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Anchana Prathep · R.H. Marrs · T.A. Norton

Spatial and temporal variations in sediment accumulation in an algal turf and their impact on associated fauna

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Abstract The relationships between the fauna inhabiting an intertidal algal turf, *Osmundea pinnatifida*, and the accumulated sediment were studied in the autumn and summer. The investigation was carried out at two levels on sheltered, moderately exposed and very exposed shores on the temperate rocky coast of the Isle of Man, British Isles. Twenty-four species of invertebrates were found associated with the turfs, and their abundance and diversity varied with season, degree of wave exposure, shore level and the amount and particle size of the sediment trapped within the turfs. Multivariate analysis indicated that most organisms were most strongly influenced by sediment accumulation and temporal changes in the turf plants. Sediment provides a heterogeneous habitat for psammophylic organisms, supplies materials for tube-building species, and is a food source for detritivores. However, it also has adverse effects; its seasonal movement resulted in an unstable community. Sediment grain size was also important; certain grades appeared to be correlated with the abundance or sparsity of some species. "Season" was, however, the overriding factor influencing this microcommunity, since the frond complexity and the productivity of the turf plant, as well as the supply and movement of sediment, vary seasonally.

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A. Prathep (✉)
Department of Biology, Faculty of Science,
Prince of Songkla University, HatYai, Songkla, 90112, Thailand

E-mail: panchana@ratree.psu.ac.th
Tel.: +66-1-542-69-77
Fax: +66-74-212917

T.A. Norton
Port Erin Marine Laboratory, School of Biological Sciences, University of Liverpool, Port Erin, Isle of Man IM9 6JA

R.H. Marrs
Applied Vegetation Dynamics Laboratory,
School of Biological Sciences, University of Liverpool,
PO Box 147, Liverpool L69 3GS, UK

Introduction

Extensive turfs of algae are a feature of the lower reaches of rocky shores in many parts of the world (Myers and Southgate 1980; Kain and Norton 1990). The crowded fronds create a labyrinth that traps sediment (Scoffin 1970; Stewart 1983; Airoldi et al. 1996) and is often inhabited by a rich and varied fauna (Nuemann 1970; Myers and Southgate 1980; Chapman 1995). The accumulation of sediment in turfs varies in time and space horizontally and vertically on the shore (Whorff et al. 1995; Airoldi et al. 1996), and seasonally, largely as a consequence of wave action (Lewis 1964; Stephenson and Stephenson 1972; Stewart 1983). Terrestrial sources of sediment washing down onto the shore as a result of deforestation and erosion may also be important in some regions (Airoldi et al. 1996).

The effects of sediment on the intertidal and subtidal zones have been well studied, but rarely with respect to turf communities. Sediment is known to scour or occlude the substratum, as well as smothering organisms or cutting off the light to juvenile attached plants (Norton 1978). Thus, it interferes with the recruitment, growth and survival of algae (Neushul et al. 1976), as well as zonation patterns and species diversity (Daly and Mathieson 1977; Little and Smith 1980; Taylor and Littler 1982; Littler et al. 1983). Sediment can also regulate the respiratory metabolism in some common shore gastropods (Marshall and McQuaid 1989; Chandrasekara and Frid 1998), clog the feeding mechanism of suspension feeders (Eleftheriou and Basford 1989; Aller and Stupakoff 1996) and inhibit the settlement of a variety of marine invertebrates (Stewart 1989).

In turf communities, studies have mostly focused on the effect of sediment on the algae themselves rather than on the fauna harboured by the turfs (but see Whorff et al. 1995). For example, the amount and type of sediment may structure both the species composition and the diversity of the algal flora (Stewart 1983;

Kendrick 1991; Airoldi et al. 1995), but there is only one report of the effects on fauna (Whorff et al. 1995).

It is well known that algal turfs can trap sediment on shores where it would otherwise be absent, but little is known about the relationships between turf communities, sediment accumulation and the interaction between physical factors, sediment supply and fauna. In an attempt to investigate these relationships, we report the results of a study of turfs of *Osmundea* (*Laurencia*) *pinnatifida* (Hudson) Lamouroux on rocky shores of the Isle of Man. *O. pinnatifida* was chosen as a model system because it forms discrete patches of short turf, with irregular branches that trap sediment. These patches represent small "islands" of favourable habitat in an otherwise adverse terrain of open rock and within them there is a greater animal diversity than on the adjacent rock.

We measured the amount and types of sediment in patches of *O. pinnatifida* in two contrasting seasons, on shores with different degrees of wave exposure and at different levels on the same shore. The fauna associated with the turfs was examined at the same time.

We hypothesised that (1) the *Osmundea* turf harbours a fauna whose composition, distribution and diversity will vary between sites and seasons and (2) the nature of the associated fauna will be determined chiefly by the amount and type of sediment that accumulates in the turf.

Materials and methods

Study site and sampling

The study sites were all in the south of the Isle of Man, in the Irish Sea. Three shores were selected with different degrees of wave exposure: sheltered (S) Port Erin (54°06′N, 4°46′W), moderately exposed (M) Port St. Mary Ledges (54°0′N, 4°44′W), and exposed (E) Scarlet Point (54°04′N; 4°39′W). Exposure was assessed using the biological exposure scale of Lewis (1964). Each shore was sampled at two shore levels within the turf zone: upper limit (h) 3.5 m above lowest astronomical tide (LAT) and lower limit (l) 2.0 m above LAT. Samples were taken in two seasons: late autumn (November 1998) and summer (August 1999). Thirty patches of turf were chosen randomly at each shore level in each season. Areas of turf measuring 10 cm×10 cm were removed using a paint scraper. This was done carefully to prevent the loss of associated organisms and sediment. Samples were immediately placed in plastic bags and transferred to the laboratory for processing.

Samples were washed with filtered sea water to remove sediment and organisms. The sediment was then filtered using distilled water and gentle suction, and dried at 60°C to constant weight. The dry sediment was then sieved into seven size fractions: >2.00 mm, 1.00–2.00 mm, 500 μm–1.00 mm, 250–500 μm, 125–250 μm, 63–125 μm and <63 μm and each fraction was weighed.

The organisms were stained using Rose Bengal which was helpful for distinguishing small specimens from sediment during sorting. Animals were preserved with 10% formalin and subsequently identified to species.

Statistical analysis

The species diversity (*H*') and equitability (*J*) of each sample were calculated for each site, level and season. The data for each variable (count of species abundance, *H*', *J* and total weight of sediment and of each size fraction separately) were analysed using ANOVA for each season using a nested design with degree of exposure (shore) as the main factor and shore level nested within the main factor. To test for temporal change, repeated measures were used; this was interpreted as a first approximation of seasonal effects. Seasonal effects were assessed using repeated measures. This analysis was done using untransformed and transformed data (species numbers $\sqrt{x}$; sediment amounts ln *x*) with PROC ANOVA (SAS 1985). Statistical results are presented based on the analyses of transformed data, but, for clarity, graphical output is based on the untransformed means.

The potential relationships between species abundance and site factors, season and sediment were then assessed using stepwise multiple regression (PROC GLM; SAS 1985). Here degree of exposure, shore elevation and season were treated as categorical variables and sediment values as an ordinal variable. The aim was not to develop predictive models, but rather to select those combinations of variables that were associated with the abundance of individual species, to give information on the types of factors that might be controlling their distribution. The univariate approach was used to generate hypotheses for individual species which could be tested experimentally in future work. Transformed data were used throughout.

Multivariate analysis was also carried out using CANOCO for WINDOWS (ter Braak and Smilauer 1998). The data (24 species, 60 samples) were analysed using a sequence of techniques; in all multivariate analyses the species data were transformed (to ln $x+1$) and the downweighting option for rare species was not used. Initially the species *x* plot data were analysed with DECORANA (DCA) to measure the gradient lengths. The gradient length on the first axis was 2.9, suggesting that the linear model should be used. Thereafter, two constrained ordinations were run using environmental variables in which wave exposure, shore elevation and season were considered as using categorical information, and the different sediment fractions were treated as ordinal data. The first constrained ordination was a redundancy analysis (RDA), in which the Forward Selection procedure was used with a Monte Carlo test with 499 permutations, to determine which environmental variables were important in explaining the variation in the species in each data set. The following variables were selected (at $P<0.05$) in order: degree of exposure, shore elevation, season, and amount of sediment in two fractions (63–125 μm, 500 μm–1 mm). In the final RDA the eigenvalues for the four axes were 0.141, 0.125, 0.029 and 0.366, and the Monte Carlo tests with 999 permutations were significant, $P=0.001$ (first canonical axis, $F=9.207$, $P<0.01$; overall model, $F=7.835$, $P<0.001$).

Results

Sediment trapped in algal turfs

The total amount of sediment trapped varied greatly, between 1,126 and 4,628 g/m^2, and the amount present differed with season, wave exposure and shore elevation. During the winter, greater amounts of sediment were found especially on the sheltered shore, and higher on the shore compared to the lower level (Figs. 1 and 2; Table 1, a). During the summer, there was less sediment on all shores and there was no significant difference between shores (Table 1, a).

Total sediment load was greater, and tended to be composed of the larger-sized particles, at the higher than the lower level on the shore, but there were no clear seasonal or spatial patterns between fractions (Fig. 2; Table 1, a).

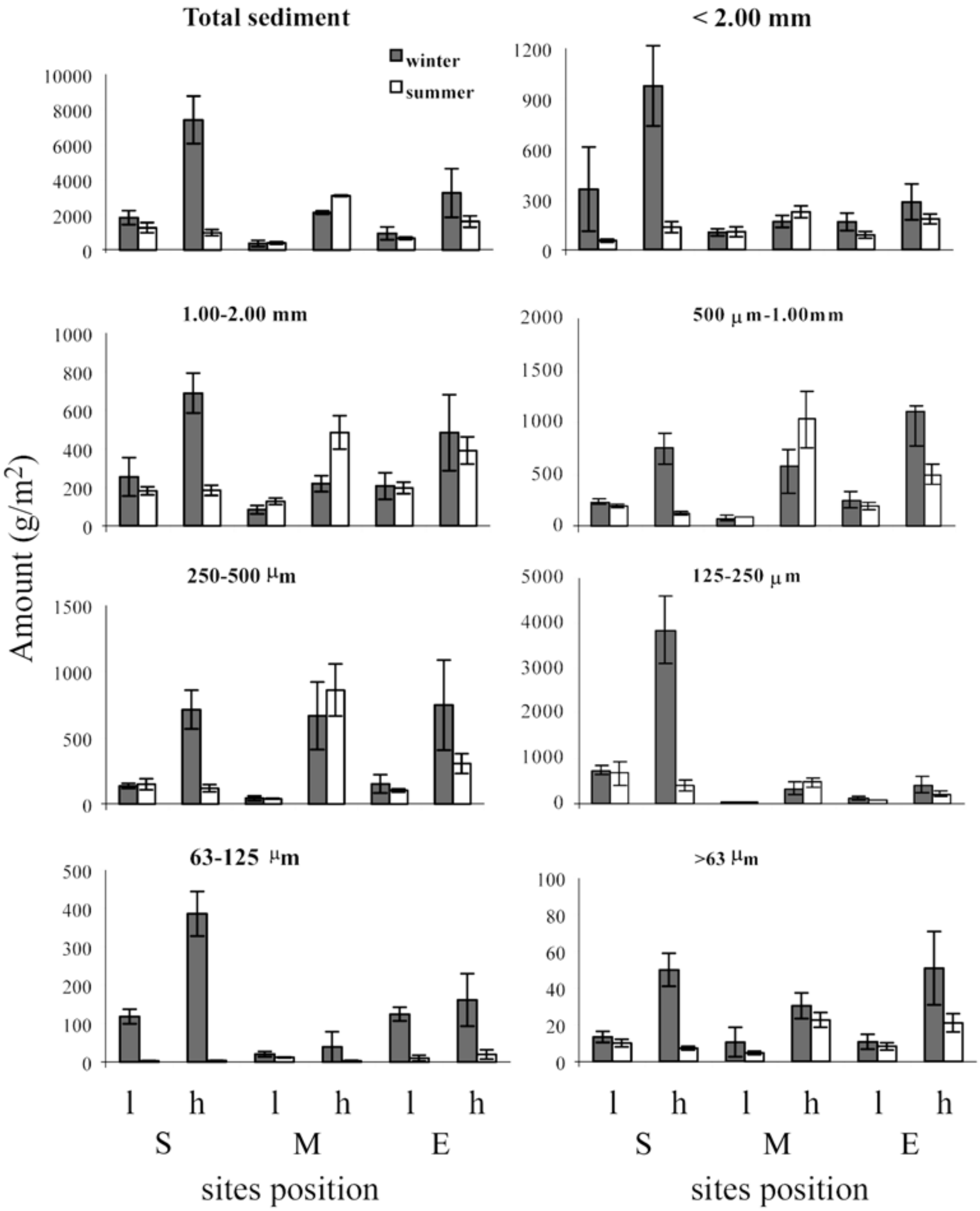

Fig. 1 *Osmundea pinnatifida* turf. Effects of wave exposure: *S* sheltered, *M* moderately exposed, *E* exposed shore at *l* low and at *h* high shore levels on associated sediment within turfs in two seasons

Fauna of algal turfs

Species composition and distribution

Twenty-four species of invertebrates were found associated with the turfs (Table 2). All came from only five phyla: Nematoda, Annelida, Arthropoda (subphylum Crustacea), Mollusca and Echinodermata. The vast majority of the individuals were molluscs, annelids and crustaceans. Most of the animals found were adults; only *Mytilus edulis* and *Modiolus modiolus* were juveniles.

The species composition and their distribution were influenced by the degree of wave exposure, shore elevation and season. *Hyale stebbingi*, *Idotea granulosa*, *Tanais dulongii*, *Pilumnus hirtellus* and *Mytilus edulis* were common over all ranges of wave exposure in both winter and summer, but *Oerstedia dorsalis*, *Owenia fusiformis*, *Amphitrite gracilis, Barleeia unifasciata*, *Gibbula umbilicalis* and *Lacuna vincta* were found only during winter and at particular sites.

Species diversity and equitability were greater on the most exposed shore, and in late autumn than in summer (Table 2). ANOVA revealed significant differences in species diversity between shores ($F = 9.34$, $P < 0.001$), and interactions between seasons and degrees of wave exposure ($F = 5.25$, $P < 0.007$), but no differences with shore level. The highest diversity was found on the exposure shore during winter and the lowest was found on the shelter shore in summer. Equitability showed similar, significant differences with degrees of wave exposure ($F = 5.84$, $P < 0.005$) and interaction between season and degrees of wave exposure ($F = 4.28$, $P < 0.020$), but not with season ($F = 0.05$, $P = 0.819$).

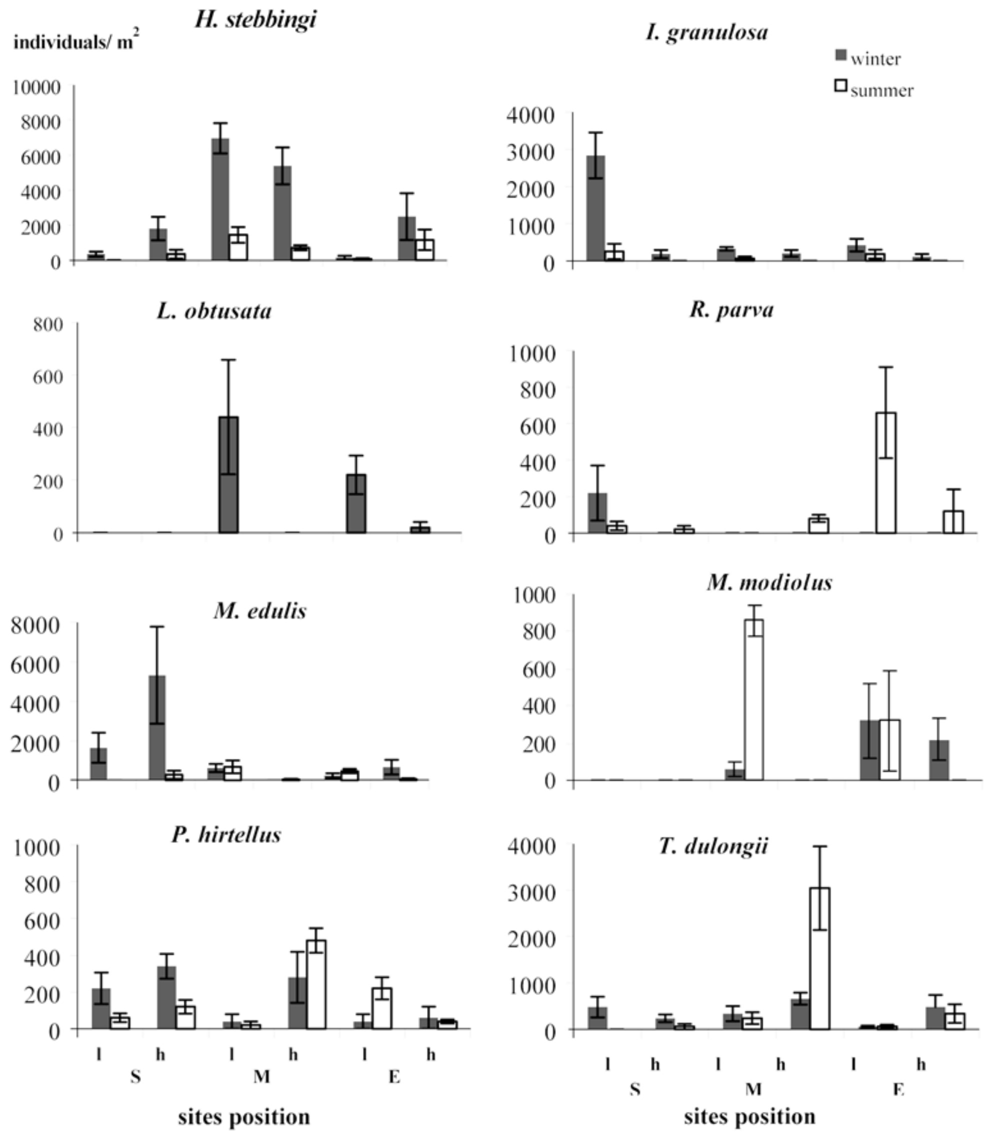

Fig. 2 *Osmundea pinnatifida* turf. Effects of wave exposure: *S* sheltered, *M* moderately exposed, *E* exposed shore at *l* low and at *h* high shore levels on species density of associated animals that showed significant relationships

Spatial and temporal variations in populations

Eight species showed significant differences in their abundance with respect to degree of wave exposure, shore elevation, seasons and their interactions (Table 1, b). *Mytilus edulis* was the most abundant species on the sheltered shore and *Hyale stebbingi*, on the moderately exposed shore during winter, but there was no dominant species on the very exposed shore. Most of the associated fauna inhabited the turfs both in winter and summer, but *Littorina obtusata* was only found during winter. The abundance of most animals decreased during summer, but *Rissoa parva*, *Modiolus modiolus* and *Tanais dulongii* greatly increased in summer (Fig. 3).

Three patterns of density were found with respect to degree of wave exposure: a lower density with increasing wave exposure (e.g. *Idotea granulosa* and *Mytilus edulis*), an increased abundance on the intermediate moderately exposed shore (*Hyale stebbingi*), and some, such as *Littorina obtusata* and *Modiolus modiolus*, were absent at certain exposures (Fig. 3). There was no uniform pattern with respect to shore elevation; for example, *I. granulosa* and *Rissoa parva* were significantly more abundant lower down, but the opposite was true for *H. stebbingi* and *Mytilus edulis* (Fig. 3).

Effects of site, season and sediment factors on species distribution

The animal species were classified into three groups on the basis of the significant factors selected in the regression analyses, i.e. group 1, only environmental factors (site and seasonal) were selected; group 2, only sediments were selected; and group 3, for which both were selected (Table 3).

Group 1 species included detritivores that feed on sediment (*Rissoa parva*), a filter feeder (*Modiolus modiolus*), and two carnivores (*Nephthys caeca* and *Nereis*

Table 1 *Osmundea pinnatifida* turf. Summary of significant results (*F*-ratio) from analysis of variance showing effects of (1) different degrees of exposure on three different shores, and (2) different levels on these shores (nested within degree of exposure) in two seasons, with seasonal effects assessed by repeated measures on (a) sediment collected, and (b) species abundance of animal species. Animal species that are not presented showed no significant relationship; otherwise, * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$; *ns* not significant

(a) Sediment collected

Sediment fraction	Winter		Summer		Repeated measures		
	Degree of exposure	Shore level	Degree of exposure	Shore level	Season	Season× exposure	Season× shore level
Total sediment	8.08***	8.61***	2.33 ns	12.92***	11.77**	9.20**	6.94**
> 2.00 mm	7.61**	2.90 ns	3.29 ns	6.27**	10.78**	8.27**	1.94 ns
1.00–2.00 mm	4.66*	4.32*	3.66*	11.06***	1.70 ns	7.25**	2.99 ns
500 μm–1.00 mm	1.18 ns	4.05*	5.62*	11.53***	1.89 ns	3.22 ns	2.19 ns
250–500 μm	0.14 ns	5.19**	6.97**	15.07***	3.36 ns	2.32 ns	2.42 ns
125–250 μm	27.53***	15.96***	5.21*	2.83 ns	18.03***	16.00***	15.64***
63–125 μm	10.35***	4.45***	2.20 ns	0.90 ns	67.89***	12.35***	10.28***
< 0.63 μm	0.71 ns	5.11***	1.99 ns	7.97***	11.83**	1.11 ns	3.23*

(b) Species abundance

Sediment fraction	Winter		Summer		Repeated measures		
	Degree of exposure	Shore elevation	Degree of exposure	Shore elevation	Season	Season× degree of exposure	Season× elevation
H. stebbingi	26.34***	4.43*	11.01***	4.72*	63.23***	15.06***	0.70 ns
I. granulosa	10.32***	16.07***	2.59	4.77**	88.52***	7.72**	11.49***
L. obtusata	10.77 ***	17.39 ns	ns	ns	42.26***	10.77***	17.38***
M. modiolus	5.19 *	0.29 ns	0.70 ns	1.03 ns	1.23 ns	2.34 ns	0.1 ns
M. edulis	1.87***	3.67**	0.80 ns	3.97*	40.19***	11.81***	3.19*
P. hirtellus	6.60**	2.21 ns	3.12 ns	8.40***	25.41***	6.56**	3.36*
R. parva	3.49*	3.49*	6.43**	3.81*	0.01 ns	6.07**	3.36*
T. dulongii	1.52 ns	2.59 ns	10.78***	9.10***	15.38***	1.08 ns	1.98 ns

Table 2 *Osmundea pinnatifida* turf. Summary species list and distribution of animals within turfs, species diversity and equitability on sheltered (*S*), moderately exposed (*M*) and exposed (*E*) shores at low (*L*) and high (*H*) shore levels within the turf zonation in winter and summer; *X* observed, – not observed

Phylum	Species	Winter						Summer					
		S		M		E		S		M		E	
		L	H	L	H	L	H	L	H	L	H	L	H
Nematoda	*Oerstedia dorsalis*	–	–	–	X	–	–	–	–	–	–	–	–
Annelida	*Amphitrite gracilis*	–	–	–	–	–	X	–	–	–	–	–	–
	Capitella sp. I	–	–	–	–	X	X	–	–	–	–	–	–
	Cirriformia tentaculata	–	–	–	X	X	–	–	X	–	–	–	–
	Nephthys caeca	–	–	–	X	–	–	–	X	–	–	–	X
	Nereis pelagica	–	X	–	X	–	–	–	X	–	–	–	–
	Owenia fusiformis	–	X	–	–	–	–	–	–	–	–	–	–
Arthropoda (subphylum Crustacea)	*Hyale stebbingi*	X	X	X	X	X	X	X	X	X	X	X	X
	Tanais dulongii	X	X	X	X	X	X	–	X	X	X	X	X
	Idotea pelagica	X	X	X	–	X	X	X	–	X	–	X	X
	Idotea granulosa	X	X	X	X	X	X	X	–	X	–	X	–
	Pilumnus hirtellus	X	X	X	X	X	X	X	X	X	X	X	X
Mollusca	*Gibbula umbilicalis*	X	–	–	–	–	–	–	–	–	–	–	–
	Barleeia unifastica	–	–	–	–	–	X	–	–	–	–	–	–
	Cingula trifasciata	–	–	–	–	–	X	–	–	–	–	–	–
	Lacuna vincta	X	–	–	–	–	–	–	–	–	–	–	–
	Littorina littorea	X	X	–	–	–	X	–	–	–	–	–	–
	Littorina obtusata	–	–	–	–	X	X	–	–	–	–	–	–
	Littorina saxtilis	–	–	–	–	–	–	–	X	–	X	–	–
	Nucella lapillus	X	X	X	–	X	X	–	–	–	–	–	–
	Rissoa parva	–	X	–	–	–	–	X	X	–	X	X	X
	Modiolus modiolus	–	–	X	–	X	X	–	X	–	–	X	–
	Mytilus edulis	X	X	X	–	X	X	–	X	X	X	X	X
Echinodermata	*Acrocnidia brachiata*	–	X	X	–	–	–	–	X	–	–	–	–
Community structure	Species diversity	2.04	1.77	1.42	1.08	2.85	2.72	0.99	2.18	1.68	1.82	2.54	1.50
	Equitability	0.44	0.39	0.31	0.24	0.62	0.60	0.22	0.48	0.37	0.40	0.56	0.33

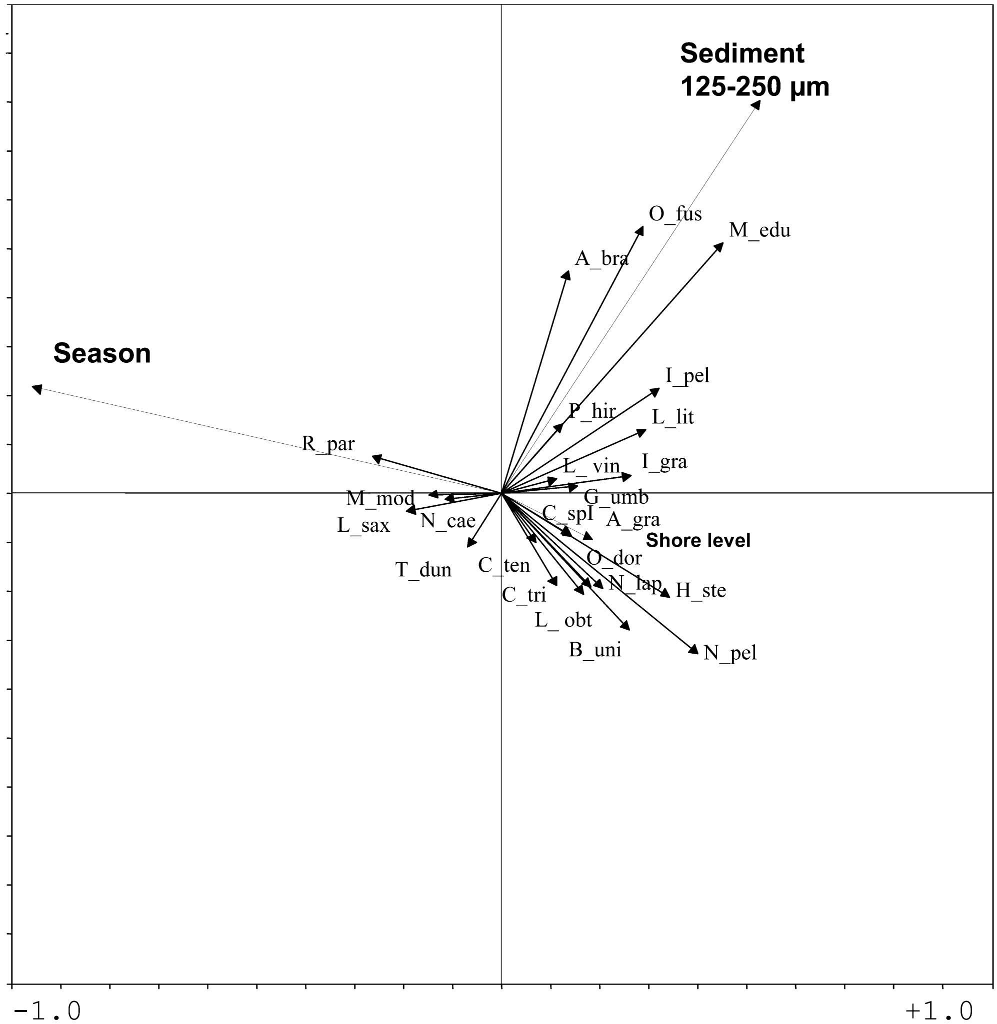

Fig. 3 *Osmundea pinnatifida* turf. RDA result showing distribution of associated animals and relationship between animals and environmental conditions. Species code: *A_bra Acrocnidia brachiata*; *A_gra Amphitrite gracilis*; *B_uni Barleeia unifastica*; *C_spI Capella* sp. I; *C_ten Cirriformia tentaculata*; *G_umb Gibbula umbilicalis*; *H_ste Hyale stebbingi*; *I_pel Idotea pelagica*; *I_gra I. granulosa*; *L_vin Lacuna vincta*; *L_lit Littorina littorea*; *L_obs L. obtusa*; *L_sax L. saxtilis*; *M_mod Modiolus modiolus*; *M_edu Mytilus edulis*; *N_cae Nephthys caeca*; *N_pel Nereis pelagica*; *N_lap Nucella lapillus*; *O_dor Oerstedia dorsalis*; *O_fus Owenia fusiformis*; *P_hir Pilumnus hirtellus*; *C_tri Cingula trifasciata*; *R_par Rissoa parva*; T_dul Tanais dulongii

pelagica). Group 2 species were mainly detritivores that feed on sediment (e.g. *Amphitrite gracilis*, *Acrocnidia brachiata*, *Mytilus edulis* and *Capitella* sp. I) and a tube-building species (*Owenia fusiformis*). However, this group also included a herbivore (*Littorina littorea*) and a predator (*Pilumnus hirtellus*), which may be indirectly influenced by sediment. Group 3 species were mostly herbivores that feed on epiphytes of *Osmundea pinnatifida* (e.g. *Hyale stebbingi*, *Idotea pelagica*, *I. granulosa*, *Gibbula umbilicalis*, *Barleeia unifasciata*, *Littorina obtusata* and *Lacuna vincta*), a detritivore (*Tanais dulongii*) and a carnivore (*Nucella lapillus*).

Faunal communities within the algal turfs

The RDA biplot (Fig. 3) showed the distribution of species with respect to the three significant ($P < 0.05$) environmental variables: season, sediment fraction (125–250 µm) and shore level. Season and sediment fraction (125–250 µm) had a greater influence than shore level, and the three variables were almost orthogonal. The species were generally distributed in the direction of one or other of these environmental variables, forming three groups: (1) associated with season – *Rissoa parva*, *Modiolus modiolus*, *Littorina saxtilis* and *Nephthys caeca*; (2) associated with sediment (125–250 µm) – *Acrocnidia brachiata*, *Owenia fusiformis*, *Mytilus edulis*, *Pilumnis hirtellus*, *Idotea pelagica* and *Littorina littorea*; and (3) associated with shore level – *Capitella* sp. I, *Cirriformia tentaculata*, *Amphitrite gracilis*, *Cingula trifasciata*, *Littorina obtusta*, *Nucella lapillus*, *Oerstedia dorsalis*, *Barleeia unifastica*, *Hyale stebbingi* and *Nereis pelagica*. A few species showed intermediate distributions – *Tanais dulongii* between seasons and shore elevation, and *Lacuna vincta*, *Idotea granulosa* and *Gibbula umbilicalis* between sediment (125–250 µm) and shore elevation. *T. dulongii* also showed a negative response with respect to sediment (125–250 µm).

Discussion

In contrast to the adjacent rock, *Osmundea* turf sustains an abundant fauna of small and juvenile animals.

Table 3 *Osmundea pinnatifida* turf. Summary of results from the stepwise multiple regression, separating species into categories for which the analysis selected species responding to: (a) site and season; (b) sediment; (c) all three factors. Final equations are presented and significance of individual variables is denoted as *ns* no significant relationship, + $P<0.10$, * $P<0.05$, ** $P<0.01$, *** $P<0.001$

	Species	r^2	Significant variables selected	Parameter	*F*-ratio	Probability
(a) Site and seasonal factors	*R. parva*	0.142	b_0	0.0169	0.13	ns
			Exposure	–0.0365	2.96	+
			Season	0.0540	6.47	*
	M. modiolus	0.1287	b_0	0.0311	0.30	ns
			Shore	0.041	5.62	*
			Exposure	–0.047	2.8	+
	N. caeca	0.0466	b_0	–0.0026	0.90	ns
			Season	0.003	2.83	+
	N. pelagica	0.1198	b_0	0.0632	12.63	***
			Season	–0.0316	7.89	**
(b) Sediment factors	*A. brachiata*	0.0797	b_0	–0.0046	0.52	ns
			Sediment 125–250 µm	0.0086	5.02	*
	P. hirtellus	0.3688	b_0	–0.1002	8.03	**
			Sediment < 63 µm	–0.1517	4.87	*
			Total sediment	0.0847	25.66	***
	A. gracilis	0.3566	b_0	0.0073	1.95	ns
			Sediment 1–2 mm	0.0101	2.90	+
			Sediment < 63 µm	0.0458	20.54	***
			Total sediment	–0.0103	7.41	**
	L. littorea	0.2617	b_0	–0.015	5.12	*
			Sediment > 2 mm	0.0166	4.98	*
			Sediment 63–125 µm	0.0233	2.59	+
	O. fusiformis	0.1279	b_0	–0.0062	2.86	+
			Sediment 125–250 µm	0.0064	8.50	**
	M. edulis	0.4710	b_0	0.7266	12.90	***
			Sediment > 2 mm	0.2086	10.08	**
			Sediment 500 µm–1 mm	0.2116	2.34	ns
			Sediment 125–250 µm	0.3026	11.23	**
			Sediment 63–125 µm	0.3357	10.61	**
			Total sediment	–0.5894	8.59	**
	Capitella sp. I	0.3326	b_0	0.042	3.01	+
			Sediment 1–2 mm	0.0450	2.63	ns
			Sediment < 63 µm	0.2090	19.74	***
			Total sediment	–0.0495	7.80	**
(c) Site, seasonal and sediment factors	*H. stebbingi*	0.5450	b_0	1.11227	38.85	***
			Sediment 125–250 µm	0.13614	2.55	+
			Sediment 250–500 µm	–0.3295	33.21	***
			Sediment < 63 µm	0.5856	6.31	**
			Shore	–0.213	17.32	***
			Exposure	0.1165	2.650	+
			Season	–0.2576	19.75	***
	I. pelagica	0.3310	b_0	0.1333	6.85	*
			Sediment > 2 mm	0.0619	7.48	**
			Shore	0.0238	4.61	*
			Exposure	–0.0463	4.53	*
			Season	–0.0343	3.42	*
			Total sediment	–0.02645	2.44	+
	I. granulosa	0.5973	b_0	0.3322	16.49	***
			Sediment 63–125 µm	0.1865	3.07	+
			Sediment < 63 µm	–0.4861	17.13	***
			Exposure	–0.181	27.05	***
			Season	–0.1013	5.01	*
			Total sediment	0.0974	10.45	**
	T. dulongii	0.4198	b_0	0.2755	6.97	*
			Sediment 250–500 µm	0.2906	37.39	***
			Sediment 125–250 µm	–0.1042	8.07	**
			Sediment < 63 µm	–0.4960	10.82	**
			Shore	–0.0573	3.02	+
			Season	–0.0685	3.35	+
	G. umbilicalis	0.2700	b_0	0.0068	1	ns
			Sediment > 2 mm	0.0180	18.04	***
			Sediment < 63 µm	–0.0236	3.70	+
			Exposure	–0.0109	5.30	*

Table 3 Contd.

Species	r^2	Significant variables selected	Parameter	F-ratio	Probability
B. unifasciata	0.2953	b_0	–0.0372	1.45	ns
		Sediment 500 μm–1 mm	0.1539	17.82	***
		Sediment 250–500 μm	–0.1455	15.76	***
		Exposure	0.0308	2.95	+
		Season	–0.0272	4.01	+
L. obtusata	0.545	b_0	0.2975	75.05	***
		Sediment >2 mm	0.0253	3.15	+
		Sediment 63–125 μm	–0.1848	26.49	***
		Exposure	–0.0313	4.76	*
		Season	–0.1286	48.19	***
L. vincta	0.3063	b_0	0.0011	0.06	ns
		Sediment >2 mm	0.0143	23.33	***
		Sediment <63 μm	–0.0212	6.19	*
		Exposure	–0.0062	3.50	+
N. lapillus	0.5346	b_0	0.2645	55.10	***
		Sediment >2 mm	0.057	14.77	***
		Sediment 63–125 μm	–0.1466	15.48	***
		Exposure	–0.0432	8.43	**
		Season	–0.1168	36.94	***

Although, 33% of these are herbivores, they do not often consume the *Osmundea* plants. Like most of its close relatives, *O. pinnatifida* contains halogenated secondary metabolites that are known to repel grazers (Erickson 1983; Hay and Fenical 1988). Indeed, *Littorina littorea*, one of the commonest grazers in the intertidal zone, is known to shun *O. pinnatifida* in preference to other algae (Watson and Norton 1985). However, since the turf-dwelling herbivores do not venture out beyond the turf, even when the tide is in, they must feed on microalgal epiphytes or diatoms that colonise the *Osmundea* fronds or on the sediment.

Unlike most intertidal microhabitats, such as crevices, overhangs, and pools, which are permanent features of the topography, algal turfs are living habitats that vary seasonally in their structure. *O. pinnatifida* has a perennial, prostrate holdfast that produces erect fronds during the late summer. Frond density rapidly develops and forms dense turfs in October and biomass reaches its maximum in early winter. Most fronds then bleach and die back in summer. It is, therefore, not surprising that 50% of the species that inhabit the turf are more abundant in late autumn when the turf is at, or near, maximum development. Exceptions include *Rissoa parva* and *Tanais dulongii* which reproduce and reach their maximum number during summer (Brown 1984; White 1987). Thus, the seasonal change in the turf structure influences the diversity and abundance of animals. Greater complexity of an algal stand supports a greater diversity of associated animals (Myers and Southgate 1980; Davenport et al. 1999).

Physical factors such as exposure to desiccation are related to shore elevation and wave action and are known to control the distribution of the most abundant species on the shore (Lewis 1964), but much less is known about such constraints upon small or juvenile organisms for which the microhabitat may be influential.

Although the fauna was sampled across the lower and upper limits of the *Osmundea* zone, only four animal species exhibited any significant effect attributable to shore level. This is probably because the effects of desiccation are greatly reduced within the turf, which even at its upper limit remains damp throughout the low tide. When the tide is out, limpets cluster around the margin of the turf patches, presumably to benefit from the proximity to moisture. Even juvenile *Modiolus*, which as adults are confined to the sublittoral zone, and suffer greatly when exposed to the air (Coleman and Trueman 1971; Gillmor 1982), colonise and, at least temporarily, survive within the turfs. Other turf dwellers, such as *Nucella lapillus*, a common intertidal carnivore, are also found in rock crevices, which also provide a damp haven when the tide retreats, but they forage for barnacles on the open rock when submerged.

Animals on intertidal rocky shores are often controlled by the degree of wave exposure and may even be washed away by the surf (Lewis 1964). However, within the microhabitat of algal turfs they are protected to some extent from wave action. It could, however, influence them indirectly through the amount of sediment accumulated in the turfs. Greater water turbulence on more exposed shores (Denny 1988) can have conflicting effects. On the one hand wave action resuspends bottom sediment thereby increasing sediment supply, but on the other hand it can prevent sediment from settling, or even flush out previously trapped sediment from the turf. Once sediment is resuspended by turbulence, the larger particles will sink more rapidly than smaller ones and are therefore more likely to be trapped by the turf. Although the effects of water turbulence are complex, we found a greater abundance of sediment on the sheltered shore, which is likely to be supplied by an adjacent sandy beach, and much less sediment accumulation on exposed shores and at the lower shore levels, where there is greater water movement.

Sediment accumulation is not only influenced by wave action but also by season. On the shore, stormy weather during winter increased sediment loads fivefold in the water over the intertidal zone compared with summer loads (Jenkins 1995). The interaction between the greater sediment supply and the longer and bushier fronds in winter explains the abundance of sediment trapped in the turfs. The great variations of sediment accumulation indicated substantial sediment movement within turfs. Sediment movement is a disturbance factor which reduces stability and limits the diversity of the animals, both on rocky shores and in soft-bottom communities (Littler et al. 1983; Snelgrove and Butman 1994) as well as in *Osmundea* turfs.

Most of the species found in the present study showed less relation to shore elevation and degree of wave exposure than to sediment accumulation, which influenced 67% of the associated animal species. Generally, localised patches of sediment induce a spatial heterogeneity which increases species diversity in rocky-shore communities (McQuaid and Dower 1990). The sediment within *Osmundea* turfs provides a habitat suitable for a range of organisms that require sediment, which is otherwise scarce elsewhere on the rocky shores we studied. We found that 46% of such animals are detritivores, including the polychaetes *Capitella* sp. I and *Cirriformia tentaculata*, which are normally found in soft sediment rather than on seaweeds.

Not surprisingly, we found that most of the detritivores showed a strong correlation with sediment accumulation. An exception was the snail *Rissoa parva* which might be more influenced by its reproduction during summer (Southgate 1982) resulting in greater density. Sediment provides a food source for filter feeders and building material for tube dwellers. The abundance of *T. dulongii*, a tube-building species, showed a strongly positive relationship with the abundance of the sediment fraction in the 250–500 μm range, which it uses for constructing its tube (White 1987), and a tube-building polychaete, *Owenia fusiformis*, in the 125–250 μm range.

Surprisingly, all the herbivores within the turfs also showed a strong relationship with sediment accumulation. Most herbivores were associated with coarse sediment (>2 mm) and had a negative correlation with finer sediment (<63–125 μm), except *Hyale stebbingi*. The coarser sediment might be expected to damage or even scour away the epiphytes that are a food source for the herbivores (D'Antonio 1986). It is also possible that the sediment encourages the growth of micro-organisms that serve as a food source for the mesograzers, which are unlikely to feed on *Osmundea pinnatifida* itself. For example, some littorinid snails prefer to feed on micro-organisms on the surface of rock, mud, sand or gravel if edible seaweeds are unavailable (Norton et al. 1990). However, coarser sediment is likely to contain less nutrients for micro-organisms (Snelgrove and Butman 1994). Therefore, it is still unclear why such coarse sediment showed a positive relationship to the herbivores. Finer sediment reduces light and oxygen levels (Devinny and Volse 1978), and we found anoxic conditions in which very fine sediment had accumulated, creating an unfavourable habitat for most animals.

However, there must also be biotic interactions between the animals in this microcommunity. *Rissoa parva*, for example, is scarce in turfs on the sheltered shore where its predator *Pilumnius hirtellus* is present, and abundant on the wave-exposed shore where turbulence eliminates *P. hirtellus*.

We conclude that the main structuring factors for most intertidal communities, desiccation and wave exposure, have less influence on the turf fauna, except in so far as they affect sediment accumulation. As for the biotic factors that are known to be influential on the shore, e.g. competition and predation, we have little knowledge of the conflicts within the crowded micro-world of algal turfs.

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References

Airoldi L, Rindi F, Cinelli F (1995) Structure, seasonal dynamics and reproductive phenology of a filamentous turf assemblage on a sediment-influenced, rocky subtidal shore. Bot Mar 38:227–237

Airoldi L, Fabiano M, Cinelli F (1996) Sediment deposition and movement over a turf assemblage in a shallow rocky coastal area of the Ligurian Sea. Mar Ecol Prog Ser 133:241–251

Aller JY, Stupakoff I (1996) The distribution and seasonal characteristics of benthic communities on the Amazon shelf as indicators of physical processes. Cont Shelf Res 16:717–751

Braak CJF ter, Smilauer P (1998) CANOCO 4 reference manual and user's guide to Canoco for Windows: software for canonical community ordination (version 4). Microcomputer Power, Ithaca, N.Y.

Brown RA (1984) Geographical variations in the reproduction of the horse mussel, *Modiolus modiolus* (Mollusca: Bivalvia). J Mar Biol Assoc UK 64:751–770

Chandrasekara WU, Frid CLJ (1998) A laboratory assessment of the survival and vertical movement of two epibenthic gastropod species, *Hydrobia ulvae* (Pennant) and *Littorina littorea* (Linnaeus), after burial in sediment. J Exp Mar Biol Ecol 221:191–207

Chapman G (1995) Aspects of the fauna and flora of the Azores. The density of animal life in the coralline alga zone. Ann Mag Nat Hist 95:801–805

Coleman N, Trueman ER (1971) The effect of aerial exposure on the activity of the mussels *Mytilus edulis* L. and *Modiolus modiolus* (L.). J Exp Mar Biol Ecol 7:295–304

D'Antonio CM (1986) Role of sand in the domination of hard substrata by the intertidal alga *Rhodomela larix*. Mar Ecol Prog Ser 27:263–275

Daly MA, Mathieson AC (1977) The effect of sand movement on intertidal seaweeds and selected invertebrates at Bound Rock, New Hampshire, USA. Mar Biol 43:45–55

Davenport J, Butler A, Cheshire A (1999) Epifaunal composition and fractal dimensions of marine plants in relation to emersion. J Mar Biol Assoc UK 79:351–355

Denny MW (1988) Biology and the mechanics of the wave-swept environment. Princeton University Press, Princeton, N.J.

Devinny JS, Volse LA (1978) The effect of sediment on the development of *Macrocystis pyrifera* gametophytes. Mar Biol 48:343–348

Eleftheriou A, Basford DJ (1989) The macrobenthic infauna of the offshore northern North Sea. J Mar Biol Assoc UK 69:123–143

Erickson KL (1983) Chemical and biological perspectives. In: Marine natural products. V. Scheuer PJ (ed) Academic Press, New York, pp 131–257

Gillmor RB (1982) Assessment of intertidal growth and capacity adaptations in suspension-feeding bivalves. Mar Biol 68:277–286

Hay ME, Fenical W (1988) Marine plant–herbivore interactions: the ecology of chemical defense. Annu Rev Ecol Sys 19:111–145

Jenkins SR (1995) The ecology of sheltered, canopy dominated shores. PhD thesis. University of Liverpool

Kain JM, Norton TA (1990) Marine ecology. In: Biology of red algae. Cole KM, Sheath RG (eds) Cambridge University Press, Cambridge, pp 377–422

Kendrick GA (1991) Recruitment of coralline crusts and filamentous turf algae in the Galapagos archipelago: effect of simulated scour, erosion and accretion. J Exp Mar Biol Ecol 147:47–63

Lewis JR (1964) The ecology of rocky shores. English Universities Press, London

Little C, Smith LP (1980) Vertical zonation on rocky shores in the Severn estuary. Estuar Coast Mar Sci 2:651–669

Littler MM, Martz DR, Littler DS (1983) Effects of recurrent sand deposition on rocky intertidal organisms: importance of substrate heterogeneity in a fluctuating environment. Mar Ecol Prog Ser 11:129–139

Marshall DJ, McQuaid CD (1989) The influence of respiratory responses on the tolerance to sand inundation of the limpets *Patella granularis* L. (Prosobranchia) and *Siphonaria capensis* Q. et G. (Pulmonata). J Exp Mar Biol Ecol 128:191–201

McQuaid CD, Dower KM (1990) Enhancement of habitat heterogeneity and species richness on rocky shores inundated by sand. Oecologia 84:142–144

Myers AA, Southgate T (1980) Artificial substrates as a means of monitoring rocky shore cryptofauna. J Mar Biol Assoc UK 60:963–975

Neushul MM, Foster MS, Coon CA, Woessner JW, Harger BWW (1976) An in situ study of recruitment, growth and survival of subtidal marine algae: techniques and preliminary results. J Phycol 12:387–408

Norton TA (1978) The factors influencing the distribution of *Saccorhiza polyschides* in the region of Lough Ine. J Mar Biol Assoc UK 58:527–536

Norton TA, Hawkins SJ, Manley NL, Williams GA, Watson DC (1990) Scraping a living. A review of littorinid grazing. Hydrobiologia 193:117–138

Nuemann AC, Gebelein CD, Scoffin TP (1970) The composition, structure and erodability of subtidal mats, Abaco, Bahamas. J Sedim Petrol 40:274–297

SAS (1985) SAS user's guide: statistics. SAS Institute Inc., Cary, N.C.

Scoffin TP (1970) The trapping and binding of subtidal carbonate sediments by marine vegetation in Bimini Lagoon, Bahamas. J Sedim Petrol 40:249–273

Snelgrove PVR, Butman CA (1994) Animal–sediment relationship revisited: cause versus effect. Oceanogr Mar Biol Annu Rev 32:111–177

Southgate T (1982) Studies on an intertidal population of *Rissoa parva* (Gastropoda: Prosobranchia) in south-west Ireland. J Nat Hist 16:183–194

Stephenson TA, Stephenson A (1972) Life between tidemarks on rocky shores. Freeman, San Francisco

Stewart JG (1983) Fluctuations in the quantity of sediment trapped among algal thalli on intertidal rock platforms in southern California. J Exp Mar Biol Ecol 73:205–211

Stewart JG (1989) Establishment, persistence and dominance of *Corallina* (Rhodophyta) in algal turf. J Phycol 25:436–446

Taylor PR, Littler MM (1982) The roles of compensatory mortality, physical disturbance, and substrate retention in the development and organization of a sand-influenced, rocky-intertidal community. Ecology 63:135–146

Watson DC, Norton TA (1985) Dietary preferences of the common periwinkle *Littorina littorea*. J Exp Mar Biol Ecol 88:193–211

White NJ (1987) Distribution, reproduction and growth in *Tanais dulongii* (Audouin) PhD thesis, University of Liverpool

Whorff JS, Whorff LL, Sweet MH III (1995) Spatial variation in an algal turf community with respect to substratum slope and wave height. J Mar Biol Assoc UK 75:429–444