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## A continental scale evaluation of the role of limpet grazing on rocky shores

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**Abstract** It is critical for our knowledge of biodiversity and ecosystem processes to understand how individual species contribute to ecosystem processes and how these contributions vary in space and time. We used a manipulative field experiment in five locations over 17° of latitude [from southern Portugal to the Isle of Man (British Isles)] to determine the relative response of rocky intertidal algal assemblages released from control by the grazing of limpets. Response ratios showed that when limpets were removed there was a trend of effects from north to south. In the north, grazing had a strong effect on algal assemblages, but removing grazers reduced spatial variability in assemblages. In the south, the effect of limpet grazing was far weaker and removal of grazers had a much reduced impact on spatial variability. Here we show a clear trophic control of an ecosystem in that grazing by limpets not only determines macroalgal abundance overall but also modifies ecosystem stability via variability in cover of algae.

**Keywords** Algae · Herbivory · Biodiversity · Meta-analysis · Community

### Introduction

Understanding how biodiversity influences ecosystem processes critically depends on our knowledge of the roles of component species (Loreau et al. 2001; Duffy 2002; Ostfeld and LoGiudice 2003). The shallow coastal benthos has been understudied in terms of the influence of species richness on ecosystem function (Bolam et al. 2002; Emmerson and Huxham 2002). If components of biodiversity are removed, food chains and trophodynamics can be disrupted in different ways (Duffy 2002; Raffaelli et al. 2002) and in order to generalize across systems it is important to understand the loss of system components in ecosystems other than temperate grasslands (Loreau et al. 2001; Paine 2002).

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Grazing is the crucial link between primary producers and consumers in food-webs and can control biomass, hence productivity of ecosystems (Paine 2002; Halpern et al. 2005). In coastal marine ecosystems, grazing has been shown to affect algal vegetation (Hawkins et al. 1992; Underwood 2000; Paine 2002). Early work (Jones 1946; Southward 1964) on the Isle of Man, and confirmed subsequently (Hawkins 1981), showed that limpet grazing, rather than wave-action, controlled algal biomass, preventing the mid-tidal region of shores in wave-exposed locations from being dominated by fucoid algae. These studies were limited by low levels of spatial replication and did not quantify the effect of limpet grazing on system properties or variability.

The balance between fucoid vegetation and limpets along the wave-exposure axis changes across a latitudinal gradient in western Europe. In the north, fucoids extend onto exposed shores, but towards the south they are increasingly restricted to sheltered conditions, including estuaries (Ballantine 1961; Hawkins et al. 1992). In addition to different climatic regimes along the European coastline, the macroalgal species pool shows a southward reduction in abundance of mid-shore canopy algae and a change towards assemblages dominated by turf algae (Ballantine 1961; Hawkins et al. 1992; Boaventura et al. 2002). Thus, in the higher northern latitudes, removal of grazers leads rapidly and deterministically to large canopy algae (Hawkins et al. 1992). Further south towards the equator, the outcomes of removal of grazers would be expected to be more stochastic due to the reduced abundance of fucoids which can dominate later stages of secondary succession (Berlow 1997, 1999). These patterns provide the opportunity to erect hypotheses on the effects of grazers on vegetation, represented by macroalgae, and on measures of small-scale spatial variance in cover of macroalgae over continental scales (Benedetti-Cecchi 2000). The effects of limpet removal on diversity of algal assemblages will be confounded by latitudinal variations in the pool of available algal species which are fundamentally different from UK to Portugal (Crisp and Southward 1958; Boaventura et al. 2002).

Whilst there has been some consideration of the effects of individual species on marine benthic processes (Emmerson and Huxham 2002), many studies concentrate on average effects, without considering variability; explaining variance in ecological processes is a key task for ecologists (Lawton 1999; Benedetti-Cecchi 2000, 2003; Underwood 2000) since the most consistent effect noted in the literature is that processes and organisms are extremely variable in space and time (Lawton 1999; Underwood 2000). Based on previous experiments (see Hawkins et al. 1992 for review) we predicted that, in the north, removal of limpets would have a strong effect on cover of algae and quickly lead to domination by large fucoid canopy algae. Removing limpets would still have an effect in southern Europe. It was likely to be weaker because of the harsher conditions, a greater range of algal colonizers and the absence of large mid-shore

canopy species, e.g. *Fucus vesiculosus*, which would channel mid-successional processes (Berlow 1997). Thus we predicted a less consistent response to the removal of grazers. We further predicted that because limpets promote small-scale spatial variability in cover of algae in the north (Johnson et al. 1997), the exclusion of limpets would lead to the deterministic colonization by canopy algae and a concomitant reduction in spatial variability in cover of algae. In contrast, limpets probably depress spatial variability in algal assemblages in the south where there are less canopy algae and a greater pool of other colonizing algae. So, the removal of grazers should increase small-scale variability. In the southern areas of Europe, algal colonization would be expected to be inhibited or at least slowed by physical stresses associated with high summer temperatures during periods of tidal emersion. In the north such stresses are expected to be less strong. Seasonal effects may be modified by the abundance of algal propagules (Kim and DeWreede 1996), this is likely to emphasize canopy dominance in the absence of grazers at northern sites due to the relatively high abundance of fucoid propagules in the summer (Hawkins 1981) compared with southern sites. To test the modulation of grazing by seasonal factors, we initiated experiments in summer and in winter.

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## Methods

### Design of experiment

Large-scale geographic effects were tested by comparison of five locations (Table 1) encompassing 17° of latitude. At each location, two randomly chosen moderately exposed shores at least 1 km apart were selected. The experiment compared summer (June and July) and winter (January/February), so two start dates were set within each season to provide temporal replication. These dates were randomized within a season for each shore by selecting four 7-day periods within a 2-month season which were possible for fieldwork, each 7-day period being separated by at least 5 days. The start dates were then randomly allocated. At each start date, two replicate sites (approximately 20 m×20 m) were established on each shore at the mid-tidal level. These were randomly selected from 16 sites previously identified as suitable on each shore. Sites for each location/season/date combinations were chosen before the experiment started. Within each site, fixed plots were established conforming to the following criteria: (1) rock as level as possible and not more than 45° slope, (2) rock surface drained at low tide, (3) more than 50% barnacle cover, (4) less than 1% algal cover, (5) limpets present and (6) each plot was more than 1 m from another plot. These criteria were necessary to standardize across locations, particularly barnacle cover as this is known to modify limpet foraging behaviour (Hawkins et al. 1992) and to ensure that we accurately measured our response variable, algal recruitment and establishment. Standardizing for greater

**Table 1** Shores used in the experiment

Location	Shore 1	Shore 2
Isle of Man (UK)	Port St. Mary 54°4'N 4°44'W	Derbyhaven 54°5'N 4°37'W
South-west England (UK)	Heybrook Bay 50°19'N 4°07'W	Wembury 50°18'N 4°05'W
Oviedo (northern Spain)	Artedo 43°34'N 6°10'W	Campaniello 43°33'N 6°24'W
Lisboa (central Portugal)	Cabo Raso 38°42'N 9°29'W	Avencas 38°41'N 9°21'W
Sines (southern Portugal)	Oliveirinha 37°53'N 8°48'W	Nascedios 37°41'N 8°48'W

levels of barnacle cover meant that plots in each location were less likely to be affected by pulses of barnacle recruitment which could impact on the recruitment of algae (Hawkins et al. 1992).

Each 0.5 m × 0.5 m plot was randomly allocated to one of three treatments: limpet exclusion (fenced), half-fenced [as a procedural control for artefacts due to presence of a fence; (Underwood 1997)], or control. There were three replicates of each treatment. If the allocation of treatments gave a grouped or regular arrangement of plots, the treatments were re-randomized. A standard construction of fences was used: square-mesh, welded plastic-coated steel wire (approximately 13 mm mesh) cut into strips 60 mm wide and bent into an 'L' shape longitudinally, with dimensions of 35 mm vertical and 25 mm horizontal. The material was formed into a 50 cm × 50 cm and screwed to the rock with rubber tap-washers over the screws to fix the mesh. Any limpets present in the plots were counted and removed. The half-fence treatment was made by fixing pieces of exclusion fence at the corners of each plot; the total length of fence material used was half that of a full exclusion treatment and allowed limpets in and out of the plot. Limpets were unmanipulated. Control plots were simply marked with drilled holes at each corner.

Plots were checked after 2 weeks and then monthly until termination (12 months). On each visit, fences were inspected, repaired, cleaned of epiphytes and all macrograzers within the exclusion plots were removed. At the end of the experiment, plots were sampled visually to assess (non-destructively) percentage cover of all algae (identified to species level wherever possible), using a 49-intersection point quadrat. Any algal species present but not recorded at any intersection point were scored as 1%. The number of each species of grazer was noted for each plot.

To facilitate comparisons across regions with different species pools (Loreau et al. 2001), we allocated algae to morphological groups (Steneck and Dethier 1994). *Patella* spp. are the dominant grazers on the mid-shore of Europe (Ballantine 1961); *P. vulgata* progressively gives way to *P. depressa* on the mid-shore further south in Europe (*P. vulgata* on open rock are 100% of all limpets on the Isle of Man; 50–80% in south-west England; > 50% in northern Spain and are absent in Portugal) (Crisp and Southward 1958; Ballantine 1961; Boaventura et al. 2002). The limpets *P. vulgata* and *P. depressa* are microphagous grazers showing similar feeding mechanisms and gut contents wherever they occur (Hawkins et al. 1989).

## Statistical analysis

In order to test for artefacts due to the presence of a fence, we formally compared differences in total algal cover for all factors, then looked at the distribution of significant SNK tests using an Anderson test (Anderson 1959; Underwood 1997). We used a meta-analysis to assess the magnitude of effects due to removal of limpets and compared this across locations (latitudinal effects) and seasons. The effect size of grazing was calculated as a response ratio using the natural log of the mean of the three control plots divided by the mean of the three exclusion plots for each experimental site (Hedges et al. 1999), giving two replicate measures of effect size for each initiation date; this estimates the relative strength of the response such that a weak effect is not significantly different from zero. These were subsequently analysed by ANOVA using WinGMAV5 (EICC, University of Sydney). This was repeated for variances from each set of controls and exclusions, which estimated the mean variability of the assemblage response to removal of limpets. Concerns over this approach (Gurevitch and Hedges 1999) do not apply as our work was from 'experiments' carried out simultaneously using identical protocols, sampling procedures and yielding a balanced data-set. Comparing effects of grazing from numerous experiments in different places, at different times, in a meta-analysis, is particularly valuable where every experiment, as here, was designed to test the same hypothesis, with identical treatments, methods and replication. Thus, heteroscedasticity between study-sets were minimized (Gurevitch and Hedges 1999; Hedges et al. 1999) enabling formal comparison. It is possible that any effects seen may be due to varying numbers of limpets at different sites (Bustamante et al. 1995). We compared the numbers of limpets present in each plot at initiation of the experiment using an ANOVA as above. We only had sizes of limpets for three locations (Isle of Man, south-west England and Southern Portugal); using a length-dry mass regression derived from limpets in south-west England (R.A. Coleman, unpublished data) as representative for the experiment, we calculated the limpet biomass in each patch for each shore at the three locations for which we had size data and compared patches using ANOVA. We used regression to test if variation in biomass of limpets influenced our four measures [effect sizes for means and variance for (1) canopy cover and (2) total algal cover in response to limpet removal].

## Results

The common effect of limpets was demonstrated in that in every location, the removal of limpet grazing led to a proliferation of macroalgae; even in summer in southern Europe. The analyses of mean percentage cover of total algal cover at 12 months showed much small-scale variation in mean percentage cover [in a 6 factor ANOVA the term  $\text{Time} \times \text{Site}(\text{Date}(\text{Season} \times \text{Shore}(\text{Location}))$ ) was significant  $F_{(80,480)} = 2.52$ ,  $P < 0.001$ ], post hoc SNK tests within this interaction ranked exclusion plots first (in an ascending sequence), significantly more often than the other treatments (69 times over 79 comparisons). These SNK tests consistently indicated that there were no differences between the half-fence controls and the full controls; thus, there were no experimental artefacts. This permitted the use of exclusions against controls as a response ratio. We therefore analysed the strength and variability in responses to the removal of limpet grazers using a standard measure of effect-size in a meta-analysis approach (Gurevitch and Hedges 1999; Osenberg et al. 1999) using means to measure the relative strength of response by the assemblage to removal of limpets and variances to estimate variability. On the whole, the effect sizes, i.e. of differences in mean cover of canopy and of total algae were negative because control areas had a lesser percentage cover of algae than did areas where limpets were removed. The effect of grazing on the development of canopy algae at 12 months was variable on different shores at two locations and between seasons

for one shore at each of two locations (Table 2). There was a north–south divide in strength of response to removal of limpets (Table 2, Fig. 1a), with the two southern-most locations showing a much reduced response. Removal of limpets had a strong effect at northern locations where canopy algae such as *F. vesiculosus* quickly dominated within a few months. Canopy algae were all but absent from Portuguese shores with only *F. spiralis* being present, hence the response to removal of limpets was minimal on this morphological group at the most southern locations (Fig. 1a). With respect to colonization by canopy algae, removing limpets increased variability in the system. Measures of effect size using variances were nearly all negative because variances were greater for areas where limpets had been excluded than in areas where grazing was allowed where the absence of canopy algae meant little or no variability. These differences were, however, minimal at the most northerly location, where canopy algae dominated and in the south where few canopy algae were present (Fig. 1b, Table 2). Seasonal differences in variability of response of canopies to removal of limpets were small and were observed at only one shore, in northern Spain.

Whilst there was significant heterogeneity of variance (Table 2) in the analysis of effect-sizes of mean percentage cover of total algae, large designs such as this experiment are robust against the consequences of this problem (Underwood 1997). Within the significant interactions, there were no seasonal effects detected by

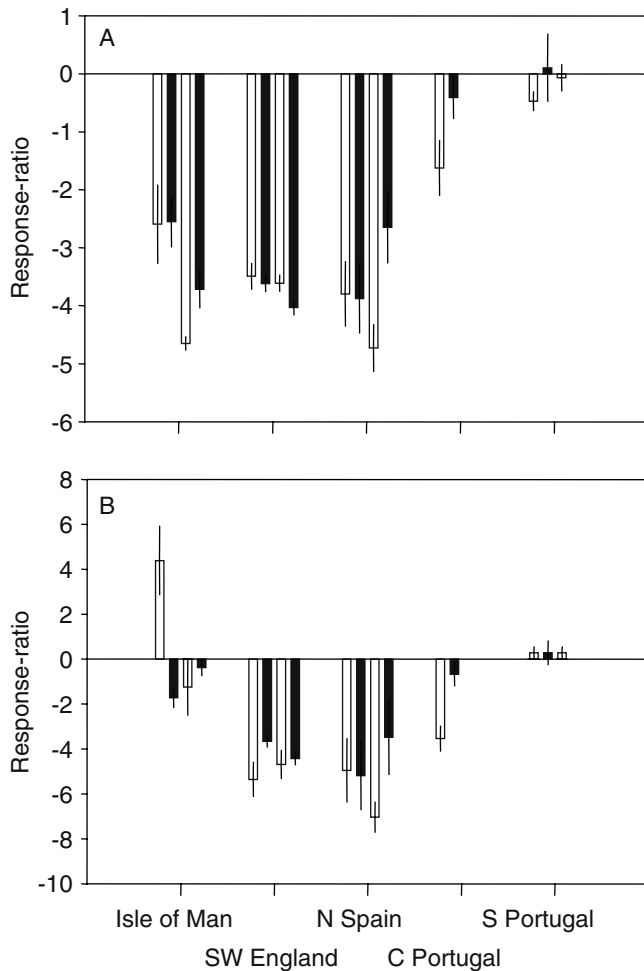
**Table 2** Analyses of response ratios as a measure of effect size of excluding limpets on growth of algae (canopy and total algae) at different locations in Europe

Source	Cochran's test												
	df	Canopy (means)			Canopy (variances)			Total algae (means)			Total algae (variances)		
		C=0.19, NS			C=0.17, NS			C=0.24, *			C=0.17, NS		
		MS	F	P	MS	F	P	MS	F	P	MS	F	P
Location Lo	4	52.9	17.72	**	109.1	15.01	**	13.5	9.55	*	32.3	6.7	*
Shore Sh(Lo)	5	3	5.85	**	7.3	1.9	NS	1.4	3.13	*	4.8	0.62	NS
Season Se	1	3.7	4.25	NS	1.4	0.11	NS	1.7	1.49	NS	13.3	1.58	NS
Date (Lo × Sh × Se)	20	0.5	0.85	NS	3.8	1.13	NS	0.5	0.74	NS	7.7	1.31	NS
Lo × Se	4	0.9	0.59	NS	12.3	0.84	NS	1.2	0.82	NS	8.5	0.69	NS
Se × Sh(Lo)	5	1.5	2.86	*	14.7	3.86	*	1.4	3.12	*	12.3	1.59	NS
Residual	40	0.6			3.4			0.6			5.9		
Total	79												

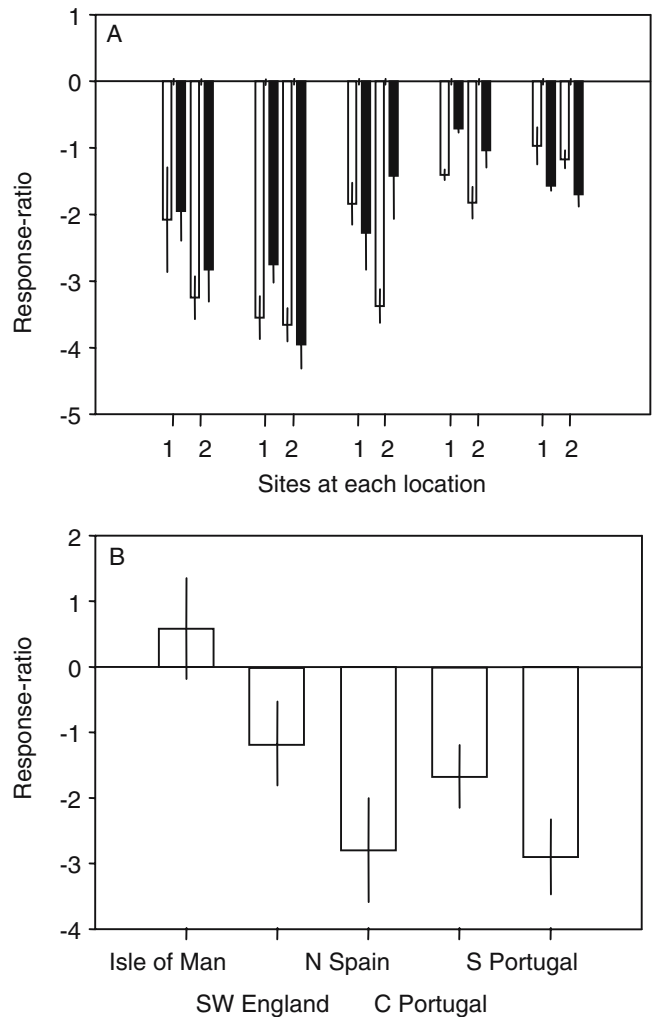
Significant factors	SNK tests			SNK tests			SNK tests			SNK tests		
	IoM = SWE = NSp > CP = Sp	IoM1 > IoM2	CP1 > CP2	SWE = NSp > IoM = CP = Sp	IoM1S > IoM2W	NSp2S > NSp2W	No logical groupings	IoM2 > IoM1	No logical groupings	No logical groupings	No logical groupings	No logical groupings
Location												
Sh(Lo)												
Se x Sh(Lo)	NSp2S > NSp2W	CP1S > CP1W		IoM1S > IoM2W	NSp2S > NSp2W		NSp2S > NSp2W					

For each functional group of algae, we used the response ratio of summary statistics of the differences between controls and exclusions. To measure the strength of the effect of limpets we used the means of treatments and to measure variability in effects we used variances. Statistical significance is denoted as follows: NS is not significant, \* < 0.05; \*\* < 0.01; \*\*\* < 0.005. The post hoc SNK tests are given under each ANOVA for the respective significant terms from the ANOVA. Rankings are given if a site or location is significantly ( $\alpha = 0.05$ ) greater than another; each location, site and season are denoted by abbreviations: *IoM* Isle of Man; *SWE* south-west England; *NSp* northern Spain; *CP* central Portugal; *sP* Southern Portugal with 1 and 2 being the different shores at each location. *S* represents summer initiation, and winter is indicated by *W*



**Fig. 1** Effects of removal of limpets on development of canopy algae 12 months after removal. For each location, *clear bars* refer to a summer initiation and *shaded bars* to a winter start; at each location the first pair of *bars* refer to shore 1 and the second set to shore 2. **a** Shows differences in response ratio of the mean of the three exclusions (per site) against the mean of the three controls. **b** Shows change in response ratio of the variance of the three exclusions (per site) against the variance of the three controls. *Error bars* are  $\pm$  SEM

SNK tests except for shore 2 in northern Spain (Table 2). SNK tests showed that differences between shores only referred to those in the Isle of Man. There were differences in response ratio at different locations, but SNK tests could not distinguish between them in strength of effect of removal of limpets. There was a trend of decreasing effect size of limpet grazers in southern locations in that the Portuguese shores appeared to have a smaller response ratio than the other locations (Fig. 2a), although the SNK tests could not distinguish logical groups (Table 2). Our expectation of differing patterns of variability in algal assemblages with respect to grazing at different latitudes was confirmed because this was the only significant factor in the ANOVA (Table 2, Fig. 2b). On the Isle of Man, variability in the grazed areas was greater than in grazer exclusions, mainly due to a strong recruitment of fucoids



**Fig. 2** Effects of removal of limpets on development of total algal cover 12 months after removal. For each location, *clear bars* refer to a summer initiation and *shaded bars* to a winter start; at each location the first pair of *bars* refer to shore 1 and the second set to shore 2. **a** Shows change in response ratio of the mean of the three exclusions (per site) against the mean of the three controls. **b** Shows change in response ratio of the variance of the three exclusions (per site) against the variance of the three controls. *Error bars* are  $\pm$  SEM

(S. J. Hawkins, unpublished observation). Further south, the greater variety of components of the macroalgal species pool and the absence of dominant canopy algae meant that the variability in cover of algae introduced by limpet activity was markedly less than the variation in possible outcomes if limpets were excluded.

Locations differed in the number of limpets present at each shore (Table 3, Fig. 3), the Isle of Man having much fewer limpets per meter square and all the other shores were broadly similar apart from northern Spain shore 1. The biomass of limpets was greatest for southwest England (mean  $50.93 \text{ g m}^{-2}$ , SEM 5.44, many medium-sized limpets) and significantly different from the Isle of Man (mean  $18.80 \text{ g m}^{-2}$ , SEM 1.84, few large limpets) and southern Portugal (mean  $15.01 \text{ g m}^{-2}$ ,



**Table 3** Analysis of variance of limpet densities in each site at the start of each experiment

Source	df	MS	F	P
Location Lo	4	9783.1	4.80	>0.05
Shore Sh(Lo)	5	2037.2	8.69	<0.001
Season Se	1	192.3	0.19	>0.6
Lo × Se	4	1015.9	3.32	>0.1
Se × Sh(Lo)	5	306.4	1.31	>0.3
Date Da(Lo × Sh × Se) <sup>a</sup>	20	234.4		
Residual <sup>a</sup>	40	395.1		
Total	79			
<sup>a</sup> Pooled data	60	341.5		

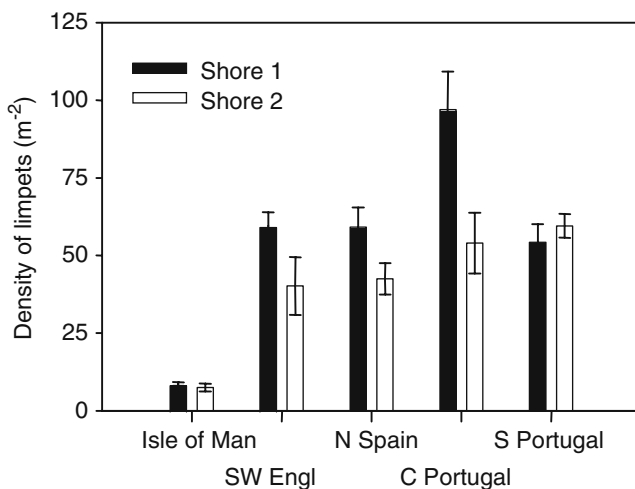
Variances were homogenous (Cochran's  $C=0.15$ , NS)

<sup>a</sup>These terms were pooled to increase the power of the test for main effects (Underwood 1997)

SEM 1.47, many small limpets) (Table 4). None of the regressions significantly explained any variation in response ratios (Table 5), hence differences in limpet biomass between the Isle of Man, south-west England and southern Portugal did not contribute to the observed changes in response ratios associated with limpet exclusion.

## Discussion

Field experiments have made numerous contributions to ecological theory and rocky shores have long proved a particularly tractable system for such work. Inevitably, there are difficulties extrapolating from local small-scale experiments to enable generalization. Hence, ecologists have often been criticized, in addition to being self-critical, because of the local contingency of many of the findings (Lawton 1999). In order to understand patterns/processes over a large spatial scale, there is clearly a need for large-scale field experiments using



**Fig. 3** Difference in limpet density at the start of the experiment. SNK tests showed that shores were significantly different except for the Isle of Man and southern Portugal. Error bars are  $\pm$ SEM

**Table 4** Analysis of variance of limpet biomass for each shore and date at the three locations

Source	df	MS	F	P
Location Lo	2	6230.3	14.72	<0.05
Shore Sh(Lo)	3	423.2	2.38	>0.08
Season Se	1	130.0	1.07	>0.4
Lo × Se	2	121.4	0.98	>0.4
Se × Sh(Lo)	3	123.6	2.70	>0.09
Date Da(Lo × Sh × Se) <sup>a</sup>	12	45.8		
Residual <sup>a</sup>	24	244.1		
Total	47			
<sup>a</sup> Pooled data	36	178.0		

<sup>a</sup>These terms were pooled to increase the power of the test for main effects (Underwood 1997)

identical experimental designs to separate generality of process from local context and small-scale variability. In spite of a long history of broadscale surveys (Menge et al. 1994; Bustamante and Branch 1996) and planned comparisons including work comparing two widely spaced locations (Worm et al. 2002), our research is the first report of such a properly replicated, broadscale manipulative field experiment over a continental scale in a natural system. Despite the obvious need for biodiversity/ecosystem experiments to be implemented over a variety of sites (Hector et al. 2002), the only comparable work to date has been large-scale projects using artificially sown assemblages in field trials in semi-agricultural systems (Hector et al. 1999; Loreau and Hector 2001) and the extensive but unreplicated iron fertilization experiments in the Pacific Ocean (Coale et al. 1998; Landry et al. 2000).

Here we demonstrate a clear role of grazers in determining ecosystem outcomes. This common effect is consistent from the Irish Sea to northern Spain. In a parallel study in western Sweden, using a similar design but with the grazers represented by littorinid snails, there were limited effects of removal of grazers on establishment of algae (Lindegarh et al. 2001). The patterns from that study (Lindegarh et al. 2001) are similar to the results from the Portuguese shores here. Thus, in harsher environments such as those exposed to winter ice (e.g. Sweden) or high summer insolation/temperatures (e.g. southern Portugal), the removal of grazers leads to more unpredictable outcomes. Unpredictable effects of limpets were also observed in exclusion experiments conducted in the north-west Mediterranean (Benedetti-Cecchi et al. 2000, 2001). Most of the variability occurred at large spatial scales (100 s of km) and among seasons. These patterns were related to variation in intensity of recruitment of algae, with limpets losing the ability to control vegetation when algal recruitment was intense. Previous studies have shown that, on low parts of shores, the effects of grazers on algal assemblages differed with respect to season (Underwood and Jernakoff 1984; Kim and DeWreede 1996). In our work, the expectation of a seasonal component in the response of mid-shore algal assemblages

**Table 5** Regression statistics for effect of limpet (ln transformed) biomass on four measures of the effects of removal of limpet grazing

Location	Regressions	Canopy algae		Total algal cover	
		Means	Variances	Means	Variances
Isle of Man	Slope, intercept	-0.42, -2.19	0.60, -1.43	-0.37, -1.49	-1.04, 3.52
	$r^2$	0.03	< 0.01	0.03	0.03
	$F_{(1,14)}, P$	0.54, > 0.47	0.18, > 0.73	0.43, > 0.52	0.49, > 0.46
South-west England	Slope, intercept	-0.08, -3.38	0.732	0.23, -4.34	0.39, -2.65
	$r^2$	0.02	0.14	0.03	< 0.01
	$F_{(1,14)}, P$	0.25, > 0.62	2.20, > 0.15	0.48, > 0.50	0.11, > 0.74
Southern Portugal	Slope, intercept	-0.24, 0.54	-0.50, 1.52	-0.54, 0.07	-1.32, 0.59
	$r^2$	0.02	0.08	0.17	0.04
	$F_{(1,14)}, P$	0.27, > 0.61	1.26, > 0.27	2.96, > 0.11	0.58, > 0.46

released from grazing pressure (Hawkins 1981) was not supported, except for a few shores (Table 2, Figs. 1, 2). The effect of limpets on rocky shore cover of algae strongly modifies system variability in a manner predicted by our knowledge of the biology of the organisms. Results were consistent with predictions of the effects of limpets on patterns of small-scale spatial variance in algal cover. The effects of removal of limpet grazing on variability of cover of macroalgae were not related to the biomass of limpets. Grazers promoted spatial variation at northern localities by preventing establishment of furoid algae which colonized the exclusion plots. In contrast, at southern locations where furoid algae were more sparse or absent, limpets reduced spatial variance in algal cover by preventing the establishment of heterogeneous assemblages. Thus, processes affecting the spatial arrangement of limpets on the shore may have important indirect effects in maintaining algal mosaics at northern locations (Johnson et al. 1998). The hypothesis that changes in spatial patterning of limpets affect the spatial organization of algal assemblages (Johnson et al. 1997; Coleman et al. 2004) warrants further investigation through appropriate experimental designs (Benedetti-Cecchi 2003).

Over the extensive latitudinal range of the study it is probably grazing, mainly by limpets, which contribute to the overall lack of abundance of algae on the mid-shore. Variations in cover of algae depend largely on escape from grazing. Whilst patterns of diversity over latitudinal scales have been discussed extensively (Gaston and Blackburn 2000; Blackburn and Gaston 2002) the underlying mechanisms are not well understood. Although the algal assemblages observed in the sites and shores used in this experiment were drawn from local species pools (Gaston and Blackburn 2000; Rivadeneira et al. 2002) and the species composition of grazers differed from area to area (Crisp and Southward 1958; Hawkins and Hartnoll 1983; Boaventura et al. 2002), the patterns were very similar over the geographic range of the experiment. This concurs with observations from work in the southern hemisphere and the north-west coast of the USA (Underwood 2000; Paine 2002; Rivadeneira et al. 2002; Menge et al. 2005).

The consequence of the grazers in this ecosystem is to determine whether the system is a net producer and

exporter dominated by macrophytes, or a net consumer dominated by filter-feeders and consumption of microbial films. The effect of removing grazers on system processes and variability did not depend on the existing biomass of the consumers present; this has important consequences for understanding trophic dynamics (Emmerson and Huxham 2002; Emmerson et al. 2004; Halpern et al. 2005). Grazing makes a major contribution to the structure of rocky shore algal assemblages over 17° of latitude on a continental scale in that it increases variation in the north, where responses of algal assemblages are deterministic (Jenkins et al. 2005) and decreases variation in the south, where outcomes are more contingent. Whilst interactions between physical conditions and recruitment dynamics were averaged across seasons, with the result that differences among seasons cannot be resolved beyond physical influences, we can propose that grazing by limpets is a key process in rocky shore ecosystem properties over much of the mid-shore of western Europe.

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## References

- Anderson RL (1959) Use of contingency tables in the analysis of consumer preference studies. *Biometrics* 15:582–590
- Ballantine WJ (1961) The population dynamics of *Patella vulgata* and other limpets. PhD Thesis, University of London
- Benedetti-Cecchi L (2000) Variance in ecological consumer–resource interactions. *Nature* 407:370–374
- Benedetti-Cecchi L (2003) The importance of the variance around the mean effect size of ecological processes. *Ecology* 84:2335–2346
- Benedetti-Cecchi L, Bulleri F, Acunto S, Cinelli F (2001) Scales of variation in the effects of limpets on rocky shores in the N. W. Mediterranean. *Mar Ecol Progr Ser* 209:131–141
- 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

- Berlow EL (1997) From canalization to contingency: historical effects in a successional rocky intertidal community. *Ecolog Monogr* 67:435–460
- Berlow EL (1999) Strong effects of weak interactions in ecological communities. *Nature* 398:330–334
- Blackburn TM, Gaston KJ (2002) Scale in macroecology. *Global Ecol Biogeog* 11:185–189
- Boaventura D, Re P, da Fonseca LC, Hawkins SJ (2002) Intertidal rocky shore communities of the continental Portuguese coast: analysis of distribution patterns. *Mar Ecol Pubbl Stn Zool Napoli* 23:69–90
- Bolam SG, Fernandes TF, Huxham M (2002) Diversity, biomass, and ecosystem processes in the marine benthos. *Ecol Monogr* 72:599–615
- Bustamante RH, Branch GM (1996) Large scale patterns and trophic structure of southern African rocky shores: the roles of geographic variation and wave exposure. *J Biogeog* 23:339–351
- Bustamante RH, Branch GM, Eekhout S, Robertson B, Zoutendyk P, Schleyer M, Dye A, Hanekom N, Keats D, Jurd M, McQuaid C (1995) Gradients of intertidal primary productivity round the coast of South Africa and their relationships with consumer biomass. *Oecologia* 102:189–201
- Coale KH, Johnson KS, Fitzwater SE, Blain SPG, Stanton TP, Coley TL (1998) IronEx-I, an in situ iron-enrichment experiment: experimental design, implementation and results. *Deep Sea Res II Topic Stud Oceanog* 45:919–945
- Coleman RA, Underwood AJ, Chapman MG (2004) Absence of costs of foraging excursions in relation to limpet aggregation. *J Anim Ecol* 73:577–584
- Crisp DJ, Southward AJ (1958) The distribution of intertidal organisms along the coasts of the English channel. *J Mar Biol Assoc UK* 37:157–208
- Duffy JE (2002) Biodiversity and ecosystem function: the consumer connection. *Oikos* 99:201–219
- Emmerson M, Bezemer TM, Hunter MD, Jones TH, Masters GJ, Van Dam NM (2004) How does global change affect the strength of trophic interactions? *Basic Appl Ecol* 5:505–514
- Emmerson M, Huxham M (2002) How can marine ecology contribute to the biodiversity-ecosystem functioning debate? In: Loreau M, Naeem S, Inchausti P (eds) *Biodiversity and ecosystem functioning: synthesis and perspectives*. Oxford University Press, Oxford, pp 139–146
- Gaston KJ, Blackburn TM (2000) *Pattern and process in macroecology*. Blackwell, Oxford
- Gurevitch J, Hedges LV (1999) Statistical issues in ecological meta-analyses. *Ecology* 80:1142–1149
- Halpern BS, Borer ET, Seabloom EW, Shurin JB (2005) Predator effects on herbivore and plant stability. *Ecol Lett* 8:189–194
- Hawkins SJ (1981) The influence of season and barnacles on the algal colonisation of *Patella vulgata* exclusion areas. *J Mar Biol Assoc UK* 61:1–15
- Hawkins SJ, Hartnoll RG (1983) Grazing of intertidal algae by marine invertebrates. *Oceanog Mar Biol Ann 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 special volume 46*. Clarendon Press, Oxford, pp 1–32
- Hawkins SJ, Watson DC, Hill AS, Harding SP, Kyriakides MA, Hutchinson S, Norton TA (1989) A comparison of feeding mechanisms in microphagous, herbivorous, intertidal, prosobranchs in relation to resource partitioning. *J Moll Stud* 55:151–165
- Hector A, Loreau M, Schmid B, Project TB (2002) Biodiversity manipulation experiments: Studies replicated at multiple sites. In: Loreau M, Naeem S, Inchausti P (eds) *Biodiversity and ecosystem functioning: synthesis and perspectives*. Oxford University Press, Oxford, pp 21–35
- Hector A, Schmid B, Beierkuhnlein C, Caldeira MC, Diemer M, Dimitrakopoulos PG, Finn JA, Freitas H, Giller PS, Good J, Harris R, Hogberg P, Huss-Danell K, Joshi J, Jumpponen A, Körner C, Leadley PW, Loreau M, Minns A, Mulder CPH, O'Donovan G, Otway SJ, Pereira JS, Prinz A, Read DJ, Scherer-Lorenzen M, Schulze ED, Siamantziouras ASD, Spehn EM, Terry AC, Troumbis AY, Woodward FI, Yachi S, Lawton JH (1999) Plant diversity and productivity experiments in European grasslands. *Science* 286:1123–1127
- Hedges LV, Gurevitch J, Curtis PS (1999) The meta-analysis of response ratios in experimental ecology. *Ecology* 80:1150–1156
- Jenkins SR, Coleman RA, Burrows MT, Hartnoll RG, Hawkins SJ (2005) Regional scale differences in determinism of limpet grazing effects. *Mar Ecol Progr Ser* 287:77–86
- Johnson MP, Burrows MT, Hartnoll RG, Hawkins SJ (1997) Spatial structure on moderately exposed rocky shores: patch scales and the interaction between limpets and algae. *Mar Ecol Progr 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 *Fucus* mosaic. *Mar Ecol Progr Ser* 169:179–188
- Jones NS (1946) The browsing of *Patella*. *Nature* 158:557
- Kim JH, DeWreede RE (1996) Effects of size and season of disturbance on algal patch recovery in a rocky intertidal community. *Mar Ecol Progr Ser* 133:217–228
- Landry MR, Constantinou J, Latasa M, Brown SL, Bidigare RR, Ondrusek ME (2000) Biological response to iron fertilization in the eastern equatorial Pacific (IronEx II). III. Dynamics of phytoplankton growth and microzooplankton grazing. *Mar Ecol Progr Ser* 201:57–72
- Lawton JH (1999) Are there general laws in ecology. *Oikos* 84:177–192
- Lindgarth M, Aberg P, Cervin G, Nilsson PG (2001) Effects of grazing on the structure of mid-shore, intertidal assemblages on moderately exposed rocky shores of the Swedish west coast. *Mar Ecol Progr Ser* 212:29–38
- Loreau M, Hector A (2001) Partitioning selection and complementarity in biodiversity experiments. *Nature* 412:72–76
- Loreau M, Naeem S, Inchausti P, Bengtsson J, Grime JP, Hector A, Hooper DU, Huston MA, Raffaelli D, Schmid B, Tilman D, Wardle DA (2001) Biodiversity and ecosystem functioning: current knowledge and future challenges. *Science* 294:804–808
- Menge BA, Allison GW, Blanchette CA, Farrell TM, Olson AM, Turner TA, van Tamelen P (2005) Stasis or kinesis? Hidden dynamics of a rocky intertidal macrophyte mosaic revealed by a spatially explicit approach. *J Exp Mar Biol Ecol* 314:3–39
- Menge BA, Berlow EL, Blanchette CA, Navarrete SA, Yamada SB (1994) The keystone species concept: variation in interaction strength in a rocky intertidal habitat. *Ecol Monogr* 64:249–286
- Osenberg CW, Sarnelle O, Cooper SD, Holt RD (1999) Resolving ecological questions through meta-analysis: goals, metrics, and models. *Ecology* 80:1105–1117
- Ostfeld RS, LoGiudice K (2003) Community disassembly, biodiversity loss, and the erosion of an ecosystem service. *Ecology* 84:1421–1427
- Paine RT (2002) Trophic control of production in a rocky intertidal community. *Science* 296:736–739
- Raffaelli D, van der Putten WH, Persson L, Wardle DA, Petchey OL, Koricheva J, van der Heijden M, Mikola J, Kennedy T (2002) Multitrophic dynamics and ecosystem processes. In: Loreau M, Naeem S, Inchausti P (eds) *Biodiversity and ecosystem functioning: synthesis and perspectives*. Oxford University Press, Oxford, pp 147–154
- Rivadeneira MM, Fernandez M, Navarrete SA (2002) Latitudinal trends of species diversity in rocky intertidal herbivore assemblages: spatial scale and the relationship between local and regional species richness. *Mar Ecol Progr Ser* 245:123–131
- Southward AJ (1964) Limpet grazing and the control of vegetation on rocky shores. In: Crisp DJ (ed) *Grazing in terrestrial and marine environments*. Blackwell, Oxford, pp 265–273



- Steneck RS, Dethier MN (1994) A functional group approach to the structure of algal-dominated communities. *Oikos* 69:476–498
- Underwood AJ (1997) Experiments in ecology: their logical design and interpretation using analysis of variance. Cambridge University Press, Cambridge
- Underwood AJ (2000) Experimental ecology of rocky intertidal habitats: What are we learning? *J Exp Mar Biol Ecol* 250:51–76
- Underwood AJ, Jernakoff P (1984) The effects of tidal height, wave exposure, seasonality, and rock pools on grazing and intertidal macroalgae in New South Wales. *J Exp Mar Biol Ecol* 75:71–96
- Worm B, Lotze HK, Hillebrand H, Sommer U (2002) Consumer versus resource control of species diversity and ecosystem functioning. *Nature* 417:848–851