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Flora and fauna associated with the introduced red alga *Gracilaria vermiculophylla*

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This paper presents the first detailed study of the spread of the introduced marine red alga *Gracilaria vermiculophylla* on the west coast of Sweden, and of the fauna and flora associated with this alga in Scandinavia and the western mid-Atlantic. *G. vermiculophylla* was discovered in the archipelago of Göteborg, Sweden, in the summer of 2003, and in 2005 its distribution range covered at least 150 km. The species is typically found as loose-lying thalli or attached to small stones and mollusc shells within low-energy bays and estuaries. Both gametophytic and tetrasporophytic specimens were found, as well as specimens with mixed reproductive stages. In order to assess the importance of this introduced alga as a habitat for native benthic organisms, attached and loose-lying individuals of *G. vermiculophylla* were sampled from invaded locations in Sweden, Denmark and Virginia (United States). In total we found 92 taxa associated with *G. vermiculophylla*. The dominant classes were Malacostraca, Gastropoda and Florideophyceae. The diversity of the associated taxa was not affected by attachment status, or *G. vermiculophylla* biomass. In Virginia and Sweden animal abundances were positively correlated with the biomass of algae and plants associated with *G. vermiculophylla*. If *G. vermiculophylla* primarily invades non-vegetated soft-sediment estuaries, the invasion may lead to an increase in abundances of small native invertebrates (e.g. gastropods and crustaceans) and epiphytic algae, with likely cascading effects on higher trophic levels.

Key words: associated organisms, community structure, distribution, diversity, invasive alga, non-indigenous

Introduction

Macroalgae are of great ecological importance, particularly as primary producers and as habitat-formers, providing space, shelter and food for a variety of associated organisms. Different species of macroalgae often support different associated organisms (Chemello & Milazzo, 2002), due to differences in growth environment, heteromorphic life cycles, chemical defence compounds (Duffy & Hay, 1994; Thornber *et al.*, 2006), morphologies, texture or architectural complexities. The attachment status of the host species (either attached to hard substratum with a holdfast structure or loose-lying) may also affect the community structure of associated species, as attached thalli baffle waves and currents, whereas loose-lying thalli drift and tumble. Drifting and tumbling cause the algae to encounter different environmental conditions (Holmquist, 1994), and the unstable and variable habitat-conditions may provide harsh conditions for associated flora and fauna, compared with attached algae that provide a more constant habitat. However, we are not aware of any studies that have compared associated biota of attached and loose-lying thalli. Many algal species survive both as attached and as loose-lying thalli. Loose-lying specimens drift with currents and may accumulate in shallow soft-bottom bays. Such drift accumulations at new locations may eventually, through spore release, lead to attached specimens scattered on stones and shells. It is also possible to become 'fixed in space' without spore release by incorporation into mussel byssal threads (Albrecht, 1998; Thomsen *et al.*, 2007) or polychaete tubes (Thomsen & McGlathery, 2005) and some algal species can re-attach to hard substratum by production of secondary rhizoids (Salinas, 1991). In soft-bottom areas loose-lying algae function as habitat modifiers (Pihl *et al.*, 1996; Wallentinus & Nyberg, 2007), structuring communities by modifying physical, chemical and biological processes.

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In 2003, a non-indigenous Asian red alga, *Gracilaria vermiculophylla* (Ohmi) Papenfuss (1967), was observed for the first time on the Swedish west coast (Wallentinus & Jenneborg, 2003), and has since accumulated in numerous shallow soft-bottom bays. This perennial species has an isomorphic life cycle with male and female gametophytes and tetrasporophytes of similar morphology (Ohmi, 1956). In 2003 it was also recorded in Horsens Fjord in Denmark (Nielsen, 2005; Thomsen *et al.*, 2007) and one year later it was confirmed that a species commonly referred to as *G. verrucosa* in Virginia, United States, was in fact *G. vermiculophylla* (Rueness, 2005; Thomsen *et al.*, 2006*a*). The vector for the introduction of *G. vermiculophylla* is unknown, but it probably arrived in the United States and Europe by oyster transplantation (or alternatively attached to vessels) and then reached Sweden and Denmark through secondary introduction from the southern or central Europe, where it has been present at least since the mid 1990s (Rueness, 2005). In the recipient areas *G. vermiculophylla* has been spreading relatively fast (this paper; Freshwater *et al.*, 2006). This coarsely branched red alga is particularly well-adapted to low energy, shallow soft-bottom bays, lagoons, estuaries, harbours and inlets (Yokoya *et al.*, 1999; Rueness, 2005; Thomsen & McGlathery, 2007). When occurring in high abundance, it may have dramatic effects on the community composition within these systems. Earlier studies on *G. vermiculophylla* focused on distribution patterns (Freshwater *et al.*, 2006; Thomsen *et al.*, 2006*b*; Thomsen *et al.*, 2007), recruitment (Thomsen & McGlathery, 2005; Thomsen *et al.*, 2006*b*), stress-tolerances (Yokoya *et al.*, 1999; Raikar *et al.*, 2001; Rueness, 2005; Nyberg, 2007, Thomsen & McGlathery, 2007), and changes in amphipod and microalgal densities (Aikins & Kikuchi, 2002). However, to our knowledge no studies have investigated the entire sessile and slow moving community associated with *G. vermiculophylla* in invaded regions.

The objectives of this study were to document the invasion of *G. vermiculophylla* in Sweden, and to compare associated community structures from invaded locations in Denmark, Sweden and Virginia, United States, as well as between attached and loose-lying thalli. We hypothesized that the associated communities would be richer and more abundant on *G. vermiculophylla* samples from Sweden (locations adjacent to rocky coastline and very high abundances of macroalgae) intermediate from Virginia (locations with near marine salinities) and lowest in Denmark (lack of hard substratum and/or brackish conditions). We also expected to find more animals and plants associated with attached, rather than loose-lying thalli, as the former are likely the more stable habitat.

Materials and methods

Gracilaria vermiculophylla *survey in Sweden*

The archipelagos of the Swedish west coast (the eastern Kattegat and Skagerrak) consist of islands and fjords with numerous shallow (0–3 m), soft-bottom bays. During the late summers of 2003–2005, the Swedish west coast between the Koster archipelago and the southern province of Halland (58°21′16.1″N; 11°24′33.9″E and 57°03′49.4″N; 12°16′39.8″E) were surveyed to document the spread of *G. vermiculophylla*. The locations visited (46 in 2003 and 50 in both 2004 and 2005) were chosen for their accessibility and environmental variables (protected to semi-exposed shallow bays with sand and/or mud). The surveys were made by wading or snorkelling and each surveyed area was about 100 m^2.

Gracilaria vermiculophylla *and associated biota*

Gracilaria vermiculophylla was collected from nine of the surveyed locations on the west coast of Sweden (September 2005), four locations in Denmark (the Danish Wadden Sea; Western Mandø, September 2005, Horsens Fjord and Holckenhavn Fjord, August 2006, cf. Thomsen *et al.*, 2007 for map of sample locations) and four locations in Hog Island Bay, Virginia on the east coast of USA (July 2006, cf. McGlathery *et al.*, 2001 for map of sample locations), see Table 1. To achieve a balanced design for statistical testing we randomly selected four of the nine Swedish sites (Underwood, 1997). We report the additional species found in the locations excluded from the statistical analysis in supplementary material (available online at http://www.informaworld.com/mpp/uploads/nyberg_et_al_supplementary_material.pdf) (for future comparison with other regions or temporal changes). All study areas were protected or semi-exposed shallow bays, lagoons and estuaries. The bottoms consisted of sand and mud with scattered shells, stones and small rocks. Sample locations in the Wadden Sea and Virginia were intertidal mudflats, whereas the remaining locations along the micro-tidal Danish and Swedish coasts were subtidal (0.2–1 m depth). All intertidal samples were collected on falling tides when the water levels were between 0.1 and 0.3 m below mean water. Sites in Virginia were typical '*Diopatra cuprea* mudflats'. *Diopatra cuprea* is a ubiquitous polychaete that anchors *G. vermiculophylla* to its tube-cap throughout Virginian lagoons and thereby provides an abundant supply of substratum (Thomsen & McGlathery, 2005). The salinities varied from 30 to 36 psu at localities in Virginia and from 15 to 36 psu at localities in Scandinavia.

At the collection sites the relative abundance of up to five of the most common algal and plant species were recorded by visual observation by two independent researchers. At each location four individual loose-lying (only Denmark and Sweden) and four attached,

Table 1. Sampling locations of *Gracilaria vermiculophylla*.

Location	Coordinates	Abundance	Attached	Semi-attached	Loose	Reproductive females (No of specimens)
Denmark						
Western Mandø	55°17′11.9″N; 8°31′00.5″E	GV, FV, CL, U		4	4	Yes (1)
Snaptun Harbour	55°48′57.4″N; 10°03′18.1″E	GV, FV	4		4	Yes (2)
Nørrevang	55°51′14.5″N; 9°52′32.8″E	GV, FV	4		4	Yes (9)
Holckenhavn Fjord	55°17′20.4″N; 10°46′42.6″E	GV, FV, U		4	4	Yes (5)
Sweden						
Särö	57°30′37.4″N; 11°56′19.6″E	FV, CF, ES, C, GV	4		4	Yes (2)
Sandö	57°28′59.6″N; 11°56′34.2″E	GV, ES, UI	3	1	4	Yes (3)
Lerkil Harbour	57°27′08.3″N; 11°54′55.6″E	GV, FV, ES	4		4	Yes (7)
Rörvik	57°37′33.8″N; 11°52′40.0″E	GV, DB, U, FV	4		4	Yes (5)
United States						
North Hog Island	37°27′90″N; 75°40′58″W	GV, U, FV, AS		4		Yes (3)
South Hog Island	37°22′17″N; 75°43′42″W	GV, U, FV		4		Yes (4)
Fisherman Island	37°06′30″N; 75°58′10″W	GV, U		4		Yes (1)
South Bay	37°17′25″N; 75°51′12″W	GV, U		4		No

Note: Number of replicates for attached, semi-attached (regarded as attached in analyses) and loose-lying specimens are shown, together with reproductive status (i.e. females with cystocarps; number of specimens in parenthesis), and the most abundant algal and plant species in decreasing order at each location.
Abbreviations: AS: *Agardhiella subulata*; C: *Ceramium spp.*; CF: *Chorda filum*; CL: *Chaetomorpha linum*; DB: *Dasya baillouviana*; ES: *Ectocarpus siliculosus*; FV: *Fucus vesiculosus*; GV: *Gracilaria vermiculophylla*; UI: *Ulva intestinalis*; U: *Ulva* spp.

or semi-attached (i.e. *G. vermiculophylla* incorporated into polychaete tubes, or mollusc byssal threads) specimens of *G. vermiculophylla* were collected separately (Table 1). The specimens were gently lifted from the water, placed in separate plastic bags and kept cold until arrival at the laboratory. Some highly motile organisms may escape using this sampling technique, but juvenile fish, shrimps and crabs were occasionally caught. Upon arrival at the laboratory *G. vermiculophylla* were blotted and wet weight was recorded. Entangled algae, seagrasses and sessile animals were identified, blotted dry and weighed. Larger mobile animals were identified and counted, while smaller mobile animals were preserved in 70% ethanol for counting later, when they were identified to the lowest possible taxonomic level. Taxa were recorded either at the specific or generic (sp.) level. For some genera we found several unspecified taxa, denoted 'spp.' (see supplementary material). These taxa were regarded as a single species to avoid overestimations of richness and diversity indices.

Statistical analyses

For the statistical analyses the semi-attached specimens of *G. vermiculophylla* were regarded as attached, since they do not drift as loose-lying thalli. To analyse the associated flora and fauna of *G. vermiculophylla* the following variables were calculated: total abundance of animal individuals (N), total number of taxa (hereafter richness, S) and algal/plant biomass, all being standardized to gram wet weight of *G. vermiculophylla*. For the animal community, diversity (Shannon–Wiener diversity, $H' = -\Sigma p_i \ln p_i$, where p_i is the number of individuals for each species divided by the total number of all individuals) and evenness (Pielou's evenness, $J' = H'/\log S$) were calculated. Analysis of variance (ANOVA) was performed on diversity, evenness, species richness, number of individuals and biomass of associated primary producers, with country and attachment status as factors. Significant differences following ANOVA were identified by Student–Newman–Keuls (SNK) post-hoc tests. The attachment status of *G. vermiculophylla* and the animal communities for the three countries were compared using Bray–Curtis similarity and non-metric Multi-Dimensional-Scaling (nMDS). Prior to the similarity analyses the raw data were transformed with the fourth root to scale down the importance of highly abundant species. Analysis of Similarities (ANOSIM) was used to test if the community structures varied between the countries, followed by Similarity Percentages (SIMPER) to detail which species caused most of the variability between countries. ANOSIM and SIMPER were run with 999 permutations. Linear regression between number of species, number of individuals and the amount of associated algae and plants were analysed with two-tailed Pearson's correlation coefficient. The PRIMER package was used to perform multivariate analyses and SPSS to perform ANOVAs and linear regression at a significance level of 0.05. All variables are reported with standard errors and all biomass-values correspond to wet weight (ww, after blotting/removal of surface water).

Results

Gracilaria vermiculophylla *survey in Sweden*

In total, 50 locations were visited on the west coast of Sweden, and *G. vermiculophylla* was found at 35 locations (through other studies in the Skagerrak and the Kattegat at least 20 additional locations have been visited but no additional *G. vermiculophylla* has been discovered, Wallentinus

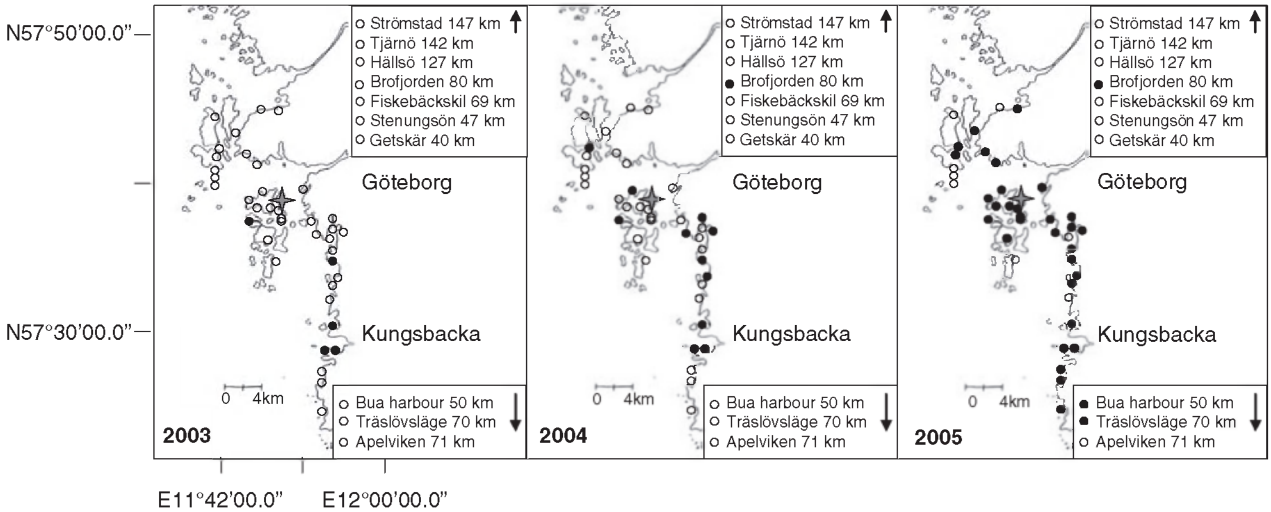

Fig. 1. Spread of *Gracilaria vermiculophylla* on the Swedish west coast 2003–2005. Grey star denotes the location of initial discovery from which the spread is measured. Positive findings are filled circles and not observed are empty circles. The northern-most discovery is Brofjorden 80 km north and the southern-most is Träslövsläge 70 km south. (Data from Brofjorden, L.-H. Jenneborg (pers. comm.) and the three northern-most discoveries on the mainland in the Göteborg area from Ahlgren (2005).

pers. obs.). In 2005, only 2 years after the first observation, *G. vermiculophylla* was observed 80 km to the north and 70 km to the south, from its original discovery location in the Göteborg archipelago (Fig. 1). *Gracilaria vermiculophylla* was primarily found in soft-bottom bays at a depth of less than 1 m. However, it can also occur deeper, particularly in eelgrass beds (*Zostera marina*). In 2003, the majority of the specimens were loose-lying, often accumulated in dense mats, while in 2005, specimens attached to stones, both living and dead gastropods and bivalves were almost as common. The largest specimen found was 1 m in length and was loose-lying. The loose-lying specimens were often partly covered with sand or mud. Female and male gametophytes, tetrasporophytes, as well as specimens with tetrasporangia in combination with either spermatangia or cystocarps were found during the surveys.

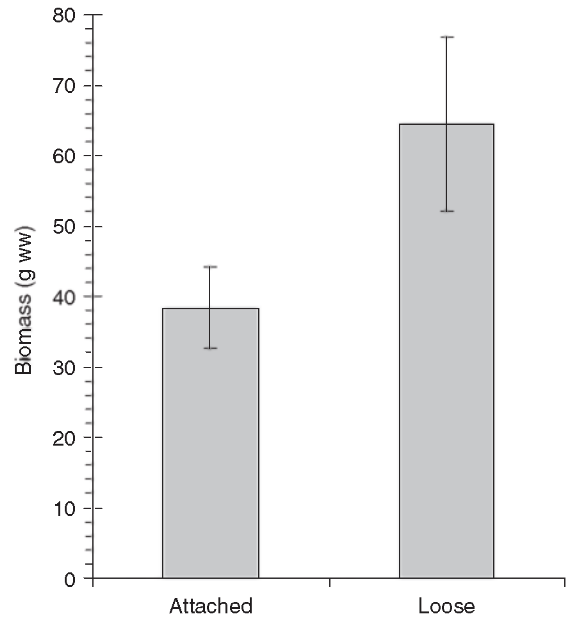

Fig. 2. Average biomass (g ww ± SE) of individual attached and loose-lying ($n = 32$) *Gracilaria vermiculophylla* specimens (pooled data for Denmark and Sweden).

Gracilaria vermiculophylla *and associated biota*

Gracilaria vermiculophylla was among the five most abundant algal/plant species at all sampled locations. *Fucus vesiculosus* and *Ulva* spp. were common native taxa at most locations. No significant difference in biomass between loose-lying and attached thalli of *G. vermiculophylla* was discovered ($p = 0.06$; Fig. 2). Focusing on the associated biota attached on or entangled in *G. vermiculophylla* we found a total of 83 taxa (92 taxa when including the additional samples not included in the statistical analyses; (see supplementary material (available online at http://www.informaworld.com/mpp/uploads/nyberg_et_al_supplementary-material.pdf)). Of these 83 taxa, 29 taxa were found in Denmark, 45 in Sweden and 25 in Virginia. Four algal/plant phyla were found and eight faunal phyla. The most abundant classes were Malacostraca (16 taxa), Gastropoda (13 taxa) and Florideophyceae (13 taxa). The most abundant primary producers entangled in *G. vermiculophylla* were the algae *Ceramium virgatum* (Virginia), *Ulva* spp. (Denmark) and *Polysiphonia* spp. (Sweden). Only eight of the 30 macroalgae and plants were attached to the thallus of *G. vermiculophylla*, the rest were entangled (e.g. Najadales, Fucales and Laminariales). The most abundant animals were amphipods

Table 2. Biomass (mean ± standard error) of sampled *Gracilaria vermiculophylla* specimens at the different locations.

Location	Attachment status	Flora			Fauna			
		G. v (g)	(S g^{-1})	(g g^{-1})	(S g^{-1})	(N g^{-1})	H′	J′
Denmark								
Western Mandø	Loose	35.28 ± 6.63	0.23	0.12	0.17	2.08	0.14	0.23
	Attached	47.33 ± 9.00	0.15	0.00	0.19	5.40	0.65	0.91
Snaptun Harbour	Loose	50.98 ± 24.21	0.18	0.08	0.08	0.11	0.47	0.76
	Attached	59.33 ± 18.25	0.17	0.10	0.12	2.54	0.09	0.17
Nørrevang	Loose	28.07 ± 12.29	0.11	0.00	0.18	0.82	0.72	1.16
	Attached	37.57 ± 7.95	0.11	0.00	0.13	0.71	0.32	0.70
Holckenhavn Fjord	Loose	19.29 ± 7.02	0.26	0.01	0.26	0.44	0.85	1.37
	Attached	34.32 ± 20.62	0.12	0.00	0.15	2.17	0.56	1.01
Sweden								
Särö	Loose	109.25 ± 33.48	0.10	0.13	0.06	0.24	0.39	0.76
	Attached	51.45 ± 34.49	0.14	0.08	0.14	0.65	0.64	1.74
Sandö	Loose	150.35 ± 62.29	0.03	0.01	0.10	0.29	0.32	0.62
	Attached	20.70 ± 5.28	0.29	0.18	0.43	3.03	0.40	0.88
Lerkil Harbour	Loose	56.03 ± 43.44	0.07	0.03	0.11	0.69	0.10	0.19
	Attached	27.28 ± 10.63	0.11	0.00	0.40	0.27	0.70	1.54
Rörvik	Loose	56.03 ± 43.44	0.07	0.03	0.11	0.69	0.10	0.19
	Attached	27.28 ± 10.63	0.11	0.00	0.40	0.27	0.70	1.54
United States								
North Hog Island	Attached	8.21 ± 2.07	0.61	0.99	1.22	6.30	0.50	1.15
South Hog Island	Attached	30.87 ± 6.89	0.19	0.25	0.29	0.69	0.65	1.43
Fisherman Island	Attached	7.83 ± 2.13	0.89	0.52	0.89	2.81	0.63	1.22
South Bay	Attached	34.00 ± 4.30	0.15	0.03	0.26	1.83	0.39	0.87

Note: Number of taxa (S), number of individuals (N) and biomass of associated algae and plants are shown per gram ww of *G. Vermiculophylla*. Shannon–Wiener diversity (H′) and Pielou's evenness (J′) are shown for the associated fauna.

(Denmark, Virginia) and the gastropod *Pusillina sarsi* (Sweden) (see supplementary material). Several animals were found both as juveniles and adults, for example the blue mussel *Mytilus edulis*, the green crab *Carcinus maenas* and the common periwinkle *Littorina littorea*, all of which were more numerous as juveniles (unpublished data).

This study did not reveal significant differences for the diversity (H′: $p = 0.92$) or evenness (J′: $p = 0.78$) of associated animals between attached and loose-lying thalli, nor between countries (H′: $p = 0.62$; J′: $p = 0.63$) (Table 2). However, thalli from Virginia had higher richness of both fauna ($p = 0.01$) and flora ($p = 0.001$) as well as larger biomass of associated algae/plants ($p = 0.0002$) compared with thalli from Denmark or Sweden (Fig. 3). A nMDS plot (Fig. 4) of the associated species showed a clear separation between countries, but no separation between attached and loose-lying *G. vermiculophylla*. This pattern was supported by the ANOSIM test that showed significant differences between countries (Global: $R = 0.89, p = 0.001$; Denmark vs Sweden: $R = 0.97, p = 0.001$; Denmark vs Virginia: $R = 0.62, p = 0.002$; Sweden vs Virginia: $R = 1.00, p = 0.002$). The taxa responsible for most of the dissimilarities (SIMPER) were Amphipoda (contribution (c) = 31% for Denmark vs Sweden; 41% for Denmark vs Virginia and 41% for Sweden vs Virginia) see Table 3.

For the US samples there was a significant positive linear relationship between both number (N g^{-1}) and richness (S g^{-1}) of animals versus biomass of associated algae and plants (g g^{-1}) ($r^2 = 0.53$, $p = 0.001$; $r^2 = 0.66$, $p = 0.0001$, respectively) and versus biomass of *G. vermiculophylla* ($r^2 = 0.37$, $p = 0.01$; $r^2 = 0.48$, $p = 0.003$). Comparison of animal number (N g^{-1}) versus biomass of associated algae/plants (g g^{-1}) was also strongly correlated ($r^2 = 0.81$, $p = 0.0002$) for the Swedish samples. No correlations were seen for the rest of the Swedish and the Danish sample comparisons.

Reproductive female gametophytes of *G. vermiculophylla* were recorded at several locations in Sweden, Denmark and Virginia (Table 1) and were present as both attached and loose-lying specimens. No significant differences were observed between the numbers of faunal individuals, the biomass of associated primary producers and the number of taxa of flora and fauna on cystocarpic versus non-cystocarpic *G. vermiculophylla* specimens (Fig. 5).

Discussion

The objective of this study was to describe the spread of the introduced red alga *G. vermiculophylla* and its associated algae/plant and animal community. From the first observation in 2003 to 2005 *G. vermiculophylla* has extended its

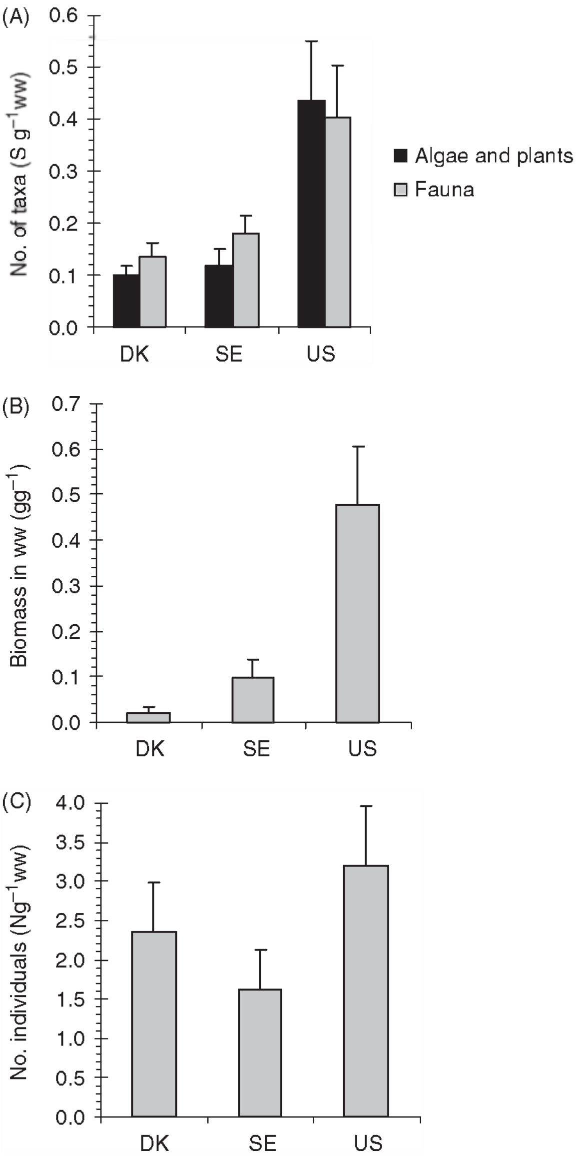

Fig. 3. (A) Number of associated taxa, (B) Biomass of associated algae and plants and (C) Number of individuals of fauna on *Gracilaria vermiculophylla* sampled in Denmark (DK), Sweden (SE) and Virginia (US). Values are means ± standard error.

range distribution in Sweden by ~150 km. This range expansion is higher than the invasive dispersal rate reported for the Japanese kelp *Undaria pinnatifida* (Harvey) Suringar along the south coast of England (44 km year^{-1}, Farrell & Fletcher, 2006) and for the Japanese brown alga *Sargassum muticum* (Yendo) Fensholt in Denmark (15–17 km year^{-1}, Staehr *et al.*, 2000). *Gracilaria vermiculophylla* has a disjunct distribution in Denmark, being common in the Horsens Fjord, Holckenhavn Fjord, Fyns Hoved, parts of the Wadden Sea and Limfjorden, and observed in smaller populations in Øster Hurup havn, Vejle Fjord, Odense Fjord, Avnø Fjord, and Sejerø Bugten, suggesting multiple introductions (Thomsen pers. comm.). Along the east coast of USA the spread has been virtually undetected,

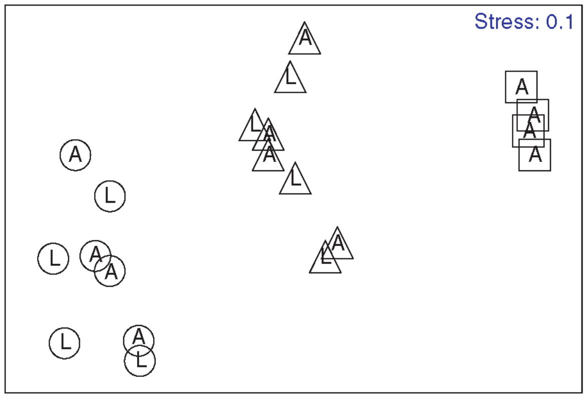

Fig. 4. Multidimensional scaling plot with the variables animal taxa and attachment type for the three locations (circle: Sweden; triangle: Denmark; square: Virginia, USA). Raw data were fourth root-transformed and run with 999 permutations. The stress is 0.1. Abbreviations: L: Loose-lying samples; A: attached samples.

because *G. vermiculophylla* invaded locations occupied by morphologically similar *Gracilaria* species (but anecdotal information suggests blooming of *G. vermiculophylla* in the late 1970s in Virginia). Today, *G. vermiculophylla* is found along the east coast of USA, at least from South Carolina to Massachusetts (Gurgel, pers. comm.). The spread of *G. vermiculophylla* (with spores and fragments down to ≥1 mm in size) (Nyberg, 2007) along the coasts will most certainly continue, with vectors including small vessels, such as fishing and leisure boats, releases from fishing gear, currents and migrating seabirds. According to the results presented by Nyberg (2007) and Yokoya *et al.* (1999), *G. vermiculophylla* can survive the salinity along the coast of the Baltic Sea to the northernmost parts of the Bothnian Bay. The alga can also survive in total darkness for more than five months (if kept cold, Nyberg & Wallentinus, in press), and the dark winters in the northern part of Scandinavia are therefore unlikely to limit its future range expansion into the Baltic Sea. Two factors that might limit the continued spread of *G. vermiculophylla* are temperature and ice coverage. However, survival over several winters on the Swedish west coast with water temperatures between −2 and 5°C and localized ice cover, suggest that these two factors will not impose major dispersal constraints.

The introduction of *G. vermiculophylla* adds structural complexity to relatively homogenous soft-bottom systems, which may affect the native communities by providing new attachment sites, shelter (Norkko *et al.*, 2000) and food for other organisms (Gustafsson, 2005; Thomsen *et al.*, 2007). This in turn may enhance local diversity, but the ability to utilize the increased habitat complexity will vary between species, due to

Table 3. Species contributing to 90% of the dissimilarities between countries as determined by the SIMPER analyses.

	DK vs SE			DK vs US			SE vs US		
	Global Dis = 96.75			Global Dis = 74.03			Global Dis = 100.00		
Species	AvDiss	Diss/SD	Contrib%	AvDiss	Diss/SD	Contrib%	AvDiss	Diss/SD	Contrib%
Amphipoda	30.16	1.16	31.17	30.00	1.57	40.52	40.75	2.71	40.75
Pusillina sarsi	24.85	1.14	25.69				17.43	1.02	17.43
Caprillida				13.05	1.04	17.62	14.37	1.07	14.37
Hydrobiidae	0.32	0.60	15.83	10.95	0.55	14.80			
Mytilus edulis	6.33	0.67	6.55						
Astyris lunata				3.82	0.81	5.17	4.34	0.83	4.34
Pagarus sp.				3.78	0.88	5.11	4.16	0.94	4.16
Rissoa membranacea	4.02	0.40	4.16				3.27	0.38	3.27
Mytilus edulis				3.71	0.52	5.01			
Nereidae				1.59	1.32	2.15	1.83	1.55	1.83
Bittium reticulatum	2.49	0.34	2.57				1.75	0.32	1.75
Littorina littorea	3.15	0.85	3.26				1.68	0.57	1.68
Idotea baltica	2.57	0.59	2.66				1.57	0.41	1.57

Abbreviations: AvDiss: average dissimilarity; Contrib%: percent contribution to the dissimilarity; Dis: dissimilarity; Diss/SD: standard deviation of dissimilarity; DK: Denmark; SE: Sweden; US: Virginia, USA.

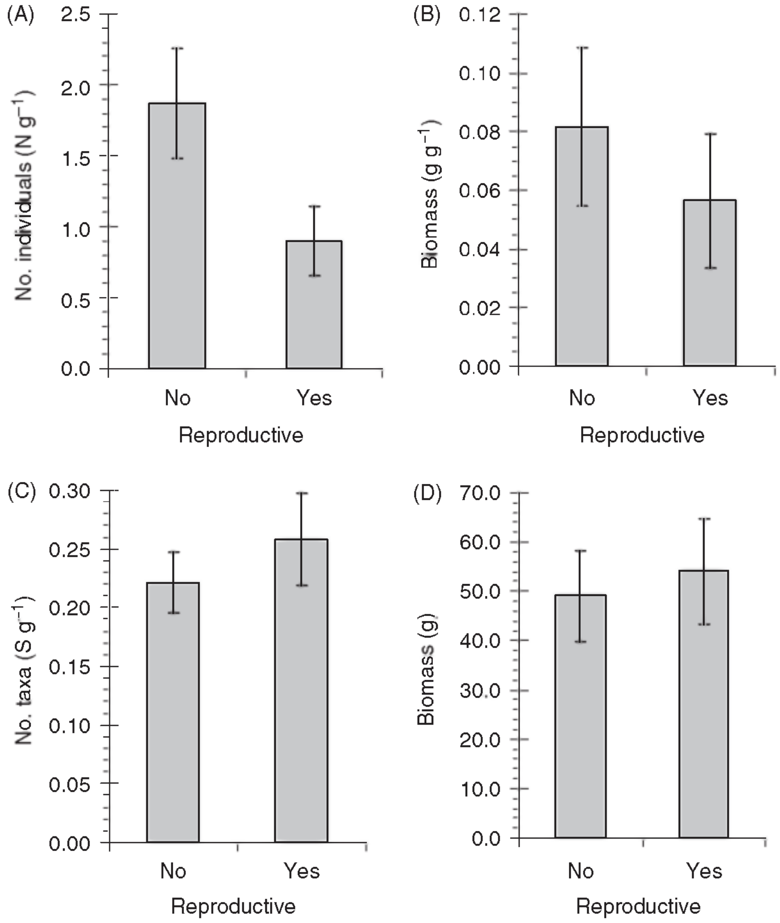

Fig. 5. The relationship between reproductive status (reproductive female gametophytes) of *Gracilaria vermiculophylla* and (A) the number of individuals (fauna), (B) biomass of associated algae and plants, (C) number of taxa of flora and fauna and (D) the biomass of *G. vermiculophylla* for the Danish and Swedish samples. Values are means ± standard error.

morphological, mobility and habitat preferences. The results from this study show that a variety of functional groups from primary producers (e.g. *Ceramium* spp. and *Polysiphonia* spp.) to filter feeders (e.g. *Mytilus edulis*), herbivores (e.g. *Littorina littorea*) and predators (e.g. *Carcinus maenas*) are found associated with *G. vermiculophylla*. Many juvenile fish have also been observed sheltering or foraging in larger loose-lying patches of *G. vermiculophylla* (pers. obs.), but most were not documented in this study due to the sampling technique. To target important motile fauna directly, cast nets, seine nets or drop nets should be utilized (Pihl & Rosenberg, 1982).

In total we observed almost 100 different macroscopic taxa associated with *G. vermiculophylla*: Sweden had the highest total number of taxa, while Virginia had the lowest. One explanation for this could be that the samples from Virginia were from *Diopatra cuprea* mud flats, which reflect a more homogenous habitat than Scandinavian bays/lagoons. Thus, the difference between Scandinavia and Virginia was expected whereas the difference between Denmark and Sweden was somewhat surprising. One reason could be that the locations in Denmark and Virginia are 'stressful' soft-sediments areas with no rocky coast anywhere near, while the Swedish locations have rocky coasts in the vicinity, from which the species pool could be recruited. The samples from Virginia lacked Magnoliophyta and macrophytic Ochrophyta. The lack of *Zostera* in the Virginia samples is likely due to the wasting disease in the 1930s that wiped out local populations, whereas lack of brown algae may be a seasonal effect, since most Virginian brown algae are typical spring bloomers (e.g. *Leathesia*, *Ectocarpus*, *Punctaria*, and *Scytosiphon*). Hall & Bell (1988) showed that there is a significant positive correlation between the density of motile fauna (copepods, nematodes, amphipods, crustacean) and the biomass of epiphytes on seagrass. This can also be the case for macroalgae (Pavia *et al.*, 1999) and a modest-to-strong positive correlation for this was seen in this study for the samples from Virginia and Sweden.

In previous years in Sweden we noted that loose-lying specimens of *G. vermiculophylla* generally appeared larger than attached specimens, potentially caused by age differences or hydrodynamic size-pruning of attached individuals. However, there was no statistically significant size-difference in this study. We expected a difference in species richness and the number of individuals on attached and loose-lying *G. vermiculophylla* due to the tumbling effect, but again no significant differences were detected. In contrast, Holmquist (1994) found more organisms on stationary algae than on drifting algae and there have been reports of shifts in dominant fauna in sandy bays due to increased cover of ephemeral algae (Isaksson & Pihl, 1992) and drifting algal mats (Soulsby *et al.*, 1982; Ólafsson, 1988; Bonsdorff, 1992; Norkko & Bonsdorff, 1996). Loose-lying *G. vermiculophylla* populations have the potential to develop into dense mats, particularly in low energy shallow embayments, estuaries, lagoons and harbours. Such mats can cause considerable habitat modifications for the benthic faunal community and bottom dwelling fish. Algal mats may also form physical barriers for settling larvae unable to encounter the sediment below the algal canopy (Ólafsson, 1988; Bonsdorff, 1992). *Gracilaria vermiculophylla* probably also affects the organisms directly in and on the sediment, through decreased light intensities and changes of water movements, which in turn modifies the sedimentation rate (Madsen *et al.*, 2001) and thus food availability for deposit feeders.

Summary and perspectives

We conclude that, over a few years, the non-indigenous red alga *G. vermiculophylla* has established many permanent and abundant populations in several European countries and along the US east coast. It has, over a short time period, spread to numerous low energy bays, estuaries and lagoons, often as abundant populations. These populations provide a 'hard and heterogeneous' habitat for a variety of associated plants and animals, often within contrasting 'barren/unvegetated' soft-bottom systems. Overall, we found native species from more than ten phyla utilizing *G. vermiculophylla* as habitat, probably for shelter, substratum for attachment, or as feeding grounds. At present no negative impacts on native species or populations have been observed, but if *G. vermiculophylla* continues its spread and accumulates as large mats in *Zostera marina* or *Fucus* beds there is a risk of a shift in the community structure of these important habitats due to shading, smothering and increased likelihood of anoxia. Accumulation of *G. vermiculophylla* could potentially also impair environmental conditions for the Swedish red-listed Charophytes and *Zostera noltii* (Gärdenfors, 2005). Finally, based on the present distribution of *G. vermiculophylla* and its ecological traits (Nyberg, 2007; Thomsen & McGlathery, 2007), we hypothesize that this successful invader will, over the next decades, become abundant in low energy, shallow soft-bottom systems throughout a large part of the Baltic Sea.

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