

Colonisation and modification of soft substratum habitats by the invasive macroalga *Sargassum muticum*

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ABSTRACT: *Sargassum muticum* is an invasive brown macroalga that originates from Japan. In the introduced range, thalli can grow in soft substratum habitats attached to embedded rock fragments and shells. Within Strangford Lough, Northern Ireland, *S. muticum* has rapidly colonised large areas of soft substrata, where dispersal by peripatetic or 'stone-walking' plants is very effective. Sediment cores were collected under and outside canopies of *S. muticum* in Strangford Lough (*S. muticum* first recorded there in 1995) and Langstone Harbour, English Channel (*S. muticum* first found there in 1974) to investigate modification of the infaunal assemblages. At both study sites, community analyses highlighted significant differences between the assemblages under the canopies and those in adjacent unvegetated areas. In Strangford Lough, the invertebrate community under the canopy contained a higher abundance of smaller, opportunistic, *r*-selected species than outside the canopy. By contrast, the communities under and outside the canopy at Langstone Harbour were similar in species composition, diversity and dominance, but overall faunal abundance was greater under the canopy. Sediment characteristics were not affected by *S. muticum* canopies, but the infaunal changes may be related to environmental modification; shading, flow suppression and temperature stratification were also investigated. The differences between these 2 sites indicate that localised conditions and/or the duration of colonisation of *S. muticum* are important in determining the nature of habitat modification.

KEY WORDS: Ecological impacts · Infauna · Introduced species · Langstone Harbour · *Sargassum muticum* · Strangford Lough

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INTRODUCTION

The number of species anthropogenically introduced outside their natural ranges is rapidly increasing (Levin et al. 2002). Although only a very small fraction of transported and introduced species becomes invasive, the ability of these species to restructure and, hence, radically change the functioning of a recipient habitat is great (Crooks 2002). Such is the volume of invasions that this issue is often considered the most severe environmental threat posed globally (Vitousek et al. 1997).

The potential impact on the environment by invasive species regarded as ecosystem engineers, i.e. species with a disproportionate influence on ecosystem functionality that are considered pivotal in habitat creation, destruction and modification (Crooks 2002), is particularly great. Invasive plant species that generate gross changes in the vegetation of an area are often regarded as highly influential ecosystem engineers. Terrestrial examples of the impacts of such species are plentiful (see Crooks 2002 for review), whereas case studies in the marine environment are rarer and often confined to the intertidal zone, e.g. hybrids of the

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cordgrass *Spartina* spp. (Neira et al. 2005), the edible winkle *Littorina littorea* (Bertness 1984) and the green seaweed *Codium fragile* (Levin & Hay 1996, Levin et al. 2002).

In the subtidal zone, submerged aquatic vegetation constitutes a functionally important component of many marine soft-sediment environments (Everett 1994). Vegetation such as seagrasses can profoundly influence animal assemblages by modification of physical, chemical and biological processes within these habitats (Everett 1994, Webster et al. 1998, Attrill et al. 2000, van Houte-Howes et al. 2004). For example, the physical presence of a plant canopy provides shelter and protection from predation for invertebrates and young fish (Summerson & Peterson 1984, Stoner & Lewis 1985, Edgar 1990, Boström & Bonsdorff 1997, De Almeida & Ruta 2000, Norkko et al. 2000, Jackson et al. 2001, Bloomfield & Gillanders 2005). Vegetation also influences localised water flow (Fonseca & Cahalan 1992, van Keulen & Borowitzka 2002), which changes the sedimentation rate and can enhance sediment organic/nutrient content and food availability for infaunal and epifaunal communities (Hull 1987, Reusch & Williams 1999). Consequently, vegetated habitats such as seagrass beds are typically characterised by high primary production, species diversity and faunal abundances (Webster et al. 1998, Bloomfield & Gillanders 2005).

Marine angiosperms have been the subject of many ecological studies on subtidal vegetation (Hemmingga & Duarte 2000). Much less is known about the influence of macroalgae that inhabit similar soft-sediment habitats, despite some of these species being abundant and clearly identifiable as potential ecosystem engineers. In Europe, few attached perennial macroalgae are associated with soft sediments. However, the invasive Japanese species *Sargassum muticum*, which was introduced into the UK in 1974 (Critchley et al. 1983), is an exception. Although restricted to hard substrata in many parts of its introduced European range (Stæhr et al. 2000), it also occupies extensive areas of subtidal soft sediments by growing in dense stands on embedded rock fragments and shells (Critchley 1983, Critchley et al. 1987). Due to its rare ability to colonise both hard and soft substrata, the total area of marine sediments open to occupation by *S. muticum* in Europe and North America is vast, and cumulative habitat modification could be very significant.

Once invasive *Sargassum muticum* has established a canopy over a previously unvegetated soft sediment substratum, there are 3 possible outcomes for the infaunal assemblages under this vegetation: (1) The canopy could reduce the diversity of infaunal and epifaunal communities, as do ephemeral algal blooms of *Ulva* (including *Enteromorpha* spp.; Hayden et al.

2003) that blanket soft substratum habitats (Soulsby et al. 1982, Everett 1994, Valiela et al. 1997, Raffaelli 2000); (2) it might enhance infaunal diversity in a similar fashion to other attached macroalgae (De Almeida & Ruta 2000) and seagrasses; or (3) it might have no detectable effects on the communities. Furthermore, the effects of a particular invasion may change over time. Biological invasion theory (Williamson 1996) suggests that changes in the abundance of invaders can occur (i.e. they become 'equilibrated'), as observed in the pondweed *Elodea canadensis* (Elton 1958) and the zebra mussel *Dreissena polymorpha* (Magoulick & Lewis 2002).

Intriguingly, adult *Sargassum muticum* are reported to be able to disperse within sediments, and further colonise them, by peripatetic 'stone-walking', i.e. peripheral movement induced when the buoyancy of the thallus exceeds the weight of the anchoring stone (Critchley 1981). The rapidly increasing geographical spread of *S. muticum* makes it one of the most striking marine introductions documented (Wallentinus 1999), yet few ecological aspects of the invasion have been investigated, and these only concern its occupation of hard substrata (e.g. Viejo 1997, Stæhr et al. 2000, Britton-Simmons 2004).

The main objective of the present study was to test the hypothesis that a canopy of invasive *Sargassum muticum* over soft sediment will affect infaunal communities in the same manner as macroalgal blooms, reducing diversity and abundance. We tested this hypothesis on both recently established populations (Strangford Lough, Northern Ireland, 5 yr after colonisation), and populations several decades after establishment (Langstone Harbour, southern England, colonised in 1974). Any effects of *S. muticum* canopies on the physical environment were determined in comparison to native macroalgal canopies, i.e. stands of *Laminaria saccharina* that can form over soft sediments when embedded stones are present. The potential ecological significance for soft-sediment communities in Europe and elsewhere was evaluated by addressing the dynamics of soft sediment habitat occupation, including peripatetic colonisation, by *S. muticum* in Strangford Lough at 2 spatial and temporal scales.

MATERIALS AND METHODS

Study sites. Strangford Lough, a large sea-lough with a narrow entrance, is situated on the east coast of Northern Ireland (Fig. 1). *Sargassum muticum* was first recorded in March 1995 at Paddy's Point on the north-western shore (Fig. 1; Boaden 1995). During 1995, 1996, 1997 and 1998, manual clearance operations were undertaken by the Environment and Heritage



Fig. 1. (a) Strangford Lough, Northern Ireland. Inset square surrounds Paddy's Point ($54^{\circ} 32' \text{ N}$, $005^{\circ} 35' \text{ W}$) and oval surrounds the Dorn ($54^{\circ} 26' \text{ N}$, $005^{\circ} 32' \text{ W}$). (b) Langstone Harbour, Portsmouth, England, redrawn from an Ordnance Survey map with inset rectangle surrounding Russell's Lagoon ($50^{\circ} 49.5' \text{ N}$, $001^{\circ} 00.05' \text{ W}$). Land and low water contours shown on both site maps

Service (EHS) Northern Ireland in an attempt to contain the invasion in this Special Area of Conservation (Davison 1999). The infaunal investigation was carried out at Paddy's Point and the study of peripatetic dispersal and modification of the physical environment was performed in a Marine Nature Reserve called the Dorn. This is an inlet on the south-eastern shore of the lough (Fig. 1) which was colonised by *S. muticum* in 1996 (Davison 1999).

Langstone Harbour, on the south coast of England (Fig. 1), is a large tidal bay between Hayling Island and Portsmouth. A narrow entrance protects the harbour from the open sea and small channels link Langstone with Portsmouth and Chichester Harbours. *Sargassum muticum* was first observed in this area in 1974 (Critchley et al. 1983). Russell's Lagoon was selected as the study site (Fig. 1) because it is the only area occupied by *S. muticum* that is shallow enough to sample at low tide without a boat.

Infaunal and sediment sampling. We randomly sampled 3 discrete stands ($>10 \text{ m}^2$) of *Sargassum muticum* at Paddy's Point (Strangford Lough) in August 2000. Sampling at Russell's Lagoon (Langstone Harbour) in July 2001 was carried out in 3 discrete areas within the only continuous stand ($>100 \text{ m}^2$) of *S. muticum*. All of the sampled stands at both sites had similar densities of *S. muticum* thalli (45 to 60 plants m^{-2}) and depth profiles (0.2 to 0.4 m below Mean Low Water of Spring Tides, MLWS). At each site, in each of the 3 *S. muticum* stands/areas, seven 110 mm diameter cores were hap-

azardly located and inserted into the sediment to a depth of 200 mm before being dug out. Haphazard sampling was considered not to introduce bias, as the feature of interest, i.e. the infaunal community, was not evident from the surface. Care was taken to avoid the vegetation and associated epiphytic fauna. From outside each stand/area, 7 infaunal and 7 sediment cores were taken at random points within a strip, at a distance of 1 to 2 m from the perimeter of the stand. The spacing between canopy and non-canopy cores and haphazard sampling follow established nested methods used for seagrass bed analysis (Webster et al. 1998, Frost et al. 1999). One infaunal sample from Russell's Lagoon was lost during sieving.

A sediment core (50 mm diameter) was taken in close proximity to each of the infaunal cores so that there were 21 under-canopy and 21 non-canopy cores at each of the 2 locations, Paddy's Point and Russell's Lagoon.

Laboratory analysis of infauna. Samples were sieved through a 500 μm mesh, fixed in 10% formalin and stained with Rose Bengal (Eleftheriou & Holme 1984). Macrofauna was sorted, identified to species level and enumerated using a dissecting microscope. One Strangford Lough canopy sample was lost. Individual biomass (wet weight) was obtained for each species by group weighing and then dividing by the number of individuals. The average body length was also determined for each species.

Sediment analysis. Granulometric analysis was performed using a Wentworth sieve series (-1.49 to 4.00ϕ)

and median grain size (ϕ), sorting coefficient and silt/clay fraction (%) calculated.

Data analysis. Spatial variation in infaunal community composition within each locality was minimal. There were no significant differences among stands/areas within localities (1-way ANOSIM; Strangford Lough global $R = -0.016$, $p = 0.56$; Langstone Harbour, global $R = -0.022$, $p = 0.54$). Therefore data from stands/areas within a locality were combined to facilitate a further 1-way ANOSIM to compare canopy versus non-canopy samples, after initial square root transformation of the species matrix. The ANOSIM tests were carried out in PRIMER (Plymouth Routines in Marine Ecological Research), a multivariate community analysis program (Clarke & Gorley 2001). SIMPER analysis within PRIMER identified which species generate the most dissimilarity between 'treatments', and thereby highlights significant species substitutions between areas. 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 within PRIMER was used to calculate the univariate community descriptive statistics.

The Infaunal Trophic Index (ITI) was also calculated for each sample and averaged according to factor and location. The purpose of the ITI is to describe the feeding behaviour of soft bottom benthic communities (Word 1979). Species are allocated to 1 of 4 groups based on whether species are suspension or deposit feeders and feed above/on or below the sediment surface. The ITI is calculated by determining the total abundance of the taxa belonging to each of the 4 groups and combining them in the following formula:

$$ITI = 100 - \{33.33 [(0n_1 + 1n_2 + 2n_3 + 3n_4)/(n_1 + n_2 + n_3 + n_4)]\}$$

where $n_1 - n_4$ is the number of individuals of (1) suspension feeders, (2) surface detritus feeders, (3) surface deposit feeders and (4) sub-surface deposit feeders. The numerators in the ITI equation are scaling factors that link feeding categories to levels of organic matter in the sedimentary environment (Pearson & Rosenberg 1978). The predominance of the ITI feeding category, reported as the 'dominant feeding guild', is considered to be indicative of the available organic material in the water and/or substratum (Cromey et al. 2002). The 'ITI score' ranges from 0 to 100 and results can be interpreted as follows: 60.0 to 100.0, community 'normal'; 30.0 to 59.9, community 'changed'; 0.00 to 29.9, community 'degraded'. This functional index is one of the indices adopted by many national monitoring programmes, including the UK National Marine Monitoring Plan (see www.cefas.co.uk/monitoring/page-b3.htm) to assess the biological quality of the benthic environment.

The univariate descriptive statistics and the sediment parameters were analysed with 1-way and 2-way ANOVA using SPSS (Statistical Package for the Social Sciences). DOMPLOT (DOMination PLOT) was used to construct Abundance/Biomass Curves (ABC) and to obtain the W (Warwick) statistic. ABC plots are an extension of k -dominance curves as they include biomass data. The W statistic describes the relationship between the cumulative abundance and biomass curves in the ABC plots (Clarke & Warwick 1994).

Physical effects of canopy. During low tide periods in the Dorn, Strangford Lough, water continuously drains from the tidal pools into the channels. Within these channels, flow is unidirectional and consistent throughout its profile. The channels form natural flumes that were used to assess flow suppression and temperature stratification within stands of *Sargassum muticum* and the native kelp *Laminaria saccharina*. All macroalgal stands studied were at least 4 m in diameter (ground cover) and there was approximately 0.4 m of water at mean low water neaps—at this depth, much of the canopy vegetation was concentrated at the surface of the water. Water movement at low tide was measured with flow meters (model MFP51, Geopacks) upstream of and within canopies (0.2 to 0.3 m below the surface). Five replicated flow readings were collected at the same location at each point in the following sampling design. Inside the canopy, 7 points were haphazardly distributed 1 m in from the upstream margin of the stand. Outside the canopy, 7 points were haphazardly distributed 0.5 m upstream of the margin of the stand. The values were converted into percentage flow reduction and analysed with 1-way ANOVA.

Canopy temperature readings were taken 0.05 m under the water surface and sub-canopy values at the surface of the substratum, 0.3 to 0.4 m from the water surface. When placing any of the probes under a canopy, care was taken not to disturb the vegetation or agitate the water excessively. The probes were allowed to stabilise for 5 min before readings were taken.

Irradiance measurements were made using a photometer (Model Li-189, LI-COR) above and below the canopies of *Sargassum muticum* and *Laminaria saccharina*, and compared to an unvegetated area. Readings were taken on a cloudless day and in a sheltered site, and the order of sampling of different canopies was randomised to minimise the effects of variation in meteorological conditions. All light, temperature and flow measurements were collected on 16 July 2000 starting at 11:30 h GMT.

Substratum occupation by *Sargassum muticum* in Strangford Lough. Distributional surveys of *S. muticum* were carried out in 1996, 1998 and 2000 by EHS and in 2002 by us. The subtidal fringe of the entire lough

shoreline was searched on foot or by boat and the length of shoreline occupied by *S. muticum* colonies was determined using either a hand-held GPS or map triangulation. The shore occupied by *S. muticum* has been expressed as a linear measure because this species is confined to a narrow vertical range in Strangford Lough. Based on original field documents and subsequent surveys, all the shoreline occupied by *S. muticum* was assigned to one of 3 types of substratum: (1) a predominantly soft substratum with $\leq 5\%$ embedded loose rock; (2) mixed small loose rock on a mud/sand base; or (3) immobile bedrock, boulder or cobble substratum.

Peripatetic colonisation and dispersal. To establish the importance of peripatetic colonisation of new habitat, a 12 m \times 2 m subtidal section of the northern shore of the Dorn was marked and all *Sargassum muticum* thalli in it were counted and removed in June 2000. From June to October 2000, the number of peripatetic thalli found in the cleared area was counted weekly.

A second experimental plot was used to assess the dispersal range of peripatetic plants of *Sargassum muticum* in Strangford Lough. For this, we selected 2 sites in the Dorn. One site with a sandy substratum was exposed to strong tidal currents; the other was sheltered from currents, with a muddy sand substratum,

Table 1. SIMPER analysis (in PRIMER) of the infaunal community under and outside canopies of *Sargassum muticum* in Strangford Lough, with dissimilarity cut-off set at 2.5% (square root transformation used for analysis). Abundance expressed as individuals per core; values in parentheses are % contribution to within-treatment similarity. The mytilid was probably *Modiolus modiolus*

Species	Mean abundance		Contribution to dissimilarity (%)
	Under canopy	Outside canopy	
Mytilid (juvenile)	102.00 (11.95)	14.64 (2.02)	21.92
<i>Tubificoides pseudogaster</i>	18.96 (5.80)	13.21 (5.62)	10.71
<i>Scoloplos armiger</i>	4.37 (4.43)	11.29 (5.96)	10.26
<i>Ophelia rathkei</i>	3.78 (2.75)	7.79 (11.09)	6.38
<i>Pygospio elegans</i>	4.15 (0.57)	5.57 (3.79)	5.69
<i>Dexamine spinosa</i>	6.04 (3.22)	0.57 (0.50)	4.95
<i>Capitellides giardi</i>	2.44 (0.73)	3.43 (1.83)	4.72
<i>Scololepis foliosa</i>	1.48 (1.69)	3.39 (1.69)	3.74
<i>Rissoella diaphana</i>	4.11 (1.38)	4.43 (0.54)	3.48
<i>Nicomache lumbricalis</i>	0.56 (1.34)	2.00 (1.34)	2.59

and perpendicular to the first site. In May 2002, a random point was generated for both sites and marked with an angle-iron post. At each site the 30 individuals of *S. muticum* closest to the post, but not attached to bedrock, were individually numbered with slightly buoyant surface markers (5 cm² bubble wrap squares: Aid-Pack). The floats were attached to the holdfast with fishing line and were small enough not to contribute to the drag or buoyancy of the peripatetic individuals. The peripatetic dispersal of each labelled individual from the initial start point was measured with a tape measure every 2 wk for 2 mo, and all distances travelled are provided along with summary statistics (Table 8).

RESULTS

Infaunal communities under and outside *Sargassum muticum* canopies in Strangford Lough

Multivariate analysis of the species matrix revealed a significant difference between infaunal samples taken under and outside the canopies of *Sargassum muticum* (1-way, ANOSIM $n = 20$, $p = 0.038$). This difference is highlighted by the MDS (multi-dimensional scaling) plot that shows the majority of unvegetated (no canopy) samples to the right of the plot and the majority of canopy samples clustered to the left of the plot (Fig. 2a). A relatively high level of overall dissimilarity between canopy and non-canopy samples (69.1%) was found with the SIMPER analysis. Table 1 lists the species that contributed the greatest amount of dissimilarity between the treatments. The most numerically important were the juvenile bivalves (probably *Modiolus modiolus*) present in greater numbers under the canopy, whereas species such as the polychaetes

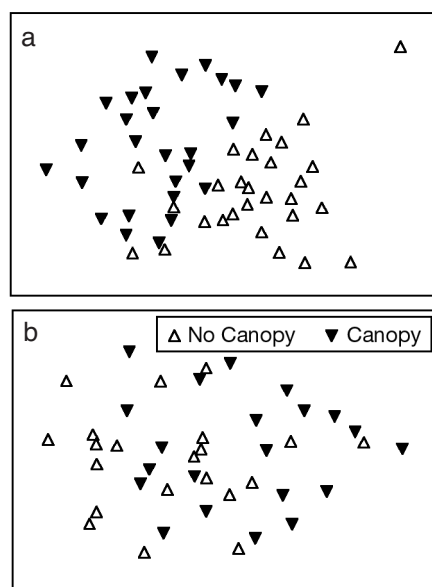


Fig. 2. Multidimensional scaling plot (PRIMER) for infaunal cores collected under (▼) and outside (△) canopies of *Sargassum muticum* at (a) Paddy's Point, Strangford Lough (stress 0.21) and (b) Russell's Lake, Langstone Harbour (stress 0.15)

Scoloplos armiger and *Ophelia rathkei* were more abundant outside the canopy (Table 1).

There were no differences in either the mean number of species or the abundance of individuals sampled from under and outside the canopies (Table 2). Several other characteristics differed significantly, however (Table 2). Samples taken from under a canopy were, on average, 20% lower for Shannon diversity and Pielou's evenness, but had a higher level of community dominance (Simpson's index). The mean body length of the infauna was almost twice as great outside than under a canopy (Table 2). The ABC for the canopy samples generated a negative *W* statistic (Table 2), i.e. the cumulative abundance curve (not shown) was well above the cumulative biomass curve. For samples from outside the canopy the ABC for cumulative abundance was just above the biomass curve, so that the *W* statistic was positive.

Table 2. Descriptive community statistics and sediment characteristics (mean \pm SD) for core samples taken under (n = 20) and outside (n = 21) canopies of *Sargassum muticum* in Strangford Lough. Data analysed using 1-way ANOVA. Dominant feeding guild: (1) suspension feeders, (2) surface detritus feeders, (3) surface deposit feeders and (4) sub-surface deposit feeders

Parameter	Under canopy	Outside canopy	p	F
Total species	15.03 \pm 3.6	15.39 \pm 4.7	0.780	0.079
Total abundance (ind.)	160.54 \pm 209.35	86.36 \pm 74.4	0.071	3.384
Shannon diversity	1.84 \pm 0.57	2.17 \pm 0.25	0.006	8.052
Pielou's evenness	0.69 \pm 0.22	0.81 \pm 0.60	0.008	7.594
Simpson's dominance index	0.29 \pm 0.21	0.17 \pm 0.04	0.005	8.447
Infaunal Trophic Index score	54.21	34.42	0.001	12.579
Dominant feeding guild	2.52	3.12	0.010	7.126
Mean body length (mm)	8.06 \pm 4.73	15.64 \pm 7.04	0.000	22.631
<i>W</i> statistic	-0.095 \pm 0.13	0.072 \pm 0.23	4.259	5.568
Median grain size (ϕ)	1.82 \pm 0.22	1.81 \pm 0.27	0.866	0.029
Sorting coefficient	0.72 \pm 0.23	0.79 \pm 0.23	0.312	1.052
Silt/clay fraction (%)	0.63 \pm 0.45	0.78 \pm 0.62	0.371	0.819

Table 3. SIMPER analysis (in PRIMER) of the infaunal assemblages under and outside a canopy of *Sargassum muticum* in Russell's Lagoon, Langstone Harbour, with dissimilarity cut-off set at 2.5% (square root transformation used for analysis). Abundance expressed as individuals per core; values in parentheses are % contribution to within-treatment similarity

Species	Mean abundance		Contribution to dissimilarity (%)
	Under canopy	Outside canopy	
<i>Cirriiformia tentaculata</i>	162.81 (41.71)	104.05 (49.80)	22.66
<i>Tubificoides pseudogaster</i>	27.14 (7.19)	18.00 (7.20)	12.00
<i>Tubificoides bendini</i>	31.67 (9.22)	21.33 (9.10)	10.94
<i>Corophium</i> sp.	3.52 (0.62)	1.67 (0.47)	6.48
<i>Capitellides giardi</i>	2.67 (0.19)	1.38 (0.34)	6.48
<i>Capitella capitata</i>	1.86 (0.18)	0.43 (0.07)	4.89
Terebellid	1.05 (0.09)	0.67 (0.09)	4.21

The dominant feeding guild calculated from the ITI analysis indicated that both surface detritus feeders and surface deposit feeders were equally abundant under the vegetation. By contrast, in unvegetated areas, the assemblages had a greater proportion of surface deposit feeders. Samples from under and outside the canopy were classified by the ITI score as having been collected from a 'changed' community.

Infaunal communities under and outside *Sargassum muticum* canopies in Langstone Harbour

There was a significant difference between macro-invertebrate communities under and outside the canopy of *Sargassum muticum* (1-way ANOSIM, $p = 0.04$). However, SIMPER analysis reported a relatively low level of dissimilarity (32.7%) between canopy and non-canopy samples. This dissimilarity appeared to be driven by a consistently higher animal abundance under the canopy than outside (Table 3). The MDS plot shows only slight separation of canopy and non-canopy samples (Fig. 2b).

Univariate analysis of the communities indicated that infaunal samples from under the canopy contained significantly more individuals (Table 4). No other univariate community statistic differed significantly between treatments and the *W* statistics obtained from ABC plots did not differ either (Table 4). Surface deposit feeders were the dominant trophic guild in both vegetated and unvegetated samples.

Sediment characteristics

Sediment composition (median size, sorting or silt/clay fraction) was not affected by the presence of a canopy of *Sargassum muticum* in either Strangford Lough (Table 2) or Langstone Harbour (Table 4).

Modification of physical environment by macroalgal canopies

In an unvegetated habitat, 89% of sub-surface irradiance penetrated to the substratum at low tide (depth 0.35 m), whereas under algal canopies this value was less than 5% (Table 5).

Table 4. Descriptive statistics for the community structure and sediment characteristics (mean \pm SD) under ($n = 21$) and outside ($n = 21$) a canopy of *Sargassum muticum* in Russell's Lagoon, Langstone Harbour. Data analysed using 1-way ANOVA. Dominant feeding guild: (1) suspension feeders, (2) surface detritus feeders, (3) surface deposit feeders and (4) sub-surface deposit feeders

Parameter	Under canopy	Outside canopy	p	F
Total species	8.62 \pm 2.71	7.48 \pm 2.06	0.132	2.363
Total abundance (ind.)	235.19 \pm 133.89	151.43 \pm 103.27	0.029	5.153
Shannon diversity	1.00 \pm 0.28	0.99 \pm 0.22	0.906	0.014
Pielou's evenness	0.47 \pm 0.11	0.51 \pm 0.10	0.328	0.981
Simpson's dominance index	0.48 \pm 0.08	0.48 \pm 0.06	0.976	0.001
Infaunal Tropic Index score	46.82	47.71	0.736	0.115
Dominant feeding guild (ITI)	2.95	2.95	0.999	0.000
Mean body length (mm)	121.72 \pm 24.48	124.42 \pm 16.87	0.727	0.124
W statistic	0.14 \pm 1.23	0.13 \pm 1.23	0.896	0.017
Median grain size (ϕ)	3.20 \pm 1.23	2.84 \pm 1.30	0.721	0.130
Sorting coefficient	4.30 \pm 1.32	3.76 \pm 1.29	0.162	2.087
Silt/clay fraction (%)	3.28 \pm 0.83	3.19 \pm 0.99	0.806	0.061

Table 5. Irradiance (mean \pm SD) and its attenuation under 2 species of macroalgae and in an unvegetated area in the Dorn, Strangford Lough (moderately sunny day without cloud cover in June 2000). Superscript letters indicate significantly different (ANOVA, 1-way, $p < 0.001$; $F_{4,150} = 7016.191$) sub-groups as identified by a Tukey-Kramer test; na: not applicable

Sensor location (depth)	Mean irradiance \pm SD ($\mu\text{mol photons m}^{-2} \text{s}^{-1}$)	Light absorption relative to unvegetated near-surface value (%)
Out of water ($n = 35$)	2595 \pm 3.7	na
Unvegetated area ($n = 35$); near surface (0.15 m)	1129 \pm 1.2 ^a	na
Unvegetated area ($n = 35$); at substratum (0.35 m)	1008 \pm 9.1 ^b	10.7
<i>Laminaria saccharina</i> stand ($n = 35$); at substratum (0.35 m)	49 \pm 9.8 ^c	95.6
<i>Sargassum muticum</i> stand ($n = 15$); at substratum (0.35 m)	31 \pm 8.9 ^d	97.2

Table 6. Flow suppression and thermal stratification within canopies of *Sargassum muticum* and *Laminaria saccharina*, based on 15 measurements under each condition. T: temperature; F: flow. *Data analysed using 1-way ANOVA where applicable; na: not applicable; nd: no data

	Sensor depth (m)	Reduction in water velocity (%)			Temperature ($^{\circ}\text{C}$)		
		Mean \pm SD	p	$F_{1,14}$	Mean \pm SD	p	$F_{1,14}$
Unvegetated areas at surface	0.05	na			12 \pm 0.4		
Within <i>Laminaria saccharina</i> canopy	T: 0.05; F: 0.30	74.6 \pm 26.8	0.419	0.717*	14 \pm 3.1	0.016	6.639*
Below <i>Laminaria saccharina</i> canopy; at substratum surface	0.35	nd			12 \pm 0.6	0.432	0.634*
Within <i>Sargassum muticum</i> canopy	T: 0.05; F: 0.30	84.0 \pm 39.7	0.115	0.736	23 \pm 5.0	<0.001	151.536*
Below <i>Sargassum muticum</i> canopy; at substratum surface	0.35	nd			10 \pm 0.7	<0.001	260.693*

Canopies of *Sargassum muticum* absorbed 97.2% of the sub-surface irradiance, compared to 95.6% for *Laminaria saccharina* canopies ($p < 0.001$) (Table 5). Suppression of current flow by *S. muticum* was not significantly different from that by *L. saccharina* (Table 6). A 2 $^{\circ}\text{C}$ warming was apparent in the canopy of *L. saccharina* when compared to the ambient seawater in unvegetated areas. Warming within the canopy of *S. muticum* was much greater, with the water temperature elevated by 11 $^{\circ}\text{C}$ above ambient. Unlike for *L. saccharina* canopies, evidence of a significant cooling to 2 $^{\circ}\text{C}$ below ambient was observed under the canopy of *S. muticum*.

Substratum occupation by *Sargassum muticum* in Strangford Lough

The total shoreline colonised by *Sargassum muticum* lengthened from 0.61 km in 1996 to 12.86 km in 1998 (Table 7). This increase was mainly due to a greater occupation of habitats with loose rock on a soft sediment base. From 1998 to 2000, although the colonised shoreline increased more than 3-fold, the relative proportions of each substratum type remained the same, 97% of the occupied shoreline being mobile, soft substrata. Between 2000 and 2002, the length of shoreline occupied decreased by nearly 50%, mostly by loss from soft rather than hard substrata. Despite this, 93% of the shoreline occupied was still loose rock on soft sediment (Table 7).

Table 7. Substratum type colonised by *Sargassum muticum* in Strangford Lough, Northern Ireland, in 1996, 1998, 2000 and 2002

Substratum	Length in km of shore colonised (% shoreline with substratum type)			
	1996	1998	2000	2002
Predominantly soft substratum with ≤5% embedded loose rock	0.46 (76)	2.27 (18)	7.66 (16)	0.53 (0.02)
Mixed small loose rock on mud/sand base	0.15 (24)	10.17 (79)	38.78 (81)	26.60 (93)
Immobile bedrock, boulder and cobble substratum	0 (0)	0.42 (3)	1.44 (3)	1.37 (5)
Total length of subtidal fringe colonised (km)	0.61	12.86	47.88	28.5

Peripatetic colonisation in the Dorn, Strangford Lough

The results summarised here are for the experiment concerning recolonisation of a cleared patch. In the monitored 24 m² subtidal section of the Dorn, the density of *Sargassum muticum* thalli before clearance in June 2000 was 14.48 plants m⁻². After 2 mo, a mean of 6.20 peripatetic thalli m⁻² had moved into the cleared site, replacing nearly half of the individuals removed. All of the newly arrived thalli within the cleared area were reproductive. At the end of September, the number of accumulated peripatetic thalli declined rapidly; field observations indicated that stormy weather was causing individuals to be stranded higher up the shore.

Determination of the distances travelled by peripatetic thalli showed that at sites characterised both by high (Site A) and low (Site B) water motion, the majority of plants remained stationary (Table 8). For those that did move, the average distances travelled at the 2 sites were similar, i.e. 4.2 m at Site A and 2.2 m at Site B. The maximum dispersal recorded at both sites was 34 m and all of the peripatetic movement was in one direction along the shore, corresponding to the residual tidal currents in the Dorn. Approximately 9 to 12% of the individuals were lost, either because they moved outside the study area or were cast up on the strandline.

Table 8. *Sargassum muticum*. Dispersal (distance from initial position, m) of peripatetic macroalgae over a 2 mo period in high tidal flow (Site A) and low tidal flow (Site B) habitats in the Dorn, Strangford Lough. Data analysed using 1-way ANOVA; $p = 0.344$, $F_{1,40} = 0.918$

	<0.5	0.5–0.9	1.0–4.9	5.0–15.0	15.1–30.0	>30.0	Lost	Mean ± SD
Site A	13	1	4	0	0	2	2	4.23 ± 9.97
Site B	18	2	1	0	0	1	3	2.23 ± 7.13

DISCUSSION

Effects of macroalgal canopies on infaunal communities

Univariate indices and multivariate community analysis of the infauna revealed significant differences between the assemblages under and outside canopies of *Sargassum muticum* in both Strangford Lough and Langstone Harbour. In Strangford Lough, the infaunal community under a canopy of *Sargassum muticum* was of a lower diversity and was characterised by a greater abundance of numerically dominant small organisms than the non-canopy community. The negative W statistic and the finding that many of the abundant species (e.g. *Tubificoides pseudogaster* and *Capitellides giardi*) under the canopy are opportunistic r -selected species (Pearson & Rosenberg 1978) also reflected the predominance of small yet abundant species. Furthermore, the greater dominance of surface detritus feeders under these conditions is consistent with the localised primary production.

The larger body size in the non-canopy community is an indicator of a stable habitat, in which disturbance is infrequent and the infauna are skewed towards K -selected strategies. K -selected species are rarely numerically dominant, but are foremost in terms of biomass (Clarke & Warwick 1994). When a community is perturbed, K -selected species are less favoured, and opportunistic r -selected species quickly proliferate (Clarke & Warwick 1994), so the enhancement of r -selected species below the canopy suggests that this assemblage was under some form of 'stress'. These results therefore support the hypothesis that a newly established canopy of the invasive macroalga *Sargassum muticum* will reduce the diversity and abundance of infaunal communities under this vegetation.

In Langstone Harbour, the differences observed between assemblages under and outside the canopy were fundamentally distinct to those found in Strangford Lough. Under the canopy, species composition remained the same and yet abundance increased substantially, which did not change the assemblage diversity, dominance, community trophic status or evenness between canopy and unvegetated areas.

Within the present study, evidence from separate locations both supports and opposes the initial hypothesis that a canopy of invasive *Sargassum muticum* over soft sediment will decrease the diversity and abundance of infaunal communities. Therefore the generality of the initial premise for both sites must be rejected. In Strangford Lough, the less diverse infaunal assemblage under the canopy suggests that some aspect of the introduced vegetation, either directly or indirectly, perturbs this community. By contrast, the Langstone Harbour infaunal community showed no signs of perturbation; rather, the presence of a canopy of *S. muticum* appeared to have enhanced the faunal abundance of the resident assemblage. It is clear that the presence of *S. muticum* does influence infaunal communities. However, perhaps due to site-specific differences between Paddy's Point and Russell's Lagoon, such as the smaller particle size, increased sorting and silt/clay fraction at the latter and other biotic and abiotic factors, the influence of this introduced vegetation can vary. The differing particle size at the 2 sites will undoubtedly result in differing infaunal composition, but it is the differences within a site between vegetated and unvegetated areas that are interesting in highlighting localised responses of the infaunal assemblages to *S. muticum*. The duration of occupation by *S. muticum* may be another factor. In Langstone Harbour, *S. muticum* has been present since 1974, providing more time for the native assemblages to potentially adapt to and ultimately exploit the presence of, and processes associated with, this species.

Our findings have several features in common with those of Neira et al. (2005), who examined the impact of hybrid invasive *Spartina* spp. at 3 intertidal areas in San Francisco Bay. As with the present study, changes in the infaunal community between vegetated and unvegetated areas differed between sites. The reason for the lack of consistency was related to either the duration of *Spartina* spp. occupation at the sites (ranging from 10 to 30 yr) or specific differences in the topography and sediment mediating the presence of *Spartina* spp. in differing ways. In accordance with the conclusions of Neira et al. (2005), only continuing temporal surveillance in Strangford Lough can test whether the impact of invasive species declines with time.

Influences of vegetation on the physical environment

One of the objectives of our study was to elucidate the causes of any changes in the infauna by establishing whether *Sargassum muticum* had modified the physical environment. The finding that sediment parti-

cle size characteristics did not differ between canopy and non-canopy habitats at either Strangford Lough or Langstone Harbour is surprising considering that there was strong flow suppression. However, unlike *S. furcatum* and seagrass communities, which show similar levels of water baffling but modify associated sediments (De Almeida & Ruta 2000, van Keulen & Borowitzka 2002), *S. muticum* sheds its canopies annually, leaving only the perennial holdfasts. This cycle leaves the sediment exposed for approximately 4 to 5 mo each year, during which time wave action and currents could re-suspend and remove sediment accumulated in the vegetated phase. The effects on infauna associated with the presence of invasive algal canopies in Strangford Lough were therefore not due to changes in sediment characteristics.

The canopy of *Sargassum muticum* had major effects on other aspects of the local environment, however. It had a strong shading effect, as previously observed (Critchley et al. 1990, Curiel et al. 1998), significantly greater than the native *Laminaria saccharina*. When one considers that in a native canopy less than 5% of the light reaches the sub-canopy, the extra 2% absorption by *S. muticum* actually represents an approximate 40% loss of the available light for the sub-canopy macroalgae.

Stands of *Sargassum muticum* in Strangford Lough caused strong temperature stratification including significant cooling of the water just above the sediment, as recorded in Lake Grevelingen, The Netherlands (Critchley et al. 1990). The extreme heating of the water associated with the surface canopy is typically restricted to a thin layer at the very surface of the water. Within the sheltered environment of Strangford Lough, the high density of *S. muticum* tends to prevent the water within the stands of vegetation from being exchanged with non-canopy areas. In addition, the dark colour of the canopy absorbs much of the light, and on a sunny day the stagnant water can become extremely warm. Such stratification did not occur in *Laminaria saccharina* beds, perhaps due to the lower standing biomass and because the vegetation does not 'interlock' as it does for *S. muticum*.

The temperature stratification documented in canopies of *Sargassum muticum* raises some interesting questions about the interaction of the warming and the physiology of this species. Norton (1977) found that the optimum temperature for growth of *S. muticum* was 25°C, and that this species was also tolerant of temperatures up to 30°C. One could hypothesize that this localised warming within the canopy might actually benefit *S. muticum* and increase its growth rate. Bouts of increased warming within the canopy may also have an impact on the extent of epiphytic colonisation by less tolerant species, for example by reducing the

fouling burden on *S. muticum*. To what extent the temperature stratification and flow suppression/water exchange persist over a tidal cycle and the implications of these factors for the infaunal community may form hypotheses for future work.

Occupation of soft-sediment habitats

Clearly, peripatetic dispersal ('stone-walking') is unlikely to be a significant factor in reported range extensions in *Sargassum muticum* of 10 to 45 km yr⁻¹ (Wallentinus 1999). However, in Strangford Lough, peripatetic dispersal contributes significantly to the rapid consolidation and, hence, invasiveness of this species. In the sheltered confines of Strangford Lough, the mean distance travelled (about 3 m in 2 mo) was not great, yet the quantity of peripatetic individuals was large enough to repopulate half of the original density in cleared sites after just 2 mo. Plants that stone-walked between July and September were reproductive and releasing propagules, so even if they were lost from favourable habitat after storm events, the released germlings ensured that the site would still be invaded. Since its first appearance in Strangford Lough 5 yr before, *S. muticum* had colonised nearly 50 km of shoreline, most of it consisting of small loose rock on a muddy sand base not previously occupied by macroalgae. Peripatetic dispersal during the growing season is also involved in the spread of the highly invasive *Codium fragile* subspecies *tomentosoides* (Ben-Avraham 1971, Dromgoole 1990).

Implications for soft-sediment communities in Europe

Sargassum muticum has successfully invaded 12 European coastal countries and produced a near-continuous distribution from Sweden to Portugal, including the British Isles, and into the Mediterranean Sea (Wallentinus 1999). The process of colonisation also continues into Pacific North America and the southern hemisphere. The unusual ability to colonise predominantly soft substrata has undoubtedly allowed this species to spread quickly, become extremely abundant and hence develop sufficient biomass to qualify as an ecosystem engineer and generate significant habitat modification.

Although often overlooked when considering the environmental impact of *Sargassum muticum*, the extensive colonisation of unvegetated soft-sediment habitats has both generated a new epibenthic habitat and modified the resident infaunal assemblages at 2 contrasting study sites. Interestingly, the resulting

influence of this species was found to differ between sites, ranging from a strong perturbation to a moderate enhancement of infaunal density. This could suggest that strong site-specific effects of *S. muticum* make generalizations about the impact of this species difficult. Nonetheless, the possibility that the long-term residence of *S. muticum* changes the nature of the influence of this species cannot be excluded. Continued surveillance within Strangford Lough could establish whether site-specific differences or the duration of colonisation is more important for determining the nature of habitat modification.

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