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Epifaunal composition and fractal dimensions of intertidal marine macroalgae in relation to emersion

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The effect of tidal emersion on the epifauna of three common British intertidal macroalgae, *Cladophora rupestris* (Chlorophyceae), *Laminaria digitata* (Phaeophyceae) and *Fucus serratus* (Phaeophyceae) was investigated. Tidally-induced migration of intertidal fauna is well documented, but the aim of this study was to determine the effect of algal complexity on the degree of change in epifaunal community structure between tidal states. The structural complexity of each algal species was determined by measuring the fractal dimension (D) of algal outlines (1.76, 1.23 and 1.11 respectively for the three species). In the case of *L. digitata*, a weighted value for D was used to take account of the varying morphologies of the holdfast, stipe and blade. The hypotheses tested were: (i) that increased algal fractal complexity is associated with increased abundance and diversity of associated epifaunal communities; (ii) that community composition is significantly reduced during emersion in intertidal algae (due to faunal migration); and (iii) that the degree of migration due to the receding tide is significantly reduced in more geometrically complex algae. Overall, faunal communities associated with *C. rupestris* were significantly more abundant and diverse than those associated with the other algal species investigated. No significant migration away from seaweeds was observed for any faunal taxon from any of the algal species studied during emersion. However, harpacticoid copepod abundance increased significantly on *L. digitata* at low tide. It is likely that these copepods were associated with the holdfast or underside of the lamina for protection from desiccation and the elements. This suggested an advantage associated with inhabiting low shore macroalgae during emersion compared with migration into the subtidal zone.

INTRODUCTION

The epifauna associated with intertidal macroalgae are exposed to a wide range of environmental extremes in factors such as temperature, salinity and levels of desiccation during tidal emersion. A significant loss of motile epifauna with receding tide on an Australian shore (Encounter Bay, South Australia) was recorded in three species of intertidal macroalgae during midwinter (July, 1996), the degree of faunal loss observed being closely correlated with the geometric complexity (measured as fractal dimension, D) of the algae (Davenport et al., 1999). Fractal dimension as one method of measuring the complexity of structures on a geometric scale was developed by Mandelbrot (1967) from the observations of Richardson (1961), and has since been used as a measure in a wide range of ecological systems (e.g. Mark, 1984; Morse et al., 1985). An increase in the diversity of faunal communities has been positively correlated with an increase in the fractal complexity of the habitats with which they were associated (Heck & Wetstone, 1977; Hicks, 1980, 1985; Lawton, 1986; Shorrocks et al., 1991; Gunnarsson, 1992; Gee & Warwick, 1994a,b). It has been shown that seaweeds can have mixed fractal characteristics and so the scales at which complexity becomes relevant to associated fauna are as important as the degree of complexity itself (Davenport et al., 1996).

The present study was conducted on UK shores in order to determine whether the findings of Davenport et al. (1999) in Australia were of general application. The hypotheses tested were: (i) that higher fractal dimension in an algal species is correlated with a higher abundance and diversity of associated epifaunal communities; (ii) that the abundance and diversity of the motile epifaunal community is significantly reduced during emersion in intertidal algae; and (iii) that the degree of migration is significantly reduced in geometrically more complex algae.

MATERIALS AND METHODS

Study sites

The sites chosen for this study were three wave-exposed localities on Great Cumbrae Island, Scotland. The sites were (Figure 1, from west to east) the Outer Eilean in Newton Bay (55°44′26″N 45°4′52″W), Farland Point (55°44′15″N 45°4′15″W) and Farland Bight (55°44′17″N 4°54′04″W). The sites were chosen on the basis of geographical closeness, relative equality in degree of wave exposure and aspect, ease of access, and adequate diversity of macroalgae. The shores are all south-west facing, and are among the most wave-exposed on the island. Due to the partially enclosed nature of the Firth of Clyde, these

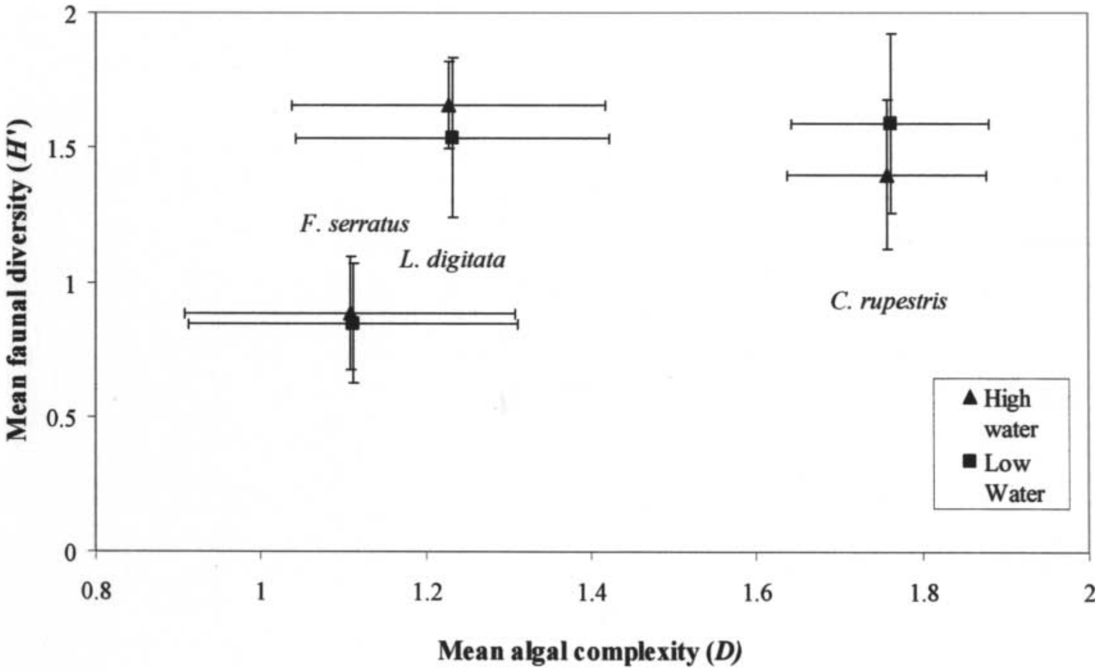

Figure 1. Relationship between mean faunal diversity (Shannon–Weiner H' ±SE) and algal complexity (fractal index D) for the epifaunal communities of *Fucus serratus*, *Laminaria digitata* and *Cladophora rupestris* at high (▲) and low tide (■).

shores have a ranking of 4 on Ballantine's scale (Norton, 1986).

Sample species

Three seaweed species were chosen based on: (i) physical appearance (visually apparent differences in complexity); and (ii) presence of all three species at each site and at the same height on the shore so that all three species were subject to similar environmental influences.

The three species chosen were *Cladophora rupestris* (Linnaeus) Kützing (Chlorophyceae), *Laminaria digitata* (Hudson) Lamouroux (Phaeophyceae) and *Fucus serratus* Linnaeus (Phaeophyceae). All were found at the uppermost edge of the *Laminaria* zone, near mean low water neaps (MLWNs), and are characteristic species of British rocky shores.

Sampling methods

Algae were collected in 1998 during high tide (immersed samples) and low tide (emersed samples). These were taken within 15 min either side of high or low tide from the Outer Eilean on 23 April, Farland Point on 25 April, and Farland Bight on 26 April, during spring tides. All samples were collected by hand, using SCUBA where necessary. The number of replicates (N=5 algae per algal species per tidal state from a single height on shore for each shore) was limited by stamina and the number of samples that could be physically carried underwater. Whilst diving, samples consisting of individual algae, carefully cut from rock surfaces with a knife or dive scissors as close to the rock as possible, were collected into plastic bags and sealed with elastic bands. There was no evidence of faunal escape during sampling. Sealed sample bags were then transferred to a net bag for carriage. Plastic fish boxes were used to support the samples once they were removed from the water for ease of transport to the laboratory.

At low tide (30–60 min after initial emersion), algal samples were carefully removed from rock substrata, gently placed in plastic bags and sealed.

Sample preservation

A 40% formalin in seawater solution was added to the sample bags to give a final concentration of about 5% formalin. Samples were then left for at least 24 h before being removed from the sample bag and placed in a white tray. The seawater was poured through a 75 μm mesh sieve and the sample bag washed three times with fresh water, the washings of which were again poured through the sieve. The algal sample wash was then washed with fresh water in the white tray three times. Each time the alga would be rubbed down with gloved (latex) hands to remove any remaining epifauna, and the washings poured through the sieve. The sieved material was then transferred to a sample jar in 70% alcohol for identification and enumeration of fauna at a later date. Seaweed samples were then carefully checked to ensure that all fauna were indeed removed, using a binocular light microscope when necessary.

Seaweeds were touch-dried with paper towels and weighed using a Mettler PE160 digital balance (to 0.1 g accuracy). They were then retained for fractal analysis.

Light microscopy

Preserved macrofauna samples were placed in Petri dishes with 70% ethanol. Faunal identifications (mainly to higher category than species level) were made under a binocular dissection microscope using relevant keys.

Samples contained large quantities of seaweed fragments and mucilaginous residue from which the meiofauna had to be separated. Hicks (1977) encountered a similar problem with separating epifauna from macrodetritus in macroalgal samples, and resorted to hand sorting. Therefore the meiofaunal component of each sample was either completely examined in this way, or if the sample was dominated by sediment and detritus, from a 20% subsample (by volume, after removal and identification of macrofauna).

Fractal analysis

Fractal dimensions were measured following the method of Davenport et al. (1999). Photographic slides were taken of each algal species (plus scale bar) using a Nikon camera and Kodak EPN 5058 colour film, and drawings of the outline of the frond edge made over a range of scales for three different parts of three different plants for each species, using a camera lucida. The Richardson plot method (Mandelbrot, 1967) was used to obtain the fractal dimension (D) of the outline of each plant. Three points were randomly marked on the camera lucida image of the sample to be analysed. Measurements of the length of the frond edges were made from this image using a pair of dividers set to specific step lengths (step lengths of 1 to 5 mm, in 1 mm increments based on the scale bar of the image). Where the step-lengths could not accurately measure the entire length of the frond edge (i.e. where the remaining edge to be measured was less than the step length used), the excess length was measured using a ruler and added to step length measurements. This was repeated at all three points so that a mean frond edge length could be calculated for each step length. The mean frond edge length for each step length was then double log plotted against step length. A line of best fit for the slope was recorded. The corresponding fractal index (D, which is equal to 1—the slope of the line of best fit) was calculated.

The above technique does not allow for an algal species that has morphologically-distinct regions. To achieve a more representative fractal index for *Laminaria digitata*, the fractal indices of the holdfast, stipe and blade were measured separately, and their contribution to overall fractal index weighted according to the contribution to total plant mass using the following equation:

$$D_o = (D_\mathrm{h} \times (\mathrm{M_h}/\mathrm{M_t})) + (D_\mathrm{s} \times (\mathrm{M_s}/\mathrm{M_t})) + (D_\mathrm{b} \times (\mathrm{M_b}/\mathrm{M_t}))$$

where: D_o=overall fractal index for *L. digitata*; $D_\mathrm{h,s,b}$=fractal indices of the holdfast (h), stipe (s) or blade (b); $\mathrm{M_{h,s,b}}$ =wet mass of the holdfast (h), stipe (s) or blade (b); and $\mathrm{M_t}$=total seaweed wet mass.

Data analysis

Analysis of experimental data and graphical representation was achieved using the computer packages Microsoft Excel '97, Minitab v. 10.1, and Primer 5ß.

RESULTS

Fractal characteristics

There was considerable variation in the fractal complexity of the seaweeds between species over a scale (step range) of 1–5 mm. The order of increasing complexity (mean D ±SE) was *Fucus serratus* (1.11 ±0.20) < *Laminaria digitata* (1.23 ±0.19) < *Cladophora rupestris* (1.76 ±0.12). *Cladophora rupestris* was significantly more complex at this scale than the other two algal species studied (analysis of variance (ANOVA): df=2, F=21.65, P=0.002). The complexity (D) of the blade, stype and holdfast of *L. digitata* were determined to be 1.06 ±0.03, 1.06 ±0.05 and 1.34 ±0.06, respectively.

Epifaunal characteristics

The faunal community compositions of each seaweed species studied were distinct from each other (Table 1). The percentage of total population for each taxon was calculated from the total faunal abundance found on each alga, to prevent any potential bias created by the conversion to number per gram of algae. Taxonomic groups were described as meiofaunal or macrofaunal based on size definition (macrofauna were retained by a 1-mm sieve, meiofauna by the 75-μm sieve), to allow a comparison of the proportion of these two size-classes for each algal species and tidal state. Harpacticoid copepods were the most dominant faunal group (by abundance), contributing over 70% of the total community on *F. serratus*, 32–52% on *L. digitata*, and 47–56% on *C. rupestris*. On *F. serratus*, nematodes, acarid mites and ostracods (at high water only) were the next greatest contributors to meiofaunal abundance. Amphipods, bivalves and dipteran larvae dominated the macrofaunal community.

There was a highly significant tidal difference in the number per gram of algae in the harpacticoid copepods on *L. digitata*, with an increased abundance during emersion (HW=3.8 ±3.29 copepods g wet mass^{-1}; LW=9.58 ±6.73 copepods g wet mass^{-1}; ANOVA: df=17, F=85.16, $P<0.001$). No other significant differences were observed. The second most abundant group were either the acarids or nematodes (depending on tidal state), followed by ostracods and foraminiferans (at high water).

Macrofaunal abundance was dominated by bivalves, amphipods, gastropods and isopods. As with *F. serratus*, no more than three macrofaunal groups achieved greater than 1% of total community abundance.

The communities associated with *C. rupestris* contained a harpacticoid copepod component similar to that of *L. digitata* communities at low water (45–50%). Nematodes/ostracods and acarid mites were the next most abundant groups, with the foraminifera contributing 1% of faunal abundance at high water. Bivalves dominated the macrofauna, followed by dipteran larvae, annelids, isopods, amphipods and gastropods.

There was no statistically significant difference in the total number of epifauna g seaweed wet mass^{-1} between tidal states (Table 1). A comparison of the epifaunal communities from each sample group showed no significant inter-site differences, and so the results for all shores were pooled for each tidal state. The data were log transformed for two-way ANOVA in order to prevent

Table 1. *Epifauna of* Fucus serratus, Laminaria digitata *and* Cladophora rupestris. *Mean abundance (no. animals g algal wet mass*$^{-1}$*, ±SE) and analysis of variance (ANOVA) of all six treatments for each faunal group, and comparison of epifaunal abundance (no. animals g seaweed wet mass*$^{-1}$*; N=90) during emersion (low tide) and immersion (high tide).*

	F. serratus				*L. digitata*				*C. rupestris*					
	HW		LW		HW		LW		HW		LW		ANOVA	
Taxonomic group	Mn	SE	Mn	SE	Mn	SE	Mn	SE	Mn	SE	Mn	SE	F	*P*
Foraminiferans	0.11	±0.20	0.09	±0.32	0.12	±0.12	0.10	±0.09	59	±116	7	±10	33.1	<0.001
Nematodes	6.46	±3.77	8.28	±6.67	1.77	±1.45	2.34	±1.80	331	±425	125	±90	62.9	<0.001
Annelids	0.07	±0.18	0.04	±0.06	0.44	±0.40	0.75	±0.55	84	±151	71	±101	39.6	<0.001
Harpacticoid copepods	40.02	±19.42	41.94	±34.25	3.80	±3.29	9.58	±6.73	1319	±1395	785	±712	85.2	<0.001
Ostracods	1.17	±1.06	0.57	±0.74	1.65	±2.05	1.07	±1.07	519	±850	119	±104	69.5	<0.001
Amphipods	1.49	±2.21	0.72	±0.78	0.22	±0.29	0.81	±0.91	37	±53	43	±48	34.6	<0.001
Isopods	0.22	±0.29	0.15	±0.18	0.03	±0.04	0.39	±0.44	14	±34	5	±6.00	28.1	<0.001
Acarid mites	1.94	±1.41	1.52	±1.81	1.77	±1.84	1.94	±1.50	80	±141	63	±53	40.7	<0.001
Gastropods	0.22	±0.20	0.06	±0.06	0.29	±0.46	0.12	±0.07	41	±69	1	±24	47.5	<0.001
Bivalves	0.63	±0.82	0.60	±0.46	0.95	±0.93	0.93	±0.86	87	±118	9	±62	65.3	<0.001
Dipteran larvae	0.31	±0.25	1.00	±1.23	0.00	±0.01	0.20	±0.26	49	±66	139	±152	36.2	<0.001
Total abundance	52.85	±22.87	55.0	±40.2	11.08	±8.38	18.26	±11.15	2669	±3063	1483	±1063	98.7	<0.001
	Two-way ANOVA					Tidal state Algal species Tide×species		*P* =0.645 *P*<0.001 *P*=0.097						

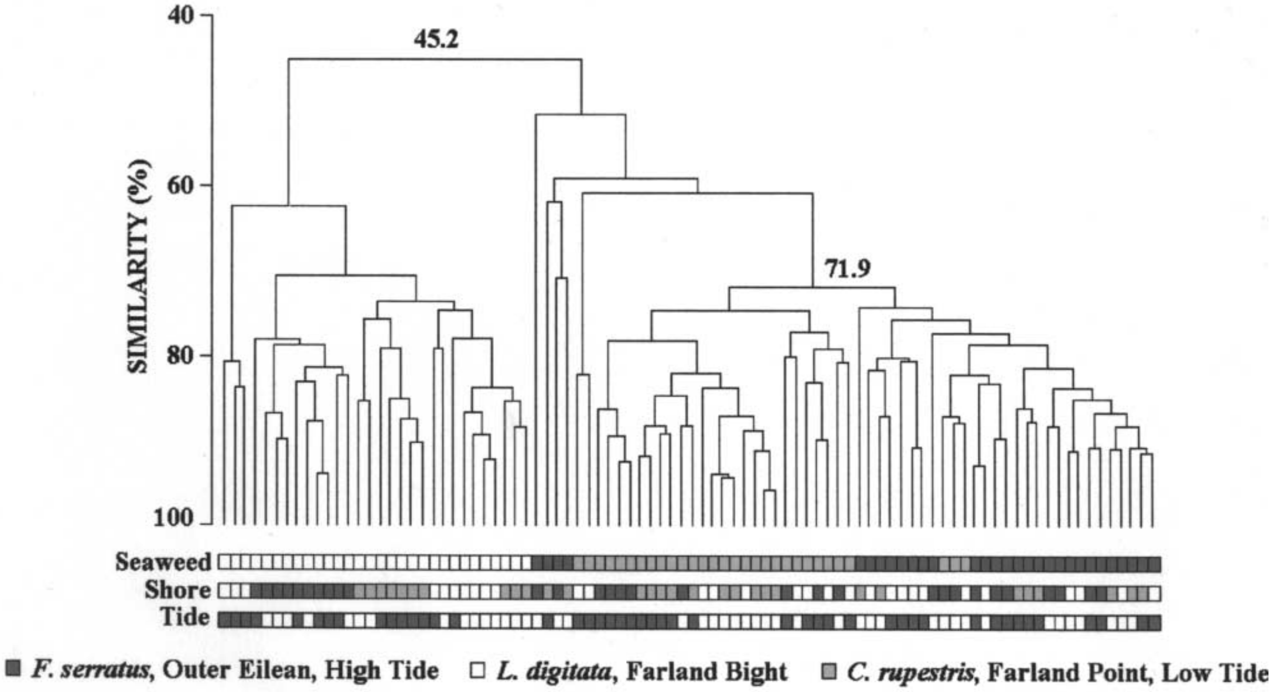

Figure 2. Epifauna of *Fucus serratus*, *Laminaria digitata* and *Cladophora rupestris*. Dendrogram using group-average linking on Bray–Curtis community similarities from fourth-root transformed abundance data. Individual samples (N=90) are grouped into seaweed species sampled, sample site (shore), and tidal state.

numerically-dominant groups masking potential abundance changes in less abundant taxa.

There was a highly significant difference in the total number of epifaunal individuals g algal wet mass^{-1} amongst the seaweed species, with the order *C. rupestris* >*F. serratus* > *L. digitata* (identified using Tukey's pairwise comparisons). Two-way ANOVA showed significant differences between seaweed species (Table 1: $P<0.001$), but no significant difference between tidal states ($P=0.645$) or interaction between the two factors ($P=0.097$).

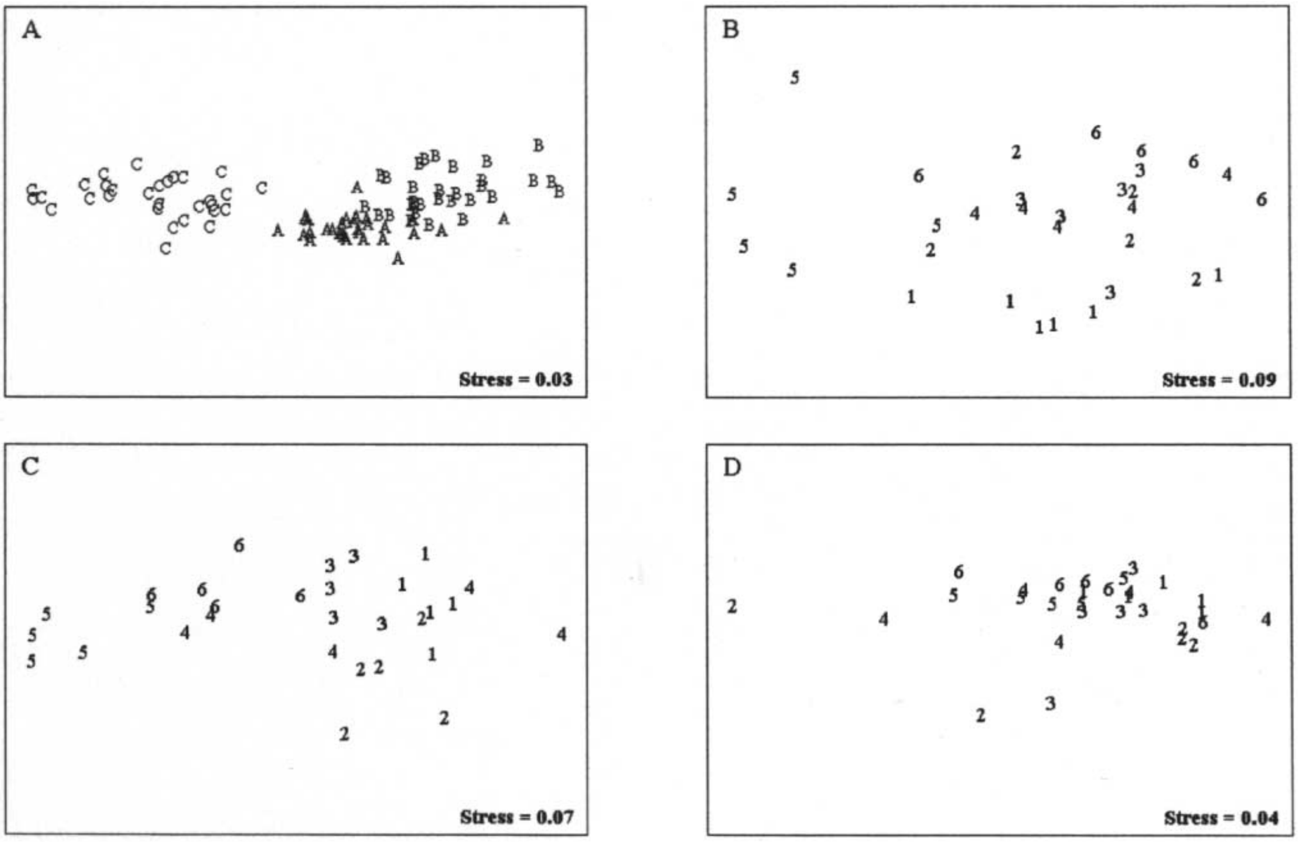

Figure 3. Multidimensional scaling (MDS) plots comparing epifaunal communities between algal species (A) *Fucus serratus*; (B) *Laminaria digitata*; and (C) *Cladophora rupestris*, and between sampling sites and tidal states for each species (B–D). 1, Outer Eilean HW; 2, Outer Eilean LW; 3, Farland Bight HW; 4, Farland Bight LW; 5, Farland Point HW; 6, Farland Point LW.

The abundance of each epifaunal taxonomic group on each alga was compared using one-way ANOVA (Table 1). *Cladophora rupestris* had a significantly greater abundance of every faunal group g seaweed wet mass^{-1} than the other two algal species studied. The only groups with significantly different abundances g^{-1} between *L. digitata* and *F. serratus* were the harpacticoid copepods and nematodes (with greater abundances on *F. serratus*; df=5, F=85.16 and 62.94 respectively, $P<0.001$ in both cases). The only faunal difference between tidal states was observed in the harpacticoid copepods associated with *L. digitata*, where a significant increase in abundance was observed during emersion (from 3.80 ±3.29 animals g algal wet mass^{-1} at HW to 9.58 ±6.73 animals g algal wet mass^{-1} at LW; df=5, F=85.16, $P<0.001$).

The diversity of the faunal community of each seaweed species at each tidal state was calculated using the Shannon−Wiener diversity index (H'; Figure 2) using untransformed faunal data. No significant difference in epifaunal community diversity within each seaweed species was found between tidal states. However, the epifaunal communities of *F. serratus* (mean $H'=0.88\pm0.21$ SE HW and 0.85 ±0.22 LW) were found to have a significantly lower diversity than those of *L. digitata* (mean $H'=1.66\pm0.16$ SE HW and 1.54 ±0.30 LW) or *C. rupestris* (mean $H'=1.40\pm0.28$ SE HW and 1.59 ±0.33 LW; ANOVA: df=5, F=29.76, $P=<0.001$).

To further analyse the community data collected, multivariate techniques were used to test the original hypotheses. The data were fourth-root transformed to prevent the dominance of harpacticoid copepods masking any prospective changes in the community as a whole. Hierarchical clustering (with group-average linking), and multidimensional scaling (MDS ordination), were both based on the results of the Bray−Curtis similarity matrix.

Both dendrogram (Figure 2) and MDS ordination plots (Figure 3A) showed that the greatest difference between the composition of epifaunal communities was related to seaweed species rather than tidal state or sample site (shore). A similarity level of 45.2% (Figure 2) characterized the *C. rupestris* faunal community in relation to those of *F. serratus* and *L. digitata*, which had a similarity of 71.9%. The MDS ordination of *C. rupestris* epifaunal communities (Figure 3C) indicated some separation of samples (N=30) into two main groupings—those from Farland Point, and those from the other two shores (Farland Bight and the Outer Eilean). The communities from *L. digitata* (Figure 3B) and *F. serratus* (Figure 3D) suggested little or no clustering due to tidal state or shore.

DISCUSSION

Complexity of Cladophora rupestris, Fucus serratus *and* Laminaria digitata

The results of the fractal analysis of the algal species investigated concurred with simple observation—that the structure of *Cladophora rupestris* was far more complex than the other two species, reflecting its multiply-branched nature. *Fucus serratus* and *Laminaria digitata* were very similar in terms of structural complexity at the scales investigated (*F. serratus* mean D=1.11, *L. digitata*=1.23). The slightly higher value for *L. digitata* reflects the incorporation of data from the holdfast—the blade and stipe are virtually Euclidean structures.

Characteristics of associated epifauna

Hypothesis (i), that higher fractal dimension in an algal species is correlated with a higher abundance and diversity of associated epifaunal communities was supported. These results concur with those of previous studies on different macroalgal species (Gee & Warwick, 1994a,b; Davenport et al., 1996, 1999), but are the first to be conducted with replication of shores.

It has recently been proposed that the size and composition of macroinvertebrate communities associated with sea grass beds (*Zostera marina*) is not determined by the structural complexity of the plants, but by the amount of plant available (Attrill et al., 2000). A strong correlation has also been reported between frond biomass of *Sargassum cymosum* and total faunal abundance per macroalgal biomass unit (Leite & Turra, 2003). This would be consistent with the established species–area concept. However, Parker et al., (2001) tested the effects of plant species composition and diversity on motile macroinvertebrate community structure, and suggested that epifaunal abundance and biomass remained higher (and evenness remained lower) among assemblages composed of branched (mostly seaweeds) relative to unbranched (mostly sea grasses) macrophytes. The current study and that of Davenport et al. (1996) found that the greatest diversity and algal mass-specific abundance of macroalgal-associated epifauna (macro- and meiofauna) were recorded from the most complex, but by far the smallest (by individual mass) algal species investigated (*C. rupestris* in the present case). The difference probably reflects the very different circumstances in a low-energy soft-bottomed habitat (sea grass bed) in which much of the invertebrate community lives in detritus, and the physically-harsh environment of the rocky shore where epifauna use seaweeds for shelter and attachment as well as feeding.

The significantly higher level of total algal mass-specific faunal abundance, abundance of harpacticoid copepods and abundance of nematodes on *F. serratus* compared with *L. digitata*, plus the significantly greater diversity of epifauna on *L. digitata* compared with *F. serratus*, may be explained by differences in plant morphology. Although fractal indices of the two algae were similar, *L. digitata* has greater differentiation into distinct blade, stipe and holdfast compared with *F. serratus*. The greater proportion of the mass of *L. digitata* is composed of the structurally-complex holdfast (61% by wet mass in this study). Simple structures have associated faunal communities that are low in abundance and diversity due to lack of shelter from predation and environmental extremes (Davenport et al., 1999), and so the blade and the stipe offset the complexity of the holdfast (which fosters diversity and abundance). Although this could not be quantified during the present study due to the methods utilized, direct observation of the different morphological regions during sampling and sample processing suggested that this was indeed the case, although further studies of the faunal communities of the different morphological regions of kelps would be required to support this.

The question of whether differences in faunal community were due to the structural heterogeneity of the seaweeds (measured using fractals) or just to differences between algae (e.g. brown algae versus green algae, interspecific differences) was addressed by direct observation of the fauna associated with each algal type. Differences between *F. serratus* and *L. digitata* have already been discussed, but significant differences were observed between the fauna of these species and communities associated with *C. rupestris*. Although the level to which fauna were identified may result in some bias in the results (by omitting species richness within taxon), which hence risks masking important trends. However, the faunal communities of *C. rupestris* were more diverse than those associated with the two species of brown seaweeds, despite being greatly dominated by harpacticoid copepods. Although there are non-structural differences between species of green and brown algae that could result in these differences (e.g. biochemical exudates, nutritional value, biofilm/epiphyte community composition), the results of faunal analysis and direct observation suggested that differences between the three algal species studied were directly associated with the morphological nature of the seaweeds (measured using fractals). Greatest faunal abundances and smallest faunal sizes were recorded from the algal species with least biomass, suggesting that habitat structure is more important in determining algal-associated faunal communities than algal biomass in this case. Highly complex algal species provide a range of ecological niches for colonization, protection from the environment and predation, but also have the potential for greater water retention properties in relation to their biomass, which is crucial for the survival of fauna of marine origin in the intertidal environment.

Tidal migration

Elements of the fauna of the intertidal zone change with the state of the tide. Motile epifauna in intertidal communities (including rocky shores) have been shown to display both vertical and horizontal movements with the ebb and flow of the tide. Unlike soft substrata, where copepods and nematodes move deeper into the sediment on the outgoing tide (McLachlan et al., 1977), the solid substratum of rocky shores prevents burrowing. However, the three-dimensional structure of marine algae does allow vertical migration. Gibbons (1989) observed tide-related intra-algal vertical movements of epifauna (particularly in the harpacticoid copepod genus *Porcellidium*) on *Gigartina radula*. During daylight hours, epifauna showed a strong movement to the base of the alga with the ebb tide, and a reverse 'migration' with the flood tide. Sanchez-Jerez et al. (1999) also noted diurnal intra-algal migrations of epifauna in *Posidonia oceanica*. Horizontal movement has been reported by Gunnill (1982, 1983), who observed the colonization of denuded *Pelvetia fastigata* by copepods, and showed that copepods retreat from high-shore algal cover to seaweeds lower on the shore. Davenport et al. (1999) confirmed migration from lower shore *Enteromorpha* sp., *Hormosira banksii* and *Corallina* sp. into the subtidal zone at low tide. This was despite the low position on the shore of the algal species studied (and hence short duration of emersion) and the season sampled (winter). The results of the study presented here could not confirm the effects of emersion on seaweed epifauna, but could confirm the effect of complexity.

Hypothesis (ii), that phytal epifaunal abundance and diversity is significantly reduced during emersion in intertidal algae was not supported for any of the seaweed species studied; in fact a significant increase in the abundance of harpacticoid copepods was observed on *L. digitata* at low tide. The reason for this is not certain, but the high density of *L. digitata* and size of collapsed fronds resulted in a large area of the lower shore being sheltered from the elements, and in the retention of some surface water and/or increased local humidity.

Even if masses of *L. digitata* would provide some protection against the elements, fauna remaining associated with this species would presumably still be exposed to greater extremes of temperature and salinity than would animals migrating to the subtidal. Intertidal animals choosing shelter over migrating to more optimal environmental conditions have been described previously. For example, Kelaher & Castilla (2005) reported no mesoscale effects of near-shore coastal upwelling on faunal assemblages or local habitat characteristics, but that sediment type and frond density of coralline turfs were strong determinants of faunal community structure. They concluded that structural complexity and habitat heterogeneity had a greater influence on the faunal assemblages of mat-like habitats of rocky shores than the environmental variables associated with mesoscale coastal upwelling. McGaw (2001) reported that purple shore crabs (*Hemigrapsus nudus*) remain in low salinity water if shelter is available, and may do so for long periods. McGaw (2001) suggested that the distribution of *H. nudus* in estuaries may depend more on the availability of suitable habitats than on the environmental tolerance of the species. This appears also to be the case for the harpacticoid copepods that associate in increased abundances with *L. digitata* at low tide.

Why the abundance of harpacticoid copepods on *L. digitata* increases during emersion is not clear. Presumably copepods grazing on adjacent rock surfaces, or occupying algae further up the shore at high water, moved onto *L. digitata* prior to emersion. However, if the concentration of copepods was simply a matter of harpacticoids moving downwards from higher on the shore, it would be expected that all three algal species would have exhibited increases in harpacticoid densities. Clearly *L. digitata* provides some advantage in terms of shelter or a metabolic advantage that the other algae do not.

Hypothesis (iii), that the degree of migration is significantly reduced in more geometrically complex algae could not be confirmed.

In conclusion, the study reinforces the concept that complex macroalgae support greater diversities and higher mass-specific abundances of epifauna than do simple macroalgae. The study also shows that loss of lower shore algal epifauna on the ebb tide (as clearly revealed for an Australian shore by Davenport et al., 1999) is not of general occurrence. The results obtained in the present study hint that migrations of the dominant epifaunal group (harpacticoid copepods) are complex, at least on UK shores. Possibly the Australian findings were clear cut simply because there was no macroalgal cover (and hence no higher source of harpacticoids) above the lower shore level, due to high summer temperatures. At Cumbrae, algal cover was extensive on the middle shore and extended up to the *Pelvetia canaliculata* zone (high water neap tide level). The study of epifauna along vertical algal transect will be needed to elucidate matters further.

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