

# The extent of grazing release from epiphytism for *Sargassum muticum* (Phaeophyceae) within the invaded range

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*The overall biotic pressure on a newly introduced species may be less than that experienced within its native range, facilitating invasion. The brown alga Sargassum muticum (Yendo) Fensholt is a conspicuous and successful invasive species originally from Japan and China. We compared S. muticum and native macroalgae with respect to the biotic pressures of mesoherbivore grazing and ectocarpoid fouling. In Strangford Lough, Northern Ireland, S. muticum thalli were as heavily overgrown with seasonal blooms of epiphytic algae as native macroalgal species were. The herbivorous amphipod Dexamine spinosa was much more abundant on S. muticum than on any native macroalga. When cultured with this amphipod, S. muticum lost more tissue than three native macroalgae, Saccharina latissima (Linnaeus) Lane et al., Halidrys siliquosa (Linnaeus) Lyngbye and Fucus serratus Linnaeus. Sargassum muticum cultured with both ectocarpoid fouling and amphipods showed a severe impact, consistent with our previous findings of large declines in the density of S. muticum observed in the field during the peak of fouling. Despite being a recent introduction into the macroalgal community in Strangford Lough, S. muticum appears to be under biotic pressure at least equal to that on native species, suggesting that release from grazing and epiphytism does not contribute to the invasiveness of this species in Strangford Lough.*

**Keywords:** co-consumption, *Dexamine spinosa*, grazing release, epiphytic algae, epiphytic amphipods, invasive alga, mesoherbivore grazing, *Sargassum muticum*

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## INTRODUCTION

A central topic in invasion ecology is why certain species are successful invaders. This involves both: (1) the intrinsic biological traits of the invasive species in question; and (2) extrinsic aspects of the invaded habitat, defined by an array of environmental and biotic parameters. The interaction between these intrinsic and extrinsic factors ultimately decides the success of a potentially introduced species. Traits that confer invasiveness have been identified in some taxonomic groups (e.g. marine macroalgae: Nyberg & Wallentinus, 2005; plants: Finnoff & Tschirhart, 2005; freshwater fish: Wonham *et al.*, 2000; Vila-Gispert *et al.*, 2005). For example, the dispersal characteristics of many successful invaders, particularly in relation to anthropogenic vectors are similar and predictable (Nyberg & Wallentinus, 2005).

The biotic pressures of predation, competition, disease and parasitism are particularly important for determining invasion success (Torchin *et al.*, 2001; Wolfe, 2002; Parker & Hay, 2005; Parker *et al.*, 2006). If the overall biotic pressure on a newly introduced species is less than in the native range, this may facilitate the invasion (Elton, 1958; Parker & Hay, 2005; Parker *et al.*, 2006). The absence of coevolved specialist enemies and the preferential consumption of native species by native generalists could give introduced

species a competitive advantage (Parker & Hay, 2005). Alternatively, non-native prey might be unable to deter native predators in the introduced range due to the absence of co-evolved defences, as in the increased susceptibility/biotic resistance hypothesis (Elton, 1958; Hokkanen & Pimentel, 1989; Colautti *et al.*, 2004; Parker *et al.*, 2006).

The relative contributions of intrinsic and extrinsic factors to the success of a particular invasion have rarely been studied. De Rivera *et al.* (2005) found that the distribution in North America of the introduced European green crab *Carcinus maenas* (Linnaeus) was partly determined by geographical variation in biotic pressures. Along a geographical gradient, the intrinsic invasive traits were eventually outweighed by predation from the native crab *Callinectes sapidus* (Rathbun). For invasive species, extrinsic factors can be compared in the native and introduced ranges (Wolfe, 2002), but it is difficult to quantitatively compare ecological processes that are similar but involve completely different sets of interacting species. An alternative approach is to contrast the biotic pressures experienced by introduced species and sympatric native species in the same habitat, potentially allowing predictive assessments of likely success within other areas.

The brown seaweed *Sargassum muticum* (Yendo) Fensholt is native to Japan and China, and has become a conspicuous and successful invasive species along vast stretches of European and North Pacific shorelines (Wallentinus, 1999). *Sargassum muticum* has many of the intrinsic traits of an invasive species (Nyberg & Wallentinus, 2005; Pedersen *et al.*, 2005; Sanchez & Fernandez, 2005) such as: (1) very high

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growth rates of 2–4 cm per day (Critchley, 1981; Lewey & Farnham, 1981; Nicholson *et al.*, 1981); (2) high fecundity, monoecious receptacles and a perennial life history (Fensholt, 1955; Norton, 1976; Norton & Deysher, 1989); and (3) multiple-range dispersal mechanisms including germling settlement, peripatetic plants and drifting fertile thalli (Norton, 1976). In Strangford Lough (Northern Ireland), *S. muticum* has been a particularly successful invader (Strong *et al.*, 2005). The habitat of *S. muticum* in Strangford Lough includes extensive soft sediment areas with only a small component of mobile hard substrata. This is a predominantly empty niche for macroalgae locally, which suggests that *S. muticum* might be benefiting from an element of release from inter-specific competition in these particular areas.

From the literature, we identified the two main elements of biotic pressure on native and introduced macroalgae in temperate marine habitats as: (1) mesoherbivore grazing, including detaching and consuming material (Duffy, 1990); and (2) epiphyte overgrowth, which can reduce photosynthesis below the compensation point and decrease gas exchange (Wahl, 1989; Steinberg & de Nys, 2002) but may also protect the alga from mesoherbivore grazing (Wahl & Hay, 1995; Karez *et al.*, 2000) and excessive light (Dodds, 1991). Clearly the effects of mesograzers in combination with epiphytes may be different from either of these factors presented alone. For example, mesograzers could preferentially graze epiphytes and thereby reduce the impact of fouling, or conversely could consume the algal basiphyte and further impact the already fouled macrophyte (Karez *et al.*, 2000).

The objective of this study was to compare the biotic pressures of mesoherbivore grazing and epiphyte fouling on *S. muticum* and three sympatric native brown macroalgae, *Saccharina latissima* (formerly known as *Laminaria saccharina*), *Halidrys siliquosa* and *Fucus serratus*. The native species were selected due to their locally high abundance, similar thallus size, and habitat overlap with *S. muticum*. These species are the most ecologically comparable to *S. muticum* although they differ morphologically and in phenology. Ultimately, this analysis should provide insights into the importance of intrinsic and extrinsic factors for *S. muticum* as an invasive species in Europe.

We tested the hypothesis that *S. muticum* will suffer less mesoherbivore grazing and algal fouling than native algal species because native grazers are not adapted to exploit it as a food source or as a substratum. This was tested by examining whether: (1) *S. muticum* has less fouling than native macroalgae; (2) fouling affects loss rate of thalli; (3) fewer mesograzers are found on *S. muticum* than on native macroalgae; (4) *Dexamine spinosa* (Montagu) (the main epiphytic mesograzer locally) prefers native macroalgae over *S. muticum*; and (5) the combined effects of *Dexamine spinosa* and epiphytic fouling differ from the effects of each alone.

## MATERIALS AND METHODS

### Study site

Strangford Lough, a large sea-lough with a narrow entrance, is situated on the north-east coast of Ireland (Figure 1). All collections were made in the Dorn (54° 26.105' N 005° 32.475' W),

an inlet on the south-eastern shore of the Lough (Figure 1) which was colonized by *Sargassum muticum* in 1996 (Davison, 1999). The substratum in the study area of the Dorn consists largely of small pebbles on mud, with some scattered loose rock fragments. In the subtidal fringe of the Dorn, *S. muticum* is found with three large native brown algae, *Saccharina latissima* (Linnaeus) C.E. Lane *et al.*, *Halidrys siliquosa* (Linnaeus) Lyngbye and *Fucus serratus* Linnaeus. *Sargassum muticum* was studied at this site over a three-year period (2000–2003) and the presence of an ectocarpoid fouling epiphyte was observed in the spring to summer periods of each year. Monthly monitoring of epiphytic algae on *S. muticum* was carried out in the Dorn from February 2000 to November 2003.

### Quantification of epiphytic algae and fauna on *Sargassum muticum* and native macroalgae

The biomass of algal epiphytes on *Sargassum muticum* and the three selected native species (*Saccharina latissima*, *Halidrys siliquosa* and *Fucus serratus*) was determined during the peak of epiphytic fouling in June 2002. Eight thalli of each species (seven of *H. siliquosa*) were randomly taken from the same depth (–0.35 m below mean low water neap tides) and carefully bagged individually to prevent loss of epiphytes. At the laboratory, each thallus was carefully washed to remove sediment then the surface epiphytes were detached. Epiphytic algal fouling was not separated into species, as preliminary investigations revealed that the vast majority was ectocarpoids (probably *Hincksia* spp.). Basiphytic and epiphytic material was blotted dry, weighed fresh, and weighed again after drying for 24 hours at 60°C in an oven.

To obtain the mobile epifauna present at the peak of the epiphytic fouling, a separate collection of basiphyte thalli was made using the method described above, with additional precautions to prevent the loss of epiphytic fauna. Each basiphyte was weighed in the field with a spring balance and only thalli weighing 400 g ± 50 g were retained. At the laboratory freshwater washes were used to detach the fauna, which was subsequently collected on a 500 µm sieve. The collection bags were also washed into the sieve to gather any epiphytic fauna that detached during transport. All material retained on the sieve was sorted by species and enumerated with a dissecting microscope.

For data analysis, wet weight epiphytic algal biomass was standardized to a value per gram dry weight of basiphyte. Comparisons between epiphytes on each basiphyte species were made with a 1-way ANOVA and Tukey–Kramer *post hoc* tests using SPSS (SPSS for Windows, Version 11.0.1). A Levene test for homogeneity was performed on all un-transformed data. Data sets not showing homogeneity of variance were Log(n) transformed and the Levene test repeated to confirm homogeneity. The mobile epiphytic fauna was analysed with the multivariate community analysis program ANOSIM in PRIMER (Plymouth Routines in Marine Ecological Research; Primer for Windows, Version 5.2.9. 2002. PRIMER-E Ltd). SIMPER analysis in PRIMER identifies which species generate the most dissimilarity between ‘treatments’. For the SIMPER routine, the raw data were square root transformed and reporting was limited to species with more than 2.5% contribution to dissimilarity. The DIVERSE program in PRIMER was used to calculate

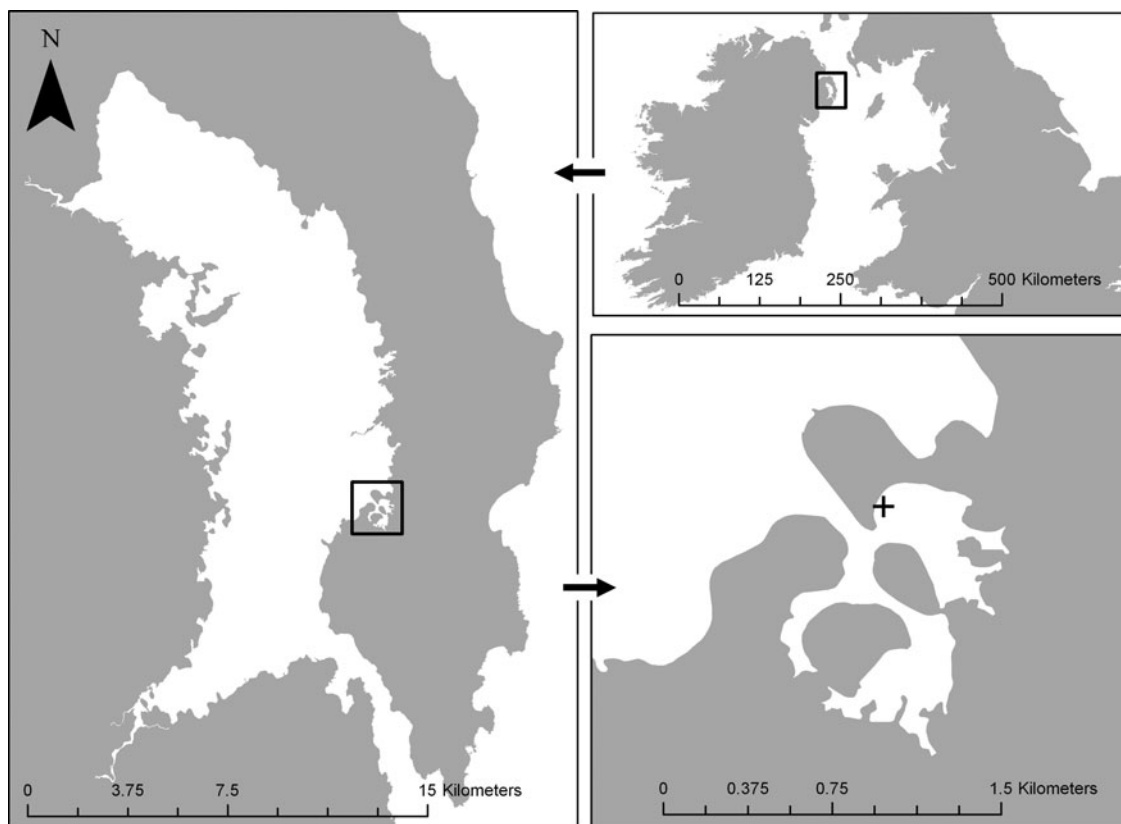


Fig. 1. Maps showing the locations of Strangford Lough in Northern Ireland (within box in top right map), the Dorn in the Lough (within box in left map) and the study site, marked with a cross, within the Dorn (bottom right map).

univariate community descriptive statistics (Clarke & Gorley, 2001). Analysis of these values was also undertaken with ANOVA in SPSS.

### Effect of *Dexamine spinosa* on *Sargassum muticum* and native macroalgae

*Dexamine spinosa* was selected as the experimental mesograzer as it was the most abundant and ubiquitous species on all basiphytes. Clean epiphyte-free tips of *Sargassum muticum*, *Saccharina latissima*, *Fucus serratus* and *Halidrys siliquosa* were obtained from the Dorn in June 2002. *Dexamine spinosa* were collected from the same four species of macroalgae by vigorously washing thalli in buckets of seawater, after which the amphipods were sorted according to species and size.

The experimental units for the grazing preference consisted of sixteen 1 l plastic containers with numerous fine perforations too small to allow loss of amphipods or algal biomass, yet sufficient to allow rapid water exchange. A cutting of each of the four macroalgal species 150 mm in length (~5–7 g wet weight) was placed in each container. In half of the containers (amphipod treatments), six large (6–12 mm) and six small (<6 mm) individuals of *D. spinosa* were added; eight containers were controls without amphipods. This density of amphipods per gram basiphyte was comparable to field observations made earlier. It was necessary for all four species to be placed into each beaker to provide equal access

and choice to the grazers added to them. The total biomass of algae and amphipods per container resulted in only a very low stocking level, hence maintaining high water quality over the 2-week treatments.

Four containers were randomly allocated into each of four vigorously aerated seawater baths containing a large volume of filtered and UV sterilized seawater which effectively made the beakers independent of each other. Seawater was maintained at ~15°C to match seasonal field values and illumination from above by two white fluorescent tubes provided ~75  $\mu\text{mol m}^{-2} \text{s}^{-1}$  in a 12/12 h light/dark cycle. Regular water changes were made throughout the experiment to maintain a high water quality and prevent nutrient limitation. After two weeks the algal tips were carefully blotted dry of surface water and weighed.

It is recognized that by having all four species present in the same containers that the consumption of each is not strictly independent: had replication been greater, one randomly chosen piece of algae from each container would have been selected to overcome this limitation (Pavia *et al.*, 1999).

Paired *t*-tests were carried out on the weights of the macroalgal cuttings before and after the experiment to establish whether there were any significant changes in weights during the experiment. The values were converted to percentage change values and a nested ANOVA was used to test for differences between amphipod and control treatments within an algal species and to determine grazing preference between macroalgal species. Unequal variances (shown by the Levene statistic) were Log(n) transformed.

## Interactions between *Sargassum muticum*, ectocarpoid epiphytes and *Dexamine spinosa*

Sixteen non-reproductive thalli of *Sargassum muticum* were collected from the Dorn (on 4 June 2002), as previously described, and branches (secondary laterals) were taken from the mid-section of each thallus. Epiphytic ectocarpoids and *Dexamine spinosa* were obtained by vigorously washing plants of *S. muticum* in a bucket of seawater; amphipods were sorted according to species and selected with a large diameter pipette. The loosely attached ectocarpoids were easily detached during the washing although other fouling species required extra effort to remove them from the thalli. The same experimental apparatus as used above was used for this series of treatments with twelve perforated containers split between six seawater baths. Each seawater bath was filled with 10 l seawater and vigorously aerated (irradiance and photoperiod were as above). In all containers, water changes were undertaken throughout the experiment to maintain high water quality conditions.

A factorial experimental design (Table 1) was used with *S. muticum* or plastic basiphytes (artificial aquarium plants of a similar architecture to *S. muticum*); each type of basiphyte was present by itself and with amphipods and/or ectocarpoid fouling. In treatments 1 and 2 the effect of amphipods on the basiphyte *S. muticum* is quantified (Table 1). Ectocarpoids on *S. muticum* in treatments 3 and 4 were used to determine the effect of amphipods when ectocarpoids were present. Treatments 5 and 6 used plastic basiphytes to isolate the interaction between epiphytic amphipods and ectocarpoids in the absence of *S. muticum*.

Treatments with amphipods received three large (6–12 mm) and two small (<6 mm) individuals of *Dexamine spinosa* (the density of amphipods differs from the experiment above as densities are standardized to the amount of basiphytic biomass). Treatments with algal epiphytes received approximately 1 g blotted ectocarpoid for each g of basiphyte (*S. muticum* or plastic basiphyte). Ectocarpoids were loosely attached to the basiphyte in a similar fashion to natural fouling observed in the Dorn. At the end of weeks three, five and seven, *S. muticum* and ectocarpoids were carefully separated, blotted and weighed. When returned to the containers, the ectocarpoids were again loosely wound round the laterals of *S. muticum*.

At the end of the experiment in week seven, changes in biomass of the basiphyte and the epiphyte were analysed separately with two-way ANOVA in SPSS. The design of this experiment had to make some compromises on the level of replication so that all of the variables could be examined. The factorial design partially helped to overcome some of these replication-related compromises. For the basiphyte,

**Table 1.** Treatments within the factorial experiment examining the interaction between basiphyte (*Sargassum muticum*), epiphytic alga (ectocarpoid species) and epiphytic fauna (*Dexamine spinosa*).

Treatment	Basiphyte	Ectocarpoids	Amphipods present
1	<i>Sargassum</i>	–	–
2	<i>Sargassum</i>	–	+
3	<i>Sargassum</i>	+	–
4	<i>Sargassum</i>	+	+
5	Plastic	+	–
6	Plastic	+	+

the two-way ANOVA included the presence of the amphipods and the epiphyte as individual factors, as well as the possible interaction between factors. The two-way ANOVA for the epiphyte had the presence of the basiphyte and amphipods as individual factors. Unequal variances (shown by the Levene statistic) were Log(n) transformed.

## Effect of ectocarpoid epiphytes on loss rates in natural *Sargassum muticum* and *Saccharina latissima* stands

To assess the effect of ectocarpoid fouling on the loss rate of basiphytes in the Dorn, four separate rectangular 18 m<sup>2</sup> areas were marked out in the subtidal fringe with similar substratum, depth and water flow and roughly equal proportions of *Saccharina latissima* and *Sargassum muticum*. The numbers of *S. latissima* (N = 167) and *S. muticum* (N = 114) were counted and each thallus was labelled with a small plastic tag inserted through the stipe of the former species and a primary lateral of the latter. Each area was split in half to produce 9 m<sup>2</sup> boxes allocated to either 'fouled' or 'cleaned' treatments. For 'cleaned' treatments, thalli of *S. latissima* and *S. muticum* were cleaned of algal epiphytism by hand each week and thereby kept artificially clear of fouling. In the 'fouled' treatments, thalli were allowed to accumulate ectocarpoid fouling naturally. After 12 weeks, the numbers of labelled *S. latissima* and *S. muticum* were recorded in each box.

The density of thalli in the fouled stands and those in the cleaned treatments were compared after 12 weeks with paired *t*-tests. Two-way ANOVA was used to compare the percentage decline of individuals between fouled and cleaned treatments and between macroalgal species.

## RESULTS

### Epiphytic algae on *Sargassum muticum* and native macroalgae

In the Dorn, fouling by epiphytic algae on *Sargassum muticum* was greatest from March to June, concurrent with the period of greatest growth of *S. muticum*, and declined rapidly in July (Figure 2). Thalli of *S. muticum* became reproductive from July onwards, by which time the epiphytism had almost completely disappeared. Similar observations showed the timing of the epiphytic bloom to be similar for all species of basiphyte considered below.

The amount of epiphytic algae on *S. muticum* was not significantly different from that on *Fucus serratus* and *Halidrys siliquosa* (Figure 3). There was a significantly lower epiphyte biomass on *Saccharina latissima* than that on the three other species of basiphyte examined. Laboratory observations indicated that the fouling biomass was almost exclusively ectocarpoids on all four basiphyte species.

### Epiphytic fauna on *Sargassum muticum* and native macroalgae

All comparisons of the mobile epiphytic fauna between basiphyte species were significantly different (Table 2). Each

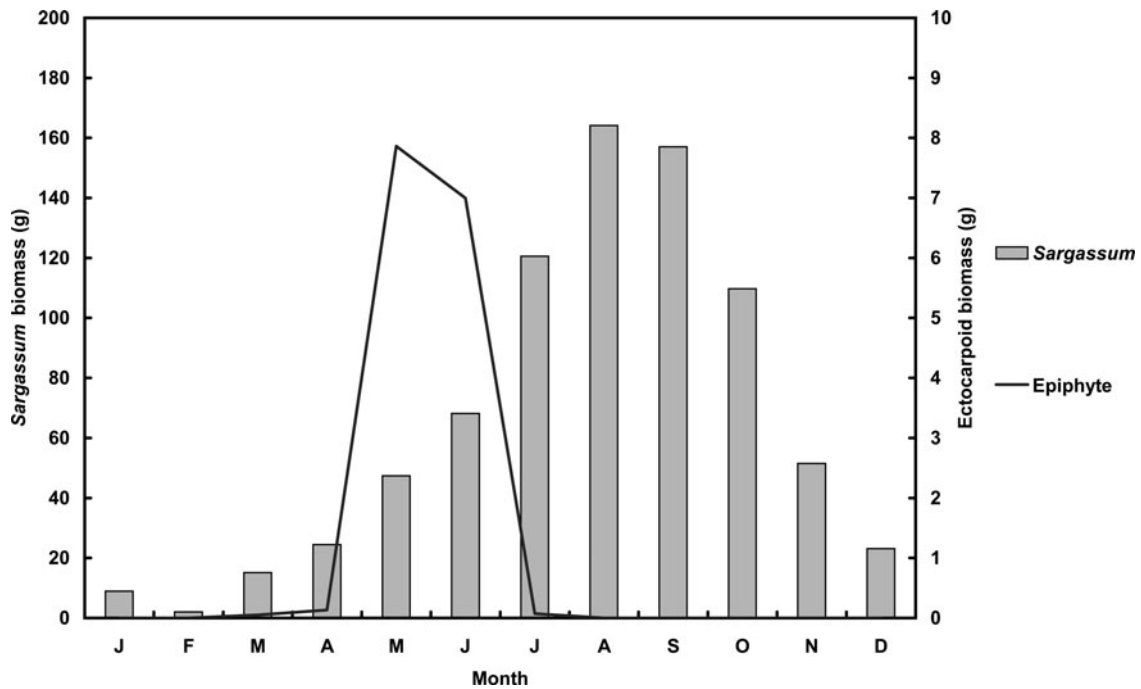


Fig. 2. Wet weight biomass of *Sargassum muticum* and attached epiphytic ectocarpoid epiphytism in 2002 in the Dorn, Strangford Lough; bars are Standard Deviation.

basiphyte species had a characteristic epiphytic faunal community during the period of greatest epiphytic fouling (Figure 4). The assemblages on *S. muticum* and *H. siliquosa* were more strongly clustered with higher levels of community similarity when compared with those found on *F. serratus* and *S. latissima*.

The mean number of mobile epiphytic species did not differ significantly between basiphytes (Table 3). The greatest variation was in the total community abundance (i.e. number of epiphytic individuals per thallus). On average, each *S. muticum* thallus hosted over 900 individuals, much

greater than *H. siliquosa*, *F. serratus* and *S. latissima*, which each supported 50–100 individuals. The species richness values on *S. muticum* were lower than for the other basiphytes, on a per thallus basis (Table 3), due to uneven distribution of the high community abundance among the species (80% of the individuals were one species).

The SIMPER analysis identified eight important epiphytic faunal species that characterize similarity within assemblages on particular basiphyte species and hence differences between basiphyte species (Table 4). There were very high

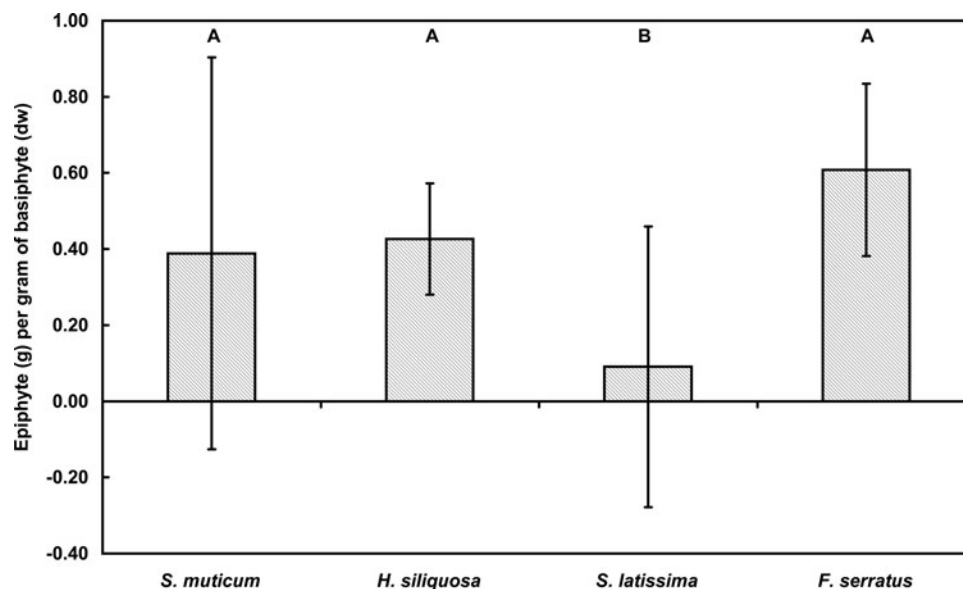


Fig. 3. Total epiphytic algal biomass on three species of native macroalgae and *Sargassum muticum* collected from hard substratum in the Dorn, Strangford Lough. ANOVA (log transformed data) was used to test epiphytic fouling between basiphytes (one-way ANOVA,  $df = 3,19$ ,  $f = 9.831$ ,  $f_{crit} = 3.072$ ,  $P = 0.001$ ). Bars are standard deviations. Letters A and B above bars indicate homogeneous sub-sets as identified by a *post-hoc* Tukey-Kramer tests.

**Table 2.** Pairwise ANOSIM comparisons of epiphytic faunal composition on four macroalgal species collected from the Dorn, Strangford Lough. As there is an element of multiple hypothesis testing, a  $P$  value of 0.008 has been used for the global significance threshold of  $P < 0.05$ .

	R value from one-way ANOSIM (PRIMER)		
	<i>Halidrys siliquosa</i>	<i>Fucus serratus</i>	<i>Saccharina latissima</i>
<i>Sargassum muticum</i>	0.872 $P = 0.001$	0.943 $P = 0.001$	0.762 $P = 0.001$
<i>Halidrys siliquosa</i>		0.903 $P = 0.001$	0.607 $P = 0.002$
<i>Fucus serratus</i>			0.531 $P = 0.001$

ANOSIM, one-way, sample statistic (Global  $R$ ): 0.729,  $P < 0.001$ .

densities of *Dexamine spinosa* (over 700 individuals) on each thallus of *S. muticum* and variable numbers on the other basiphyte species (Table 4). Moderate numbers of *Littorina mariae* and Isopoda were characteristic of *F. serratus* (Table 4). *Saccharina latissima* supported a broad community with many species contributing to similarity, although *Gibbula umbilicalis*, *Corophium volutator* and *Ischyrocarus anguipes* were particularly characteristic. However, the overall abundance of fauna not found on *S. muticum* but present on the other species was very low and inconsistent between the native species.

### Effect of *Dexamine spinosa* on *Sargassum muticum* and native macroalgae

The wet weight of control samples of *F. serratus*, *S. latissima* and *H. siliquosa* increased during the experiment (Figure 5). Control samples of *S. muticum* decreased in weight by 0.05% (Figure 5). In the amphipod treatments *F. serratus* and *H. siliquosa* still increased in weight—this was not statistically different to the controls. Conversely, *S. latissima* declined by approximately 10% when amphipods were present, not significantly different from the control treatment. Samples

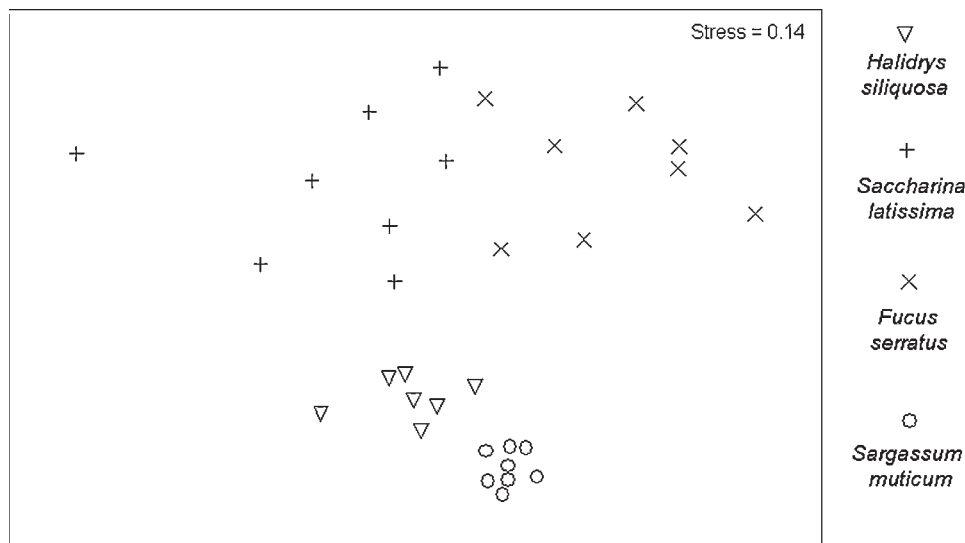
of *S. muticum* grown with amphipods declined by 62% after two weeks, significantly different from control values for this species: observations during the experiment indicated that the leaflets were consumed first and many of the bladders detached. The loss of basiphytic material, in the presence of *Dexamine spinosa*, follows this series: *H. siliquosa* < *F. serratus* < *S. latissima* < *S. muticum*.

### Interactions between *Sargassum muticum*, ectocarpoid epiphytic algae and *Dexamine spinosa*

In the absence of ectocarpoids, *Sargassum muticum* grown without amphipods gained significantly more wet weight than thalli cultured with amphipods, which were consumed as quickly as the algal laterals grew over the experimental period (Figure 6). In the presence of ectocarpoid fouling, the biomass of *S. muticum* remained constant when there were no amphipods but when amphipods were present it decreased throughout the seven-week period (Figure 6), and finally appeared to be mostly consumed. Ectocarpoid biomass placed onto plastic basiphytes without amphipods increased in weight over the 7-week period (Figure 7). When ectocarpoids were present on the plastic basiphytes with amphipods, the biomass remained constant over the experimental period (Figure 7).

### Effect of ectocarpoid epiphytes on loss rates in natural *Sargassum muticum* and *Saccharina latissima* stands

The epiphytized *S. muticum* thalli suffered a mean loss of 70% of the plants, whereas the stand of fouled *S. latissima* thalli experienced a significantly lower (ANOVA) loss of 9% (Table 5). By contrast, in the 'cleaned' treatments, there was no significant change in the plant density of *S. latissima* or *S. muticum* over the 12 week period (Table 5).



**Fig. 4.** Multidimensional scaling plot (PRIMER) of the epiphytic assemblages on *Sargassum muticum* and three native macroalgae collected from the Dorn, Strangford Lough.

**Table 3.** Univariate descriptive statistics for the mobile epiphytic fauna diversity per thallus on four macroalgal species collected from the Dorn, Strangford Lough. All values are per thallus (all thalli weighed 400 g ± 50 g).

Basiphyte	Number of replicate basiphyte thalli	Number of species ±SD	Number of individuals ±SD	Species richness (Margalef) ±SD	Pielou's evenness ±SD
<i>Sargassum muticum</i>	8	6.50 ± 1.41 <sup>a</sup>	906.00 ± 196.80 <sup>a</sup>	0.81 ± 0.20 <sup>a</sup>	0.33 ± 0.12 <sup>a</sup>
<i>Saccharina latissima</i>	8	7.25 ± 3.06 <sup>a</sup>	84.13 ± 58.45 <sup>b</sup>	1.51 ± 0.59 <sup>b</sup>	0.78 ± 0.13 <sup>c</sup>
<i>Halidrys siliquosa</i>	7	6.88 ± 1.64 <sup>a</sup>	96.50 ± 57.38 <sup>b</sup>	1.33 ± 0.36 <sup>b</sup>	0.58 ± 0.18 <sup>b</sup>
<i>Fucus serratus</i>	8	7.00 ± 1.93 <sup>a</sup>	65.125 ± 42.17 <sup>b</sup>	1.51 ± 0.32 <sup>b</sup>	0.77 ± 0.12 <sup>b,c</sup>

Number of species: ANOVA one-way,  $df = 3,28$ ,  $f = 0.317$ ,  $P = 0.813$ ; number of individuals (log transformed): ANOVA one-way,  $df = 3,28$ ,  $f = 25.294$ ,  $P < 0.000$ ; species richness (log transformed): ANOVA one-way,  $df = 3,28$ ,  $f = 6.789$ ,  $P = 0.001$ ; Pielou's evenness: ANOVA one-way,  $df = 3,28$ ,  $f = 18.513$ ,  $P < 0.000$ . Superscript letters are homogeneous sub-sets as identified by *post-hoc* Tukey–Kramer tests.

## DISCUSSION

### Epiphytic algae and fauna on subtidal macroalgae in the Dorn, Strangford Lough

*Sargassum muticum* was heavily epiphytized and grazing by a common and generalist native herbivore was substantial. The peak in fouling algal biomass occurred in May and June within the Dorn. Unlike the findings of most other reports (e.g. Bjæke & Fredriksen, 2003), but as in the Danish study by Thomsen *et al.* (2006), the peak of epiphytism on *S. muticum* was during the period of greatest growth rather than later in the season after reproduction. During this peak in ectocarpoid fouling, the attached epiphytic biomass on *S. muticum* was similar to that seen on the three sympatric species. The biomass of algal fouling was greater on the branched and complex algae, i.e. *S. muticum* and *Halidrys siliquosa*, where their architecture retained loosely attached epiphytic biomass, especially the main bushy ectocarpoid species. It was also interesting that some silt was also associated with the ectocarpoid biomass

that will have exacerbated smothering and shading of the basiphyte. Future work will have to account for the impact from both the epiphytic biomass and the silt bound within the fouling mass.

With regard to the epiphytic fauna, herbivorous amphipods associated with *S. muticum* were exceptionally numerous, which corresponds with previous studies on their habitat preferences and macroalgal structure (Gee & Warwick, 1994; Heckscher *et al.*, 1996; Schmidt & Scheibling, 2007) and is probably related to the complex morphology of the basiphyte. Equally, the complex morphology of *S. muticum* is also likely to trap more suspended sediment and thereby modify the abundance and nature of epiphytic fauna with a detrital component to their diet.

The epiphytic community on *S. muticum* in Strangford Lough was very similar to fauna observed on *S. muticum* by Norton & Benson (1983) at Friday Harbor, Washington, and Viejo (1999) in El Truhan Inlet, northern Spain. Both studies found assemblages characterized by abundant amphipods. However, Norton & Benson (1983) also reported a high abundance of the herbivorous gastropod *Lacuna variegata*, whereas very few epiphytic gastropods were seen on this alga in Strangford Lough. In contrast, thalli of *S. muticum* collected in the Solent from 1975 to 1978 by Gray (1978) had a substantially different epiphytic fauna characterized by sedentary and encrusting filter feeders confined to the older parts of the thallus (Withers *et al.*, 1975). Gray (1978) reported that a few species of amphipods were numerous, with *Gammarus locusta* being the most abundant (up to 150 individuals per thallus), compared to single-species abundances in Strangford Lough that consistently exceeded 700 per thallus. Equally, the analysis of *S. muticum* in Limfjorden (Denmark) by Wernberg *et al.* (2004) also found a rich epiphytic fauna which differed substantially from that found in this study. The differing composition of epiphytic faunal assemblages may be due to environmental and community differences in each area. It is a clear indication also of how biotic pressure from native species can vary throughout the introduced range.

Grazing preference experiments using *Dexamine spinosa* indicate that *S. muticum* was consumed in preference to the native macroalgae, hence thalli provide both habitat and grazing material for this amphipod. Norton & Benson (1983) also reported that several members of the epiphytic fauna at Friday Harbor were herbivorous—grazing experiments confirmed that the abundant gastropod *Lacuna variegata* and the amphipod *Ampithoe mea* consumed substantial

**Table 4.** SIMPER analysis (PRIMER) of the epiphytic faunal communities on four macroalgal species collected from the Dorn, Strangford Lough.

Epiphytic species	Mean number of animals per basiphyte thallus* (percentage contribution to intraspecific basiphyte similarity)			
	<i>Sargassum muticum</i>	<i>Fucus serratus</i>	<i>Halidrys siliquosa</i>	<i>Saccharina latissima</i>
<i>Caprella linearis</i> (Linnaeus)	104.75 (15.48)	7.13 (22.20)	8.38 (15.17)	10.38 (22.20)
<i>Dexamine spinosa</i> (Montagu)	727.75 (65.84)	18.38 (27.59)	68.75 (49.19)	5.50 (11.14)
<i>Littorina mariae</i> (Linnaeus)	9.50 (<5.00)	6.38 (18.43)	1.50 (<5.00)	0.88 (9.87)
<i>Gibbula umbilicalis</i> (da Costa)	0.00 (<5.00)	0.50 (<5.00)	0.00 (<5.00)	1.00 (8.77)
<i>Corophium volutator</i> (Pallas)	0.00 (<5.00)	0.50 (<5.00)	1.50 (<5.00)	2.88 (11.15)
<i>Ischyrocerus anguipes</i> (Kryer)	0.00 (<5.00)	0.25 (<5.00)	0.00 (<5.00)	9.50 (4.21)
Isopoda spp.	0.00 (<5.00)	12.38 (20.39)	0.00 (<5.00)	0.00 (<5.00)
<i>Jassa falcata</i> (Montagu)	43.25 (9.89)	2.63 (<5.00)	4.00 (6.84)	2.00 (<5.00)

\*All thalli weighed 400 g ± 50 g, N = 8.

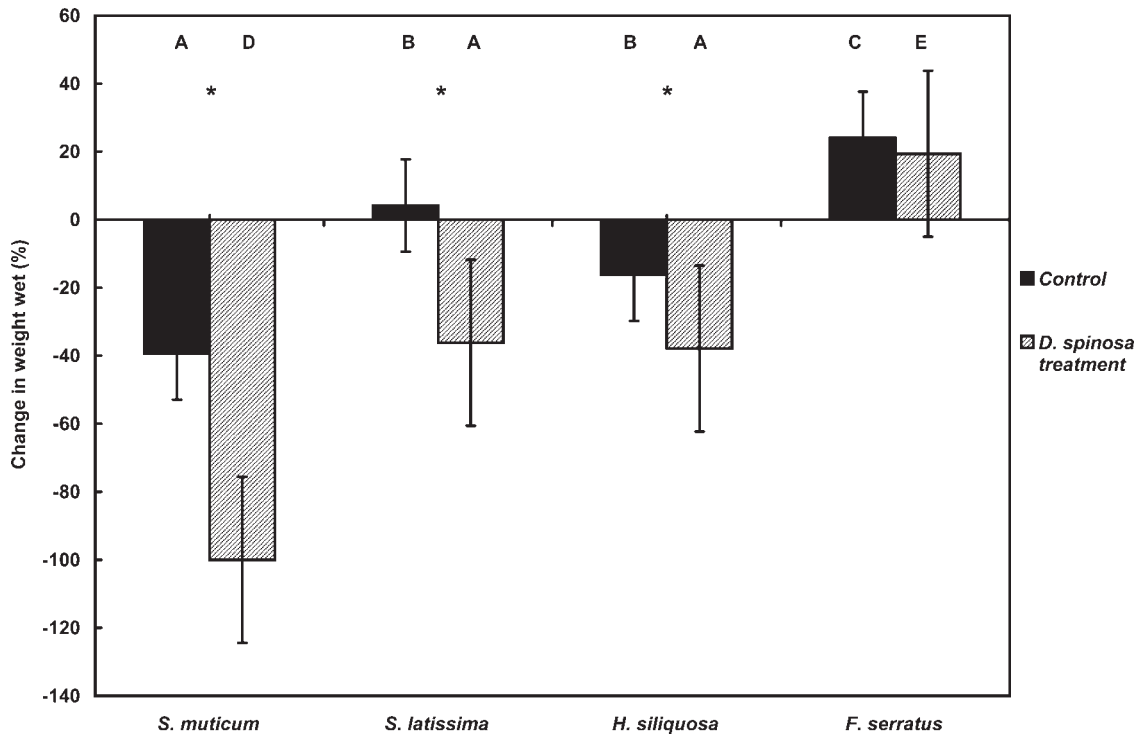


Fig. 5. Percentage change in wet weight of four macroalgal species after two weeks in control (no amphipods present) or amphipod (*Dexamine spinosa*) grazing treatments. Asterisks indicate significant differences (*post-hoc*: Tukey HSD) between amphipod and control treatments within a macroalgal species (two-way ANOVA;  $df = 1, f = 39.405, P = 0.000$ ). Comparisons between seawater baths (nested ANOVA;  $df = 15, f = 1.136, P = 0.352$ ).

quantities of *S. muticum*. Field observations of *S. muticum* by Norton & Benson (1983) revealed that 78% of the primary laterals lacked tips and secondary laterals exhibited progressively more damage away from the apices. Gray (1978), Norton & Benson (1983), Viejo (1999) and Withers *et al.* (1975) have

all documented grazing of *S. muticum* by herbivorous amphipods.

Mesoherbivore feeding preferences vary among macroalgae for several reasons. Commonly, preferences are set by either the concentration or potency of chemical defences in

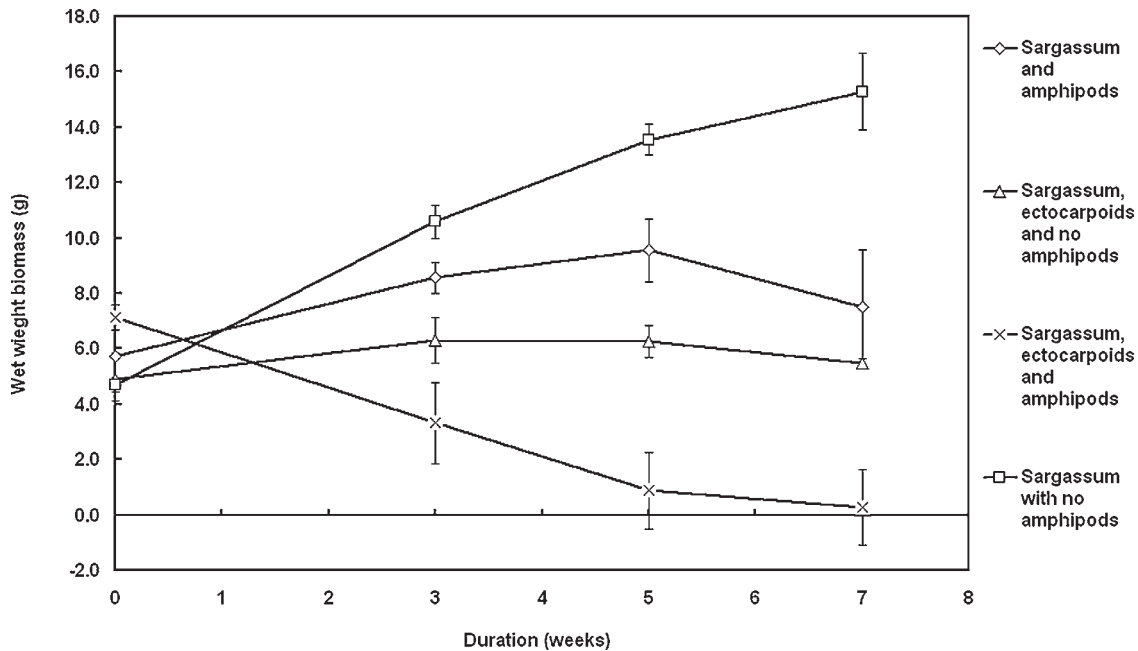
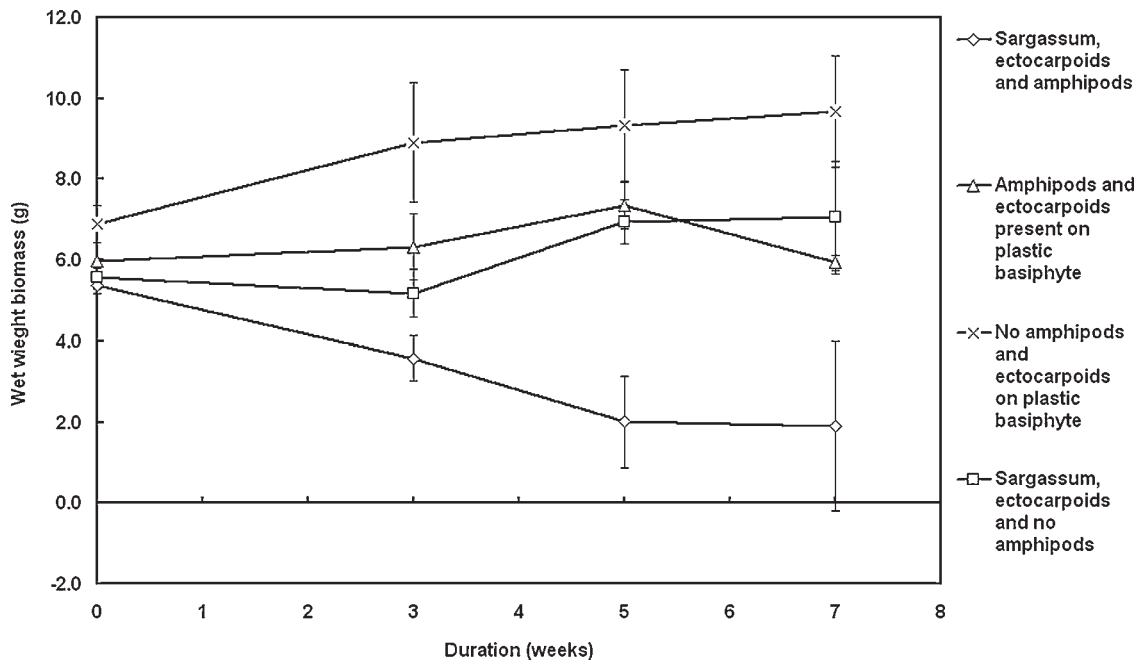


Fig. 6. Effect of *Dexamine spinosa* and ectocarpoid epiphytes on the growth of *Sargassum muticum* in a factorial experimental. Mean ( $\pm$  standard deviation,  $N = 2$ ) wet weight biomass of thalli of *S. muticum* shown. Letter indicates significant difference between treatments at week 7; two-way ANOVA (presence/absence of ectocarpoid),  $df = 1, f = 23.868, f_{crit} = 7.709, P = 0.008$ ; two-way ANOVA (presence/absence of amphipods)  $df = 1, f = 41.070, f_{crit} = 7.709, P = 0.003$ ; interaction  $df = 1, f = 0.971, f_{crit} = 7.709, P = 0.380$ . Power analysis states that replication used will detect differences of 5.00023 g with a power of 0.8.





**Fig. 7.** Effect of *Dexamine spinosa* and basiphyte presence on the growth of ectocarpoid epiphytism. Mean ( $\pm$  standard deviation,  $N = 2$ ) change in the wet weight biomass of ectocarpoid shown. A plastic basiphyte was used for treatments without *Sargassum muticum*. Letters indicate significant difference between treatments; ANOVA two-way (presence/absence of *S. muticum*),  $df = 1$ ,  $f = 9.348$ ,  $f_{crit} = 7.709$ ,  $P = 0.038$ ; ANOVA two-way (presence/absence of amphipods)  $df = 1$ ,  $f = 5.233$ ,  $f_{crit} = 7.709$ ,  $P = 0.084$ ; interaction  $df = 1$ ,  $f = 0.236$ ,  $f_{crit} = 7.709$ ,  $P = 0.652$ . Power analysis states that replication used will detect differences of 5.00023 g with a power of 0.8.

the algal thallus (Hay & Fenical, 1988), local abundance or the nutritional requirements of the mesoherbivore (Cruz-Rivera & Hay, 2001). The density, size and isolation of host basiphytes can also influence the grazing pressure placed upon them. Certain mesograzers will change algal preference depending on the relative abundance of each macroalgal species, hence poorer hosts are often selected over more nutritious ones when they are more abundant (Poore, 2004). The levels of phlorotannin compounds were not measured in this study, but all of the macroalgal species examined are known to contain tannin-like substances (*S. muticum*; Conover & Sieburth, 1964; Glombitza *et al.*, 1982; Hay & Fenical, 1988; Plouguerne *et al.*, 2006). Within single and mixed species treatments, *S. muticum* was preferentially grazed. Cruz-Rivera & Hay (2001) found that the amphipod *Ampithoe longimana* did not rely on mixed macroalgal diets but underwent compensatory feeding (increased consumption of material of a lower nutritional value) to obtain the required

nutritional balance/intake within its diet. The range of herbivore responses to macroalgal foodstuffs is highly varied. Without knowing more about the nutritional and defensive properties of the algae used in this study it is difficult to understand the grazing response. What was apparent from this study is that *S. muticum* was heavily populated with *D. spinosa* and that native biotic resistance from grazing is strong.

### Interactions between basiphyte and epiphytic algae and fauna

The cumulative interactive impact of epiphytic algae and mesoherbivore grazing resulted in the rapid decline of young and non-reproductive *S. muticum* thalli. *Dexamine spinosa* was able to consume both basiphyte and epiphyte, like other epiphytic mesograzers including amphipods (Cruz-Rivera & Hay, 2000; Karez *et al.*, 2000). Although

**Table 5.** Density of *Sargassum muticum* and *Saccharina latissima* stands before and after 12 weeks with and without cleaning of epiphytic ectocarpoid fouling (Dorn, Strangford Lough).

Treatment	Basiphyte species	May 2002: mean no. thalli $m^{-2}$ $\pm$ SD	July 2002: mean no. thalli $m^{-2}$ $\pm$ SD	N	<i>t</i> value	<i>P</i> value	Thalli density loss (%)
Fouled	<i>Sargassum</i>	6.80 $\pm$ 2.33	2.00 $\pm$ 0.56	4	5.24	0.013	70.5 <sup>a</sup>
Cleaned	<i>Sargassum</i>	5.90 $\pm$ 2.11	5.10 $\pm$ 2.00	4	1.95	0.146	13.2 <sup>b</sup>
Fouled	<i>Saccharina</i>	8.60 $\pm$ 3.67	7.80 $\pm$ 3.56	4	3.97	0.028	9.1 <sup>b</sup>
Cleaned	<i>Saccharina</i>	9.90 $\pm$ 4.44	9.50 $\pm$ 4.67	4	2.45	0.092	4.5 <sup>b</sup>

Before and after comparisons of actual thalli density: paired *t*-test two-tailed, critical  $t = 3.182$  at 3 degrees of freedom. Superscript letters: ANOVA two-way (comparisons between fouled and unfouled treatments)  $df = 1$ ,  $f = 129.084$ ,  $f_{crit} = 4.747$ ,  $P = <0.001$  and (comparisons between macroalgal species)  $df = 1$ ,  $f = 104.435$ ,  $f_{crit} = 4.747$ ,  $P = <0.001$ , interaction  $df = 1$ ,  $f = 74.983$ ,  $f_{crit} = 4.747$ ,  $P = <0.001$ . Homogeneous sub-set as identified by *post-hoc* Tukey–Kramer tests.

most mesoherbivores consume the epiphyte in preference to the basiphyte, many species will consume both types of vegetation (Bulthuis & Woelkerling, 1983; Cattaneo, 1983; Duffy & Hay, 2000). Grazers can often switch diet depending on the relative abundance of epiphyte and basiphyte vegetation (Brawley & Fei, 1987) or on the nutritional requirements needed to sustain optimum fitness. The amphipod, *Ampithoe marcuzzii* Ruffo, strongly preferred *Sargassum filipendula* Agardh over the epiphyte, *Ectocarpus siliculosus* (Dillwyn) Lyngbye (Duffy, 1990). Fitness of this amphipod was no greater in a mixed algal treatment (hypothesized to generate greatest fecundity and hence fitness) than when fed on either the basiphyte or epiphyte alone (Cruz-Rivera & Hay, 2000).

Karez *et al.* (2000) documented enhanced negative effects on basiphytes during the interaction between epiphytism and mesograzing, which they termed 'co-consumption'. The epiphytic isopod *Idotea granulosa* consumed significantly more *Fucus vesiculosus* when it was fouled by an epiphyte than when presented as an unfouled basiphyte. Co-consumption may also explain why basiphyte biomass declined so quickly in our experiment when both amphipods and epiphytic algae were in the same culture.

The presence of fouling itself can have many disadvantages for the basiphyte. In culture, when the epiphyte was present on *S. muticum* (no amphipods), there was no net growth of basiphyte suggesting that ectocarpoid fouling had a detrimental effect, possibly through competition for nutrients, dissolved gases and light. Photosynthetic studies of *S. muticum* have revealed that this species requires high irradiance levels (Hales & Fletcher, 1989; Rico & Fernandez, 1997) (approximate saturation at  $700 \mu\text{mol photons m}^{-2} \text{s}^{-1}$ ; Strong unpublished), hence it was presumed that fouling always represented an impact, most likely from shading, and no mutualism would be evident.

Comparison between 'fouled' and 'cleaned' thalli of *S. muticum* and *S. latissima* in the field showed that smothering by ectocarpoids caused a significant loss of thalli of the former species. Field observations also found that fouling was much greater on *S. muticum*, probably due to the complex architecture of the thalli. Individuals of both species were attached to loose rock. The loss of *S. muticum* thalli was probably related to excessive shading and grazing, as well as the high levels of fouling generating more drag, which will have pulled individuals out of the monitored area. The fate of the individuals lost from the experimental site is not known but field observations suggest some were cast high on the shore and died. The occupation of loose substrata by *S. muticum* is characteristic of large areas of Strangford Lough and leads to very high rates of peripatetic movement that may not be seen in other areas of this species distribution (Strong *et al.*, 2005).

The impact of epiphytism in field experiments has been best studied in seagrass habitats. The decline of seagrass beds is particularly likely in nutrient-enriched water, where it is largely caused by the excessive growth of algae on the seagrass blades (McGlathery, 2001). Phytoplankton biomass and total suspended particles also increase in nutrient-enriched water and further reduce light penetration to benthic communities (McGlathery, 2001). Algal fouling of submerged aquatic vegetation has been found to reduce light by 80%, and thereby reduce photosynthesis of some basiphytes below their compensation point (Bulthuis & Woelkerling, 1983; Bronmark,

1985). In Chesapeake Bay *Zostera marina* transplants into areas previously occupied by this species failed to survive, which has been related to seasonal variation in light attenuation and the accumulation of a dense epiphyte layer during late spring (Moore *et al.*, 1996).

In response to the original hypothesis, our results suggest that:

- 1) Ectocarpoid fouling on *S. muticum* was comparable to that on native macroalgae.
- 2) Herbivorous amphipod abundance was much greater on *S. muticum* in comparison with other native macroalgae.
- 3) Basiphytes of *S. muticum* were preferentially consumed by *D. spinosa* over native macroalgae.
- 4) *Dexamine spinosa* consumed both *S. muticum* and ectocarpoid biomass (even when given the option of either vegetation).
- 5) The combination of amphipod grazing and ectocarpoid fouling led to a rapid decline of both *S. muticum* and ectocarpoid biomass.
- 6) Heavy fouling by epiphytic ectocarpoids resulted in thalli loss from natural stands of *S. muticum*.

Both the periodic ectocarpoid fouling and the continuous mesograzing presence represent significant biotic pressures on the population of *S. muticum*, with sizable declines in the density of this species being observed during the bloom period; based on these observations, hypotheses 1, 3 and 4 should be rejected. It is apparent that *S. muticum* is thoroughly exploited as a substratum for epiphytic algae and a food source for epiphytic mesoherbivores. This exploitation represents a serious biotic pressure that generates a thinning mechanism on the invasive population.

Despite being a recent introduction to Strangford Lough, *S. muticum* is under substantial pressure from epiphytic algae and mesoherbivores, probably resulting in a high biotic resistance. On balance of the available data, it is highly likely that extrinsic factors, in the form of ecological release, are only of minor importance in determining the success of *S. muticum* as an invasive species, although interspecific competition between macroalgae cannot be ruled out. It is highly likely that the fundamental intrinsic traits of this species, e.g. fast growth, multiple dispersal mechanisms and high fecundity, ultimately underpin its ability to disperse and invade such large areas of new habitat. Only through the balanced investigation of intrinsic and extrinsic factors of particular invasions can the concepts of invasive traits and habitat invasibility be understood. These studies may also yield interesting insights into the control of established invasion and the mechanisms behind permanent control and naturalization.

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