael Kemp

Horn Point Laboratory, University of Maryland Center for Environmental Science, Cambridge, Maryland

Abstract

Although physical and biogeochemical properties of an environment determine distribution and health of biota, some organisms modify habitat conditions through complex interactions with their surroundings. We quantified effects of the canopy-forming submersed plant species *Stuckenia pectinata* on local hydrodynamics and explored resulting positive and negative feedbacks on plant growth. Measurements of waves and tidal currents were made outside, at the edge of, and within a plant bed located in the mesohaline region of Chesapeake Bay. Clear feedback effects on light, nutrients, and sediments were observed, and were found to vary seasonally with plant growth cycle. During the June period of peak plant biomass, significant wave heights were attenuated by ~37% within the plant stand; this resulted in an ~60% reduction of total suspended solids, which was stable and relatively unaffected by periods of high wind speed or water depth. Deployments of artificial substrates showed that epiphytic accumulation was greatly reduced within the plant bed, further increasing available light for plants to 25% of incoming irradiance (as compared to 0.2% outside the plant bed). In addition, higher particle trapping rates and sediment organic content augmented bed pore-water nutrient pools (CO_2 , NH_4^+ , PO_4^{3-}) sufficiently to satisfy plant demands. These processes generated negative feedback effects on plant growth, including elevated pore-water sulfide ($> 700 \mu\text{mol L}^{-1}$) and depressed water-column O_2 concentrations ($< 2 \text{ mg L}^{-1}$), but levels were ephemeral and generally outside reported stress thresholds. Dominant positive feedbacks provide an explanation for bed survival in this environment despite degraded water quality during summer months.

Seagrasses and other submersed angiosperms are the foundation for some of the world's most diverse and productive ecosystems, providing significant services relevant to human interests (Costanza et al. 1997). Beds of these submersed plants represent valuable coastal habitats that serve as food and refugia for a variety of ecologically important benthic and pelagic animals (Lubbers et al. 1990; Hemminga and Duarte 2000). Submersed plant communities are also sites of enhanced nutrient cycling, facilitating the stabilization of nutrient levels in coastal systems (Caffrey and Kemp 1992; McGlathery et al. 2007). Unfortunately, many coastal waters worldwide (including Chesapeake Bay, Maryland) have experienced degraded water quality due to increased anthropogenic loading of nutrients and sediment (Kemp et al. 2005). The resulting decreased light penetration and overgrowth of algal epiphytes on leaf surfaces have led to large-scale declines in submersed plants (Duarte 1995; Orth et al. 2006).

Established beds of submersed plants can modify their physical environment by attenuating wave and current energy through leaf-associated frictional drag (Gambi et al. 1990; Peterson et al. 2004). Canopy-forming species are known to be particularly effective in attenuating waves (Fonseca and Cahalan 1992). This important group of submersed plants, which commonly inhabits estuaries and coastal bays, often exhibits two seasonally shifting growth forms: a dense highly branched reproductive form with tall flowering shoots occurring in summer, and a shorter vegetative (nonflowering) form that occurs throughout the year (van Wijk 1988).

Modification of local hydrodynamics by plant beds can alter environmental conditions in ways that enhance growth through “positive feedbacks” or retard it through “negative feedbacks” (de Boer 2007; van der Heide et al. 2007). One important positive feedback is increased water clarity and light penetration due to enhanced sinking of suspended particles (Ward et al. 1984) and reduced resuspension within the plant bed (Gacia and Duarte 2001). Decomposition of this trapped particulate organic material tends to increase nutrient recycling and augment sediment pore-water nutrient pools (Kemp et al. 1984; Hemminga et al. 1991). However, decomposition can also increase pore-water concentrations of phytotoxic metabolites, including hydrogen sulfide, the accumulation of which represents a negative feedback on plant growth (Holmer and Bondgaard 2001). Little is known about conditions that influence the presence and magnitude of feedbacks in canopy-forming plant beds, but plant-growth form has been previously identified as being particularly important (Rybicki et al. 1997; Hasegawa et al. 2008).

Although substantial research has demonstrated the influence of submersed plants on individual factors such as nutrients or sediment type, few studies have assessed a full suite of physical and biogeochemical processes in natural plant communities. Additionally, many studies detailing hydrodynamics within plant beds have been conducted in flumes and have focused on meadow-forming seagrasses (Fonseca 1996). Given the importance of submersed plants to the coastal environment, studies of complex interactions within plant beds are necessary to understand and preserve bed health and stability. The aims of this study were, therefore, to explore positive and negative feedback effects on light, nutrients, and sediments in an established canopy-forming submersed plant bed and to assess seasonal changes in feedbacks related to plant-growth form.

* Corresponding author: Renee.Gruber@environment.nsw.gov.au

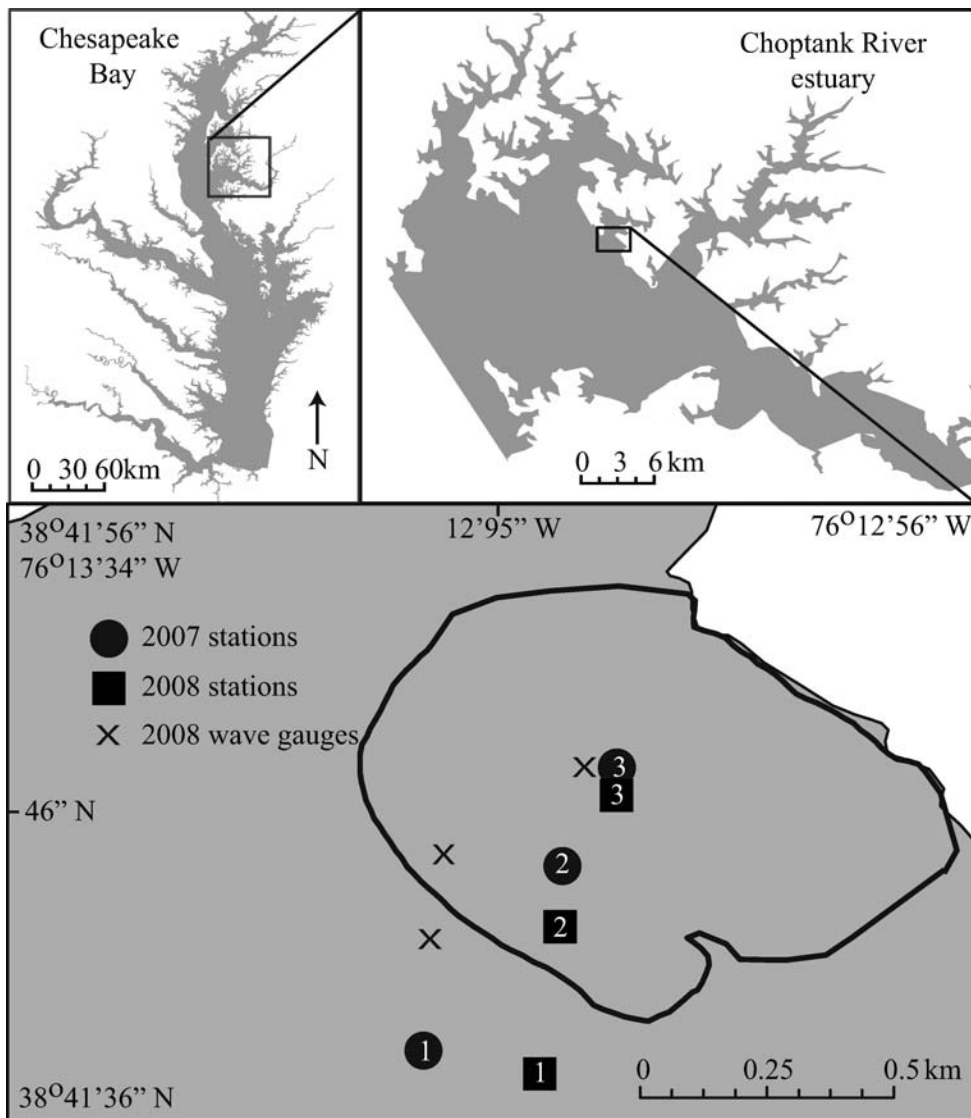


Fig. 1. Locations of sampling platforms and wave gauges at the Irish Creek study site (*Stuckenia pectinata* bed perimeter shown in black). Bare (1), Edge (2), and Bed (3) stations are shown for 2007 (circles) and 2008 (squares). Black X's indicate the locations of Bare, Edge, and Bed station wave gauges (when deployed) in 2008.

Methods

Study site—This study spanned a 17-month period (June 2007–October 2008) and involved intensive sampling of a 0.15-km² monospecific stand of the canopy-forming submersed plant *Stuckenia pectinata* (previously known as *Potamogeton pectinatus*). The plant bed was located on the northern shore of the Choptank River estuary adjacent to a small embayment (Fig. 1). To support sampling equipment, three wooden platforms were placed along a cross-bed transect forming station locations at: (1) the dense inner portion of the bed ~ 200 m inside the seaward perimeter (“Bed”), (2) a patchy vegetated region ~ 60 m inside the seaward perimeter (“Edge”), and (3) an unvegetated site ~ 150 m outside the bed’s seaward perimeter (“Bare”). Despite the transect length, water

depths were similar among Bare, Edge, and Bed stations at 1.40, 1.14, and 1.13 m mean low low water (MLLW), respectively.

Water quality—Water samples (~ 800 mL) were collected using automated discrete samplers (Teledyne Isco, Model 6712) secured to each platform. Programmed collection occurred at 2–4-h intervals for week-long deployments during June 2007, August 2007, and May 2008. Sampler intakes were positioned at mid-water-column depth (~ 70 cm above sediment surface), and each sampler contained an ice block to preserve samples, which were retrieved daily, placed on ice, and transported to the laboratory for immediate processing.

Water samples were shaken to homogenize them and passed through preweighed and ashed filters (0.45 μ m GF/

F). Filters were rinsed with deionized (DI) water to remove salt and then dried to determine total suspended solid (TSS) concentrations. Weight loss of filters on combustion (4 h at 550°C) provided an estimate of percent particulate organic material (%POM). An additional known volume of water sample (60–120 mL) was passed through filters, which were then frozen in darkness for chlorophyll *a* (Chl *a*) analysis. Within 6 months of collection, the filters were thawed, extracted in the dark with 100% acetone, sonicated, filtered, and read on a fluorometer (10-AU, Turner Designs). Additional filters were retained for analysis of particulate carbon (PC) and nitrogen (PN) (Exeter Analytical, CE-440) and particulate phosphorus (PP). Filters retained for PP analysis were ashed, digested in 1 mol L⁻¹ HCl (Aspila et al. 1976), and analyzed colorimetrically for phosphate (PO₄³⁻) (Technicon Auto Analyzer II). Concentrations of dissolved ammonium (NH₄⁺), nitrate (NO₃⁻), and PO₄³⁻ in filtrate were also determined colorimetrically (U.S. EPA 1993a,b).

During water-sample retrieval in June, vertical profiles of photosynthetically available radiation (PAR, LICOR, LI-1000 hand-held 2π sensor) were taken at each site to calculate diffuse downwelling attenuation coefficients (*K_d*). Because light measurements made at the Bed station included shading from the plant canopy, profiles were also taken in an adjacent patch (1 m²) with aboveground plant tissue removed.

To detect high-frequency changes in selected water-quality variables, data sondes (YSI 6600, Yellow Springs Instruments) equipped with a series of sensors for turbidity, chlorophyll, conductivity, temperature, pH, dissolved oxygen (O₂), and water depth were deployed at each station; sensors were placed adjacent to water sampler intakes and programmed to record every 15 min. Sondes were deployed 1–2 weeks coincident with water samplers and for 2 additional weeks in August and October 2008. The latter deployments included additional data-logging sensors (YSI 600XLM) placed 5 cm above the sediment surface at Bare and Bed stations.

Plant canopy—Aboveground plant material was collected monthly (twice in May 2008) in triplicate from June 2007 through August 2008. Quadrat frames (0.25 m × 0.25 m) were tossed haphazardly between Bed and Edge stations, and all biomass within the frame was clipped at the sediment surface, bagged, and chilled. Within 3 d of collection, samples were washed in freshwater, scraped free of epiphytes, and 10 reproductive (flowering, when present) and vegetative (nonflowering) shoots were selected for length measurement. During the months of August and September, with the onset of senescence, shoots were no longer oriented vertically but tended to lie prone near the sediment surface in a compact mat. In order to quantify vertical space occupied by the canopy, “effective canopy height” was defined as the mean shoot length (presenescent period, April through July) or the mean in situ height of the mat (senescent period, August and September). Finally, tissue samples were dried (60°C overnight) and weighed to determine aboveground biomass, and ~ 1 g was set aside for particulate C, N, and P analysis (as conducted previously).

Physical measurements—During the May 2008 instrument deployment, a data-logging anemometer (Campbell Scientific) was placed at the Bare station atop a pole 3 m above the water surface. In addition, wind data were downloaded for each deployment from a long-term land-based station on the south side of the Choptank River estuary, 13.5 km away (Chesapeake Bay Observing System, Horn Point Weather Station). For the study site, which was partially protected by land, only winds directed from 155° to 280° had significant fetch (1–10 km).

Data-logging wave gauges (MacroWave Pressure Gauge, Coastal Leasing) were deployed monthly (April–October 2008) inside and outside the plant bed (Fig. 1) and burst-sampled pressure at a frequency of 5 Hz. Raw data were Fast-Fourier transformed to determine significant wave height (Platt and Denman 1975). Relative wave attenuation (%*WA*) by the plant canopy was calculated as

$$\%WA = \left(1 - \frac{H_{s\text{Bed}}}{H_{s\text{Bare}}} \sqrt{\frac{c_{\text{Bed}}}{c_{\text{Bare}}}} \right) \times 100, \quad (1)$$

where *H_s* is significant wave height, and *c* is group velocity ($\sqrt{g \times h}$, where *h* = water depth) (Koch et al. 2006). Additionally, the effect of shoaling could be measured by predicting *H_s* at a station using

$$H_{s\text{Bed}} = H_{s\text{Bare}} \times \sqrt[4]{\frac{h_{\text{Bare}}}{h_{\text{Bed}}}} \quad (2)$$

and comparing predicted to measured values of significant wave height. Assuming waves were linear, wave orbital velocity was calculated as

$$u = \frac{A}{h} \sqrt{g \times h}, \quad (3)$$

where wave amplitude (*A*) is one-half of *H_s*. In addition, tidal current speed and direction were burst-sampled at a frequency of 2 Hz using an acoustic Doppler current profiler (Nortek AS, AquaDopp) at Bare and Bed stations (within the devegetated patch).

Epiphytes—To provide an index of epiphytic material effects on light availability to plants, epiphytes were sampled using artificial substrates during each week of automated sampler deployment. Plant leaf mimics were fastened to the sediment surface near platforms and collected after 8–10 d (Gruber 2009). Mimics were then scraped of all accumulated material and rinsed with DI water. This homogenized mixture was passed through pre-ashed filters (Stankelis et al. 2003) for total and inorganic epiphyte dry weight (dry wt) and Chl *a* analysis (as conducted previously).

Sediment—During each deployment period, triplicate surface sediment samples (upper 1 cm) were collected at each station with a cutoff 60-mL syringe (2.6 cm diameter). Sediment bulk density was measured with dry and wet weights, and sediment organic matter was measured as weight loss on ignition. Sediment grain size was determined through a combination of wet and dry sieving of sand (63–

Table 1. Summary of physical measurements over the 2007 and 2008 periods of instrument deployment.

Deployment date	Length (d)	Salinity*	Temperature (°C)*	Wind†			$H_{s\ddagger}$	
				Direction (true)	Mean speed (m s ⁻¹)	Max speed (m s ⁻¹)	Mean (m)	Max (m)
25 Jun 2007	8	11.0(0.07)	27.3(1.27)	214(24.6)	1.80(0.752)	5.07	—	—
20 Aug 2007	8	14.9(0.20)	25.9(1.68)	103(25.9)	1.86(0.787)	5.26	—	—
01 May 2008	10	—	—	258(21.4)	2.36(1.110)	6.46	0.17(0.091)	0.50
23 May 2008	14	10.3(0.29)	21.4(1.64)	278(23.3)	2.44(0.982)	5.22	—	—
25 Jun 2008	17	—	—	283(22.2)	1.89(0.895)	5.14	0.18(0.087)	0.66
08 Aug 2008	15	11.5(0.24)	26.5(0.87)	331(21.6)	2.20(1.151)	5.40	0.14(0.055)	0.36
05 Sep 2008	7	—	—	151(20.5)	2.53(1.400)	8.19	0.16(0.092)	0.59
16 Oct 2008	8	17.8(0.97)	17.3(2.48)	22(19.5)	2.63(1.991)	8.65	0.18(0.096)	0.47

All values are mean (SD).

* Measured by data sonde deployed at Bare station.

† Recorded at long-term land-based station.

‡ Significant wave height, measured by gauge deployed near Bare station.

500 μm) plus silt and clay ($< 63 \mu\text{m}$) fractions (Ingram 1971).

Triplicate dialysis pore-water samplers (“peepers”) were installed during the automated sampler deployments in random locations near each station. Peepers contained five holes covered by a polycarbonate membrane (0.2 μm) centered at 5, 8, 11, 15, and 20 cm below the sediment surface (Hesslein 1976). Peepers were filled with deoxygenated DI water and inserted into the sediment for 10 d until equilibration was achieved (Hesslein 1976). Pore-water samples were filtered (Acrodisc, 0.25 μm), aliquoted into vials for NH_4^+ and PO_4^{3-} analysis, placed on ice, and immediately frozen upon return to the laboratory. Nutrient analyses followed the same procedures as for water-column samples. Additional pore-water aliquots were made for hydrogen sulfide analysis; these were immediately fixed with diamine reagent (Cline 1969) and stored at room temperature until reading with a spectrophotometer (Shimadzu UVmini 1240).

Statistical methods—Measurements were tested for significant differences among stations within each month at $\alpha = 0.05$ using ANOVA. Assumptions of homoscedasticity and normality were met as indicated by Levene’s test and Shapiro–Wilk normality test, respectively, and by visual assessment of residuals. For some variables, transformation was necessary to meet ANOVA assumptions, and back-transformations were applied to means and their 95% confidence limits. Post-ANOVA testing included all possible pairwise comparisons (Ryan’s Q or Tukey–Kramer Honestly Significant Difference, depending on evenness of sample size). Multiple one-way Model II ANOVA was used for time-series water-quality data, with time treated as a random factor, and one-way Model I ANOVA was applied to pore-water, sediment, wave, and epiphyte data. Different measures of variance are reported for means, including standard error (SE, used for small n), standard deviation (SD, used for high-frequency measurements), and 95% confidence limits (95% CL, used for back-transformed means). Differences in TSS (Bare–Bed) from data taken with automated samplers and grab samples

(July, October) were regressed against aboveground plant biomass with Model I linear regression.

Turbidity (nephelometric turbidity units, NTU+) collected by data sondes was converted to equivalent TSS (mg L^{-1}) using significant regression equations generated for these data and concurrent direct measurements of TSS in May ($Y = 1.41X + 8.53$, $n = 107$, $R^2 = 0.72$, $p < 0.0001$) and June ($Y = 1.04X + 3.00$, $n = 72$, $R^2 = 0.47$, $p < 0.0001$). To assess the interaction between suspended particles and physical processes, TSS attenuation (%TSSA) was defined as

$$\%TSSA = \left(1 - \frac{\text{TSS}_{\text{Bed}}}{\text{TSS}_{\text{Bare}}} \right) \times 100 \quad (4)$$

and was compared across multiple levels of wind speed (winds from 155° to 280° only) and water depth (entire time series).

Results

Physical conditions at the study site showed seasonal trends typical of Chesapeake Bay. Daily maximum water temperatures were measured in midsummer ($27.3^\circ\text{C} \pm 1.27^\circ\text{C}$, mean \pm SD), and daily mean salinity increased from lowest values in spring (10.3 ± 0.29) to highest values in fall (17.8 ± 0.97) (Table 1). During the study period, mean wind speeds tended to be high during spring months, decrease during summer, and increase again in the fall. For spring and summer instrument deployment periods, winds were directed out of the south and west (coinciding with the axis of the study transect $\sim 200^\circ$). During the fall, winds reversed and were directed primarily out of the north and east. Mean significant wave height (H_s) varied between 0.14 and 0.18 m by deployment, with the maximum measured in July 2008 (0.66 m) (Table 1).

Dramatic changes were observed in this submersed plant bed over the growing season, with minimal difference between summers of 2007 and 2008; thus, results are presented out of chronological order to emphasize distinct phases of the annual growth cycle. Monthly aboveground plant biomass and effective canopy height increased during

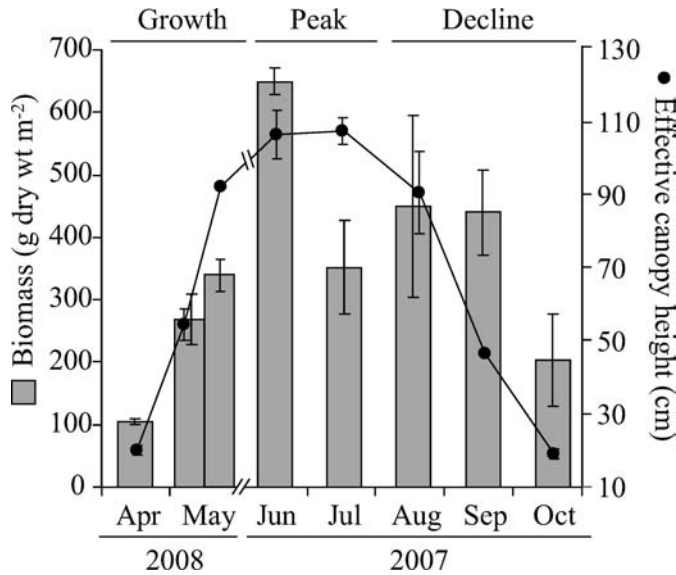


Fig. 2. Aboveground plant biomass (bars) and effective canopy height (points) during the study period (means \pm SE). Collection occurred once monthly ($n = 3$), except in May (sampled twice). Aboveground biomass included all live plant material, and effective canopy height consisted of the average vertical space occupied by plants, accounting for horizontal shoot orientation during fall months. Note that seasonal patterns are emphasized in presenting data by month rather than chronologically.

spring, reached maximum values during June (mean \pm SE of 641 ± 21 g dry wt m^{-2} and 106 ± 7 cm, respectively), and decreased with fall senescence (Fig. 2). Aboveground plant material was composed of $34.9\% \pm 0.3\%$ C, $2.08 \pm 0.09\%$ N, and $0.19 \pm 0.02\%$ P (mean \pm SE).

Average wave attenuation within the plant bed was greatest ($37\% \pm 13.0\%$, mean \pm SD) during the maximum biomass period of late June (Fig. 3), and was measured up to 85% during that time. Wave attenuation also occurred to a lesser extent in late August ($17\% \pm 5.7\%$). Multiple wave gauges contemporaneously deployed at Bare, Edge, and Bed stations during August (Fig. 1) showed significantly greater mean H_s (\pm SD) at Edge (0.16 ± 0.053 m) than Bare (0.14 ± 0.055 m) or Bed (0.12 ± 0.044 m) stations (ANOVA, $p < 0.0001$). The early May period of low biomass and short canopy corresponded to greater and highly variable significant wave heights within the plant stand ($-20\% \pm 23.4\%$). During the September period of senescence, there was little difference in wave height inside and outside the bed ($-3\% \pm 18.9\%$) (Fig. 3). Large wave attenuation was also measured during October ($21\% \pm 5.2\%$), when landmasses sheltered the Bed site from strong northerly winds (Table 1). Tidal current velocities were fairly low ($4\text{--}6$ cm s^{-1} , max 9 cm s^{-1}) inside and outside the plant bed (data not shown); wave orbital velocities exceeded tidal current velocities, averaging 26.4 cm s^{-1} during June.

Mean suspended particle concentrations (TSS and Chl *a*) decreased significantly along the transect (Bare > Edge > Bed) in June and August, although this trend was less pronounced in May (Fig. 4, $p < 0.0001$ for all months). The greatest differences between Bare and Bed in both TSS

and Chl *a* (9.2 mg L^{-1} and 4.11 μg L^{-1} , respectively) occurred during June. An inverse pattern was observed for %POM, where organic material composed a significantly larger fraction of suspended particles at the Bed station as compared to the Bare station ($p < 0.0001$ in all cases). As a result of reduced TSS and Chl *a* concentrations within the plant bed, water clarity increased during June, with average K_d values of 0.88 m^{-1} at Bed station (within clipped patch) and 1.20 m^{-1} at Bare station. Within the plant stand, overall light attenuation was much stronger ($K_d = 3.21$ m^{-1}) due to shading by the dense canopy. During May and August, patterns in water clarity were similar to those for suspended particles.

Concentrations of dissolved NO_3^- , NH_4^+ , and PO_4^{3-} were low and not significantly different among stations each month, with means in June of 0.28 ± 0.04 μmol L^{-1} , 1.73 ± 0.25 μmol L^{-1} , and 0.17 ± 0.02 μmol L^{-1} , respectively (\pm SE). On the other hand, suspended particulate nutrients (PC, PN, and PP) followed patterns similar to TSS, which were significant in June ($p < 0.007$ in all cases) and significant for PN in August ($p < 0.04$). Values of pH were elevated at the Bed station during May (data not available for June), a mean (\pm SD) of 8.6 ± 0.56 (max 9.6) as compared to 7.9 ± 0.01 (max 8.6) at the Bare station. Accumulation of epiphytic material also exhibited seasonal patterns paralleling those of suspended material. In July and August, accumulated epiphytic material was mainly inorganic and significantly heavier at Bare as compared to Edge and Bed stations when measured by total dry wt and Chl *a* ($p < 0.003$) (Fig. 5).

Key sediment characteristics differed among stations during the months studied (Table 2). Sediment wet bulk density (WBD) was significantly lower at the Bed station in June and August, and organic content was also elevated at this station during these months ($p < 0.003$ for all). A significant difference in percent silt and clay ($p < 0.0001$) was measured among stations during August (replicates not available for June). Vertical profiles of nutrients and sulfide showed similar patterns of significantly elevated concentrations ($p < 0.01$) and high variability within the plant bed during June (Fig. 6), with no significant differences during May (data not shown). Low O_2 concentrations were recorded near the sediment surface at the Bed station for nearly the entire sonde deployment in August 2008 (Fig. 7), and hypoxic conditions ($O_2 < 2.0$ mg L^{-1}) were observed for 2.8% and 0.3% of this period at Bed and Bare stations, respectively.

Seasonal variability in suspended material at Bare and Bed stations was evident in a regression relating aboveground plant biomass (*B*) to differences in directly measured TSS (bare – bed) over five different months ($TSS_{\text{Bare-Bed}} = 0.034 B - 9.28$, $R^2 = 0.52$, $p < 0.0001$). Additionally, the pattern of reduced TSS at the Bed station persisted regardless of water depth or wind speed (a proxy for wave height) in June (Fig. 8). In May, TSS concentrations at the Bed station significantly ($p < 0.03$) exceeded those at the Bare station ($\%TSSA < 0$) above wind speed and water depth thresholds of 4 m s^{-1} and 1.8 m, respectively. Wind speeds reaching $4\text{--}5$ m s^{-1} were infrequent, occurring just 4% of the time during the years 2007 and 2008; typically, wind speed remained between 1 and 2 m s^{-1} .

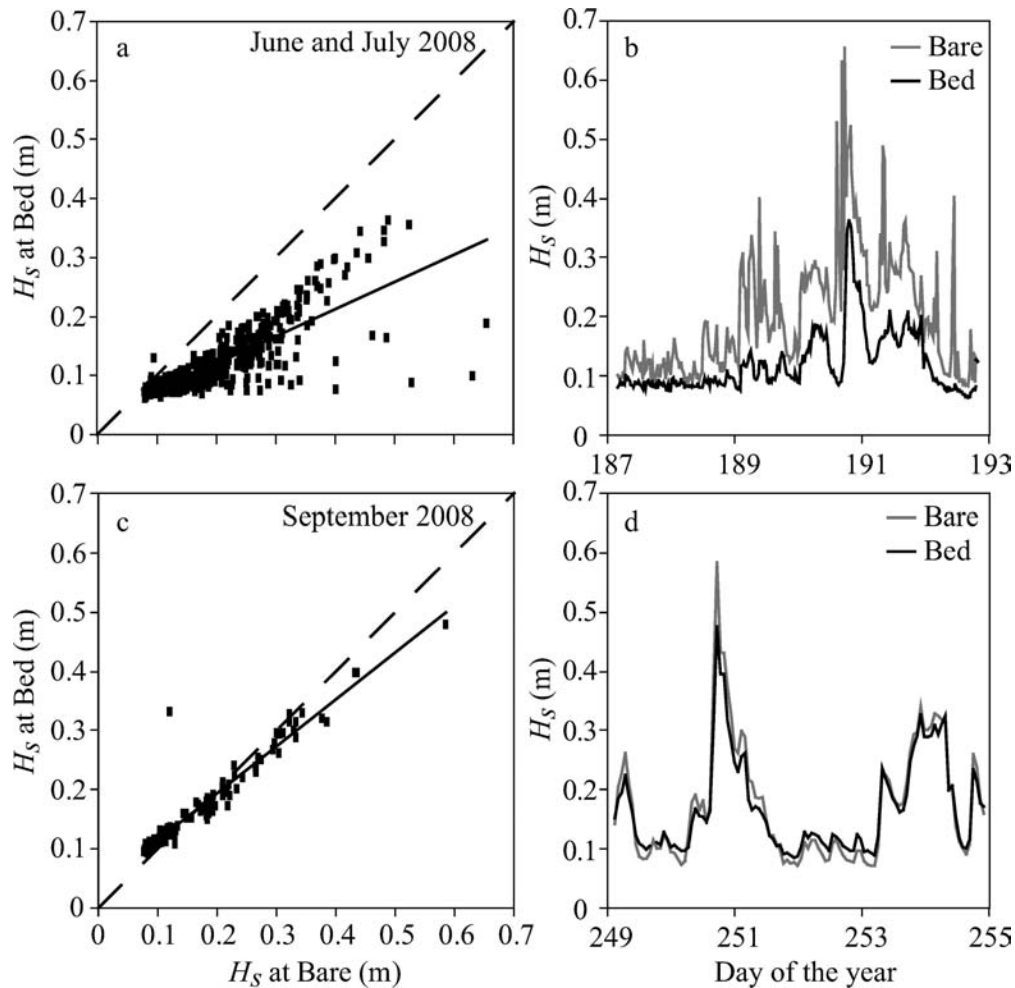


Fig. 3. Contrast in wave attenuation by the plant canopy in (a) June and July (peak plant biomass) and (c) September (senescence). Dashed lines represent a 1:1 relationship between Bare and Bed station measurements of significant wave height (H_s). Solid lines represent significant linear regressions of wave height relationships for (a) ($y = 0.46x + 0.03$, $R^2 = 0.70$) and (b) ($y = 0.79x + 0.03$, $R^2 = 0.93$). Examples of time-series H_s measurements at both stations during the periods of (b) peak biomass and (d) senescence are also shown.

Discussion

Effects on hydrodynamics—The presence of this *Stuckenia pectinata* bed had a clear effect on wave height, which was inversely related to plant presence. Peak wave attenuation (37% in June) was similar to previous reports from laboratory studies of canopy-forming species (Fonseca and Cahalan 1992). In our study, however, water depth typically exceeded shoot height, making the large effect of the plant canopy on H_s even more remarkable.

Although plants were expected to reduce tidal current velocities (Fonseca et al. 1982), this was not observed at our study site. Wave orbital velocities greatly exceeded tidal current velocities, indicating that site hydrodynamics were primarily dominated by waves (Worcester 1995; Koch and Gust 1999). Tidal current directions changed as expected with tidal phases, but current speed was variable and not related to phase of tide. Reproductive shoots of this *S. pectinata* bed were thin and cylindrical for most of their length, but became highly branched approaching the water's surface (van Wijk 1988). Given this vertical

structure, we expected to find higher current speeds in the lower portion of the water column, where plant surface area was minimal (Verduin and Backhaus 2000). The absence of flow intensification in the lower portion of the *S. pectinata* canopy is consistent with our conclusion that the hydrodynamic regime of this site was wave-dominated.

Positive feedbacks: Light—Water-quality conditions at the study site were relatively poor during summer deployments; mean TSS levels measured during June were elevated above the maximum value (15 mg L^{-1}) associated with submersed plant survival in Chesapeake Bay (Dennison et al. 1993). However, concentrations of suspended material and attenuation of diffuse downwelling light were significantly reduced within the plant bed as a consequence of the plant canopy (see Fig. 9). This pattern, which has been reported in previous in situ studies (Moore 2004), can be attributed to two complementary mechanisms. Wave action within the plant stand is reduced, and resuspension of previously deposited material is decreased (Terrados and Duarte 2000; Gacia and Duarte 2001). Suspended particles

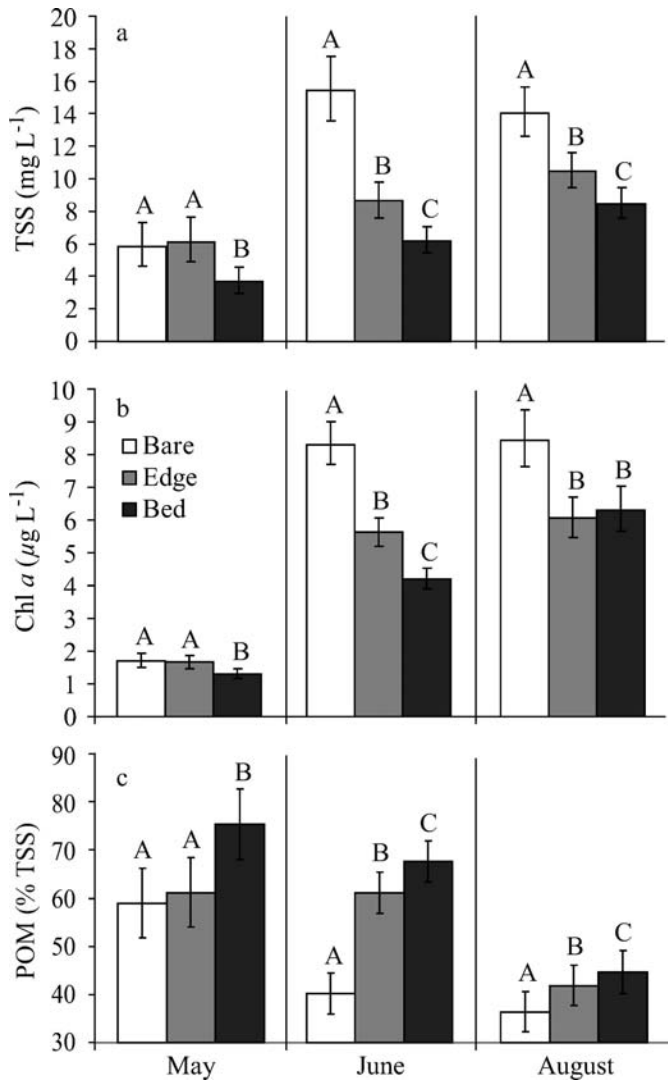


Fig. 4. Mean values for suspended particles including (a) TSS, (b) Chl *a*, and (c) particulate organic material (%POM) collected with automated samplers at Bare (white), Edge (gray), and Bed (black) stations by month. Error bars indicate the 95% confidence intervals around means, and uppercase letters indicate significant differences among stations (ANOVA, $p < 0.0001$) within May ($n = 55$), June ($n = 78$), and August ($n = 42$).

are intercepted by plant leaves and subsequently deposited (Agawin and Duarte 2002; Palmer et al. 2004).

Light attenuation by epiphytes was also reduced within this plant bed by retarded accumulation of epiphytic material; accumulation rates were an order of magnitude less at the Bed as compared to Bare station during peak plant biomass (0.62 and 8.47 g dry wt m⁻² d⁻¹, respectively). Epiphytic accumulations were primarily composed of inorganic particles, especially outside the plant stand, which highlights the importance of algal biofilms as collectors of suspended particles (van Dijk 1993). There are many potential explanations for plant bed control on epiphyte growth, including reduced nutrient uptake, shading by the plant canopy, increased herbivorous grazing, and increased mechanical removal (Lavery et al. 2007), but our goal was simply to quantify this effect.

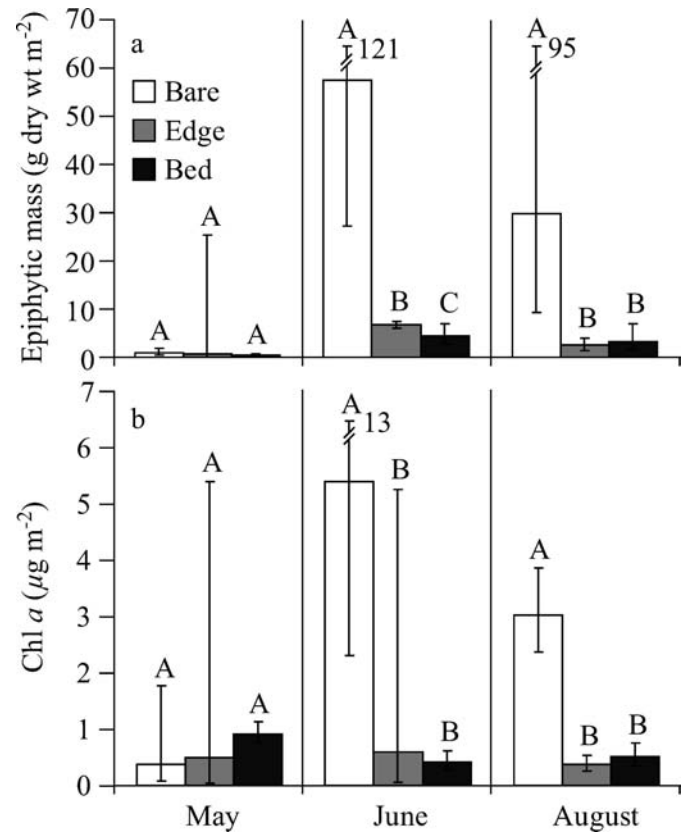


Fig. 5. Accumulation of epiphytic material on artificial substrates measured in (a) dry wt and (b) Chl *a* per substrate surface area during May ($n = 3$), June ($n = 3$), and August ($n = 5$). Error bars indicate the 95% confidence interval around back-transformed means. Uppercase letters indicate significant differences among stations within each month.

The light attenuation coefficient of epiphytic material (K_e) was estimated with the empirical relationship, $K_e = 0.07 + 0.32 \times (B_e/B_{de})^{-0.88}$, where B_{de} and B_e represent epiphyte mass and Chl *a* (respectively) normalized to plant mass (Kemp et al. 2004). The percent of light passing through the water column (PLW) was estimated as $PLW = e^{K_d z} \times 100$, assuming a depth (z) of 1.2 m; the percent of light reaching the leaf surface (PLL) was estimated as $PLL = e^{K_e B_{de}} \times PLW$. During June, 25% of incident light reached the leaf surface within the plant bed, as opposed to 0.2% for a plant growing outside the bed without the benefits of feedbacks. The light climate outside the bed was clearly insufficient to support the growth of most submersed plants, which require at least 15% of incident light (Kemp et al. 2004). Therefore, feedback effects in this bed relieved light limitation and allowed for plant growth that could not otherwise have occurred. Canopy development of this species occurred during the spring period of clearer water, initiating feedbacks before the onset of poor summer water quality.

Positive feedbacks: Sediment and nutrients—Key sediment characteristics at the study site revealed evidence of bed-induced alterations, which reflect feedback mechanisms enhancing nutrient cycling (see Fig. 9). Compared to

Table 2. Summary of key sediment properties by month at each station.

Month	Property*	Station		
		Bare	Edge	Bed
May 2008	WBD (g cm^{-3})	1.84(1.77–1.90)	1.82(1.72–1.93)	1.77(1.61–1.94)
	% organic	0.84(0.64–1.03) ^A	0.72(0.56–0.87) ^A	1.10(0.94–1.25) ^B
	% silt and clay	3.9(1.0–6.8)	6.6(0–17.8)	9.8(7.0–12.5)
Jun 2007	WBD (g cm^{-3})	1.77(1.74–1.81) ^A	1.82(1.79–1.85) ^B	1.68(1.64–1.72) ^C
	% organic	0.72(0.66–0.77) ^A	0.74(0.66–0.81) ^A	1.42(1.27–1.57) ^B
	% silt and clay	6.6 [†]	7.2 [†]	13.4 [†]
Aug 2007	WBD (g cm^{-3})	1.87(1.83–1.91) ^A	1.88(1.82–1.94) ^A	1.69(1.52–1.85) ^B
	% organic	0.90(0.29–1.51) ^A	0.76(0.61–0.90) ^A	1.52(1.16–1.88) ^B
	% silt and clay	4.0(3.0–5.1) ^A	7.4(4.7–10.2) ^A	20.3(13.6–27.1) ^B

All values are means with 95% confidence intervals in parentheses ($n=3$). Superscript letters denote significant differences among sites within months (ANOVA, $p < 0.05$).

* WBD, wet bulk density.

† Single sample ($n=1$).

Bare, Bed sediments in June had lower WBD, higher % organic matter, and smaller grain size. The differences between stations were less pronounced early in the season, but became large and significant with peak plant biomass in June. These observations, coupled with patterns along the transect, indicate that high plant biomass had the effect of enhancing particle deposition and reducing resuspension within the plant bed, thereby increasing accumulation of lighter organic material within the plant bed.

Enhanced deposition and decomposition of organic particles in plant bed sediment generated relatively high pore-water concentrations of NH_4^+ and PO_4^{3-} to support plant growth (Barko et al. 1991; Lee and Dunton 1999). Pore-water NH_4^+ concentrations during June were well above levels limiting growth for submersed plants (Dennison et al. 1987), and PO_4^{3-} was significantly elevated in the upper sediment layers. Although we did not measure rates of sediment nutrient production, plant uptake represents a large nutrient sink that would tend to lower pore-water concentrations in Bed sediments (compared to Bare)

(Caffrey and Kemp 1990). Thus, pore-water pools under-represent differences in sediment nutrient availability inside vs. outside the bed. Based on measurements of tissue nutrient content, this *S. pectinata* bed was not limited by N or P (Gerloff and Krombholz 1966), despite low water-column concentrations (van Wijk 1989) and quiescent hydrodynamic conditions that likely retarded plant uptake (Morris et al. 2008). Therefore, particle trapping augmented nutrient recycling and pore-water pools, providing a critical nutrient source for plant growth (Wigand et al. 2001).

Negative feedbacks—High rates of dissolved inorganic carbon (DIC) uptake coupled with reduced water mixing within the plant stand resulted in relatively elevated pH values in May (data not available for June). *S. pectinata* does not utilize bicarbonate as readily as other macrophytes (Sand-Jensen 1983), and bicarbonate and carbonate species dominate DIC at the observed mean pH of 8.6 (~ 99%) and peak pH of 9.6 (~ 100%) (Stumm and

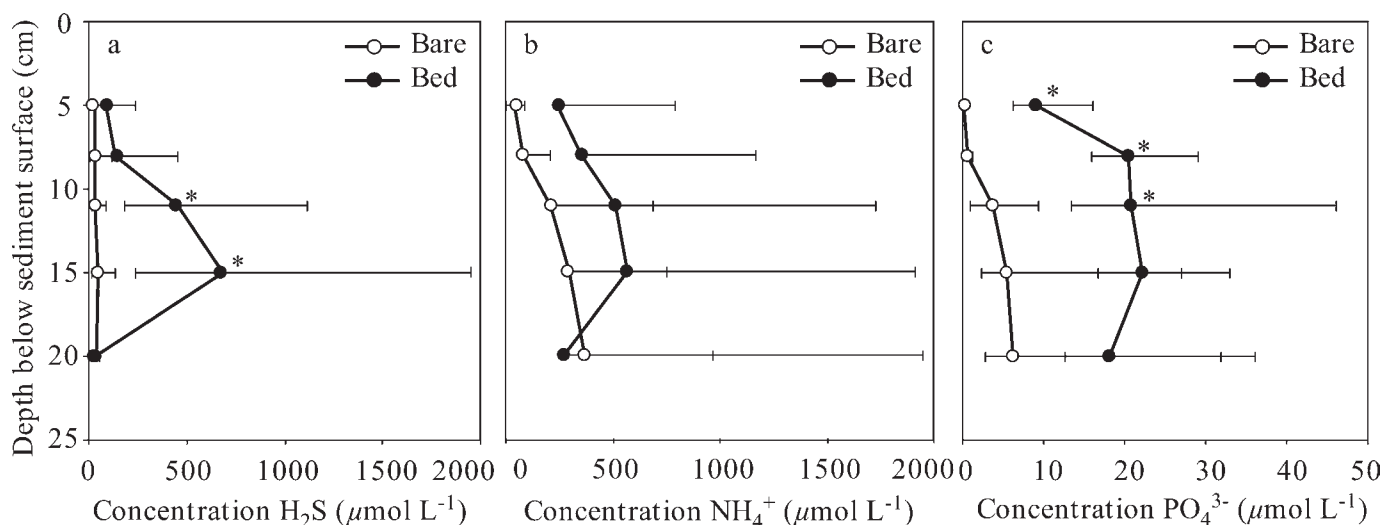


Fig. 6. Vertical profiles of means and 95% confidence limits of sediment pore-water dissolved (a) sulfide, (b) ammonium, and (c) phosphate concentrations at each station ($n = 3$) during June. Depths are below the sediment surface (0 cm). Asterisks indicate significant differences between means (ANOVA, $p < 0.05$). The negative lower confidence limits of (b) are not shown for clarity.

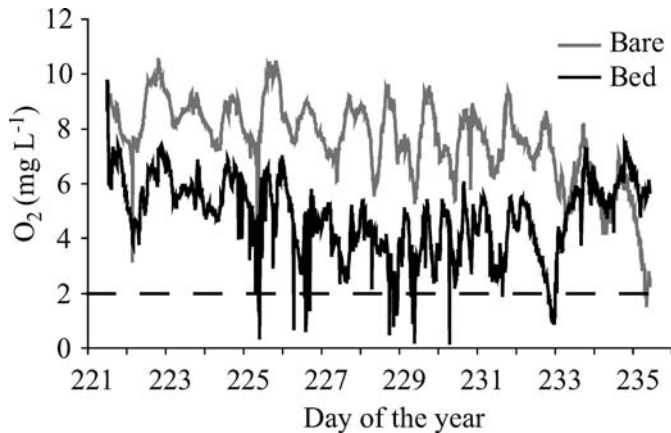


Fig. 7. Time series of dissolved oxygen concentrations measured by data sondes deployed during August near the sediment surface at Bare (light gray) and Bed (black) stations. Concentrations $< 2.0 \text{ mg L}^{-1}$ (dashed line) are considered hypoxic.

Morgan 1996). The massive production and accumulation of plant biomass, however, suggest that DIC limitation was an ephemeral factor, likely confined to late afternoons under low-mixing conditions. In addition, trapped organic material probably fueled high respiration rates and CO_2 production in the plant bed (Gacia et al. 2002), circumventing carbon limitation.

Rapid decomposition of organic material and associated oxygen consumption within the bed contributed to frequent but brief hypoxic events measured near the sediment surface in August (Fig. 7). Oxygen depletion has been reported in submersed plant beds (Caraco and Cole 2002; Goodwin et al. 2008) and is known to be deleterious to seagrass health (Holmer and Bondgaard 2001). However, *S. pectinata* is relatively tolerant of low- O_2 conditions in freshwater systems, and anoxic sediment can even stimulate tuber germination (Dixon et al. 2006). Thus, it is likely that

hypoxic events recorded in this study had little detrimental effect on plant growth.

The sediment organic content measured in this plant bed was much lower than levels reported to be deleterious for most submersed plant species (Koch 2001) and *S. pectinata* in particular (van Wijck et al. 1992). Despite this, microbial decomposition of organic material was rapid and resulted in elevated ($> 700 \mu\text{mol L}^{-1}$) and highly variable levels of sediment pore-water sulfide (Fig. 6). Threshold values for sulfide toxicity vary by species, but concentrations $> 1000 \mu\text{mol L}^{-1}$ are known to negatively affect plant growth (Koch 2001). Although *S. pectinata* may be relatively tolerant of high sulfide levels (van Wijck et al. 1992), photosynthetic inhibition has been reported for some submersed plants at concentrations $< 400 \mu\text{mol L}^{-1}$ (Goodman et al. 1995). Effects of plant root-release of dissolved oxygen (Kemp and Murray 1986; Pedersen et al. 2004) tend to reduce sulfide concentrations in microzones around roots (Lee and Dunton 2000; Holmer et al. 2005), leading to an under-representation of sulfide production rates. Therefore, the accumulation of pore-water hydrogen sulfide as a consequence of organic particle trapping within this plant bed represents a potential negative feedback that may, however, be balanced by increases in O_2 loss from plant roots.

Controls on feedbacks: Plant canopy—Strong seasonal patterns in feedbacks attributable to the changing plant canopy were observed in this *S. pectinata* bed. Although earlier studies have suggested that cylindrical seagrasses do little to reduce sediment movement (Fonseca and Fisher 1986), our results demonstrate that under variable wave-dominated field conditions, suspended material concentrations were strongly regulated by biomass in this *S. pectinata* bed. In addition, differences among stations in key properties of sediments (e.g., pore-water nutrient and sulfide concentrations) and suspended material (TSS and %POM) were less pronounced in May when only vegetative shoots were present. However, differences in the same

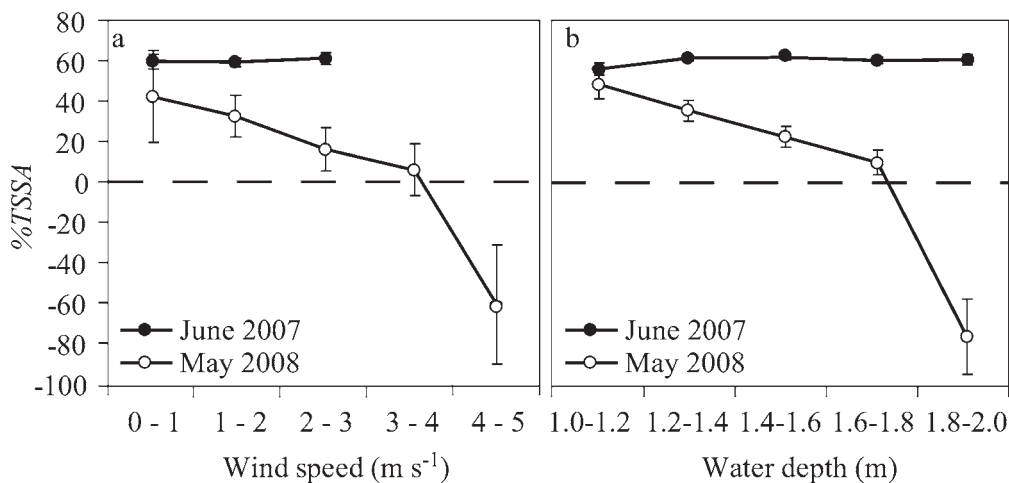


Fig. 8. TSS attenuation (see Eq. 4) by the plant bed over a range of (a) wind speeds and (b) water depths in June (filled circles) and May (open circles). Values are means, and error bars represent 95% confidence limits. The dashed line at 0% represents $\text{TSS}_{\text{Bare}} = \text{TSS}_{\text{Bed}}$. Only winds directed from 155° to 280° were included (proxy for wave height), while water depths consisted of the entire time series (atmospheric and tidal components).

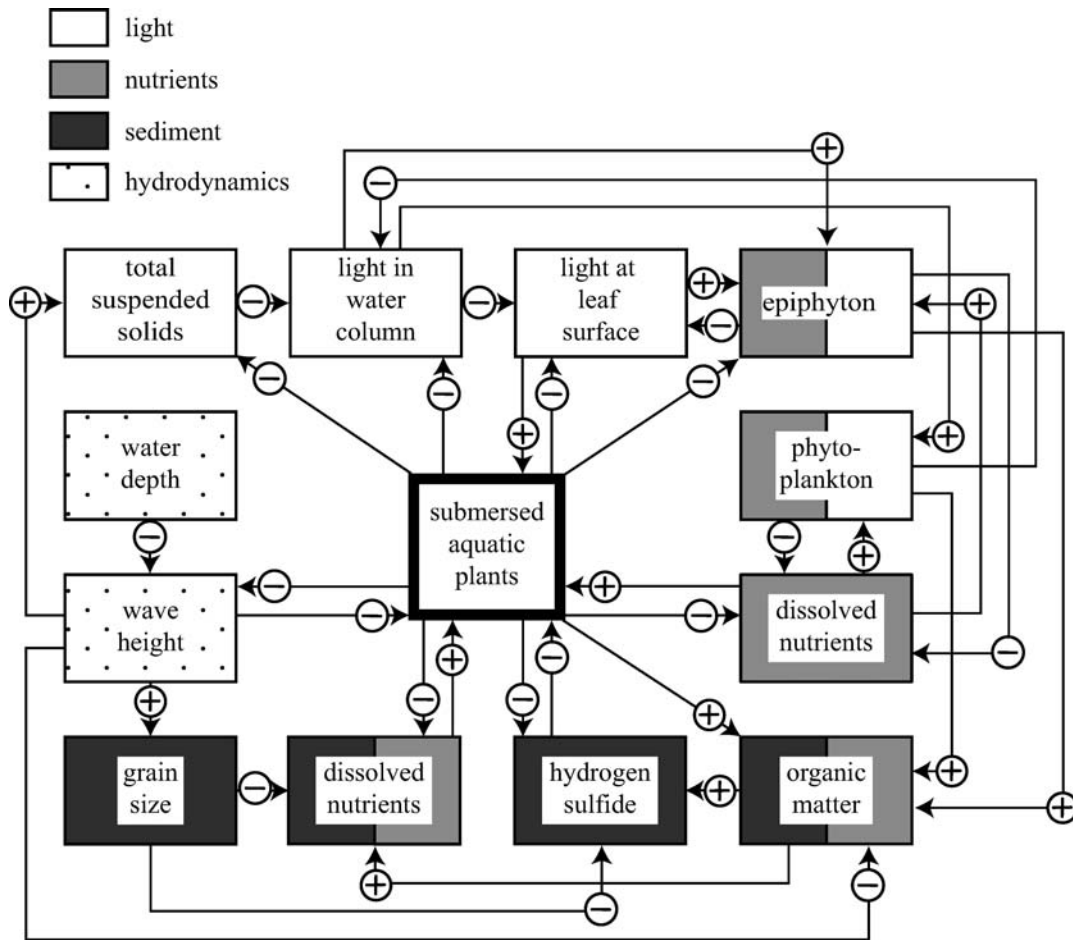


Fig. 9. Summary of key feedback processes resulting from modification of local hydrodynamics by a canopy-forming submersed plant bed. The growth of plants is principally driven by factors associated with the availability of dissolved nutrients (gray boxes) and light (white boxes), as well as certain sediment properties (black boxes). These factors are influenced by feedbacks resulting from the effects of plant bed friction on water flow (dotted boxes). Changes in a given variable tend to influence other variables (black arrows) in either positive (plus) or negative (minus) ways.

properties were much greater in June when a tall reproductive canopy had been formed. These observations can be attributed to the morphology of *S. pectinata* reproductive shoots, which have a large biomass and are highly branched (Stevenson and Confer 1978), enabling more effective particle trapping (Harvey et al. 1995). As a consequence, the partitioning of biomass in canopy-forming plants can have major effects on suspended particles, greatly enhancing feedbacks during reproductive periods.

Controls on feedbacks: Physical perturbations—Physical conditions associated with high-energy storm events can exceed the plant canopy's capacity to reduce wave energy and modulate bed effects on hydrodynamics and TSS (Ward et al. 1984). Therefore, the effect of waves and water depth on within-bed TSS levels (James and Barko 1994; Granata et al. 2001) can provide a measure of feedback strength and persistence, elucidating thresholds at which feedbacks cease to operate.

In this study, plant bed effects on TSS attenuation did not vary with wind speed (a proxy for wave height) during

June peak plant biomass (Fig. 8). This suggests that plant canopy friction was sufficient to enhance particle sinking and reduce shear stress at the sediment surface, maintaining low within-bed turbidity even under higher-energy conditions (James et al. 2004). During the May period of lower biomass, however, TSS concentrations within the bed gradually approached those at the Bare station as wind speed increased beyond 2 m s^{-1} , and Bed concentrations eventually exceeded Bare concentrations ($\%TSSA < 0$) at wind speeds $> 4 \text{ m s}^{-1}$. The source of this additional suspended material was likely previously deposited fine-grained particles (Bos et al. 2007), as well as particles trapped on plant leaves in algal epiphyte matrices (Agawin and Duarte 2002). Winds during the June deployment were, however, always $< 3 \text{ m s}^{-1}$, and therefore a full comparison with May is not possible.

Mean water level varied widely during both months due to a combination of atmospheric and astronomical tides. Previous studies suggested that water levels elevated above canopy height ($> 1.2 \text{ m}$) would reduce the capacity of the plant bed to attenuate wave energy, and would thus increase inputs of suspended particles into the bed (Ward

et al. 1984). Instead, variations in water level during June had little effect on bed attenuation of TSS, suggesting that waves were effectively reduced at all observed water levels. During late May, the pattern of water-level effect on TSS attenuation was similar to that of wind speed, suggesting a combination of a reduced capacity of the plant bed to damp waves and increased particulate inputs from overlying water when water depth > canopy height. It appears that water depth of 1.8 m represents a threshold (Fig. 8) beyond which resuspension of fine particles surpassed depositional processes within the plant bed. Under conditions observed in this study, feedbacks involving suspended particles were generally resilient to perturbation by higher-energy events during peak plant biomass, but were less resilient prior to canopy development.

Feedbacks at the edge—While canopy effects on hydrodynamics and associated feedbacks were strong and consistent in the inner portion of the plant bed, conditions at the bed's edge were more variable. Previous researchers have suggested that the edge of a seagrass bed is a dynamic region characterized by increased deposition of suspended particles (den Hartog 1971), and numerical model simulations suggest that the seaward perimeter of submersed plant beds is an active site of sediment accumulation (Chen et al. 2007). However, scant evidence of particle trapping in natural bed edges exists in the literature.

Over the course of this study, some interesting edge effects were observed that contribute to a spatially integrated understanding of feedbacks. During the August deployment of wave gauges at all three sites, waves were attenuated within the plant bed as expected, but H_s was observed to increase at the edge of the bed. Predicted values of significant wave height due to shoaling only explained approximately one third of this 15% increase. Previous reports based on modeling analysis (Mendez et al. 1999) and field studies corroborate this finding and suggest that the leading edge of vegetation may act as an impenetrable "step" to waves, increasing H_s and resulting in wave reflection (Bradley and Houser 2009). It is likely that the effects of the June plant canopy on hydrodynamics at the bed's edge were even more pronounced, and further study of natural plant communities is necessary to elucidate this phenomenon.

If wave momentum is immediately reduced at the bed's edge, large particles would tend to fall out of suspension rapidly. Significantly higher surface sediment WBD at the Edge station suggests that deposition of larger suspended particulate material may be focused primarily in this region. Additionally, despite decreasing water-column Chl *a* along the transect, the organic fraction of TSS steadily increased with distance into the bed (similar to Moore 2004), further implicating the edge as a zone of intense deposition of coarser-grained inorganic particles. Although conclusions cannot be drawn about the mechanisms behind these edge phenomena, this region experienced water and sediment quality less favorable for plant growth than the dense inner region of the plant bed. The edge region (~ 0–100 m inward from perimeter) therefore functioned as a buffer zone where hydrodynamic modification and subse-

quent water-clarity improvement occurred during summer months, primarily benefiting plants located in the inner bed region. Clearly, more research is necessary to understand edge effects and the ways in which they pertain to overall health and resilience of submersed plant beds.

This study has demonstrated that positive and negative feedback effects involving light, nutrients, and sediment are highly interactive in submersed canopy-forming plant beds (Fig. 9). Positive feedbacks affecting light penetration (through the water column and epiphytic layer) resulted in vigorous plant growth that could not otherwise have occurred under the conditions of poor water clarity and heavy epiphytic growth that characterize this region outside the bed. Trapping and subsequent decomposition of particulate organic material led to increases in pools of sediment pore-water nutrients, which augmented low water-column nutrient concentrations and helped plants circumvent limitation. Particle trapping also resulted in the negative feedback of sediment pore-water sulfide accumulation, but concentrations were not high enough to significantly impair plants. High productivity and quiescent conditions within the bed resulted in low O₂ levels, but hypoxic events were likely too intermittent to negatively affect plant growth. Wave and TSS attenuation varied seasonally with bed biomass, and feedbacks were most prominent and stable during peak plant biomass. These results indicate that once established, a plant bed can significantly modify its local environment, allowing for growth under suboptimal conditions. However, colonization or reestablishment of plant stands without the benefit of feedbacks would require much more stringent initial conditions. Further research is clearly necessary to understand the influence of habitat quality and perturbations on plant beds at various stages of succession. Ultimately, continued growth and survival of this and other aquatic species will depend on the balance between positive and negative feedbacks, especially under the degraded environmental conditions that characterize many aquatic systems worldwide.

Acknowledgments

Sampling systems and instruments were generously provided by Walter Boynton, Lou Codispoti, Jeff Cornwell, Evamaria Koch, and Court Stevenson. Debbie Hinkle's expertise in the field and laboratory was critical to the success of this project. Extensive technical support was also provided by Eva Bailey, Dale Booth, and Katie McKone. Laura Murray, Larry Sanford, and Evamaria Koch gave guidance and careful reviews of these findings. Mark Fonseca and an anonymous reviewer are gratefully acknowledged for their careful edits and thoughtful suggestions on an earlier version of this paper. Funding was provided by Maryland Sea Grant, National Oceanographic and Atmospheric Administration (award NA05/OAR4171042), Waterfowl Festival Inc., and the University of Maryland Center for Environmental Science Horn Point Laboratory.

References

- AGAWIN, N. S. R., AND C. M. DUARTE. 2002. Evidence of direct particle trapping by a tropical seagrass meadow. *Estuar. Coasts* **25**: 1205–1209, doi:10.1007/BF02692217

- ASPILA, K. I., H. AGEMIAN, AND A. S. Y. CHAU. 1976. Semi-automated method for determination of inorganic, organic, and total phosphate in sediments. *Analyst* **101**: 187–197, doi:10.1039/an9760100187
- BARKO, J. W., D. GUNNISON, AND S. R. CARPENTER. 1991. Sediment interactions with submersed macrophyte growth and community dynamics. *Aquat. Bot.* **41**: 41–65, doi:10.1016/0304-3770(91)90038-7
- BOS, A. R., T. J. BOUMA, G. L. J. DE KORT, AND M. M. VAN KATWIJK. 2007. Ecosystem engineering by annual intertidal seagrass beds: Sediment accretion and modification. *Estuar. Coast. Shelf Sci.* **74**: 344–348, doi:10.1016/j.ecss.2007.04.006
- BRADLEY, K., AND C. HOUSER. 2009. Relative velocity of seagrass blades: Implications for wave attenuation in low-energy environments. *J. Geophys. Res. Earth Surf.* **114**: 1–13.
- CAFFREY, J. M., AND W. M. KEMP. 1990. Nitrogen cycling in sediments with estuarine populations of *Potamogeton perfoliatus* and *Zostera marina*. *Mar. Ecol. Prog. Ser.* **66**: 147–160, doi:10.3354/meps066147
- , AND ———. 1992. Influence of the submersed plant, *Potamogeton perfoliatus*, on nitrogen cycling in estuarine sediments. *Limnol. Oceanogr.* **37**: 1483–1495, doi:10.4319/lo.1992.37.7.1483
- CARACO, N. F., AND J. J. COLE. 2002. Contrasting impacts of a native and alien macrophyte on dissolved oxygen in a large river. *Ecol. Appl.* **12**: 1496–1509, doi:10.1890/1051-0761(2002)012[1496:CIOANA]2.0.CO;2
- CHEN, S. N., L. P. SANFORD, E. W. KOCH, F. SHI, AND E. W. NORTH. 2007. A nearshore model to investigate the effects of seagrass bed geometry on wave attenuation and suspended sediment transport. *Estuar. Coasts* **30**: 296–310.
- CLINE, J. D. 1969. Spectrophotometric determination of hydrogen sulfide in natural waters. *Limnol. Oceanogr.* **14**: 454–458, doi:10.4319/lo.1969.14.3.0454
- COSTANZA, R., AND OTHERS. 1997. The value of the world's ecosystem services and natural capital. *Nature* **387**: 253–260, doi:10.1038/387253a0
- DE BOER, W. F. 2007. Seagrass–sediment interactions, positive feedbacks and critical thresholds for occurrence: A review. *Hydrobiologia* **591**: 5–24, doi:10.1007/s10750-007-0780-9
- DEN HARTOG, C. 1971. The dynamic aspect in the ecology of seagrass communities. *Thalassia Jugoslavica* **7**: 101–112.
- DENNISON, W. C., R. C. ALLER, AND R. S. ALBERTE. 1987. Sediment ammonium availability and eelgrass (*Zostera marina*) growth. *Mar. Biol.* **94**: 469–477, doi:10.1007/BF00428254
- , AND OTHERS. 1993. Assessing water quality with submersed aquatic vegetation. *BioScience* **43**: 86–94, doi:10.2307/1311969
- DIXON, M. H., S. A. HILL, M. B. JACKSON, R. G. RATCLIFFE, AND L. J. SWEETLOVE. 2006. Physiological and metabolic adaptations of *Potamogeton pectinatus* L. tubers support rapid elongation of stem tissue in the absence of oxygen. *Plant Cell Physiol.* **47**: 128–140, doi:10.1093/pcp/pci229
- DUARTE, C. M. 1995. Submerged aquatic vegetation in relation to different nutrient regimes. *Ophelia* **41**: 87–112.
- FONSECA, M. S. 1996. The role of seagrasses in nearshore sedimentary processes: A review, p. 261–286. *In* K. F. Nordstrom and C. T. Roman [eds.], *Estuarine shores: Evolution, environments, and human alterations*. Wiley.
- , AND J. A. CAHALAN. 1992. A preliminary evaluation of wave attenuation by four species of seagrass. *Estuar. Coast. Shelf Sci.* **35**: 565–576, doi:10.1016/S0272-7714(05)80039-3
- , AND J. S. FISHER. 1986. A comparison of canopy friction and sediment movement between 4 species of seagrass with reference to their ecology and restoration. *Mar. Ecol. Prog. Ser.* **29**: 15–22, doi:10.3354/meps029015
- , ———, J. C. ZIEMAN, AND G. W. THAYER. 1982. Influence of the seagrass, *Zostera marina* L., on current flow. *Estuar. Coast. Shelf Sci.* **15**: 351–358, doi:10.1016/0272-7714(82)90046-4
- GACIA, E., AND C. M. DUARTE. 2001. Sediment retention by a Mediterranean *Posidonia oceanica* meadow: The balance between deposition and resuspension. *Estuar. Coast. Shelf Sci.* **52**: 505–514, doi:10.1006/ecss.2000.0753
- , ———, AND J. J. MIDDELBURG. 2002. Carbon and nutrient deposition in a Mediterranean seagrass (*Posidonia oceanica*) meadow. *Limnol. Oceanogr.* **47**: 23–32, doi:10.4319/lo.2002.47.1.0023
- GAMBI, M. C., A. R. M. NOWELL, AND P. A. JUMARS. 1990. Flume observations on flow dynamics in *Zostera marina* (eelgrass) beds. *Mar. Ecol. Prog. Ser.* **61**: 159–169, doi:10.3354/meps061159
- GERLOFF, G. C., AND P. H. KROMBOLZ. 1966. Tissue analysis as a measure of nutrient availability for growth of angiosperm aquatic plants. *Limnol. Oceanogr.* **11**: 529–537, doi:10.4319/lo.1966.11.4.0529
- GOODMAN, J. L., K. A. MOORE, AND W. C. DENNISON. 1995. Photosynthetic responses of eelgrass (*Zostera marina* L.) to light and sediment sulfide in a shallow barrier island lagoon. *Aquat. Bot.* **50**: 37–47, doi:10.1016/0304-3770(94)00444-Q
- GOODWIN, K., N. CARACO, AND J. COLE. 2008. Temporal dynamics of dissolved oxygen in a floating-leaved macrophyte bed. *Freshw. Biol.* **53**: 1632–1641, doi:10.1111/j.1365-2427.2008.01983.x
- GRANATA, T. C., T. SERRA, J. COLOMER, X. CASAMITJANA, C. M. DUARTE, AND E. GACIA. 2001. Flow and particle distributions in a nearshore seagrass meadow before and after a storm. *Mar. Ecol. Prog. Ser.* **218**: 95–106, doi:10.3354/meps218095
- GRUBER, R. K. 2009. Interactions between an estuarine submersed plant bed and its physical and biogeochemical environment: Seasonal and spatial patterns. M.Sc. thesis. Univ. of Maryland.
- HARVEY, M., E. BOURGET, AND R. G. INGRAM. 1995. Experimental evidence of passive accumulation of marine bivalve larvae on filamentous epibenthic structures. *Limnol. Oceanogr.* **40**: 94–104, doi:10.4319/lo.1995.40.1.0094
- HASEGAWA, N., M. HORI, AND H. MUKAI. 2008. Seasonal changes in eelgrass functions: Current velocity reduction, prevention of sediment resuspension, and control of sediment–water column nutrient flux in relation to eelgrass dynamics. *Hydrobiologia* **596**: 387–399, doi:10.1007/s10750-007-9111-4
- HEMMINGA, M. A., AND C. M. DUARTE. 2000. *Seagrass ecology*. Cambridge Univ. Press.
- , P. G. HARRISON, AND F. VANLENT. 1991. The balance of nutrient losses and gains in seagrass meadows. *Mar. Ecol. Prog. Ser.* **71**: 85–96, doi:10.3354/meps071085
- HESSLEIN, R. H. 1976. In situ sampler for close interval pore water studies. *Limnol. Oceanogr.* **21**: 912–914, doi:10.4319/lo.1976.21.6.0912
- HOLMER, M., AND E. J. BONDGAARD. 2001. Photosynthetic and growth response of eelgrass to low oxygen and high sulfide concentrations during hypoxic events. *Aquat. Bot.* **70**: 29–38, doi:10.1016/S0304-3770(00)00142-X
- , M. S. FREDERIKSEN, AND H. MOLLEGAARD. 2005. Sulfur accumulation in eelgrass (*Zostera marina*) and effect of sulfur on eelgrass growth. *Aquat. Bot.* **81**: 367–379, doi:10.1016/j.aquabot.2004.12.006
- INGRAM, R. L. 1971. Sieve analysis, p. 49–67. *In* R. E. Carver [ed.], *Procedures of sediment petrology*. Wiley.
- JAMES, W. F., AND J. W. BARKO. 1994. Macrophyte influences on sediment resuspension and export in a shallow impoundment. *Lakes Reserv. Res. Manag.* **10**: 95–102.

- , ———, AND M. G. BUTLER. 2004. Shear stress and sediment resuspension in relation to submersed macrophyte biomass. *Hydrobiologia* **515**: 181–191, doi:10.1023/B:HYDR.0000027329.67391.c6
- KEMP, W. M., W. R. BOYNTON, R. R. TWILLEY, J. C. STEVENSON, AND L. G. WARD. 1984. Influences of submersed vascular plants on ecological processes in upper Chesapeake Bay, p. 367–394. In V. S. Kennedy [ed.], *Estuaries as filters*. Academic Press.
- , AND L. MURRAY. 1986. Oxygen release from roots of the submersed macrophyte *Potamogeton perfoliatus* L.: Regulating factors and ecological implications. *Aquat. Bot.* **26**: 271–283, doi:10.1016/0304-3770(86)90027-6
- , AND OTHERS. 2004. Habitat requirements for submerged aquatic vegetation in Chesapeake Bay: Water quality, light regime, and physical–chemical factors. *Estuaries* **27**: 363–377, doi:10.1007/BF02803529
- , AND ———. 2005. Eutrophication of Chesapeake Bay: Historical trends and ecological interactions. *Mar. Ecol. Prog. Ser.* **303**: 1–29, doi:10.3354/meps303001
- KOCH, E. W. 2001. Beyond light: Physical, geological, and geochemical parameters as possible submersed aquatic vegetation habitat requirements. *Estuar. Coasts* **24**: 1–17, doi:10.2307/1352808
- , AND G. GUST. 1999. Water flow in tide- and wave-dominated beds of the seagrass *Thalassia testudinum*. *Mar. Ecol. Prog. Ser.* **184**: 63–72, doi:10.3354/meps184063
- , L. P. SANFORD, S. N. CHEN, D. J. SHAFER, AND J. MCKEE SMITH. 2006. Waves in seagrass systems: Review and technical recommendations. U.S. Army Corps of Engineers, Engineer Research and Development Center. Report ERDC TR-06-15.
- LAVERY, P. S., T. REID, G. A. HYNDES, AND B. R. VAN ELVEN. 2007. Effect of leaf movement on epiphytic algal biomass of seagrass leaves. *Mar. Ecol. Prog. Ser.* **338**: 97–106, doi:10.3354/meps338097
- LEE, K. S., AND K. H. DUNTON. 1999. Inorganic nitrogen acquisition in the seagrass *Thalassia testudinum*: Development of a whole-plant nitrogen budget. *Limnol. Oceanogr.* **44**: 1204–1215, doi:10.4319/lo.1999.44.5.1204
- , AND ———. 2000. Diurnal changes in pore water sulfide concentrations in the seagrass *Thalassia testudinum* beds: The effects of seagrasses on sulfide dynamics. *J. Exp. Mar. Biol. Ecol.* **255**: 201–214, doi:10.1016/S0022-0981(00)00300-2
- LUBBERS, L., W. R. BOYNTON, AND W. M. KEMP. 1990. Variations in structure of estuarine fish communities in relation to abundance of submersed vascular plants. *Mar. Ecol. Prog. Ser.* **65**: 1–14, doi:10.3354/meps065001
- MCGLATHERY, K. J., K. SUNDBACK, AND I. C. ANDERSON. 2007. Eutrophication in shallow coastal bays and lagoons: The role of plants in the coastal filter. *Mar. Ecol. Prog. Ser.* **348**: 1–18, doi:10.3354/meps07132
- MENDEZ, F. J., I. J. LOSADA, AND M. A. LOSADA. 1999. Hydrodynamics induced by wind waves in a vegetation field. *J. Geophys. Res. Oceans* **104**: 18383–18396, doi:10.1029/1999JC900119
- MOORE, K. A. 2004. Influence of seagrasses on water quality in shallow regions of the lower Chesapeake Bay. *J. Coastal Res.* **45**: 162–178.
- MORRIS, E. P., G. PERALTA, F. G. BRUN, L. VAN DUREN, T. J. BOUMA, AND J. L. PEREZ-LLORENS. 2008. Interaction between hydrodynamics and seagrass canopy structure: Spatially explicit effects on ammonium uptake rates. *Limnol. Oceanogr.* **53**: 1531–1539.
- ORTH, R. J., AND OTHERS. 2006. A global crisis for seagrass ecosystems. *BioScience* **56**: 987–996, doi:10.1641/0006-3568(2006)56[987:AGCFSE]2.0.CO;2
- PALMER, M. R., H. M. NEPF, AND T. J. R. PETERSSON. 2004. Observations of particle capture on a cylindrical collector: Implications for particle accumulation and removal in aquatic systems. *Limnol. Oceanogr.* **49**: 76–85, doi:10.4319/lo.2004.49.1.0076
- PEDERSEN, O., T. BINZER, AND J. BORUM. 2004. Sulphide intrusion in eelgrass (*Zostera marina* L.). *Plant Cell Environ.* **27**: 595–602, doi:10.1111/j.1365-3040.2004.01173.x
- PETERSON, C. H., R. A. LUETTICH, F. MICHELI, AND G. A. SKILLETER. 2004. Attenuation of water flow inside seagrass canopies of differing structure. *Mar. Ecol. Prog. Ser.* **268**: 81–92, doi:10.3354/meps268081
- PLATT, T., AND K. L. DENMAN. 1975. Spectral analysis in ecology. *Annu. Rev. Ecol. Systemat.* **6**: 189–210, doi:10.1146/annurev.es.06.110175.001201
- RYBICKI, N. B., H. JENTER, V. CARTER, R. BALTZER, AND M. TUTORA. 1997. Observations of tidal flux between a submersed aquatic plant stand and the adjacent channel in the Potomac River near Washington, D.C. *Limnol. Oceanogr.* **42**: 307–317.
- SAND-JENSEN, K. 1983. Photosynthetic carbon sources of stream macrophytes. *J. Exp. Bot.* **34**: 198–210, doi:10.1093/jxb/34.2.198
- STANKELIS, R. M., M. D. NAYLOR, AND W. R. BOYNTON. 2003. Submerged aquatic vegetation in the mesohaline region of the Patuxent estuary: Past, present, and future status. *Estuaries* **26**: 186–195, doi:10.1007/BF02695961
- STEVENSON, J. C., AND N. M. CONFER. 1978. Summary of available information on Chesapeake Bay submerged vegetation. U.S. Department of Interior, Fish and Wildlife Service Report FWS/OBS-78/66.
- STUMM, W., AND J. J. MORGAN. 1996. *Aquatic chemistry: Chemical equilibria and rates in natural waters*, 3rd ed. Wiley.
- TERRADOS, J., AND C. M. DUARTE. 2000. Experimental evidence of reduced particle resuspension within a seagrass (*Posidonia oceanica* L.) meadow. *J. Exp. Mar. Biol. Ecol.* **243**: 45–53, doi:10.1016/S0022-0981(99)00110-0
- U.S. EPA. 1993a. Method 350.1: Determination of ammonia nitrogen by semi-automated colorimetry. In J. W. O'DELL, [ed.], CWA methods of interest approved for use at 40 CFR 136. EPA-600/4-79-020. Environmental Monitoring Systems Laboratory.
- U.S. EPA. 1993b. Method 365.1: Determination of phosphorus by semi-automated colorimetry. In J. W. O'DELL, [ed.], CWA methods of interest approved for use at 40 CFR 136. EPA-600/4-79-020. Environmental Monitoring Systems Laboratory.
- VAN DER HEIDE, T., E. H. VAN NES, G. W. GEERLING, A. J. P. SMOLDERS, T. J. BOUMA, AND M. M. VAN KATWIJK. 2007. Positive feedbacks in seagrass ecosystems: Implications for success in conservation and restoration. *Ecosystems* **10**: 1311–1322, doi:10.1007/s10021-007-9099-7
- VAN DIJK, G. M. 1993. Dynamics and attenuation characteristics of periphyton upon artificial substratum under various light conditions and some additional observations on periphyton upon *Potamogeton pectinatus* L. *Hydrobiologia* **252**: 143–161, doi:10.1007/BF00008152
- VAN WIJCK, C., C. J. DEGROOT, AND P. GRILLAS. 1992. The effect of anaerobic sediment on the growth of *Potamogeton pectinatus* L.: The role of organic matter, sulfide and ferrous iron. *Aquat. Bot.* **44**: 31–49, doi:10.1016/0304-3770(92)90079-X
- VAN WIJCK, R. J. 1988. Ecological studies on *Potamogeton pectinatus* L. 1. General characteristics, biomass production and life-cycles under field conditions. *Aquat. Bot.* **31**: 211–258, doi:10.1016/0304-3770(88)90015-0
- . 1989. Ecological studies on *Potamogeton pectinatus* L. 5. Nutritional ecology, in vitro uptake of nutrients and growth limitation. *Aquat. Bot.* **35**: 319–335, doi:10.1016/0304-3770(89)90005-3

- VERDUIN, J. J., AND J. O. BACKHAUS. 2000. Dynamics of plant-flow interactions for the seagrass *Amphibolis antarctica*: Field observations and model simulations. *Estuar. Coast. Shelf Sci.* **50**: 185–204, doi:10.1006/ecss.1999.0567
- WARD, L. G., W. M. KEMP, AND W. R. BOYNTON. 1984. The influence of waves and seagrass communities on suspended particulates in an estuarine embayment. *Mar. Geol.* **59**: 85–103, doi:10.1016/0025-3227(84)90089-6
- WIGAND, C., M. FINN, S. FINDLAY, AND D. FISCHER. 2001. Submersed macrophyte effects on nutrient exchanges in riverine sediments. *Estuaries* **24**: 398–406, doi:10.2307/1353241
- WORCESTER, S. E. 1995. Effects of eelgrass beds on advection and turbulent mixing in low current and low shoot density environments. *Mar. Ecol. Prog. Ser.* **126**: 223–232, doi:10.3354/meps126223

Associate editor: Anthony Larkum

Received: 09 December 2009

Accepted: 15 June 2009

Amended: 06 July 2010