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How an introduced seaweed can affect epibiota diversity in different coastal systems

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Abstract Invasions by non-indigenous species have the potential to alter the biodiversity of recipient systems. The magnitude of this effect often depends on the nature of the invaded communities and the ecology of the invader. We investigated the impacts of the Japanese seaweed *Sargassum muticum* (Phaeophyceae, Fucales) on biodiversity in a rocky and sedimentary environment on two islands in the North Sea. In each case, we compared the epibiota of non-indigenous *S. muticum* with epibiota communities on taxonomically related and structurally similar native seaweed hosts. Total and average species richness on *S. muticum* were similar on the rocky shore (60 species and 22 ± 6 species, respectively) and the sandy shore (64 species and 20 ± 3 species, respectively). However, community structure and species composition differed significantly between the environments. On the rocky shore, another native fucoid seaweed, *Halidrys siliquosa*, supported an epibiota community very similar to that of the invader. On the sandy shore, the only other abundant native habitat-providing algal species was *Fucus vesiculosus*. This species supported a different and less diverse assemblage of associated taxa. We conclude that *S. muticum* enhances epibiota diversity in the sedimentary

environment, probably by increasing the substratum availability and habitat heterogeneity. In contrast, it has negligible impacts on epibiota diversity in the rocky shore environment, where it does not represent a fundamentally new habitat component. We conclude that even within the same region, the consequences of non-indigenous species on biodiversity cannot be generalised but depend on the composition and structural complexity of the species in the recipient community.

Introduction

Biological invasions by non-indigenous (alien/non-native) species can have strong ecological impacts on resident communities by changing population dynamics, community structure and ecosystem processes (e.g. Bertness 1984; Vitousek et al. 1996; Grosholz et al. 2000; Sakai et al. 2001; Steneck and Carlton 2001; Ross et al. 2004). These impacts may vary greatly depending on the invaded communities (Berman et al. 1992; Chapman 1999). For example, the Japanese seaweed *Codium fragile* (Sur.) Harriot ssp. *tomentosoides* (van Goor) Silva (hereafter *Codium*) was introduced to the European and North American coasts of the Atlantic Ocean at the beginning and in the latter half of the 20th century, respectively. While *Codium* occurs in low abundances intertidally on many European shores, it can have detrimental effects on subtidal kelp communities in the northeast Atlantic Ocean, where the seaweed often reaches nuisance proportions (Chapman 1999; Chapman et al. 2002).

Once established, introduced species can affect biodiversity of the recipient communities. In particular, in a sedimentary environment epibenthic invaders such as macroalgae and mussels create additional, structurally complex habitats that may increase epibiota diversity (Willan 1987; Jones et al. 1994; Crooks 1998, 2002; Dame et al. 2001). For example, the Asian mytilid mussel *Musculista senhousia* (Benson in Cantor) has

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formed dense aggregations on soft sediments of the Pacific coast of North America since the 1920s. The physical structure of these bivalve mats provides a suitable habitat for many native species and, consequently, total densities and species richness of macrofauna are higher inside mussel aggregations (Crooks 1998; Crooks and Khim 1999). As these examples illustrate, the impacts of exotic species can thus be diverse. They are often unpredictable and cannot be generalised, and must be assessed separately for each invaded assemblage. To our knowledge, only few studies compare the impacts of the same invasive species in different systems (Berman et al. 1992; Grosholz and Ruiz 1996; Chapman 1999).

The objective of this study was to assess the biodiversity effects of the Japanese seaweed *Sargassum muticum* (Yendo) Fensholt on neighbouring but distinct species communities in the south-eastern North Sea (German Bight) through a comparison of associated organisms in two fundamentally different environments. We chose the rocky shore of the island of Helgoland and a soft sediment environment near the island of Sylt as our study areas. Their proximity of less than 100 km enabled us to compare the effects of *S. muticum* on the biodiversity of associated epibiota in two contrasting but nearby coastal systems.

The Japanese seaweed *S. muticum* was first described from Japan by Yendo (1907). The brown alga was accidentally introduced to North America in the 1940s and then to Europe in the early 1970s, probably associated with the international transportation of Japanese oysters *Crassostrea gigas* (Thunberg) (Druehl 1973; Critchley 1983). It has subsequently spread along the Atlantic coast of western Europe from Portugal to Scandinavia (Rueness 1989; Karlsson and Loo 1999). In 1980, the first attached specimens were found in the Dutch Wadden Sea on the island of Texel. Since 1988, *S. muticum* has been observed regularly on the German island of Helgoland, and since 1993 on the island of Sylt (Kornmann and Sahling 1994). Currently, *S. muticum* has an almost worldwide distribution. Because of its fast growth and large thallus size (> 3 m), its very successful reproductive strategy by self fertilisation (Fletcher 1975; Norton 1976, 1977a) and several successful dispersal mechanisms (including floating thalli), the alga has been highly invasive and was believed to out-compete native algal species and the organisms associated with them (Norton 1977b).

To assess consequences of the introduction of *S. muticum* on the epibiota diversity of the invaded communities, we compared species associated with *S. muticum* and with the structurally very similar and related native brown alga *Halidryx siliquosa* (L.) Lyngb. on the rocky shores of Helgoland. On soft sediment tidal flats (near the island of Sylt), the species assemblage inhabiting *S. muticum* was compared with biota on the bladder wrack *Fucus vesiculosus* forma *mytili* (Nienburg) Nienhuis because *Fucus* represents the only other abundant habitat-providing macroalgal in the Wadden Sea (Schories et al. 1997; Albrecht 1998).

We hypothesised that *S. muticum* would have different effects on epibiota diversity in the two coastal systems. We expected a neutral effect of *S. muticum* for Helgoland's rocky shore, because the introduced and the native seaweed hosts have very similar morphologies and occur in overlapping habitats (Wernberg et al. 2004). In contrast, an increase in epibiota diversity was expected for Sylt. Predicting that *S. muticum* increases habitat heterogeneity and substratum availability providing suitable living conditions for many associated organisms in a sedimentary environment, we hypothesised that species numbers would be higher on *S. muticum* than on the comparatively unstructured, native *Fucus vesiculosus* forma *mytili*.

Materials and methods

Study sites

We selected the soft sediment tidal flats near the island of Sylt (54°55'N, 008°20'E) and the rocky shore of Helgoland (53°11'N, 007°53'E) in the North Sea (German Bight) as our field sites (Fig. 1). Both sites belong to the cold temperate region.

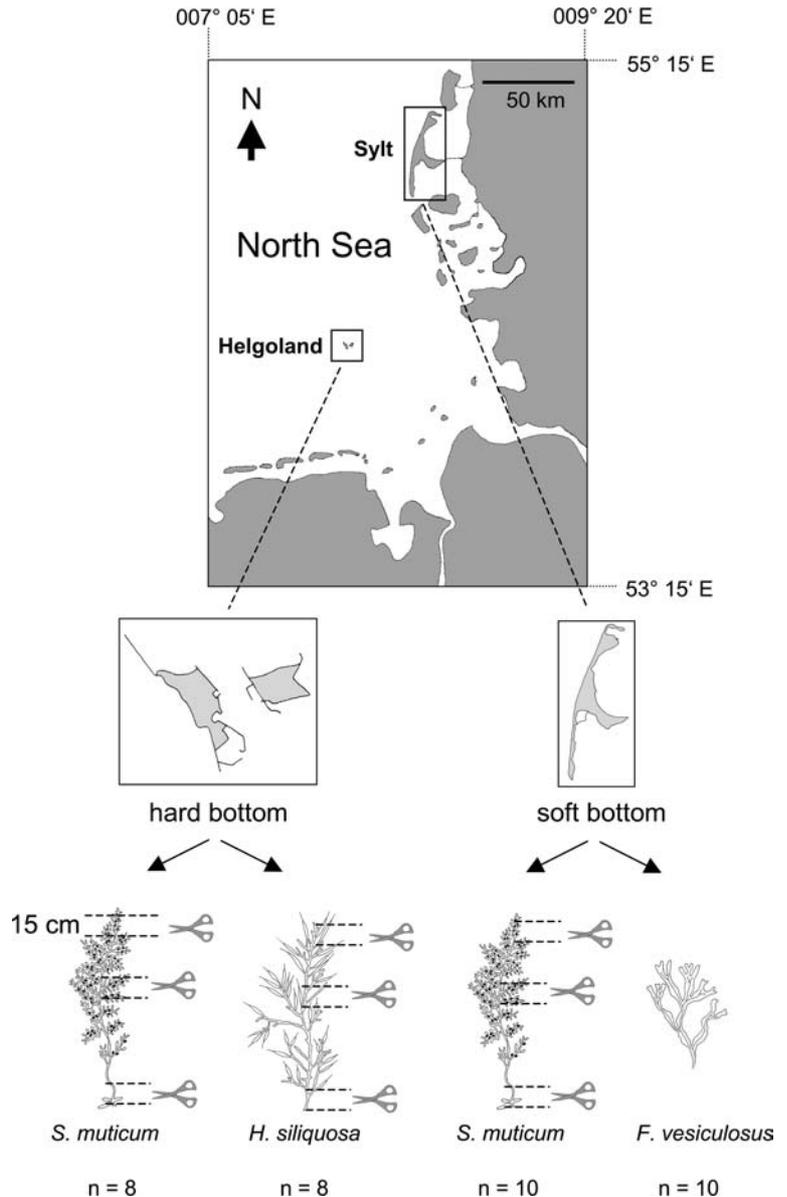
The mean annual water temperature off Sylt is about 9°C, with a summer average of 15°C and a winter average of 4°C. Tides are semi-diurnal with an average tidal range of about 2 m. Salinity usually remains between 30 and 32 psu. A detailed description of the hydrography, geology, sediments and biota of the study area is given by Reise (1985), Austen (1994a, b), Bayerl and Higelke (1994) and Gätje and Reise (1998). Assemblages of macroalgae are scarce on the sedimentary tidal flats where *F. vesiculosus* presents the only abundant native habitat-providing seaweed. An overview of the macroalgal community off the island of Sylt is provided by Schories et al. (1997).

The island of Helgoland represents the only rocky shore in the south-eastern part of the North Sea. It lies about 75 km south-west of the island of Sylt. Average tidal range is 2.2 m and average salinity is 32 psu. Mean water temperature is 17°C in summer and 4°C in winter. Detailed information on abiotic factors, the ecology and geology was provided by Hagmeier (1930), Wurster (1962) and Janke (1986, 1990). The shore is populated by a rich macroalgal community including many habitat-providing furoids such as *Ascophyllum nodosum* (L.) Le Jol., *Fucus* sp. and kelps (e.g. *Laminaria* sp.). A comprehensive description of the biotopes and the algal community of Helgoland is given by Kornmann and Sahling (1977), Bartsch and Kuhlenkamp (2000) and Bartsch and Tittley (2004).

Sampling of algae and associated organisms

For identification and quantification of associated organisms, samples of the alien *S. muticum* and the two native species of *F. vesiculosus* (on Sylt) and *H. siliquosa*

Fig. 1 Study sites in the south-eastern part of the North Sea and schematic diagram of the sampling protocol



(on Helgoland) were collected in July and August 2003 (Fig. 1), when associated organisms are most abundant on all investigated algal species (Viejo 1999; Rindi and Guiry 2004; Wernberg et al. 2004) and potential differences between epibiota communities are expected to be most pronounced. At both study sites, sampling was performed during tidal submergence and at the same tidal elevation, i.e. just below the mean low water spring tide level. In both cases, native and non-native algae were collected within an area of 50 m×50 m.

On tidal flats around the island of Sylt, we collected *S. muticum* and *F. vesiculosus* (ten specimens each) from shallow subtidal mussel beds of *Mytilus edulis* (L.) near the mean low water tide mark. In the Wadden Sea, both seaweed species are largely restricted to mussel beds as the only major natural hard substratum available. *S. muticum* is attached by a holdfast to mussel shells or to other biogenic hard substrata and, locally, may achieve

densities of about ten individuals per m² (Buschbaum, unpublished data). *F. vesiculosus* in this habitat lacks a holdfast and is, instead, permanently attached to the bivalve bed by mussel byssus threads. It may cover up to 70% mussel bed surface area (Albrecht and Reise 1994). This specific form of bladder wrack was first described as *Fucus mytili* (Nienburg 1925, 1927) and is now referred to as *F. vesiculosus* forma *mytili* (Nienburg 1925; Albrecht 1998). Despite the differences in morphology between *S. muticum* and *F. vesiculosus* forma *mytili* (hereafter “*Fucus*”) in the soft sediment habitat, we chose *Fucus* for a comparison of associated organisms because it represents the only other furoid, as well as the only other habitat-providing seaweed growing in significant abundances in the Wadden Sea (Schories and Albrecht 1996; Albrecht 1998). Furthermore, *Fucus* and *S. muticum* occur in overlapping habitats. In the hard bottom system, we chose *H. siliquosa* instead of *Fucus*

sp. as the native species for our comparison, because it is not only a close relative, but is also highly similar in morphology and structure and co-occurs with *Sargassum* on rocky shores (Fig. 1). Both species reached densities of approximately 5–10 specimens per m² at our study site (Chapman and Saier, personal observations), making them dominant components of the vegetation at this location. Sampling ($n=8$) on the island of Helgoland took place by means of SCUBA diving. For *Fucus*, we sampled whole specimens ranging between 40 and 50 cm in total lengths. For *Sargassum* and *Halidrys* (both between 1 and 3 m in length), we took 45 cm samples of the thallus by cutting three full 15 cm sections (proximal, central and distal thallus parts) from each specimen (Fig. 1). In the current analysis, we pooled these three thallus segments into one sample per thallus.

Sample processing was identical on Sylt and on Helgoland: plastic bags were carefully placed over individual thalli (or segments) and closed immediately after detachment of the algae. Through this procedure we were also able to sample motile organisms closely associated with the host seaweed, e.g. gastropods and amphipods. In the laboratory, samples were transferred into buckets with filtered seawater and shaken vigorously. A repetition of this process effectively removed the majority of all motile species (Norton and Benson 1983). Then, the water was sieved (500 µm mesh size). The remaining organisms within the sieves and epibionts directly attached to the algae were counted and identified to species (or nearest possible taxonomic) level. In colony-forming species such as hydrozoans or bryozoans, colony numbers were recorded. Many species associated with the algae were extremely abundant and it was impractical to count individuals. Therefore, we categorised abundances as follows: 0 individuals/colonies per sample (absent): category 0; 1–5 individuals/colonies per sample (present): category 1; 6–20 individuals/colonies per sample (common): category 2; 21–50 individuals/colonies per sample (abundant): category 3; more than 50 individuals/colonies per sample (dominant): category 4.

Statistical analysis

Species richness was compared by means of univariate statistical techniques (ANOVA). Data were tested for homoscedasticity using Cochran's test and were transformed if necessary (see Results section). Differences between group means were tested using Spjotvoll/Stoline posthoc test for unequal replication. Results were considered statistically significant at $P \leq 0.05$.

Whole communities were analysed using multivariate, non-parametric ordination techniques [Multidimensional Scaling, analysis of similarities (ANOSIM) and similarity percentages (SIMPER)] based on the Bray-Curtis similarity comparisons from the PRIMERTM software package (Clarke and Warwick 2001). For epibiota analyses including all fauna and flora data

(see Results section), we worked with presence–absence records as the only reliable means of standardisation across all species.

Results

Species richness (S)

The total number of associated species encountered across replicate samples of *Sargassum*, *Halidrys* and *Fucus* ranged from 38 (*Fucus*) to 70 (*Halidrys*). Species richness on *Sargassum* was intermediate in both regions (64 on Sylt and 60 on Helgoland, Tables 1, 2). These richness ranks of associated species were reflected by both epifauna and epiflora (Table 2). The average richness (including flora and fauna) of epibiota per sample differed significantly between species (one-way ANOVA, $F_{3,32} = 18.73$, $P < 0.001$, $MS_{\text{error}} = 22.74$). Again, *Halidrys* stood out as the seaweed species with the highest average richness of epibiota (29.88 ± 5.5 , $n=8$). *Fucus* had the lowest average richness in epibiota (13.10 ± 4.98 , $n=10$), and the richness of associated epibiota on *Sargassum* was intermediate, both on Helgoland (22.38 ± 5.95 , $n=8$) and on Sylt (20.00 ± 2.16 , $n=10$). Posthoc tests (Spjotvoll/Stoline tests) revealed significant differences between mean species richness for all pairwise comparisons of the four algal hosts except for *Sargassum* Sylt (SS) compared to *Sargassum* Helgoland (SH) ($P = 0.753$).

Community analysis

Comparing the species communities of epifauna and flora between seaweed hosts on Sylt (soft sediment) and Helgoland (rocky substratum), we found differences between the two environments, as well as between *Sargassum* and *Fucus* on Sylt (Fig. 2). In contrast, epibiont communities did not differ between *Sargassum* and *Halidrys* on Helgoland. The ANOSIM procedure revealed an overall R -statistic of 0.85 ($P < 0.001$) for differences among epibiont communities of the four groups when samples are identified by the seaweed species and region (Fig. 2). This overall difference of epibiota communities among the four seaweed hosts [*Sargassum* Helgoland (SH), *Halidrys* Helgoland (HH), *Sargassum* Sylt (SS) and *Fucus* Sylt (FS)] is based on significant differences between all host pairs (significant at $P < 0.001$ with R -values between 0.49 and 1), except when comparing associated communities on SH and HH, in which case R was close to 0 ($R = 0.007$), indicating that these communities were very similar (Fig. 2).

These differences were confirmed when the data were analysed separately for flora and fauna.

By means of SIMPER analysis, we identified the main species responsible for similarities in epibiota communities within seaweed groups, and those accounting for differences between epibiota of seaweed hosts (Table 3). On Helgoland, motile epifauna, especially gastropods and the amphipod *Apherusa bispinosa*,

Table 1 List of species associated with *Sargassum muticum* and *Halidrys siliquosa* on the island of Helgoland (hard bottom) and *S. muticum* and *Fucus vesiculosus forma mytili* on the island of Sylt (soft bottom)

Species	Hard bottom		Soft bottom	
	<i>Sargassum</i>	<i>Halidrys</i>	<i>Sargassum</i>	<i>Fucus</i>
Fauna				
Porifera				
<i>Halichondria panicea</i> (Pallas)			p	
<i>Halisarca dujardini</i> Johnston		p		
Coelenterata				
<i>Bougainvillia ramosa</i> (Van Beneden)			p	
<i>Clytia hemisphaerica</i> (L.)		p	p	
<i>Coryne pusilla</i> Pallas		p		
<i>Dynamena pumila</i> (L.)	c	a		
<i>Edwardsia claparedii</i> (Panceri)	p			
<i>Eudendrium rameum</i> (Pallas)	p	c		
<i>Halecium halecinum</i> (L.)	p	p		
<i>Laomedea flexuosa</i> Alder	p	p	p	
<i>Metridium senile</i> (L.)			p	p
<i>Obelia dichotoma</i> (L.)			p	
<i>Obelia longissima</i> (Pallas)	p	p	p	p
<i>Obelia</i> sp.			p	p
<i>Sagartiogeton undatus</i> (Müller)			p	
<i>Sarsia tubulosa</i> (M. Sars)	p			
Nemertea				
<i>Amphiporus lactifloreus</i> (Johnston)	p	p		p
<i>Lineus viridis</i> (Müller)				p
<i>Oerstedia dorsalis</i> (Abildgaard)	p	p		
<i>Tetrastemma vermiculus</i> (Quatrefages)	p			
Nemertini (unidentified species)	p	p		
Annelida				
<i>Anaitides maculata</i> (L.)	p			
<i>Autolytus</i> sp.			p	p
<i>Eumida sanguinea</i> (Oersted)				p
<i>Fabricia sabella</i> (Blainville)	p	p		
<i>Harmothoe imbricata</i> (L.)			p	p
<i>Janua pagenstecheri</i> (Quatrefages)	p	p		
<i>Kefersteinia cirrata</i> (Keferstein)		p		
<i>Lanice conchilega</i> (Pallas)			p	
<i>Lepidonotus squamatus</i> (L.)			p	
<i>Neodexiospira</i> sp.		p		
<i>Nereis</i> sp.	p		p	
<i>Nicolea venustula</i> (Montagu)	p	p		
<i>Polydora ciliata</i> (Johnston)			p	
<i>Polydora</i> sp.	p	p		
<i>Proceratea cornuta</i> (Agassiz)				p
<i>Spirorbis spirorbis</i> (L.)	p	p		
<i>Spirorbis tridentatus</i> Levinsen	p	p		
Phyllodocidae (unidentified species)	p	p		
Syllidae (unidentified species)		p		
Terebellidae (unidentified species)	p	p		
Mollusca				
<i>Aeolidia papillosa</i> (L.)			p	
<i>Crepidula fornicata</i> (L.)			p	p
<i>Cuthona</i> sp.		p		
<i>Gibbula cineraria</i> (L.)	p	p		
<i>Hydrobia ulvae</i> (Pennant)		p	p	
<i>Lacuna pallidula</i> (da Costa)	c	c		
<i>Lacuna vineta</i> (Montagu)	c	c		
<i>Littorina fabalis</i> (Turton)			p	p
<i>Littorina littorea</i> (L.)			p	p
<i>Mytilus edulis</i> L.	p	p	p	p
<i>Pusillina inconspicua</i> (Alder)	a	c		
<i>Rissoa parva</i> (da Costa)				p
<i>Tergipes tergipes</i> (Förskal)			p	
Crustacea				
<i>Apherusa bispinosa</i> (Bate)	p	c	p	
<i>Apherusa jurenei</i> (Milne Edwards)		p		
<i>Apherusa ovalipes</i> Norman & Scott		p		

Table 1 (Contd.)

Species	Hard bottom		Soft bottom	
	<i>Sargassum</i>	<i>Halidrys</i>	<i>Sargassum</i>	<i>Fucus</i>
<i>Apherusa</i> sp.	p	p		
<i>Balanus crenatus</i> Bruguière	p		p	a
<i>Calliopius laeviusculus</i> (Krøyer)			p	p
<i>Caprella linearis</i> (L.)			p	
<i>Carcinus maenas</i> (L.)	p	p	p	p
<i>Chaetogammarus marinus</i> Leach	p	p	p	p
<i>Corophium</i> sp.	p	p	p	p
<i>Elminius modestus</i> Darwin				p
<i>Gammarus locusta</i> (L.)			d	p
<i>Hyas araneus</i> (L.)			p	
<i>Idotea granulosa</i> Rathke	p	p		
<i>Idotea pelagica</i> Leach	p	p		
<i>Idotea</i> sp.			p	
<i>Jaera albifrons</i> Leach		p	p	p
<i>Jassa falcata</i> (Montagu)	c	c	p	
<i>Pagurus bernhardus</i> (L.)			p	
<i>Praunus</i> sp.			p	p
Pycnogonida				
<i>Anoplodactylus</i> sp.	p	p		
<i>Nymphon</i> sp.			p	
Bryozoa				
<i>Acyonidium gelatinosum</i> (L.)		p		
<i>Acyonidium mytili</i> (Dalyell)			p	p
<i>Bowerbankia gracilis</i> (Leidy)	p	p	p	p
<i>Bowerbankia imbricata</i> (Adams)			p	
<i>Conopeum reticulum</i> (L.)			p	p
<i>Electra pilosa</i> (L.)	p	p	p	p
Tunicata				
<i>Botryllus schlosseri</i> (Pallas)	c	a		
<i>Clavelina lepadiformis</i> (Müller)	p	p		
<i>Didemnum</i> sp.	p	p		
<i>Molgula</i> sp.	p		p	p
<i>Sidnyum turbinatum</i> Fleming	p	p		
<i>Styela clava</i> Herdman			p	
Algae				
Chlorophyta				
<i>Chaetomorpha</i> sp.	p	p		
<i>Chaetomorpha tortuosa</i> (Dillw.) Kütz.	p	p		
<i>Cladophora</i> sp.	p	p		p
<i>Enteromorpha flexuosa</i> (Wulfen ex Roth) J.G.Ag.			p	
<i>Enteromorpha</i> spp. Link	p	p	p	p
<i>Rhizoclonium riparium</i> (Roth) Harvey			p	
<i>Ulva lactuca</i> L.	p	p	p	
<i>Ulva</i> sp.	p	p		
Phaeophyta				
<i>Ectocarpus siliculosus</i> (Dillw.) Lyngb.		p	a	
<i>Ectocarpus</i> spp. Lyngbye	p	c	p	
<i>Elachista fucicola</i> (Velle) Aresch.				d
<i>Giffordia granulosa</i> (Sm.) Hamel			p	
<i>Laminaria</i> sp.	p	p		
<i>Petalonia fascia</i> (O.F. Müll.) O. Kuntze	p	p		
<i>Scytosiphon lomentaria</i> (Lyngbye)		p		
Rhodophyta				
<i>Acrochaetium secundatum</i> (Lyngb.) Dixon			p	c
<i>Antithamnion plumula</i> (Ellis) Thur. in Le Jolis			p	p
<i>Ceramium nodulosum</i> (Lightf.) Ducluz.	p	a	a	p
<i>Ceramium</i> sp.	p	p		
<i>Chondrus crispus</i> Stackhouse	p	p		
<i>Erythrotrichia carnea</i> (Dillw.)			a	c
<i>Erythrotrichia reflexa</i> (Crouan et Crouan) De Toni sensu Rosenv.			p	p
<i>Membranoptera alata</i> (Hudson) Stackhouse		p		
<i>Plocanium cartilagineum</i> (L.) Dixon	p	p		
<i>Polysiphonia elongata</i> (Huds.) Sprengel			p	
<i>Polysiphonia fibrillosa</i> (Dillw.) Sprengel			p	
<i>Polysiphonia fucoides</i> (Huds.) Grev.			p	p

Table 1 (Contd.)

Species	Hard bottom		Soft bottom	
	<i>Sargassum</i>	<i>Halidrys</i>	<i>Sargassum</i>	<i>Fucus</i>
<i>Polysiphonia</i> sp.	c	p		
<i>Porphyra umbilicalis</i> (L.) Kütz.			p	
<i>Rhodochorton floridulum</i> (Dillw.) Näg.			p	
<i>Rhodomela confervoides</i> (Huds.) Silva	p	p		
Unidentified red crust	p	p		
Others				
<i>Asterias rubens</i> L. (Echinodermata)			p	p
<i>Chunio marinus</i> Haliday (Insecta)		p		
<i>Convoluta convoluta</i> (Abildgaard) (Platyhelminthes)	p	p		
Nematoda (unidentified species)			p	
<i>Pedicellina</i> sp. (Entoprocta)			p	
<i>Pomatoschistus</i> sp. (Pisces)		p		
Total number of species 126	60	70	64	38

Semi-quantitative data on species abundances are given as: *p* present, 1–5 individuals/colonies per sample; *c* common, 6–20 individuals/colonies per sample; *a* abundant, 21–50 individuals/colonies per sample; *d* dominant, > 50 individuals/colonies per sample

Table 2 Species richness (S) of epibiota on seaweeds from Helgoland and Sylt

	Overall S (all samples)			Mean S per thallus (Flora and Fauna, all segments)		
	Flora	Fauna	Total	Mean	sd	<i>n</i>
Helgoland						
<i>Sargassum muticum</i>	16	44	60	22.38	5.95	8
<i>Halidrys siliquosa</i>	19	51	70	29.88	5.54	8
Sylt						
<i>Sargassum muticum</i>	17	47	64	20.00	2.16	10
<i>Fucus vesiculosus</i> f. <i>mytili</i>	9	29	38	13.10	4.98	10

Overall richness (all samples) and mean richness (averaged per thallus) including standard deviation (sd) and replication (*n*)

characterises epibiota on *S. muticum*. However, the hydroid *Dynamena pumila* and the colonial ascidian *Botryllus schlosseri* are also common. All seven species

characterizing the *Sargassum* epibiota community, including a filamentous red algal species (*Polysiphonia* sp.), are also typical for the assemblage on *H. siliquosa* (Table 3).

The significance of macroalgal epiphytes as characteristically associated with algal hosts is greater on Sylt (*Erythrotrichia* sp. on both *Sargassum* and *Fucus*, *Polysiphonia* sp. and *Enteromorpha flexuosa* on *Sargassum*, and *Elachista fucicola* on *Fucus*). In addition, particularly amphipods (*Gammarus locusta* and *Corophium* sp.) account for similarities of epibiota in *Sargassum* samples on Sylt, and the barnacle *Balanus crenatus* for epibiota similarities on *Fucus*.

Average dissimilarities between epibiota are higher when comparing *Sargassum* on Helgoland and Sylt, and *Sargassum* and *Fucus* on Sylt than between *Sargassum* and *Halidrys* on Helgoland, a result that had already become apparent in the Bray-Curtis similarity ordination (see above, Fig. 2). Analysing the species accounting for dissimilarities between these groups (Table 4) reveals that it is largely the same species that were also characteristic for identifying epibiota of the respective seaweed hosts (Table 3), i.e. epibiota are distinguished primarily by comparison of common species, rather than

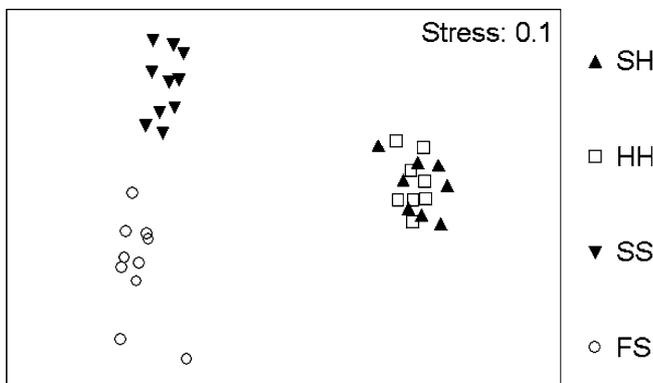


Fig. 2 Multidimensional scaling image of epibiota (flora and fauna) on different species of seaweed from Sylt and Helgoland. Analysis is based on the presence/absence data of species and on Bray-Curtis similarities. Samples are identified by seaweed species and region: SH (*Sargassum* Helgoland, *n*=8), HH (*Halidrys* Helgoland, *n*=8), SS (*Sargassum* Sylt, *n*=10), FS (*Fucus* Sylt, *n*=10)

Table 3 Similarity percentages (SIMPER) analysis of epibiota (flora and fauna) on native and alien seaweed hosts from Sylt and Helgoland. Average epibiota community similarities among replicate samples in percent (SH Sargassum Helgoland, $n = 8$; HH Halidrys Helgoland, $n = 8$; SS Sargassum Sylt, $n = 10$; FS Fucus Sylt, $n = 10$), and the relative contribution of dominant species (to cumulative 50%) in replicate samples (presence/absence data)

Seaweed species (average similarity %)	SH 51.38%		HH 54.75%		SS 50.49%		FS 55.91%	
	%	Contribution	%	Contribution	%	Contribution	%	Contribution
Species dominating epibiota								
	8.94		6.19		9.95		9.95	
<i>Pusillina inconspicua</i>				<i>Pusillina inconspicua</i>				<i>Elachista fucicola</i> ^d
<i>Dynamena pumila</i>	8.94		6.19	<i>Lacuna pallidula</i>				<i>Balanus crenatus</i>
<i>Apherusa bispinosa</i>	8.94		6.19	<i>Lacuna vineta</i>				<i>Erythrotrichia reflexa</i> ^a
<i>Polysiphonia</i> sp. ^a	6.91		6.19	<i>Dynamena pumila</i>				<i>Erythrotrichia carnea</i> ^a
<i>Lacuna pallidula</i>	6.66		6.19	<i>Apherusa bispinosa</i>				
<i>Lacuna vineta</i>	6.66		6.19	<i>Botryllus schlosseri</i>				
<i>Botryllus schlosseri</i>	6.57		4.78	<i>Ceramium nodulosum</i> ^a				
			4.56	<i>Polysiphonia</i> sp. ^a				
			51.04	<i>Jassa falcata</i>				
Cumulative percentage > 50%	Σ	53.62	Σ	Σ	Σ	53.86	Σ	51.70

^a Algal epiphytic species

by rare or missing species. In addition, it becomes apparent that *Sargassum* is colonised by a distinctive group of species, depending on the host pool in the two environments.

Discussion

Epibiota of *Sargassum muticum* in different coastal systems

This study demonstrates that the associated species community of an introduced alga may vary considerably on spatial scales of kilometres. Whereas the richness of species associated with *S. muticum* was similar on the rocky shore of Helgoland and on the sedimentary shore around Sylt, community structure and species composition differed significantly between islands. Only 17 species associated with *S. muticum* on Helgoland were also found on *S. muticum* on Sylt, i.e. less than one third of the total species found on algal hosts of either island were common to Sargassum on Helgoland and Sylt.

In cold waters, *S. muticum* is pseudo-perennial. The lateral branches detach in summer and early autumn, leaving only a short perennial stipe from which branches regenerate during the following spring (e.g. Jephson and Gray 1977; Critchley et al. 1987; Fernández 1999). Thus, each year the associated species community is lost with the branches shed, and an annual re-colonisation of the alga is necessary because only few species stay attached to the basal system, maintaining their presence over winter (Norton and Benson 1983; Jephson and Gray 1977). This may explain why species communities in both environments differ so clearly from one another, and why almost all species found associated with *S. muticum* on Helgoland and Sylt originate from the regional species pool of the respective environments. Only one species on Sylt (*Bougainvillia ramosa*) and two species on Helgoland (*Edwardsia claparedii*, *Sarsia tubulosa*) are uncommon in other habitats of the islands (Janke 1986; Buschbaum 2002; Reichert 2003).

Often, introduced species serve as vectors and habitat for further associated non-indigenous organisms. The Pacific oyster *C. gigas* (Thunberg), for example, has been imported into European waters for aquaculture since the 1960s. It has become established as a dominant and permanent member in the coastal systems of the southern North Sea (Wolff and Reise 2002). These imports were accompanied by the introduction of more than 20 species of associated animals, and some of the exotics have since become an integral part of the species community of the newly developed *C. gigas* beds in the area (Buschbaum, unpublished data). However, no further invader associated with *S. muticum* has been found on the rocky shore of Helgoland, and only one alien species (the tunicate *Styela clava*) has been detected on the soft sediments near Sylt. Explanations may be that (1) *S. muticum* is not a suitable habitat for further invaders of

Table 4 Similarity percentages (SIMPER) analysis of epibiota (flora and fauna) on native and alien seaweed hosts from Sylt and Helgoland. Average epibiota community dissimilarities between seaweed host pairs, and relative contribution of six major distinguishing species in each paired comparison

Seaweed species comparisons (average dissimilarity %)	SH-HH 47.02%		SH-SS 84.73%		SS-FS 70.84%		HH-FS 89.56%		
	% Contribution	%	% Contribution	%	% Contribution	%	% Contribution	%	
Species distinguishing epibiota of different seaweeds									
	2.63	<i>Chaetomorpha</i> sp. ^a	2.84	<i>Erythrotrichia carnea</i> ^a	4.37	<i>Elachista fucicola</i> ^a	2.67	<i>Elachista fucicola</i> ^a	
	2.48	<i>Coryne pusilla</i>	2.84	<i>Pusillina inconspicua</i>	3.98	<i>Polysiphonia</i> sp. ^a	2.67	<i>Pusillina inconspicua</i>	
	2.40	<i>Eudendrium rameum</i>	2.84	<i>Dynamena pumila</i>	3.97	<i>Enteromorpha flexuosa</i> ^a	2.67	<i>Lacuna pallidula</i>	
	2.38	<i>Cladophora</i> sp. ^a	2.84	<i>Gammarus locusta</i>	3.53	<i>Corophium</i> sp.	2.67	<i>Lacuna vineta</i>	
	2.24	<i>Chaetomorpha tortuosa</i> ^a	2.58	<i>Enteromorpha flexuosa</i> ^a	3.50	<i>Balanus crenatus</i>	2.67	<i>Dynamena pumila</i>	
	2.19	<i>Enteromorpha</i> sp. ^a	2.57	<i>Obelia</i> sp.	3.20	<i>Rhizoclonium riparium</i> ^a	2.67	<i>Apherusa bispinosa</i>	
Cumulative percentage	Σ	14.32	Σ	16.51	Σ	22.55	Σ	16.02	

^aAlgal epiphytic species

the southern North Sea and (2) as mentioned above, *S. muticum* is an unstable habitat due to the annual shedding of branches.

Associated species communities of *Sargassum muticum* and native macroalgae

On the rocky shores of Helgoland, associated species richness and community composition on the introduced *S. muticum* and native *H. siliquosa* were similar, while the composition of the epibiotic assemblages differed significantly between *S. muticum* and the indigenous *Fucus* in the sedimentary environment near the island of Sylt.

Abundance and community composition of associated organisms can be strongly influenced by the architecture of the host algae, and morphological complexity of seaweeds is often positively correlated to the number of species associated with them (e.g. Hacker and Steneck 1990; Gee and Warwick 1993, 1994; Taylor and Cole 1994). Higher diversity and abundance in a more complex habitat are caused by enhanced living space, increased variety of food organisms, more suitable feeding surfaces and a higher protection against predation and wave action (Taylor and Cole 1994; Kraufvelin and Salovius 2004, references therein).

S. muticum and the native *H. siliquosa* examined on the island of Helgoland show strong structural similarities. Both algae have a similar highly complex thallus morphology. We suggest this as a likely explanation for the similarities between their communities of associated species. The likeness of the two epibiotic assemblages on Helgoland also indicates that most of the associated species are non-selective and have a non-specific relationship with their host plant, an observation confirmed by other studies investigating epibiota on morphologically similar algae (e.g. Taylor and Cole 1994; Viejo 1999; Wernberg et al. 2004). Wernberg et al. (2004) argue that this general pattern (lack of host specificity) may resemble an adaptation of epibiota to the fluctuating environment of temperate regions, because the seasonality of many epibiota species tracks that of the algae.

Despite morphological similarities, *S. muticum* and *H. siliquosa* are functionally different because *H. siliquosa* is a truly perennial macroalgae whereas *S. muticum* has a perennial holdfast which produces an annual vegetative thallus (Wernberg et al. 2000). The different strategies (pseudo-perennial in *S. muticum* and perennial in *H. siliquosa*) and associated habitat provision for epibiota seem to have no effect on the occurrence and abundance of associated organisms, emphasizing the facultative host selection of epibionts.

The native seaweed *Fucus* from the island of Sylt is rather unstructured in comparison with the much more branched *S. muticum*. This may explain the lower species richness of associated organisms found in this abundant indigenous furoid. Another apparent difference between

native *Fucus* and the exotic *Sargassum* on Sylt was the high degree of epiphyte cover on the latter algal host. It contributed to the richness of algal epiphytes being twice as high (20 species) on *Sargassum* as on *Fucus* (ten species). The heavy epiphyte load in *S. muticum* enhances the living space and the structural complexity of the host algae. Consequently, it provides suitable conditions for further organisms and may indirectly increase the community diversity of *S. muticum*.

Although chemical antifouling defences may also affect the associated species communities of the seaweeds we studied we conclude that morphological characteristics of host algae seem mainly responsible firstly for similarities in epibiota communities of *S. muticum* and *H. siliquosa* on the rocky shore of Helgoland and secondly for dissimilarities between *S. muticum* and *Fucus* on soft bottoms near Sylt.

Consequences of *Sargassum muticum* invasion

The impact of an exotic algal invasion on the native assemblages of epibionts depends on the host-plant specificity of the organisms and the similarities between invasive and native seaweed hosts. Furthermore, it is also related to the effects of the invasion on the indigenous macroalgal assemblage (Viejo 1999).

Since the introduction of *S. muticum* in the 1980s in the south-eastern North Sea, the species has become established as a permanent member of the algal community in the low intertidal and upper subtidal zones in both, rocky and sedimentary environments (Bartsch and Kuhlenskamp 2000; Buschbaum 2005). Despite its successful dispersal and increasing densities, *S. muticum* has not replaced other indigenous macroalgae, and there is no evidence that the native species in either system are negatively affected by the newcomer. Thus, to date, no negative effects on the local pool of macroalgae have been detected in the systems we investigated. In other areas, however, *S. muticum* has been shown to displace indigenous macroalgal species by competition for hard substratum and light (Stæhr et al. 2000; Britton-Simmons 2004), and observations by Bartsch and Tittley (2004) suggest that competition for space between *S. muticum* and *H. siliquosa* is likely on Helgoland. Therefore, we do not exclude detrimental effects of *S. muticum* on the native macroalgal community in the future.

In terms of the associated organisms, similarities between the species assemblages of *S. muticum* and *H. siliquosa* indicate that the introduction of *S. muticum* to the island of Helgoland has caused no major changes in local macroalgal epibiota. Therefore, it can be considered primarily as an addition to the native macroalgal pool, providing additional habitat space and consequently facilitating epibiota abundances. This was also observed on other European coasts (Withers et al. 1975; Viejo 1999; Wernberg et al. 2004). Wernberg et al. (2004) point out, however, that, in the absence of pre-invasion

data, this conclusion warrants caution, as it is equally possible that the epibiota community of native algae undergoes radical change following the invasion of an exotic species. Nevertheless, on Helgoland we found only associated species originating from the local species pool that had already been known from the area prior to the *S. muticum* invasion (Kormann and Sahling 1977; Janke 1986), and no further exotic species was detected on *S. muticum*. This indicates that the species assemblage on the new algal host closely resembles the suite of epibionts that already existed before the invasion of *S. muticum*.

On soft sediment substrata near Sylt, the higher number of species associated with *S. muticum* suggests that the newcomer is a more favourable host than native *Fucus*. However, eight species occurring on *Fucus* were not observed on *S. muticum*, suggesting that *Fucus* has a distinctive species community associated with it. Although *Fucus* and *S. muticum* occur in overlapping habitats in the Wadden Sea, strong competition between the species is unlikely because *Fucus* occurs mainly on intertidal mussel beds, while *S. muticum* is predominantly restricted to the upper subtidal zone (Buschbaum 2005). Hence, associated species communities of both algal hosts can also coexist in the area.

On the unstable sediments of soft bottom environments, suitable substrata for colonisation by sessile and epibenthic mobile organisms are generally rare. Biogenic structures such as mussel beds, seagrass beds and benthic macroalgae provide the only suitable habitats for many associated organisms. With the arrival of *S. muticum* in the Wadden Sea area, another epibenthic structure has been added to the assemblage. In this system, *S. muticum* functions as an ecosystem engineer (see Crooks 2002). Although thalli of *S. muticum* are not available all year round because of its pseudo-perennial life cycle, the additional habitat structure has been adopted by a diverse community of native epibionts that might otherwise be absent or rare. Consequently, *S. muticum* has strongly enriched biodiversity in the area.

Interestingly, *S. muticum* may provide a suitable habitat for species which have become rare in the Wadden Sea because of human impact. For example, epiphytic red algae were once abundant on the subtidal beds of the European oyster *Ostrea edulis* L. which, together with a rich community of associated species, disappeared in the 1950s due to overexploitation (Reise 1994). The fact that many red algal species are now found on *S. muticum* (this study) indicates that the invader is used by resident algal species as an alternative habitat and, hence, may stabilise endangered populations.

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