

# Role of biological habitat amelioration in altering the relative responses of congeneric species to climate change

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**ABSTRACT:** The distribution of most species is expected to alter in response to climate change. Predictions for the extent of these range shifts are frequently based on 'climate envelope' approaches, which often oversimplify species responses because many do not consider interactions between physical and biological factors. The local persistence of some species, however, is likely to be strongly modulated by microhabitat-forming organisms. Using congeneric patellid gastropods with northern/boreal and southern/lusitanian distributions, we have demonstrated how the loss of habitat-forming macroalgal species could modify species responses to climate change. The northern limpet *Patella vulgata* preferentially aggregates beneath *Fucus* spp. When *Fucus vesiculosus* was experimentally removed, to simulate a decline in macroalgal abundance in response to climatic warming, *P. vulgata* suffered increased mortality or relocated home scars, often to nearby *Fucus* spp. patches. In contrast, the southern limpet *P. depressa* did not aggregate beneath *Fucus* spp. and showed no response in terms of movement or mortality to the loss of *F. vesiculosus*. Based on these results, we predict that the loss of *Fucus* spp. will influence the relative abundance of these 2 limpet species, particularly at the distributional limit of *Fucus* spp. In addition, differences in the aggregative behaviour of these limpet species will result in changes in the spatial distribution of grazing in the intertidal, with likely consequences for community dynamics. These outcomes could not be anticipated from predictions based on direct responses to temperature alone, highlighting the need for biotic and abiotic factors to be incorporated into predictions of species responses to climate change.

**KEY WORDS:** Biological interactions · Biologically generated habitat · Climate change · Climate envelope · Limpets · Macroalgae

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## INTRODUCTION

Global air temperatures have risen by  $0.6 \pm 0.2^\circ\text{C}$  in the last 100 yr and further increases of between 2 and  $3^\circ\text{C}$  are predicted by 2100 (Hulme et al. 2002), prompting the need to understand how species and assemblages respond to climate change. To date, forecasts of species-level responses have used a 'climate envelope' approach, whereby a single climatic variable, usually

temperature, is mapped in 'climate space' (the area in which a species can survive because the environment is suitable). If the climatic space alters, then it is predicted that the geographical distribution of species found within that climatic space will alter accordingly (Pearson & Dawson 2003). This approach can be useful (Hodkinson 1999, Pearson & Dawson 2003), but it has also been criticised because it tends to predict a species' fundamental (or potential) niche and does not

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take into account biological interactions, dispersal capability, habitat quality, together with habitat availability and connectivity, all of which influence a species' realised niche (Davis et al. 1998, Pearson & Dawson 2003). Here, we use the rocky intertidal as a convenient model system to investigate the role of behaviourally mediated direct and indirect biological interactions in modifying species' responses to climate change and the likely consequence for community structure and dynamics.

The British Isles straddle 2 major marine biogeographic zones, with both warm lusitanian and cool boreal biota (Lewis 1964). As a consequence, many of the species present are at either the northern or southern edge of their biogeographic ranges (Southward et al. 1995), resulting in sets of ecologically comparable species, with northern and southern centres of distribution co-existing and with abundances which have been shown to fluctuate with climatic changes (Southward 1967, Southward et al. 1995). Therefore, south-west Britain provides an ideal region in which to investigate how species with northern and southern biogeographic distributions respond to climate change and, in particular, the way in which biotic interactions may modify these responses.

A general poleward movement of species' ranges in response to global warming has been predicted (Parmesan 1996), although see Helmuth et al. (2006) for discussion of local factors, such as time of low water, influencing species' range shifts. Evidence of changes in the relative abundance of species with northern and southern biogeographic distributions, as well as poleward and upward latitudinal shifts in species' ranges, have been observed in a wide range of taxonomic groups during the twentieth century (Walther et al. 2002). These shifts are evident in both aquatic and terrestrial habitats, including coastal waters where plankton (Beaugrand & Ibanez 2004), intertidal organisms (Southward et al. 1995) and fish (Genner et al. 2004, Perry et al. 2005) have all shown responses.

Canopy-forming furoid algae are conspicuous members of the community of all but the most exposed rocky shores of the NE Atlantic (Lewis 1964). Midshore furoids are a cold temperate/boreal group of species that becomes less abundant with decreasing latitude (Ballantine 1961). Thus, it is anticipated that furoids will become restricted to more northerly latitudes or buffered environments if temperatures rise (Franklin & Forster 1997). For example, 'climate envelope' models predict that, with an increase in temperature of 1 to 2°C, *Fucus vesiculosus*, the dominant midshore algal species on moderately exposed shores, would be lost from most of south-west Britain (M. T. Burrows unpubl. data). There is some evidence to suggest that this

northward range retraction has already started, with some cold-temperate canopy-forming species, such as *Laminaria* spp. (Breeman 1990, A. E. F. Murias Dos Santos unpubl. data), *Himantalia elongata* and *Pelvetia canaliculata* (A. E. F. Murias Dos Santos unpubl. data), already becoming scarcer at their southern range limits.

Canopy-forming algae influence community structure by modifying the environment (Menge 1978). Higher concentrations of microalgal food are found beneath algal canopies (Thompson et al. 2004), where environmental conditions are ameliorated and habitats are generated for other species (Leonard 2000), often resulting in increased diversity (e.g. *Fucus* spp. at mid-shore heights in Britain, Thompson et al. 1996; and *Cystoseira* spp. at low-shore levels in the Mediterranean, Benedetti-Cecchi et al. 2001). Hence, it is likely that the presence/absence of canopy-forming algae will have a disproportionate effect on the distribution and diversity of species in the intertidal, with implications for assemblage dynamics.

Limpets are key grazers on rocky shores in the NE Atlantic, and strongly influence community structure and dynamics by controlling macroalgal abundance (Southward & Southward 1978, Hawkins et al. 1992). Two species of limpet co-exist at midshore levels on moderately exposed shores of south-west Britain: *Patella vulgata*, a cold-temperate/boreal limpet, distributed from northern Norway to southern Portugal, and *P. depressa*, a southern/lusitanian limpet, distributed from Senegal in West Africa to north Wales, UK (Southward et al. 1995). It is predicted that *P. depressa* will become the dominant limpet on the shores of south-west Britain, at the expense of *P. vulgata*, in response to increased climatic warming (Southward et al. 1995), and there is evidence to suggest this is already occurring on some shores (S. J. Hawkins unpubl. data).

Both species of limpet exhibit 'homing' behaviour, returning to the same home scar between foraging excursions (Hawkins et al. 1992), and their spatial distribution influences the probability of *Fucus* spp. (here after *Fucus*) becoming established via escapes from grazing (Hartnoll & Hawkins 1985). Conversely, *Fucus* influences the distribution of many intertidal species including limpets (Menge 1978, Hawkins et al. 1992, Thompson et al. 1996, Leonard 2000, Jenkins et al. 2005). Thus, whilst *Patella* spp. control the initial development of furoid stands, once established, furoids provide 'nursery' grounds for juvenile *P. vulgata* and a microhabitat for adult *P. vulgata* that aggregate under patches of *Fucus*. In contrast, *P. depressa* does not appear to aggregate under *Fucus* patches (S. J. Hawkins unpubl. data).

Here, we explore the direct and indirect effects of *Fucus* canopy loss on these 2 closely related limpet

species to demonstrate how responses to climate change can be modulated by biological interactions mediated by intrinsic differences in behaviour. Such interactions are likely to alter predictions for species' range shifts based on the direct effects of climate change on setting distributional limits. The relationships between *Fucus* patches and both *Patella vulgata* and *P. depressa* were examined to determine the extent to which each species aggregates beneath *Fucus*. Manipulative field experiments were then used to investigate the responses of both limpet species to the loss of *Fucus*. Responses were quantified in terms of changes in behaviour—in this case, both the distance moved to locate a new home scar and mortality. Specifically, we examined the hypothesis that the loss of *Fucus* would have a much greater effect on the behaviour and mortality of *P. vulgata* than on that of *P. depressa*, by effectively reducing *P. vulgata*'s preferred habitat.

## MATERIALS AND METHODS

**Spatial distribution of northern and southern limpet species in relation to *Fucus* patches.** The spatial distribution of the limpets *Patella depressa* and *P. vulgata* in relation to *Fucus* were compared independently of each other at each of 2 locations: Trevone (50° 55' N, 4° 98' W) and Crackington Haven (50° 74' N, 4° 64' W), on the north coast of Cornwall, UK. The abundance of *P. vulgata* and *P. depressa* was recorded in *Fucus* patches and on areas of open rock using 10 randomly placed 0.5 × 0.5 m quadrats for each species–habitat combination. The effect of macroalgal canopy on the relative abundance of *P. vulgata* and *P. depressa* was then compared using a 3-factor ANOVA, with the factor location (2 levels) considered random and the factors habitat (2 levels: with or without macroalgal canopy) and species (2 levels: *P. vulgata* or *P. depressa*) considered fixed.

To provide an indication of the differences in temperature limpets may experience beneath *Fucus* patches and on open rock, 3 temperature data loggers (Thermochron® ibutton DS1921G) were allocated to each of 3 areas of open rock and beneath *Fucus* patches at Crackington Haven during typical summer low-tide weather conditions in 2004.

**Limpet mortality and behaviour following loss of *Fucus*.** The effect of the loss of *Fucus vesiculosus* (hereafter *Fucus*) on the mortality and behaviour of *Patella vulgata* and *P. depressa* was investigated experimentally at Trevone and Crackington Haven. Both shores are moderately exposed, with areas of open rock, barnacle-covered rock and a mosaic of *Fucus* patches. Experiments were run between June and September

in both 2002 and 2003. At midshore level, 20 areas with patches of *Fucus* of approximately 0.09 m<sup>2</sup> in size were randomly allocated to 2 treatments: *Fucus* present (unmanipulated control) or *Fucus* removal. In the *Fucus* removal treatments, *Fucus* canopy (including holdfast) was removed from the substrate with a scalpel. Ten areas of open rock were also selected to act as controls. Responses of *P. vulgata* and *P. depressa* were monitored independently of each other in each of 5 replicate plots for each of the 3 treatments. Five *P. vulgata* or *P. depressa* were randomly selected within each experimental plot; these individuals were measured and double tagged with micro-numbers glued to the shell with cyanoacrylate.

The response variables measured were distance moved to a new home scar and mortality. To quantify relocation to new home scars the position of each limpet was recorded using coordinates from a 1 m<sup>2</sup> grid separated into 0.03 m<sup>2</sup> grid squares. Limpet positions prior to treatment manipulations were taken to be the limpets' initial home scars, as limpets are generally inactive and on their home scars at midshore levels while the tide is out. Analyses were carried out on the distance limpets moved from their initial home scar at the completion of the experiment 4 mo later. The position of each individual was then determined every 14 d during low water when the limpets were not active (i.e. on their home scars) to ensure that micro-numbers were still attached to limpet shells and to monitor mortality. In cases in which limpets had relocated from their original home scar, the habitat to which they had moved was noted. Where limpets were missing from plots, a 15 min search of the surrounding area (approximately 9 m<sup>2</sup>) was made, and, if the limpets were not found, they were assumed to have died. Total mortality across the 4 mo of the experiment was used for analysis.

In 2002, a large number of limpets from all treatments at Trevone died, probably as a consequence of natural sand scour in some of the experimental areas; therefore, only the Crackington Haven experiment was analysed for this period. In 2003, comparisons were possible between Trevone and Crackington Haven. Two-factor ANOVA was used to compare differences in response variables (distance moved from original home scar at the completion of the experiment and mortality over the course of the experiment) between the 3 treatments at Crackington Haven in 2002. The factors treatment (3 levels) and species (2 levels) were considered fixed. In 2003, a third factor, location (2 levels and random), was also examined to establish spatial consistency. The number of individual limpets available for analysis of distance moved to a new home scar was unequal, due to differential mortality between treatments, so data were randomly

removed from treatments to create a balanced design. For all analyses, heterogeneity of variance was examined using Cochran's test, and, where appropriate, data were  $\log(x + 1)$  transformed. In order to increase the power when comparing factors of interest, post-hoc pooling was utilised to remove non-significant terms ( $p > 0.25$ ). Student-Newman-Keuls (SNK) post-hoc tests were carried out on significant results ( $p < 0.05$ ).

## RESULTS

### Spatial distribution of northern and southern limpet species in relation to *Fucus* patches

There were significant differences in the spatial distribution of *Patella vulgata* and *P. depressa* in relation to *Fucus* patches at both Trevone and Crackington Haven. The abundance of *P. vulgata* was significantly higher beneath *Fucus* patches than on open rock (Table 1). In contrast, the abundance of *P. depressa* was significantly higher on open rock than beneath *Fucus* patches ( $F_{1,73} = 133.87$ ;  $p < 0.01$ ; Fig. 1).

Temperature data loggers confirmed the potential for *Fucus* patches to ameliorate conditions during low tide, with temperatures beneath *Fucus* patches (mean  $\pm$  SE:  $20.59 \pm 0.11^\circ\text{C}$ ) on average  $5^\circ\text{C}$  cooler than temperatures experienced on open rock ( $25.68 \pm 0.22^\circ\text{C}$ ).

### Limpet mortality and behaviour following loss of *Fucus*

*Patella vulgata* experienced significantly higher mortality in *Fucus* removal treatments (approximately 40%) than in unmanipulated *Fucus* patches (approximately 20%) and on open rock (approximately 24%). There was no difference in the levels of mortality for *P. depressa* amongst the 3 treatments. These patterns were evident at Crackington Haven in 2002 ( $F_{2,17} = 4.66$ ,  $p < 0.05$ ; Table 2, Fig. 2a) and were consistent at both Trevone and Crackington Haven in 2003 ( $F_{2,50} = 3.75$ ,  $p < 0.05$ ; Table 2, Fig. 2b). At Crackington Haven in 2002, *P. depressa* suffered significantly higher levels of mortality compared to *P. vulgata* in the open rock treatments.

The distance moved to a new home scar by *Patella vulgata* following experimental removal of *Fucus* was greater than that of *P. depressa* in all treatments and than that of *P. vulgata* under *Fucus* patches and on open rock. This behaviour was consistent at Crackington Haven in 2002 ( $F_{2,66} = 8.97$ ,  $p < 0.01$ ; Table 3, Fig. 2c) and across locations in 2003 ( $F_{2,194} = 3.4$ ,  $p <$

Table 1. ANOVA for the abundance of *Patella vulgata* and *P. depressa* beneath *Fucus* patches and on emergent rock at 2 locations (Crackington Haven and Trevone) in south-west Britain [ $\ln(x + 1)$  transformation; Cochran's test:  $C = 0.2008$ , non-significant]. Location  $\times$  habitat  $\times$  species was non-significant ( $p > 0.25$ ) and was thus pooled with the residual to increase the power of the test for the treatment  $\times$  species interaction

Source	SS	df	MS	F	p	F vs.
Location (Lo)	3.84	1	3.84	15.54	<0.01	1-Pooled
Habitat (Ha)	9.70	1	9.70	99.57	0.06	Lo $\times$ Ha
Species (Sp)	30.46	1	30.46	504.05	<0.05	Lo $\times$ Sp
Lo $\times$ Ha	0.10	1	0.10	0.39	0.53	1-Pooled
Lo $\times$ Sp	0.06	1	0.06	0.24	0.62	1-Pooled
Ha $\times$ Sp	33.07	1	33.07	133.87	<0.01	1-Pooled
Lo $\times$ Ha $\times$ Sp	0.04	1	0.04	0.15	0.70	1-Pooled
Residual	17.99	72	0.25			
Total	95.25	79				
1-Pooled		73	0.25			

SNK tests  
*P. vulgata*, *Fucus* patch > *P. vulgata*, open rock  
*P. depressa*, open rock > *P. depressa*, *Fucus* patch

0.05; Table 3, Fig. 2d). The maximum distance an individual *P. vulgata* moved to relocate their home scar following *Fucus* removal was approximately 2 m. Of the *P. vulgata* that survived following *Fucus* removal, 36% from Crackington Haven in 2002 and 25% from Trevone and Crackington Haven in 2003 relocated home scars to beneath another *Fucus* patch.

In contrast, *Patella depressa* at both locations in 2003 stayed loyal to their home scars in all treatments, irrespective of the presence or absence of *Fucus*. At Crackington Haven in 2002, *P. depressa* moved a small, but significant, distance from their home scars in unmanipulated *Fucus* patch treatments (mean  $\pm$  SE:  $12.2 \pm 2.9$  cm) compared to in *Fucus* removal ( $3.3 \pm$

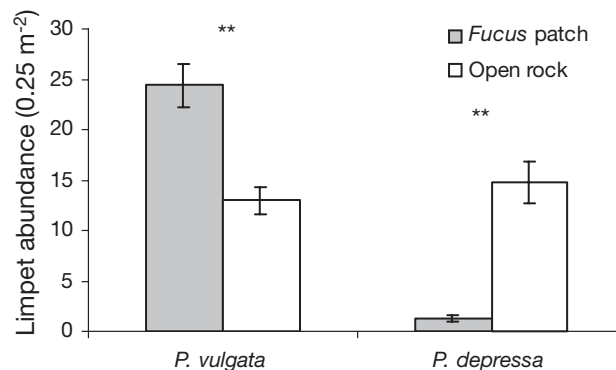


Fig. 1. *Patella vulgata* and *P. depressa*. Effect of macroalgal cover (*Fucus vesiculosus*) on the relative abundance of limpets at Crackington Haven and Trevone (means  $\pm$  1 SE) (\*\* $p < 0.01$ )

1.2 cm) and open rock treatments ( $2 \pm 0.7$  cm; Fig. 2a). However, all individuals remained beneath the *Fucus* patch in which they were initially tagged.

## DISCUSSION

### Responses of northern and southern species of limpet to furoid microhabitats

We have shown that *Patella vulgata* aggregates beneath *Fucus* patches. In contrast *P. depressa* appears to prefer open rock habitats. Our findings support previous work for *P. vulgata* (Hartnoll & Hawkins 1985, Hawkins et al. 1992), but data on the patterns of distribution of *P. depressa* in relation to *Fucus* patches have not been previously reported. These differences in behaviour in relation to *Fucus* patches may lead to changes in the spatial distribution of grazers on the

Table 2. ANOVA of limpet mortality in 3 treatments: *Fucus* removal (FR), *Fucus* patch (FP) and open rock (OR) for Crackington Haven, south-west Britain, in 2002 (Cochran's test:  $C = 0.4943$ , non-significant), and Trevone and Crackington Haven, south-west Britain, in 2003 (Cochran's test:  $C = 0.1932$ , non-significant). Location  $\times$  treatment  $\times$  species was non-significant ( $p > 0.25$ ) and was thus pooled with the residual to increase the power of the test for the treatment  $\times$  species interaction

Source	SS	df	MS	F	p	F vs.
<b>Crackington Haven (2002)</b>						
Treatment (Tr)	0.96	2	0.48	2.72	0.12	Residual
Species (Sp)	0.02	1	0.02	0.09	0.77	Residual
Tr $\times$ Sp	1.64	2	0.82	4.66	0.03	Residual
Residual	2.12	12	0.18			
Total	4.74	17				
SNK tests						
Tr $\times$ Sp interaction			Sp $\times$ Tr interaction			
<i>P. vulgata</i> : FR > FP = OR			FR: <i>P. vulgata</i> = <i>P. depressa</i>			
<i>P. depressa</i> : FR = FP = OR			FP: <i>P. vulgata</i> = <i>P. depressa</i>			
			OR: <i>P. vulgata</i> < <i>P. depressa</i>			
<b>Trevone and Crackington Haven (2003)</b>						
Location (Lo)	1.67	1	1.67	2.30	0.13	1-Pooled
Treatment (Tr)	3.23	2	1.62	1.59	0.39	Lo $\times$ Tr
Species (Sp)	3.27	1	3.27	49.00	0.09	Lo $\times$ Sp
Lo $\times$ Tr	2.03	2	1.02	1.40	0.26	1-Pooled
Lo $\times$ Sp	0.07	1	0.07	0.09	0.77	1-Pooled
Tr $\times$ Sp	5.43	2	2.72	3.75	0.03	1-Pooled
Lo $\times$ Tr $\times$ Sp	1.03	2	0.52	0.71	0.50	1-Pooled
Residual	35.20	48	0.73			
Total	51.93	59				
1-Pooled	36.23	50	0.72			
SNK tests						
Tr $\times$ Sp interaction			Sp $\times$ Tr interaction			
<i>P. vulgata</i> : FR > FP = OR			FR: <i>P. vulgata</i> = <i>P. depressa</i>			
<i>P. depressa</i> : FR = FP = OR			FP: <i>P. vulgata</i> = <i>P. depressa</i>			
			OR: <i>P. vulgata</i> < <i>P. depressa</i>			

shore if the relative abundance of these 2 species alters as is expected with increased climatic warming.

Experimental removal of *Fucus* led to two-thirds of *Patella vulgata* individuals at Trevone and Crackington Haven either relocating their home scars to beneath other *Fucus* patches or dying. This may have been caused by the greater thermal and desiccation stress experienced on open rock compared to beneath *Fucus* patches. Similar subtle changes in temperature have been shown to influence the survival of other intertidal species such as barnacles (Bertness et al. 1999, Leonard 2000).

In contrast, the southern/lusitanian congeneric limpet species *Patella depressa* was more abundant on open rock, and the removal of *Fucus* had little effect on its behaviour or mortality. *P. depressa* did, however,

Table 3. ANOVA for distance limpets moved to a new home scar for 3 treatments: *Fucus* removal (FR), *Fucus* patch (FP) and open rock (OR) for Crackington Haven, south-west Britain in 2002 [ $\ln(x + 1)$  transformation; Cochran's test:  $C = 0.2154$ , non-significant] (Due to unequal levels of mortality  $n = 12$  limpets treatment<sup>-1</sup> were used to formally analyse the distance moved from a home scar.) and Trevone and Crackington Haven, south-west Britain, in 2003 [ $\ln(x + 1)$  transformation; Cochran's test:  $C = 0.1496$ , non-significant). Location  $\times$  habitat  $\times$  species was non-significant ( $p > 0.25$ ) and was thus pooled with the residual to increase the power of the test for the treatment  $\times$  species interaction. (Due to unequal levels of mortality  $n = 17$  limpets treatment<sup>-1</sup>)

Source	SS	df	MS	F	p	F vs.
<b>Crackington Haven (2002)</b>						
Treatment (Tr)	35.07	2	17.53	4.28	0.02	Residual
Species (Sp)	1.19	1	1.19	0.29	0.59	Residual
Tr $\times$ Sp	73.51	2	36.76	8.97	<0.01	Residual
Residual	270.57	66	4.10			
Total	380.34	71				
SNK tests						
Tr $\times$ Sp interaction			Sp $\times$ Tr interaction			
<i>P. vulgata</i> : FR > FP = OR			FR: <i>P. vulgata</i> > <i>P. depressa</i>			
<i>P. depressa</i> : OR < FP;			FP: <i>P. vulgata</i> < <i>P. depressa</i>			
FR < FP; OR = FR			OR: <i>P. vulgata</i> = <i>P. depressa</i>			
<b>Trevone and Crackington Haven (2003)</b>						
Location (Lo)	9.45	1	9.45	8.68	0.00	1-Pooled
Treatment (Tr)	4.33	2	2.17	0.89	0.53	Lo $\times$ Tr
Species (Sp)	7.39	1	7.39	35.55	0.11	Lo $\times$ Sp
Lo $\times$ Tr	4.86	2	2.43	2.23	0.11	1-Pooled
Lo $\times$ Sp	0.21	1	0.21	0.19	0.66	1-Pooled
Tr $\times$ Sp	7.39	2	3.7	3.4	0.04	1-Pooled
Lo $\times$ Tr $\times$ Sp	0.73	2	0.37	0.34	0.72	1-Pooled
Residual	210.5	192	1.1			
Total	244.86	203				
1-Pooled	211.23	194	1.09			
SNK tests						
Tr $\times$ Sp interaction			Sp $\times$ Tr interaction			
<i>P. vulgata</i> : FR > FP = OR			FR: <i>P. vulgata</i> > <i>P. depressa</i>			
<i>P. depressa</i> : FR = FP = OR			FP: <i>P. vulgata</i> = <i>P. depressa</i>			
			OR: <i>P. vulgata</i> = <i>P. depressa</i>			

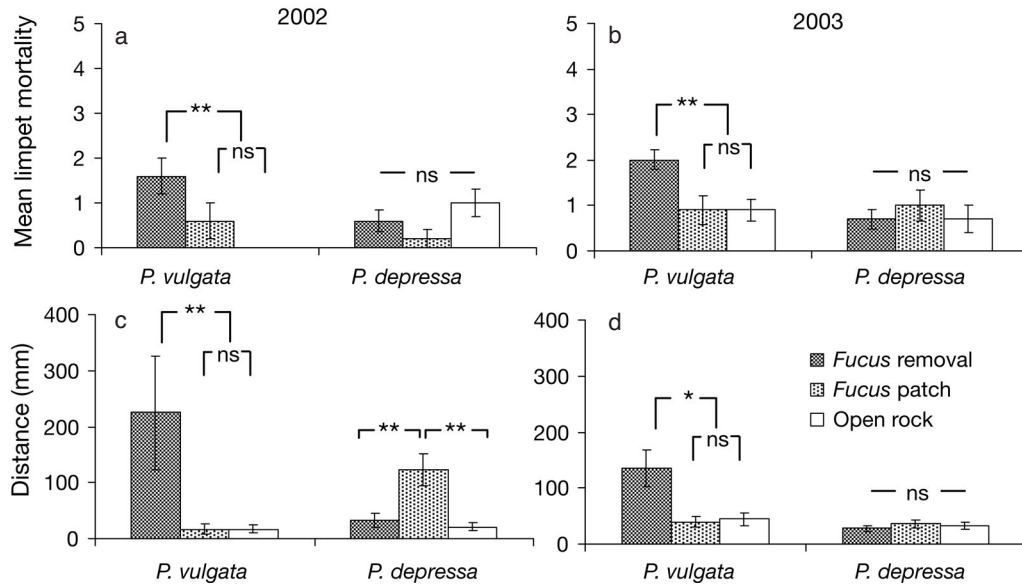


Fig. 2. *Patella vulgata* and *P. depressa*. Response to the experimental loss of *Fucus vesiculosus* for: treatment  $\times$  species interaction for mortality at (a) Crackington Haven in 2002 and (b) Trevone and Crackington Haven in 2003; treatment  $\times$  species interaction for distance moved to a new home scar at (c) Crackington Haven in 2002 and (d) Trevone and Crackington Haven in 2003 (means  $\pm$  1 SE) (\* $p$  < 0.05; \*\* $p$  < 0.01, ns: non-significant)

suffer increased levels of mortality on open rock compared to *P. vulgata*, but this perhaps reflects greater intrinsic rates of mortality of *P. depressa* compared to *P. vulgata* (Boaventura et al. 2002). The reasons for the difference in behaviour between *P. vulgata* and *P. depressa* in relation to *Fucus* are not clear. *Fucus* is absent over much of the biogeographic range of *P. depressa*, so the lack of a response by *P. depressa* to the loss of *Fucus* patches may be a direct result of the limited overlap in their biogeographic ranges. Alternatively, there is some evidence to suggest that *P. depressa* does less well beneath *Fucus* patches compared to on open rock (Southward & Southward 1978, Moore et al. in press), and may actively avoid creating home scars beneath *Fucus* patches.

In laboratory studies both species of limpet have been shown to withstand and recover from exposure to temperatures close to 43°C (lethal temperatures: *Patella vulgata*, 42.8°C and *P. depressa*, 43.3°C; Evans 1948); however, no work has been done on the temperature tolerances of these 2 species in the field. Recent work has shown that congeneric species with cold/boreal biogeographic distributions were more temperature sensitive than those with warmer/lusitanian distributions (Stillman 2003). In addition species may be able to initially survive exposure to extreme temperatures, but thermal damage experienced as a result of the exposure may prove fatal in the future (Stenseng et al. 2005). Therefore, although both species have been shown to survive similar temperature extremes, *P. vulgata* may still be more temperature sensitive than *P.*

*depressa*. The amelioration of temperature extremes beneath canopy algae may explain the preferential aggregation of *P. vulgata* beneath *Fucus* patches and the relocation of home scars beneath new *Fucus* patches as well as the increased mortality when canopy algae is experimentally removed. Hence, the local persistence of *P. vulgata* may be partly reliant on the presence of its preferred habitat, *Fucus* patches.

It is unlikely that selective predation resulted in the increased mortality of *Patella vulgata* in *Fucus* removal treatments. The main predators of limpets are birds, crabs, whelks and fish (Thompson et al. 2000). There is no evidence of any selection for *P. vulgata* or *P. depressa* by these predators (e.g. Coleman et al. 1999 for birds and Thompson et al. 2000 for crabs), or, in the case of oystercatchers, a preference for foraging on open or *Fucus*-covered rock (Coleman et al. 1999).

#### Biotic interactions modify species responses to climate change

Amelioration of environmental conditions by organisms such as canopy-forming algae has been well documented. However, the role of these habitat-generating species will become more important as warming increases, since limpets, littorinids, whelks, anemones and numerous other species will increasingly become restricted to habitats where climatic extremes are buffered (Leonard 2000, Jenkins et al. 2005). For example, in the USA, habitat amelioration has been

shown to increase the survival and persistence of the northern barnacle *Semibalanus balanoides*, whose survivorship was increased by shading by macroalgae at hotter southern sites, but not at cooler northern sites (Bertness et al. 1999, Leonard 2000). Furthermore, a study of high-level salt marsh plants in New England found that the plants experienced facilitative effects of neighbouring plants at hotter southern sites, but not at cooler northern sites (Bertness & Ewanchuk 2002). Therefore, if warming continues as predicted, the local persistence of many species may become more dependent on the presence of others, and shifts in species' distributions may become magnified where biologically generated habitats are lost or reduced.

If climatic warming increases, the abundance of *Patella depressa* at sites in Britain is predicted to increase, while the abundances of *P. vulgata* and *Fucus* are predicted to decrease. However, when the interaction of these 2 limpet species with *Fucus* is incorporated, it is apparent that a stepped response in the relative abundance of the 2 limpet species is likely to occur, particularly at the edge of the distributional boundary of *Fucus*. At this boundary the abundance of *P. vulgata* may decrease sharply as a consequence of increased environmental stress resulting from the loss of its preferred micro-habitat (*Fucus* canopy). In contrast, the abundance of *P. depressa* may rapidly increase at the boundary as more of its preferred habitat (open rock) becomes available. This switch in the relative abundance of *P. vulgata* and *P. depressa* is apparent when the proportion of the 2 limpet species is compared between shores in south-west Britain (mean proportion of *P. depressa*, 0.30; Jenkins et al. 2001), where *Fucus* can be abundant, and shores 7° (approximately 800 km) further south in northern Spain (mean proportion of *P. depressa*, 0.81; Jenkins et al. 2001), where *Fucus* becomes rare on open coasts (Ballantine 1961). If, as predicted, canopy algae, such as *Fucus vesiculosus*, respond to increased warming faster than *P. vulgata*, without incorporation of the modifying ('engineering') effect of *Fucus* on local microhabitats, predictions of future range shifts are likely to be inaccurate. For example, 'climate envelope' models based solely on changes in sea-surface temperature and wave action forecast little change in the distribution of *P. vulgata* in the British Isles (M. T. Burrows unpubl. data). This is unlikely to be the case if canopy-forming algae disappear, as expected, on shores in south-west Britain.

#### Community-level responses to local changes in grazer distribution

The grazing behaviour of *Patella vulgata* contributes to the conspicuous mosaic of variously aged macro-

algal patches common on many moderately exposed shores of the NE Atlantic (Lewis 1964, Hartnoll & Hawkins 1985, Hawkins et al. 1992), which, in turn, influence the community structure of rocky shores, because a higher diversity of organisms is found beneath *Fucus* patches compared to in areas of adjacent emergent rock (Thompson et al. 1996). *P. vulgata* plays a key role in structuring rocky shore communities because of its aggregative behaviour, which can lead to a patchy distribution of grazing intensity that enables *Fucus* escapes to occur (Hartnoll & Hawkins 1985). Our data show that *P. depressa* does not preferentially aggregate beneath *Fucus* patches, and this is likely to result in a more even distribution of grazing activity. Initial studies also indicate that *P. depressa* may be less effective at controlling macroalgal abundance than *P. vulgata* on shores in south-west Britain (Moore et al. in press). Hence, changes in the spatial distribution of grazers and the level of grazing intensity could have broad-scale implications for macroalgal abundance. Manipulation of canopy-forming algae has been shown to result in changes in the diversity and abundance of other algal species (Dayton 1975, Benedetti-Cecchi et al. 2001) and results in a reduction in the diversity and abundance of invertebrates (Benedetti-Cecchi et al. 2001). Therefore, changes in macroalgal cover are likely to have broad-scale implications for rocky shore community dynamics.

#### Predicting responses to climate change

Our findings are supported by work carried out in mesocosms (Davis et al. 1998) and by experimental field studies (Bertness et al. 1999, Leonard 2000), which have highlighted the need to incorporate biotic interactions into predictions of species' future biogeographic distributions. The present study has shown, in the case of *Patella vulgata* and *P. depressa*, that the presence or absence of *Fucus* canopy may alter the speed at which these 2 species respond to increased climatic warming. Therefore, if future predictions on the effects of climate change do not include effects on the survival of *Fucus*, then it is unlikely that realistic predictions of range shifts by these limpet species can be made. Recent work has also shown that variability in the physical environment is often greater within sites than that experienced over larger geographic areas (Benedetti-Cecchi et al. 2000); therefore, future predictions of species' range shifts need to be made at appropriate spatial (and temporal) scales. 'Climate envelope' models may be able to provide a first approximation of species' responses to climate change; however, these models have the potential to be highly inaccurate if they do not take into account biotic

interactions and are undertaken at an inappropriate scale (Hellmuth et al. 2006). 'Climate envelope' models incorporating multiple species, to account for biotic interactions, and measurements of the physical environment made at the appropriate scales are therefore fundamental in providing more biologically realistic predictions of species' range and abundance shifts in response to climatic change.

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