

The effects of grazing on the distribution and composition of low-shore algal communities on the central coast of Portugal and on the southern coast of Britain

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Abstract

A red algal turf is often found just below the barnacle/limpet zone of many European shores, especially on steep shores of moderate exposure. The hypothesis that grazing by limpets determines the upper limit of distribution of this red algal turf was tested on moderately exposed shores in Portugal and Britain. We also aimed to assess whether the grazing effect is modified at various spatial scales. Grazers were excluded by fences, with half-fenced and unfenced controls. Exclusion plots were rapidly colonised by green ephemeral algae in the months immediately after the beginning of the experiment (summer); these algae were later replaced by perennial algae. The percentage cover of turf-forming macroalgae showed a significant increase at both locations. The upper limit of distribution extended more than 50 cm on most of the shores studied. In contrast, control and half-fenced plots remained devoid of algae. After 2 years, ungrazed plots were mainly colonised by a red algal turf (e.g. *Caulacanthus ustulatus*, *Gelidium* spp., *Laurencia pinnatifida*) in Portugal, while canopy cover (*Fucus serratus* and *Himantalia elongata*) dominated in Britain in marked contrast to

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the grazed plots. Physical factors acting at both local and geographical scales may explain these differences. However, although physical factors probably have an important influence on the identity, size and abundance of sublittoral fringe macroalgae, grazers play a major role in directly setting their upper limits. The effect of grazing by limpets was not consistent for all of the morphological algal groups and spatial scales considered in the present study. The effect of grazing on the cover of turf algae varied between Portugal and Britain (location scale), while effects on ephemeral and canopy algal cover varied at the shore scale within location. © 2002 Elsevier Science B.V. All rights reserved.

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1. Introduction

Considerable attention has been devoted to the study of the causes of vertical distribution patterns of algae and sessile animals on rocky shores. In the 1970s a paradigm emerged that upper limits were set by physical factors and lower limits by biological interactions (Connell, 1972). Physical factors had long been thought to set the upper limits of most intertidal species (e.g. Baker, 1909), and subsequent experiments and observations of high shore kills during extreme events have shown the importance of stress associated with desiccation in directly setting the upper limits of high and midshore fucoid species (e.g. Schonbeck and Norton, 1978; Hawkins and Hartnoll, 1985). Lower on the shore, physical factors have also been shown to set the upper extent of some red algal species (Lubchenco, 1980; Carter and Anderson, 1991).

In addition to extensive experimental evidence that biological interactions can set lower limits (reviewed in Connell, 1972; Norton, 1985), evidence has accumulated that grazing and competition can set upper limits of some species (e.g. Schonbeck and Norton, 1980; Hawkins and Hartnoll, 1985). Underwood (1980) and co-workers (Underwood and Jernakoff, 1981, 1984) clearly demonstrated that the upper limit of foliose macroalgae in Australian shores was primarily set by herbivorous molluscs. Thus, the upper limits of these lower algal beds would depend on the grazing of algal propagules by gastropods and only in the absence of grazers would physical factors become important in determining the upper limit of macroalgae (Jernakoff, 1983; Underwood, 1985).

On many European rocky shores the low shore is dominated by a turf of red algae. It is especially prevalent on more steeply sloping shores and often there is a very sharp boundary giving way to limpets and barnacles. This pattern occurs throughout the British Isles (Lewis, 1964) and further south down to Portugal (Saldanha, 1974). In Europe, less work has been done on the upper limits of low-shore species than elsewhere in the world. Observations of broad-scale death of limpets following the Torrey Canyon oil spill has suggested that grazing restricts the upper limit of low-shore algae (Southward and Southward, 1978).

The overall aim of this work was to understand what factors determine vertical distribution patterns on the shore. The hypothesis that grazing by limpets directly determines the upper limit of distribution of the red algal turf was tested. The work was

undertaken in both Portugal and Britain with a nested experimental design to enable spatial scale comparisons.

Most experimental work on the effects of grazing on rocky shore distribution patterns has been restricted to one locality (but see Benedetti-Cecchi et al., 2000). We have taken a broader approach, making comparisons between locations, shores within locations and patches within shores to test for generality of process in setting the upper limit of turf-forming algae by limpet grazing.

2. Methods

2.1. Study sites and organisms

This study was carried out on the central coast of Portugal and southern coast of Britain. Two shores were chosen in each country (location): Cabo Raso (38°42' N, 9°29' W) and Estoril (38°42' N, 9°23' W) in Portugal, Heybrook Bay (50°22' N, 4°11' W) and Swanage (50°37' N, 1°57' W) in Britain (see Grubb, 1936 for description of Swanage). These shores were selected as they showed a red algal zone with a sharp upper limit of distribution. The reefs with these characteristics had a slope of more than 25°.

The Portuguese shores have a mean tidal range during spring tides of 2.84 m. The substratum is limestone bedrock that faces the open Atlantic Ocean. Strong surf action is frequent in winter but storms are interspersed with periods of sufficient calm to allow shore visits. Mean tidal range of spring tides at Heybrook Bay and Swanage is 4.70 and 1.50 m, respectively. Both are typical moderately exposed English Channel shores. Although the Portuguese shores were more exposed than those in the UK, a similar clearly visible boundary existed between the limpets and barnacles zone and a band dominated by a red algal turf.

The experimental area comprised the upper part of the red algal turf and the lower mid-shore zone composed of bare rock, limpets, encrusting algae and few barnacles, between mean low water of neap and mean low water of spring tides. The algal turf was essentially composed of articulated coralline and corticated macrophyte algae. Some differences in species composition and abundance were found in Portugal and in the UK. *Gelidium* spp. and *Caulacanthus ustulatus* (Mertens) Kützing were more abundant in Portugal, while *Mastocarpus stellatus* (Stackhouse) Guiry was more frequent in Britain. Canopy-forming algae such as *Himanthalia elongata* (L.) S.F. Gray and *Fucus serratus* L. only occurred in Britain and the encrusting alga *Lithophyllum lichenoides* Philippi was only found at the Portuguese location. Other macroalgae in both locations comprised a variety of filamentous red and foliose green algae, encrusting coralline algae and noncalcareous crusts. The most common herbivores were limpets although trochids (*Gibbula* spp.) were also present at Heybrook Bay and in Portugal. Limpet species on the Portuguese shores included *Patella depressa* Pennant and *P. ulyssiponensis* Gmelin (often called *P. aspera* Röding). On British shores, *P. vulgata* L., *P. depressa* and *P. ulyssiponensis* were all present in the experimental area.

2.2. Experimental design

In order to test the null hypothesis that there was no influence of grazing by limpets (*Patella* spp.) on the upper limits of distribution of the red algal turf, the limpets were excluded by fences with half-fenced and unfenced controls. In exclusion treatments (E), fences were put on the shore and all macrograzers were removed. Half-fenced plots (HF) were used as controls with no manipulation of grazers to test if there was any artifact in the experiment due to the use of fences. The half-fences allowed limpet grazing and tested whether algal settlement was enhanced or reduced by the fence structure either by direct or indirect effects. Unfenced control plots (C) were marked with screws in each corner but with no fences and no manipulation of grazers. Two “patches” were chosen on each of the shores and three replicates of each treatment were randomly assigned within each “patch”.

Similar fixed plots of 1 × 0.5 m were chosen in each patch and the treatment and controls were allocated randomly to them. These strips comprised the upper part of the red algal belt (approximately 40 cm) and the lower part of the mid-shore devoid of macroalgae (except for some encrusting species). This region of the shore was chosen to see if the red algal zone would extend up the shore in the absence of limpets, either from propagules or vegetative growth. The plots were selected according to the following criteria: the presence of red algal turf with a sharp upper limit of distribution, rock slope greater than 25°, presence of limpets in the plots prior to any manipulation.

Fences made of a square mesh (13 × 13 mm) welded plastic-coated steel wire were attached to the rock by screws fixed into rawl-plugs in holes drilled by a petrol-driven drill (Ryobi ER160). On the first day of the experiment, fences were put on the shore, limpets and other grazers were removed from exclusion plots. The plots were sampled non-destructively on this and subsequent occasions. The percentage cover of algae and sessile animals was estimated in 50 × 50-cm quadrats by the intersection point method (49 points). To quantify algal abundance, substrate cover and canopy cover were always distinguished. Thus, a quadrat with several layers of different algal species could have more than 100% of total algal cover. The remaining sessile species present inside the quadrat that did not match any intersection point were recorded and arbitrarily assigned 1% value. The total numbers of limpets and trochids were counted. Plots were sampled either directly in the field or in the laboratory from 35-mm colour slides of the plots (with the sampling quadrat) analysed under a binocular stereoscopic microscope. Photographic estimates were only used when the weather and sea conditions did not allow time for observation in the field. This procedure was only applied to plots with a single algal layer and to sessile species. Thus, British plots, which often had a canopy layer, were always assessed on the shore.

This experiment was started in the summer of 1996 in both countries. The patches were sampled at monthly intervals for the first 6 months and then about every 2 months until the end of the second year. The top and bottom quadrats were sampled in each plot but only the data from the top quadrats were analysed in this study. During each visit to the shore, fences were checked and repaired if necessary. Any invading limpets were also removed from exclusion plots. Herbivore exclusion seemed to be more effective in Britain than in Portugal. Small limpets persistently entered the exclusions in Portuguese shores. This is probably related to the size and density of limpets on these shores. Additionally, fences in

Portugal needed frequent repair during the winter due to wave action. Thus, the “exclusion treatment” of this experiment should be regarded as a significant decrease but not total absence of grazers.

2.3. Morphological groups

A morphological group approach was also adopted for the analysis and presentation of results. Such an approach can be applied more broadly in space for making biogeographical comparisons (Steneck and Dethier, 1994). Algae were grouped in functional form groups as described by Littler and Littler (1980, 1984) and Steneck and Watling (1982). In our study, the following morphological groups were designated: microalgae, ephemeral algae, turf-forming algae, canopy, calcareous turf-forming algae, crustose coralline algae, noncalcareous crusts. Data on individual species are also presented where appropriate.

2.4. Data analysis

Total algal cover, algal species richness, and algal cover of the different morphological groups were analysed using a four-way mixed model ANOVA. The factors tested were “grazing treatments” (fixed, orthogonal, three levels), “locations” (random, orthogonal, two levels), “shores” (random, nested within location, two levels), and “patches” (random, nested within shores and location, two levels). Note that the location factor is random and should not be regarded as a Portugal vs. Britain comparison.

Cochran’s *C*-test was used to check homogeneity of variance. Where this assumption was violated, arcsine transformations were used (Underwood, 1997). When variances remained heterogeneous after transformation, significant results were still discussed but should be regarded with some caution. Nonsignificant results are perfectly acceptable since this problem can lead to excessive type I error (rejecting the null hypothesis when it is true) (Underwood, 1997).

For each morphological group, data were analysed at two dates. Only spatial differences were tested at each one of these dates. Time-related comparisons were not made due to nonindependence of repeatedly sampled plots. Tests of homogeneity, ANOVA and SNK (Student–Newman–Keuls) a posteriori comparison tests were done using GMAV5 for Windows Statistical Software (Institute of Marine Ecology, Sydney, Australia).

3. Results

3.1. Limpet density

There were no differences in the abundance of limpets in control and half-fenced treatments (12 months $F_{1,1}=3.26$, $P>0.05$; 24 months $F_{1,1}=0.01$, $P>0.98$). Grazer abundance fluctuated greatly during the 2 years but with the same trends in control and half-fenced plots (Fig. 1). There were significant differences in the number of limpets in

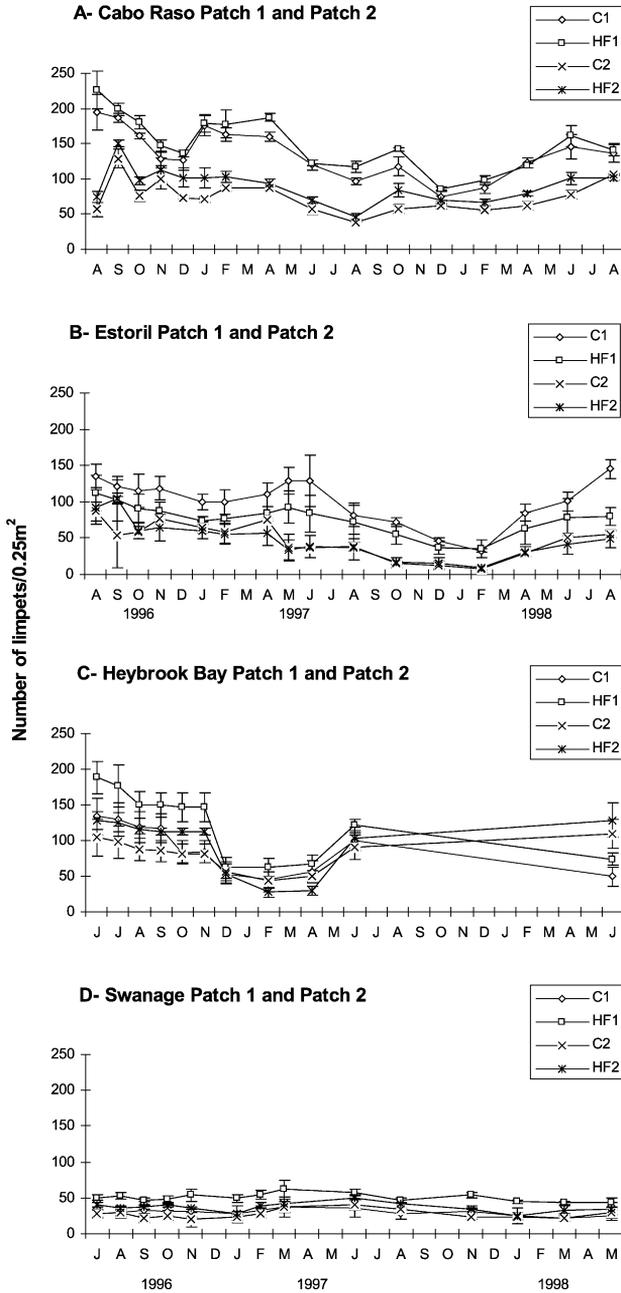


Fig. 1. Mean number (\pm SE) of limpets in grazed treatments. C—control, HF—half-fenced; -1—patch 1, -2—patch 2.

different patches after both 12 ($F_{4,32} = 11.63$, $p < 0.001$) and 24 months ($F_{4,32} = 13.08$, $p < 0.001$). The mean number of limpets was higher in patch 1 than patch 2 in Cabo Raso and Estoril and also in Heybrook Bay on the last sampling date (Fig. 1). Swanage consistently registered lower limpet density and less variation than the other shores.

3.2. Total algal cover

Percentage cover of total macroalgae was far greater in exclusions than either in control or half-fenced treatments (Fig. 2) throughout the experiment. On all shores except Heybrook Bay, treatment effects were apparent after 1 month (Fig. 2, Table 1). Two years after the starting date, algal cover was significantly higher in exclusion plots than unfenced control and half-fenced control for all the shores (Table 1, SNK test).

In addition to the clear differences between ungrazed and grazed areas, there were some differences in the effect of grazers from shore to shore (Table 1, $\text{Gr} \times \text{Sh}(\text{Lo})$ significant at 1 and 24 months). Cabo Raso showed an initial increase of algal cover (80%) with a subsequent decline of 15% on the second month; then there was a more gentle recovery and after February (6 months), percentage cover values remained above 85% until the end of the experiment (Fig. 2a). At Estoril, variation in algal cover was greater, and only approached maximal levels from 12 months onwards (Fig. 2b). Rapid increase in cover had occurred by the end of the first month at Swanage (62% cover, Fig. 2d); such an increase was only apparent, however, by the sixth month at Heybrook Bay (Fig. 2c). Both sets of controls remained almost devoid of macroalgae at Swanage (Fig. 2d). At Heybrook Bay, however, there was some algal colonisation of other plots (Fig. 2c).

3.3. Algal colonisation

Limpet exclusion experiments had different effects on the algal assemblage, depending upon the experimental spatial scale and the morphological group considered (see Figs. 3, 4 and 5 and Table 2 for the most important morphological algal groups). Abundance of individual important species is also given (Fig. 6), plotted for exclusion only as virtually no new species colonised half-fenced and control plots, although encrusting forms persisted.

There were no significant differences among treatments for any of the three major morphological groups at the start of the experiment (Table 2). Only turf algae showed a significant difference between patches at Swanage at time zero (Table 2, SNK tests) but mean values were still very low ($P1 = 3.5\%$, $P2 = 0.2\%$) and had no influence on the outcome of the experiment. Thus, the start conditions were very similar in all plots.

Ephemeral algae significantly increased in exclusion plots in the first month on all shores except Heybrook Bay (Table 2, SNK tests). The response of this morphological group to removal of grazers was much more evident at the beginning of the experiment (Fig. 3a,b,d). Variances were heterogeneous, so these significant differences should be regarded with some caution. From the first month onwards, differences between exclusions and controls were observed occasionally on a specific shore (e.g. Estoril and Swanage, see Fig. 3b,d). Although some variability was evident, ephemeral algae (mainly

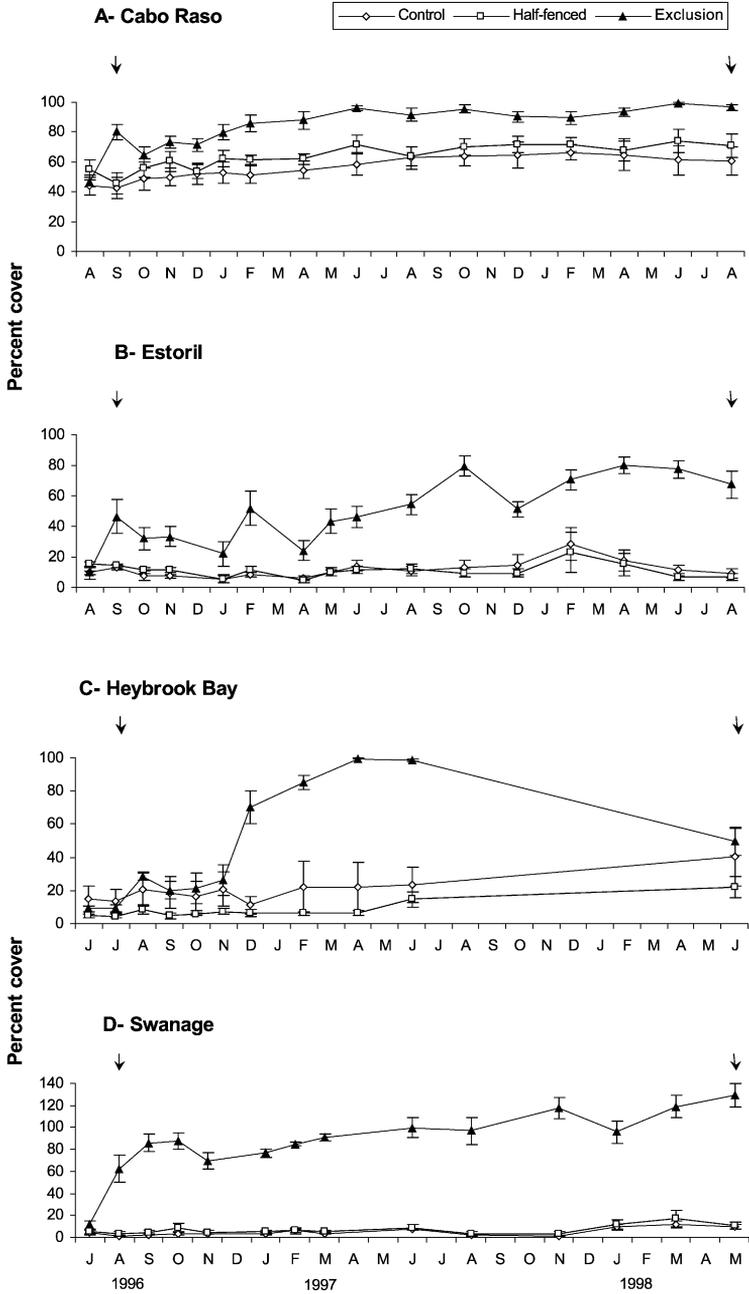


Fig. 2. Effects of limpet exclusion on mean (\pm SE)% of total algal cover on the different shores. Arrows indicate dates for which data were analysed. Data were pooled across patches at each shore.

Table 1
ANOVA on the total percentage cover in response to limpet exclusion

Source of variation	df	Total algal cover			
		1 month		24 months	
		MS	F	MS	F
Grazing = Gr	2	4241.18	162.47**	26 690.90	40.71*
Location = Lo	1	6701.65	3.14 ns	4118.54	0.39 ns
Shore (Lo) = Sh(Lo)	2	2130.89	9.96*	10 622.96	24.14**
Patch (Lo × Sh) = Pa (Lo × Sh)	4	213.94	2.42 ns	440.06	2.23 ns
Gr × Lo	2	26.10	0.02 ns	655.58	0.15 ns
Gr × Sh(Lo)	4	1089.98	6.74*	4245.69	27.54***
Gr × Pa(Lo × Sh)	8	161.84	1.83 ns	154.18	0.78 ns
Residual	48	88.46		197.62	
Cochran's test		C = 0.30, $p < 0.01$		C = 0.16 ns	
Transformation:		ArcSin (%)		none	
SNK tests		Gr × Sh(Lo), SE = 5.19		Gr × Sh(Lo), SE = 5.07	
		Cabo Raso, C = HF < E*		Cabo Raso, C = HF < E**	
		Estoril, C = HF < E*		Estoril, C = HF < E**	
		Heybrook Bay, ns		Heybrook Bay, C = HF < E*	
		Swanage, C = HF < E**		Swanage, C = HF < E**	

ns = not significant.

* $p < 0.05$.

** $p < 0.01$.

*** $p < 0.001$.

Ulva sp. and *Enteromorpha* sp.) generally declined at all Portuguese shores after the second month. This pattern was shown clearly at patch 1 in Cabo Raso (Fig. 6a). At Estoril (patch 2) the cover of ephemeral algae showed considerable fluctuations throughout the remainder of the experiment (Fig. 6d). At Swanage, cover remained relatively high during the first year (Fig. 6g,h). This ephemeral phase was missing at Heybrook Bay (Fig. 6e,f). The lack of ephemeral algae on this shore explains the absence of differences in total algal cover after 1 month as reported above.

The effects of grazers on structurally more complex algae such as turfs became evident only after 6 months at Cabo Raso (Fig. 4a), and even later on the other shores. An interaction between grazing treatments and location was found after 2 years, indicating that the effect of limpets varied with the location. Percentage cover of turf algae was significantly higher in exclusion treatments in both Portugal and UK but this effect was greater in the southern European location (mean value for exclusion plots of 43.5% in Portugal and of 19.6% in the UK). In Portugal (Fig. 6a,b,c,d), the turf-forming *C. ustulatus* dominated the exclusion plots at the end of the experiment (values between 39% and 41% in the different patches), followed by the turf-forming *Gelidium* sp. in patch 1 of Cabo Raso (Fig. 6a) and patch 2 at Estoril (Fig. 6d).

Very different colonisation patterns occurred in Britain. Despite the significant increase in red algae, the exclusions eventually became dominated by canopy-forming brown algae, which started to colonise the plots after the fifth month. Canopy cover became very dense

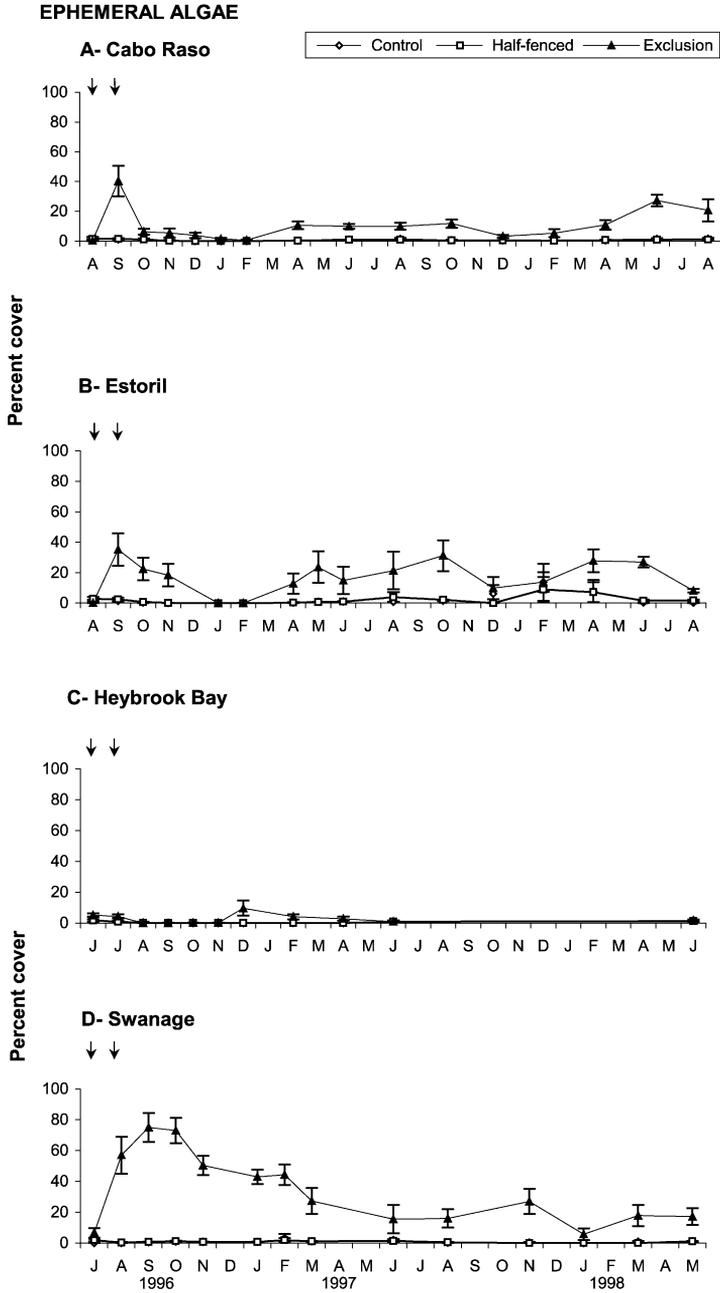


Fig. 3. Effects of limpet exclusion on the mean% cover (\pm SE) of ephemeral algae on the different shores. Arrows indicate dates for which data were analysed. Data were pooled across patches at each shore.

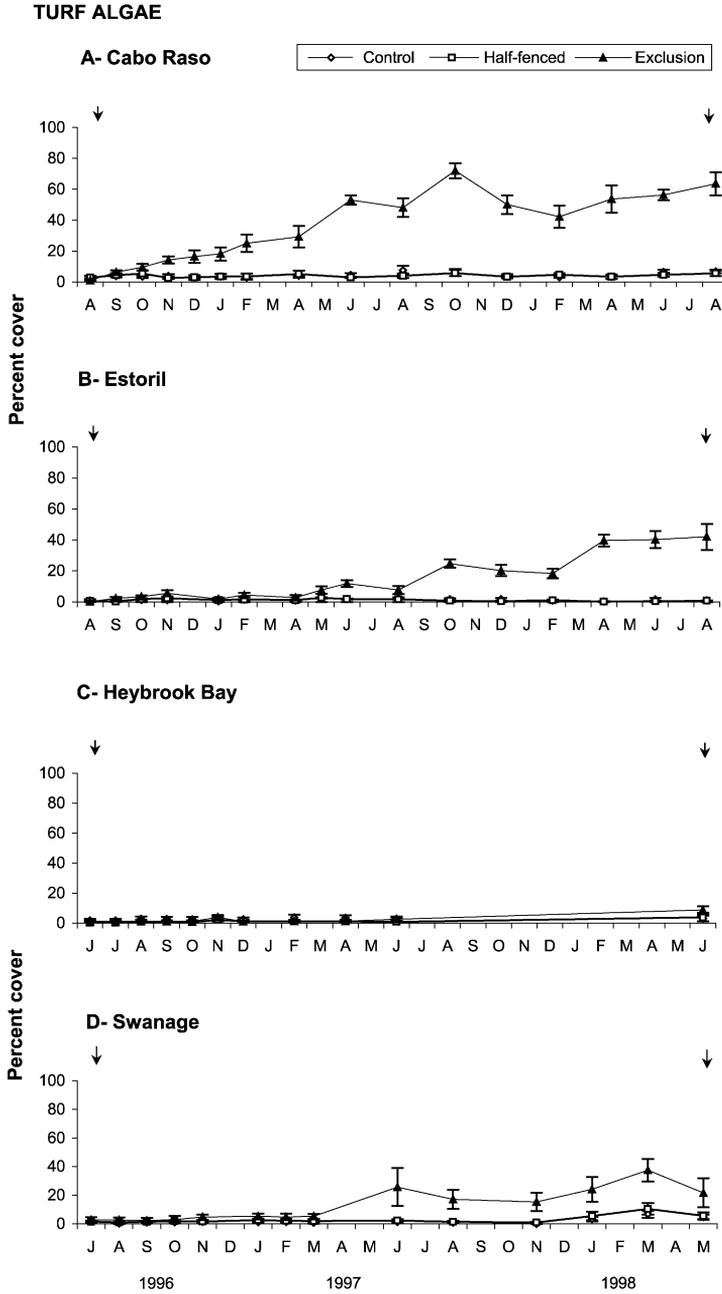


Fig. 4. Effects of limpet exclusion on the mean% cover (\pm SE) of turf algae on the different shores. Arrows indicate dates for which data were analysed. Data were pooled across patches at each shore.

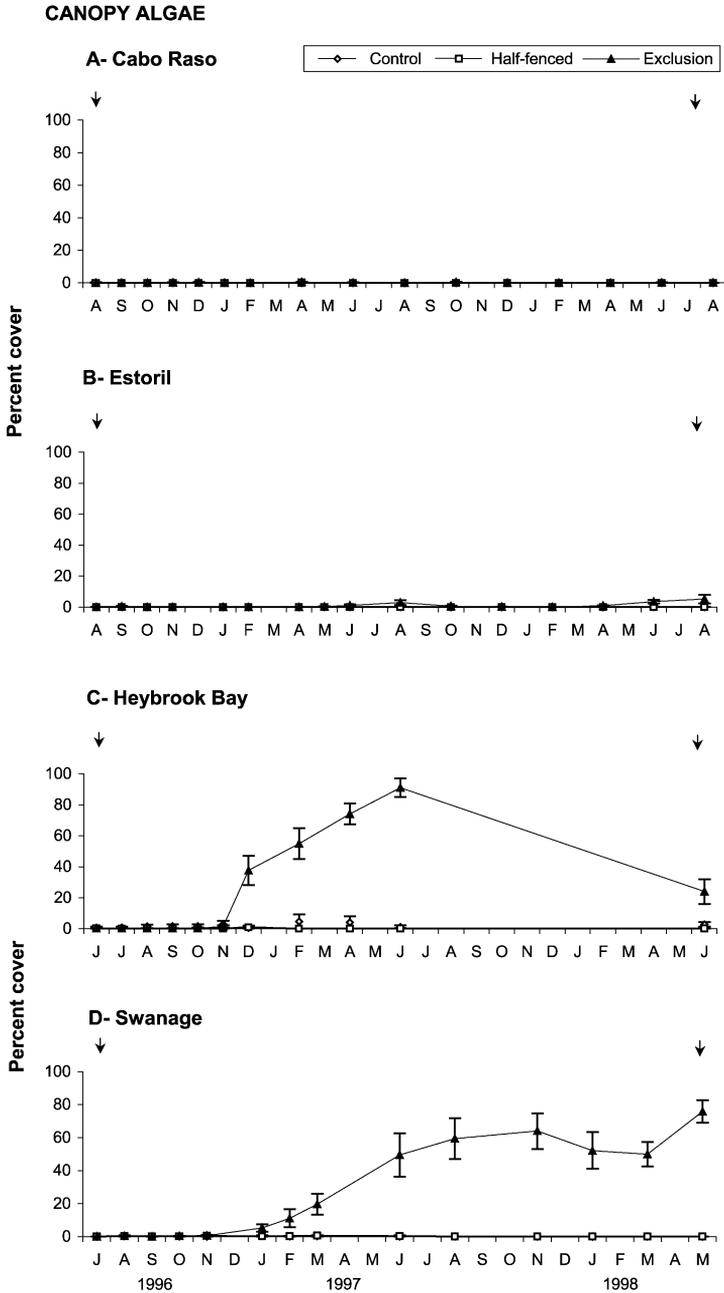


Fig. 5. Effects of limpet exclusion on the mean% cover (\pm SE) of canopy algae on the different shores. Arrows indicate dates for which data were analysed. Data were pooled across patches at each shore.

Table 2
ANOVA on the percentage cover of three morphological algal groups in response to limpet exclusion

Source of variation	df	Ephemeral algae				Turf algae				Canopy algae			
		0 month		1 month		0 month		24 months		0 month		24 months	
		MS	F	MS	F	MS	F	MS	F	MS	F	MS	F
Gr	2	5.10	0.02 ns	6513.59	226.99**	10.18	0.45 ns	4152.98	3.51 ns	5.90	4.52 ns	4611.56	1.51 ns
Lo	1	212.65	4.75 ns	253.81	0.59 ns	2.69	0.02 ns	1067.58	1.94 ns	0.01	0.00 ns	4137.75	11.02 ns
Sh(Lo)	2	44.78	2.50 ns	426.61	3.11 ns	115.19	1.20 ns	549.02	1.31 ns	9.20	2.08 ns	375.34	10.59*
Pa(Lo × Sh)	4	17.94	0.65 ns	137.21	1.77 ns	95.99	5.01 **	418.01	9.26***	4.42	0.81 ns	35.43	0.84 ns
Gr × Lo	2	243.79	3.62 ns	28.70	0.03 ns	22.70	2.02 ns	1184.87	129.25***	1.30	1.40 ns	3061.97	3.74 ns
Gr × Sh(Lo)	4	67.32	3.29 ns	998.95	6.57 *	11.24	0.76 ns	9.17	0.10 ns	0.93	0.16 ns	818.76	23.71***
Gr × Pa(Lo × Sh)	8	20.46	0.75 ns	152.15	1.96 ns	14.74	0.77 ns	89.71	1.99 ns	5.94	1.09 ns	34.53	0.82 ns
Residual	48	27.40		77.71		19.15		45.14		5.44		42.05	
Cochran's test		C=0.2698, $p < 0.05$		C=0.4785 $p < 0.01$		C=0.13 ns		C=0.19 ns		C=0.34 $p < 0.01$		C=0.37 $p < 0.01$	
Transformation:		ArcSin (%)		ArcSin (%)		ArcSin (%)		ArcSin (%)		ArcSin (%)		ArcSin (%)	
SNK tests				Gr × Sh(Lo), SE=5.04		Pa(Lo × Sh), SE=1.46		Gr × Lo, SE=0.87		Gr × Sh(Lo), SE=2.40			
				Cabo Raso, C=HF<E**		Cabo Raso, P1=P2 ns		Portugal, C=HF<E**		Cabo Raso, C=HF=E ns			
				Estoril, C=HF<E**		Estoril, P1=P2 ns		U.K., C=HF<E**		Estoril, C=HF=E ns			
				Heybrook Bay, C=HF=E ns		Heybrook Bay, P1=P2 ns				Heybrook Bay, C=HF<E**			
				Swanage, C=HF<E**		Swanage, P1>P2**				Swanage, C=HF<E**			

ns = not significant.

* $p < 0.05$.

** $p < 0.01$.

*** $p < 0.001$.

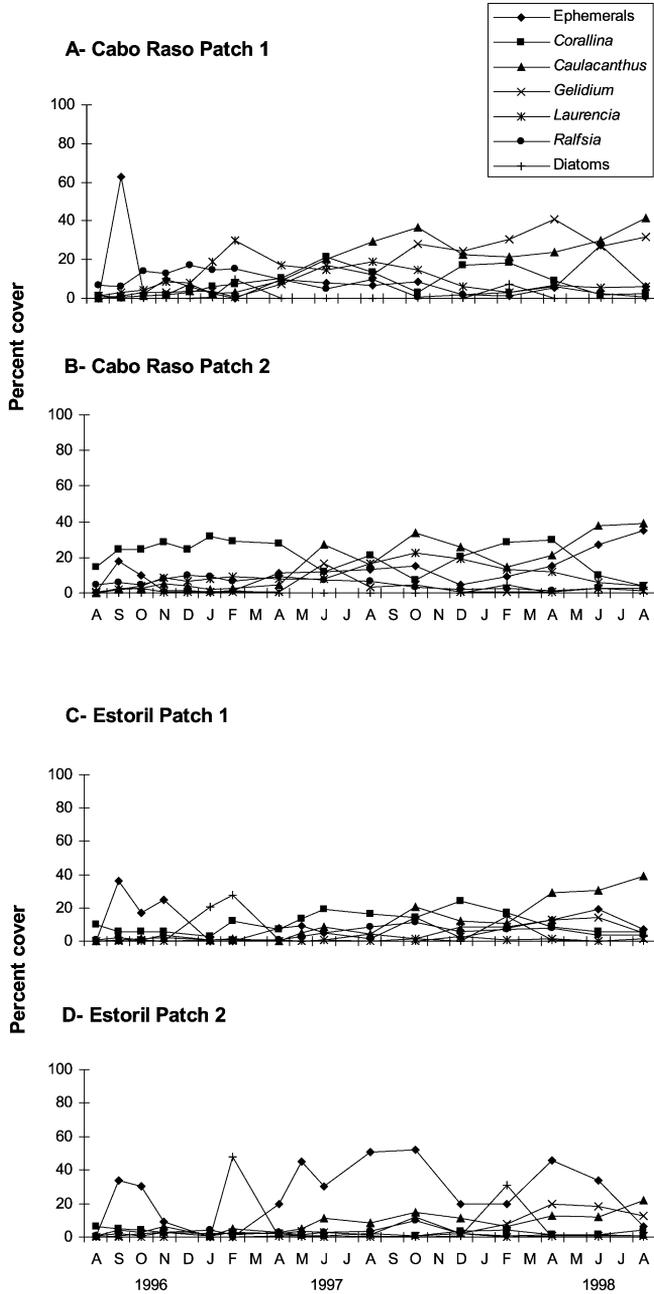


Fig. 6. Effects of limpet exclusion on patterns of algal colonisation in the ungrazed treatments on the different patches.

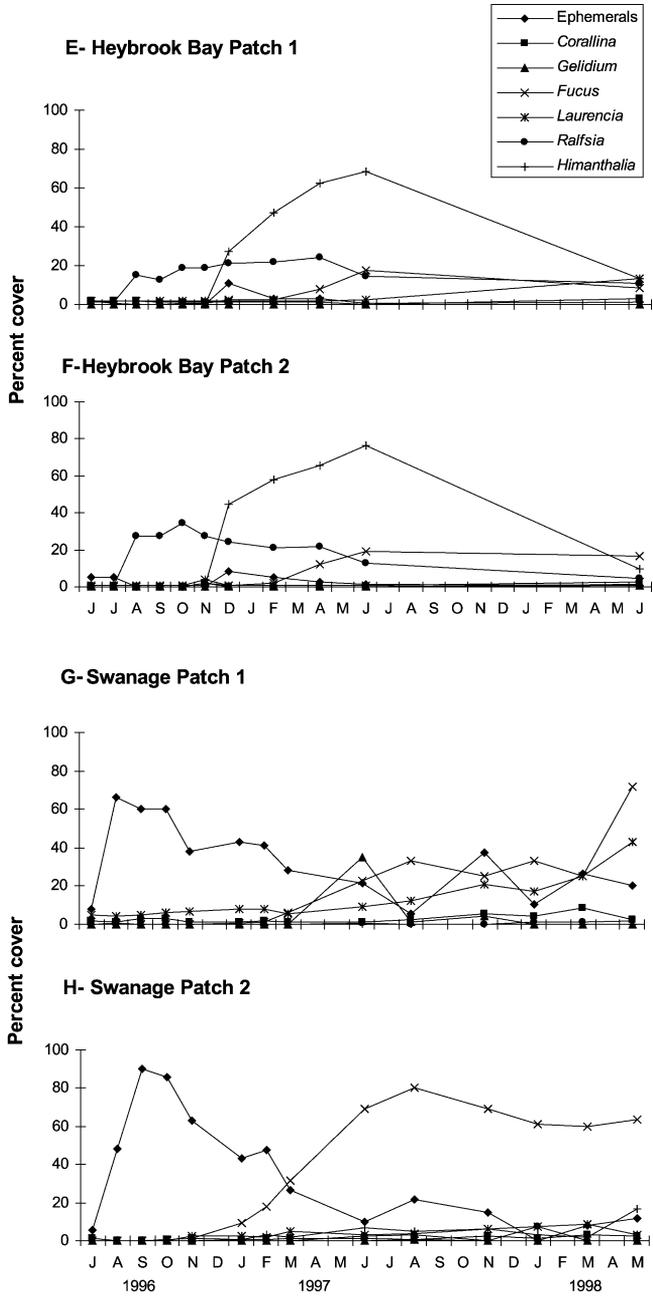


Fig. 6 (continued).

in ungrazed areas being significantly higher 2 years post limpet removal at both Heybrook Bay and Swanage (Fig. 5c,d; Table 2, SNK tests). The interaction is due to differences among shores in the cover of canopy in exclusion treatments. The most abundant algal species differed on the two shores. After 1 year, *H. elongata* accounted for 69% and 77% cover in Heybrook Bay (patch 1 and 2, respectively) (Fig. 6e,f). In contrast, *F. serratus* was more abundant at Swanage; at that time reaching percentage cover of 23% and 69% in patch 1 and 2, respectively (Fig. 6g,h). The dense cover of *F. serratus* persisted until the end of the experiment in Swanage, while a reduction of *H. elongata* was observed in the second year at Heybrook Bay. At Swanage, *F. serratus* was more abundant in patch 2, whereas *Laurencia pinnatifida* (Hudson) Lamouroux showed higher values in patch 1. In Portugal, the exclusion of limpets did not lead to an increase in canopy cover during the study period. The only canopy-forming algae included in this morphological group in Portugal was *Codium tomentosum* Stackhouse, which never reached values greater than 10%.

The response of other morphological algal groups to reduction of grazing was not so evident. Microalgae showed an increase in February (6 months) on Portuguese shores ($F_{Gr \times Sh(Lo)}_{4,8} = 7.78, P < 0.01, SNK \text{ test} < 0.05$). A brown slick of diatoms occurred in February at Cabo Raso, but seemed to be a seasonal event rather than part of a successional sequence since it occurred again in the second winter, although at a reduced level as less space was available. A peak of diatoms was also observed in both patches at Estoril (27% and 48%) after the reduction in ephemeral algal cover (Fig. 6c,d). Patch 2 showed a less dense cover of late colonisation stages and thus a relatively high cover of both ephemeral algae and diatoms in the second year. No significant differences were obtained for any other shores or dates. Calcareous turf-forming algae showed no clear difference among treatments, although an increase to 20% in the cover of corallines was observed at Cabo Raso (patch 1) and 10% cover was reached at Estoril (patch 1). This occurred in exclusion plots after 12 months, but generally these algae died back in the summer. Crustose coralline algae showed no discernible changes through time; their

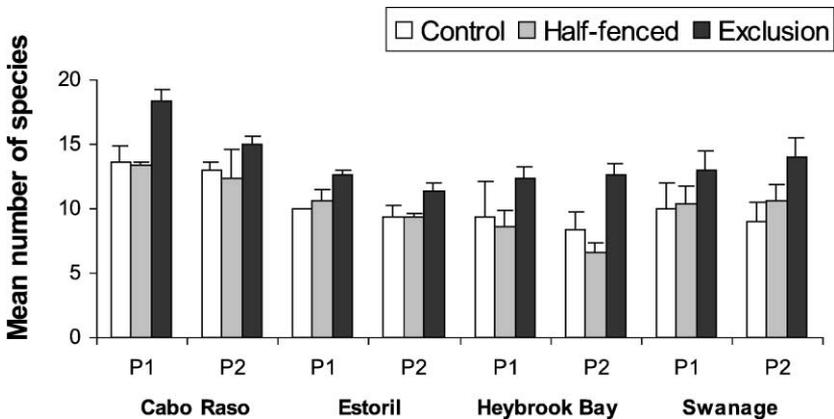


Fig. 7. Effects of limpet exclusion on the mean number (\pm SE) of algal species. P1—patch 1, P2—patch 2.

Table 3
ANOVA on the cumulative number of algal species in response to limpet exclusion

Source of variation	df	\sum number of algal species in 2 years	
		MS	F
Gr	2	91.17	45.58*
Lo	1	72.00	0.99 ns
Sh(Lo)	2	72.47	13.38*
Pa(Lo \times Sh)	4	5.42	1.11 ns
Gr \times Lo	2	2.00	0.61 ns
Gr \times Sh(Lo)	4	3.30	1.89 ns
Gr \times Pa(Lo \times Sh)	8	1.75	0.36 ns
Residual	48	4.86	
Cochran's test		C = 0.21 ns	
Transformation:		none	
SNK tests		Gr, SE = 0.29	
		C = HF < E*	

ns = not significant.

* $p < 0.05$.

abundances decreased and increased as the other algae covered them and disappeared. Noncalcareous crusts increased in response to limpet removal after 6 months, but only at Heybrook Bay ($F_{\text{Gr} \times \text{Sh(Lo)}}_{4,8} = 5.83$, $P < 0.02$, SNK test < 0.01).

3.4. Species richness

The number of algal species was greater in exclusion treatments on all of the shores investigated (Fig. 7, Table 3). The highest mean number of algal species was recorded in Portugal, particularly at Cabo Raso (Fig. 7). The algal species that occurred in ungrazed areas were essentially the same as those observed in grazed treatments, but they occurred only occasionally in controls. Different species pools were present in north and south Europe at the two studied locations.

4. Discussion

4.1. Approach

The experimental design and methodology used in these experiments proved to be effective to test the initial hypotheses. No artifacts occurred and there were no significant differences in percentage cover of algae between controls and half-fenced treatments. Moreover, the design included several spatial scales (Locations, Shores, Patches) and it was possible to compare the effects of grazing across this range of spatial scales. Few studies have investigated the effects of grazing at more than one spatial scale (but see Benedetti-Cecchi et al., 2000). The morphological group approach was also adopted and proved to be useful for broad-scale comparison of different communities.

4.2. Distribution patterns

Our study shows that grazing by limpets sets the upper limits of low-shore macroalgae on North-east Atlantic coasts. In both Portugal and the UK, red algal turf extended upshore by at least 50 cm in vertical height. In the UK, however, they were eventually covered by canopy algae, which were not present in controls and also extended upshore in the experimental plots. These results support the work of Underwood (1980) who was first to experimentally demonstrate that grazing was a major determinant of the upper limits of low-shore foliose algae in Australia. In his work, however, most species were ephemerals and perennials did not persist unlike in our experiments in Europe. Underwood (1980) also manipulated the physical environment. While we did not do such experiments, observations of run off from pools in both UK and Portugal, and drainage from crustacean holding tanks at Cabo Raso (Boaventura, 2000) suggest that red algae can extend higher up the shore when emersion stress is reduced. Thus, it is likely that the ultimate extent of algae up the shore is set by physical factors. The ability of algae to outpace grazers is determined by physical factors, but at certain level on the shore, grazers win and here grazing directly sets upper limits.

4.3. Patterns of algal colonisation and diversity

Our results indicate that the diversity of species was always higher in ungrazed areas than in grazed areas (Table 3), as found by Lubchenco (1978) for emergent substrata, and in other low-shore studies (e.g. Raffaelli, 1979; Williams, 1993). Thus, where turf develops it lessens mortality due to desiccation and grazing pressure (Hay, 1981; Steneck and Watling, 1982; Littler and Littler, 1984) and facilitates the settlement and persistence of a variety of species.

The overall pattern of colonisation was of ephemeral greens, followed by perennial algal turfs, which in the UK alone gave way to canopy-forming brow algae. Although ephemeral algae were the earliest colonisers in most cases except Heybrook Bay (see also May et al., 1970; Sousa, 1979; Littler and Littler, 1980; Hawkins, 1981a,b; Jara and Moreno, 1984; Carter and Anderson, 1991; Dye, 1995), there were some differences from what has been considered the typical sequence of diatoms, ephemerals and then perennials (Dayton, 1971, 1975; Underwood, 1980; Hawkins, 1981a,b; Underwood and Jernakoff, 1984; Jernakoff, 1985). A slick of diatoms never occurred first, but only appeared later in the winter. Green algae did not colonise rapidly at Heybrook Bay. Absence of both diatoms and green algae has been observed in other summer-initiated experiments in the North-east Atlantic (Hawkins, 1981a). Ephemerals were eventually replaced by perennial species, which took over as the ephemerals died. In some patches in Portugal (e.g. Cabo Raso), noncalcareous crusts were prevalent before giving way to perennial turfs (see Carter and Anderson, 1991 for work in South Africa). In Portugal, a rich turf of various red algae dominated. Although a turf of red algae began to form in the UK, they were rapidly dominated by canopy-forming species (*F. serratus* more abundant at Swanage, *H. elongata* more abundant at Heybrook Bay). The different canopy species colonising in the UK can best be explained by slightly more exposed conditions favouring *H. elongata* (see Ballantine, 1961; Lewis, 1964). Large fucoids have been shown to colonise in the

absence of grazers on northern hemisphere temperate shores (e.g. Jones, 1948; Lubchenco, 1978; Southward and Southward, 1978; Hawkins, 1981a,b; Kim and DeWreed, 1996; Jenkins et al., 1999a,b; and many others) although most of these studies have been in the midshore. Dominance by red algae following grazer exclusion has been more common in warm temperate waters (e.g. Sousa, 1979; Sousa et al., 1981; Benedetti-Cecchi and Cinelli, 1992) including the southern hemisphere (Jara and Moreno, 1984; Carter and Anderson, 1991), especially lower on the shore.

4.4. Variation of grazing effects on the different algal groups and at various spatial scales

As in previous work (e.g. Duggins and Dethier, 1985; Benedetti-Cecchi et al., 1996), ephemerals, turf and canopy algae were the morphological algal groups that responded more to the cessation of limpet grazing. Lack of grazing had little discernible effect on calcareous turf and encrusting algae, in contrast to the indirect effects noted by Benedetti-Cecchi et al. (1996), who observed that calcareous turf algae declined as the coarsely branched algae increased in the absence of herbivores.

Few studies have analysed the effects of grazing at different spatial scales although Benedetti-Cecchi et al. (2000) undertook an extensive study in the North-west Mediterranean. Our work revealed that the effect of limpets was not consistent for all of the morphological algal groups and spatial scales considered in the present study. In general, the effects of grazing were consistent at the scale of patches (i.e. no interaction occurred between grazing and patch). Most of the analysed categories (e.g. total algal cover, ephemeral algae, canopy algae), however, showed that the effect of grazing varied between shores. Despite the significant effect of grazing on the cover of ephemeral and canopy algae, both morphological groups showed a great variation from shore to shore. This lack of consistency on the effects of limpets at the scale of shore was also found by Benedetti-Cecchi et al. (2000) on rocky shores in the North-west Mediterranean. The particular hypothesis proposed in our study was to see if grazing by limpets determined the upper limit of distribution of the red algal turf and to see whether its effects varied at different spatial scales. Limpet removal resulted in a significant increase in algal turf above its usual level on both shores at both locations. However, this effect was not homogeneous at the location scale. Percentage cover of algal turf was much greater in Portugal. Removal of limpets allows natural variation in algal colonisation to be expressed by allowing recruitment. The different responses at various scales reflect different pools of species and their propagules. These will vary at small spatial scales and temporally, especially for ephemerals. On larger scales such as latitude different types of species will be available to colonise.

5. Conclusions

Grazers play a major role in directly setting upper limits of low-shore turfs in intertidal rocky shores. Turf algae extended their upper limits of distribution in ungrazed areas at both locations studied. Furthermore, turf-forming algae exclusively dominated ungrazed areas in Portugal, while canopy—also extending upshore—eventually became the dom-

inant morphological algal group in Britain. The response to removal of grazing by limpets was not consistent for all of the several morphological algal groups and spatial scales considered in the present study. The effect of grazing varied between countries (location scale) on the cover of turf algae, while on ephemeral and canopy algal cover varied at the shore scale.

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