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Influence of Seagrasses on Water Quality in Shallow Regions of the Lower Chesapeake Bay

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ABSTRACT

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The influence of seagrasses on water quality was investigated seasonally from permanent stations located along transects across vegetated and formerly vegetated sites in shoal regions of the Chesapeake Bay National Estuarine Research Reserve in Virginia. The effect of the seagrass bed on conditions inside compared to outside the bed varied seasonally and could be related to bed biomass and development. During spring (April to June), the rapidly growing seagrass bed was a sink for nutrients, suspended inorganic particles, and phytoplankton, whereas during the summer, as bed dieback progressed, resuspension and release of nutrients were observed. Reductions in suspended particle concentrations and light attenuation were generally not measurable until bed biomass exceeded 50–100 gdm/m^2 or 25–50% vegetative cover. During April, when nitrate levels in adjacent channel waters were observed to be highest (>10 μM), rapid uptake, equivalent to 48% of nitrogen requirements for seagrass growth, reduced inorganic nitrogen standing stocks by 73% within the bed compared to outside of it. An unvegetated site that previously supported seagrass demonstrated little capacity to reduce measurable levels of suspended particles or nutrients, and resuspension of bottom sediments contributed to higher levels of suspended particle concentrations and turbidity in the unvegetated shallows compared to adjacent waters. The capacity of seagrass beds to improve local water-quality conditions, such as turbidity and nutrients, during the spring when suspended particle concentrations are highest may be key to their continued long-term survival in this lower bay region. High levels of spring turbidity, which have been related to seagrass declines in this area, can be mediated by dense seagrass structure, but largely unvegetated areas are unlikely to modify conditions to permit survival of first-year recruits or transplants through the summer. Therefore, water-quality conditions that are suitable for recovery are likely greater than those required for continued survival of existing seagrass beds. Given this, statistically derived estimates of water-quality conditions or habitat requirements that are usually obtained from measurements in areas adjacent to existing seagrass beds should be used with caution. Although suitable for predicting the maintenance of existing beds with adequate biomass and structure, they may underestimate the levels needed for restoration and recovery of many currently unvegetated sites.

ADDITIONAL INDEX WORDS: *SAV, submerged aquatic vegetation, eelgrass,* Zostera marina, Ruppia maritima, *management, biomass, chlorophyll, inorganic phosphorus, nitrate, ammonium, dissolved oxygen, anoxia, hypoxia.*

INTRODUCTION

Low levels of submersed macrophytes in the Chesapeake Bay over the past 30 years (MOORE, WILCOX, and ORTH, 2000; ORTH *et al.,* 2002) have been related to suboptimal water-quality conditions such as water column nutrient concentrations and turbidity (DENNISON *et al.,* 1993; KEMP *et al.,* 1983; MOORE *et al.,* 1996; ORTH and MOORE, 1983). However, water quality in vegetated shallows may be distinctly different from that in adjacent channel or unvegetated shoal areas (BATIUK *et al.,* 1992, 2000; WARD, KEMP, and BOYNTON, 1984). This capacity of the vegetative community to modify local conditions may provide a key to their continued survival or recovery in some areas where water quality is of marginal quality for growth or where stresses are seasonal or pulsed in nature (MOORE, WETZEL, and ORTH, 1997; ZIMMERMAN *et al.,* 1991). Estimates of water-quality conditions needed for seagrass recovery that are obtained from water column measurements in existing beds (BATIUK *et al.,* 1992, 2002; DENNISON *et al.,* 1993, 2000) may therefore underestimate the levels required for recovery into unvegetated areas, given sufficient capacity of the vegetation to improve conditions for growth.

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In the lower Chesapeake Bay, seagrasses occur at depths of <1.5 meters (ORTH and MOORE, 1983), where their capacity to modify local conditions may be significant. In such shallow environments, the plant communities can effectively attenuate waves and baffle tidal currents (FONSECA *et al.,* 1982; FONSECA, 1992; KOCH, 1999), and nutrient uptake from the water column may be rapid (MOORE and WETZEL, 2000; SHORT and MCROY, 1984). In the upper Chesapeake Bay, WARD, KEMP, and BOYNTON (1984) have demonstrated that suspended particulate matter concentrations can be significantly lower inside a bed of *Ruppia maritima* than outside of it. However, the effects of seagrass on water-quality conditions over small spatial and temporal scales within vegetated areas, especially as they compare to adjacent channel areas and formerly vegetated sites, are not well known.

Here is described a series of seasonal studies designed to investigate the water-quality characteristics of vegetated and formerly unvegetated sites in one southwestern tributary of the lower Chesapeake Bay, the York River, using fixed-station, high-frequency water-quality monitoring in combination with seagrass habitat measurements. The York River system is the location of the reserve site of the Chesapeake Bay National Estuarine Research Reserve in Virginia (CBNERRVA). The CBNERRVA was designated in 1991 and is managed by the Virginia Institute of Marine Science. Seagrass populations declined in this system between 1971 and 1974 (ORTH and MOORE, 1983), and today many areas remain devoid of vegetation (ORTH *et al.,* 2002). The objectives of this study were to determine if water quality in these shallow, littoral zones is distinct from that in adjacent deeper areas and how the presence of seagrass may modify these conditions.

METHODS

Two sites were chosen for study in the lower region of the York River to examine the relationships between seagrass bed development and water quality (Figure 1). The sites extended channelward from the shorelines of small uninhabited islands across shallow subtidal flats to water depths of 1.5 to 2.0 meters. Because the islands are isolated from the upland, inputs of nutrients from direct surface runoff and groundwater discharge were considered negligible. The first site, Goodwin Island, is an area that has remained consistently vegetated with seagrass vegetation (ORTH *et al.,* 2002) since declines in the early 1970s in this region were first documented (ORTH and MOORE, 1983). It is a CBNERRVA reserve site. The second site, Mumfort Island, is located 12 kilometers upriver. The shallow flats adjacent to the island had been vegetated with *R. maritima* (widgeon grass) and *Zostera marina* (eelgrass) prior to 1972 (MARSH, 1973). However, following complete loss of vegetation by 1974 (ORTH and MOORE, 1983), the area has remained unvegetated, and periodic attempts to transplant *Z. marina* have been unsuccessful (BATIUK *et al.,* 1992; MOORE *et al.,* 1996).

At the Goodwin Island site (37°12′ N, 76°23′ W), four stations were established along a transect running approximately northwest-southeast, beginning in the shallow subtidal flat adjacent to the east shoreline of the island, and extending 1.25 kilometers channelward (Figure 1). Station G1 (0.4 meters mean low water [MLW]) and station G2 (0.6 meters MLW) were within the seagrass bed, 130 meters and 270 meters, respectively, from the island shoreline (Figure 2). Station G3 (0.8 meters MLW) was located at the outer edge of the bed, 525 meters from the island shoreline. Station G4 (1.5 meters MLW) was located outside the bed in an area of bare bottom, 1.15 kilometers from the island. At each station a permanent pole, which supported a box that housed the remote sampling equipment, was placed in the bottom.

Three stations were established along a transect at the Mumfort Island site (37°15′ N, 76°30′ W) beginning in the shallow water adjacent to the island and extending ~0.50 kilometers channelward in a northeast-southwest direction (Figure 1). Station M1 (0.7 meters MLW) and station M2 (0.9 meters MLW) were located 140 meters and 310 meters, respectively, from the island (Figure 3) in locations that had been vegetated prior to 1974. Station M3 was located outside of the historically vegetated region, approximately 500 meters from the island. As with Goodwin Island, a permanent pole, which supported a box that housed the remote sampling and support equipment, was established at each station.

Water-Quality Sampling

At each of the stations, water-quality sampling (Table 1) was conducted during four 10-day periods in June, August, and October 1994 and in April 1995. During each study period, 1-liter ali-

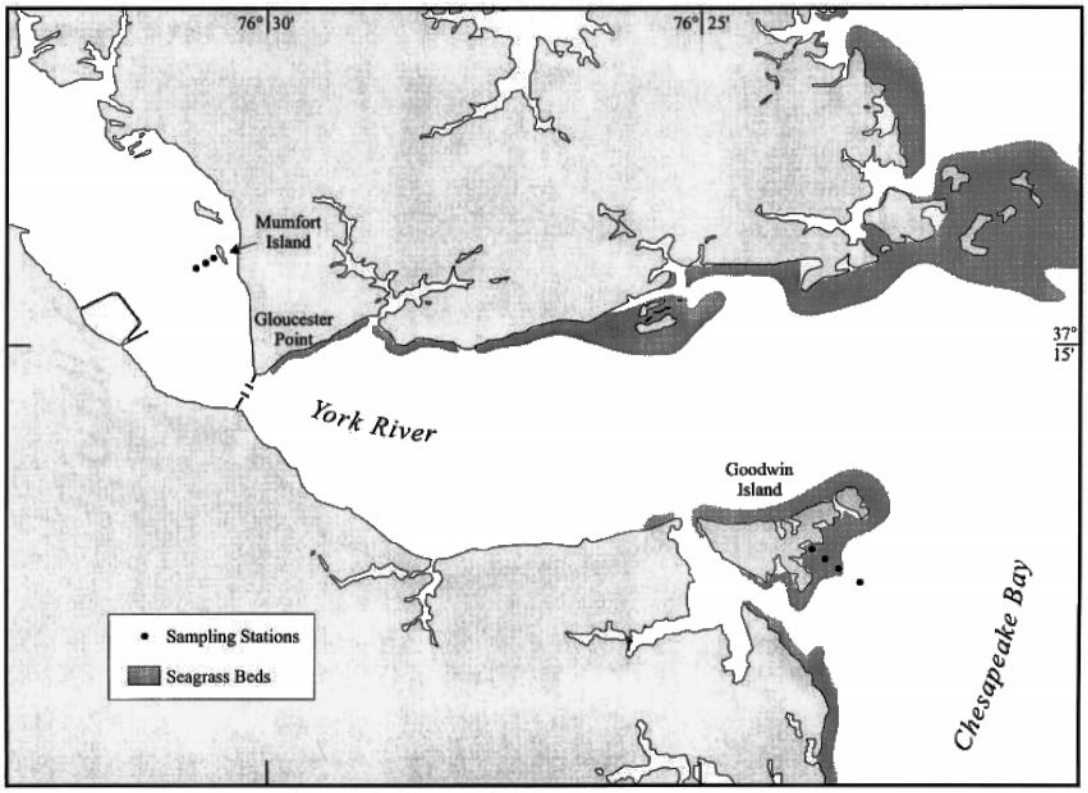

Figure 1. Lower York River CBNERRVA study areas showing sampling stations and seagrass distribution.

quots of water were sampled at 3-hour intervals at each station using automated samplers (Teledyne ISCO, Inc., Lincoln, NE; Table 1). Samples were pumped from fixed depths of 0.3 meters above the bottom at all stations, except for the channel-most station at Mumfort, where an additional series of samples were pumped from near the surface (Station 3Ms; −0.3 meters MLW).

All samples were preserved with a 100-μM solution of sodium azide (NaN_3), stored in ice for no more than 24 hours, then filtered through 0.45-micrometer filters and analyzed in duplicate for dissolved inorganic nutrients and suspended particles. Ammonium (NH_4^+) was determined spectrophotometrically after PARSONS, MIATA, and LALLI (1984). Nitrite (NO_2^-), nitrate (NO_3^-), and orthophosphate (PO_4^{3-}) were measured using an Alpkem Autoanalyzer (Alpkem Corporation, Clackamas, OR) equipped with a Model 510 Spectrophotometer. Total suspended solids (TSS) were determined by filtration (precombusted Gelman, Type A/E; Pall Corporation, East Mills, NY), rinsing with freshwater, and drying at 60°C. Percentage combustible matter was obtained by ashing at 550°C. Chlorophyll *a* (Chl *a*)was extracted using dimethyl sulfoxide/acetone (SHOAF and LIUM, 1976) and analyzed by fluorometry.

Dissolved oxygen (O_2), pH, salinity, temperature, and water depth were measured at 15-minute intervals using Hydrolab Data Sonde instrument systems (Hydrolab Corporation, Austin, TX) placed adjacent to the ISCO sampler intakes (Tables 2 and 3). These instruments were individually calibrated before each field deployment. In situ,

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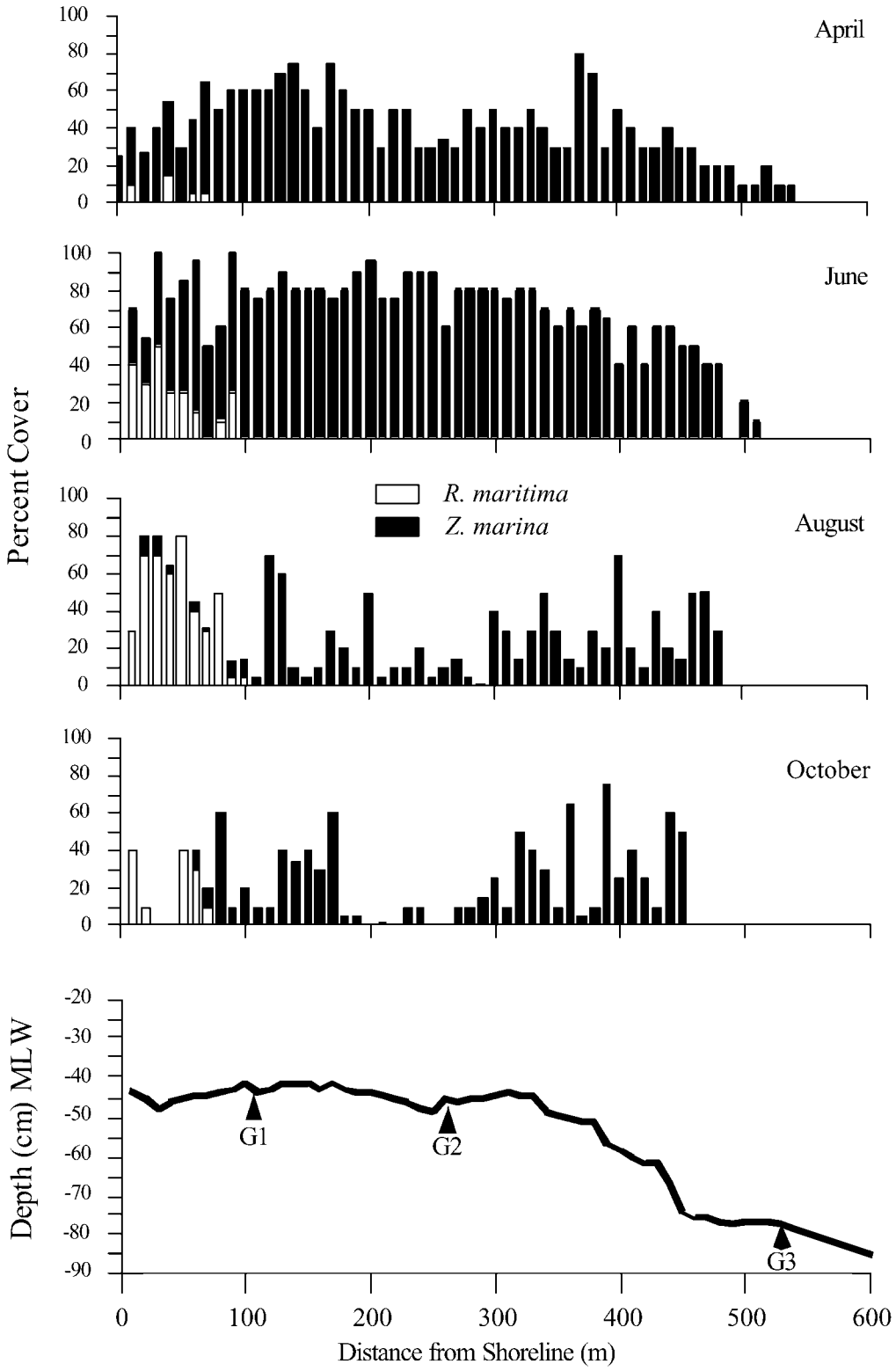
Figure 2. Percentage seagrass cover, depth profile, and sampling stations at Goodwin Island.



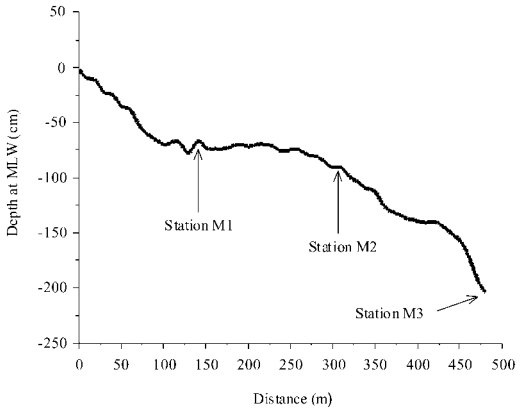


Figure 3. Depth profile and sampling stations at Mumfort Island.

photosynthetically active radiation (PAR) light attenuation was measured continuously and integrated over 15-minute periods using fixed arrays of underwater, scalar (4π), quantum sensors (LI-193SA, LI-COR, Inc., Lincoln, NE). The sensors were calibrated by the manufacturer prior to use and cleaned daily to remove fouling. The downwelling attenuation coefficient (K_d) was calculated according to Beer's Law. Atmospheric, downwelling irradiance (2π quantum, LI-190SA, LI-COR, Inc.) and 6-minute, vector-averaged wind speed and direction were continuously recorded ~10 kilometers from the sites at the Gloucester Point, Virginia, meteorological station (37°14.8′ N, 76°30.0′ W; height +45 meters above mean sea level).

Macrophyte Sampling

Monthly, from May 1994 through April 1995, 10 replicate 0.1-m^2 rings were placed on the bottom at random locations along the transect in the vegetated area at Goodwin Island between Stations G1 and G2. All seagrass, including roots and rhizomes to a depth of 0.2 meters, was removed, gently shaken to remove sediments, placed in plastic bags on ice, and returned to the lab for morphometric and mass determinations (Figures 4 and 5). Each sample was separated by seagrass species; the shoots were rinsed, counted, measured for length, cleaned of epiphytes, and separated into shoots and roots/rhizomes (cut distal to the fifth node). Shoot leaf area was determined using a meter (Model 3100 area meter, LI-COR, Inc.). Dry mass of the shoot and root/rhizome samples was determined after drying at 60°C to constant weight. Subsamples of shoot and root/rhizome tissue were freeze dried, ground in a Wiley mill, and analyzed in duplicate for total carbon and nitrogen (Perkin-Elmer CHN analyzer, Wellesley, MA). Duplicate portions of the subsamples were analyzed colorimetrically for phosphorus content after di-

Table 1. *Summary of parameters and sampling intervals for site and water-quality measurements at Goodwin Island and Mumfort Island, Virginia, study areas.*

Parameter	Interval
Site description	
Community transect (% cover, depth profile)	Seasonal (June, August, October, April)
Submerged aquatic vegetation (Goodwin only)	
Above/belowground mass; tissue C, N, P; density; shoot length; epiphyte mass	Monthly
Water-quality parameters	Seasonal (June, August, October, April)
TSS (inorganic, organic)	Every 3 h for 10 d
Chl *a*	Every 3 h for 10 d
NO_2	Every 3 h for 10 d
NO_3	Every 3 h for 10 d
NH_4	Every 3 h for 10 d
PO_4	Every 3 h for 10 d
K_d	Every 15 min for 10 d
Temperature	Every 15 min for 10 d
Salinity	Every 15 min for 10 d
Dissolved oxygen	Every 15 min for 10 d
pH	Every 15 min for 10 d
Tidal depth	Every 15 min for 10 d
Wind direction/speed	Every 15 min for 10 d

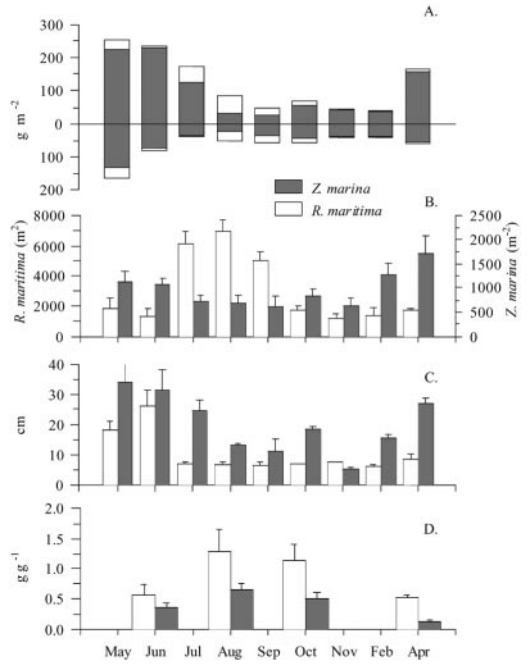


Figure 4. Seagrass biomass at Goodwin Island. (A) Aboveground and belowground biomass (gdm/m^2); (B) shoot density (count per m^2); (C) shoot length (cm); and (D) epiphyte biomass (gdm epiphyte per gdm). Error bars are standard error.

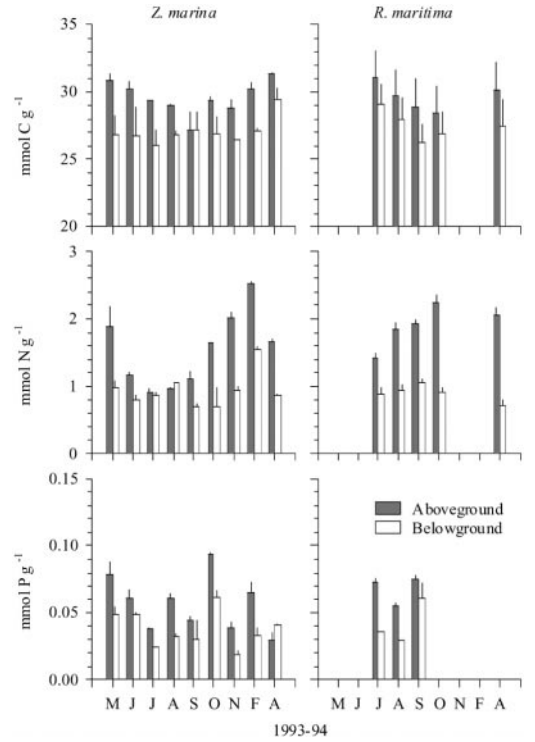


Figure 5. Aboveground and belowground tissue carbon (C), nitrogen (N), and phosphorus (P). (Error bars are standard error.)

gestion following SOLORZANO and SHARP (1980) as modified by FOURQUREAN and ZIEMAN (1992).

Separate samples were obtained for epiphyte mass determinations in June, August, and October 1994 and in April 1995. Individual shoots were carefully placed in plastic bags in the field and were returned immediately to the lab, where they were gently scraped to remove attached epiphytes. The epiphytic material was collected on glass fiber filters, rinsed with freshwater, and dried at 60°C. Leaf areas of shoots used to obtain each subsample of epiphytes were determined as before.

Macrophyte Relative Abundance and Depth Profiles

Macrophyte abundance was determined along the station transect during each of the seasonal 10-day sampling periods in June, August, and October 1994 and April 1995 at Goodwin Island. At 10-meter intervals, beginning at the island edge and continuing past the channelward edge of the bed, macrophyte standing crop was estimated by a point-intercept method (ORTH and MOORE, 1988). At each 10-meter point, a diver, who arbitrarily placed a 0.1-m^2 ring on the bottom, estimated percentage cover of macrophytes by species. At each measurement, water depth, distance along the transect, and time were recorded. A fixed tidal-reference staff was used to measure water height change. These relative depth data were then normalized to MLW using referenced tidal measurements at the National Ocean Survey, Gloucester Point tidal gauging station located ~10 kilometers west in the York River (37°14.8′ N, 76°30.0′ W).

A similar transect was conducted at Mumfort Island in June 1994. However, because the site was not vegetated with seagrass, only depth, distance, and water height were recorded.

Three 5-centimeter-deep sediment cores were randomly obtained along the transect both inside the bed between stations G1 and G2 and outside the bed between G3 and G4 at Goodwin Island, and between stations M1 and M3 at Mumfort Is-

Table 2. *Medians of water-quality parameters by station for June 1994 and August 1994 study periods at Goodwin and Mumfort islands. Identical superscripts denote no significant differences* ($p > 0.05$) *among stations within each study period and site.*

	Goodwin Island				Mumfort Island			
Parameter	Station G1	Station G2	Station G3	Station G4	Station M1	Station M2	Station M3s	Station M3d
June								
NO_2 (μM)	0.04[a]	0.04[a]	0.07[a]	0.02[a]	0.25[a]	0.35[b,c]	0.32[a,b]	0.39[c]
NO_3 (μM)	0.24[a]	0.18[a]	0.24[a]	0.31[a]	0.93[a]	2.06[b]	1.25[a]	2.28[b]
NH_4 (μM)	1.05[a]	1.15[a]	1.19[a]	2.01[a]	1.42[a]	1.41[a]	2.00[b]	1.94[b]
DIN (μM)	1.40[a]	1.53[a]	1.54[a]	2.30[b]	2.94[a]	3.61[a]	3.91[a]	4.67[b]
PO_4 (μM)	0.41[a]	0.48[a]	0.48[a]	0.48[a]	0.22[a]	0.26[a]	0.24[a]	0.28[a]
TSS (mg/L)	3.58[a]	3.90[a]	7.35[b]	7.50[b]	6.36[b]	5.88[b]	3.73[a]	7.25[c]
Chl *a* (μg/L)	8.48[a]	14.40[b]	24.80[c]	24.80[c]	24.72[b]	24.72[b]	22.80[a]	26.24[c]
pH	8.70[c]	—	7.85[a]	8.08[b]	—	8.16[b]	8.01[a]	8.17[b]
DO (mg/L)	9.29[a]	—	9.80[b]	10.54[c]	—	10.0[b]	—	9.51[a]
Salinity (psu)	15.84[c]	—	14.80[a]	15.00[b]	—	17.7[c]	17.2[b]	17.0[a]
Temp (°C)	25.35[c]	—	23.89[b]	23.76[a]	—	23.45[c]	23.41[b]	22.92[a]
K_d (per m)	0.98[a]	1.13[b]	1.05[a,b]	1.55[c]	1.91[c]	1.64[b]	1.33[a]	—
August								
NO_2 (μM)	0.10[b]	0.03[a]	0.02[a]	0.03[a]	0.13[a]	—	0.23[b]	0.22[b]
NO_3 (μM)	0.28[a]	0.21[a]	0.30[a]	0.29[a]	0.00[a]	—	0.00[a]	0.00[a]
NH_4 (μM)	1.77[b]	1.17[a]	0.87[a]	0.98[a]	2.31[a]	—	2.60[a]	2.23[a]
DIN (μM)	2.30[b]	1.51[a]	1.22[a]	1.33[a]	2.40[a]	—	2.84[a]	2.50[a]
PO_4 (μM)	0.34[a]	0.30[a]	0.32[a]	0.29[a]	0.35[a]	—	0.42[a]	0.39[a]
TSS (mg/L)	4.05[a]	6.11[b]	3.91[a]	4.58[a]	5.59[a]	—	5.38[a]	6.51[b]
Chl *a* (μg/L)	9.12[a]	10.96[b]	9.44[a]	10.48[b]	42.32[a]	—	40.32[a]	39.76[a]
pH	7.98[b]	8.13[c]	7.66[a]	8.17[c]	7.91[b]	—	7.75[a]	7.79[a]
DO (mg/L)	5.02[a]	6.46[b]	7.82[c]	6.78[b]	6.63[a]	—	6.80[b]	8.90[c]
Salinity (psu)	17.90[a]	19.70[d]	18.30[b]	18.70[c]	20.2[a]	—	21.20[b]	20.80[c]
Temp (°C)	27.20[d]	27.00[c]	26.79[a]	26.83[b]	25.23[c]	—	24.93[a]	25.05[b]
K_d (per m)	1.19[c]	0.80[a]	0.90[b]	0.94[b]	1.37[a]	1.39[a]	1.61[a]	—

DO = dissolved oxygen, Temp = temperature.

land. These cores were analyzed for grain size using standard pipette and dry-sieving techniques (FOLK, 1961).

Statistical Analyses

Friedman's analysis of variance (ZAR, 1984), a nonparametric procedure for testing repeated measures, was used to compare dissolved nutrients, TSS, Chl *a,* and physical variables for significant differences among stations located along each transect at each sampling period. Analyses were accomplished using Statistica/Mac (StatSoft Inc., Tulsa, Oklahoma). If medians were determined to be significant ($p \leq 0.05$), multiple, pairwise comparison analysis (ZAR, 1984) was used to compare individual station effects.

RESULTS AND DISCUSSION

Site Characteristics and Seagrass Community Development

The site characteristics of the seagrass bed at Goodwin Island were similar to other seagrass areas in the region (ORTH and MOORE, 1986; WETZEL and PENHALE, 1983). The shoreline of the island consisted of a *Spartina alterniflora* (smooth cordgrass) marsh that was separated from the landward edge of the bed by a narrow (10- to 20-meter), unvegetated, intertidal and subtidal zone. Seagrass first occurred at depths of approximately −40 centimeters MLW and extended channelward a distance of 550 meters to depths of −70 to −80 centimeters MLW (Figure 2). Greatest cover occurred in June, when nearly the entire bed exceeded 60%. *Zostera marina* dominated at all seasons, whereas *R. maritima* was found in the shallowest areas near the island. The topography of the seagrass bed was quite flat with only 0.1-meter relief over the first 350 meters of width. After this point, the depth gradually increased in the offshore direction. Bed width varied with season. During June, the bed extended nearly 550 meters from shore.

Zostera marina reached maximum abundance (300 gdm/m^2) and canopy height (33 centimeters)

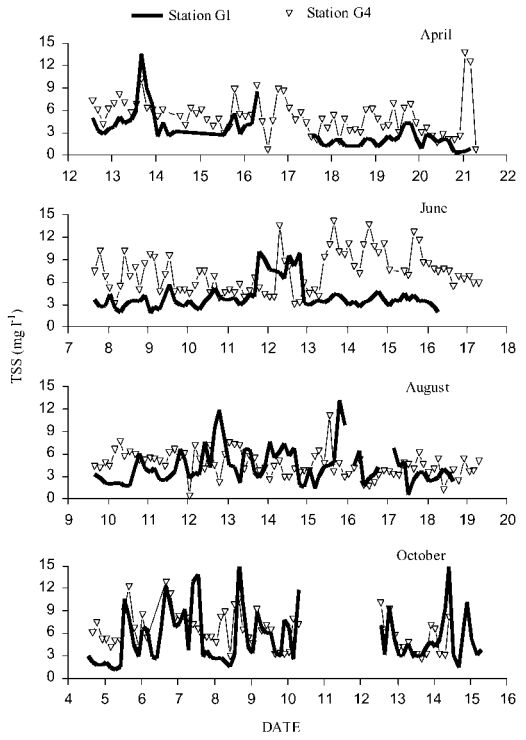


Figure 6. Goodwin Island total suspended solids (TSS).

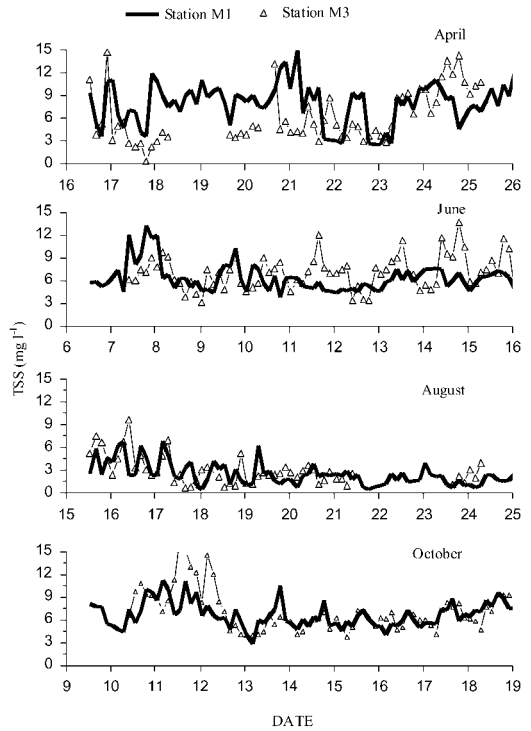


Figure 7. Mumfort Island total suspended solids (TSS).

in June, with *R. maritima* occurring largely as an understory at inshore areas (15 gdm/m^2, 10 centimeters; Figure 4). By August, a large dieback of *Z. marina,* particularly in the shallow, inshore areas was evident. *Ruppia maritima,* however, reached its greatest biomass (85 gdm/m^2) and density (>500 per m^2) during this summer period. Large accumulations of decaying macrophyte shoot material were present throughout the bed at this time. By October, *R. maritima* density (175 per m^2) and biomass (22 gdm/m^2) had decreased, and although *Z. marina* biomass was still low (80 gdm/m^2), new shoot production and seedling germination (MOORE *et al.,* 1995) of that species were evident. The bed maintained low (81 gdm/m^2) biomass of both *Z. marina* and *R. maritima* throughout the winter. By April, significant regrowth of the bed had occurred, with *Z. marina* predominating throughout.

The changing patterns of abundance of *Z. marina* and *R. maritima* observed here support the observations of EVANS, WEBB, and PENHALE (1986) that small-scale differences in the distribution of these two species may be related to their different photosynthetic capacities relative to light and temperature. *Ruppia maritima* occurred only at the most inshore zone, where depths were shallowest and light availability was greatest. Although *Z. marina* dominated in this zone from October through June it was rapidly replaced by *R. maritima* throughout the summer as water temperatures increased to their seasonal maximum.

The depth distribution of seagrass at the Goodwin Island site appeared to be controlled by environmental conditions. Annual recruits of *Z. marina,* identified through their rhizome structure, were commonly observed both in the shallowest and deepest areas early each year (Figure 2). By April, they accounted for ~10–25% of bottom cover in these areas. However, these recruits were unsuccessful colonizers of these zones, because inshore recruits were gone by June, and the outer, deeper edge of the bed retreated landward several hundred meters throughout the summer. The lower depth limit of the seagrass bed reported here is shallower than other nearby beds in this area

Table 3. *Medians of water-quality parameters by station for October 1994 and April 1995 study period at Goodwin and Mumfort islands. Identical superscripts denote no significant differences* ($p > 0.05$) *among stations within each study period and site.*

	Goodwin Island				Mumfort Island			
Parameter	Station G1	Station G2	Station G3	Station G4	Station M1	Station M2	Station M3s	Station M4d
October								
NO_2 (μM)	0.08[b]	0.11[b]	0.02[a]	0.02[a]	0.54[b]	0.58[c]	0.054[b]	0.49[a]
NO_3 (μM)	0.35[a]	0.40[a]	0.57[b]	0.53[b]	0.47[a]	0.79[b]	0.50[a]	0.41[a]
NH_4 (μM)	1.78[a]	1.77[a]	1.80[a]	1.70[a]	3.47[a]	4.27[b]	4.23[b]	3.52[a]
DIN (μM)	2.40[a]	2.35[a]	2.67[a]	2.29[a]	4.58[a]	5.91[b]	5.37[b]	4.47[a]
PO_4 (μM)	0.26[a]	0.32[a]	0.32[a]	0.29[a]	0.45[a]	0.52[b]	0.54[b]	0.42[a]
TSS (mg/L)	3.95[a]	4.84[a,b]	5.73[a,b]	6.51[b]	6.43[b]	6.05[a]	7.38[c]	6.59[a]
Chl *a* (μg/L)	5.96[a]	8.32[b]	14.24[c]	13.92[c]	18.16[b]	13.91[a]	15.59[a]	13.31[a]
pH	—	8.03[a]	8.12[c]	8.10[b]	7.83[c]	7.73[a]	7.82[c]	7.79[b]
DO (mg/L)	—	7.12[a]	7.94[c]	7.77[b]	8.34[b]	8.04[a]	8.42[b]	8.04[a]
Salinity (psu)	—	23.90[a]	24.10[b]	24.20[c]	22.00[c]	21.50[b]	21.40[a]	22.00[c]
Temp (°C)	—	19.06[a]	19.62[b]	19.74[c]	17.66[a]	17.79[b]	17.94[d]	17.92[c]
K_d (per m)	1.37[a]	1.47[b]	1.33[a]	1.23[a]	1.32[a]	1.49[b]	1.30[a]	—
April								
NO_2 (μM)	0.19[a]	0.43[b]	0.52[c]	0.51[c]	0.33[a]	—	0.34[a]	0.32[a]
NO_3 (μM)	0.64[a]	5.50[b]	9.53[c]	9.74[c]	0.14[a]	—	0.00[b]	0.00[b]
NH_4 (μM)	1.36[a]	0.85[a]	1.11[a]	1.08[a]	3.16[a]	—	3.78[b]	4.14[b]
DIN (μM)	3.07[a]	6.84[b]	11.41[c]	11.27[c]	3.84[a]	—	4.18[a]	4.49[a]
PO_4 (μM)	0.31[a]	0.33[a]	0.32[a]	0.28[a]	0.23[a]	—	0.29[a]	0.19[a]
TSS (mg/L)	5.65[a]	6.06[a,b]	5.82[a,b]	6.72[b]	7.76[a]	—	3.15[b]	5.08[a]
Chl *a* (μg/L)	6.34[a]	10.11[b]	15.96[c]	15.04[c]	21.92[a]	—	20.32[a]	23.10[b]
pH	8.73[a]	8.63[a]	8.32[b]	8.33[b]	7.47[b]	7.66[c]	7.87[d]	7.33[a]
DO (mg/L)	—	11.02[a]	8.25[c]	9.52[b]	10.55[b]	—	10.21[a]	10.15[a]
Salinity (psu)	—	12.50[a]	12.62[b]	13.10[c]	19.40[a]	19.64[b]	19.90[c]	19.40[a]
Temp (°C)	17.26[a]	15.92[b]	15.75[b]	15.70[b]	16.10[a,c]	16.01[c]	15.84[a]	15.87[b]
K_d (per m)	0.95[a]	0.92[a]	—	0.79[b]	—	2.67[b]	2.37[a]	—

DO = dissolved oxygen, Temp = temperature.

(Moore *et al.,* 1996; Orth and Moore, 1986) and may be related to local water clarity conditions. The loss of vegetation throughout the summer is, however, similar to the annual pattern of loss of transplants of *Z. marina* at upriver sites, which has been related to a period of high turbidity in the spring. Turbidities at the channel station G4 at Goodwin were highest in June (Table 2, Figure 6), suggesting a similar mechanism at this location.

Differences in sediment grain size inside and outside of the bed suggest that the vegetation at Goodwin Island is effective in trapping fine suspended sediments. Inside the bed, sand accounted for approximately 85%, silts and clays 13%, and shell and other material larger than 1.0 millimeter approximately 2% of total sediment weight. Outside of the bed, sands, silts and clays, and particles larger than 1.0 millimeter accounted for 92%, 6%, and 2% of weight, respectively. These differences are similar to differences in surface sediments inside and outside of *Z. marina*–dominated beds observed elsewhere (Kenworthy, Zieman, and Thayer, 1982; Orth, 1977).

Patterns of C, N, and P in aboveground and belowground tissue contents of both seagrass species varied seasonally (Figure 5) and are in the range of levels reported for other eelgrass populations (Harrison and Mann, 1975; Moore and Wetzel, 2000; Thayer, Engel, and La Croix, 1977). Nitrogen content in shoot tissues of both *Z. marina* and *R. maritima* demonstrated annual minima in July and maxima in the fall and winter when they exceeded 2 mmol nitrogen per gram. During the summer (July–September), shoot tissue N was higher in *R. maritima* than *Z. marina* (1.2–1.8 mmol nitrogen per gram *vs.* 1.0 mmol nitrogen per gram). Belowground tissue N demonstrated less annual variability and remained consistently around 1 mmol nitrogen per gram in both species throughout the year. Phosphorus levels were quite variable throughout the year for both aboveground and belowground tissues of both species, ranging from 0.02 to 0.06 mmol phosphorus per gram of

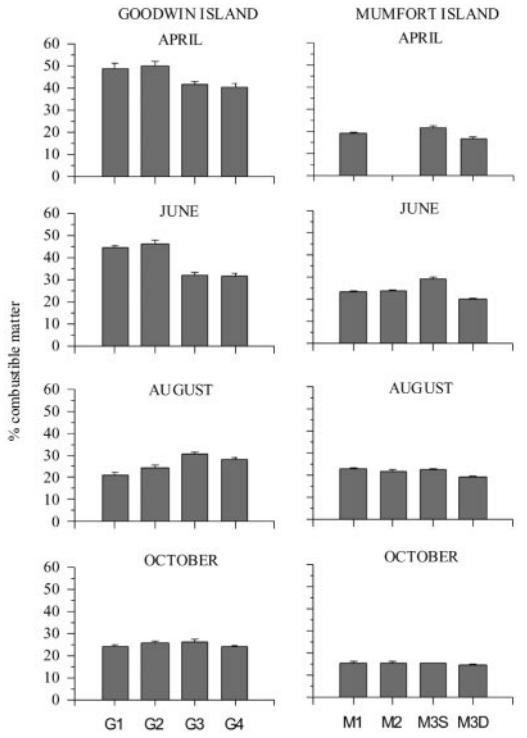


Figure 8. Combustible suspended matter as percentage of total suspended solids. (Mean + standard error.)

belowground and 0.03 to 1.0 mmol phosphorus per gram of aboveground tissue mass. Aboveground tissue carbon was seasonally highest in the fall and winter (>30 mmol carbon per gram) and decreased throughout the summer to annual minima (27–28 mmol carbon per gram) in September in both species. Belowground tissue C in *R. maritima* paralleled the pattern of decreasing aboveground tissue C levels throughout the summer; however, *Z. marina* belowground tissue remained nearly constant throughout this period.

Epiphyte mass varied seasonally from April minima to August maxima (Figure 4), and levels for *Z. marina* were consistent with levels reported for other vegetated areas in the region (MOORE *et al.,* 1996). Seagrass leaf tissue–specific levels were always higher on *R. maritima* than *Z. marina,* exceeding 1 gdm epiphyte per gdm leaf during August and October.

In contrast to Goodwin Island, the shoal area of Mumfort Island remained unvegetated throughout the study, and no evidence of seagrass recruits or seedlings was observed throughout the area (Figure 3), even though seagrass beds are located within several kilometers of the site (Figure 1). The transect extended channelward from a small sandy island vegetated with *S. alterniflora* and *Spartina patens.* The surface sediments of the submersed shoal consisted of ~96% medium to fine sands, 2% silts and clays, and 2% shell and other material 1 millimeter or greater in size by weight and were similar to the unvegetated station G4 at Goodwin Island. Such sediment characteristics are comparable to those reported by others who have worked in this area over the past 30 years (MARSH, 1973; RIZZO, 1986), suggesting that there has been little change in sediment conditions over that time.

Water-Quality Conditions in Relation to Seagrass Community Development

Suspended Particles and Light

Suspended particle concentrations in the water column were clearly reduced by the presence of vegetation at Goodwin Island compared to Mumfort Island, especially during April and June when the seagrass community development was greatest (Figures 6 and 7). Levels of TSS and Chl *a* were consistently lower in the bed than outside of it during these study periods (Tables 2 and 3), and midday light attenuation was significantly lower in the bed than outside of it during June. In addition to lower overall medians, the high variability of TSS at the channel station was greatly dampened within the bed. However, during August, when seagrass biomass was low, the effects of the vegetation on suspended particle concentrations were not evident. Resuspension of bottom material at station G2 resulted in significantly higher TSS ($p < 0.05$) than at all other stations at that time.

The percentage combustible matter in TSS reflected the source and sinks of the suspended particles at Goodwin Island. The organic matter in the suspended load was lower outside the bed than inside of it during April and June (Figure 8), as the organic component was diluted by resuspension of the principally inorganic bottom sediments. Overall, percentage combustible matter increased proportionally as TSS decreased (Figure 9), and in June, during periods when suspended loads were lowest within the bed, organic matter comprised nearly all the suspended particles. Interestingly, Chl *a* decreased significantly from outside to inside the bed during April and June, when per-

centage suspended organic matter was increasing (Tables 2 and 3). These data suggest that much of the organic component by mass of the suspended load may be detrital or other fine-grained organic material. During August, percentage combustible matter in the suspended load was lower in the bed than out of it, likely reflecting resuspension of inorganic sediments. The proportion of combustibles in the suspended matter at Goodwin Island decreased throughout the year (Figure 8) as evidenced by the marked decrease in percentage combustible matter at TSS concentrations <5 mg/L. It may be that much of the organic matter in the suspended load is buried or exported throughout the year as the seagrass vegetation dies back.

Although direct measures of sediment deposition at Goodwin Island were not made, sediment deposition (D) within the bed may be approximated using the following equation (after WARD, KEMP, and BOYNTON, 1984):

$$D = 1/A \int_{to}^{tf} (C_t Q_t p^{-1})\, dt$$

Here, A is a unit area of seagrass bed; C_t is the difference in TSS concentration between stations inside and outside of the bed; Q_t is the volume of water transported into and outside of the bed due to tides, assuming a mean tidal range of 0.6 meters; and p is dry bulk density of 1 g/cm^3. Net sediment accumulations within the bed were estimated to be ~0.007 and 0.012 cm/month during the April and June studies, respectively, a net loss of 0.007 cm/month during August and no net deposition during October.

These levels are much lower than the sediment accretion rates of 0.2–0.3 cm/month estimated for a submersed macrophyte bed in the Choptank River, Maryland, by WARD, KEMP, and BOYNTON (1984). However, mean concentrations of suspended particulate matter in their offshore sampling site were 40–110 mg/L, compared with 5–8 mg/L for Goodwin Island. Therefore, the potential source for depositional material there would have been much greater. Others have similarly observed the deposition of sediments within *Vallisneria americana* and *Zannichellia palustris* beds in other regions of the Chesapeake Bay (MOORE *et al.,* 1995, 1996). Thus, submersed macrophyte beds throughout the bay have a potentially great capacity for suppressing resuspension and enhancing deposition even under very turbid conditions. The net loss of sediment during August at Goodwin Island and the lack of net deposition during October suggest that in lower bay seagrass beds much of the material trapped during the spring may be resuspended and exported once the vegetation declines in midsummer. In upper bay sites dominated by *R. maritima* such as those studied by WARD, KEMP, and BOYNTON (1984), peak biomass is not attained until the midsummer. Resuspension and transport from the vegetated shallows there may occur later in the year.

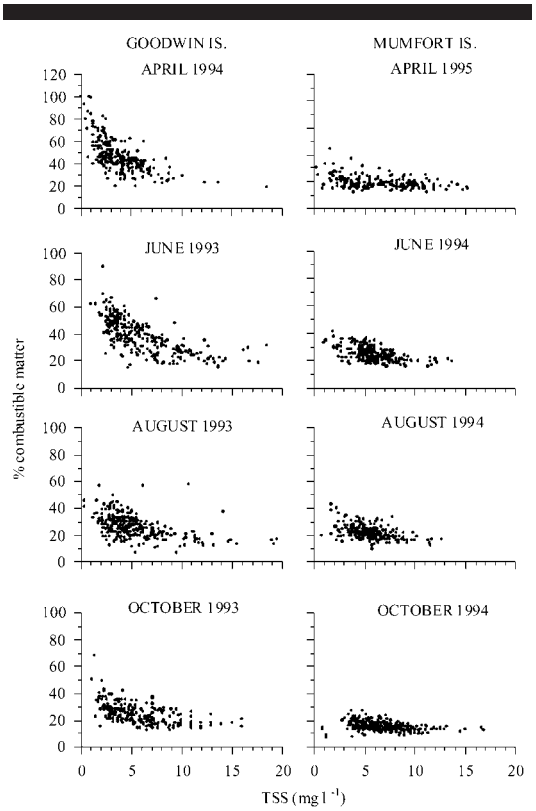


Figure 9. Percentage combustible matter *vs.* total suspended solids.

In contrast to Goodwin Island, where the presence of seagrass was associated with lower TSS concentrations and decreased turbidity in the bed than outside of it during the spring, Mumfort Island was characterized by significantly greater suspended particle concentrations and increased light attenuation inshore than offshore during the April and June studies (Tables 2 and 3, Figure 7). This may have important implications for recovery of seagrasses into formerly vegetated areas. Evidence suggests that light conditions during the

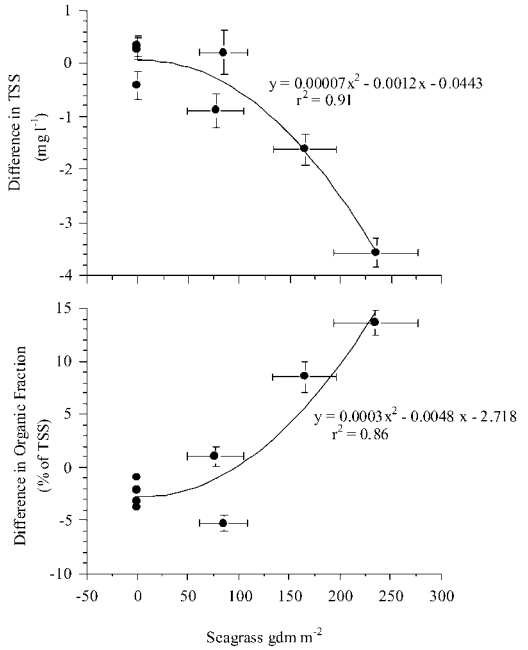


Figure 10. Differences in TSS and organic fraction of TSS between channel and shoal stations at Goodwin and Mumfort islands (G1–G4 and M1–M3) during all study periods *vs.* seagrass aboveground biomass. (Error bars are + standard error.)

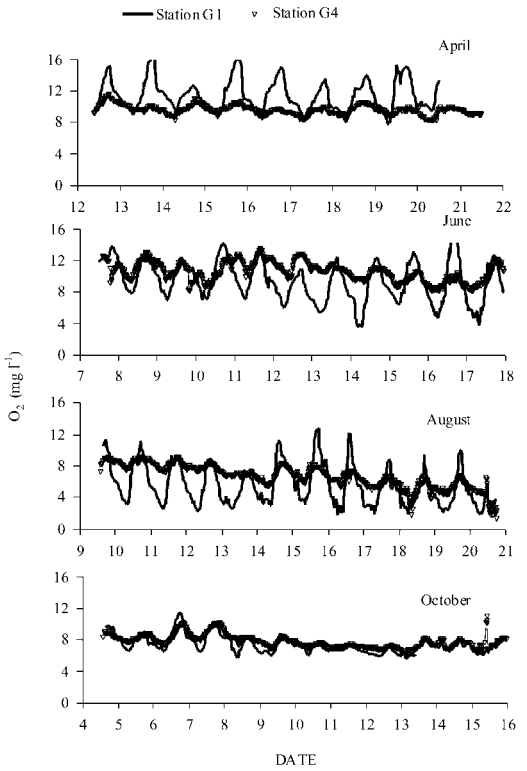


Figure 11. Goodwin Island water column dissolved oxygen (O_2).

spring are critical to long-term survival in this region (MOORE, WETZEL, and ORTH, 1997). Given the seasonally high levels of TSS observed in this region during the spring (Tables 2 and 3; MOORE *et al.,* 1996; MOORE, WETZEL, and ORTH, 1997) and the lack of existing vegetation to reduce resuspension and enhance deposition, it appears that seagrass recovery into this former habitat will be very slow.

The effects of bed biomass and density on the attenuation of suspended particles in the shallows observed here suggest that there may be a critical level of development below which little effect on the level or compositions of TSS may be evident. Comparison of the mean seasonal differences in TSS concentrations between the most inshore and channelward stations at Goodwin and Mumford islands and the mean seasonal seagrass biomass (Figure 10) reveals, in fact, that at shoot biomass levels of <50–100 gdm/m^2, little effect of bed structure on suspended particle concentrations and light attenuation may be expected. WARD, KEMP, and BOYNTON (1984) evaluated sedimentological activity using sediment traps and suggested that resuspension of bottom sediments in the macrophyte bed was no longer occurring at bed biomass values >175 gdm/m^2. Using a relationship between percentage cover and gdm per square meter shoot biomass of 1 : 3, which is determined here from the Goodwin Island data, and the above relationships between seagrass biomass and suspended particle reduction, ~25% to 50% of the bottom would have to be vegetated with seagrass before significant TSS reduction could be expected. Dieback in midsummer of the outer 200 meters of the bed at Goodwin Island may, in part, be related to a reduced baffling effect, as seagrass cover early in the year was generally <50% in this outer zone. In addition, seagrass transplant experiments in unvegetated upriver sites have been generally small in area, with coverage usually <50% (MOORE *et al.,* 1996; R.J. ORTH personal communication). Little capacity for localized improvements in water quality would therefore be expect-

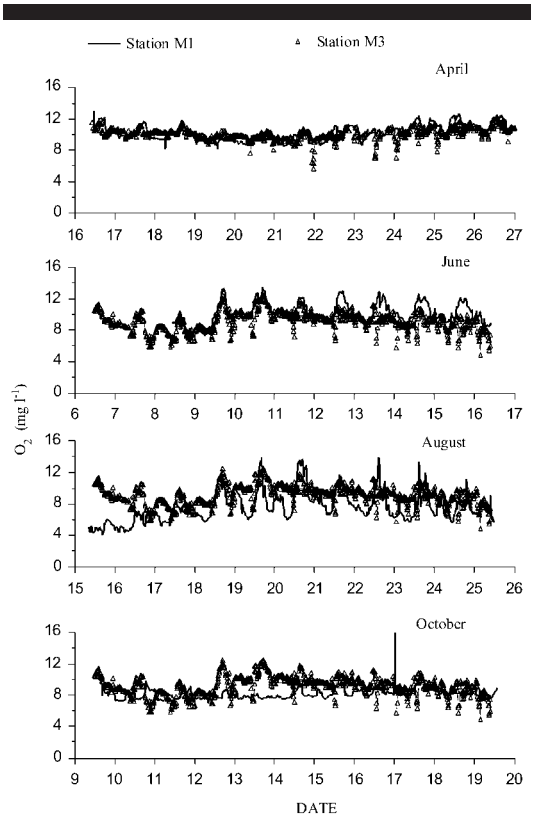


Figure 12. Mumfort Island water column dissolved oxygen (O_2).

ed, and the transplanted plots were largely unsuccessful. Given adequate bed size and density, however, seagrass may persist through periods of high turbidity (MOORE, WETZEL, and ORTH, 1997), which are currently limiting recovery in some areas. During June at Goodwin Island, for example, K_d dropped from 1.5 to 1.0 per meter from outside to inside the bed. This corresponded to an increase in water column PAR of 63%.

Water Column Oxygen and Nutrients

Large diurnal ranges in water column O_2 within the seagrass bed at Goodwin Island during April, June, and August (8–10 mg/L; Figure 11) reflect the large macrophyte, algal, and phytoplankton production by day and the community respiration at night constrained within the relatively shallow water column of the seagrass bed (MURRAY and WETZEL, 1987; NIXON and OVIATT, 1972). These water column values contrast with those of channel stations where daily ranges were typically 1–4 mg/L. At Mumfort Island diel ranges of O_2 (2–6 mg/L; Figure 12) were less than those at Goodwin Island. Ranges at inshore stations at Goodwin Island were greater than those of offshore stations during June and August. Median concentrations (Tables 2 and 3) generally were not significantly different among stations within sites, although median O_2 concentrations were significantly lower at station G1 than all other stations during August, suggesting highest respiration rates there.

Ammonium comprised 60% to 90% of dissolved inorganic nitrogen (DIN) during most seasons at both Goodwin Island and Mumfort Island (Tables 2 and 3). Nitrate predominated in the water column only during the April study at Goodwin Island. Few significant differences among stations were observed in the individual DIN species at Mumfort Island, although bottom water samples at station M3 were slightly higher than surface samples during June. However, at Goodwin Island ammonium was significantly higher within the bed than out, especially at night, during August, and nitrate was significantly lower in the bed than out throughout the April study.

Dissolved inorganic phosphate concentrations were quite consistent among stations and sites (0.2 to 0.5 μM; Tables 2 and 3). There were generally no significant differences in median water column inorganic phosphate concentrations between channel and shoal sites. At Goodwin Island in August, however, inorganic phosphate concentrations inside the bed were elevated for several hours each day as O_2 concentrations reached daily minima, suggesting temporary phosphate release from the sediments.

When distinct differences in nutrient concentrations between shoal and near channel stations occur, they may be reflective of processes regulating the cycling of nutrients in these areas given an absence of external sources. During August at Goodwin Island, for example, distinct diel periodicities in ammonium and inorganic phosphate were observed. Figure 13 presents time series–aggregated data of the 3-hour ammonium and inorganic phosphate concentrations and the 15-minute O_2 concentrations for all stations. At channel stations G3 and G4, no apparent diel changes in nutrient concentrations were observed. However, at vegetated stations G1 and G2, ammonium levels in the water column were observed to increase markedly at night from ~1 to 3 μM. No similar changes were observed in nitrate or nitrite. In ad-

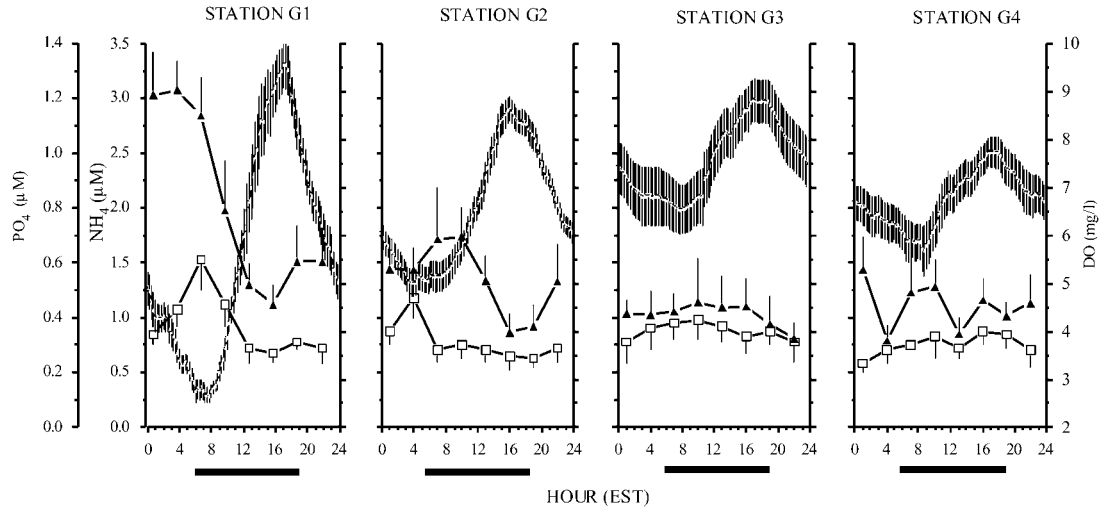


Figure 13. Goodwin Island 10-day mean diel water column dissolved oxygen (circle), NH_4^+ (triangle), and PO_4^{-3} (square). Shaded bars are photoperiods. (Means ± standard error.)

dition, as O_2 concentrations dropped to <5 mg/L at the 30-centimeter sensor height, inorganic phosphate concentrations increased, on average, from 0.3 to 0.6 μM.

Flux rates of O_2 and NH_4^+ were calculated from hourly changes in nutrient and oxygen concentrations at night at station M1 (Figure 13). The slope of the relationship between O_2 and NH_4+ was ~38 : 1 (Figure 14), which was considerably higher than the Redfield ratio of 17.25 : 1 if ammonium is the end product (Redfield, 1934; Redfield, Ketchum, and Richards, 1963). Assuming a 1 : 1 molar relationship between oxygen uptake and carbon release, the C : N ratio of 19 : 1 is very similar to the average annual C : N ratio of 18.5 for *Z. marina* at the site. The O : N fluxes were greater on average than summertime benthic fluxes across the sediment–water interface reported for Chesapeake Bay channel stations (Boynton and Kemp, 1985) and may be the result of higher denitrification in the seagrass sediments in this region (Caffrey and Kemp, 1990). Average release rates of inorganic phosphate were ~0.03 mmol/m²/h, with similar rates of reabsorption. Such rates are similar to rates reported for inorganic phosphate flux by Boynton and Kemp (1985) for the Chesapeake Bay but low for other estuaries (Nixon, 1981). The fluxes corresponded directly to water column O_2 levels and may represent desorption from bound complexes under anoxic sediment conditions.

The seagrass bed at Goodwin Island also demonstrated a strong capacity to remove nutrients when available in relatively high concentrations from the water column, as observed in other studies (Short and McRoy, 1984; Thursby and Harlin, 1982). During April, unusually high levels of nitrate (>10 μM) were measured at the channel stations throughout the study period. These nitrate concentrations were rapidly reduced within the seagrass bed as median levels decreased 10-fold to <1 μM by station G1. Assuming a mean tidal range of 0.6 meters, the net daily uptake is estimated as ~10 mmol N/m²/d. Growth requirements of the seagrasses can account for a large proportion of this uptake. Using tissue N levels reported here (Figure 5), a mean total biomass of 227 gdm/m² for April, a growth rate of 3%/d, and an estimated internal recovery and root uptake of 50% (Borum, Murray, and Kemp, 1989), the N requirement for growth of the seagrasses would be 4.75 mmol N/m²/d or 48% total uptake.

CONCLUSIONS

The feedbacks described here between increasing seagrass bed biomass and improvements to local water-quality conditions that are important for survival may be either positive or negative depending on a number of factors. The capacity of seagrass beds in the lower Chesapeake Bay to re-

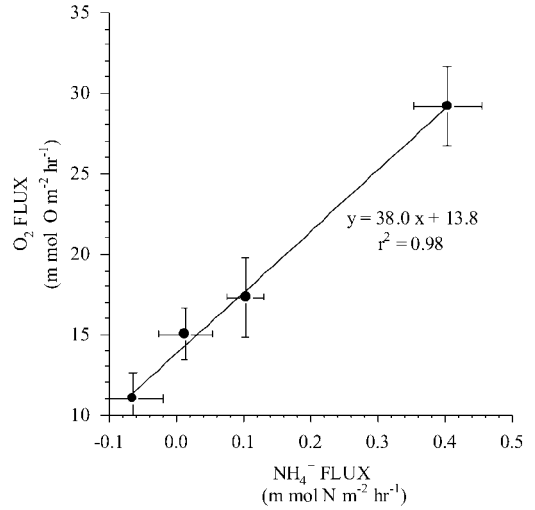


Figure 14. Relationship between O_2 and NH_4^+ flux at Goodwin Island station G1, August 1994. (Means ± standard error.)

duce suspended particle concentrations and modify water-quality conditions may be a key to their continued survival in stressed environments. Given sufficient biomass of seagrass to modify local conditions, current water-quality levels in formerly vegetated sites in lower bay tributaries may not necessarily be limiting to seagrass. However, given no existing vegetation, recovery of sites, such as Mumfort Island, may be very difficult unless conditions improve such that a critical mass of seagrass can be established. This process may involve a number of years of low freshwater flow to the bay or other factors that would improve water quality beyond existing levels. Seagrass habitat quality criteria that are based on correspondence between existing seagrass vegetation and adjacent water-quality conditions (BATIUK *et al.,* 1992, 2000; DENNISON *et al.,* 1993) may underestimate the water-quality levels needed for recovery into many areas by not considering seagrass bed effects. Such levels, although suitable for the maintenance of existing seagrass, may not be sufficient for restoration of unvegetated sites.

Seagrass beds surviving under stressed conditions could be very susceptible to short-term events or conditions (such as storms, dredging activities, or other disturbances) that may reduce bed biomass below threshold levels of 25–50% cover. Reduced bed biomass would then likely result in increased local resuspension, with a cascade of negative effects including lower light availability, lower plant growth, and consequently further resuspension and bed loss.

The influence of seagrass on water quality in shallow waters varies seasonally and reflects the capacity of these communities to act as sources and sinks for nutrients and suspended particles. Uptake and deposition in the spring are balanced by release and resuspension later in the year. The dynamic roles that these communities play throughout the year, however, are as yet not well understood. The diurnal patterns of nutrient exchange evident here during the summer at the Goodwin Island Estuarine Research Reserve site suggest that processes responsible for the transformation of nutrients and metabolism in shallow water areas are complex and can be different among vegetated shallows, unvegetated shallows, and adjacent channel areas.

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