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THE INFLUENCE OF MUSSEL- MODIFIED HABITAT ON *FUCUS SERRATUS* L. A ROCKY INTERTIDAL CANOPY-FORMING MACROALGA

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ABSTRACT

The influence of habitat modification by *Mytilus edulis* L. on the settlement and development of *Fucus serratus* populations was investigated on rocky shores of the Isle of Anglesey, North Wales. Settlement of fucoids was higher inside mussel habitat than outside on one of two shores studied. The effect of microhabitat on survival of fucoid germlings was examined by transplanting the germlings into and outside mussel habitats, each with and without the exclusion of grazers. Observation showed that periwinkles and top shells were abundant in mussel habitat, while limpets dominated bare rock. Exclusion of grazers greatly enhanced the survival of fucoid germlings in both habitats, indicating that while mussel habitat supports a different grazer assemblage to bare rock, both assemblages are important in limiting fucoid recruitment. Risk of dislodgement was assessed and compared between fucoids growing on mussel shells and bare rock. *In situ* pull-tests showed less force was required to detach large fertile thalli growing on mussel shells than those growing on the rock. Adhesion was generally broken between the mussel and the rock rather than between the holdfast and the mussel. These observations indicate that mussels provide an unstable substrate for mature fucoids. Overall results suggest a negative effect of mussel-modified habitat on fucoids is profound in adults; but the effect is context-dependent in juveniles and can be positive at settlement. Results from a survey on population structure of fucoids across two shores showed that there were greater numbers of large fertile fucoids growing directly attached to rock than on mussel shells, while there was no difference for juvenile fucoids confirming the experimental results. Moreover thalli larger than 60 cm were found only on the rock but not on shells. This finding suggests that mussel

dominated habitat may have a significant impact on reproductive output in fucoid populations.

Keywords: mussels, fucoids, rocky intertidal, grazing, population structure, wave dislodgement

1. INTRODUCTION

Primary space at mid to low shore levels of intertidal rocky shores in temperate latitudes is usually utilized by mussels and canopy-forming macroalgae (Ballantine, 1961; Lewis, 1964; Raffaelli and Hawkins, 1996). The general pattern of community structure over the wave exposure gradient in the north-western and north-eastern Atlantic is similar, with fucoid macroalgae dominating at sheltered sites and secondary consumers, such as barnacles and mussels, increasing in cover with exposure to wave action (Menge, 1976; Lubchenco and Menge, 1978; Jenkins et al., 2008). On the Atlantic coast of North America, it is proposed that this pattern is regulated by the effect of predation on mussels, the competitively superior space occupiers. At exposed locations predation on mussels is low, but intense predation at sheltered sites by crabs and dogwhelks allows algal canopies to dominate (Dayton, 1971; Lubchenco and Menge, 1978). On European shores mussel recruitment shows strong spatial irregularities and they are not generally considered the dominant competitor (Jenkins et al., 2008). Instead a wealth of experimental work has focused on the role of patellid limpets as key to determining spatial patterns of community structure over the wave exposure gradient (Jones, 1946; Hawkins, 1981; Hawkins and Hartnoll, 1983; Jenkins et al, 2005; Coleman et al., 2006; Jenkins et al., 2008). Interactions between mussels and canopy-forming macroalgae have rarely been examined on European shores (but see Crowe et al., 2011). Studying how these key taxa interact when they co-exist in the same area may help to explain the distribution patterns outlined above.

The biogenic structure created by living mussels can affect survivorship of fucoids in different life-history phases in different ways. Mussels can ingest and digest fucoid zygotes and gametes leading to pre-settlement mortality of the fucoids (Harding, 1993). Moreover, thick sediment trapped within mussel beds, which includes mussel pseudofaeces, prevents zygotes from attaching to hard substrates, (Chapman and Fletcher, 2002) and may also increase mortality of early settlers (Albrecht, 1998; Chapman and Fletcher, 2002). Presumably this is because when embryos are buried by the sediment, availability of light, nutrients and dissolved gas decreases and mussel biodeposits can enhance bacterial infection of embryos (Chapman and Fletcher, 2002). However, there are likely positive effects on early fucoid stages. Bracken (2004) and Pfister (2007) found that the supply of inorganic nitrogen and phosphorus from mussel excretion promoted algal growth. Within the mussel bed matrix, desiccation stress is ameliorated (Seed, 1996) and damaging wave action effects are significantly reduced (O'Donnell, 2008). The extent to which mussel beds modify the likelihood of fucoid escape from grazing is unclear. The complex topography may provide a refuge from the grazing of patellid limpets, (Erlandsson et al., 1999) although several studies have demonstrated grazing effects of limpets and other grazers within the mussel bed (Albrecht, 1998; O' Connor and Crowe, 2008; Crowe et al., 2011). For larger fucoids, the effect of mussels appears to be generally negative. Mussels can cause the loss of the entire thalli when the stipes are abrading against the sharp shell edges (Grant, 1977), or when holdfasts are degenerated by the accumulation of anaerobic sediments within the mussel beds (McCook and Chapman, 1991). Moreover, mussels can overgrow fucoid thalli by attaching byssal threads to the thalli and pulling them down (McCook and Chapman, 1991). Dislodgement of thalli by breaking waves is a key mechanism influencing mortality of large fucoids (Carrington, 1990); growing on mussel shells can increase fucoid loss because mussels are less stable substrate and both fucoids and mussels can be moved together by strong waves (Malm, 1999).

Canopy-forming macroalgae appear to exhibit both positive and negative impacts on mussels (McCook and Chapman, 1991; Bertness et al., 1999; O'Connor et al., 2006). Fucoids can facilitate the settlement of mussels under their canopy (McCook and Chapman, 1991; Bertness et al., 1999), as well as enhance mussel growth rate (Bertness et al., 1999). However canopy macroalgae present a suitable environment for a range of predators which predate on mussels (Menge, 1978). Also experiments by Witman and Suchanek (1984), Witman (1987) and O'Connor et al. (2006) showed that epibiotic macroalgae enhance the dislodgement of mussels from the substrata. Mussels overgrown by macroalgae encountered greater flow-induced forces when compared to mussels alone (O’ Connor et al., 2006).

Here we investigate the effects of mussel-modified habitat on the settlement and survivorship and consequent population structure of a dominant low shore species *Fucus serratus*. Surveys and experiments were carried out on two exposed rocky shores on the Isle of Anglesey where these two organisms coexist, to test the general hypothesis that the mussel habitat influences fucoid life history processes, resulting in population level effects on fucoids. We specifically tested the hypotheses that mussel dominated habitat causes a reduction in fucoid settlement but enhancement of germling survival through impairment of top-down control by molluscan grazers and amelioration of physical extremes. Experimental work on fucoid adults also tested the hypothesis that the risk of dislodgement of fucoid thalli growing on mussel shells is higher than it is for thalli growing on primary substrate. Survey work was conducted to determine the outcome of mechanisms operating at different life history stages on fucoid population structure.

2. METHODS

2.1 Study sites

The surveys and experiments were carried out on the exposed rocky shores at Moelfre and Traeth Bychan on the Isle of Anglesey, off the north coast of Wales, at the low-mid shore level (1.5 - 2.5 m above LAT) where *F. serratus* and *Mytilus edulis* co-exist. This level on each shore was characterised by a mosaic of mussels and patches of bare rock (variously covered with filamentous algae, mud and sand especially during summer). Mussels were generally monolayered and occurred in patches not usually less than ~1 m^2. Most barnacles were found epibiotically on mussel shells while they were rarely found on the primary rock surface. Fucoids of different sizes were found growing on both mussel shells and on rock substrate. Dominant grazers were the limpet *Patella vulgata*, the periwinkles *Littorina littorea*, and *L. saxatilis*, and the top shell *Gibbula umbilicalis*.

2.2 Sampling

2.2.1 Population structure of fucoids growing in mussel-modified habitat

A survey was made within a patchy mussel bed in October 2014 to assess fucoid abundance in areas with different degrees of mussel cover. On both shores, the percentage cover of mussels was estimated in forty 25×25 cm quadrats and all fucoid thalli with holdfasts within the quadrats were counted, assessed for fertility status, and their lengths measured to the nearest cm. The type of substrate (mussel shell or rock) upon which each individual thallus was growing was also noted. Thalli smaller than 10 cm were categorized as juveniles.

Fucoid abundance, within and outside mussel habitat across two shores, was calculated as adjusted density to reflect the relative abundance of mussel/ rock habitat within each quadrat. Adjusted density (number of individuals per quadrat assuming that there is 100% cover of a habitat in a quadrat), was calculated as [100 × number of fucoids either on mussels or rock / percentage cover of that habitat in the quadrat]. The adjusted densities of fucoids growing within mussel habitat were calculated from data randomly selected from 20 quadrats on each shore, while data from the other 20 quadrats were used to calculate adjusted density of fucoids growing on bare rock.

2.2.2 Effect of mussel-modified habitat on fucoid settlement

In December 2015 the intensity of *Fucus serratus* propagule settlement was assessed over a period of spring tides inside and outside mussel habitat using artificial settlement panels. Ten 10×10 cm PVC panels were placed within each habitat on both shores. The panels were scrubbed using coarse abrasive paper before use. Within the mussel patch a few mussels were first pulled out from the rock and the panel then inserted into the space and fastened to the substrate using a single stainless steel screw. The panel was at least 10 cm away from the edge of the mussel patch. Outside mussel patches, each panel was secured within a 20×20 cm area cleared of all organisms. All panels were retrieved three days after installation and kept for three days in a plastic tank fed with a constant supply of seawater at ~10 °C, until they could be processed. All fucoid settlers on the panels were counted using a dissecting microscope at 30x magnification, except those on the peripheral 5 mm of the panels to avoid edge effects.

2.2.3 Effect of mussel-modified habitat on survival of fucoid germlings

The effect of mussel habitat and grazing on fucoid germling survival was tested in a factorial experiment in November 2014 at Moelfre and Traeth Bychan. Slate tiles with 4 week old fucoid germlings were transplanted to positions inside and outside mussel habitat and three grazing treatments applied: tiles were exposed to grazers; a cage was used to exclude molluscan grazers; or a procedural control using roofs of the cage material but allowing full grazer access applied.

To obtain germlings for the experiment, *F. serratus* gametes were fertilized in the laboratory, and then the zygotes were seeded onto the slate tiles. The procedure of releasing the fucoid gametes and isolation of zygotes was adapted from McLachlan et al., (1971) and Creed (1993). Fifty male and fifty female receptacles of *F. serratus* were collected in the field and brought to the lab. Black dots within conceptacles are clearly visible on female receptacles, while the male conceptacle is an opaque orange. The receptacles were laid onto blue paper towel, left to dry slightly and then stored in a freezer (-20 °C) for two hours. After the cold shock the receptacles were washed in tap water for one minute, as a freshwater shock to trigger gamete release. Female and male receptacles were placed separately in plastic trays (30×50×6 cm) under illumination from 60W halogen lamps for 30 minutes, then, while still illuminated, covered with seawater for two hours. Eggs and spermatozoids were released with mucus; thus the solutions were diluted with approximately one litre of seawater in each container. Fertilization took place when the solutions containing the male and female gametes were combined, and left undisturbed for one hour. The mixture was then added to a 36×56×20cm plastic tank 75% filled with seawater into which sixty 5×5 cm slate tiles had been placed. Zygotes were allowed to settle onto the panels for 6 hours, after which the tank was connected to a constant supply of seawater. The propagules were kept in the aquarium at 15-17°C under 24 h artificial light for four weeks, and then transferred to the field. The number of germlings at the onset of the experiment was assumed to be equal over all treatments.

On each shore an area was chosen with mixed cover of mussels and open bare rock. Fifteen 10×10 cm mussel patches (100% mussel cover) in the mussel-dominated area were designated for mussel treatment. All organisms and sediment within a 7 cm radius from the mussel patch were removed. Fifteen 10×10 cm areas outside mussel habitat served as no-mussel treatment on each shore. In each of the two habitats the three grazer treatments were applied (thus 5 replicates of each treatment). Cages and roofs were fastened to the rock using stainless steel screws and washers and the control plots were labelled by fastening a plastic label with a screw and washer onto the rock. Cages were 7x10x10 cm height, width and length respectively, and were made from a rigid metal mesh (1.6 cm diagonal in mesh size) coated with green plastic. Roofs were similar to cages but two vertical opposite sides of mesh material were removed, thus, allowing access to grazers. Experimental plots were at least one metre apart. In each plot, a slate tile with fucoid propagules was fastened to the rock using a single screw. Any grazers found within the cages or within a 30 cm radius were removed.

After two weeks in the field all slate tiles were removed and transported back to the laboratory in plastic boxes. The tiles were kept in an aquarium at ~15°C water temperature overnight until processing. The germlings on the tiles were counted in four randomly selected microscope fields at 25× magnification (a total area of 254.47 mm^2), avoiding the peripheral 5 mm of the tile. Data from these fields of view were pooled to obtain an estimate of the number of germlings per tile.

A survey to monitor the abundance of key grazers (littorinids, top shells and limpets) inside and outside mussel habitat was made in April 2015. Thirty 10×10 cm quadrats were placed inside and outside patches of mussels on each shore and all molluscan grazers identified and counted. Patellid limpets and *Littorina littorea* with sizes < 1 cm were classified as small, and those ≥ 1 cm as large.

2.2.4 Influence of mussel substrate on survival of adult fucoids at risk from dislodgement

In order to test if mussels provide a stable substrate for fucoids to grow and reach fertility a tagging experiment was performed in the winter when risk of dislodgement from waves was highest. In November 2014, a total of 80 *F. serratus* thalli in the mussel-dominated area on each shore were tagged using coloured cable ties. The thalli were divided into 4 categories: 1) 20 small thalli (20-30 cm) growing on mussel shells; 2) 20 small thalli growing on rock; 3) 20 large thalli (40-50 cm) growing on mussel shells; and 4) large thalli growing on rock. The fucoids growing on mussel shells were within mussel matrix, whereas the fucoids growing on rock substrate were those outside mussel patches. The length of the thallus was measured from holdfast to tip of the longest frond. At this time of the year on both shores the majority of the large fucoids were producing gametes and the receptacles were clearly visible, while few of the small thalli were doing so. Therefore, the small and large thalli were associated with being sterile and fertile, respectively. Only small sterile thalli and large fertile thalli were tagged. Each shore was visited again in March 2015, when the tagged fucoids remaining were counted.

Measurements of the critical breaking stress of fucoids were made *in situ* during low tide periods in November 2014. Fucoids within the same categories as in the previous experiment were subjected to simulated hydrodynamic drag using a method adapted from Jonsson et al. (2006). A Pesola® macro-line spring scale (10 kg) with a maximum force recorder was secured to a wooden clamp with a nylon rope and the wooden clamp attached to the fucoid stipe 1 cm from the substrate. It was then pulled approximately perpendicular to the substratum until the thallus was detached from the substrate. The breaking forces were recorded in kilograms and then converted into newtons (N). For plants growing on mussel shells, the position of adhesive failure was classified as holdfast-mussel (i.e., plants were detached from mussel shells) or mussel-rock (i.e., mussels were detached from rock and both mussels and algae were removed).

2.3 Statistical Analyses

Analyses of variance (ANOVA) were used to examine effects of mussel-modified habitat on abundance of fucoids, grazers and breaking forces of fucoids. The factor shore was treated as a random factor in all analyses, while the others were fixed. Further details of the models are provided in the relevant sub-sections of the Results. Cochran's tests (Winer, 1971) were used to test for heterogeneity of variance. Multiple comparisons of levels within significant factors were made using Student Newman Keuls (SNK) tests. In the case where data were heterogeneous even after transformation, Mann-Whitney U tests were used instead of ANOVA. Between-habitat differences in size frequency distribution of fucoids, frequency of survived-tagged fucoids, and frequency of the thalli that broke away from substrate at different positions were analysed using chi-square contingency test.

3. RESULTS

3.1 Population structure of fucoids growing in mussel-modified habitat

Two way ANOVA (random factor – shore, orthogonal to fixed factor –habitat) revealed no effect of habitat on the adjusted density of juvenile fucoids (Table 1) but there was a clear effect on fertile adults (Table 1, Fig. 1). SNK tests of the significant Shore × Habitat interaction showed significantly greater density of fertile adults outside mussel habitat at Traeth Bychan but not Moelfre (Fig. 1). The adjusted density of all fucoids, irrespective of developmental stage, was significantly greater outside mussel habitat (Table 1, Fig. 1).

On both shores, the size distributions of fucoids (considering both sterile and fertile combined) within and outside mussel habitat were different: Moelfre ($\chi 2 = 37.81$, $P < 0.001$) and at Traeth Bychan ($\chi 2 = 90.73$, $P < 0.001$) with greater numbers of larger thalli found outside the mussel habitat than within (Fig. 2). Fucoid individuals reached a maximum length of 60 cm within mussel patches, but grew up to 100 cm outside. 87% of the thalli larger than 60 cm were fertile while only 6% of those smaller than 60 cm were. Thus the proportion of fertile thalli was very low inside mussel habitat compared to outside.

3.2 Effect of mussel-modified habitat on fucoid settlement

At Moelfre fucoid settlement was significantly greater inside mussel habitat (over 18 times greater density) than outside ($U = 79.50$, $P < 0.05$, Fig. 3). At Traeth Bychan no effect of mussel habitat was detected ($U = 55.0$, $P > 0.05$), although it is worth noting that the mean abundance of propagules inside mussel habitat was twice that outside.

3.3 Effects of mussel modified habitat on survival of fucoid germlings

There was a clear positive effect of grazer exclusion on the survival of fucoid germlings both inside and outside the mussel habitat (Fig 4, Table 2). In the absence of grazers the number of germlings following 2 weeks in the field was on average 170 per tile (pooled across both shores and habitat type) compared to an average of 44 across the two control treatments. Post hoc analysis of the significant 3 way interaction in the 3 way factorial ANOVA (random factor-shore, orthogonal to fixed factors-habitat and grazing treatment) showed significantly higher fucoid numbers in caged treatments (grazer exclusion) compared to both control treatments (grazers present) at all shore × habitat combinations. Although there was a trend for greater survival of fucoids protected from grazing inside the mussel habitat, post hoc analyses of the 3 way interaction indicated no significant effect of habitat on the effect of caged treatments at either shore.

The distribution of grazers between mussel and bare rock habitat showed some clear patterns, although there was variation between the two shores. Overall there was greater abundance of grazers (all species combined) inside the mussel habitat at Moelfre but not Traeth Bychan (Table 4; post hoc analysis of significant Shore × Habitat interaction from Table 3). On both shores large limpets were more abundant outside than inside the mussel habitat (Table 4; Fig. 5). The pattern for small limpets was less clear. At Traeth Bychan small limpets were found only outside the habitat; whereas at Moelfre they were only found living on mussel shells inside mussel habitat (although densities were very low) (Fig. 5). *L. littorea* of both sizes were more abundant inside mussel habitat than outside; a similar pattern was found for top shells. Habitat had no significant effect on *L. saxatilis* (Table 4). No other grazers except limpets were found outside mussel habitat at Traeth Bychan (Fig. 5).

3.4 Influence of mussel substrate on survival of adult fucoids at risk from dislodgement

In the tagging experiment, comparisons of the proportions of thalli which survived were made between thalli growing on mussel shells within mussel habitat and on primary substrate outside mussel habitat. The effect of size on the probability of dislodgement was also examined. The effect of habitat on dislodgement was significant only for small fucoids at Moelfre, where the number of lost thalli was higher for thalli growing on mussel shells (Table 5, Fig. 6). No discernible effect of size was found in any comparison (Table 5).

In the dislodgement force experiment, a factorial ANOVA testing the effect of size of fucoid (fixed factor), substrate type (fixed factor) and shore (random factor) revealed that significant interactions were found between shore and substrate, as well as shore and size (Table 6). The force required to pull thalli from rock was double that required from mussel shells (averaged across shores and sizes; SNK tests on the shore × substrate interaction, $P < 0.05$, Fig. 7). Breaking forces were 3 times greater for large thalli than small thalli (averaged across shores and substrates; SNK tests on the shore × size interaction, $P < 0.05$, Fig. 7). It is interesting to note that the difference in breaking forces between substrates seemed greater for large thalli than small thalli (Fig. 7).

Chi-square contingency tests were used to examine whether there was a difference in position of adhesive failure for small and large thalli growing on mussel shells. At Traeth Bychan, the number of large thalli that broke at the mussel-rock position was 1.5 time greater than at the holdfast-mussel position ($\chi2 = 7.20$, $P < 0.01$, Fig. 8), but the difference was not found in small thalli ($\chi2 = 0.00$, $P = 0.99$), nor for thalli of both sizes at Moelfre (small: $\chi2 = 0.20$, $P = 0.65$; large; $\chi2 = 1.8$, $P = 0.18$).

4. DISCUSSION

Mussel-modified habitat differentially influences fucoids of different life-history stages. Mechanisms and processes demonstrated in the experiments potentially contribute to the variation in population structure found on the shores. When the fucoids are young the effect of mussel-modified habitat on settlement and survival of germlings can be positive but is context-dependent. Overall there was no difference in abundance of juvenile fucoids inside and outside mussel habitat. Negative effects were more evident when the fucoids were older, as shown by a higher risk of dislodgement found in large fertile thalli. Thus, there were lower numbers of large fucoids in the mussel habitat, and the maximum size of the thalli inside the mussel habitat was considerably smaller than outside.

The effect of mussel-modified habitat on the settlement of fucoid propagules appeared to be positive, as settlement was higher in mussel habitat in one of the two shores studied. This may be due to reduced water current velocities and wave forces within the mussel beds (Van Duren et al., 2006; O'Donnell, 2008), facilitating settlement. A reduction in turbulence within the mussel habitat may also reduce gamete dilution, and hence aid fertilization (Serrão et al., 1996; Ladah et al, 2008). Negative effects of sedimentation (Albrecht, 1998; Chapman and Fletcher, 2002) were unlikely as the panels were deployed in the field for only a short time period (3 days).

The mussel habitat harboured more grazing snails with positive associations for periwinkles and top shells, but not limpets. Limpets were associated with bare rock, except for small limpets at Moelfre, which were found only on mussel shells. Limpets need an area of smooth surface that they use as a 'home-scar' to which they can return to after each foraging event (Hartnoll and Wright, 1977) and tend to avoid moving and foraging directly over surface irregularities (Erlandsson et al., 1999). At Moelfre, however, sedimentation outside mussel reefs was high, so small limpets may avoid sediment by living on mussel shells (Airoldi and Hawkins, 2007). For periwinkles and top shells surface irregularities of the mussel matrix are not an impediment to effective grazing (Albrecht, 1998; O'Connor and Crowe, 2008; Griffin et al., 2009).

Exclusion of grazers resulted in enhanced survival of fucoid germlings in both mussel dominated and bare rock habitats. Thus while mussel reefs support a different grazer assemblage to bare rock, both assemblages are important in limiting fucoid recruitment. As the survival rate of germlings was more than 40 times lower when grazers were allowed to forage in the experimental plots, the grazing effect on fucoid abundance was very strong and the effect of differences in the physical environment between mussel patches and bare rock seems negligible. Grazer assemblages in the mussel reef are dominated by periwinkles and top shells that have been shown to have a lower impact on macroalgal cover than limpets (Hawkins et al., 1989; O'Connor and Crowe, 2005; Crowe et al., 2011; Griffin et al 2010). However our results show clear top down control by grazer assemblages dominated by these species and thus correspond with previous work (e.g. Lubchenco, 1983; Harding, 1993) which suggests that when these grazers occur in high numbers they can control abundance of macroalgae effectively. Given the strong top down control observed in mussel modified habitat and the observation that grazer assemblages within mussel patches vary spatially (compare the grazer assemblage at Moelfre and Traeth Bychan in this study) it is likely that the question of whether mussel dominated habitat influences fucoid abundance and distribution is dependent to a large extent on how mussels modify grazer identity and abundance. Thus context specific modification by mussel habitat of the grazer assemblage is perhaps key to understanding the mechanisms by which mussel habitat influences fucoid distribution.

Dislodgement by hydrodynamic forces generated by breaking waves is a key mechanism influencing macroalgae mortality and subsequent population structure (Gunnill, 1985; Carrington, 1990). The level of wave induced mortality is influenced to a large degree by factors such as substratum type (Barnes and Topinka, 1969; van Tamelen and Stekoll, 1997) and levels of epiphytic fouling (Witman and Suchanek, 1984; Brosnan, 1994; O'Connor et al., 2006). We showed that the risk of dislodgement for large fucoids growing on mussel shells was significantly greater than for those growing on the rock surface. Hence, mussel shells are not a stable substrate for fucoids to grow and reach fertility. A positive relationship between thallus size and breaking force has been demonstrated in numerous studies (e.g. Thomsen and Wernberg, 2005). Our experiments showed that for large thalli the position of adhesion failure is likely to be between the mussels and the rock surface. Therefore, when algae grow on mussel shells, the breaking force required to detach algae from the shore is not a function of the strength of the attachment by the algal holdfast; rather it is the strength of mussel attachment, especially in large thalli.

Large reproductive thalli have a higher chance of being lost through dislodgement in mussel habitat compared to open rock. Thus it is likely that the greater the area occupied by mussels on a shore, the less the reproductive output of the fucoid population will be. In addition, while many marine organisms have long-living planktonic larvae, algal propagules have a shorter life span, rarely dispersing elsewhere, with successful settlement commonly occurring near to the parent plants (Chapman, 1995; Johnson et al., 1998). Both local reproductive failure and the lack of propagule supply from outside can cause a reduction in fucoid populations in mussel-dominated areas. On some rocky shores on the east coast of the Isle of Anglesey, such as Penysarn, where mussels densely aggregate on primary rocky substrate forming extensive beds, fucoids are very rare to almost absent. This suggests that the negative effects of mussels resulting in low fucoid cover can be consistent over time.

Our work contributes towards understanding the interaction between two widely distributed and abundant groups of organisms on exposed rocky shores of NW Europe. We showed that the direction and magnitude of effects of mussels on fucoid abundance and distribution was dependent on the specific life-history stage, and to a certain extent was also context dependent. Such context dependency may be mediated through the way in which mussels modify grazer assemblages living within the mussel matrix. (see also Crowe et al, 2011). Overall however, our observational work suggests that mussel-modified habitat had a negative effect on fucoid abundance on the shores of N Wales, with experimental work suggesting mussels fail to provide a stable substrate for the maintenance of large mature individuals rather than out-competing them. The extent to which mussels may out-compete fucoids in NW Europe is likely to be a function of local and regional variation in mussel recruitment. Where permanent, dense beds occur, it is likely they will have a negative effect on fucoid populations. Such beds are, however, less common on British coasts than in the Gulf of Maine where much of the experimental work in North America has been conducted (Menge, 1976; Lubchenco and Menge, 1978; Bertness et al, 2004). Less deterministic and intense recruitment, coupled with different grazing species and grazing regime may lead to subtle differences in ecological processes influencing outcomes of mussel-fucoid interactions between NW Europe and the Atlantic coast of North America and their interpretation (Jenkins et al, 2008).

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REFERENCES

Airoldi, L., Hawkins, S. J., 2007. Negative effects of sediment deposition on grazing activity and survival of the limpet *Patella vulgata*. Mar. Ecol. Prog. Ser. 332, 235-240.

Albrecht, A. S., 1998. Soft bottom versus hard rock: Community ecology of macroalgae on intertidal mussel beds in the Wadden Sea. J. Exp. Mar. Biol. Ecol. 229(1), 85-109.

Ballantine, W. J., 1961. A biologically-defined exposure scale for the comparative description of rocky shores. Field Studies 1, 1-19.

Barnes, H., Topinka, J. A., 1969. Effect of the nature of the substratum on the force required to detach a common littoral alga. Am. Zool., 9(3), 753-758.

Bertness, M. D., Leonard, G. H., Levine, J. M., Schmidt, P. R., Ingraham, A. O., 1999. Testing the relative contribution of positive and negative interactions in rocky intertidal communities. Ecology 80(8), 2711-2726.

Bertness, M. D., Trussell, G. C., Ewanchuk, P. J., Silliman, B. R., Mullan Crain, C. 2004. Consumer-controlled community states on Gulf of Maine rocky shores. Ecology 85(5), 1321-1331.

Blanchette, C. A., 1997. Size and survival of intertidal plants in response to wave action: a case study with *Fucus gardneri*. Ecology 78(5), 1563-1578.

Bracken, M. E., 2004. Invertebrate-mediated nutrient loading increase growth of an intertidal macroalga. J. Phycol. 40(6), 1032-1041.

Brosnan, D. M., 1994. Environmental factors and plant-animal interactions on rocky shores along the Oregon coast. Doctoral dissertation. Oregon State University, Oregon.

Carrington, E., 1990. Drag and dislodgment of an intertidal macroalga: consequences of morphological variation in *Mastocarpus papillatus* Kützing. J. Exp. Mar. Biol. Ecol. 139(3), 185-200.

Chapman, A. R. O., 1995. Functional ecology of fucoid algae: twenty-three years of progress. *Phycologia* 34(1), 1-32.

Chapman, A. S., Fletcher, R. L., 2002. Differential effects of sediments on survival and growth of *Fucus serratus* embryos (Fucales, Phaeophyceae). J. Phycol. 38(5), 894-903.

Coleman, R. A., Underwood, A. J., Benedetti-Cecchi, L., Åberg, P., Arenas, F., Arrontes, J. Castro, J., Hartnoll, R. G., Jenkins, S. R., Paula, J., Santina, P. D., Hawkins, S. J., 2006. A continental scale evaluation of the role of limpet grazing on rocky shores. Oecologia 147(3), 556-564.

Creed, J. C., 1993. Intraspecific competition in seaweeds. PhD Thesis, University of Liverpool.

Crowe, T. P., Frost, N. J., Hawkins, S. J., 2011. Interactive effects of losing key grazers and ecosystem engineers vary with environmental context. Mar. Ecol. Prog. Ser. 430, 223-234.

Dayton, P.K., 1971. Competition, disturbance, and community organization: the provision and subsequent utilization of space in a rocky intertidal community. *Ecol Monograph* 41:351–389.

Dudgeon, S. R., Johnson, A. S., 1992. Thick vs. thin: thallus morphology and tissue mechanics influence differential drag and dislodgement of two co-dominant seaweeds. J. Exp. Mar. Biol. Ecol. 165(1), 23-43.

Erlandsson, J., Kostylev, V., Williams, G. A., 1999. A field technique for estimating the influence of surface complexity on movement tortuosity in the tropical limpet *Cellana grata* Gould. Ophelia, 50(3), 215-224.

Gaylord, B., Blanchette, C. A., Denny, M. W., 1994. Mechanical consequences of size in wave-swept algae. Ecol. Monograph, 287-313.

Grant, W. S., 1977. High intertidal community organization on a rocky headland in Maine, USA. Mar. Biol. 44(1), 15-25.

Griffin, J. N., Jenkins, S. R., Gamfeldt, L., Jones, D., Hawkins, S. J., Thompson, R. C., 2009. Spatial heterogeneity increases the importance of species richness for an ecosystem process. Oikos, 118(9), 1335-1342.

Griffin, J. N., Noël, L. L., Crowe, T. P., Burrows, M. T., Hawkins, S. J., Thompson, R. C., Jenkins, S. R., 2010. Consumer effects on ecosystem functioning in rock pools: roles of species richness and composition. Mar. Ecol. Prog. Ser. 420, 45-56.

Gunnill, F. C., 1985. Population fluctuations of seven macroalgae in southern California during 1981–1983 including effects of severe storms and an El Nino. J. Exp. Mar. Biol. Ecol. 85(2), 149-164.

Harding, S.P., 1993. Seston dynamics, algal propagule availability and the role of mussels on a moderately exposed shore. PhD Thesis. University of Liverpool, Liverpool.

Hartnoll, R. G., Wright, J. R., 1977. Foraging movements and homing in the limpet *Patella vulgata* L. Anim. Behav. 25, 806-810.

Hawkins, S. J., 1981. The influence of season and barnacles on the algal colonization of *Patella vulgata* exclusion areas. J. Mar. Biol. Assoc. UK 61(01), 1-15.

Hawkins, S. J., Hartnoll, R. G., 1983. Grazing of intertidal algae by marine invertebrates. Oceanogr. Mar. Biol. 21, 195-282.

Hawkins, S. J., Watson, D. C., Hill, A. S., Harding, S. P., Kyriakides, M. A., Hutchinson, S., Norton, T. A., 1989. A comparison of feeding mechanisms in microphagous, herbivorous, intertidal, prosobranchs in relation to resource partitioning. J. Mollusc. Stud. 55(2), 151-165.

Jenkins, S. R., Coleman, R. A., Della Santina, P., Hawkins, S. J., Burrows, M. T., Hartnoll, R. G., 2005. Regional scale differences in the determinism of grazing effects in the rocky intertidal. Mar. Ecol. Prog. Ser. 287, 77-86.

Jenkins, S. R., Moore, P., Burrows, M. T., Garbary, D. J., Hawkins, S. J., Ingólfsson, A., Sebens, K. P., Snelgrove, P. V. R., Wethey, D. S., Woodin, S. A., 2008. Comparative ecology of North Atlantic shores: do differences in players matter for process? Ecology, 89(sp11), S3-S23.

Jones, N. S. 1946. Browsing of *Patella*. Nature 158, 557-558.

Johnson, L. E., Brawley, S. H., 1998. Dispersal and recruitment of a canopy-forming intertidal alga: the relative roles of propagule availability and post-settlement processes. Oecologia, 117(4), 517-526.

Jonsson, P. R., Granhag, L., Moschella, P. S., Åberg, P., Hawkins, S. J., Thompson, R. C., 2006. Interactions between wave action and grazing control the distribution of intertidal macroalgae. Ecology, 87(5), 1169-1178.

Knight, M., Parke, M., 1950. A biological study of *Fucus vesiculosus* L. and *F. serratus* L. J. Mar. Biol. Assoc. UK, 29(02), 439-514.

Ladah, L. B., Feddersen, F., Pearson, G. A., Serrão, E. A., 2008. Egg release and settlement patterns of dioecious and hermaphroditic fucoid algae during the tidal cycle. Mar. Biol. 155(6), 583-591.

Lewis, J. R., 1964. The ecology of rocky shores, English Universities Press, London.

Lubchenco, J., Menge B. A., 1978. Community development and persistence in a low rocky intertidal zone. Ecol. Monograph 59, 67–94.

Lubchenco, J., 1983. *Littorina* and *Fucus*: effects of herbivores, substratum heterogeneity, and plant escapes during succession. Ecology 64(5), 1116-1123.

Malm, T., 1999. Distribution patterns and ecology of *Fucus serratus* L. and *Fucus vesiculosus* L. in the Baltic Sea. PhD Thesis, Stockholm University, Stockholm.

McCook, L. J., Chapman, A. R. O., 1991. Community succession following massive ice-scour on an exposed rocky shore: effects of *Fucus* canopy algae and of mussels during late succession. J. Exp. Mar. Biol. Ecol. 154(2), 137-169.

McLachlan, J., Chen, L. M., Edelstein, T., 1971. The culture of four species of *Fucus* under laboratory conditions. Can. J. Bot. 49(8), 1463-1469.

Menge, B. A. 1976. Organization of the New England rocky intertidal community: role of predation, competition, and environmental heterogeneity. Ecol Monograph 46(4), 355-393.

Menge, B. A. 1978. Predation intensity in a rocky intertidal community: Effect of an algal canopy, wave action and desiccation on predator feeding rates. Oecologia 34(1), 17-35.

O'Connor, N. E., Crowe, T. P., McGrath, D., 2006. Effects of epibiotic algae on the survival, biomass and recruitment of mussels, *Mytilus* L. (Bivalvia: Mollusca). J. Exp. Mar. Biol. Ecol. 328(2), 265-276.

O'Connor, N. E., Crowe, T. P., 2005. Biodiversity loss and ecosystem functioning: distinguishing between number and identity of species. Ecology 86(7), 1783-1796.

O'Connor, N. E., Crowe, T. P., 2008. Do mussel patches provide a refuge for algae from grazing gastropods? J. Mollusc. Stud. 74(1), 75-78.

O'Connor, N. E., Donohue, I., Crowe, T. P., Emmerson, M. C., 2011. Importance of consumers on exposed and sheltered rocky shores. Mar. Ecol. Prog. Ser., 443, 65-75.

O’Donnell, M. J., 2008. Reduction of wave forces within bare patches in mussel beds. Mar. Ecol. Prog. Ser. 362, 157-167.

Pfister, C. A., 2007. Intertidal invertebrates locally enhance primary production. Ecology 88(7), 1647-1653.

Raffaelli, D., Hawkins, S. 1996. Intertidal Ecology. Chapman and Hall, London.

Seed, R., 1996. Patterns of biodiversity in the macro-invertebrate fauna associated with mussel patches on rocky shores. J. Mar. Biol. Assoc. UK 76(1), 203-210.

Serrão, E. A., Pearson, G., Kautsky, L., Brawley, S. H., 1996. Successful external fertilization in turbulent environments. Proc. Natl. Acad. Sci. USA, 93(11), 5286-5290.

Thomsen, M. S., Wernberg, T., Kendrick, G. A., 2004. The effect of thallus size, life stage, aggregation, wave exposure and substratum conditions on the forces required to break or dislodge the small kelp *Ecklonia radiata*. Bot. Mar., 47(6), 454-460.

Thomsen, M. S., Wernberg, T., 2005. Miniview: What affects the forces required to break or dislodge macroalgae? Eur. J. Phycol. 40(2), 139-148.

van Duren, L. A., Herman, P. M., Sandee, A. J., Heip, C. H., 2006. Effects of mussel filtering activity on boundary layer structure. J. Sea Res. 55(1), 3-14.

van Tamelen, P. G., Stekoll, M. S., 1997. The role of barnacles in the recruitment and subsequent survival of the brown alga, *Fucus gardneri* (Silva). J. Exp. Mar. Biol. Ecol., 208(1), 227-238.

Winer, B. J. 1971. Statistical Principles in Experimental Design. McGraw-Hill, Tokyo.

Witman, J. D., Suchanek, T. H. 1984. Mussels in flow: drag and dislodgement by epizoans. Mar. Ecol. Prog. Ser. 16, 259-268.

Witman, J. D., 1987. Subtidal coexistence: storms, grazing, mutualism, and the zonation of kelps and mussels. Ecol. Monograph. 57(2), 167-187.

FIGURE LEGENDS

Fig.1 Abundance (Mean ± SE) of juvenile, fertile and total thalli growing within mussel habitat and outside at Moelfre and Traeth Bychan.

Fig.2 Size frequency distributions of sterile (white bars) and fertile (black bars) fucoids.

Fig.3 Density of fucoid setters (Mean ± SE) inside and outside mussel habitat at Moelfre and Traeth Bychan.

Fig.4 Number of fucoid germlings (Mean ± SE) survived in each treatment in mussel habitat and outside.

Fig.5 Grazers (Mean ± SE) living inside mussel habitat and outside. S = small gastropods; L = large gastropods.

Fig.6 Frequency of tagged fucoids that survived or lost after winter 2015. Small = 20-30 cm thalli; Large = 40-50 cm thalli; Rock = rock substrate; Mussel = mussel shells.

Fig.7 Breaking forces (Mean ± SE) of small (20-30 cm) and large (40-50 cm) fucoid thalli growing on mussel shells and on rock.

Fig.8 Frequency of small (20-30 cm) and large (40-50 cm) fucoids growing on mussel shells that broke from substrates at holdfast-mussel and mussel-rock positions.

TABLES

Table 1 Analyses of variance for abundances of fucoids at different stages inside and outside mussel habitats. ns = not significant.

Source	*df*	Juvenile			Fertile			Total			F test denominator
		MS	F	P	MS	F	P	MS	F	P	
Shore	1	0.53	0.24	0.63	0.89	1.64	0.20	0.21	0.14	0.71	Residual
Habitat	1	1.38	0.26	0.70	7.97	1.79	0.41	4.75	1054.	<0.01	Sh × Ha
Sh × Ha	1	5.21	2.36	0.13	4.45	8.15	<0.01	0.00	0.00	0.98	Residual
Residual	76	2.21			0.54			1.53			
Cochrans C		C = 0.32; ns			C = 0.42; ns			C= 0.35; ns			
Transformation		ln (x+1)			ln (x+1)			ln (x+1)			

Table 2 Analysis of variance of fucoid germling survival following grazer manipulation inside and outside mussel habitat at Moelfre and Traeth Bychan. Transformation = ln (x+1); Cochrans C = 0.32, not significant.

Source	*df*	MS	F	*P*	F test
Shore	1	1.45	2.99	0.09	Residual
Habitat	1	1.53	0.28	0.69	Sh × Ha
Grazing	2	92.11	67.74	<0.05	Sh × Gr
Sh × Ha	1	5.49	11.36	<0.01	Residual
Sh × Gr	2	1.36	2.81	0.07	Residual
Ha × Gr	2	0.50	0.09	0.92	Sh × Ha × Gr
Sh × Ha × Gr	2	5.65	11.68	<0.001	Residual
Residual	36	0.48			

Table 3 Analysis of variance on abundance of all grazers (all species combined). No transformation; Cochrans C = 0.37, not significant.

Source	df	MS	F	P	F test Denominator
Shore	1	21.67	16.56	<0.001	Residual
Habitat	1	3.67	0.16	0.76	Sh × Ha
Sh × Ha	1	23.41	17.88	<0.001	Residual
Residual	116	1.31			

Table 4 Results from Mann-Whitney U tests on abundances of grazers in mussel habitat and outside. [- = absent in both habitats; M = most abundant in mussel habitat; O = most abundant outside mussel habitat]

Taxa	*U*	P	Habitat
Patella vulgata (small)			
- Moelfre	435.00	0.317	M
- Traeth Bychan	540.00	<0.05	O
Patella vulgata (large)			
- Moelfre	555.00	<0.01	O
- Traeth Bychan	573.00	<0.01	O
Littorina littorea (small)			
- Moelfre	269.50	<0.01	M
- Traeth Bychan	-	-	-
Littorina littorea (large)			
- Moelfre	285.50	<0.01	M
- Traeth Bychan	390.00	<0.05	M
Gibbula umbilicalis			
- Moelfre	390.00	0.08	M
- Traeth Bychan	390.00	<0.05	M
Littorina saxatilis			
- Moelfre	435.00	0.317	M
- Traeth Bychan	-	-	-

Table 5 Results from chi-square tests comparing the proportion of surviving tagged fucoids between different substrate types and between fucoid individual sizes.

Source of variation	Moelfre		Traeth Bychan	
	χ^2	*P*	χ^2	*P*
Between substrates				
- Both sizes	3.41	0.06	1.35	0.24
- Small fucoids	3.96	<0.05	0.00	1.00
- Large fucoids	0.42	0.52	2.67	0.10
Between sizes				
- Both substrates	0.05	0.82	0.05	0.82
- Mussel shell	1.13	0.29	0.48	0.49
- Rock	0.10	0.75	0.92	0.34

Table 6 Analysis of variance testing the effects of shore, substrate and size of fucoids on breaking forces. Data were from the mussel-dominated area. Transformation = Square root (x+1); Cochrans C = 0.23, not significant.

Source	df	MS	F	P	F test
Shore	1	52.25	27.88	<0.001	Residual
Substrate	1	67.11	4.62	0.28	Sh × Su
Size	1	320.42	32.73	0.11	Sh × Si
Sh × Su	1	14.52	7.75	<0.01	Residual
Sh × Si	1	9.79	5.22	<0.05	Residual
Su × Si	1	96.37	26.56	0.12	Sh × Su × Si
Sh × Su × Si	1	3.63	1.94	0.17	Residual
Residual	152	1.87			

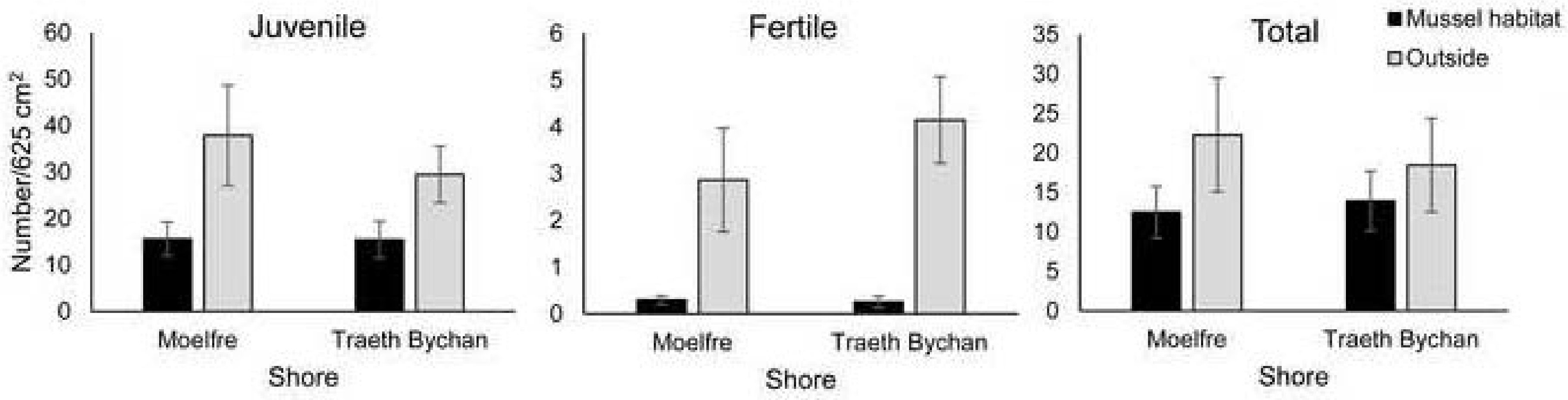
Juvenile
Fertile
Total
■ Mussel habitat
□ Outside
Number/625 cm^2
60
50
40
30
20
10
0
6
5
4
3
2
1
0
35
30
25
20
15
10
5
0
Moelfre
Traeth Bychan
Shore

Figure2

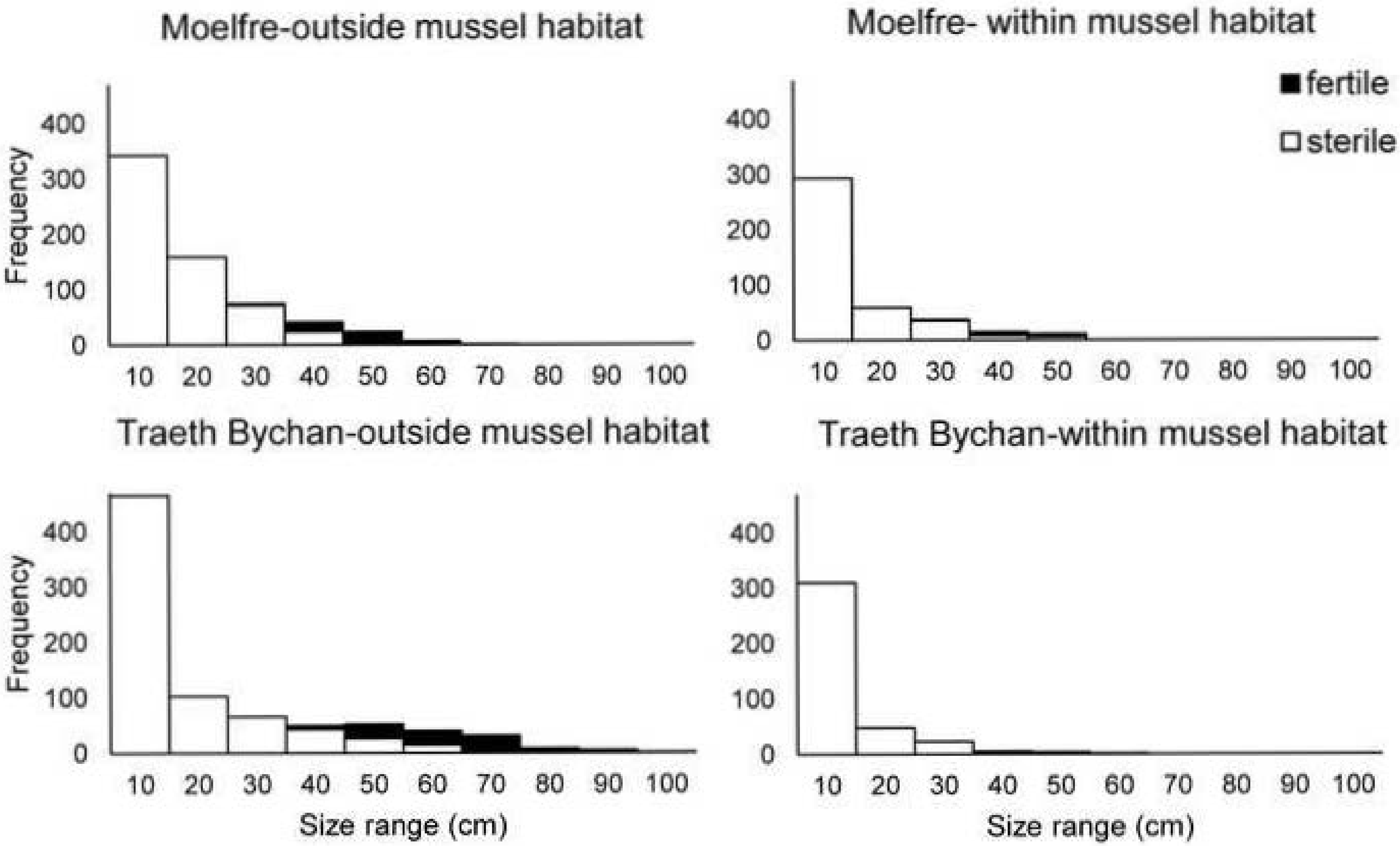
Moelfre-outside mussel habitat
Moelfre- within mussel habitat
■ fertile
□ sterile
Frequency
400
300
200
100
0
10
20
30
40
50
60
70
80
90
100
Traeth Bychan-outside mussel habitat
Traeth Bychan-within mussel habitat
Size range (cm)

Figure3

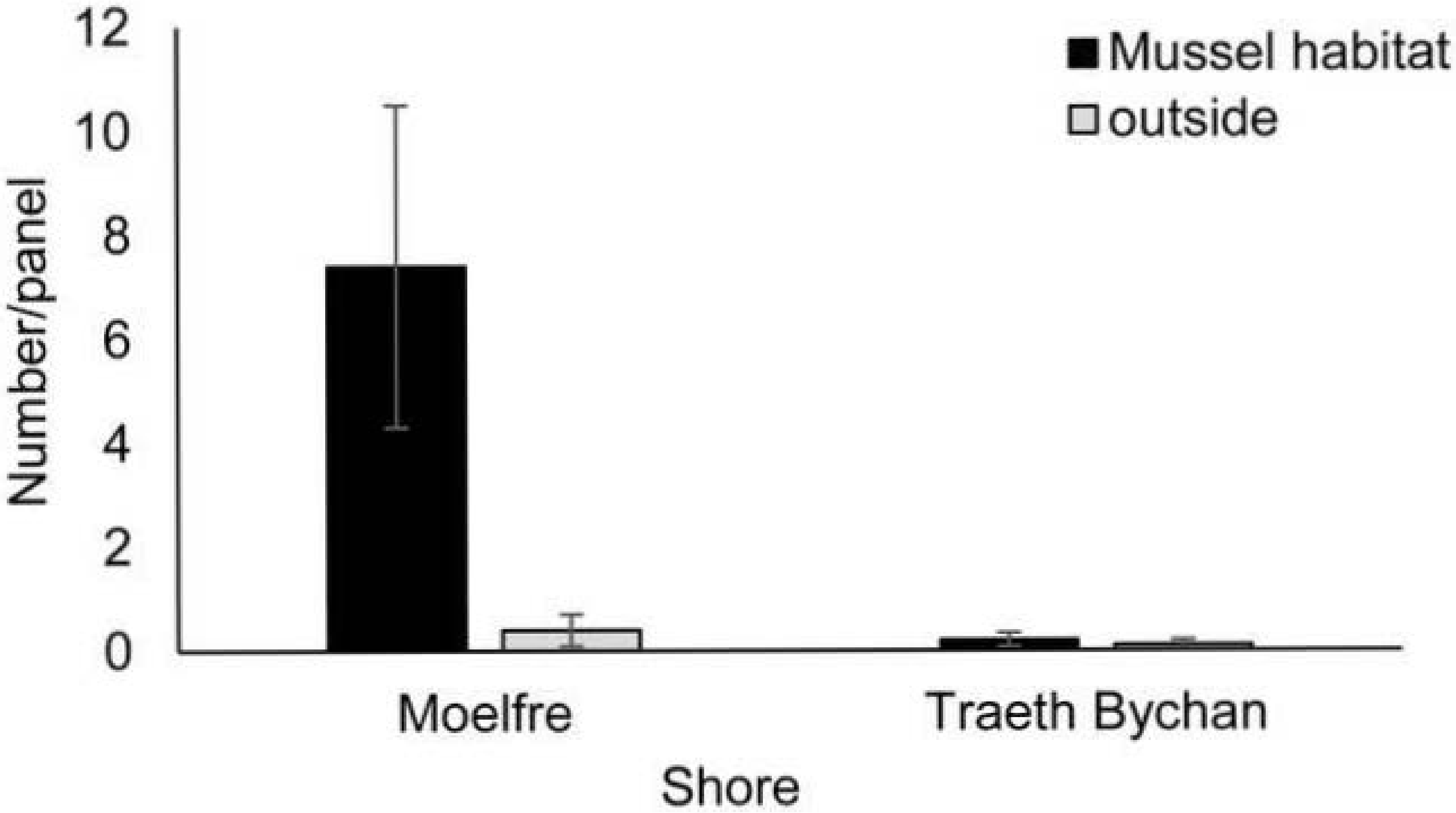
12
10
8
6
4
2
0
Number/panel
■ Mussel habitat
□ outside
Moelfre
Traeth Bychan
Shore

Figure4

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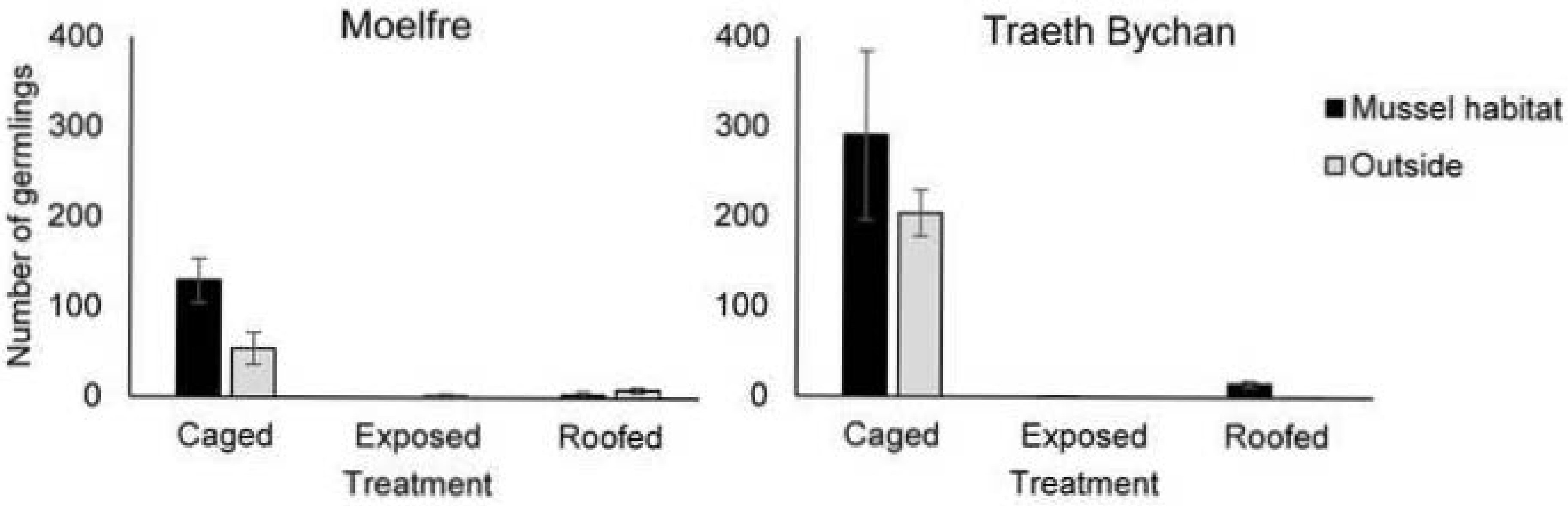
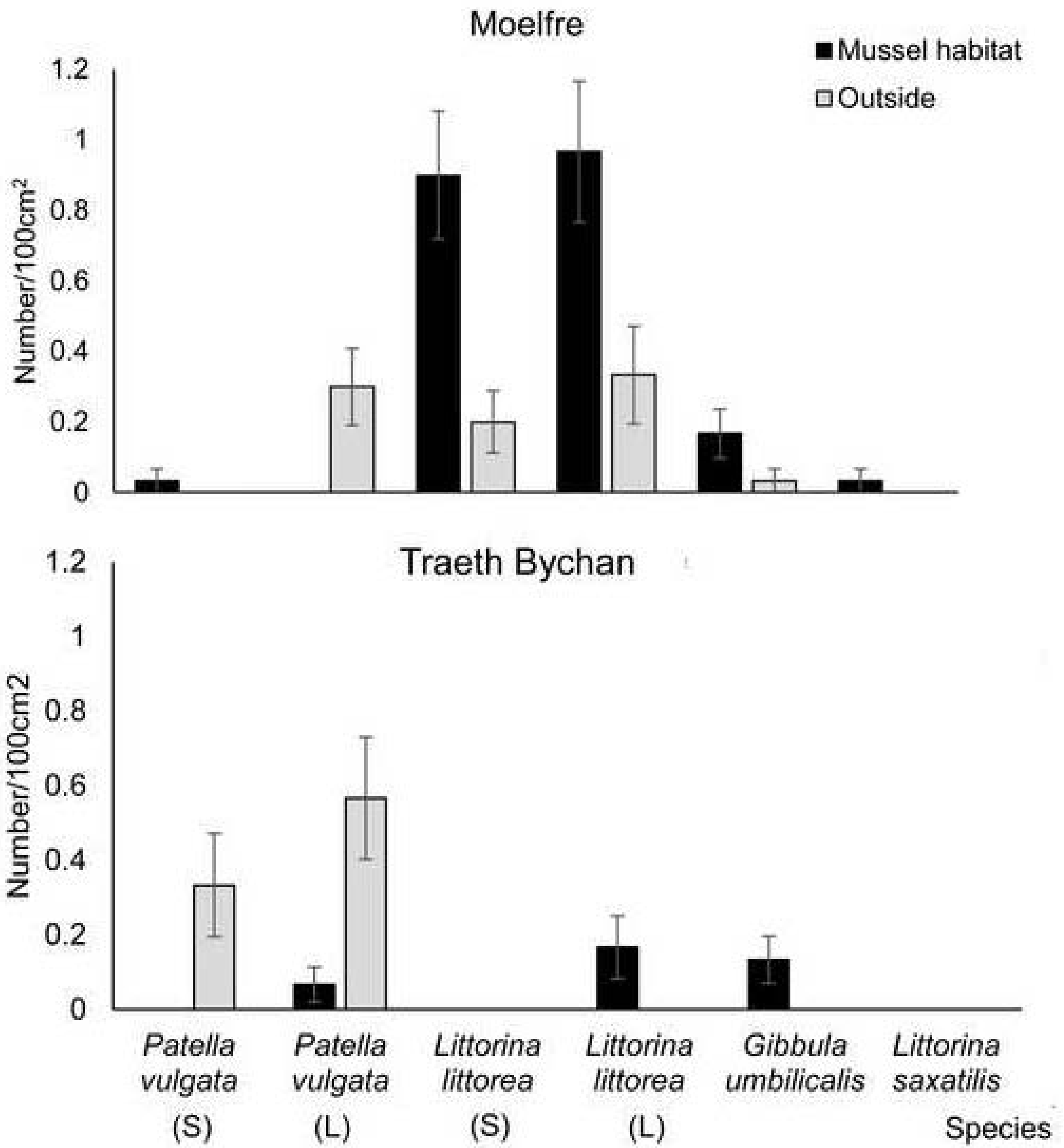


Figure5

Click here to download high resolution image



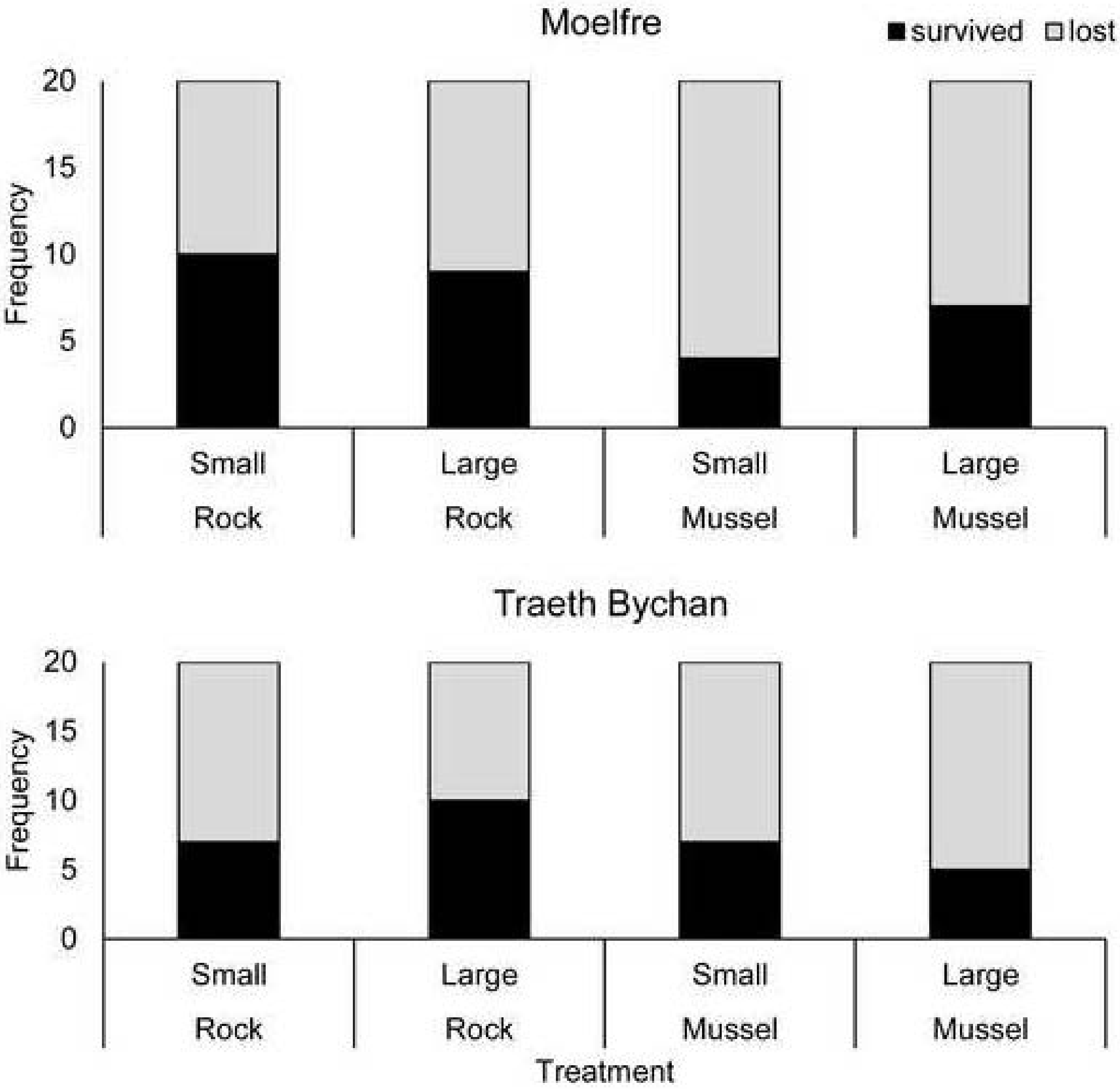

Moelfre
■ survived
□ lost
Frequency
20
15
10
5
0
Small
Rock
Large
Rock
Small
Mussel
Large
Mussel
Traeth Bychan
Frequency
20
15
10
5
0
Small
Rock
Large
Rock
Small
Mussel
Large
Mussel
Treatment

Figure7

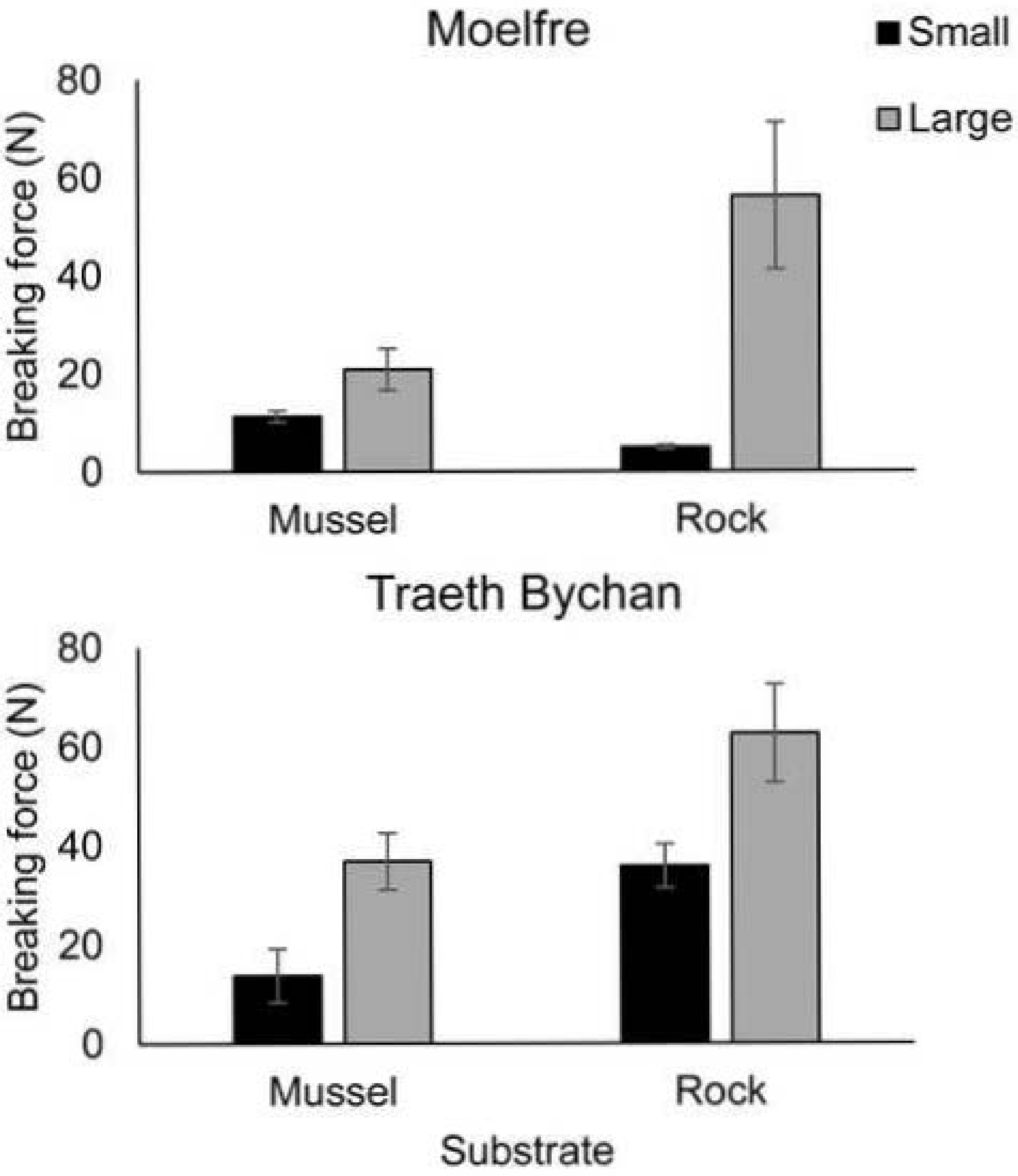
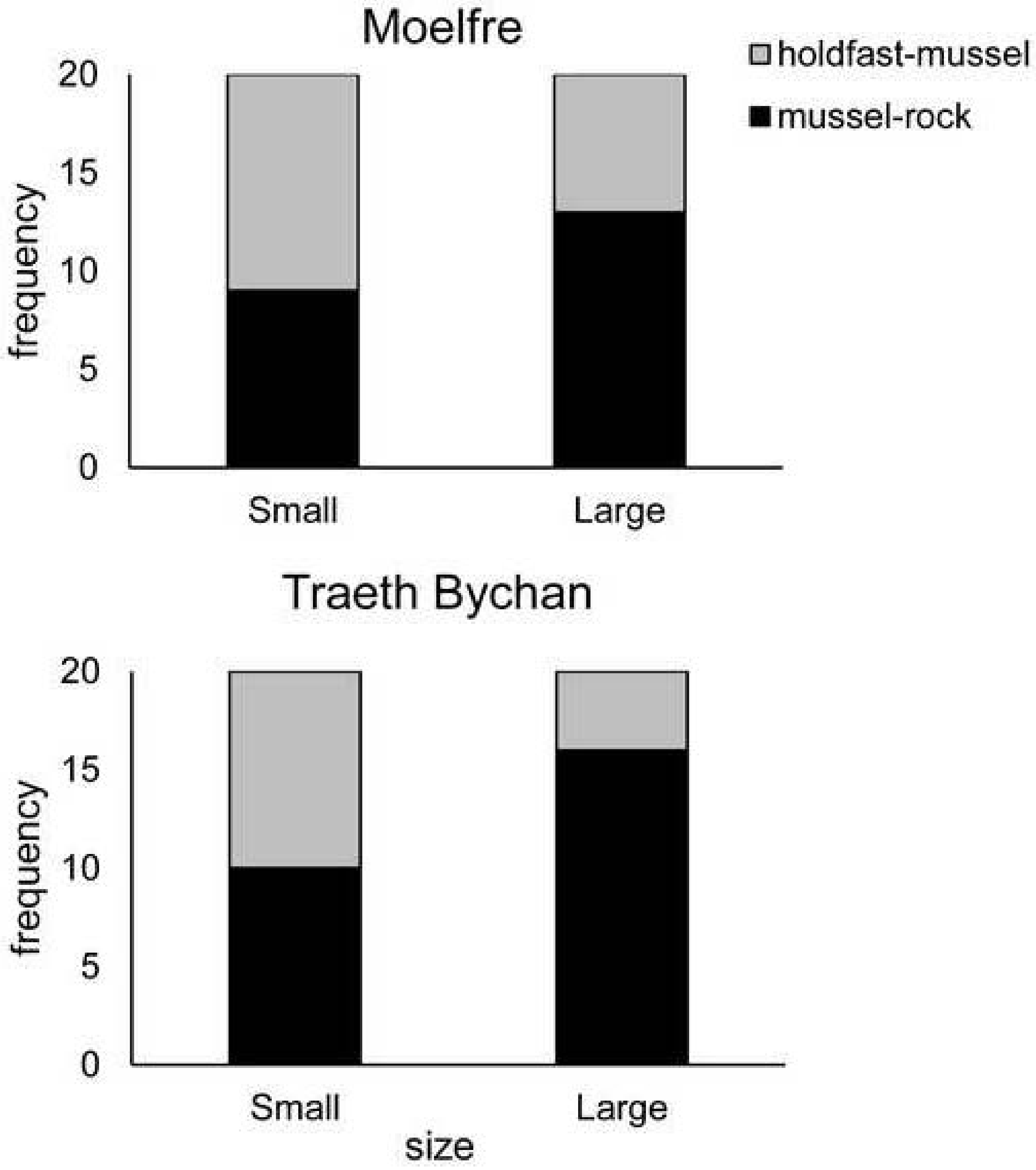

Moelfre
■ Small
▨ Large
Breaking force (N)
80
60
40
20
0
Mussel
Rock
Traeth Bychan
Breaking force (N)
80
60
40
20
0
Mussel
Rock
Substrate

Figure8


Moelfre
▨ holdfast-mussel
■ mussel-rock
frequency
20
15
10
5
0
Small
Large
Traeth Bychan
frequency
20
15
10
5
0
Small
Large
size