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Distribution and ecological role of the non-native macroalga *Gracilaria vermiculophylla* in Virginia salt marshes

M. S. Thomsen · K. J. McGlathery · A. Schwarzschild · B. R. Silliman

Abstract Intertidal salt marshes are considered harsh habitats where relatively few stress-resistant species survive. Most studies on non-native species in marshes describe terrestrial angiosperms. We document that a non-native marine macroalga, *Gracilaria vermiculophylla*, is abundant throughout Virginia's Atlantic coastline. We sampled eight marshes, characterized by low slopes and by the presence of the tube-building polychaete *Diopatra cuprea* on adjacent mudflats, which have been shown previously to be associated with *G. vermiculophylla*. *G. vermiculophylla* was found in 71% of the sampled quadrats on the border between the mudflat and tall *Spartina alterniflora*, 51% within the tall *S. alterniflora* zone, and 12% further inland. We also tagged *G. vermiculophylla* from two habitats: (1) unattached *G. vermiculophylla* within marshes and (2) *G. vermiculophylla* 'incorporated' onto *D. cuprea* tubes on the adjacent mudflats. Of the incorporated thalli, 3–9% ended up in the marsh, demonstrating connectivity between habitats. In addition, 21% of unattached thalli remained for 2 weeks within the marsh, suggesting that entanglement around marsh plants reduces tidal drift. Growth experiments in mesh bags indicate that most of the *G. vermiculophylla* transferred from the lagoon to the marsh decomposed there, potentially enhancing local nutrient levels. Finally, we document that *G. vermiculophylla* in marshes had a reduced associated flora and fauna compared to *G. vermiculophylla* on the adjacent *Diopatra* mudflats. In conclusion, unattached *G. vermiculophylla* is abundant along marsh borders in the tall *S. alterniflora* zone in Virginia, and we hypothesize that this non-native species has significant impacts in terms of marsh habitat complexity, species abundance and diversity, nutrient dynamics, productivity, and trophic interactions.

Keywords Non-native macroalgae · Salt marsh *Gracilaria vermiculophylla* · *Spartina alterniflora*

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Introduction

Intertidal salt marshes are highly productive ecosystems, typically composed of halophytic plants, benthic diatoms, visiting fish and birds, and stress-tolerant invertebrates that can survive both emergence and submergence (Chapman 1974; Adam 1990). In this context, marine macroalgae are only rarely mentioned (but see Brinkhuis et al. 1976; Brinkhuis 1977; Fong et al. 1998; Moseman et al. 2004; Boyer and Fong 2005), and wetland textbooks typically treat macroalgae in a rudimentary way (e.g., Chapman 1974; Adam 1990; Keddy 2000). However, macroalgae can occasionally be an abundant component of the lower marsh zone, such as fast-growing opportunistic green algae (*Blidingia*, *Rhizoclonium,* and *Ulva* including former *Enteromorpha*), slow-growing stress tolerant and long-lived brown algae (*Fucus* and *Ascophyllum*), and inconspicuous slow growing red algae (*Bostrychia* and *Caloglossa*). When these algae are abundant, they may affect primary production rates, biogeochemical cycling, trophic interactions, and environmental conditions, such as evapotranspiration, infiltration, and sediment characteristics (Brinkhuis et al. 1976; Brinkhuis 1977; Fong et al. 1998; Moseman et al. 2004; Boyer and Fong 2005).

Salt marshes are relatively rarely reported to be dominated by non-native species, and the vast majority of existing studies on non-native species describe a few fast-growing angiosperms, in particular *Phragmites australis* or various *Spartina* species (e.g., Daehler and Strong 1996; Benoit and Askins 1999; Amsberry et al. 2000; Hedge and Kriwoken 2000; Able and Ragan 2003; Chambers et al. 2003; Nieva et al. 2003; Silliman and Bertness 2004; Bart et al. 2006; Brusati and Grosholz 2006; Neira et al. 2006; Brusati and Grosholz 2007; Chen et al. 2007; Cottet et al. 2007). In contrast, we are not aware of studies that describe non-native macroalgae in marshes. In the present paper, we document that the Pacific macroalga, *Gracilaria vermiculophylla* (Ohmi) Papenfuss, is a conspicuous member of the lower *Spartina alterniflora* marsh zone in Virginia. *G. vermiculophylla* is an estuarine alga that only recently has been identified as a non-native species in the West Atlantic (based on molecular analysis, Thomsen et al. 2006). This non-native species was long thought to be the native, morphologically similar, sibling species *G. tikvahiae* McLachlan,

and as a result, it is unknown exactly when, where and how *G. vermiculophylla* was introduced. Given its high abundance on oyster reefs (Thomsen et al. 2006, 2007a, b), it is possible that *G. vermiculophylla* introduction occurred associated with oyster imports. Today, *G. vermiculophylla* co-exists with other large macroalgae, e.g., *Agardhiella subulata* (C. Agardh) Kraft & Wynne, *Codium fragile* (Suringar) Hariot (another non-native species), *Fucus vesiculosus* L, and *Ulva curvata* (Kützing) De Toni, in many lagoons from South Carolina to Massachusetts (F. Gurgel, Personal communication; Schneider and Searles 1991; Freshwater et al. 2006; Thomsen et al. 2006, 2007a). Interestingly, *G. vermiculophylla* differs in morphology, taxonomy and ecology from other marsh algae, in that it is red, coarsely branched, large, relatively fast growing, and yet still tolerant of temperature and desiccation stresses (Thomsen and McGlathery 2007).

Within Virginia, the distribution of *G. vermiculophylla* has so far only been reported in the peer-reviewed literature from two adjacent lagoons on the eastern shore of the Delmarva Peninsula (Thomsen et al. 2006). In both of these lagoons, this non-native species is associated with the ubiquitous polychaete, *Diopatra cuprea* Bosc (hereafter *Diopatra*), which actively incorporates drift algae, in particular *G. vermiculophylla*, into its sediment protruding tube cap (Thomsen 2004a, 2004b; Thomsen and McGlathery 2005; Thomsen et al. 2006). This 'gardening behavior' potentially influences algal persistence, diversity and assemblage structure by converting mudflats into semi-stable *Gracilaria* meadows (Thomsen and McGlathery 2005). We focused our surveys and experiments on marshes characterized by adjacent *Diopatra*-mudflat colonies. Although there have been no studies that have quantified how common *Diopatra* mudflats are adjacent to salt marshes on a large scale, in Virginia we have observed them to be a common feature along low-sloping marshes connected to open lagoon waters. This 'targeted survey' approach increases the likelihood of detecting *G. vermiculophylla* and is generally considered an efficient method for ground monitoring of non-native species (Wittenberg and Cock 2001). Thus, the objective of our study was to provide a first record of *G. vermiculophylla*'s distribution, stability, survival, growth, and associated flora and fauna in Virginia marshes adjacent to *Diopatra* mudflats.

Methods

Distribution of G. vermiculophylla. Eight coastal bay marshes dominated by *S. alterniflora* were surveyed in June and July 2006 (Fig. 1). The marshes were all located in coastal barrier-island systems on the eastern shore of the Delmarva Peninsula in Virginia. Within each marsh, presence–absence of *G. vermiculophylla* was recorded in 15 random quadrats (0.32×0.32 m^2) in three zones: (1) the border between the *S. alterniflora* zone and the mudflat, (2) 1–5 m inside the *S. alterniflora* marsh, and (3) 20–30 m further upland. The upland zone was not sampled at Fishermans Island and Chincoteague Island as the first area is a Nature

Reserve and the latter marsh is less than 20 m deep. All marshes were characterized by a low slope and *Diopatra* colonies on the adjacent mudflats. We also recorded whether *G. vermiculophylla* was unattached or attached to stones, bivalves, or living *S. alterniflora* stems and if visible carpogoniums were present to indicate fertile thalli. Documenting attached and reproductive individuals on living stems is important because it provides evidence that the entire algal life cycle can be completed at that specific place. Chi-squared tests were used to test if distribution patterns differed between zones and marshes.

Stability and habitat linkage. Given that *G. vermiculophylla* is found in a semi-attached state on

Fig. 1 Sample locations of *Gracilaria vermiculophylla* along the eastern shore of Virginia on the Delmarva Peninsula. The peninsula is situated on the US mid-Atlantic coast and separate Chesapeake bay to the west from the Atlantic ocean to the east. *1* Toms Cove (southern Assateague Island), *2* Chincoteague Channel, *3* north Hog Island, *4* south Hog Island, *5* Castle Ridge Creek, *6* Elkin Marsh (outside of Oyster Harbor), *7* Oyster Harbor, and *8* Fishermans Island
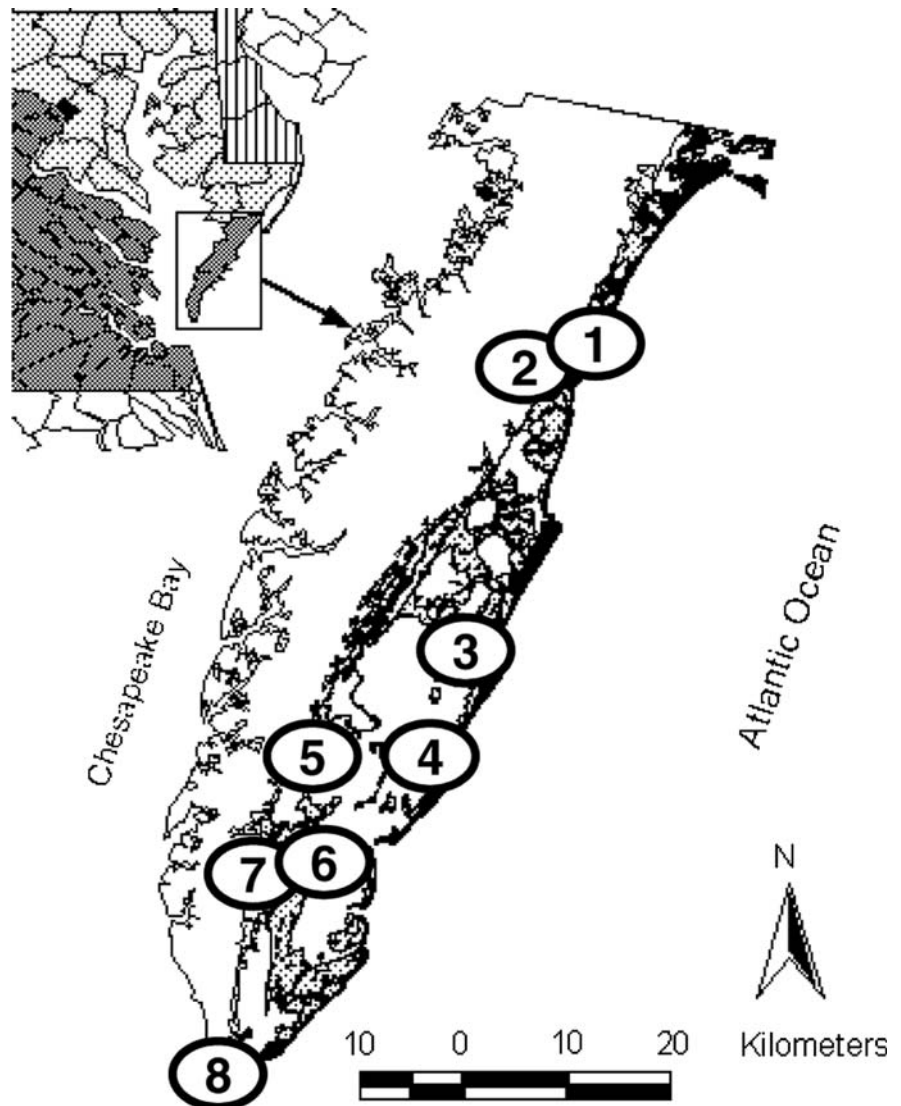
the mudflats (incorporated into *Diopatra* tubes, cf. introduction) but mainly as un-attached thalli in the marsh (see survey data), we used three tagging experiments to quantify (1) the stability of *G. vermiculophylla* relative to other common bay algae in marshes and (2) algal transfer rates between *Diopatra* mudflats and marshes. These experiments were designed to quantify if marsh populations are less stable and if there is a 'drift-fragment-linkage' between the two adjacent habitats. All algae were tagged by tying a 15 × 1 cm strip of flagging tape around the thallus, each with a unique identifier (Thomsen and McGlathery 2005). In the first experiment, ten unattached thalli (5–10 g wet weight) of *G. vermiculophylla, A. subulata, C. fragile, F. vesiculosus*, and *U. curvata* (Kützing) De Toni were tagged. Tagged thalli were scattered around *S. alterniflora* stems within 1–5 m from the mudflat border on 10 July 2006 in South Hog Island Bay and on 20 July 2006 in Oyster Harbor. We also tagged ten *F. vesiculosus* thalli that were attached to the bivalve *Geukensia demissa* (Dillwyn). The attached *F. vesiculosus* population is known to be stable on long time scales (Thomsen, Personal observation) and provided procedural controls to ensure tags did not break off from thalli. All remaining tags were counted on 21 July 2006 (South Hog Island Bay) and 29 July 2006 (Oyster Harbor). In the second experiment, 20 thalli of *G. vermiculophylla* and *U. curvata* incorporated into tube caps on the *Diopatra* mudflat were tagged (locations and sample dates similar to Experiment 1). Also, 20 tube caps were tagged as stable procedural controls (Fig. 2). Tags were searched for in the adjacent marshes to calculate the tag-transfer rate from mudflat to marsh. In the third experiment, 50 larger clumps of unattached *G. vermiculophylla* (average of 20 g wet weight) and 50 thalli incorporated into tube caps were tagged. Unattached thalli were scattered around *S. alterniflora* stems (similar to Experiment 1). The experiment was initiated on 4 November 2006 at Oyster Harbor and Ramshorn Channel; the remaining tags were counted on 5 and 18 November 2006 to quantify both stability and bi-directional habitat-transfer.

Stress tolerances. We tested if *G. vermiculophylla, A. subulata, C. fragile, G. tikvahiae*, and *U. curvata* had net growth or loss in the marsh habitat (the other species were again included as a background to evaluate if stress tolerance of *G. vermiculophylla* should be considered high or low). Nine mesh bags, each containing 0.3–0.8 g wet weight of each species, were incubated on 20 July 2006 1–5 m within the marsh, on the marsh-mudflat border, and on the adjacent mudflat (30 cm lower elevation than the marsh border). *F. vesiculosus* was not included in this experiment because it is already known to survive, grow, and reproduced in *S. alterniflora* marshes (e.g., evidenced by the large attached thalli commonly found on marsh *G. demissa*). The bags had 3 mm mesh size openings to allow for basic water exchange and light penetration (ca. 40% reduction, Apogee PAR-meter). Mesh bags simultaneously reduce light and water flow (negative effects) but also reduce grazing and fragmentation caused by physical disturbances and hydrodynamic forcing (positive effects). Still, keeping these limitations in mind, the growth results remain comparable between algal species and habitats.

Three bags were collected from each habitat after 4, 6, and 9 days. After collection, the algae were added to 250 ml aerated containers with salt water from Hog Island Bay and kept at favorable growth conditions (12:12 L:D cycle, 21°C, 100 $\mu Em^{-2} s^{-1}$). The biomass of all thalli was measured on July 30, 2006. This procedure ensured that most dead thalli disintegrated before the final biomass measurements, partially safeguarding against wrongful conclusions regarding the ability to survive in the marsh habitat. To further ensure that the remaining algal biomass was productive, photosynthetic yields were quantified with pulse amplitude modulated fluorometry using a Mini-PAM (©Heinz Walz, yield being interpreted as a proxy for photosynthetic capacity, Heinz 1999). The fiber optic was aimed at a piece of the thalli that appeared healthy with respect to coloration and texture, using standard settings (0.7 cm distance, 30° angle, Heinz 1999). All fluorescence measurements (one yield per thalli) were conducted in randomized order in less than 1 h to minimize differences in ambient environmental conditions. Yield values below 0.2 indicate highly stressed thalli (Mouget and Tremblin 2002; Macinnis and Ralph 2001). We also compared the experimental yield values with yields measured on non-manipulated *G. vermiculophylla* thalli collected randomly from the low *S. alterniflora* zone at the South Hog Island Bay site on June 20, 2006 (N = 67). These latter
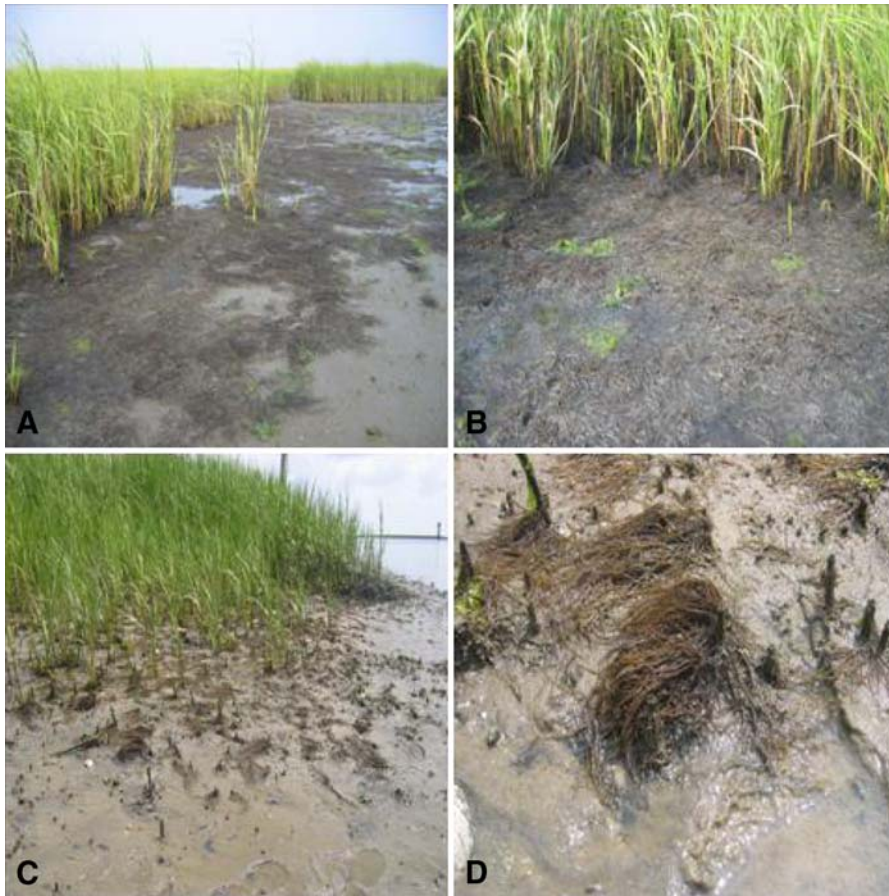
Fig. 2 *Gracilaria vermiculophylla* in *Spartina alterniflora* salt marshes. **a** *G. vermiculophylla* mat covering the mud-*Spartina* border at south Elkorn marsh. Note scattered *G. vermiculophylla* and *Ulva spp.* incorporated into *D. cuprea* tube caps (*low-right corner*). **b** Close-up of *G. vermiculophylla* and scattered *Ulva spp.* at mud-*S. alterniflora* interface at south Assateague Island. **c, d** *G. vermiculophylla* attached to *S. alterniflora* stems at the mud-*Spartina* border at Oyster Harbor, documenting recruitment, survival, and growth in this zone

values indicate if thalli from natural salt marsh populations are 'healthy' and capable of photosynthesis. Percent change in biomass and photosynthetic yield were analyzed for each species with two-way fixed ANOVA's (4, 6, and 9 field days corresponding to 'short', 'medium', and 'long' incubation time), followed by SNK tests to differentiate treatments.

Associated biota. 'Epibiota samples' were collected from Toms Cove, southern Elkin Marsh, Oyster Harbor, and Fisherman Islands to (1) quantify if native marsh flora and fauna are found associated with *G. vermiculophylla* and (2) test if this non-native species hosts different macrobiotic assemblages in marshes and *Diopatra* mudflats (Fig. 1, see Wernberg et al. 2004 for similar sampling methodology on another non-native macroalgae). Random thalli

($n = 9$–11 per location) were collected in the *S. alterniflora* marsh (1–5 m from the edge) and from adjacent *Diopatra* mudflats. At the time of collection thalli were covered by 10–20 cm water. Samples were collected by a rapid sweep, gripping the thalli (including the *Diopatra* tube cap that extends above the sediment surface), and placing it into a ziploc bag. We did not sample tube caps without incorporated algae for comparison because they were generally absent (i.e., all caps had typically some level of incorporated algae). A more 'careful' sampling of only the algal component would have resulted in loss of fast moving decapods. In the laboratory, samples were rinsed in freshwater to release mobile species, and sessile species (macroalgae and the bryozoa *Bugula* sp.) were scraped off. Conspicuous taxa were

identified to species, whereas more complex groups, such as amphipods and small sedentary polychaetes, were identified to family or order. The mobile animals were counted and the sessile species weighed if found in abundance of more than 1 g wet weight. For small quantities of sessile species (<1 g wet weight), we used a fast ranking scheme of three categories; 0–0.3, 0.3–0.6, and 0.6–0.9 g wet weight (several training sessions were used to standardize our ability to allocate abundances correctly to each ranking). The mid-point of these intervals was used in the statistical analyses (Stæhr et al. 2000). The effects on *G. vermiculophylla* biomass, taxonomic richness, biomass, and density of either sessile or mobile species between locations and habitats were tested with two-way ANOVA. All variables, except 'biomass of sessile species', had homogeneous variances (this variable could not be transformed to variance homogeneity using standard formulas but we proceeded with the analysis being cautious about marginally significant results, Quinn and Keough 2002). Finally, two-way permutational multivariate analysis of variance (PERMANOVA, Anderson 2004) was used to test if assemblages differed between locations and habitats. We used Euclidian distances and presence–absence transformations because units differed between sessile and mobile species (trials with other test combinations showed similar results), followed by SIMPER (Clarke 1993) to identify the key taxa that determined significant effects.

Results

Distribution. G. vermiculophylla was observed in all the surveyed marshes, but with significant differences in presence–absence counts both between zones ($\chi^2 = 71.64$, $df = 2$, $P < 0.001$) and locations ($\chi^2 = 28.22$, $df = 7$, $P < 0.001$, Table 1). The zonation pattern was particularly strong, with highest abundance at the mudflat-marsh border (71% of the quadrats examined), intermediate abundance 1–5 m inside the marsh (51%) and lowest abundance in the inland zone (12%). Of the 330 sampled quadrates, a total of 157 quadrats contained *G. vermiculophylla* (loose-lying or attached), 11 quadrats contained attached thalli, and 3 quadrats contained both attached and reproductive individuals. Attached individuals were only found in the mudflat-*S. alterniflora* border zone. In general, most thalli appeared 'healthy' with normal brown coloration and structural integrity(firm branches).

Stability and habitat linkage. In the first experiment, 31 and 39% of *G. vermiculophylla,* 12 and 28% of *C. fragile*, 11 and 19% of *F. vesiculosus*, 0 and 0% of *A. subulata*, and 100 and 100% of attached *F. vesiculosus* were recaptured at, respectively, Oyster Harbor and South Hog. In the second experiment, the transport of tube cap incorporated *G. vermiculophylla* and *U. curvata* into the adjacent marsh was calculated to be 7% (Oyster Harbor) and 11% (South Hog) for *G. vermiculophylla* and 2%

Table 1 Number of quadrates with *G. vermiculophylla* (attached or unattached) in Virginia marshes characterized by low slopes and adjacent *D. cuprea* mudflats (see Fig. 1 for study locations)

Zone	Categories	Chincoteaque Channel	Castle Ridge	Elkin Marsh	North Hog	Oyster Harbor	Smith Island	South Hog	Toms Cove	Total
Border *Spartina*-mud	Absent	2	10	2	3	5	4	7	2	35
	Unattached	11	5	12	10	5	11	7	13	74
	Attached	2	0	1	2	5	0	1		11
1–5 m inland *Spartina*	Absent	7	11	5	4	8	9	7	8	59
	Unattached	8	4	10	11	7	6	8	7	61
	Attached	0	0	0	0	0	0	0	0	0
20–30 m Inland *Spartina*	Absent	NA	14	15	8	15	NA	13	14	79
	Unattached	NA	1	0	7	0	NA	2	1	11
	Attached	NA	0	0	0	0	NA	0	0	0

NA 'Not Available', i.e., we could not sample these zones (cf. method section)

Table 2 Tagging experiment three: *G. vermiculophylla* recapture rates (%) after 1 and 14 days from two adjacent habitats and two locations ($n = 50$ per combination)

Habitat	Location	1 Day	14 Days
Diopatra	Oyster Harbor	96	66
	Ramshorn Channel	98	20
Diopatra Total		97	43
Marsh	Oyster Harbor	96	32
	Ramshorn Channel	92	10
Marsh Total		94	21
Grand Total		95.5	32

Zero (Oyster Harbor) and three (Ramshorn Channel) tags from tube-cap incorporated *G. vermiculophylla* were recaptured in the adjacent marsh after 2 weeks (i.e., were transferred between habitats)

(Oyster Harbor) and 8% (South Hog) for *U. curvata* (i.e. average transfer of 9 and 5%, respectively). In contrast, there was no transport of tags attached around the tube caps, as they all remained on the *Diopatra*-mudflat. In the third experiment, >90% of *G. vermiculophylla* was recaptured after 1 day (Table 2) but after 2 weeks, the recapture percentages were reduced to 43% for tube cap incorporated algae and 21% for marsh algae. In this third experiment, after 2 weeks, 0 and 6% of the *G. vermiculophylla* from the *Diopatra*-mudflat were recaptured in the marsh at Oyster Harbor and Ramshorn Channel, respectively (i.e. average transfer of 3%).

Stress tolerances. We detected a significant habitat effect on the change in *G. vermiculophylla* biomass in the marsh ($F_{2,27} = 13.979$, $P = 0.000$), but no effects on photosynthetic yield (average of 0.40 ± 0.10, all variability measures refer to standard errors, hereafter SE, Fig. 3). The smallest biomass loss was observed on the mudflat ($-3\% \pm 19$), followed by the marsh ($-38\% \pm 39$), and the border zone ($-75\% \pm 20$). Net growth (i.e., biomass change >0%) was detected in two out of nine marsh bags as well as in five mudflat bags, suggesting that *G. vermiculophylla* can sometimes survive in the marsh habitat. This was supported by the yield values from randomly collected marsh thalli that appeared healthy. The average yield for these plants was 0.42 ($\pm$ 0.14; with 85% of the values being about 0.3, 7% between 0.2 and 0.3 and only 7% < 0.2). In general, *G. vermiculophylla* performed

well compared to other bay algae. *A. subulata* lost almost all its biomass under all test conditions ($99\% \pm 4$) and had very low yield ($0.01 + 0.06$; cf. Fig. 3). The biomass of *C. fragile* was not affected by either habitat or time (average = $-55\% \pm 18$), but yields were significantly affected by habitat ($F_{2,27} = 5.28$, $P = 0.016$), with lower values on the border (0.16 ± 0.14) than in the marsh (0.48 ± 0.32) or mudflat (0.49 ± 0.25). There was a significant effect of time on *G. tikvahiae* biomass change ($F_{2,27} = 5.864$, $P = 0.011$), but no effect on yields (average = 0.06 ± 0.11). Much higher biomass loss were observed after 4 and 6 days ($-0.93\% \pm 9$ and $-0.92\% \pm 13$) than 3 days ($-69\% \pm 24$) incubation. Finally, no significant effects were found on either *U. curvata* biomass change or yield (average biomass change and yield of, respectively, $-49\% \pm 36$ and 0.55 ± 0.16). *U. curvata* was the only other alga where net growth was detected in a few bags.

Associated biota. Since *G. vermiculophylla* differed in thalli sizes between locations (Table 3) we tested for differences in the epibiota on standardized data (per g wet weight *G. vermiculophylla*). We found a total of 38 taxa in the 78 epibiota samples. There were significant interactions between habitat and location for both taxonomic richness and biomass of sessile species. The highest taxonomic richness and biomass were found at the *Diopatra* mudflats (Fig. 4), a finding supported by highly significant single factor effects of habitat ($P < 0.01$ for all tests, cf. Table 3). For the taxonomic richness and density of mobile species, only the habitat factor was significant, again with highest values at the *Diopatra* mudflat. Finally, we detected a significant location and habitat interaction between assemblages, of which seven out of the eight pair-wise comparisons had different assemblages ($P < 0.002$; the *Diopatra* epibiota samples from Toms Cove vs. Fishermann Island were alike, $P = 0.11$). A SIMPER analyses of the habitat factor (the factor that explained most of the variability, cf. Table 3) showed that eight taxa contributed to 90% of the multivariate variability for both *Diopatra*- (average similarity = 53.31) and marsh- (average similarity = 33.03) associated biota (Table 4). In contrast, 21 taxa contributed to 90% of the differences between the two assemblages (average dissimilarity = 69.80). The five most important taxa that separated the marsh and *Diopatra* epibiota samples were *Polysiphonia denudata* (Dillwyn) Kutz,

Fig. 3 Performance experiment. Changes in biomass (%) and photosynthetic yields after incubations inside the marsh (1–5 m), at the marsh-mudflat border and on the mudflat, collected after 3 (*T1*), 4 (*T2*) and 6 (*T6*) days (n = 3, ±1 SE)
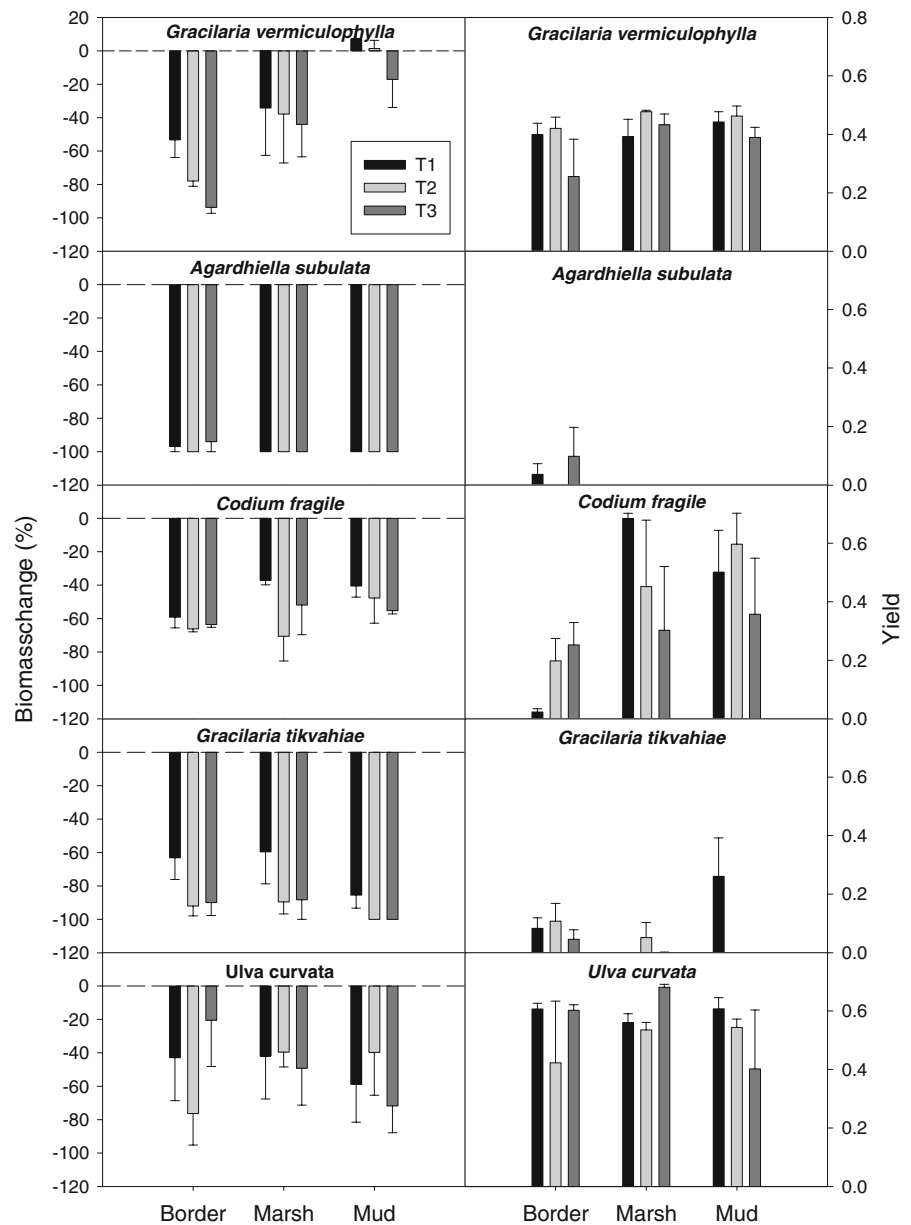
Ceramium "rubrum" (Huds.) C. Ag., *Caprella* spp., *Bryopsis plumosa* (Hudson) C. Ag., and *U. curvata* that were all more abundant in *Diopatra* samples. In contrast, *Ilyanassa obsoleta*, *Ulva* spp. (former *Enteromorpha*), *Bostrychia rivularis* Harvey, *Hydrobia* spp., and *Ovatella myosotis* (Draparnaud) were all more abundant in the marsh samples. A few juvenile individuals of larger highly mobile fish, shrimps and crabs were also found in marsh epibiota samples, including *Fundulus* sp., *Sesarma* sp., *Uca* sp.,

Palaemonetes sp., *Panopeus* sp., and *Callinectes sapidus* Rathbun.

Discussion

We documented that the Pacific macroalga, *G. vermiculophylla*, is a non-native species in many salt marshes in Virginia, mainly found as relatively unstable unattached individual thalli. However,
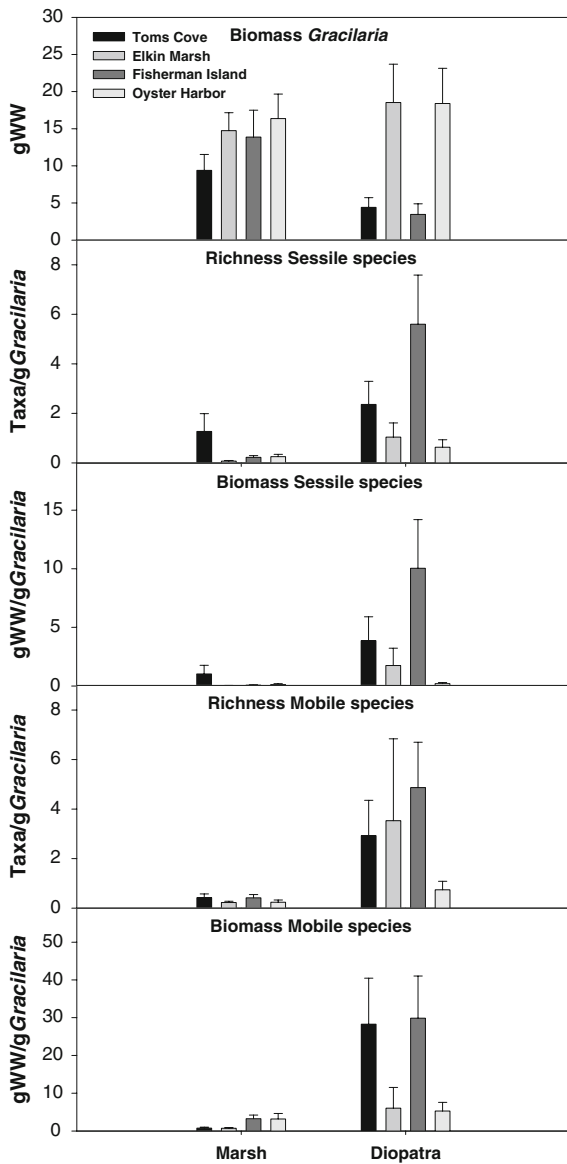
Fig. 4 Biomass of *G. vermiculophylla* thalli and associated taxonomic richness of sessile and mobile species, biomass of sessile species, and number of mobile species in marshes and incorporated onto *D. cuprea* tube caps ($n = 39$, ± 1 SE, pooled from four different sites). Data for sessile and mobile species are shown per *G. vermiculophylla* thalli. *Asterisks* correspond to significant differences

Table 3 Epibiota on *G. vermiculophylla*. ANOVA tests on univariete variables and PERMANOVA (999 permutations) on assemblage data

Test factor	Source	SS	df	F	P
Biomass	Location	1,707.5	3	5.671	**0.002**
Gracilaria	Habitat	111.1	1	1.107	0.296
	Loc × Hab	613.2	3	2.037	0.117
	Error	7,025.5	70		
Richness	Location	77.6	3	3.461	0.021
Sessile	Habitat	74.2	1	9.921	**0.002**
	Loc × Hab	75.7	3	3.375	**0.023**
	Error	523.5	70		
Biomass	Location	267.5	3	2.911	0.040
Sessile	Habitat	258.6	1	8.444	**0.005**
	Loc × Hab	271.7	3	2.957	**0.038**
	Error	2,144.0	70		
Richness	Location	45.2	3	0.818	0.488
Mobile	Habitat	140.7	1	7.637	**0.007**
	Loc × Hab	39.4	3	0.713	0.547
	Error	1,289.7	70		
Density	Location	2,701.4	3	2.294	0.085
Mobile	Habitat	4,602.6	1	11.727	**0.001**
	Loc × Hab	2,684.0	3	2.280	0.087
	Error	27,473.8	70		
Assemblage	Location	32.25	3	4.23	**0.001**
	Habitat	39.78	1	15.60	**0.001**
	Loc × Hab	35.55	3	4.65	**0.001**
	Error	178.45	70		

All test data, except 'biomass of *Gracilaria*', were standardized to gram wet weight of *G. vermiculophylla*. Significant *P* values are in bold

many thalli die in the marsh, some thalli may survive and grow if they are 'deposited' in pockets of favorable microclimatic conditions.

Distribution. Although the interpretation of our data is confined to areas where *S. alterniflora* marshes lie adjacent to mudflats inhabited by *Diopatra*, we have observed *G. vermiculophylla* in marshes without adjacent *Diopatra* mudflats and suspect that *G. vermiculophylla* has a broader distribution in marshes than what we have reported here. More work is needed to determine the distribution of *G. vermiculophylla* in marshes, especially those in Europe, and in the regions north and south of Virginia, as well as in west Pacific marshes where *G. vermiculophylla* is native (Yokoya et al. 1999; Rueness 2005;

G. vermiculophylla marsh populations may be more stable on larger spatio-temporal scales than investigated here due to a continuous fragment supply provided from adjacent '*Diopatra–Gracilaria*'-mudflats (Thomsen and McGlathery 2005; Thomsen et al. 2007b; this study). Our data also indicate that while

Table 4 Key taxa associated with *G. vermiculophylla* in marshes and adjacent *D. cuprea* tube caps (pooling locations)

Species	%Dis-similarity	%Marsh similarity	%Diopatra similarity	Diopatra abundance	Marsh abundance
Polysiphonia denudata	7.99	3.56	15.5	0.92	0.32
Ceramium "rubrum"	7.9	4.35	15.85	0.69	0.13
Caprella spp.	7.78		10.21	3.26	0.03
Bryopsis plumosa	6.96		8.95	0.43	0.05
Ulva curvata	6.73	7.31	9.67	1.75	0.14
Illyanasa obsoleta	6.71	20.89		0.21	1.26
Pagurus Spp.	6.44		6.88	1.9	0.03
Ulva Spp.	6.12	11.99	4.86	0.11	0.14
Amphipoda spp.	4.09	35.07	21.76	20.85	8.49
Astyris lunata	3.97			1.77	0.33
Bostrychia spp.	3.52	5.18		0	0.1
Hydrobia spp.	3.44	4.59		0.03	7.79
Ovatella myosotis	3.4			0.1	5.21
Nereis spp.	3.16			0.41	0
Polychaeta spp.	2.97			0.21	0.1
Hypnea musciformis	2.65			0.17	0.03

Data represent species contribution to assemblage differences between the two habitats (column 1) and species contribution to within-habitat assemblage structure (columns 2, 3) based on a SIMPER analysis. The taxa are arranged after contribution to dissimilarity between habitats. The last two columns refer to the average abundance of each key taxa per habitat and per *G. vermiculophylla* thallus (g wet weight for sessile species and number of individuals for mobile species)

Thomsen and McGlathery 2005; Freshwater et al. 2006; Thomsen et al. 2007b).

Stability and habitat linkage. The importance of habitat linkages in stabilizing metapopulations has been recognized for some time (Hanski 1998; Grimm et al. 2003). Our study shows that individual *G. vermiculophylla* thalli were relatively unstable within a marsh, but also suggests that metapopulation stability may be conserved due to advection from the more stable populations associated with the adjacent *Diopatra* mudflats. This builds on our previous work which established that *G. vermiculophylla* is commonly incorporated into polychaete tubes, and that this phenomena increases algal population stability (Thomsen and McGlathery 2005). It is well known that these worms often live adjacent to marshes (Mangum et al. 1968), yet until now no link has been made between the habitats with respect to algal population stability. Fragmentation of the algae as it is being incorporated into the tube cap (unpublished data; Thomsen and McGlathery 2005) is also important in ensuring a constant supply of fragments that could potentially reach areas in the marsh where growth is possible.

Our results indicated that this transfer is mainly unidirectional; *G. vermiculophylla* biomass is primarily produced in the lagoon (Thomsen and McGlathery 2007), fixed into polychaete tubes (Thomsen and McGlathery 2005), and transported to the marsh where it may enter the detritus chain (this study). This advection and accumulation of biomass can result in a nutrient transfer between the lagoon and the marsh. In a recent mesocosm study, Boyer and Fong (2005) used ^{15}N as a tracer and showed that the nitrogen incorporated into an opportunistic macroalgae (*Ulva*) was subsequently taken up by a marsh succulent (*Salicornia*) after decomposition of the algae, and they suggested that nutrient transfer via algae from the lagoon to the marsh is a potentially important process. Our data from the mesh bag stress resistance experiment indicates that a substantial amount of biomass (40%) can be lost in 1 week, suggesting that the nitrogen contained in this mass would also be released into the environment. Clearly, more field studies are needed on this potential nutrient subsidy from the lagoon to the marsh. Similar habitat linkages have been described for other marine systems, e.g., between limestone

reefs and seagrass beds (Wernberg et al. 2006) or between oyster reefs and mudflats (Thomsen and McGlathery 2006). It is also important to reiterate that a few adult *G. vermiculophylla* thalli were found attached to stems with perennial holdfast structures, documenting that settlement, survival, and long-term growth is possible in certain marsh zones. Such attachment in marshes is only known for macroalgae of unusually high desiccation resistance, including *Ulva* (Boyer and Fong 2005), *Caloglossa*, *Bostrychia*, and *Fucus* (Humm 1979) and has, to our knowledge, not been described before for *Gracilaria* species.

Stress tolerances. The mesh bag experiment indicates that *G. vermiculophylla* is more stress-resistant in the marsh compared to other common coarsely branched algae found in lagoons and estuaries, including *A. subulata*, *C. fragile*, and *G. tikvahiae* (Cowper 1978; Virnstein and Carbonara 1985). However, even though *G. vermiculophylla* is relatively stress-resistant, net growth is probably only possible under very specific environmental conditions (e.g., we only found net growth in two out of nine growth bags and only 11 quadrats with attached *G. vermiculophylla* out of 330), for example, where drainage is restricted, where shading reduces desiccation, or where other micro-climatic conditions reduce abiotic stress (Gabriela et al. 2000; Theodose and Martin 2003). High stress resistance of *G. vermiculophylla*, compared to common bay algae, has previously only been observed in the lagoon/marine habitats in this region (Thomsen and McGlathery 2006, 2007; Thomsen et al. 2007a). This suggests that many different traits, including high recruitment and high tolerance to sedimentation, desiccation, grazers, and light and salinity extremes, may explain the success of this non-native species across diverse habitats (Raikar et al. 2001; Rueness 2005; Freshwater et al. 2006; Nyberg 2006; Thomsen et al. 2007b).

Associated biota. The significant differences in biota associated with *G. vermiculophylla* in lagoonal and salt marsh habitats, with lower species richness and biomass in the marsh, indicate very different assemblages in the two habitats. We suggest that the associates of *G. vermiculophylla* should be characterized as (1) a marine stenohaline and desiccation-intolerant assemblage that is most common on lagoonal *G. vermiculophylla* (e.g., *Ceramium* spp., *Polysiphonia* spp., *Hypnea musciformis* (Wulfen)

Lamour, *Caprella* spp., *Pagarus* spp., many amphipods), (2) a marine stress-tolerant euryhaline assemblage that colonizes *G. vermiculophylla* in the lagoon but can survive conditions in the lower marsh (e.g., *Ulva* spp., and to some extent *Astyris lunata* (Say) and several polychaetes), and (3) an assemblage that mainly colonizes *G. vermiculophylla* in the marsh (e.g., *Bostrychia* spp., *Hydrobia* spp., *O. myosotis*, *I. obsoleta* Say, *Sesarma* sp., *Uca* sp.) (Daiber 1982; Adam 1990). It should be noted that from the latter group both *Hydrobia* and *I. obsoleta* are also common on intertidal mudflats and are not obligate marsh organisms (Lippson and Lippson 1997). This suggested algal-mediated transfer of organisms between habitats (lagoon to marsh) has also been documented previously between sand patches and seagrass assemblages (Holmquist 1992; Holmquist 1994).

It is interesting that a few juvenile fish (killifish and silversides) and blue crab recruits were found associated with *G. vermiculophylla* in both *Diopatra* mudflats and within the marsh. The economically important blue crabs have declined in population size in recent decades (Lipcius and Stockhausen 2002). We suggest that the complex structure of *G. vermiculophylla* could potentially create a predation refuge for blue crab and fish recruits as well as shrimps and amphipods (Hay et al. 1988; Hay et al. 1990) in both the upper intertidal and lower marsh zone. This may be ecologically important on large spatial scales if *G. vermiculophylla* continues its spread. It has been shown previously that *G. vermiculophylla* is an important foundation species that supports an array of associated organisms (Thomsen and McGlathery 2005; Thomsen et al. 2006; Wallentinus and Nyberg 2007). This type of habitat facilitation also has been observed for several non-native macroalgae in shallow subtidal systems in Europe (Wernberg et al. 2004; Wikstrom and Kautsky 2004; Buschmann et al. 2006).

Possible temporal effects. Our study did not intend to address temporal effects. However, we expect that our results would vary significantly on decadal (ongoing colonization process and climate changes), annual (cold vs. warm or wet vs. dry years), seasonal (light and warm summers vs. cold and dark winters), lunar (strong vs. weak peak tides), and daily (sporadic storms, grazer appearances, tides) scales. There is strong seasonality in both abitotic and biotic factors

in temperate salt marshes, for example, with freezing and low light levels over winter months (Thomsen 2004a; for detailed account of salt marsh seasonality see Adam 1990). As our data are summer collections, we assume that they represent a general summer maxima, and that abundances, including associated flora and fauna, will decrease towards the cold and dark winter season as has been shown for the abundance (Thomsen et al. 2006), recruitment (Thomsen 2004a; Thomsen and McGlathery 2006; Thomsen et al. 2007a) and ecological performance (Thomsen 2004a; Thomsen and McGlathery 2007) of macroalgae in the adjacent lagoons. Nevertheless, the recording of a few attached and reproductive thalli in the marsh-border documents that *G. vermiculophylla* at least in these cases have survived adverse winter conditions in the marsh and managed to complete its life cycle (spores attached to stems and grew into adult and reproductive perennial thalli).

In conclusion, *G. vermiculophylla,* a non-native coarsely branched large red algae, is today a conspicuous component of Virginia marshes characterized by low slopes and adjacent *Diopatra* mudflats. Most thalli are relatively unstable, even though a few individuals may recruit, survive and grow for long periods. Metapopulation stability may be maintained by the transfer of fragments from adjacent *Diopatra* mudflats. *G. vermiculophylla* is more resistant to the stresses of desiccation and low salinity than several native algal species and thus may be able to survive for longer periods in the low marsh habitat. The advection, accumulation, and subsequent decomposition of *G. vermiculophylla* are likely to have important implications for nutrient cycling and trophic dynamics in the *S. alterniflora* dominated low marsh. *G. vermiculophylla* contains a relatively abundant epiflora and fauna, showing utilization by native marsh plants and animals. We suggest that future studies should focus on possible ecological impacts of the introduction, by combining manipulative impact studies from locations where *G. vermiculophylla* is present, e.g., using addition or removal designs, with correlative space-for-time substitution, e.g., comparing mid-Atlantic sites where *G. vermiculophylla* is present with similar habitats from northern and southern regions where *G. vermiculophylla* is absent (Williams and Smith 2007). We also hypothesize that *G. vermiculophylla,* similar to many non-native marine species (Williams and

Grosholz 2008), will be difficult to control or eradicate, due to its high abundance, stress-resistance, and high sexual and asexual reproductive success.

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