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## Invasion of a habitat-forming seaweed: effects on associated biota

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**Key words:** epifauna, epiphytes, *Fucus evanescens*, *Fucus vesiculosus*, host specificity, introduced species, invasion

### Abstract

*Fucus evanescens* is a brown alga of arctic origin that has invaded European coasts. The epiphytic community of *F. evanescens* in southern Sweden was compared with that of the native *Fucus vesiculosus*, to examine to what extent an invading seaweed can modify local biodiversity. *F. evanescens* was much less fouled than *F. vesiculosus*, supporting both less biomass and fewer species of epiphytes. Multivariate analysis of the most common epiphyte taxa showed that the epiphytic community composition of *F. evanescens* was not entirely separated from that of *F. vesiculosus*, but host species contributed significantly to explain the variation in community composition. The biomass of free-living invertebrates was also lower on *F. evanescens*, although the pattern differed between taxonomic groups. While the biomass of amphipods was lower on *F. evanescens*, there was no significant difference in biomass of isopods or gastropods between the *Fucus* species. The good correlation between biomass of epiphytes and free-living animals suggests that the epiphytes play an important role in providing a suitable habitat for many species of free-living epifauna. The study shows that the invasion of *F. evanescens* affects the environmental conditions for many species associated with the *Fucus* community but that the direct effect on biodiversity is probably low.

### Introduction

The increasing rate of species invasions in most ecosystems has become a common concern and is regarded as one of the major agents of global environmental change (Vitousek et al. 1996; Mack et al. 2000). One of the central questions in invasion research is to what extent an invader may modify biodiversity and ecosystem processes in the native community. Several studies in terrestrial systems have shown that the invasion of key-stone species, e.g. habitat-forming or habitat-modifying species, may have a dramatic effect on the recipient biota (e.g. Braithwaite et al. 1989; Vitousek and Walker 1989). In contrast, there are very few studies on effects of invaders, especially invasive plants, in marine coastal systems (Grosholz 2002).

The large brown macroalgae, e.g. members of Fucales, are ecologically dominant species in temperate coastal hard-bottom communities. These perennial

seaweeds are believed to contribute importantly to the biodiversity of the littoral community by providing substratum for a diverse epiphytic community (Seed and O'Connor 1981; Hay 1986). Primary space is often the limiting resource in marine hard-substrate communities (Dayton 1971; Sutherland and Karlson 1977) and epiphytism on macroalgae is a common strategy both for algae and sessile invertebrates. The macroalgae and their epiphytes also provide food and shelter for a diverse fauna of free-living invertebrates, e.g. small herbivorous crustaceans and gastropods (Brawley 1992). The role of seaweeds as substratum for epiphytes distinguishes them from most terrestrial plants (except perhaps trees) and indicates that changes associated with the introduction and establishment of a dominant seaweed may have great impact on biodiversity and ecosystem processes in the coastal zone.

The magnitude of this effect depends in part on the ability of epiphytic organisms and free-living epifauna

to colonise the introduced species. Most marine epiphytes are believed to be relatively unspecific in their host choice, although a high host specificity has been found in a few epiphytic algae (e.g. Correa and McLachlan 1991; Lining and Garbary 1992) and invertebrates (reviewed by Seed and O'Connor 1981). Despite the proposed low host specificity, the patterns of distribution and abundance of epiphytes differ among algal species. Factors suggested to influence the attractiveness of an alga to epiphytic organisms include plant size (area available for establishment), plant longevity, cell-wall structure, surface texture, and the presence of allelopathic substances (Seed and O'Connor 1981; Schmitt et al. 1995; Hay 1996; Steinberg et al. 1998; Dawes et al. 2000).

Distribution of free-living epifauna on different macroalgae is generally attributed to an active choice of the animals, based on either food or habitat preferences (e.g. Hacker and Steneck 1990; Duffy and Hay 1991; Martin-Smith 1993). The free-living invertebrates are generally believed to be rather unspecific in their choice of macroalgal host (reviewed by Arrontes 1999), although a few species show high host specificity (Hay et al. 1990; Poore et al. 2000). Studies on macroalgal invasions have produced conflicting evidence for the ability of motile epifauna to colonise new species. In the Mediterranean, the introduced *Caulerpa taxifolia* had fewer species and individuals of associated invertebrates than native algae (Bellan-Santini et al. 1996). In contrast, the invasive *Sargassum muticum* Yendo (Fensholt) on the Atlantic coast of Spain have an associated fauna very similar to that of the native seaweeds it replaces (Viejo 1999).

The brown alga *Fucus evanescens* C. Ag. is an arctic species, originally found in North America and the arctic regions of Europe (Powell 1957a). It was first recorded outside the native range in the Oslofjord in southern Norway in 1894 (Simmons 1898) and since then it has spread southwards in northern Britain (Powell 1957b) and Scandinavia (Hylmö 1933; Lund 1949; Wikström et al. 2002). The recent record of *F. evanescens* in the western Baltic Sea (Schueller and Peters 1994) suggests that the species is still expanding its range. In the inner parts of the Oslofjord *F. evanescens* has become the most common fucoid, locally replacing the native congeners *Fucus vesiculosus* L., *Fucus serratus* L. and *Ascophyllum nodosum* (L.) Le Jol. (Bokn and Lein 1978; Bokn et al. 1992). In other areas, the invader has principally established in eutrophicated or otherwise polluted areas

where other fucoids are scarce (e.g. Powell 1957b; Schueller and Peters 1994).

As *F. evanescens* is functionally and morphologically similar to the native congeners, it could be expected to house a similar epibiota. Other authors have however observed that in its new range, *F. evanescens* is less overgrown by epiphytic algae than native fucoids (Bokn et al. 1992; Schueller and Peters 1994). In the Baltic Sea, one of the most abundant grazers, the isopod *Idotea baltica* Pallas, was shown to prefer the native *F. vesiculosus* to *F. evanescens* in laboratory grazing experiments (Schaffelke et al. 1995).

The aim of this study was to investigate how the invasion of *F. evanescens* affects the littoral community in a newly invaded area, by comparing the associated flora and fauna of the invader with that of the native *F. vesiculosus*. We chose to work purely mensuratively, since the long time required to build up a natural epiphytic community makes manipulative experiments less tractable. Specifically, the following questions were addressed: (1) does *F. evanescens* support less epiphytes (in terms of biomass and/or species richness) than the native *F. vesiculosus*? (2) similarly, is the biomass of free-living epifauna lower on *F. evanescens*? (3) does the epiphytic species composition of *F. evanescens* differ from that of the native fucoid? (4) does substratum species interact with abiotic factors (salinity and wave exposure) in structuring epiphytic community composition?

## Materials and methods

Sampling of *F. evanescens*, *F. vesiculosus* and their associated biota was carried out in Öresund, southern Sweden, during June 2000. Öresund is one of the straits connecting the brackish Baltic Sea with the more marine Kattegat. The salinity in the area is very variable but there is generally a salinity gradient, from on average 9 to 15‰ S, along the 100 km coastal stretch (Öresunds vattenvårdsförbund, Sweden). *F. evanescens* was first recorded in this area in 1948 (Lund 1949) and has since then spread and established throughout the strait. In a recent study of the distribution of *F. evanescens* in Öresund, the species was present at half of the investigated sites, mostly in areas subjected to anthropogenic influence (Wikström et al. 2002). It dominated the algal vegetation at several sites, the native *F. vesiculosus* being scarce or absent. In the present study we included all 14 sites at which

*F. evanescens* and *F. vesiculosus* occurred together according to Wikström et al. (2002). *F. evanescens* dominated the algal vegetation (> 50% cover) at 9 sites, *F. vesiculosus* being scarce (< 5% cover) at 7 and more common (5–50% cover) at two of the sites. *F. vesiculosus* dominated at one site, *F. evanescens* being scarce, and at the four remaining sites the two *Fucus* species were equally abundant. At each site, 5 plants of *F. evanescens* and *F. vesiculosus*, > 10 cm in length, were randomly collected at 0.5 m depth, using a fine-meshed bag to catch the motile fauna.

In the laboratory, the length of the *Fucus* plant was measured and the macroscopic epiphytes were carefully scraped off using a scalpel and identified. Specimen of the genus *Enteromorpha* were identified to species when possible but the genus was analysed as one taxon in subsequent analyses. Motile animals were removed and identified. Epiphytes and motile animals were then dried at 70 °C to constant weight, together with the cleaned *Fucus* fronds. Animals from the three most abundant taxonomic groups, amphipods, isopods, and snails, were dried separately. In all analysis, the biomass (mg dry wt) of associated biota was related to gram biomass of *Fucus*.

The effective fetch (Håkanson 1981) was calculated for each sampling site as a measure of wave exposure. The effective fetch value ( $L_f$ ) is calculated from the formula  $L_f = (\sum \chi_i \cos \gamma_i) / (\sum \cos \gamma_i)$ , where  $\chi_i$  is the distance in kilometres to nearest land, measured in 15 directions with deviation angles ( $\gamma_i$ )  $\pm 6$ ,  $\pm 12$ ,  $\pm 18$ ,  $\pm 24$ ,  $\pm 30$ ,  $\pm 36$ , and  $\pm 42$  from a central radius. The central radius was put in the direction giving the highest value of  $L_f$ . The calculated  $L_f$ -values varied between 0 and 7.6. We obtained a relative measure of the salinity gradient by measuring the salinity at each site at one occasion (within 4 h) during the sampling period with a hand refractometer (measure accuracy 0.5‰). The relative salinity differences between sampling sites in our study were comparable to the differences in median salinity from monthly measurements during four years at four near-shore sites along the coast (Öresunds vattenvårdsförbund, Sweden).

The epiphytic species composition of the two *Fucus* species was analysed with ordination and canonical ordination using CANOCO 4.0 (ter Braak and Šmilauer 1998). In the analyses, the 5 plants collected from each *Fucus* species and site were treated as one entity and the abundance of an epiphytic species was measured as the number of *Fucus* plants (0–5) where it occurred. The analyses were done on the 14 commonest taxa (total

frequency > 3 *Fucus* plants). Detrended correspondence analysis (DCA, Hill and Gauch 1980) was used to examine the epiphytic assemblages on the different *Fucus* species and sites, and which epiphytic species discriminated best between the two *Fucus* species.

In addition, canonical correspondence analysis (CCA) was performed to assess how much of the variation in epiphytic community composition could be explained by the measured environmental factors (*Fucus* species, salinity and wave exposure). Firstly, CCA was performed using each environmental factor separately and all factors together. Secondly, the unique explanatory power of host species was assessed by eliminating the effects of salinity and exposure covariables with partial CCA (ter Braak 1988). The epiphytic community of the two *Fucus* species was also analysed separately with CCA, using salinity and wave exposure as constraining variables. The hypothesis of non-significant deviation of variation explained by the variables from that explained by a random variable was tested with Monte Carlo randomisation test with 999 unrestricted permutations of the constraining variables. In both the indirect and direct ordination analysis, species data were root transformed to reduce influence of species with very high abundance. Effective fetch was  $\log_{10}$  transformed to obtain linearity.

## Results

The biomass of epiphytes on *F. vesiculosus* was highly variable between sites, while *F. evanescens* was generally very little epiphytised (Figure 1). Epiphytic biomass consisted mostly of filamentous algae, sessile animals constituting only a small part (Figure 2a). Two-way analysis of variance (ANOVA) showed that both site, *Fucus* species and the interaction had significant effect on epiphytic biomass (Table 1). The difference in epiphytic load between species was largest at sites where *F. vesiculosus* was heavily overgrown. Tukey's *post hoc* test showed that the biomass of epiphytes was significantly lower on *F. evanescens* than on *F. vesiculosus* at 11 of the 14 sites. The ratio of epiphytic animals to epiphytic algae did not differ between sites or *Fucus* species.

The sampled *F. vesiculosus* plants were on average larger than the *F. evanescens* plants (*t*-test,  $P < 0.001$ ), the mean plant length was  $240 \pm 11$  and  $166 \pm 6$  mm, respectively. This difference in size may reflect a

different age structure in populations of the two species which may be important for the epiphytic community. However, the biomass of epiphytes per *Fucus* biomass was not significantly correlated with plant length for either of the *Fucus* species, indicating that the large differences in epiphytic load cannot be explained by plant size.

The biomass of motile animals also differed both between sites and *Fucus* species, *F. vesiculosus*

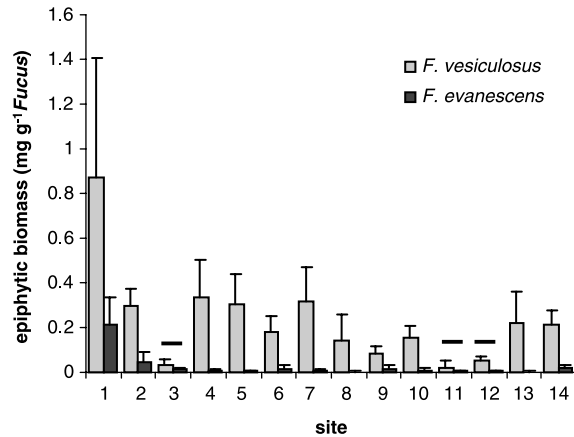


Figure 1. Biomass (mg dry weight) of epiphytes (per gram dry weight of *Fucus*) on *Fucus vesiculosus* and *Fucus evanescens* from the different sites. Error bars show 95% confidence limits ( $n = 5$ ). A line above a species pair indicates that the species were not significantly different due to Tukey's *post hoc* test.

supporting more animals than *F. evanescens* (Table 2, Figure 2b). There were significantly more amphipods on *F. vesiculosus*, while the biomass of isopods did not differ between the two species. Gastropods, that constituted the largest part of the animal biomass, also tended to be more abundant on *F. vesiculosus* although the difference between species was not significant due to large between-plant differences. Biomass of motile epifauna was positively correlated with epiphytic algal biomass ( $R^2 = 0.24, P < 0.001$ ).

Table 3 presents all taxa of epiphytes (epiflora and epifauna) and motile fauna, and the percentage of *Fucus* plants where they were found. In total, 33 epiphytic taxa were documented, 28 algae and

Table 1. Two-way ANOVA of the biomass of epiphytes and the ratio of epifauna to epiflora at *Fucus evanescens* and *Fucus vesiculosus* from different sites. Data were fourth-root transformed to obtain homogeneity of variances.

Source of variation	df	All epiphytes		Ratio epifauna/epiflora	
		MS	F	MS	F
<i>Fucus</i> species (F)	1	4.03	222.28***	0.25	1.57 ns
Site (S)	13	0.17	9.40***	0.23	1.46 ns
F × S	13	0.05	2.71**	0.24	1.48 ns
Residual	112	0.02		0.16	

\*\*  $P < 0.01$ ; \*\*\*  $P < 0.001$ ; ns = not significant.

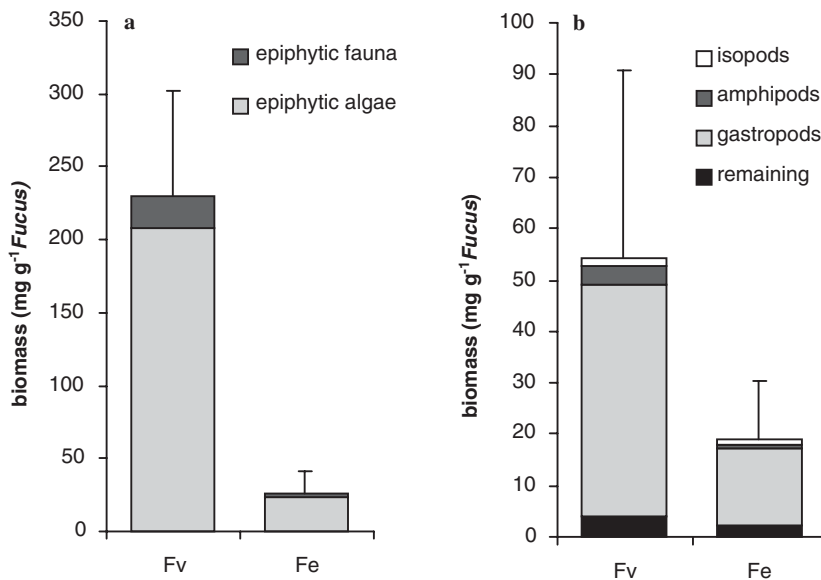


Figure 2. The biomass (mg dry weight) of epiphytes (a) and associated free-living fauna (b) of *Fucus vesiculosus* (Fv) and *Fucus evanescens* (Fe), per gram dry weight of the *Fucus* plant. Error bars show 95% confidence limits ( $n = 70$ ).

Table 2. Two-way ANOVA of the biomass of free-living fauna in plants of *Fucus evanescens* and *Fucus vesiculosus* from different sites. Data were fourth-root transformed to obtain homogeneity of variances.

Source of variation	df	All animals		Isopods		Amphipods		Gastropods	
		MS	F	MS	F	MS	F	MS	F
<i>Fucus</i> species (F)	1	0.59	18.45***	0.02	2.07 ns	0.45	59.30***	0.01	0.33 ns
Site (S)	13	0.14	4.32***	0.02	2.34**	0.05	7.19***	0.15	3.93***
F × S	13	0.02	0.53 ns	0.01	1.48 ns	0.02	2.04*	0.01	0.38 ns
Residual	112	0.03		0.01		0.01		0.04	

\*  $P < 0.05$ ; \*\*  $P < 0.01$ ; \*\*\*  $P < 0.001$ ; ns = not significant.

Table 3. Percentage of plants of *Fucus evanescens* and *Fucus vesiculosus* where the different epiphytic taxa were found ( $n = 70$ ).

	<i>F. evanescens</i>	<i>F. vesiculosus</i>
Epiflora		
Rhodophyceae		
<i>Callithamnion</i> sp.		1
<i>Ceramium nodulosum</i> (Lightf.) Ducluz.	1	4
<i>Ceramium tenuicorne</i> (Kütz.) Waern	4	11
<i>Dumontia contorta</i> (S.G.Gmel.) Rupr.	3	1
<i>Membranoptera alata</i> (Huds.) Stackh.		1
<i>Phycodrys rubens</i> (L.) Batters		1
<i>Polysiphonia fucoides</i> (Huds.) Grev.	3	21
<i>Polysiphonia stricta</i> (Dillwyn) Grev.		7
<i>Porphyra purpurea</i> (Roth) C. Agardh		1
<i>Rhodomela confervoides</i> (Huds.) P.C. Silva		3
<i>Stylonema alsidii</i> (Zanardini) K.M. Drew**		1
Phaeophyceae		
<i>Dictyosiphon foeniculaceus</i> (Huds.) Grev.		1
<i>Ectocarpus</i> sp./ <i>Pilayella littoralis</i> (L.) Kjellm.	50	73
<i>Elachista fucicola</i> (Vellay) Aresch.**	53	83
<i>Spongonema tomentosum</i> (Huds.) Kütz.*	1	7
Chlorophyceae		
<i>Chaetomorpha aerea</i> (Gooden. ex Dilwyn) Kütz.		1
<i>Cladophora</i> sp. <sup>a</sup>	14	16
<i>Cladophora rupestris</i> (L.) Kütz.	14	17
<i>Enteromorpha</i> spp. <sup>b</sup>	16	69
<i>E. clathrata</i> (Roth) Grev.		(1)
<i>E. compressa</i> (L.) Nees		(1)
<i>E. flexuosa</i> (Wulfen) J. Agardh	(3)	(3)

Table 3. Continued.

	<i>F. evanescens</i>	<i>F. vesiculosus</i>
<i>E. intestinalis</i> (L.) Nees	(3)	(19)
<i>E. linza</i> (L.) Agardh	(1)	(7)
<i>E. prolifera</i> (O.F. Müll.) J. Agardh	(1)	(11)
<i>Spongomorpha aeruginosa</i> (L.) C. Hoek*		1
<i>Ulotrix</i> sp.	1	3
<i>Ulva</i> sp.	1	1
<i>Ulvopsis grevillei</i> (Thur.) Gayral	3	7
Epifauna		
Hydrozoa		
<i>Clava multicornis</i> Forskål		3
<i>Laomedea flexuosa</i> Alder	17	16
Crustacea		
<i>Balanus improvisus</i> Darwin		6
Bryozoa		
<i>Electra pilosa</i> L.*	17	10
<i>Membranipora membranacea</i> L.**		3
Motile fauna		
Isopoda		
<i>Idotea</i> sp.	14	28
<i>Jaera</i> sp.	34	46
Amphipoda		
<i>Gammarus</i> sp.	31	84
<i>Corophium volutator</i>	1	6
Gastropoda		
<i>Hydrobia</i> sp.	11	11
<i>Littorina littorea</i> L.	9	14
<i>Littorina obdusata</i> L.	3	10
<i>Theodoxus fluvatilus</i> L.	1	3
Bivalvia		
<i>Cardium</i> sp.	1	3
Oligochaeta		
		6
Insecta		
Chironomidae	24	57

<sup>a</sup> Only *Cladophora rupestris* was extinguished.

<sup>b</sup> Specimen of the genus *Enteromorpha* were only identified to species when possible, why the figures for the particular species are underestimated. Species most often growing epiphytic are indicated with \* and obligate or near-obligate epiphytes are indicated with \*\* (information from Ruess 1977; Hayward and Ryland 1995).

5 animals. Of these, only three are regarded as obligate epiphytes. All taxa were present on *F. vesiculosus* but only 18 were found on *F. evanescens* plants. The mean number of taxa found on a single *F. vesiculosus* plant was  $3.7 \pm 2.0$  compared to  $2.2 \pm 1.6$  on *F. evanescens*, the difference being highly significant (*U*-test,  $P < 0.001$ ). It was consistently the rare species that were absent from *F. evanescens*. Almost all taxa of motile animals were more commonly found on *F. vesiculosus* plants, but all taxa except *Oligochaeta* were found on both *Fucus* species.

Detrended correspondence analysis of the 14 most common epiphytic taxa showed a clear tendency of the samples from *F. evanescens* and *F. vesiculosus* to separate along the first canonical axis, which explained 24.6% of the total variation (Figure 3). The species mainly responsible for this pattern were *Enteromorpha* spp., *Ceramium nodulosum*, *Polysiphonia fucoides*, *Polysiphonia stricta*, and *Spongonema tomentosum*, that occurred relatively more often on *F. vesiculosus*.

Canonical correspondence analysis showed that 20.6% of the total variation (total inertia) was explained by the three constraining variables (*Fucus* species, salinity and wave exposure). *Fucus* species alone explained 10.3% and was the only variable that was significant according to the Monte Carlo test, although wave exposure was almost significant (Table 4). When

the effects of salinity and wave exposure were removed using a partial CCA, *Fucus* species still explained 9.3% of the total variation.

Canonical correspondence analysis with only *F. vesiculosus* showed that salinity explained as much as 20.0% of the variation in epiphytic community ( $P < 0.01$ ), while the effect of wave exposure was non-significant. In contrast, neither salinity nor exposure had significant effect on the epiphytic community of *F. evanescens*, when analysed separately.

## Discussion

Our study demonstrated that the two closely related species *F. evanescens* and *F. vesiculosus* differ in substrate quality for epiphytic organisms even when growing at the same site. While the native *F. vesiculosus* is heavily overgrown by epiphytes at some sites, *F. evanescens* rarely has much epiphytes. The number of associated epiphytic species also differed between the *Fucus* species. *F. evanescens* plants had consistently lower species richness and half of the species in the material were not found on this species at all. The epiphytes that were absent from *F. evanescens* were all among the rarest species. It is thus unclear whether these species are completely unable to grow epiphytic on *F. evanescens*, or if they only are more likely to

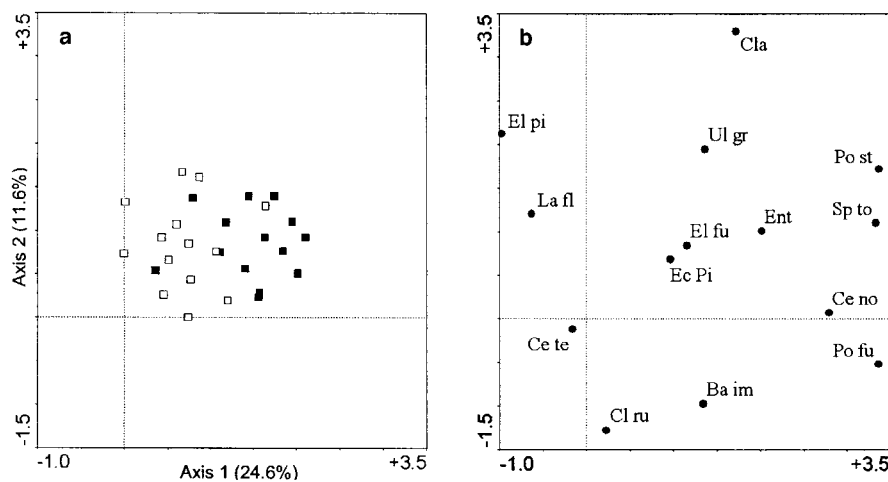


Figure 3. Plot of the first two ordination axes from DCA of the epiphytic species composition, using the 14 most common taxa; (a) Plot of *Fucus* species and sites. Filled quadrats represent *Fucus vesiculosus* at different sites and empty represents *Fucus evanescens*. Percentage of the total variation explained by the canonical axes is also indicated. (b) Plot of species scores. The species names are abbreviated to the part in italics as follows: *Balanus improvisus*, *Ceramium nodulosum*, *Ceramium tenuicorne*, *Cladophora* spp., *Cladophora rupestris*, *Ectocarpus* spp./*Pilayella littoralis*, *Elachista fucicola*, *Electra pilosa*, *Enteromorpha* spp., *Laomedea flexuosa*, *Polysiphonia fucoides*, *Polysiphonia stricta*, *Spongonema tomentosum*, *Ulvopsis grevillei*.

Table 4. The percentage of total variation in epiphytic species composition (% inertia) explained by the different environmental factors according to CCA and partial CCA with the 14 most common taxa. The constraining variables were host species (Spe), salinity (Sal) and wave exposure (Exp). *P*-values of the constraining variables from Monte Carlo test with 999 unrestricted permutations are indicated.

	Both <i>Fucus</i> species		<i>F. vesiculosus</i>		<i>F. evanescens</i>	
	% inertia	<i>P</i>	% inertia	<i>P</i>	% inertia	<i>P</i>
All factors	20.6	0.001	26.6	0.015	14.1	0.136
Spe	10.3	0.006	—	—	—	—
Sal	5.9	0.092	20.0	0.007	6.7	0.072
Exp	6.6	0.051	9.3	0.261	13.9	0.062
Spe/(Sal × Exp) <sup>a</sup>	9.3	0.003	—	—	—	—

<sup>a</sup>The effect of host species when effects of salinity and wave exposure are partialled out.

be found on *F. vesiculosus* due to its larger epiphytic biomass and possibly higher age.

The mechanism behind the low epiphytic growth on *F. evanescens* is not clear. Differential fouling on other macroalgal species has in several cases been attributed to morphological features, e.g. thallus morphology, thickness of cell-wall and surface texture (Hayward 1980; Correa and McLachlan 1991; Jennings and Steinberg 1997; Dawes et al. 2000). *F. evanescens* is morphologically similar to *F. vesiculosus*, but lacks air bladders and consequently does not stand up in the water column. This may influence settlement of spores or larvae and may affect growth or survival of algal epiphytes by shading them to a larger degree. Jennings and Steinberg (1997) found that thallus pieces of the kelp *Ecklonia radiata* suspended higher in the water column became more overgrown by epiphytes than pieces placed near the bottom. The relatively smoother surface of *F. evanescens* fronds may also inhibit settling.

Another explanation of differences in epiphytic load between macroalgal species is the presence of an antifouling defence. Several studies have shown that epiphytes may have a negative impact on the marine macrophytes, e.g. by shading the plant and competing for limited nutrients (Sand-Jensen 1977; Worm and Sommer 2000). These processes could select for seaweed characteristics that inhibit colonisation of epiphytic organisms. Regular shedding of the outer epidermis has been evoked as a defence mechanism for fucoids (Filion-Myklebust and Norton 1981; Moss 1982) and crustose algae (e.g. Johnson and Mann 1986). Several studies have also demonstrated an effect of algal secondary metabolites on establishment or survival of epiphytic species (Sieburth and Conover 1965; Schmitt et al. 1995; Steinberg et al. 1998; but see Jennings and Steinberg 1997). The possible presence

of an effective antifouling mechanism in *F. evanescens* will be experimentally tested.

Despite the considerable difference in species richness between the *Fucus* species, CCA showed that only some part of the variation in community composition could be explained by substratum species. A few taxa, e.g. *Enteromorpha* spp., *P. fucoides* and *P. stricta*, were relatively more common on *F. vesiculosus* than on *F. evanescens*, but the two species did not have distinctly different epibiotas. Some populations of *F. evanescens* had an epiphytic community that more closely resembled certain *F. vesiculosus* populations than other populations of the same species, and vice versa. The similarity of community composition suggests that most epiphytic species show low host specificity. This is not surprising, since most species found epiphytic on the two *Fucus* species are not obligate epiphytes but can grow also on rocks and other hard-substrata. Whatever restricts the establishment or survival of epiphytes on *F. evanescens*, it seems to influence all epiphytes to a similar degree.

While the differences in epiphytic community composition could be partly explained by *Fucus* species, neither wave exposure nor salinity had any significant effect. The small influence of exposure was unexpected, since wave exposure has been identified as one of the most important single factors influencing intertidal rocky shore communities (Lewis 1964; Jones and Demetropoulos 1968). The exposure gradient in our material is however very short, since *F. evanescens* is only present at sheltered sites in this area (Wikström et al. 2002). Since the study was performed in the transition zone between a marine and a brackish area with partly different biota, where many species have their distribution limits due to salinity tolerance (Wallentinus 1991; Nielsen et al. 1995), the salinity gradient would also be expected to influence species



composition. While salinity had no significant effect when *F. evanescens* and *F. vesiculosus* were analysed together, it did explain much of the variation in community composition for *F. vesiculosus* alone. It seems as if the epiphytic community of *F. evanescens* is too species-poor to show this gradient.

As with the epiphytes, the biomass of free-living animals associated with the seaweed was considerably lower on *F. evanescens* than on *F. vesiculosus*, suggesting that *F. evanescens* is a less suitable host also for free-living animals. Most of the epifaunal biomass consisted of herbivorous crustaceans and gastropods (mesograzers *sensu* Brawley 1992), grazing on the host seaweed or its epiphytes. The macroalgae thus serve both as food and habitat for the motile epifauna and *F. evanescens* may be avoided either because it offers less-suitable substratum or is a less-preferred food source than the native *F. vesiculosus*.

Laboratory grazing experiments show that *F. evanescens* is a less-preferred food source than the native *F. vesiculosus*, both for the common isopod *I. baltica* Pallas (Schueller and Peters 1994) and the periwinkle *Littorina obdusata* (S.A. Wikström, unpubl. data). If this is a general pattern, a lower palatability may explain why *F. evanescens* is avoided by species that forage directly on the *Fucus* plant. As expected, we found *Idotea* sp. and *L. obdusata* on fewer *F. evanescens* than *F. vesiculosus* plants. However, the mean biomass of isopods (including the genus *Idotea*) did not differ significantly between the *Fucus* species, suggesting that the preference demonstrated in the laboratory may have less importance in the field situation.

While *Idotea* species and *L. obdusata* are known to graze directly on the *Fucus* plant (Watson and Norton 1987; Pavia et al. 1999; Jormalainen et al. 2001), many mesograzers, as *Littorina littorea* (Watson and Norton 1985) and gammarid amphipods (D'Antonio 1985; Pavia et al. 1999) prefer feeding on epiphytic species. Macroepiphytes may also favour the free-living epifauna by increasing the substrate complexity, offering shelter from predators and physical stress (e.g. Nicotri 1980; Brawley 1992). Earlier studies have demonstrated a positive correlation between the biomasses of seaweed epiphytes and free-living epifauna, showing that the epiphyte cover may affect the amount of free-living epifauna that can be supported by a seaweed (Martin-Smith 1993; Worm and Sommer 2000). We found a similar correlation in our study, indicating that the observed preference for *F. vesiculosus* may, at

least partly, be an indirect effect of the larger abundance of epiphytes on this species. However, experimental studies of the food and habitat choice of different epifaunal species are needed to elucidate the mechanism behind the low colonisation of *F. evanescens*.

The low epiphytic growth on *F. evanescens* is a possible explanation to the observed success of the species in eutrophicated areas (Powell 1957b; Bokn et al. 1992; Wikström et al. 2002). Increased nutrient load has been shown to favour the growth of filamentous epiphytic algae on *F. vesiculosus*, resulting in lower growth rate of the seaweed (Worm and Sommer 2000). If *F. evanescens* is better at resisting heavy epiphytic overgrowth, eutrophication may induce a change in the seaweed community by affecting competitive interactions between the *Fucus* species. In this case, a human-driven change in coastal water quality may actually have promoted the invasion of *F. evanescens*, supporting the notion (e.g. Elton 1958; Burke and Grime 1996) that anthropogenic disturbances may render a biotic community more susceptible to invasion.

In conclusion, our study indicates that most epiphytic species show low host specificity among *Fucus* species. In addition, most of the species found on the *Fucus* plants are not obligate epiphytes and do not depend on seaweeds for their presence in the littoral. The only obligate epiphytes absent from *F. evanescens* were the red alga *Stylonema alsidii* and the bryozoan *Membranipora membranacea*, that were overall very rare in the material. Thus, although *F. evanescens* constitutes a less favourable substratum for epiphytes than *F. vesiculosus*, the species richness of algae and sessile invertebrates in the *Fucus* belt is probably little affected by the invasion. By supporting comparatively little epiphytic growth, *F. evanescens* provides less living-space for free-living animals dependent on epiphytes for food or habitat. However, further studies comparing the abundance of free-living fauna between sites with different degree of *F. evanescens* dominance are needed to conclude that the shift from *F. vesiculosus* to *F. evanescens* has actually affected the epifaunal populations in the invaded region.

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## References

- Arrontes J (1999) On the evolution of interactions between marine mesoherbivores and algae. *Botanica Marina* 42: 137–155
- Bellan-Santini D, Arnaud PM, Bellan G and Verlaque M (1996) The influence of the introduced tropical alga *Caulerpa taxifolia*, on the biodiversity of the Mediterranean marine biota. *Journal of the Marine Biological Association of the United Kingdom* 76: 235–237
- Bokn T and Lein TE (1978) Long-term changes in fucoid association of the inner Oslofjord, Norway. *Norwegian Journal of Botany* 25: 9–14
- Bokn TL, Murray SN, Moy FE and Magnusson JB (1992) Changes in the fucoid distributions and abundances in the inner Oslofjord, Norway: 1974–1980 versus 1988–1990. *Acta Phytogeographica Suecica* 78: 117–124
- Braithwaite RW, Lonsdale WM and Estbergs JA (1989) Alien vegetation and native biota in tropical Australia: the spread and impact of *Mimosa pigra*. *Biological Conservation* 48: 189–210
- Brawley S (1992) Mesoherbivores. In: John DM, Hawkins SJ and Price JH (eds) *Plant–animal Interactions in the Marine Benthos*, pp 235–263. Clarendon Press, Oxford
- Burke MJW and Grime JP (1996) An experimental study of plant community invasibility. *Ecology* 77: 776–790
- Correa JA and McLachlan JL (1991) Endophytic algae of *Chondrus crispus* (Rhodophyta). III. Host specificity. *Journal of Phycology* 27: 448–459
- D'Antonio C (1985) Epiphytes on the rocky intertidal red alga *Rhodomela larix* (Turner) C. Agardh: negative effects on the host and food for herbivores? *Journal of Experimental Marine Biology and Ecology* 86: 197–218
- Dawes CJ, Teasdale BW and Friedlander M (2000) Cell wall structure of the agarophytes *Gracilaria tikvahiae* and *G. cornea* (Rhodophyta) and penetration by the epiphyte *Ulva lactuca* (Chlorophyta). *Journal of Applied Phycology* 12: 567–575
- Dayton PK (1971) Competition, disturbance, and community organization: the provision and subsequent utilization of space in a rocky intertidal community. *Ecological Monographs* 41: 351–389
- Duffy JE and Hay ME (1991) Food and shelter as determinants of food choice by an herbivorous marine amphipod. *Ecology* 72: 1286–1298
- Elton CS (1958) *The Ecology of Invasions by Animals and Plants*. Methuen, London, 181 pp
- Filion-Myklebust CC and Norton TA (1981) Epidermis shedding in the brown seaweed *Ascophyllum nodosum* L. *Le Jolis. Marine Biology Letters* 2: 45–51
- Grosholz E (2002) Ecological and evolutionary consequences of coastal invasions. *Trends in Ecology and Evolution* 17: 22–27
- Hacker SD and Steneck RS (1990) Habitat architecture and the abundance and body-size-dependent habitat selection of a phytal amphipod. *Ecology* 71: 2269–2285
- Håkanson L (1981) *A Manual of Lake Morphometry*. Springer-Verlag, Berlin, 78 pp
- Hay ME (1986) Associational plant defences and the maintenance of species diversity: turning competitors into accomplices. *The American Naturalist* 128: 617–641
- Hay ME (1996) Marine chemical ecology: what's known and what's next? *Journal of Experimental Marine Biology and Ecology* 200: 103–134
- Hay ME, Duffy JE and Fennical W (1990) Host-plant specialization decreases predation on a marine amphipod: an herbivore in plant's clothing. *Ecology* 71: 733–743
- Hayward PJ (1980) Invertebrate epiphytes of coastal marine algae. In: Price JH, Irvine DEG and Farnham WF (eds) *The Shore Environment, Vol II, Ecosystems*, pp 761–787. Academic Press, London
- Hayward PJ and Ryland JS (eds) (1995) *Handbook of the Marine Fauna of North-west Europe*. Oxford University Press, Oxford, 800 pp
- Hill MO and Gauch HG (1980) Detrended correspondence analysis, an improved ordination technique. *Vegetatio* 42: 47–58
- Hylmö DEV (1933) Algenimmigration nach der schwedischen Westküste. *Botaniska Notiser* 1933: 377–390
- Jennings JG and Steinberg PD (1997) Phlorotannins versus other factors affecting epiphyte abundance on the kelp *Ecklonia radiata*. *Oecologia* 109: 461–473
- Johnson CR and Mann KH (1986) The crustose coralline alga *Phymatoliton* Foslie inhibits the overgrowth of seaweeds without relying on herbivores. *Journal of Experimental Marine Biology and Ecology* 199: 249–267
- Jones WE and Demetropoulos A (1968) Exposure to wave action: measurements of an important ecological parameter on rocky shores on Anglesey. *Journal of Experimental Marine Biology and Ecology* 2: 46–63
- Jormalainen V, Honkanen T and Heikkilä N (2001) Feeding preferences and performance of a marine isopod on seaweed hosts: cost of habitat specialization. *Marine Ecology Progress Series* 220: 219–230
- Lewis JR (1964) *The Ecology of Rocky Shores*. English Universities Press, London, 323 pp
- Lining T and Garbary DJ (1992) The *Ascophyllum/Polysiphonia/Mycosphaerella* Symbiosis. III. Experimental Studies on the interactions between *P. lanosa* and *A. nodosum*. *Botanica Marina* 35: 341–349
- Lund S (1949) Immigration of algae into Danish waters. *Nature* 164: 616
- Mack RN, Simberloff D, Lonsdale WM, Evans H, Clout M and Bazzaz FA (2000) Biotic invasions: causes, epidemiology, global consequences, and control. *Ecological Applications* 10: 689–710
- Martin-Smith KM (1993) Abundance of mobile epifauna: the role of habitat complexity and predation by fishes. *Journal of Experimental Marine Biology and Ecology* 174: 243–260
- Moss BL (1982) The control of epiphytes by *Halidrys siliquosa* (L.) Lyngb. (Phaeophyta, Cystoceiraceae). *Phycologia* 21: 185–188
- Nicotri ME (1980) Factors involved in herbivore food preference. *Journal of Experimental Marine Biology and Ecology* 42: 13–26
- Nielsen R, Kristiansen A, Mathiesen L and Mathiesen H (1995) Distributional index of the benthic macroalgae of the Baltic Sea area. *Acta Botanica Fennica* 155: 1–51
- Pavia H, Carr H and Åberg P (1999) Habitat and feeding preferences of the crustacean mesoherbivores inhabiting the brown seaweed *Ascophyllum nodosum* (L.) Le Jol. and its epiphytic macroalgae. *Journal of Experimental Marine Biology and Ecology* 236: 15–32

- Poore AGB, Watson MJ, Nys Rd, Lowry JK and Steinberg PD (2000) Patterns of host use among alga- and sponge-associated amphipods. *Marine Ecology Progress Series* 208: 183–196
- Powell HT (1957a) Studies in the genus *Fucus* L. I. *Fucus distichus* L. Emend. Powell. *Journal of the Marine Biological Association of the United Kingdom* 36: 407–432
- Powell HT (1957b) Studies in the genus *Fucus* L. II. Distribution and ecology of forms of *Fucus distichus* L. Emend. Powell in Britain and Ireland. *Journal of the Marine Biological Association of the United Kingdom* 36: 663–693
- Rueness J (1977) *Norsk Algeflora*. Universitetsforlaget, Oslo, 266 pp
- Sand-Jensen K (1977) Effect of epiphytes on eelgrass photosynthesis. *Aquatic Botany* 3: 55–63
- Schaffelke B, Evers D and Walhorn A (1995) Selective grazing of the isopod *Idotea baltica* between *Fucus evanescens* and *F. vesiculosus* from Kiel Fjord (western Baltic). *Marine Biology* 124: 215–218
- Schmitt TM, Hay ME and Lindquist N (1995) Constraints on chemically mediated coevolution: multiple functions for seaweed secondary metabolites. *Ecology* 76: 107–123
- Schueller GH and Peters AF (1994) Arrival of *Fucus evanescens* (Phaeophyceae) in Kiel Bight (Western Baltic). *Botanica Marina* 37: 471–477
- Seed R and O'Connor RJ (1981) Community organization in marine algal epifaunas. *Annual Review of Ecology and Systematics* 12: 49–74
- Sieburth JM and Conover JT (1965) *Sargassum* tannin, an antibiotic which retards fouling. *Nature* 208: 52–53
- Simmons HG (1898) *Algologiska notiser*. II. Einige Algenfunde bei Drøbak. *Botaniska Notiser* 1898: 117–123
- Steinberg PD, De Nys R and Kjelleberg S (1998) Chemical inhibition of epibiota by Australian seaweeds. *Biofouling* 12: 227–244
- Sutherland JP and Karlson RH (1977) Development and stability of the fouling community at Beaufort, North Carolina. *Ecological Monographs* 47: 425–446
- ter Braak CJF (1988) Partial canonical correspondence analysis. In: Bock HH (ed) *Classification and Related Methods of Data Analysis*, pp 551–558. North Holland, Amsterdam
- ter Braak CJF and Šmilauer P (1998) *CANOCO Reference Manual and User's Guide to Canoco for Windows*. Software for Canonical Community Ordination (version 4). Centre for Biometry Wageningen, Wageningen, The Netherlands and Microcomputer Power, Ithaca, New York, 352 pp
- Viejo RM (1999) Mobile epifauna inhabiting the invasive *Sargassum muticum* and two local seaweeds in northern Spain. *Aquatic Botany* 64: 131–149
- Vitousek PM and Walker LR (1989) Biological invasion by *Myrica faya* in Hawai'i: plant demography, nitrogen-fixation, ecosystem effects. *Ecological Monographs* 59: 247–265
- Vitousek PM, D'Antonio CM, Loope LL and Westbrooks R (1996) Biological invasions as global environmental change. *American Scientist* 84: 468–478
- Wallentinus I (1991) The Baltic Sea gradient. In: Mathieson AC and Nienhuis PH (eds) *Ecosystems of the World 24: Intertidal and Littoral Ecosystems*, pp 83–108. Elsevier, Amsterdam
- Watson DC and Norton TA (1985) Dietary preferences of the common periwinkle, *Littorina littorea* (L.). *Journal of Experimental Marine Biology and Ecology* 88: 193–211
- Watson DC and Norton TA (1987) The habitat and feeding preferences of *Littorina obtusata* (L.) and *L. marie* Sacchi et Rastelli. *Journal of Experimental Marine Biology and Ecology* 112: 62–72
- Wikström SA, von Wachenfeldt T and Kautsky L (2002) Establishment of the exotic species *Fucus evanescens* C. Ag. (Phaeophyceae) in Öresund, Southern Sweden. *Botanica Marina* 45: 510–517
- Worm B and Sommer U (2000) Rapid direct and indirect effects of a single nutrient pulse in a seaweed-epiphyte grazer system. *Marine Ecology Progress Series* 202: 283–288