

Regional scale differences in the determinism of grazing effects in the rocky intertidal

S. R. Jenkins^{1,*}, R. A. Coleman², P. Della Santina³, S. J. Hawkins^{1,3},
M. T. Burrows⁴, R. G. Hartnoll⁵

¹Marine Biological Association, Citadel Hill, Plymouth PL1 2PB, UK

²Marine Biology and Ecology Research Group, School of Biological Sciences, University of Plymouth, Drake Circus, Plymouth PL4 8AA, UK

³Biodiversity and Ecology Division, School of Biological Sciences, Southampton University, Southampton SO16 7PX, UK

⁴Scottish Association for Marine Science, Dunstaffnage Marine Laboratory, Oban, Argyll PA37 1QA, UK

⁵Port Erin Marine Laboratory, University of Liverpool, Port Erin, Isle of Man IM9 6JA, UK

ABSTRACT: Patellid limpets are dominant grazers on intertidal rocky shores of NW Europe with a key role in structuring the eulittoral community. Localised loss of limpets and the subsequent reduction in grazing pressure is known to result in important changes in community structure, through the development of canopy-forming macroalgae, and an associated increase in species diversity and community complexity. The level of determinism in the community level response to localised loss of patellid limpets was assessed at spatial scales from 100s of kilometres to 10s of metres and temporal scales from weeks to months at mid-tide level of exposed rocky shores. Limpets were removed and excluded from experimental plots to simulate localised limpet loss and appropriate controls established. Experimental plots were established in replicate patches at 2 shores at each of 2 regional locations, separated by approximately 500 km: the Isle of Man and SW England. Removals were conducted on 2 dates within each of 2 seasons (summer and winter) and the community level response monitored for a period of 12 mo. There was a clear effect of limpet loss at all spatial and temporal scales, with rapid development of green ephemeral algae followed by a furoid canopy. However, the degree of determinism in the development of canopy-forming algae differed markedly between the 2 locations. At the northerly location, the Isle of Man, furoid algae developed quickly and dominated all areas of limpet exclusion; there was little variability between plots. In contrast, in SW England, the abundance of furoid algae was significantly lower and much more variable. Such geographic changes in the development of macroalgae in the absence of the dominant grazer are discussed in relation to rocky shore community dynamics and the latitudinal change in balance between grazers and algae over the wave exposure gradient.

KEY WORDS: Herbivory · Large scale · Macroalgae · Rocky shore

Resale or republication not permitted without written consent of the publisher

INTRODUCTION

Experimental work on rocky shores has frequently demonstrated that intertidal grazers have the ability to almost completely control the species composition, distribution and dynamics of algal communities (Lubchenco & Gaines 1981, Paine 2002). Patellid limpets are some of the best-known and most studied of marine herbivores, and have a profound effect on the

community structure of intertidal rocky shores of NW Europe (see Southward 1964, Hawkins & Hartnoll 1983, Hawkins et al. 1992 for reviews). Limpet-removal experiments on the Isle of Man first demonstrated that canopy-forming algae, particularly mid-shore *Fucus vesiculosus*, were directly prevented from establishing on wave-exposed shores by limpet grazing (Jones 1946, 1948, Lodge 1948, Burrows & Lodge 1950, Southward 1956, 1964). Experimental removal of

*Email: sjen@mba.ac.uk

limpets resulted in the rapid development of various ephemeral or opportunistic species (*Enteromorpha* spp., *Ulva* spp., *Blidingia* spp.) followed by growth of a furoid canopy which persisted for up to 5 yr. This successional sequence was confirmed in the British Isles, following the widespread mortality of limpets on the shores of west Cornwall following a massive oil spill (Southward & Southward 1978, Southward 1979), and in follow-up experiments on the Isle of Man (Hawkins 1981a,b, Hartnoll & Hawkins 1985).

In the British Isles and northern France, moderately exposed shores support a mid-shore community composed of patches of *Fucus* spp., barnacles and bare rock, interspersed with grazing patellid limpets (Lewis 1964). On such shores, localised areas of low grazing pressure allow 'escapes' of macroalgae to occur (Hartnoll & Hawkins 1985). Once beyond a size of around a few centimetres, such macroalgae are rarely consumed by microphagous grazers such as limpets and hence, persist to form clumps of canopy. The dynamics of this patchy mosaic community have been the subject of a number of empirical (Hawkins 1981a, Hartnoll & Hawkins 1985, Johnson et al. 1997) and modelling studies (Burrows & Hawkins 1998, Johnson et al. 1998) that have demonstrated the importance of individual limpet behaviour in maintaining the mosaic community.

The role of patellid limpets in structuring the mid-shore assemblage of the NE Atlantic at exposed sites is undoubted, though they have much less influence amongst canopies, low on the shore (Jenkins et al. 1999b) or at sheltered sites (Jenkins et al. 1999a). Ballantine (1961) observed a latitudinal trend in the balance between furoid algae and limpet/barnacle-dominated areas down the coast of western Europe, with fucoids being restricted further into shelter in the south. Both he and subsequent authors (Hawkins & Hartnoll 1983, Hawkins et al. 1992) suggested that the balance between the effectiveness of grazers and the ability of fucoids to grow, changed with latitude, thereby affecting the probability of successful colonisation by fucoids in areas of reduced grazing pressure. The development of a furoid canopy on barnacle-dominated shores has important implications for community dynamics and energy flow. Macroalgal canopies regulate community structure in a number of ways: (1) by altering the quality and quantity of light reaching the substratum (e.g. Reed & Foster 1984), (2) by whiplash or sweeping effects of fronds (e.g. Velimirov & Griffiths 1979, Jenkins et al. 1999c) or (3) by providing shelter from wave action (McCook & Chapman 1991) and from physical extremes such as high temperatures, desiccation or freezing (Leonard 2000). Furoid clumps provide a complex habitat and shelter for a wide range of animal species, the more obvious

of these including anemones, dogwhelks, littorinids, isopods and amphipods. In addition, the development of furoid canopy algae on exposed shores, dominated by barnacles and mussels, results in a distinct change from a community dominated by the secondary production of filter feeders to one dominated by primary production of macroalgae. Hence, the eulittoral zone can change from a net importer of primary production, when barnacle-dominated, to a net exporter, when dominated by macroalgae (Hawkins et al. 1992).

We aimed to test the determinism of the assemblage response (and particularly the development of a furoid canopy) to limpet loss at a realistic spatial scale, from small (0.5 × 0.5 m) patches. We tested the general hypothesis that loss of limpets from small patches at mid-tide level of moderately exposed shores results in macroalgal growth. Many factors may affect the likelihood of macroalgal development in the absence of limpet grazing, including the supply of macroalgal propagules (Arrontes 2002), mortality of germlings in unfavourable microclimates (Brawley & Johnson 1991), dislodgement of propagules by wave action (Vadas et al. 1990) and grazing of propagules or germlings by other non manipulated grazers such as crustacean mesoherbivores (Brawley 1992). Given the variability of these and other ecological processes on rocky shores, from place to place, and time to time, we used a complex experimental design to test the general hypothesis applied over a number of spatial and temporal scales. In addition, we examined the effect of latitude within the British Isles on the community response to limpet loss by conducting the experiment at 2 locations: the Isle of Man and SW England. In this way, we tested the hypothesis developed from the original observations of Ballantine (1961) that loss of limpets would have a larger and more consistent effect at northern compared to southern latitudes.

MATERIALS AND METHODS

Study sites. Experimental work was undertaken at 2 locations separated by approximately 450 km, the SW of England near Plymouth (50° 19' N, 04° 06' W) and the south of the Isle of Man (54° 5' N, 04° 40' W) in the Irish Sea. Both locations were in areas of full salinity with maximum tidal ranges of 5 and 6 m, respectively. Two moderately exposed rocky shores on open coastlines, separated by a minimum of 2 km, were selected at both locations: Wembury and Heybrook Bay in SW England, Port St. Mary and Derbyhaven in the Isle of Man. The main criteria in shore selection was topographical simplicity, a gentle slope (<30°) and domination at mid-tide level by an extensive cover of barnacles, with

abundant patellid limpets. The shores in both areas, the Isle of Man (Southward 1953, Hartnoll & Hawkins 1985) and the Plymouth area (Colman 1933, Boalch et al. 1974) have been well described. At both shores at each location, the mid-shore, though dominated by barnacle cover, had patches of furoid canopy algae. These were less common in the Plymouth area. Experimental plots were located in the mid-shore, well within the barnacle zone and at a mean tidal height above Chart Datum of 2.3 m at Wembury (range 1.9 to 2.9 m), 2.1 m at Heybrook Bay (range 1.9 to 2.2 m), 3.6 m at Port St. Mary (range 3 to 4.3 m) and 3.5 m at Derbyhaven (range 2.6 to 4.8 m).

Experimental design. The experiment consisted of 3 treatments: (1) complete removal of all patellid limpets and exclusion using 3 cm high fences of plastic-coated wire mesh with 13 mm square openings, (2) a half-fenced treatment using the same fence structure but only encompassing half the quadrat perimeter, and allowing free movement of limpets, and (3) a control treatment with only the 4 corners of the quadrat marked by screws. The half-fenced treatment was used as a procedural control to determine whether the use of fences in the exclusion treatment had any effect on community succession, other than that caused by exclusion of limpets.

In order to fully explore the variability in the effect of limpet grazing on mid-shore community structure, this basic design was implemented over a number of spatial and temporal scales. Spatial variability was assessed at 3 scales, between locations (100s of kilometres), between shores within each location (kilometres) and among patches within each shore (10s to 100s of metres). Temporal variability was assessed at 2 scales, between seasons (summer and winter) and between dates within seasons. At each shore, experiments were established during 2 different seasons, summer 1996 and winter 1996/1997, and in each season, 2 start dates were selected at random from within a 3 mo period, with a minimum separation of 4 wk. Start dates were independently selected at all shores over both locations. At each start date, 2 patches were selected at each of the 2 shores at both locations. Within each patch, nine 0.5×0.5 m quadrats were chosen and the 3 treatments, replicated 3 times, were applied at random. All 8 patches for each shore were selected in advance of experimental set-up, over a horizontal distance of between 250 and 400 m, with a minimum separation of 30 m between individual patches. The choice of the 2 patches, at each start date, from amongst the 8 selected was made at random.

Maintenance and sampling of the experiment. Following establishment of the experiment, sampling was undertaken at regular intervals after each individual start date, monthly for the first 6 mo and then bi-

monthly until termination of the experiment at 12 mo. At each sampling date, a 0.5×0.5 m quadrat, subdivided to give 49 intersection points, was used to estimate the percentage cover of all macroalgae using the point intersect method (e.g. Benedetti-Cecchi et al. 1996). At selected sampling dates, all experimental quadrats were photographed. At least monthly, experimental plots were checked for damage to fences and repairs made. Any limpets that had invaded exclusion treatments plus any other 'macro-grazers' (littorinids, topshells) were removed.

Data analysis. The experiment was designed to allow partitioning of sources of variance using a 6-factor mixed-model ANOVA, where the factors Season, Location and Treatment were fixed, and Date, Shore and Patch were random. This analysis was used to determine the spatial and temporal consistency of treatment effects (i.e. differences between the control, fenced and exclusion treatments). Significant effects of the treatment give no information on the magnitude of the effect and how this varies over different spatial and temporal scales. For this, data from exclusion plots alone were used in a 5-factor mixed-model ANOVA. Prior to ANOVA, data were examined for heterogeneity of variance using Cochran's test and heterogenous data transformed appropriately. Significant factors were analysed further using SNK (Student Newman Keuls) multiple comparisons.

In any experiment examining development of biota over a number of sampling dates, choice of the dependent variable is paramount to interpretation of the experiment. In theory, a separate analysis could be performed for each sampling date but this would only lead to an over complex interpretation. For the key species in our analysis, 2 dependent variables were selected, maximal cover during the 12 mo period and the area under the curve for each individual plot. Maximal cover indicates the peak response to perturbation, while the area under the curve integrates the pattern of development for any particular species over time and, thus, takes into account the rate and temporal trajectory of algal colonisation.

RESULTS

General patterns of colonisation

Three main algal groups developed in experimental plots as a result of limpet removal: ephemeral green algae made up of a mixture of *Enteromorpha* and *Blidingia* spp. with some *Ulva* spp., and *Monostroma* spp., soft algal crusts, predominantly *Ralfsia* spp. and furoid canopy algae made up almost entirely of *Fucus vesiculosus*. The patterns of colonisation of these 3 groups

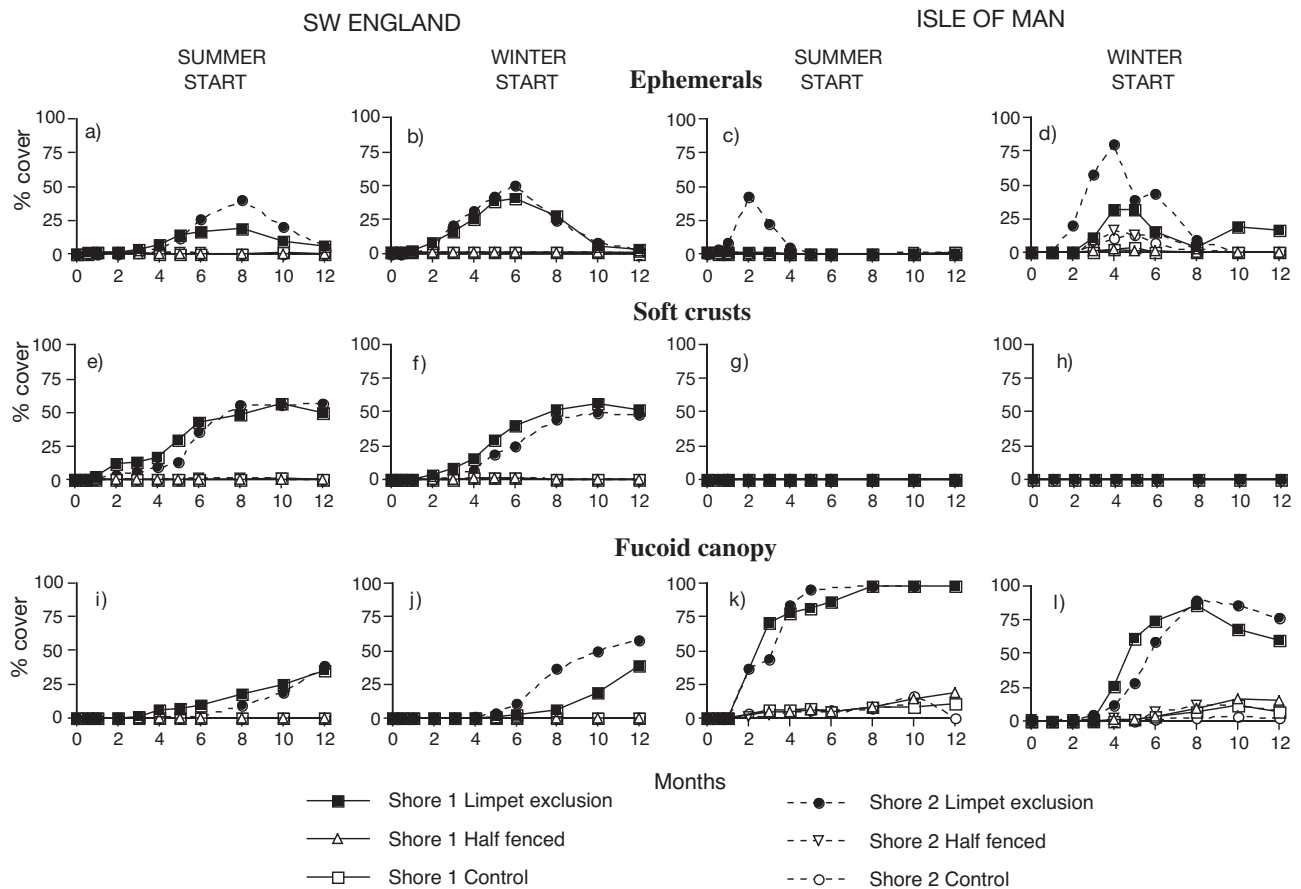


Fig. 1. Percentage cover of the 3 main algal functional groups in experimental plots over the 12 mo period of observation, for summer and winter seasonal start dates in SW England and the Isle of Man. Each line represents the mean percentage cover for a single shore in 1 of 3 treatments, with data pooled over start dates within a season and patches within a shore. Error bars are omitted for clarity. a–d: ephemeral green algae, predominantly *Enteromorpha* spp.; e–h: soft crustose algae, predominantly *Ralfsia* spp.; i–l: fucoid canopy algae, predominantly *Fucus vesiculosus*

over the 12 mo period of study are shown in Fig. 1. Data are grouped into mean levels per shore and season and, thus, do not display smaller temporal (date) and spatial (patch) scale variability. Of immediate note is that for all 3 algal groups, there was a marked effect of limpet removal; algal cover in exclusion plots differed markedly from control and half-fenced treatments. There was very little difference between control and half-fenced treatments indicating few or no artefacts caused by the placement of fences. This was confirmed in statistical analyses. For example, SNK multiple comparisons of the significant Treatment \times Patch interaction in the 6-factor mixed-model ANOVA, showed that fucoid macroalgae (measured as the area under the fucoid curve over 12 mo) were more abundant in half-fenced compared to control treatments in only 2 out of 32 patches at both locations. A similar result was obtained for ephemeral green algae. As a result of the general lack of a fence artefact, the half-fence treatment was ignored in further analyses.

Soft crustose species only developed in SW England, being completely absent from experimental plots on the Isle of Man. There was little difference between shores or between seasons in the development of soft crusts and on average, they covered 50% of exclusion plots at the end of the 12 mo period in the south west for both summer and winter start dates. Despite high values of percentage cover in some plots, the biomass of soft crusts was consistently low. Soft crusts were absent from half-fenced and control plots.

Development of green ephemeral algae in limpet exclusion plots differed between the 2 locations in timing, abundance and variability. In SW England, peak ephemeral algal cover occurred at 8 mo (summer start date) and 6 mo (winter start date), and generally showed the same pattern of colonisation between seasons and shores. On the Isle of Man, green algae developed soon after limpet removal, showing peaks at 2 mo (summer start date) and 4 mo (winter start date) before declining as fucoid canopy algae developed.

Development of *Fucus vesiculosus* showed marked differences between the 2 locations. Colonisation occurred more quickly and percentage cover reached a higher level on the Isle of Man compared to SW England. Maximum cover approached 100% for both start dates on the Isle of Man, while in SW England it was little over 50%. There was little difference in the timing of furoid development between seasons in SW England; however, on the Isle of Man, furoid cover developed more quickly in the summer experiment, on average 2 mo in advance of the winter experiment. The decline in cover of furoids between 8 and 12 mo following the winter but not the summer start date on the Isle of Man is noteworthy. This occurred as large mature plants were lost in autumn and winter storms. For both ephemeral green algae and furoids, there was greater development in control plots on the Isle of Man than SW England. Furoids were virtually absent from control plots in the southern location, whilst on the Isle of Man they developed high cover in a minority of plots.

Relationship with physical variables

For each shore at each location, the relationships between tidal height, substratum roughness, slope and aspect for each experimental plot, and the main dependent variables (maximal cover and area under the curve) for ephemeral algae and furoids were investigated to determine potential causes of variability. There was no correlation between any of the physical variables measured and either of the measures of algal cover.

Spatial and temporal variability of limpet effects

The degree to which limpet removal allowed algal growth in the experimental manipulations can be examined in a number of different ways. Firstly, we used data from control and exclusion plots but ignoring those from the half-fenced treatment to determine the level of consistency of the treatment (limpet removal). Secondly, we used data solely from limpet exclusion plots to determine how the level of algal growth following localised loss of limpets varied at all temporal and spatial scales.

Consistency of treatment effect

A 6-factor mixed-model ANOVA was applied to the data and the consistency of the treatment determined by applying the SNK multiple comparison test to the highest order significant interaction involving the factor 'treatment'. For ephemeral algae, the effects of limpet removal were variable, with some limpet exclu-

sion plots leading to little or no algal growth. For both maximum cover and area under the curve, there was a significant interaction between treatment and the smallest spatial scale, that of patch (maximum cover: $F_{16,128} = 2.88$; $p < 0.001$; Area: $F_{16,128} = 2.27$; $p < 0.01$). SNK tests of this interaction show that there was no effect of the treatment at 3 patches at Port St. Mary on the Isle of Man and 1 patch at Heybrook Bay in SW England for the summer start dates. At all other patches, limpet removal resulted in significantly higher growth of ephemeral algae than in control plots.

For maximum furoid cover, there was also a significant interaction between treatment and patch (Table 1); SNK tests of this interaction showed that at all 16 patches, at each location, the exclusion treatment was significantly greater than the control. Thus, limpet removal always resulted in significantly greater furoid cover than when limpets were present, at both locations. For area under the furoid curve, the highest order significant interaction of the factor treatment was Treatment \times Location; SNK tests showed a significant difference between the 2 treatments at both locations.

Variation in exclusion plots

There were no clear differences between locations in the level of ephemeral green algae in limpet exclusion plots (Table 2). Both locations showed small scale variability at the scale of patch, although such differences between patches only occurred in the summer start dates on the Isle of Man (SNK of significant Patch factor). Differences between shores only occurred on the Isle of Man; such differences can be clearly seen in the summer experiment where ephemerals did not grow at all at Port St. Mary, but reached up to 50% cover at Derbyhaven. Temporal differences were only observed at the seasonal scale with greater maximum ephemeral cover in winter on the Isle of Man (SNK of Location \times Season). For soft algal crusts, differences between locations were clear; there was no development of this algal group on the Isle of Man. In SW England, variability only occurred at the smallest spatial scale; differences between patches occurred in both the winter and summer experiments.

Removal of limpets led to significantly greater furoid development (both maximum cover and area under the curve) on the Isle of Man compared to SW England (Fig. 1, Table 3). These differences between locations were consistent between experimental start dates and seasons. There was significant variability at the spatial scales of patches and marginally insignificant variability (at the 5% level) at the scale of the shore; SNK tests of these factors, for both measures of furoid cover, showed that such variability only occurred in SW Eng-

Table 1. Mixed-model ANOVA of furoid canopy cover in experimental plots of the control and grazer exclusion. Half-fenced treatment is not included. Tr: treatment; Loc: location; Sh(Loc): shore (location); Se: season; Da: date; Pa: patch

Source	df	Maximum cover			Area under curve			F-ratio versus
		MS	F	p	MS	F	p	
Tr	1	193675	507.5	<0.01	2947110	1656	<0.001	Tr × Sh(Loc)
Loc	1	47313	132.1	<0.01	1966680	769	<0.01	Sh(Loc)
Sh(Loc)	2	358	1.8	>0.2	2554	0.2	>0.8	Da[Se × Sh(Loc)]
Se	1	0.02	0.007	>0.9	186750	12.8	>0.06	Se × Sh(Loc)
Tr × Loc	1	21042	55.1	<0.05	1386350	779	<0.01	Tr × Sh(Loc)
Tr × Sh(Loc)	2	381	2.4	>0.1	1778	0.7	>0.5	Tr × Da[Se × Sh(Loc)]
Tr × Se	1	295	0.9	>0.4	103277	9.3	>0.09	Tr × Se × Sh(Loc)
Loc × Se	1	1485	5.7	>0.1	257803	17.7	>0.05	Se × Sh(Loc)
Tr × Se × Loc	1	462.5	1.4	>0.3	157580	14.2	>0.06	Tr × Se × Sh(Loc)
Se × Sh(Loc)	2	261.3	1.3	>0.3	14530	1.2	>0.3	Da[Se × Sh(Loc)]
Tr × Se × Sh(Loc)	2	329	2.1	>0.15	11110	4.2	>0.05	Tr × Da[Se × Sh(Loc)]
Da[Se × Sh(Loc)]	8	193	0.6	>0.7	11981	1.3	>0.3	Pa{Da[Se × Sh(Loc)]}
Tr × Da[Se × Sh(Loc)]	8	156	0.4	>0.8	2673	0.8	>0.6	Tr × Pa{Da[Se × Sh(Loc)]}
Pa {Da[Se × Sh(Loc)]}	16	320	2.6	<0.01	9056	3.9	<0.001	Residual
Tr × Pa{Da[Se × Sh(Loc)]}	16	325	2.6	<0.01	3358	1.5	>0.1	Residual
Residual	128	123			2302			

land (Table 3). For example, for SNK comparisons of maximum furoid cover between patches established on the same date, 5 out of 8 tests were significant in SW England compared to none on the Isle of Man. At the spatial scale of shores, there were significant differences in SW England but not the Isle of Man; thus, for furoid algae, there was less, but more variable cover in SW England in limpet removal plots than in the more northerly locality.

Small-scale variability in furoid cover

Examination of variability at the smallest spatial scale, that between individual experimental plots, was made by determining the frequency distribution of maximal percentage cover for exclusion and control plots (Fig. 2). On the Isle of Man, the frequency distribution for maximum furoid cover in exclusion plots was skewed strongly to the right; 43 of the 48 exclusion

Table 2. Mixed-model ANOVA of ephemeral green algal cover in limpet exclusion plots. Loc: location; Sh(Loc): shore (location); Se: season; Da: date; Pa: patch

Source	df	Maximum cover			Area under curve			F-ratio versus
		MS	F	p	MS	F	p	
Loc	1	163	0.03	>0.8	16.07	1.05	>0.4	Sh(Loc)
Sh(Loc)	2	5553	9.15	<0.01	15.31	6.93	<0.02	Da [Se × Sh(Loc)]
Se	1	10185	56.73	<0.02	56.35	14.22	>0.05	Se × Sh(Loc)
Loc × Se	1	2660	14.82	>0.05	14.79	3.73	>0.1	Se × Sh(Loc)
Se × Sh(Loc)	2	179	0.3	>0.7	3.96	1.79	>0.2	Da [Se × Sh(Loc)]
Da [Se × Sh(Loc)]	8	606	1.62	>0.1	2.21	1.55	>0.2	Pa {Da[Se × Sh(Loc)]}
Pa {Da[Se × Sh(Loc)]}	16	375	4.15	<0.001	1.43	5.21	<0.001	Residual
Residual	64	90			0.27			
SNK test of Sh(Loc)		SE = 5.03			SE = 0.304			
		Isle of Man: Shore 1 < Shore 2			Isle of Man: Shore 1 < Shore 2			
		SW England: Shore 1 = Shore 2			SW England: Shore 1 = Shore 2			
SNK test of Loc × Se		SE = 2.74						
		Isle of Man: Summer < Winter						
		SW England Summer = Winter						
		Summer and winter: Isle of Man = SW England						
SNK test of Pa		SE = 5.49			SE = 0.303			
		Isle of Man: 2/8 comparisons significant			Isle of Man: 2/8 comparisons significant			
		SW England: 4/8 comparisons significant			SW England: 4/8 comparisons significant			

Table 3. Mixed-model ANOVA of furoid canopy algal cover in limpet exclusion plots. Loc: location; Sh(Loc): shore (location); Se: season; Da: date; Pa: patch

Source	df	Maximum cover			Area under curve			F-ratio versus
		MS	F	p	MS	F	p	
		Transformation: none Cochran's C = 0.4604, p < 0.01			Transformation: ln(x) Cochran's C = 0.1834, p > 0.05			
Loc	1	65730	90.89	<0.02	92.88	117.28	<0.01	Sh(Loc)
Sh(Loc)	2	723	3.68	>0.05	0.79	4.11	>0.05	Da [Se × Sh(Loc)]
Se	1	150	0.33	>0.6	0.19	0.08	>0.8	Se × Sh(Loc)
Loc × Se	1	1802	4.00	>0.1	5.55	2.42	>0.25	Se × Sh(Loc)
Se × Sh(Loc)	2	450	2.29	>0.1	2.29	11.89	<0.01	Da [Se × Sh(Loc)]
Da [Se × Sh(Loc)]	8	196	0.54	>0.8	0.19	0.30	>0.9	Pa {Da[Se × Sh(Loc)]}
Pa {Da[Se × Sh(Loc)]}	16	365	2.98	<0.01	0.63	4.57	<0.001	Residual
Residual	64	122			0.14			
SNK test of Sh(Loc)		SE = 2.86 Isle of Man: Shore 1 = Shore 2 SW England: Shore 1 < Shore 2			SE = 0.09 Isle of Man: Shore 1 = Shore 2 SW England: Shore 1 < Shore 2			
SNK test of Pa		SE = 6.39 Isle of Man: 0/8 comparisons significant SW England: 5/8 comparisons significant			SE = 0.21 Isle of Man: 0/8 comparisons significant SW England: 4/8 comparisons significant			

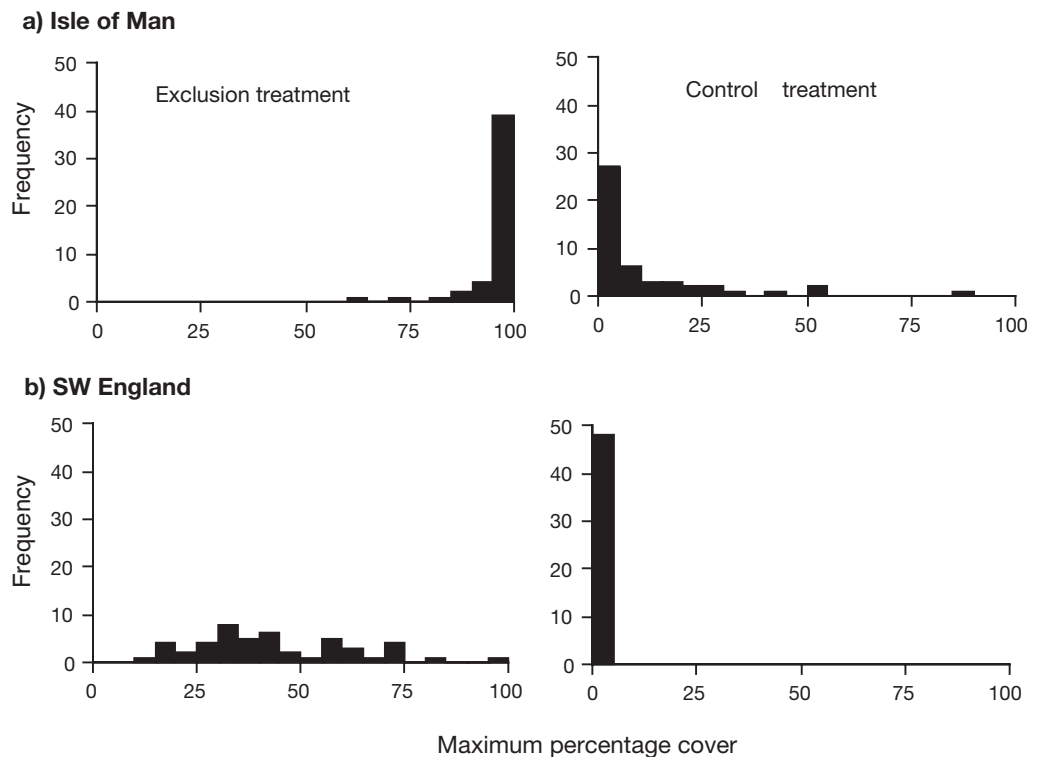


Fig. 2. Frequency distribution of maximal furoid canopy cover values for limpet exclusion and control plots on (a) the Isle of Man and in (b) SW England

plots established throughout the experiment had a maximal cover of furoids of over 90%. In contrast, the frequency distribution in SW England was approximately normal, with the maximum cover of furoids in exclusion plots showing high variability. Maximum

cover in control plots showed no variation in SW England, with no furoid growth at all, while on the Isle of Man, although over half the experimental plots showed no furoid growth, there was extensive growth in a minority of plots (Fig. 2)

DISCUSSION

Local scale experimental studies have provided considerable insight into the way shallow subtidal and intertidal communities are structured and organised. The tractable nature of rocky intertidal systems has allowed them not only to provide a means of testing ecological theory, but means that rocky shore communities are some of the best understood in the world, in either terrestrial or marine environments. Despite this, it is well recognised that the results of many community-based field studies are context-dependent to a large extent (Lawton 1999), making generalisations difficult. The key role played by grazing patellid limpets in controlling macroalgal development on rocky shores of NW Europe has been recognised for decades. The huge changes in community structure after removal of limpets, especially on a large scale (Jones 1948, Southward & Southward 1978), suggest that these are 'keystone' grazers (sensu Paine 1966). However, the keystone effects of limpets are not universal (e.g. Jenkins et al. 1999a), just as the effects of the original keystone predator *Pisaster ochraceus* are limited to certain habitats (Menge et al. 1994). In addition, the geographical generality of limpet-grazing effects on exposed shores of Europe are not fully known. The majority of effective manipulations of patellid limpets in the mid-shore zone have been concentrated on the Isle of Man (see Hawkins et al. 1992 for review). More recently, however, extensive experimental manipulations of patellid grazers have been made in the Mediterranean (Benedetti-Cecchi et al. 2000, 2001). This work has shown extremely inconsistent grazing effects at different spatial and temporal scales with only occasional strong effects on macroalgal abundance. Low on the shore at exposed sites, Boaventura et al. (2002) have convincingly shown that limpet grazing can limit the vertical extent of turf forming and canopy algae in both England and Portugal.

The results of the present study show, that within the British Isles, the community response to small-scale loss of limpets is similar; at both locations, macroalgae developed after limpet removal. However, the level of determinism in response to simulated localised release of grazing pressure varies considerably. It is clear that the more northerly locality, the Isle of Man, experiences a strong, deterministic community response to localised reductions in grazing pressure. In contrast, further south in the British Isles, the response is weak and more variable. These results support, and provide a mechanistic insight into, the observations of Ballantine (1961) of a latitudinal gradient in the balance between grazers and macroalgae across the wave-exposure gradient. It should be noted that while the main focus of our experiment was in manipulation of

the dominant patellid limpet grazers (*Patella vulgata* on the Isle of Man and both *P. vulgata* and *P. depressa* in SW England), regular maintenance of the experiment prevented other macrograzers, including *Littorina littorea*, *L. obtusata*, *Gibbula umbilicalis* and *Osilinus lineata*, from exerting a large effect. Other grazers within the eulittoral zone, such as crustacean mesoherbivores, which were not manipulated, could potentially contribute to the spatial and temporal differences observed. However, from our observations and the known effects of these grazers (see Brawley 1992 for review), it is unlikely that they contributed significantly to the large differences between locations.

The probability of early post-settlement stages of furoid macroalgae (zygotes, young germlings and germlings of Vadas et al. 1992) escaping grazing by microphagous molluscs is critical in determining community structure at the mid-tide level of rocky shores. We propose that an increase in the probability of escape with increasing latitude is the prime driver for the increasing dominance of macroalgae to the north, with fucoids extending further onto wave-exposed shores. Such probability will change with the abundance, activity and possibly diversity of grazers, and the growth rate of algae. In areas of naturally reduced grazing intensity or experimental exclusions, the probability of furoid development lies solely with the supply of propagules and/or their ability to develop and grow. The dominant furoid in experimental exclusion plots, *Fucus vesiculosus*, has a European range stretching from northern Norway as far south as Morocco (Luhning 1990). A detailed study into the biology of *F. vesiculosus* on the Isle of Man and Devon (SW England) by Knight & Parke (1950) showed little difference in the growth rate, reproductive period or ability to repopulate areas cleared within stands of adults. Hence, in SW England, *F. vesiculosus* is well within its distributional range and so expected to respond well to the release of grazing pressure. It appears unlikely that furoid zygotes and germlings are unable to cope with slightly higher air and sea temperatures at the southern location, although this remains to be tested experimentally.

Another explanation for the lower effect size in SW England is a generally lower, less predictable supply of macroalgal propagules. Dispersal patterns of algal propagules are generally poorly understood, but assessment of the distance of recruits from adult sources have invariably suggested short dispersal shadows, in the order of metres to 10s of metres (see Santelices 1990 for review). Limited dispersal distances can be increased if the number of source plants is increased. The effect of large stands of adult plants on propagule supply was graphically demonstrated by the early experiments of Burrows & Lodge (1950) when

extensive furoid development in a large limpet clearance (over 10×100 m) resulted in high furoid recruitment downstream of the original experimental area. In mid-shore experiments in northern Spain, increasing distance from stands of *Fucus* spp. results in a decline in the colonisation and development of *Fucus* spp. canopy in grazer exclusion plots (F. Arenas pers. comm.). In the present study, no quantitative measures were made of the distribution of adult stands of *F. vesiculosus* in relation to experimental plots at either location. However, *F. vesiculosus* was generally abundant on the Isle of Man and stands of adults were rarely if ever more than 30 m away from experimental plots. In contrast, on the 2 shores of SW England, stands of *F. vesiculosus* were rarer and more patchily distributed, supporting the hypothesis that propagule supply was limiting.

It could be argued that the lower response to grazer loss in SW England indicates a reduction in the role of limpet grazing in structuring mid-shore communities. However, Jenkins et al. (2001) demonstrated an increase in abundance and overall grazing pressure of patellid limpets in SW England compared with the Isle of Man, consistent with a general increase in grazing pressure with declining latitude in Europe. These observations would suggest an increase in the importance of grazers further south. One explanatory model to account for these results is that the activity of microphagous grazers, of which patellid limpets are undoubtedly the most important, limits the development of furoid macroalgae in the south to such an extent that adult plants are rare; thus, when localised areas of reduced grazing pressure arise, through natural or experimental means, there is insufficient supply of propagules. Small scale experimentation cannot be used to determine the importance of limpet grazing at a shore-wide scale under this scenario.

Variability in propagule supply in SW England may be one cause of the high variability in furoid development at this location. Within the experiment, none of the physical variables measured, shore height, aspect, slope nor surface roughness could explain variability in either ephemeral or furoid development. This is, however, not surprising as experimental plots at both locations were chosen with relatively strict physical criteria, which minimised differences in the physical environment. Another explanation is based simply on the inherent probabilities of patch occupancy within each exclusion quadrat for high and low mean values of furoid cover. Percentage cover can be considered as a measure of occupancy of a number of possible sites, or patches (Johnson et al. 1997), for *Fucus* spp. plants within each quadrat. If the presence of *Fucus* spp. in single patches is independent of the occupancy of other patches in a quadrat, then percentage cover for the

whole quadrat would be expected to follow a binomial distribution defined by the number of possible patches and the likelihood of occupancy of single patches. Lower likelihood of patch occupancy as seen in SW England would give much greater variability in percent cover as a result of such a binomial expectation.

In summary, we show that the level of determinism in the community response to small-scale limpet loss, in particular the development of a furoid canopy, varies considerably within the British Isles. The level of furoid development was consistently high on the Isle of Man, compared to a low and more variable response further south in SW England. This work supports the observations of Ballantine (1961) of a latitudinal gradient in the balance between grazers and macroalgae. Further experimental work is required to determine the causal mechanisms driving this change in balance.

Acknowledgements. This study was supported by the Mast III project EUROROCK MAS3-CT95-0012. Thanks to E. LaCroix, M. Roberts, S. Kimmance and D. Boaventura for assistance with the experimental set-up and sampling. S.R.J. and S.J.H. were supported during data analysis and write-up by NERC Grant-In-Aid to the MBA.

LITERATURE CITED

- Arrontes J (2002) Mechanisms of range expansion in the intertidal brown alga *Fucus serratus* in northern Spain. *Mar Biol* 141:1059–1067
- Ballantine WJ (1961) A biologically defined exposure scale for the comparative description of rocky shores. *Field Stud* 1:1–19
- Benedetti-Cecchi L, Airoldi L, Abbiati M, Cinelli F (1996) Estimating the abundance of benthic invertebrates: a comparison of procedures and variability between observers. *Mar Ecol Prog Ser* 138:93–101
- Benedetti-Cecchi L, Bulleri F, Cinelli F (2000) The interplay of physical and biological factors in maintaining mid-shore and low-shore assemblages on rocky coasts in the north-west Mediterranean. *Oecologia* 123:406–417
- Benedetti-Cecchi L, Bulleri F, Acunto S, Cinelli F (2001) Scales of variation in the effects of limpets on rocky shores in the northwest Mediterranean. *Mar Ecol Prog Ser* 209: 131–141
- Boalch G, Holme N, Jephson N, Sidwell J (1974) A resurvey of Colman's intertidal traverses at Wembury, South Devon. *J Mar Biol Assoc UK* 54:551–553
- Boaventura D, Alexander M, Della Santina P, Smith ND, Re P, Da Fonseca LC, Hawkins SJ (2002) 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. *J Exp Mar Biol Ecol* 267:185–206
- Brawley S (1992) Mesoherbivores. In: John DM, Hawkins SJ, Price JH (eds) *Plant-animal interactions in the marine benthos*. Oxford University Press, Oxford
- Brawley SH, Johnson LE (1991) Survival of furoid embryos in the intertidal zone depends upon developmental stage and microhabitat. *J Phycol* 27:179–186
- Burrows EM, Lodge SM (1950) Note on the inter-relationships of *Patella*, *Balanus* and *Fucus* on a semi-exposed coast. *Rep Mar Biol Stn Port Erin* 62:30–34

- Burrows MT, Hawkins SJ (1998) Modelling patch dynamics on rocky shores using deterministic cellular automata. *Mar Ecol Prog Ser* 167:1–13
- Colman JS (1933) The nature of intertidal zonation of plants and animals. *J Mar Biol Assoc UK* 18:435–476
- Hartnoll RG, Hawkins SJ (1985) Patchiness and fluctuations on moderately exposed rocky shores. *Ophelia* 24:53–64
- Hawkins SJ (1981a) The influence of *Patella* grazing on the fucoid-barnacle mosaic on moderately exposed rocky shores. *Kiel Meeresforsch* 5:537–543
- Hawkins SJ (1981b) The influence of season and barnacles on algal colonization of *Patella vulgata* (L.) exclusion areas. *J Mar Biol Assoc UK* 61:1–15
- Hawkins SJ, Hartnoll RG (1983) Grazing of intertidal algae by marine invertebrates. *Oceanogr Mar Biol Annu Rev* 21: 195–282
- Hawkins SJ, Hartnoll RG, Kain JM, Norton TA (1992) Plant animal interactions on hard substrata in the North-east Atlantic. In: John DM, Hawkins SJ, Price JH (eds) Plant-animal interactions in the marine benthos. Systematics Association Spec Vol 46. Clarendon Press, Oxford, p 1–32
- Jenkins SR, Hawkins SJ, Norton TA (1999a) Direct and indirect effects of a macroalgal canopy and limpet grazing in structuring a sheltered inter-tidal community. *Mar Ecol Prog Ser* 188:81–92
- Jenkins SR, Hawkins SJ, Norton TA (1999b) Interaction between a fucoid canopy and limpet grazing in structuring a low shore intertidal community. *J Exp Mar Biol Ecol* 233: 41–63
- Jenkins SR, Norton TA, Hawkins SJ (1999c) Settlement and post-settlement interactions between *Semibalanus balanoides* (L.) (Crustacea: Cirripedia) and three species of fucoid canopy algae. *J Exp Mar Biol Ecol* 236:49–67
- Jenkins SR, Arenas F, Arrontes J, Bussell J and 10 others (2001) A European scale analysis of seasonal variability in limpet grazing activity and microalgal abundance. *Mar Ecol Prog Ser* 211:193–203
- Johnson MP, Burrows MT, Hartnoll RG, Hawkins SJ (1997) Spatial structure on moderately exposed rocky shores: patch scales and the interactions between limpets and algae. *Mar Ecol Prog Ser* 160:209–215
- Johnson MP, Burrows MT, Hawkins SJ (1998) Individual based simulations of the direct and indirect effects of limpets on a rocky shore *Fucus* mosaic. *Mar Ecol Prog Ser* 169:179–188
- Jones NS (1946) Browsing of *Patella*. *Nature* 158:557
- Jones NS (1948) Observations and experiments on the biology of *Patella vulgata* at Port St. Mary, Isle of Man. *Proc Trans Liverpool Biol Soc* 56:60–77
- Knight M, Parke MW (1950) A biological study of *Fucus vesiculosus* and *Fucus serratus*. *J Mar Biol Assoc UK* 29:439–514
- Lawton J (1999) Are there general laws in ecology? *Oikos* 84: 177–192
- Leonard GM (2000) Latitudinal variation in species interactions: a test in the New England rocky intertidal zone. *Ecology* 81:1015–1030
- Lewis JR (1964) The ecology of rocky shores. English Universities Press, London
- Lodge SM (1948) Algal growth in the absence of *Patella* on an experimental strip of foreshore, Port St. Mary, Isle of Man. *Proc Trans Liverpool Biol Soc* 56:78–85
- Lubchenco J, Gaines SD (1981) A unified approach to marine plant-herbivore interactions. I. Populations and communities. *Annu Rev Ecol Syst* 12:405–437
- Luhning K (1990) Seaweeds, their environment, biogeography and ecophysiology. John Wiley & Sons, London
- McCook, Chapman ARO (1991) Community succession following massive ice scour on an exposed rocky shore: effects of *Fucus* canopy algae and of mussels during late succession. *J Exp Mar Biol Ecol* 154:137–169
- Menge BA, Berlow EL, Blanchette CA, Navarette SA, Yamada SB (1994) The keystone species concept: variation in interaction strength in a rocky intertidal habitat. *Ecol Monogr* 64:249–286
- Paine RT (1966) Food web complexity and species diversity. *Am Nat* 100:65–75
- Paine RT (2002) Trophic control of production in a rocky intertidal community. *Science* 296:736–739
- Reed DC, Foster MS (1984) The effect of canopy shading on algal recruitment and growth in a giant kelp forest. *Ecology* 65:937–948
- Santelices B (1990) Patterns of reproduction, dispersal and recruitment in seaweeds. *Oceanogr Mar Biol Annu Rev* 28:177–276
- Southward AJ (1953) The ecology of some rocky shores in the south of the Isle of Man. *Proc Trans Liverpool Biol Soc* 59:1–50
- Southward AJ (1956) The population balance between limpets and seaweeds on wave-beaten rocky shores. *Rep Mar Biol Stn Port Erin* 68:20–29
- Southward AJ (1964) Limpet grazing and the control of vegetation on rocky shores. In: Crisp DJ (ed) Grazing in terrestrial and marine environments. Blackwell Scientific Publications, Oxford, p 265–273
- Southward AJ (1979) Cyclic fluctuations in population density during 11 years recolonisation of rocky shores in West Cornwall following the Torrey Canyon oil spill in 1967. In: Naylor E, Hartnoll RG (eds) Cyclic phenomena in marine plants and animals. Pergamon Press, Oxford, p 85–92
- Southward AJ, Southward EC (1978) Recolonization of rocky shores in Cornwall after use of toxic dispersants to clean up the Torrey Canyon spill. *J Fish Res Board Can* 35: 682–706
- Vadas RL, Wright WA, Miller SL (1990) Recruitment of *Ascophyllum nodosum*: wave action as a source of mortality. *Mar Ecol Prog Ser* 61:263–272
- Vadas RL, Johnson S, Norton TA (1992) Recruitment and mortality of early post-settlement stages of benthic algae. *Br Phycol J* 27:331–351
- Velimirov B, Griffiths CL (1979) Wave-induced kelp movement and its importance for community structure. *Bot Mar* 22:169–172

Editorial responsibility: Roger Hughes (Contributing Editor), Bangor, UK

Submitted: April 6, 2004; Accepted: August 24, 2004
Proofs received from author(s): January 31, 2005