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Macroalgal Distribution Patterns in a Shallow, Soft-bottom Lagoon, with Emphasis on the Nonnative *Gracilaria vermiculophylla* and *Codium fragile*

MADS SOLGAARD THOMSEN*, KAREN J. MCGLATHERY, and ANNA CHRISTINA TYLER

Department of Environmental Sciences, University of Virginia, 291 McCormick Road, P. O. Box 400123, Charlottesville, Virginia 22903

ABSTRACT: We determined the distribution of macroalgae in Hog Island Bay, a shallow coastal lagoon in Virginia, USA, seasonally at 12 sites from 1998 to 2000 and at 3 representative sites from 2000 to 2002. We analyzed macroalgal biomass, taxonomic richness, and abundance of two non-native species, the cryptic invader *Gracilaria vermiculophylla* and the conspicuous *Codium fragile*, with respect to season, location (mainland, mid lagoon, barrier island sites), and elevation (intertidal, subtidal). Taxonomic richness, total algal biomass, and nonnative biomass peaked in the summer months when temperature and light availability were highest. A few stress tolerant and ephemeral algae dominated the algal assemblage. *G. vermiculophylla* constituted 74% of the entire algal biomass, was the most abundant alga in all seasons, locations, and elevation levels, and was positively correlated with taxonomic richness and abundance of filamentous species. *Ulva curvata*, *Bryopsis plumosa*, and *C. fragile* accounted for an additional 16% of the algal biomass. There are distinct habitats in Hog Island Bay that can be classified into low diversity-low biomass regions near the mainland and barrier islands and high diversity-high biomass regions in the open mid lagoon, where abundant shells for attachment and intermediate levels of water column nutrients and turbidity likely create better growth conditions. Taxonomic richness and biomass were higher in subtidal than intertidal zones, presumably due to lower desiccation stress. This study provides an example of how a single invasive species can dominate an entire assemblage, both in terms of biomass (being most abundant in all seasons, locations, and tidal levels) and species richness (correlating positively with epiphytic filamentous taxa). By adding hard-substratum structural complexity to a relatively homogenous soft-substratum system, *G. vermiculophylla* increases substratum availability for attachment and entanglement of other algal species and enhances local diversity. Without widespread and abundant *G. vermiculophylla*, taxa like *Polysiphonia*, *Ceramium*, *Bryopsis*, *Ectocarpus*, and *Champia* would likely be much less common. This study also highlights the importance of using DNA analysis of voucher specimens in monitoring programs to accurately identify cryptic invaders.

Introduction

Shallow lagoons are important land-margin ecosystems worldwide, constituting at least 14% of the world's coastline (Cromwell 1971). These soft-bottom systems provide extensive areas for seagrasses and macroalgae (Norton and Mathieson 1983; Sand-Jensen and Borum 1991; Boynton et al. 1996). Seagrasses and low density algal mats are important habitats, providing nursery grounds for fish, substrate for attachment of sessile organisms, shelter from predation, food supply, and amelioration of adverse stresses such as desiccation (Norkko 1998; Norkko et al. 2000). Dense drift algal mats have become increasingly abundant in coastal lagoons and this proliferation has had a negative effect on seagrass meadows (Lee and Olsen 1985; Taylor et al. 1995; Hauxwell et al. 2001). These changes are well documented by quantitative surveys and baseline data sets from northern and southern United States Atlantic lagoons (e.g., Cowper 1978; Thorne-Miller et al. 1983; Virnstein and Carbonara 1985) and have been related to nutrient overenrichment (Fletcher 1996; Hauxwell et al. 2001; McGlathery 2001). Comparatively less is known about mid Atlantic lagoons, where existing data on algal distributions are based on presence-absence or dominance scales (e.g., Wulff and Webb 1969; Rhodes 1970; Humm 1979; Connor 1980). Quantitative distribution data are needed to track biotic changes associated with anthropogenic stressors such as nutrient enrichment or invasion by nonnative species.

Our main objective was to provide a first quantitative data set of macroalgal distribution patterns from the mid Atlantic region and to describe spatial and temporal variations in distribution, taxonomic richness, and abundance of key species. Much of the previous work on macroalgal distribution has correlated spatiotemporal variability with individual factors related to season (light or temperature effects; Connor 1980; Wolfe and Harlin 1988), location or distance from a mainland (nutrient

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* Corresponding author; current address: Edith Cowan University, School of Natural Sciences, Faculty of Computing, Health and Science, Joondalup Campus, 100 Joondalup Drive, Joondalup, Western Australia 6027; tele: +61 8 6304 5674; fax: +61 8 6304 5762; e-mail: mads_thomsen@mailcity.com

effects; McGlathery 1992; Castel et al. 1996; Flindt and Kamp-Nielsen 1997), or elevation (desiccation effects; Doty 1946; Dromgoole 1980). These environmental factors typically covary across spatiotemporal gradients, and few studies on soft-bottom systems have addressed the simultaneous effects of multiple factors on macroalgal distribution.

In addition to nutrient overenrichment, invasions by nonnative species have been detrimental to biodiversity and ecosystem function in many coastal ecosystems (Ruiz et al. 1997, 1999). In Hog Island Bay, we have identified two nonnative species, *Gracilaria vermiculophylla* and *Codium fragile* ssp. *tomentosoides* (hereafter *C. fragile*), that both originated from the western Pacific (Thomsen 2004a; Thomsen et al. 2005). *C. fragile* has no close relatives in the northwest Atlantic and its arrival and spread were easily recognized (Hillson 1976; Trowbridge 1998). *G. vermiculophylla* arrived into a region with morphologically similar relatives, such that the invasion was cryptic until recent discovery by molecular analysis (Rueness 2005; Thomsen et al. 2005). Because of the potential effect of invasive macroalgae on estuarine ecosystems (Ruiz et al. 1997, 1999), we focus a substantial portion of our analysis on these two species.

Materials and Methods

STUDY LOCATION

Hog Island Bay is located within the Machipongo drainage basin on the Delmarva Peninsula, and is c. 100 km^2 in area (Fig. 1). It is part of the Virginia Coast Reserve (VCR) Long Term Ecological Research (LTER) site. The bay bottom consists of sands and muds, with scattered unconsolidated bivalve shells and oyster reefs providing hard substratum for sessile organisms. These reef structures are particularly extensive in the mid lagoon region. The average water depth is 1.5 m; 37% of the lagoon surface area is intertidal and 80% is less than 3 m deep (Oertel 2001). The semidiurnal tidal range is c. 1.2–1.5 m (Oertel 2001), although storm surges can add at least an extra meter of water.

Water and sediment properties differ along the mainland-lagoon-barrier island transect. Typical values of water transparency, water column nutrients, and sediment organic matter are reported in McGlathery et al. (2001), with concentrations highest at sites near the mainland, intermediate in the mid lagoon region, and lowest at barrier island sites (Table 1). These physiochemical data are representative for the mainland-lagoon-barrier island transect based on the LTER water quality data set (http://www.vcrlter.virginia.edu/data/). Air temperature can vary seasonally from −5°C to 35°C and water temperature from 2°C to 28°C (http://www.vcrlter.virginia.edu/data/). Salinity ranges from 27‰ to 34‰ within the bay, depending on precipitation events and tidal flushing (Thomsen 2004a).

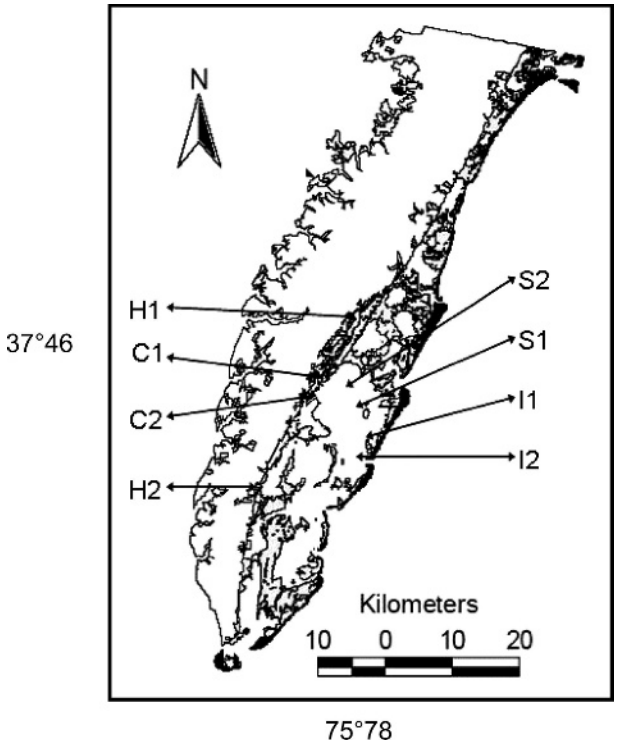

Fig. 1. Sample locations in Hog Island Bay and nearby areas on the Delmarva peninsula: H1 (Harbor1 at Willis Wharf, 75°819′3825″W, 37°461′7235″N) and H2 (Harbor2 at Oyster, 75°933′0825″W, 37°281′3235″N) are harbor sites, C1 (Creek1, 75°819′3825″W, 37°470′7435″N) and C2 (Creek2, 75°819′3831″W, 37°470′7438″N) are near mainland creek sites, S1 (Shoal1, 75°773′9025″W, 37°434′6635″N) and S2 (Shoal2, 75°785′2725″W, 37°461′7235″N) are open mid lagoon shoal sites, and I1 (Island 1 behind Hog, 75°728′4225″W, 37°371′5235″N) and I2 (Island2 behind Cobb, 75°739′7925″W, 37°353′4835″N) are near ocean back barrier island sites. All sites were subtidal, but note that C1, C2, I1, and I2 also had matching nearby intertidal sample locations (c. 100 m apart) but these could not be distinguished on the map.

SAMPLING DESIGN

Twelve soft-bottom sites (Fig. 1) were sampled 13 times from summer 1998 to spring 2000. Eight of the sites were shallow subtidal (c. 0.7–1.0 m below mean sea level [MSL]) and 4 were intertidal (c. 0.5–0.2 m below MSL). We classified sites into 2 subtidal mainland harbor sites (H1 = Harbor1 at Willis Wharf, H2 = Harbor2 at Oyster), 4 mainland creek sites (C1 = Creek1, C2 = Creek2, both with paired subtidal and intertidal sites), 2 subtidal mid lagoon shoal sites at intermediate distances from the peninsula (S1 = Shoal1, S2 = Shoal2), and 4 barrier island sites furthest away from the peninsula

TABLE 1. Mean values of key physical and chemical characteristics along the lagoonal transect in Hog Island Bay (±1 SE, data based on McGlathery et al. 2001).

	Near Mainland Creek (Creek1)	Mid Lagoon Shoal (Shoal1)	Near Ocean Island (Island1)
Dissolved inorganic nitrogen (μM)	4.4 (0.9)	2.3 (2.5)	1.2 (0.4)
Dissolved organic nitrogen (μM)	15.4 (1.9)	12.1 (3.7)	11.8 (1.6)
Dissolved inorganic phosphorous (μM)	1.4 (0.2)	0.8 (0.1)	0.5 (0.1)
Sediment organic content (% dw)	3.8 (0.2)	2.1 (0.3)	0.5 (0.3)
Sediment nitrogen content (% dw)	0.11 (0.00)	0.03 (0)	0.01 (0)
Light extinction coefficient (m^{-1})	2.2 (0.6)	1.9 (0.8)	1.7 (0.7)

(I1 = Island1 behind Hog Island, I2 = Island2 behind Cobb Island, both with paired subtidal and intertidal sites). Following the initial 13 surveys, sampling was reduced to 3 representative subtidal sites (Creek1, Shoal1, Island1), which are part of a database maintained by the VCR LTER program (http://atlantic.evsc.virginia.edu/). These 3 sites were sampled 14 additional times from summer 2000 to fall 2002. Sampling was conducted in June, July, August, October 1998, January, March, May, June, July, August, October 1999, February, March, May, June, July, August, October 2000, February, April, June, July, August, October 2001, and February, June, November 2002. For each survey, 6 random quadrats were sampled at each site using 0.15 m^2 circular plastic cores. The person collecting the sample was spun around several times to face a random direction and walked with eyes closed between 5 and 20 steps. When present, macroalgae within the core were collected and divided in the field into unattached and attached (on bivalve shells and polychaete tube-caps) groupings; samples with zero biomass were also recorded. We found that there were no differences in assemblage structure between attachment groupings and so report pooled results (see Thomsen [2004a] for an analysis of attachment groupings). Samples were separated into different species or genera (Humm 1979; Schneider and Searles 1991), rinsed in deionized water to remove sediments, and freeze-dried to determine dry weight (dw). Note that the cylindrical and flat forms of *Gracilaria* from Hog Island Bay, previously described as *G. verrucosa* and *G. foliifera* (Thomsen 2004a,b; Thomsen and McGlathery 2005) are referred to here as *G. vermiculophylla* and *G. tikvahiae*, respectively (Gurgel and Fredericq 2004; Rueness 2005; Thomsen et al. 2005).

STATISTICAL ANALYSES

Three separate single factor analysis of variance (ANOVA) were used to test for the effects of season, location (mainland creeks versus mid lagoon shoals versus barrier island sites), and elevation (intertidal versus subtidal sites) on taxonomic richness, total algal biomass, and biomass of *G. vermiculophylla*. The distribution of *C. fragile* was not analyzed with ANOVA as it was only found in 23 samples and we relied instead on graphical analysis (cf., Figs. 2–4).

Effects of season were tested using the entire 4 yr data set. Tests for location and elevation were conducted on separate, balanced data subsets, extracted from the first 13 surveys. Since the mid lagoon was not sampled in the intertidal zone and the location factor was unreplicated from summer 2000 onward, location effects were tested on the subtidal sites from Creek1, Creek2, Shoal1, Shoal2, Island1, and Island2. The two mainland harbor sites (Willis Wharf, Oyster) were not included in the location analysis because these harbors are less representative of typical mainland habitats along the Delmarva Peninsula. Elevation effects were tested on the subset of sites that included both intertidal and subtidal areas, i.e., Creek1, Creek2, Island1, and Island2. All data were log(x + 1) transformed to reduce variance heterogeneity and the influence of outliers and to increase effect sizes (η^2, SPSS 8.0, Pallant 2001). Because the season and location factors still had heterogeneous variances following transformation ($p < 0.05$, Levene test), statistical significance was evaluated based on $p < 0.01$ (Underwood 1981). Filamentous taxa were often attached to, or entangled in, *G. vermiculo-*

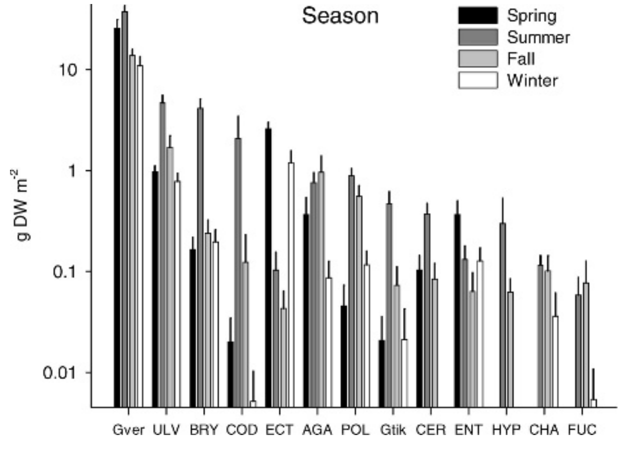

Fig. 2. Dominance patterns during 4 seasons (all sites and surveys, +SE, Spring = 252, Summer = 558, Fall = 198, and Winter = 180 samples). See Table 2 for species abbreviations. Note logarithmic scale.

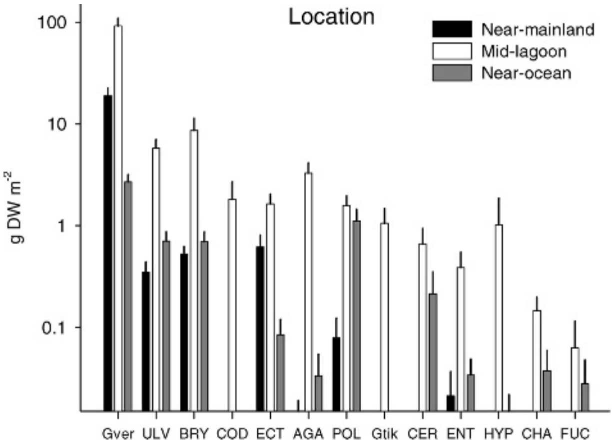

Fig. 3. Dominance patterns at near mainland creek, mid lagoon shoal, and near ocean island sites (subtidal sites only, first 13 surveys. +SE, n = 156 per site). See Table 2 for species abbreviations. Note logarithmic scale.

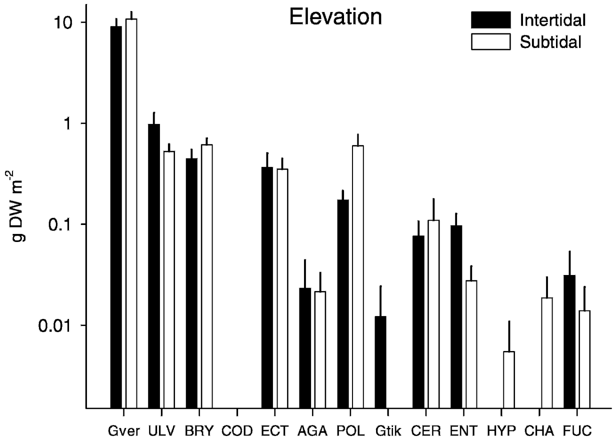

Fig. 4. Dominance patterns at intertidal and shallow subtidal elevations (creek and island sites, first 13 surveys, +SE, n = 312 per elevation level). See Table 2 for species abbreviations. Note logarithmic scale.

phylla, so we included a correlation analysis (Pearson's r) of *G. vermiculophylla* biomass against taxonomic richness, total algal biomass, and the biomass of the most common of these filamentous species, both as separate species and using pooled biomass (data were log(x + 1) transformed).

Results

The macroalgal assemblage in Hog Island Bay was species poor. Only 13 species constituted 98% of the algal biomass. The 4 most abundant algae, which included the 2 nonnative species, corresponded to more than 90% of the total algal biomass (*G. vermiculophylla, Ulva curvata, Bryosis plumosa, C. fragile,* cf., Table 2). Of the 1188 collected samples, macroalgae were present in 60%, and there was an average taxonomic richness of 1.62 taxa per sample and an average total algal biomass of 36.5 g dw m^{-2}.

Most species were found year-round, but there were significant patterns of abundance across seasons. Taxonomic richness, total algal biomass, and biomass of *G. vermiculophylla* were affected significantly by season ($p < 0.001$, $F_{4,1188} = 337$, 156, 136, respectively), with highest values in summer (1.77 ± 0.09 taxa per sample, 53.71 ± 7.08 g dw m^{-2}, 37.50 ± 5.53 g dw m^{-2}, dispersal values hereafter correspond to 1 standard error) and lowest in winter (1.32 ± 0.12 taxa per sample,

TABLE 2. Species constituting 98% of the total algal biomass in Hog Island Bay. B = brown, G = green, and R = red algae. Abr = abbreviations used in Figs. 2–4. Mean (±SE) in g dw m^{-2} and number of recordings (# Obs) are based on 1,188 samples.

Taxonomic Unit	Abr	Mean	# Obs
Gracilaria vermiculophylla (R)	Gver	27.02 (2.93)	643
Ulva curvata (G)[1]	ULV	2.79 (0.43)	320
Bryopsis plumosa (G)	BRY	2.04 (0.47)	229
Codium fragile (G)	COD	1.00 (0.64)	23
Ectocarpus spp. (B)	ECT	0.78 (0.11)	177
Agardhiella subulata (R)	AGA	0.61 (0.12)	107
Polysiphonia spp. (R)[2]	POL	0.54 (0.08)	137
Gracilaria tikvahiae (R)	Gtik	0.24 (0.07)	28
Ceramium spp. (R)[3]	CER	0.21 (0.05)	62
Enteromorpha spp. (G)[4]	ENT	0.17 (0.04)	60
Hypnea musciformis (R)	HYP	0.15 (0.11)	29
Champia parvula (R)	CHA	0.08 (0.02)	39
Fucus vesiculosus (B)	FUC	0.04 (0.4)	10

Less common taxa arranged after abundances: *Leathesia difformis, Calithamnium* sp., *Punctaria latifolia, Gelidium pusillum, Scytosiphon lomentaria, Grinnellia americana, Lomentaria baileyana, Cladophora* sp., *Rhizoclonium* sp., and *Dasya baillouviana.* Taxa observed outside sample cores: *Ralfsia verrucosa, Sargassum natans, Porphyra* sp., *Spyridia filamentosa, Chondria baileyana, Melobesia membranacea,* and *Caloglossa leprideurii.*

[1] Potentially with a minor component of *U. rotunda* and *Monostroma* sp.

[2] *P. denudata* and *P. nigrescens.*

[3] *C. rubrum* and *C. strictum.*

[4] *E. prolifera* and *E. intestinalis.*

11.94 ± 2.62 g dw m^{-2}, 10.94 ± 2.55 g de m^{-2}). *G. vermiculophylla* was the most abundant species in every season (Fig. 2). *C. fragile* biomass was highest in summer (2.08 ± 1.36 g dw m^{-2}) and lowest in winter (0.01 ± 0.01 g dw m^{-2}). While many species were most abundant in summer and least abundant in winter (*G. vermiculophylla, U. curvata, C. fragile, B. plumosa*), *Ectocarpus* spp. and *Enteromorpha* spp. were most abundant in winter and spring, and *Agardhiella subulata* was most abundant in fall (Fig. 2).

Taxonomic richness, total algal biomass, and *G. vermiculophylla* biomass also varied significantly among locations ($p < 0.001$, $F_{3,468} = 316, 174, 144$, respectively), with highest values at mid lagoon sites (3.39 ± 0.19 taxa per sample, 128.44 ± 20.63 g dw m^{-2}, 92.15 ± 16.95 g dw m^{-2}), intermediate values at mainland sites (1.23 ± 0.09 taxa per sample, 19.40 ± 3.66 g dw m^{-2}, 18.96 ± 3.63 g dw m^{-2}), and lowest values at barrier island sites (1.11 ± 0.13 taxa per sample, 4.58 ± 0.89 g dw m^{-2}, 2.70 ± 0.46 g dw m^{-2}). *C. fragile* also had highest abundance at mid lagoon sites (Fig. 3; 1.82 ± 0.87 g dw m^{-2}), but was absent at both mainland and barrier island sites in the initial 2 yr data set. In the additional sampling in 2000–2002, *C. fragile* was found at the barrier island sites (Thomsen unpublished data). *G. vermiculophylla* was again the most abundant macroalgae regardless of location. With the exception of *G. vermiculophylla*, mainland and barrier island sites were characterized by a few structurally simple ephemerals (*U. curvata, B. plumosa, Ectocarpus* spp., *Ceramium* spp., *Polysiphonia* spp., Fig. 3). Mid lagoon sites generally had higher abundance of more structurally complex perennials (*C. fragile, A. subulata, Gracilaria tikvahiae, Hypnea musciformis,* and *Fucus vesiculosus*).

Taxonomic richness, total algal biomass, and *G. vermiculophylla* biomass were affected significantly by elevation ($p < 0.001$, $F_{2,624} = 284, 111, 110$, respectively), with higher values in the subtidal zone (1.17 ± 0.08 taxa per sample, 11.99 ± 1.93 g dw m^{-2}, 10.83 ± 1.89 g dw m^{-2}) than the intertidal zone (0.97 ± 0.07 taxa per sample, 10.68 ± 1.91 g dw m^{-2}, 9.07 ± 1.76 g dw m^{-2}). Although significant, these differences were less pronounced than differences associated with season or location. *G. vermiculophylla* was the most abundant species regardless of elevation. *C. fragile* was not present in any samples used for this analysis. Other species showed variable patterns: *U. curvata, Enteromorpha* spp., and *F. vesiculosus* were more common in the intertidal than subtidal zone, whereas *B. plumosa, Polysiphonia* spp., *Ceramium* spp., and *Champia parvula* were more common in the subtidal than intertidal zone (Fig. 4).

The biomass of *G. vermiculophylla* was correlated significantly ($p < 0.001$, $n = 1,188$) with taxonomic richness ($r = 0.65$), total algal biomass ($r = 0.94$), and the pooled biomass of the most common filamentous algae ($r = 0.41$). The biomass of *G. vermiculophylla* also was correlated with individual filamentous species as follows: *B. plumosa* ($r = 0.37$), *Polysiphonia* spp. ($r = 0.29$), *Ceramium* spp. ($r = 0.23$), *C. parvula* ($r = 0.20$), and *Ectocarpus* spp. ($r = 0.10$). This corresponds well with our observations that *G. vermiculophylla* provides an abundant and widely distributed substratum for these taxa.

Discussion

Algae were generally patchily distributed and low in abundance in the extensive shallow soft-bottom portions of Hog Island Bay. There was a general pattern of low diversity-low biomass regions near the mainland and barrier islands and high diversity-high biomass in the mid lagoon regions. The main factors that vary along this mainland-island transect include light (highest availability at barrier island sites), nutrients (highest concentrations at mainland sites), burial by fine suspended solids (highest total suspended sediment concentrations and finest sediments at mainland sites), and substrate for attachment (most bivalve shells at mid lagoon sites; Table 1; McGlathery et al. 2001; Lawson 2003; Thomsen 2004a). Algae are probably limited by low light penetration and sedimentation of fine organic-rich particles at mainland sites and low nutrient concentrations at barrier island sites, particularly in summer months when the growth demand for nutrients is typically highest (Tyler et al. 2001; Thomsen 2004a). Similar patterns have been observed in other soft-bottom systems, although these patterns have been attributed primarily to a nutrient gradient (Borum 1985; Pedersen 1995; Castel et al. 1996; Tagliapietra et al. 1998). In the mid lagoon region, abundant shell substrata available for algal attachment are important in stabilizing populations (Connor 1980; Thomsen 2004b) and likely contribute to the high biomass and taxonomic richness in this region. Tidal currents also are important in facilitating the capture and accumulation of drift algae in the more conspicuous reef structures that occur here (Lenihan 1999; Thomsen and McGlathery 2006). Gradients of multiple environmental factors similar to that observed for Hog Island Bay likely occur in many lagoonal systems, and we hypothesize that our results can be generalized to these types of systems.

In addition to their horizontal position with respect to environmental gradients, marine organisms also occupy different vertical elevations relative to tides because desiccation, light levels, sedimentation, grazing, and hydrodynamic forces depend on the depth of the overlying water column. In Hog Island Bay, although most species were most abundant in the subtidal zone compared the intertidal zone, these differences were less pronounced compared to seasonal or location effects. It is noteworthy that the filamentous taxa associated with *G. vermiculophylla* were most abundant in the subtidal zone. This pattern can reflect upward growth limitation by desiccation (Thomsen 2004a), higher abundance of the host *G. vermiculophylla*, or accumulations of algae that drift in denser mats in the subtidal zone because currents are slower and wave action is less (Flindt et al. 1997; Lawson 2003). The species that were most common in the intertidal zone, *F. vesiculosus*, *U. curvata*, and *Enteromorpha* spp., are most resistant to desiccation, more susceptible to grazing, and have the highest recruitment in the intertidal zone (Thomsen 2004a; Thomsen and McGlathery 2006).

The algal assemblage in Hog Island Bay was species poor and was structurally similar to drift algal associations known worldwide that are characterized by the dominance of relatively few red and green filamentous, sheet-like, and coarsely branched species (e.g., Thorne-Miller et al. 1983; Lowthion et al. 1985; Virnstein and Carbonara 1985; Cecere et al. 1992; Fletcher 1996). Both perennial (e.g., *G. vermiculophylla*, *A. subulata*, *C. fragile*) and ephemeral (e.g., *U. curvata*, *Ectocarpus* spp., *B. plumosa*) algae were found year-round, although for most species densities were lowest in the cold and low-light winter months (Rhodes 1970; Connor 1980). The peak in algal biomass and taxonomic richness in summer is similar to many temperate algal communities (Rhodes 1970; Sears 1975; Humm 1979; Connor 1980; Wolfe and Harlin 1988). *Ectocarpus*, a well known bloom-forming genus (Fletcher 1996; Morand and Briand 1996; Raffaelli et al. 1998), differed from most species in being more common in spring, a pattern also found in Danish shallow water turbid systems (Thomsen et al. 2006). The invasive *G. vermiculophylla* explained a large proportion of the algal taxonomic richness by providing attachment sites for filamentous species. *G. vermiculophylla* enhanced local diversity by adding structural complexity to a relatively homogenous soft-bottom system. This alga plays a similar role as a facilitator (sensu Bruno and Bertness 2001; Bruno et al. 2003; Thomsen and McGlathery 2005) of species diversity as oyster reefs (Thomsen and McGlathery 2006), seagrass beds (Cancino 1981), and kelp forests (Cancino 1981). Other nonnative species that have been shown to facilitate species diversity include the brown alga *Sargassum muticum* (Wernberg et al. 2004; Thomsen et al. 2006), the tunicate *Pyura praeputialis* (Castilla et al. 2004), and the polychaete *Ficopomatus enigmaticus* (Schwindt et al. 2001). When entire assemblages are introduced together, local diversity can increase rapidly and significantly (Ruiz et al. 1997, 1999; Simberloff and Von Holle 1999).

Of the two nonnative species in Hog Island Bay, *C. fragile* is considered to be the less successful invader. *C. fragile* is a well-known invader in northern estuaries (Carlton and Scanlon 1985; Trowbridge 1998). This is the first report of the distribution pattern of this species in the mid Atlantic region (Hillson 1976), and our data show that this species has clearly expanded its range in this region over the past 30 yr (Hillson 1976). Our data do not support the notion that *C. fragile* is a successful invader due to its ability to occupy a wide range of environmental conditions and habitats (e.g., Malinowski and Ramus 1973; Hanisak 1979a,b; Carlton and Scanlon 1985; Trowbridge 1998). *C. fragile* was found only rarely at the barrier island sites or in the intertidal zone and appeared to be restricted to mid lagoon shallow subtidal locations where hydrodynamic forces are low, oyster shells abundant, desiccation and sediment burial limited, and light adequate (this study; Thomsen 2004a,b; Thomsen and McGlathery 2005; Thomsen and McGlathery 2006). Many native algae (e.g., *A. subulata*, *U. curvata*, *Enteromorpha* spp., *B. plumosa*, *Ceramium* spp., *Polysiphonia* spp., *Ectocarpus* spp.) had wider distributions and were found in more samples (as smaller individuals). *C. fragile* was the fourth most abundant alga in terms of biomass, but this was based on a few samples with large and heavy individuals, and it would be considered less successful if evaluated on a presence-absence basis (cf., Table 2).

Our data indicate that the invasion of *G. vermiculophylla* in Hog Island Bay is widespread, with this species being the most abundant alga during all seasons and all locations and elevation levels. This wide distribution suggests that *G. vermiculophylla* has a wide tolerance to variable temperature, light availability, and dessication stress (Humm 1979; Connor 1980; Rueness 2005), and supports the results of laboratory experiments that have shown its tolerance to environmental extremes (Yamamoto and Sasaki 1988; Yokoya et al. 1999; Rueness 2005). This is the first report of distribution data for *G. vermiculophylla* in the mid Atlantic region and to our knowledge the first report of its abundance in any invaded system, in spite of its rapid advance in Europe and along east and west North American coastlines (Bellorin et al. 2004; Rueness 2005; Thomsen et al. 2005). Because of the cryptic nature of this invasion, with positive identification only after recent molecular analysis (Gurgel and Fredericq 2004; Thomsen et al. 2005), it is unknown when or how *G. vermiculophylla* arrived at the U.S. east coast and in how many systems it is present. The high abundance of *G. vermiculophylla* in Hog Island Bay is matched by its efficient recruitment onto hard substratum (Thomsen and McGlathery 2006) and the intermediate to high growth rates of fragments under stressful conditions of high grazer densities, low light conditions, and high sedimentation (Thomsen 2004a). Separate recruitment and growth data have shown that *G. vermiculophylla* is more desiccation tolerant than *C. fragile* (Thomsen 2004a; Thomsen and McGlathery 2006). *G. vermiculophylla* also was found incorporated onto the tubecap of the ubiquitous polychaete *Diopatra cuprea* throughout Hog Island Bay (Thomsen and McGlathery 2005). Facilitation by this association (Woodin 1978; Bell and Coen 1982), along with its environmental tolerance, may lead to a high invasion potential along the U.S. east coast and in other areas where soft-bottom polychaetes can facilitate spatial fixation (Reise 1983; Zuhlke 2001). This has been observed in the recently invaded Wadden Sea, where *G. vermiculophylla* is found frequently in lugworm associations as described by Reise (1983) for green algal mats (Thomsen personal observation, Mandoe, Wadden Sea).

In addition to its influence on biotic structure in Hog Island Bay, *G. vermiculophylla* also affects patterns of primary production and biogeochemical cycling (McGlathery et al. 2001; Tyler et al. 2001, 2003), similar to other highly invasive macroalgae (Pedersen et al. 2005). During most of the year, algae in Hog Island Bay occurred at low densities that can have a positive effect on the system, by acting as a filter for land-derived nutrients, creating habitats for invertebrates and fish, and providing food for grazers (Holmquist 1994; Raffaelli et al. 1998; Norkko et al. 2000; McGlathery et al. 2001). Approximately 10% of our samples (typically summer samples from the mid lagoon region) contained more than 100 g dw m^{-2}, and the maximum recorded was nearly 2 kg dw m^{-2}. Most of this biomass was comprised of *G. vermiculophylla*, which suggests that the system may have changed greatly since the introduction of this species. Such accumulations can have negative consequences by creating anoxia when they decompose and by outcompeting seagrasses (Fletcher 1996; Norkko and Bonsdorff 1996; Raffaelli et al. 1998; Hauxwell et al. 2001). We observed several summer anoxic events in the mid lagoon region and have shown a reduction in faunal biomass and diversity associated with algal biomass over 100 g dw m^{-2} (McGlathery et al. 2001; Tyler et al. 2001; Rosinski 2004). These dense accumulations were of the same magnitude as those reported for highly nutrient-enriched estuaries (McGlathery 2001), but in Hog Island Bay the accumulations may be initiated by hydrodynamic conditions that accumulate drifting algae against shallow shoals and oyster reef structures (Thomsen 2004a,b; Thomsen and McGlathery 2006). Once trapped, the rapid turnover of nutrients in the sediments supports a large part of the local algal nitrogen demand (McGlathery et al. 2001; Tyler et al. 2003). Even though nutrient inputs to this system are low compared to nearby areas (Boynton et al. 1996; Goshorn et al. 2001; Stanhope 2003), algal accumulations provide an important reference point for the enhanced ecosystem metabolism that would be caused by future eutrophication (Goshorn et al. 2001; Stanhope 2003).

This first published report of macroalgal biomass distribution from the western mid Atlantic region documents the dominance of two nonnative species, in particular the cryptic west Pacific invader *G. vermiculophylla* that can be confused with native *Gracilaria* species. This species also has been observed in the eastern Pacific and eastern Atlantic in the last few years, suggesting an aggressive ongoing global spread. Today, *G. vermiculophylla* is the single most abundant alga in Hog Island Bay at all sampled seasons, locations, and elevations levels, but the wider geographical extent of this invasion along the U.S. east coast remains unknown. As no previous biomass sampling or older *Gracilaria* DNA data exist from this region, it is virtually impossible to quantify the effects associated with the initial invasion. It is important that future studies outline how common this non-native *G. vermiculophylla* is on larger geographical scales and measure distribution patterns in noninvaded adjacent lagoons to provide preinvasion reference data.

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