

# Physical and biological control of furoid recruitment in range edge and range centre populations

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**ABSTRACT:** The structure of rocky shore assemblages is determined to a large extent by the interaction between abiotic and biotic processes. Understanding of the strength and interactive nature of these processes over different spatial and temporal scales provides insight into key structuring mechanisms and clarifies what sets species' distributions. Here we examine the potential interactive effect of physical environment (insolation stress) and grazing pressure on recruitment success of furoid species (*Fucus* spp.) in North Wales and Portugal, in order to understand patterns of distribution at the centre and equatorward edge of their range. Contrary to expectations, amelioration of the physical environment through reduction of insolation stress did not improve recruitment in either geographical region. Grazing activity of patellid limpets was found to be an important process regulating furoid recruitment only on northern European shores. The top-down control of furoid recruitment at the northern latitude was apparent, even at half the normal densities of patellid limpets. The use of reduced light levels and reduced grazing pressure in southern regions was expected to improve furoid recruitment, but results indicate amelioration of physical and biological pressures cannot compensate for an inherently low supply of propagules. Our study confirms that strong top-down control by grazers (*Patella* spp.) can directly determine the distribution and abundance of furoid algae in core areas of its range, but toward the range edge factors other than those examined are responsible for low recruitment and, ultimately, the observed decline in furoid abundance in southern European regions.

**KEY WORDS:** Reproductive success · Geographical differentiation · Biotic stress · Grazing pressure · Abiotic stress · Solar radiation · *Fucus spiralis* · *Fucus vesiculosus* · *Patella* spp.

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## INTRODUCTION

Furoid species are important intertidal ecosystem engineers and primary producers (Chapman 1995, Connell & Irving 2008, Jenkins et al. 2008); hence, they are central to both community structure and ecosystem functioning. Due to their size and 3-dimensional structure, furoid canopies are able to influence the physical environment, providing microhabitats that are utilized by other organisms (Thompson et al.

1996). Furoid canopy algae modify the presence and activity of other organisms in the intertidal through a range of both positive and negative interactions, including amelioration of temperature and desiccation extremes (Moore et al. 2007a), reduction of wave action (McCook & Chapman 1991) and reduction of light levels (Jenkins et al. 1999a). Sweeping effects of furoid fronds across the substratum can also have a strong community structuring role (Hawkins 1983, Hawkins & Harkin 1985, Jenkins et al. 1999b).

Furoid populations occur over much of the European coast, but their abundance decreases with declining latitude towards their southern limit of distribution (Ballantine 1961, André 1970, Ferreira 2012), leading to the development of smaller and more fragmented populations (Guo et al. 2005, Bridle & Vines 2007, Araujo et al. 2011). Species composition also changes markedly in southern European regions (Lüning 1990, Lima et al. 2007, Tuya et al. 2012), with some furoid species reaching (e.g. *Fucus vesiculosus*; Nicastro et al. 2013) or approaching (e.g. *Fucus spiralis*; Ribera et al. 1992) their southern limit of distribution at Portugal. Model predictions based on 3 IPCC (Intergovernmental Panel on Climate Change) climate change scenarios suggest that shores south of 45°N will become unsuitable for important furoid species in the future (Jueterbock et al. 2013). The reasons for the decline of furoid populations and consequent changes in community structure across such latitudinal scales are not clearly understood, but are likely to be the result of a combination of physical and biological processes (Dethier et al. 2005, Jenkins et al. 2008, Ferreira et al. 2014).

As sessile organisms living in a tidally dominated environment, furoid species are adapted to variable environmental conditions (Lubchenco 1980, Norton 1983), although differences in tolerance to stress (Schonbeck & Norton 1978) and grazing pressure (Hartnoll & Hawkins 1985, Boaventura et al. 2002), as well as competitive hierarchies (Schonbeck & Norton 1980, Hawkins & Hartnoll 1985) set vertical patterns of zonation. The effects of minimum and maximum temperatures combined with extreme climate events, such as unusually cold or warm periods or storms, are important in setting the geographic distribution and range limits of seaweeds (Crisp 1964, Underwood 1999, Smale & Wernberg 2013). Other physical factors such as solar radiation can also be extremely important. Both low and high solar radiation levels can control macroalgal species distribution by limiting or damaging their photosynthetic system (Creed et al. 1997, Martínez et al. 2012, Ferreira et al. 2014). In addition to physical control of macroalgal distribution and population structure (Arrontes 1993, Altamirano et al. 2003), biological interactions, especially top-down control by grazers, can also have a strong effect on the abundance and distribution of algal species. Removal of top-down herbivore control can lead to dramatic increases in the abundance of algae (Southward & Southward 1978, Hartnoll & Hawkins 1985, Jenkins et al. 2005). Such an increase can lead to further disequilibrium in the ecosystem owing to enhanced primary production (Lubchenco 1978,

Paine 2002). Experimental work since the 1940s in Britain (Jones 1946, Hawkins 1981, Jonsson et al. 2006) has shown how grazing can be an important factor in controlling furoid recruitment, especially on moderately exposed and exposed shores. In southern Europe, however, probably due to differences in the available species pool, recruitment levels of algae and harsher environmental stress, the effects of grazing pressure though influential have more unpredictable effects (Benedetti-Cecchi et al. 2001, Boaventura et al. 2002, Coleman et al. 2006).

Physical and biological processes are especially important in determining survival rates of early furoid life stages on rocky intertidal shores (Thompson et al. 2004, Jonsson et al. 2006); these stages are generally seen as the most critical for the maintenance of viable furoid populations (Santelices 1990, Vadas et al. 1992). Intertidal furoid recruits are subjected to severe and variable physical factors and are part of the diet of multiple intertidal grazer species (Lubchenco 1980, Jenkins et al. 2001, Nielsen et al. 2003). Their vulnerability to environmental stresses, when compared with adult algae, makes them especially susceptible to high mortality, leading to a possible bottleneck effect in successful survival of furoid species (Santelices 1990, Lotze et al. 2001, Jenkins et al. 2005).

The decline of furoid abundance from central to range-edge populations could be due to physico-chemical or biological effects, in isolation or combined, and their impact is likely to be greater on the more vulnerable early recruitment stages. Disentangling the effects of possible physical and biological controlling mechanisms on early mortality across a latitudinal range is the basis for the development of our work. We aimed to explore the role played by different levels of grazing pressure by patellid limpets combined with different levels of light irradiance in the control of furoid settlement and recruitment at both northern (central range) and southern (range edge) wave-exposed shores of western Europe. Many factors can determine the effectiveness of grazers and the probability of furoid recruitment success (Vadas et al. 1990, Arrontes 2002, Jenkins et al. 2008), but taking into consideration information from such studies, we hypothesised strong top-down control by grazers at northern latitudes irrespective of physical conditions, but no effect of irradiance on recruitment. A reduction in irradiance was hypothesised to negatively impact biomass of early recruits through effects on productivity. Towards the south, grazer control is more unpredictable (e.g. Benedetti-Cecchi et al. 2001, Coleman et al. 2006); we hypothe-

sised that under less stressful physical conditions (reduced light irradiance) furoid recruitment would be enhanced and under these conditions grazer control would be more important, hence leading to an interaction between physical and biological factors close to the range edge.

## MATERIALS AND METHODS

### Study areas

Manipulative experiments were undertaken in 2 geographical regions separated by 11° of latitude (~1300 km): northern Portugal and northern Wales. Two replicate shores, separated by a minimum of 10 km, were chosen in each region: Carreço (41.7293°N, 8.8735°W), Vila Praia de Âncora (41.8233°N, 8.8755°W) in Portugal; Porth Cwyfan (53.1803°N, 4.4899°W) and Cemlyn Bay (53.4149°N, 4.5174°W) in Wales. These fully saline rocky shores were selected because of their similar geomorphology, wave exposure and the presence of patches of furoids and limpets on rocky surfaces with gentle slopes (<45°). A wave fetch model, created by Burrows et al. (2008), was used to independently determine wave exposure indices for each of the shores. Maximal tidal ranges were 3.8 and 6.3 m on the Portuguese and Welsh shores, respectively. Experimental plots were established within the equivalent biological zone in Portugal and Wales (between 2.1 to 4.7 m above Chart Datum in Wales and 2.3 to 3.2 m above Chart Datum in Portugal), so they were emersed for similar periods of time at both locations. *Fucus vesiculosus* (Linnaeus, 1753) and *Fucus spiralis* (Linnaeus, 1753) (both Ochrophyta, Fucales) were present at both locations at these tidal levels.

### Experimental designs

In order to show generality across shores and geographical regions the design was replicated on 2 shores in Portugal and 2 shores in Wales. Portuguese shores were affected by warmer temperatures than Welsh shores during the experimental period (e.g. from the end of July to beginning of October 2010, mean temperature [mean ± SE; n = 6048] on the Portuguese shores was 18.8 ± 1.0°C at Carreço and 18.5 ± 0.9°C at Vila Praia de Âncora, while on Welsh shores it was 15.5 ± 0.9°C at Porth Cwyfan and 15.5 ± 0.9°C at Cemlyn Bay). To test for the effect of light intensity and grazing level on furoid recruitment at

these 2 geographical regions, a factorial experiment was established with 3 levels of each factor. Limpet grazing was manipulated to include natural densities of grazers, half densities and no grazers present, while light intensity included natural radiance levels, shaded plots and a procedural control consisting of a transparent Perspex cover. Thus, the experiment consisted of 9 treatments each replicated 4 times.

### Experimental setup and sampling

On each shore 36 randomly spread plots (41 × 41 cm), at least 1 m apart, were created in areas of rock with no furoid presence at the specified tidal height. The 9 treatments were randomly allocated to experimental plots. In order to create plots with reduced light intensity, a plastic mesh (model: Figured 45 from Conwed Plastics Ltd) that reduced photosynthetically active radiation (PAR) by 84% on cloudy and 80% on sunny days (Rauh 2006) was used in a third of the plots. As a procedural control for shading, another third of the plots were covered with a 4 mm perforated clear Perspex sheet. This material was used because it replicates the potential artefacts imposed by the shade treatment (a physical barrier to water movement when immersed and modification of humidity levels when emersed), whilst allowing natural levels of light to reach the plots (light transmission efficiency >92%). Grazing pressure was manipulated using grazer inclusion fences. After estimating the density of *Patella* spp. (the main grazer) for each shore, plots with natural, half and no grazing pressure were established by removal of limpets from the plots. Natural grazing levels varied between shores, with mean values (mean ± SE; n = 25) in Portugal reaching 131 ± 5.0 (Vila Praia de Âncora) and 77 ± 4.2 (Carreço) limpets m<sup>-2</sup> and in Wales reaching 155 ± 7.8 (Porth Cwyfan) and 95 ± 4.3 (Cemlyn Bay) limpets m<sup>-2</sup>. Only limpets larger than 13 mm were used in the study. Inclusion fences were created using 3 cm high fences of plastic-coated wire mesh (mesh size 13 mm). To test whether enclosing limpets in this way modified their behaviour and ability to control furoid recruitment, an additional 4 plots marked only by screws in the corners were created allowing grazing to occur at normal levels. These plots were compared to fenced plots with natural levels of grazing.

The experiment started at the beginning of May 2010, ahead of the peak in fertility (Knight & Parke 1950, Vernet & Harper 1980, Ladah et al. 2003) and recruitment (Hawkins 1981, Jenkins et al. 2005, Coleman et al. 2006) of both *F. vesiculosus* and *F. spiralis*.

From May 2010 to May 2011, macroalgae were allowed to establish and grow on plots under the manipulated grazing and light radiance treatments. Measurements of the density of *Fucus* spp. (no attempt was made to identify juveniles to species level) were made at all shores at 3 different dates: 70, 145 and 365 d after deployment. After 1 yr, all the fucoid individuals were destructively sampled to measure density and dry weight of fucoids from each of the plots. During the entire period of the experiment, plots on every shore were checked, fences and shades repaired if needed, and limpet densities assessed and adjusted when required.

### Statistical analysis

Differences in total weight after 1 yr plus differences in densities of fucoid species over the 3 sampling dates were evaluated using a mixed model ANOVA with 4 factors. Comparisons were made among geographical regions (fixed, 2 levels), shores (random nested in geographical regions, 2 levels), light intensity (fixed, 3 levels) and grazing pressure (fixed, 3 levels). Results from different sampling dates were not compared due to the non-independence of repeatedly sampled plots. In designing the experiment, procedural controls were also used to determine whether artefacts were introduced by the use of Perspex screens and fencing material. These procedural artefacts were tested by using post hoc tests of significant factors. Prior to analysis, heterogeneity of variance of the data was tested with Cochran's test (Cochran 1951), and, when necessary, appropriate transformation of heterogeneous data was undertaken. For further analysis of significant factors post hoc Student-Newman-Keuls (SNK) tests were applied. Only SNK results showing differences are displayed in the 'Results' section. All the analyses

were performed using WinGMAV5 (EICC, University of Sydney).

## RESULTS

### Experimental artefacts

No procedural artefacts were detected. The control areas (natural level of grazing in unfenced plots) did not differ significantly from inclusion plots at natural grazing levels for any of the response variables (fucoid density and fucoid weight at 365 d), thus indicating that the behaviour of limpets was not modified to a significant extent in inclusion plots (Table 1). Similarly, there were no obvious artefacts from the shading structures; no significant difference was found between unshaded plots and those where the shade procedural control (Perspex covers) were used (Table 2).

### Densities of fucoids (across the entire period)

The levels of natural fucoid (*Fucus* spp.) recruitment in the presence of *Patella* spp. grazers at full and half densities resulted in similar recruitment levels in Wales and Portugal. In contrast, fucoid recruitment in the absence of grazers differed between geographical regions across all sampling dates (Table 2: density [70, 145 and 365 d] – SNK of Re × Gr; Fig. 1). Ungrazed areas in Wales showed significantly greater mean recruitment levels compared to ungrazed areas in Portugal (Table 2: density [70, 145 and 365 d] – SNK of Re × Gr; Fig. 1). After 1 yr, recruitment levels in Wales ( $1091.4 \pm 876.1$  ind. m<sup>-2</sup> [mean ± SE; n = 24]) were 2 orders of magnitude higher than those in Portugal ( $5.2 \pm 8.1$  ind. m<sup>-2</sup> [mean ± SE; n = 24]), which were very low.

There was a significant effect of grazing on fucoid densities at all sampling dates on Welsh shores (Table 2: density [70, 145 and 365 d] – SNK of Re × Gr; Fig. 1). Absence of grazing pressure in Welsh plots promoted the survival of significantly higher numbers of fucoid recruits (density after 145 d on the shore was  $1893.7 \pm 1524.1$  ind. m<sup>-2</sup> [mean ± SE; n = 24]) compared with grazed plots (density after 145 d on the shore was  $1.7 \pm 3.6$  ind. m<sup>-2</sup> [mean ± SE; n = 24]). It is also interesting to point out that the

Table 1. Mixed model ANOVA of density and weight of fucoids *Fucus* spp. produced after 365 d on the shore to test the effect of fence. Re: geographical region; Sh: shore; Fe: fence; Res: residual. **Bold** values are significant at  $p < 0.05$

Source	df	Density (365 d)		Weight (365 d)		F ratio vs
		F	p	F	p	
Re	1	0.6	0.535	0.6	0.518	Sh (Re)
Sh (Re)	2	5.4	<b>0.012</b>	4.1	<b>0.031</b>	Res
Fe	1	1.9	0.306	1.9	0.305	Fe × Sh (Re)
Re × Fe	1	0.1	0.743	0.1	0.752	Fe × Sh (Re)
Fe × Sh (Re)	2	1.2	0.331	0.7	0.533	Res
Res	24					
Cochran test		C = 0.434, p > 0.05		C = 0.430, p > 0.05		

Table 2. Mixed model ANOVA of density of furoids *Fucus* spp. produced after 70, 145 and 365 d and biomass produced after 365 d on the shore. Post hoc Student-Newman-Keuls (SNK) tests of significant differences are presented. Re: geographical region (Por: Portugal; Wal: Wales); Sh: Shore (Vil: Vila Praia de Âncora; Car: Carreço; Cwy: Porth Cwyfan; Cem: Cemlyn Bay); Li: light intensity; Gr: grazing level (-G: ungrazed; ½G: half grazing pressure; +G: grazed at natural densities); Res: residual. **Bold** values are significant at  $p < 0.05$

Source	df	Density (70 d)		Density (145 d)		Density (365 d)		Weight (365 d)		F ratio vs
		F	p	F	p	F	p	F	p	
Re	1	8.8	0.097	2.1	0.281	1.7	0.325	1.9	0.305	Sh (Re)
Sh (Re)	2	6.6	<b>0.002</b>	16.8	<b>&lt;0.001</b>	15.7	<b>&lt;0.001</b>	13.4	<b>&lt;0.001</b>	Res
Li	2	3.2	0.149	2.6	0.191	2.5	0.199	3.3	0.144	Li × Sh (Re)
Gr	2	25.3	<b>0.005</b>	25.5	<b>0.005</b>	30.7	<b>0.004</b>	33.5	<b>0.003</b>	Gr × Sh (Re)
Re × Li	2	0.2	0.823	0.2	0.802	2.3	0.219	2.8	0.171	Li × Sh (Re)
Re × Gr	2	23.4	<b>0.006</b>	26.5	<b>0.005</b>	24.3	<b>0.006</b>	26.2	<b>0.005</b>	Gr × Sh (Re)
Li × Sh (Re)	4	0.4	0.832	0.2	0.924	0.8	0.562	0.4	0.802	Res
Gr × Sh (Re)	4	2.5	<b>0.050</b>	2.9	<b>0.025</b>	2.9	<b>0.024</b>	2.5	<b>0.047</b>	Res
Li × Gr	4	0.8	0.573	1.5	0.298	0.6	0.650	0.6	0.652	Gr × Li × Sh (Re)
Re × Li × Gr	4	2.4	0.136	2.4	0.140	2.6	0.120	2.0	0.195	Gr × Li × Sh (Re)
Gr × Li × Sh (Re)	8	0.5	0.875	0.4	0.904	0.6	0.758	1.1	0.353	Res
Res	108									
Cochran's test		C = 0.141, $p > 0.05$		C = 0.158, $p > 0.05$		C = 0.157, $p > 0.05$		C = 0.159, $p > 0.05$		
SNK		<u>Gr × Sh (Re)</u>		<u>Gr × Sh (Re)</u>		<u>Gr × Sh (Re)</u>		<u>Gr × Sh (Re)</u>		
		Cwy & Cem:		Cwy & Cem:		Cwy & Cem:		Cwy & Cem:		
		+G = ½G < -G		+G = ½G < -G		+G = ½G < -G		½G = +G < -G		
		-G: Vil < Car		-G: Vil < Car		-G: Vil < Car		-G: Vil < Car		
		-G: Cwy < Cem		½G: Vil < Car		½G: Vil < Car		½G: Vil < Car		
				+G: Vil < Car		+G: Vil < Car		-G: Cwy < Cem		
				-G: Cwy < Cem		-G: Cwy < Cem				
		<u>Re × Gr</u>		<u>Re × Gr</u>		<u>Re × Gr</u>		<u>Re × Gr</u>		
		-G: Por < Wal		-G: Por < Wal		-G: Por < Wal		-G: Por < Wal		
		Wal: +G = ½G < -G		Wal: +G = ½G < -G		Wal: +G = ½G < -G		Wal: ½G = +G < -G		

removal of half the limpets from Welsh plots did not significantly increase recruitment levels, when compared with full-grazing-pressure plots (Table 2: density [70, 145 and 365 d] – SNK of Re × Gr; Fig. 1). In contrast, there was no significant effect of decreased grazing pressure in Portugal, leading to similar levels of recruitment occurring across all treatments on each of the Portuguese shores (Table 2, Fig. 1).

Providing increased shade protection, to reduce exposure to light radiance, did not promote increased levels of furoid recruitment at either geographical region (Table 2, Fig. 1).

There were significant differences in recruitment levels between shores within each geographical region on all sampling dates (Table 2: density [70, 145 and 365 d] – SNK of Gr × Sh[Re]). After 1 yr on the shore in Portugal, higher densities of furoid recruits occurred at Carreço than at Vila Praia de Âncora across treatments. In Wales, significant differences after 1 yr were only observed between ungrazed plots, showing higher recruitment densities at Cemlyn Bay than at Porth Cwyfan (Table 2: density [365 d] – Gr × Sh[Re]).

### Furoid biomass (after 1 yr)

Furoid biomass after 1 yr showed a similar response to grazing as furoid recruitment, with significant interaction between the region and grazer treatments. Within Portugal biomass was consistently low across all the grazer treatments (weight of  $4.4 \pm 11.0 \text{ g m}^{-2}$  in ungrazed,  $3.4 \pm 8.9 \text{ g m}^{-2}$  in ½ grazed and  $1.3 \pm 3.5 \text{ g m}^{-2}$  in grazed plots [mean ± SE;  $n = 24$ ]). In contrast, the complete removal of grazers in Wales greatly enhanced furoid biomass production (weight of  $269.4 \pm 247.2 \text{ g m}^{-2}$  [mean ± SE;  $n = 24$ ]), while in Welsh ½ grazed or grazed plots recruitment and growth were virtually non-existent (weight of  $0.0 \pm 0.0 \text{ g m}^{-2}$  and  $0.1 \pm 0.2 \text{ g m}^{-2}$  [mean ± SE;  $n = 24$ ], respectively) (Table 2: weight [365 d] – SNK of Re × Gr; Fig. 2). Comparison among regions showed that ungrazed plots had significantly higher biomass in Wales (Table 2: weight [365 d] – SNK of Re × Gr; Fig. 2). Increased shading did not promote differences in biomass at either geographical region (Table 2).

Differences in total biomass of recruits were observed between shores (Table 2: weight [365 d] –

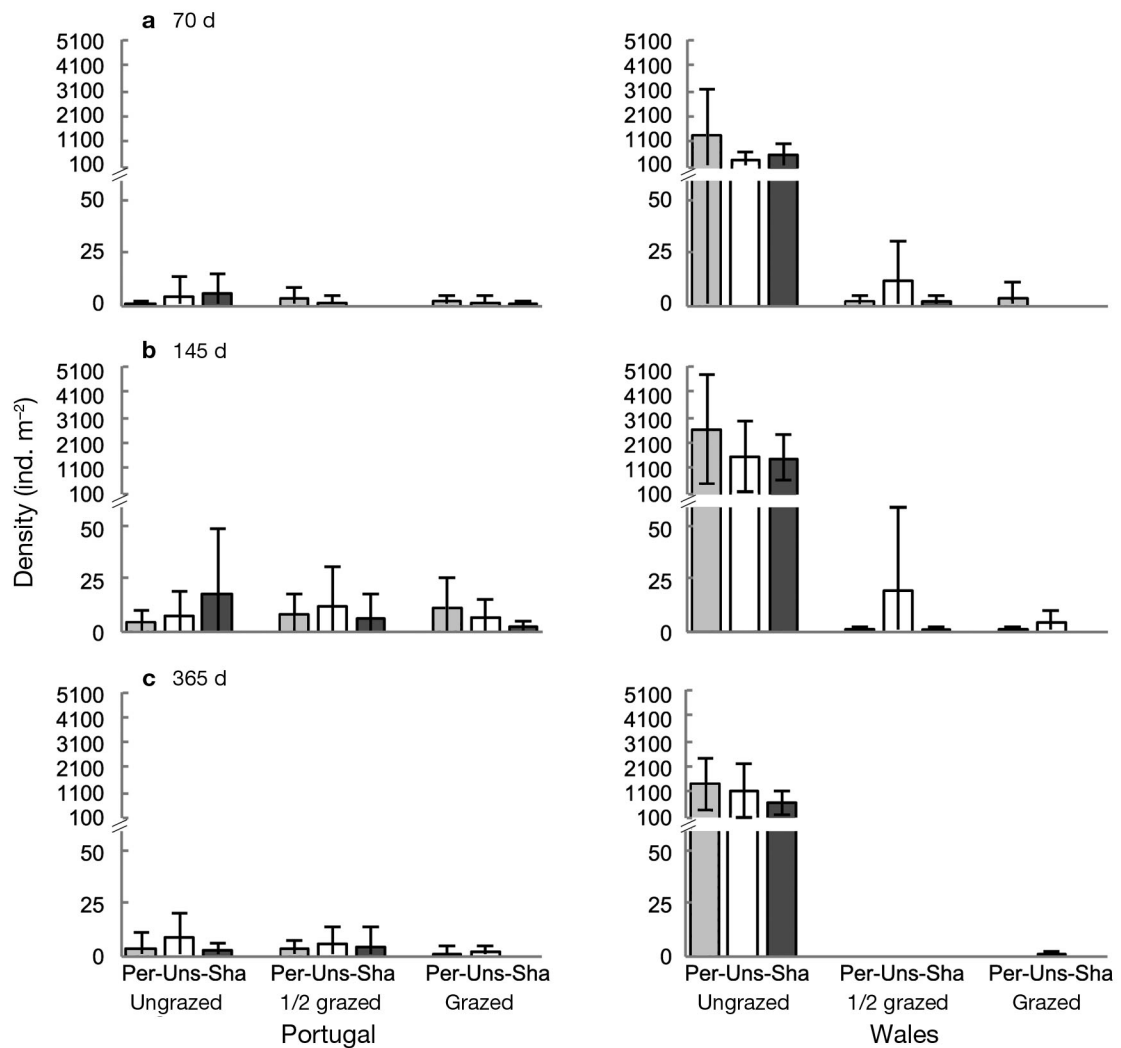


Fig. 1. Densities of fucoid *Fucus* spp. individuals ( $m^{-2}$ ) present after (a) 70, (b) 145 and (c) 365 d on the shore under different light intensities (Per: Perspex, procedure control; Uns: unshaded, subjected to natural solar radiance levels; Sha: shaded, under reduced solar radiance levels) and grazing treatments (ungrazed, half grazing pressure, grazed at natural densities) at 2 geographical regions (Portugal, Wales). Error bars =  $\pm 1$  SE

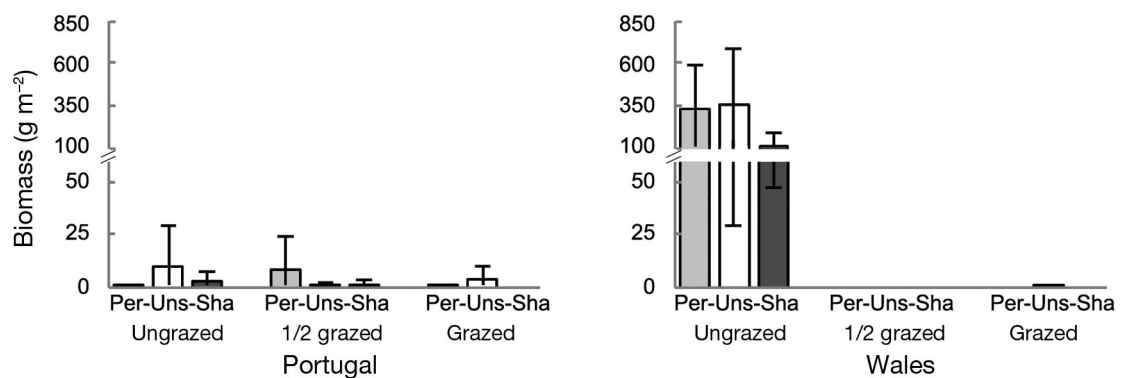


Fig. 2. Total fucoid *Fucus* spp. biomass ( $g\ m^{-2}$ ) produced after 365 d on the shore under different light intensities (Per: Perspex, procedure control; Uns: unshaded, subjected to natural solar radiance levels; Sha: shaded, under reduced solar radiance levels) and grazing treatments (ungrazed, half grazing pressure, grazed at natural densities) at 2 geographical regions (Portugal, Wales). Error bars =  $\pm 1$  SE



Gr  $\times$  Sh[Re]). On Portuguese shores the biomass of total recruits was higher in ungrazed and  $\frac{1}{2}$  grazed plots at Carreço than at Vila Praia de Âncora, while in Wales variation occurred only between ungrazed plots, where recruitment was higher at Cemlyn Bay than at Porth Cwyfan (Table 2: weight [365 d] – Gr  $\times$  Sh[Re]).

## DISCUSSION

Our experiment aimed to understand the combined effects of physical and biological processes through an experimental design that explored the effects of both processes simultaneously on furoid recruitment across Europe.

The results showed important geographical differences with a clear differentiation in furoid (*Fucus vesiculosus* and *Fucus spiralis*) settlement/recruitment levels between Welsh and Portuguese shores. In the absence of grazing pressure by limpets, northern populations developed higher numbers of furoid recruits than range edge populations, irrespective of light-reduction. These increased levels of recruitment in central range populations have also been reported for *F. serratus* growing under natural conditions (Araujo et al. 2011), indicating that these furoid species have lower recruitment success in range edge populations.

The role played by grazers in the control of macroalgae has long been highlighted as a major factor controlling algal abundance and spatial distribution in different geographical regions (Lubchenco 1978, Underwood & Jernakoff 1984, Boaventura et al. 2002). The probability of macroalgae escaping grazers, especially during the early post-settlement stages, can determine community composition on the shore (Burrows & Hawkins 1998, Johnson et al. 1998). The probability of escapes will greatly depend on the identity, abundance and diversity of the grazer community (Jenkins et al. 2001, Coleman et al. 2006, Moore et al. 2007b). Field experiments have consistently shown patellid limpets to have a stronger grazing impact than other abundant grazing molluscs in western Europe (e.g. O'Connor & Crowe 2005, Griffin et al. 2010), and in the absence of patellid limpets, for example in Sweden, littorinid grazers can have little control on algal recruitment (Lindegarh et al. 2001). The exclusion of *Patella* spp. grazers generally promotes an increase of macroalgal recruitment, although this is clearly dependent on supply of algal propagules (Johnson et al. 1997, Coleman et al. 2006).

In our experiment, the effects of *Patella* spp. grazing pressure were strongly felt on central range furoid populations. In Wales, an increase in the recruitment of macroalgae occurred in plots where limpets were absent, independently of the levels of radiance arriving at the plots, indicating that furoid recruitment on moderately exposed shores in Britain is mostly determined by the level of limpet grazing pressure, as previously proposed by other studies (Hawkins 1981, Jenkins et al. 2005, Coleman et al. 2006). Manipulation of limpet density indicated that half the natural grazing pressure by limpets is enough to control furoid recruitment levels on these shores. In contrast, the impact of limpet grazing in southern European algal communities is more variable (Benedetti-Cecchi et al. 2001, Jenkins et al. 2005, Coleman et al. 2006). A possible combination of reduced grazing pressure and amelioration of physical factors may promote furoid recruitment in these harsher range edge environments (Underwood 1980, Williams 1994, Kaehler & Williams 1998). Our results from Portuguese shores show that even in the absence of patellid grazers and under a benign environment, where light stress is reduced, recruitment is still very low. These results could potentially be due to the presence of different grazer species affecting recruitment in Portugal (e.g. mobile fishes: Ruitton et al. 2000; crabs: Cannicci et al. 2002), although this seems unlikely given the limited access of such species beneath shade canopies. Our results seem to indicate that the level of supply of new individuals, and not their subsequent success, limits furoid abundance on southern European shores. Differences in habitat availability across regions could limit propagule supply since the Portuguese coast comprises large stretches of sandy shoreline. However, our study shows that even in areas where fucoids are present, supply of new recruits is limited, giving support to the idea that the reduced reproductive capacity of furoid adults (Viejo et al. 2011, Ferreira 2012) is a crucial factor contributing to the observed decline in furoid abundance from northern to southern European regions. It is also worth noting the presence of some furoid biomass in control areas, where limpets were free to graze, in Portugal compared to its virtual absence in Wales. This raises the question of the effectiveness of patellid grazers in Portugal compared to Wales, although evidence from work on patellid grazing activity by Jenkins et al. (2001) suggests overall grazing pressure is high in Portugal relative to the British Isles.

Climatic conditions during the summer period are harsher at Portugal. Therefore, reducing solar irradi-

ance levels, especially during harsh summer conditions on Portuguese shores, was expected to influence survival of furoid recruits (Ladah et al. 2003, Schoenwaelder et al. 2003). Harsher environmental conditions in summer can affect intertidal communities (Helmuth et al. 2002) and have been highlighted as a possible reason for the decline in algal abundance in southern Europe (Viejo et al. 2011, Martínez et al. 2012, Ferreira et al. 2014). Thermal and desiccation stresses, particularly at the upper levels of the shore, can affect the ability of macroalgae to survive (Doty 1946, Davison & Pearson 1996). High levels of solar radiation during summer in Portugal have also been shown to negatively affect the photophysiological performance of furoids (Ladah et al. 2003, Viejo et al. 2011, Martínez et al. 2012, Ferreira et al. 2014). Effects of shading treatments applied in our experiment did not, however, significantly raise recruitment above its very low level in Portugal. That no effect of ameliorating such conditions was observed on recruitment suggests that improving environmental conditions does not mitigate the effects of low levels of supply and settlement of propagules in experimental plots from sparse adult populations. In the north we hypothesised that reducing light level would have a negative effect on biomass production. That this did not occur indicates that furoid populations have the capacity to adjust their photosynthesis to deal with a range of light intensities and promote normal levels of growth and survival. In order to determine the level of recruitment reduction suffered by each furoid species we recommend that future studies focus on the direct measurement of propagule supply of each furoid species both at central and range edge populations.

In summary, our experiments allowed us to clearly show the strong control that *Patella* spp. can exert on populations of furoids in the centre of their range and the lack of influence of physical factors, in this case light irradiance. On Portuguese shores, ameliorating stress from light and reducing limpet grazing pressure had little impact on recruitment levels. The likely variable and low propagule supply in our experimental plots in southern regions limits our ability to understand how the physical environment and grazing activity affect early recruits of *Fucus* spp. toward the range edge, but supports the idea that the reduced reproductive capacity of furoid adults (Viejo et al. 2011, Ferreira 2012) is an essential factor contributing to the observed decline in furoid abundance from northern to southern European regions.

The low likelihood of furoid recruitment in southern Europe reduces the ceiling of potential produc-

tivity (Raffaelli & Hawkins 1996), in clear contrast with northern Europe where escapes from grazing contribute to higher furoid productivity (Coleman et al. 2006, Ferreira 2012). Aggravation of climatic conditions in the south has led to contraction of the southern range edges of furoid species (Nicastro et al. 2013), with consequent impacts on the associated community and on local levels of intertidal primary productivity. Thus further focus on how changing environmental conditions modify adult performance and hence determine potential recruitment is justified and of great interest.

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