SPATIAL COMPARISONS OF POPULATIONS OF AN INDIGENOUS LIMPET *SCUTELLASTRA ARGENVILLEI* AND AN ALIEN MUSSEL *MYTILUS GALLO-PROVINCIALIS* ALONG A GRADIENT OF WAVE ENERGY

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In the 1970s, the Mediterranean mussel *Mytilus galloprovincialis* invaded the South African coast and spread rapidly to dominate much of the West Coast, indicating either the opportunity to occupy a vacant niche or its superior competitive capability over indigenous species. In Namaqualand on the West Coast it appears to compete with a large indigenous limpet, *Scutellastra argenvillei*, which is capable of forming dense, almost monospecific stands low on the shore. A survey on the Namaqualand coast indicated that the abundance of *M. galloprovincialis* changes with wave exposure. At wave-exposed locations, the mussel covered up to 90% of the primary substratum, whereas in semi-exposed situations it was never abundant. As the cover of *M. galloprovincialis* increased, the abundance and size of *S. argenvillei* on rock declined and it became confined to patches within a matrix of mussel bed. Both species were absent from sheltered shores and diminished where wave action was extreme. Comparisons with previous surveys indicated that exposed sites now largely covered by the alien mussel were once dominated by dense populations of the limpet. Therefore, the results of this survey provide circumstantial correlative evidence of a competitive interaction between *M. galloprovincialis* and *S. argenvillei,* and suggest that wave action mediates the strength of this interaction. The presence of mussel beds provides a novel settlement and living substratum for recruits and juveniles of *S. argenvillei*, albeit at much lower densities than in limpet patches. Adult limpets were virtually excluded from the mussel beds owing to their large size, which indicates the unsuitability of this habitat as a replacement substratum after competitive exclusion from primary rock space.

Key words: alien invasive, limpet, mussel, spatial competition, wave action

Throughout the world, mussels of the genus *Mytilus* are highly successful competitors for primary space on rocky intertidal shores (Paine 1974, Paine and Levin 1981, Suchanek 1985, Seed and Suchanek 1992, Petraitis 1995). *Mytilus* spp. are widely distributed in the cooler waters of both northern and southern hemispheres (Gosling 1992), but are not native to southern African shores. In South Africa, the dominant indigenous mussels on rocky shores are the mytilids *Aulacomya ater* and *Choromytilus meridionalis*, which inhabit the cool West Coast, and *Perna perna* from the warmer South and East coasts (van Erkom Schurink and Griffiths 1990). The West Coast is further characterized by high densities and biomasses of limpets (Stephenson 1939, Bustamante *et al.* 1995). On moderately exposed to exposed shores, bordered by subtidal kelp beds, the presence of a conspicuous low-shore band (1–3 m wide) of densely packed limpets is a striking feature. This band is called the Argenvillei Zone (Stephenson 1939), after the most dominant component species *Scutellastra argenvillei* (Krauss). In this zone, *S. argenvillei* is able to achieve average densities of up to 200 m^{-2}. Coupled with its maximum size of nearly 100 mm shell length, this results in higher biomasses per unit area than those reported for

any other intertidal invertebrate grazer worldwide (Bustamante *et al.* 1995). The limpet can maintain such high biomasses because of a subsidy of food from the subtidal. The upper limits of subtidal kelp forests extend up to the low-water mark where the fronds of the kelps are accessible to the limpet. When it reaches 40-mm shell length it becomes capable of trapping these kelp fronds, and this subtidal food supply is a vital component of the adult limpets' food resource, >50% of their gut contents comprising kelp (Bustamante *et al.* 1995).

Invasion of the South African west coast by the Mediterranean mussel *Mytilus galloprovincialis* (Lamarck) has, however, dramatically changed and modified rocky coasts in many ways (Griffiths *et al.* 1992, Hockey and van Erkom Schurink 1992). Compared with the indigenous mussels, *M. galloprovincialis* has a fast growth rate, high fecundity and high tolerance to desiccation – all traits making it an aggressive invasive species (van Erkom Schurink and Griffiths 1991, 1992, 1993, Hockey and van Erkom Schurink 1992). Since its arrival in southern Africa in the 1970s (Grant *et al.* 1984, Grant and Cherry 1985), it has become an established and thriving invader and has largely displaced the indigenous mussels *A. ater* and

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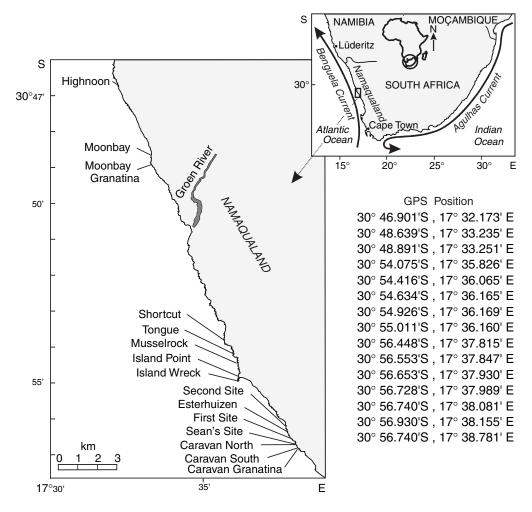
Fig. 1: Map of the study region showing the 15 sites. GPS positions are given in sequence from north to south

C. meridionalis. The appearance of *M. galloprovincialis* has greatly increased the standing stock of mussels and it now constitutes around 74% of intertidal mussel biomass (Griffiths *et al.* 1992). As a competitor for primary rock space, *M. galloprovincialis* is superior to adults of the midshore limpet *Scutellastra granularis*, but it does serve as a good settlement and recruitment ground for that limpet (Hockey and van Erkom Schurink 1992).

Observations suggest that *M. galloprovincialis* also competes for primary space with the limpet *S. ar-* *genvillei* in the Argenvillei Zone (Eekhout *et al.* 1992). The intensity of competition, however, seems to vary spatially as a function of wave exposure. Several studies have shown that the intensity of biological interactions can differ along physical gradients (Dayton 1975, Santelices *et al.* 1980, Race 1982, Griffiths and Hockey 1987, Safriel and Sasson-Frostig 1988, Navarette and Menge 1996, Vallarino and Elias 1997, Dudgeon *et al.* 1999). The environmental stress model developed by Menge and Sutherland (1987) predicts that, in highly stressful environments

(such as those with high wave impact or situated high on the shore), both mobile and sessile organisms are regulated mainly by the direct effects of stress. With decreasing stress levels, first competition becomes important and then, in more benign environments, predation becomes the dominant structuring process. A number of studies have further shown that, although inferior competitors may be excluded from the primary space by competitively superior mussels, they can thrive on the secondary substratum provided by the mussel bed (Lee and Ambrose 1989, Hockey and van Erkom Schurink 1992, Lohse 1993a, b).

Preliminary observations on the South African west coast led to the formulation of the hypotheses that (1) the alien mussel *M. galloprovincialis* and the indigenous limpet *S. argenvillei* compete for space in the Argenvillei Zone, but that (2) this competition is moderated by wave action. At moderate wave exposure *S. argenvillei* is abundant, but with increasing wave force the mussel appears to dominate the low intertidal and outcompete the limpets for primary space. It was further hypothesized that (3) the mussel bed cannot serve as a suitable alternative habitat for adult *S. argenvillei* owing to the large size of the limpet.

The aim of this study was to use a comparative approach to determine the patterns of distribution, abundance and biomass of *S. argenvillei* and *M. galloprovincialis* and the influence of wave force on these patterns. For this purpose, a once-off survey was made of several sites along the coast of Namaqualand on the west coast of South Africa; wave exposures were measured at each site. The stability of the observed patterns over time is described in Steffani and Branch (2003).

MATERIAL AND METHODS

Study sites

The survey was conducted between October 1996 and April 1997 at 15 sites spread along a 25-km long stretch of coastline lying north and south of the Groen River Estuary in Namaqualand, and covering a range of wave-exposure regimes from very sheltered to extremely exposed (Fig. 1). The estuary is usually closed off from the sea by a sandbank, and only breaks through during years with very high rainfall (about every 10 years). The study sites included two types of rocky shores: (1) boulder beaches (Caravan Granatina, Moonbay Granatina), which were sheltered from direct wave action, accumulated large amounts of drift kelp, and were characterized by large stable boulders that

were firmly anchored to the ground and therefore constituting a stable substratum equivalent to that on rocky platforms; (2) gently sloping continuous rocky outcrops with variable exposure to wave action (all other sites).

Maximum wave force

Intertidal wave forces at the sites were measured using a maximum wave-force dynamometer. A description of the device and the calculations involved is detailed in Palumbi (1984). On six different occasions, spanning two years, 10 devices were simultaneously mounted to the rock on the low shore at each site, left for 24 h (two full tidal cycles) and then retrieved. Each device provided a single measurement of maximum wave force during the two tidal cycles, which was expressed in $N\ m^{-2}$.

Transects

At each site a 12×1-m transect was laid down parallel to and low on the shoreline – within the zone normally occupied by *S. argenvillei*. Because fronds of live kelp are an important food source for *S. argenvillei*, their availability in the transect was recorded at each site as being either present or absent. Each transect was divided into contiguous squares of 1×1 m and each square was photographed using a 1×1 m quadrat as a scale. The photographs were then electronically scanned. Areas of rock inhabited by *S. argenvillei* and surrounded on all sides by mussels or other sessile organisms were defined as "limpet patches". By employing the software programme IMAGE (NIH IMAGE version 1.62), the area covered by sessile organisms, the dimensions of the limpet patches, the amount of rock occupied by *S. argenvillei* within the limpet patches, and the amount of bare rock outside the patches could be determined from the scanned images. If limpet patches included encrusting corallines and/or *Ralfsia verrucosa*, their coverage was incorporated in the patch dimensions because the limpets occur on and are associated with these algae (Branch 1971, Eekhout *et al.* 1992, Bustamante *et al.* 1995, pers. obs.). Sessile organisms were classed as mussels, algae (foliose, upright corallines or encrusting algae), the sessile polychaete *Gunnarea capensis* or the sea anemone *Aulactinia* (=*Bunodactis*) *reynaudi*.

In the field, all *S. argenvillei* found inside the transect and living on rock were counted and measured to the nearest 0.5 mm using a vernier caliper. The limpets were classed as adults (>45 mm shell length, the size

at which sexual maturity is reached according to Eekhout *et al.* 1992), juveniles (10–45 mm) or recruits (<10 mm). The data for each limpet patch were kept separate. In naturally dense limpet stands, small *S. argenvillei* typically occur on the shells of larger conspecifics (Branch 1971, Bosman *et al.* 1990, Day *et al.* 2000). The measurements of these limpets were pooled with those of adult limpets on the rock surface (and are hereafter collectively referred to as "limpets on rock"). Within each transect 12 × 1 m, four 50 × 50 cm quadrats were positioned randomly on the mussel beds, the degree of mussel cover was recorded and all *S. argenvillei* on mussel shells ("limpets on mussels") falling within the quadrats were counted and measured. Only animals >2 mm were included in the measurements, because individuals smaller than that could not be identified.

Limpet biomass was calculated using a regression for wet somatic mass (total flesh mass excluding gonad mass) to shell length according to Bosman *et al.* (1990):

$$\log(\text{somatic mass}) = 3.36 \log(\text{length}) - 4.999 (r^2 = 0.98, \ df = 121, \ p < 0.001)\ .$$

Wet mass was converted to dry mass by subtracting the water content of the somatic mass (75.38 ± 2.24% *SD*, *n* = 136).

Regressions of flesh dry mass to shell length of *M. galloprovincialis* were determined in January 1999 for seven of the study sites, representatively spread across the range of wave exposures (Table I) and covering animals from 10-mm shell length and larger. The gonad material could not be dissected cleanly from the flesh, so it is therefore included in the dry flesh mass. For the remaining sites, the regression from the measured site most similar in wave action was applied.

In April 1997, five 10 × 10 cm mussel samples were collected at each site. All *M. galloprovincialis* within the samples were counted and the shell lengths measured to the nearest 1.0 mm. Using the percentage cover of mussels derived from each transect, the mean densities and size frequencies of the samples, and the calculated dry flesh mass/shell length regressions, the total dry flesh biomass (expressed per m^2 of shore) of *M. galloprovincialis* could be estimated for the entire transect at each site. The conversion between mussel percentage cover (*x*) and adult mussel density (*y*, number per m^2 of shore) was

$$y = 43.712 x^{1.031} \ (r^2 = 0.86, \ df = 11, \ p < 0.001)\ .$$

The calculation was based on adult mussels (de-

Table I: The flesh dry mass/shell length equations for *M. galloprovincialis* at the seven sites where measurements were made (underlined) and the eight remaining sites (not underlined). Log(flesh dry mass, g) = *a* + *b* × log(shell length, mm); *a* = Y intercept, *b* = slope, *r^2* = coefficient of determination; *n* = 55 and *p* < 0.001 in all cases

Sites	*a*	*b*	*r^2*
*Caravan Granatina, Moonbay Granatina	–	–	–
Caravan North	-4.378	2.632	0.95
Caravan South, Highnoon, Moonbay	-4.250	2.215	0.95
Sean's Site	-4.829	2.582	0.96
Musselrock, Island Wreck	-4.961	2.832	0.96
First Site, Island Point	-4.641	2.537	0.91
Second Site, Esterhuizen	-5.229	2.787	0.94
Shortcut, Tongue	-5.524	3.052	0.86

* No mussels found

fined as animals >10 mm); mussel recruits (≤ 10 mm) were excluded because their biomass is a small fraction of the total biomass (<1%).

Statistical analyses

Wave-force measurements were conducted on randomly chosen dates, which resulted in a two-way mixed model design, with dates as a random effect and sites as a fixed effect. This design was analysed by variance components estimation. The ANOVA-based Expected Mean Squares Method provided an integrative approach for the estimation of variance components (Variance Components Module, STATISTICA 5.5 for Windows, StatSoft, Inc. 2000). The significances of the variance components and of the fixed effect (site) were tested using Satterthwaite's method of denominator synthesis for constructing error terms (Satterthwaite 1946). This method can result in fractional degrees of freedom. Usually, some of the wave-force dynamometers were lost during each measurement period, resulting in an unbalanced design, which makes estimates of the mean squares sensitive to heterogeneous variances. However, the implementation of Satterthwaite's approximation by STATISTICA addresses the problem of heterogeneous variances. Differences among sites were further analysed by multiple comparisons Tukey HSD tests for unequal sample sizes (Zar 1999).

Data from the transects were examined with least-squares-fit regression analyses with linear, polynomial or power curve equations. In all regressions, mean wave-force data were used, and when limpet densities or biomasses were expressed per m^2 of habitat, their mean values were used as well. When relationships
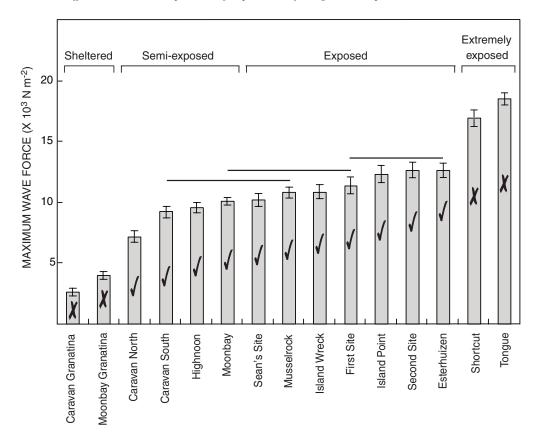
Fig. 2: Mean (± *SE*, *n* = 6) maximum wave force ($\times 10^3$ N m^{-2}) at the 15 study sites. Kelp accessibility at the sites is indicated by presence (✓) or absence (✗). Solid lines above the bar columns connect sites that were not significanty different from each other (Tukey tests, *p* > 0.05)

were non-linear and included zero values, the data were $y + 1$ transformed. The regression analyses were restricted to the range of wave action in which one or both species occurred. The significance level for all analyses was $\alpha = 0.05$.

Definition of limpet density

Limpet densities can be expressed in two different ways: per m^2 of utilized habitat (either rock or mussel bed habitat) or per m^2 of total shoreline, including habitats that are not occupied by limpets. The latter expression can also be calculated separately for limpets occurring on rock space or on the mussel bed. Consequently, the densities of limpets were expressed either

per m^2 of total shoreline ("on rock per m^2 of shore" or "on mussel bed per m^2 of shore") or per m^2 of habitat ("per m^2 of limpet patch" or "per m^2 of mussel bed").

RESULTS

Maximum wave force

The maximum wave forces at the 15 sites investigated were measured simultaneously on six different dates (Fig. 2). Differences in weather conditions among dates might have influenced their comparability. However, the components of variance in the de-
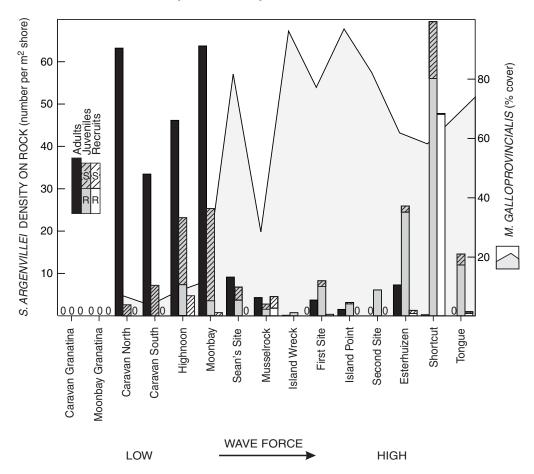
Fig. 3: Densities of adults, juveniles and recruits of *S. argenvillei* on rock and percentage cover of *M. galloprovincialis*. Densities of limpets on shells of larger conspecifics (S) and on rock (R) are indicated. Zeros indicate an absence of any particular size-class. The line shows *M. galloprovincialis* cover

pendent variable (wave force) attributable to the interaction between the factors (site × date) and to the random factor (date) were very small (0.054252 and 0.000377 respectively) and had no significant effects ($F_{70,496} = 1.153$, $p = 0.199$; $F_{5,65.40} = 1.014$, $p = 0.417$ respectively). On the other hand, the fixed factor (site), had a significant effect, showing differences among sites ($F_{14,62.88} = 247.086$, $p < 0.001$). The sites at either end of the spectrum differed significantly from those in the middle of the scale ($p < 0.05$). However, sites at both ends of the wave-force scale also differed significantly from each other ($p < 0.05$). Sites in the middle of the spectrum were most often not signifi-

cantly different from each other ($p > 0.05$), but showed a slow, gradual gradient in wave force (Fig. 2). Because the component of variance attributable to the different dates was not significant (see above), statistical analyses were conducted on the means of the maximum wave-force measurements averaged over the six dates per site. Four grades of wave action were selected: (a) sheltered shores, below 7×10^3 N m^{-2}; (b) semi-exposed shores, $7–10 \times 10^3$ N m^{-2}, (c) exposed shores, $>10–15 \times 10^3$ N m^{-2}; and (d) extremely exposed shores, $>15 \times 10^3$ N m^{-2}.

Fronds of live kelp were accessible to *S. argenvillei* at all the sites, except at the two least exposed
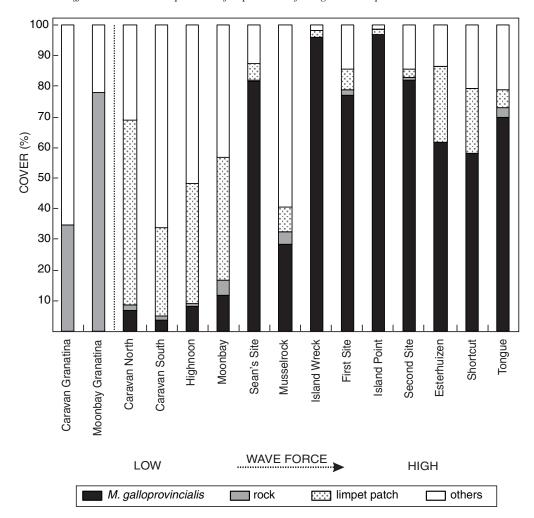
Fig. 4: Percentage cover of *M. galloprovincialis*, rock, limpet patches and other sessile organisms (including *Gunnarea capensis*, foliose algae, coralline turfs, encrusting algae, the sea anemone *Aulactinia* (=*Bunodactis*) *reynaudi* and, for the sites Caravan Granatina and Moonbay Granatina, rock occupied by *C. granatina*); the dotted line separates the sites at which *S. argenvillei* and *M. galloprovincialis* were absent

sites (Caravan Granatina and Moonbay Granatina), and the two most exposed sites (Shortcut and Tongue, Fig. 2).

Cover of mussels and density of limpets

S. argenvillei or *M. galloprovincialis* were not found at the two most sheltered sites (Fig. 3). These sites were dominated by the limpet *Cymbula granatina*, which favours very sheltered sites (Bustamante *et al.* 1995). This suggests that the distribution range of *S. argenvillei* and *M. galloprovincialis* commences above a certain threshold of wave exposure. Of the sites surveyed in this study, the least exposed site at which they were found was Caravan North, with wave forces of 7.2×10^3 N m^{-2}, but limpets were extremely abundant there (Fig. 3). The focus of this work is on the inter-

action between *S. argenvillei* and *M. galloprovin-cialis* over the range of wave actions within which they are capable of living. Therefore, only the data for sites at which either species was present are included in the statistical analyses that follow, although all sites are represented graphically.

At all sites at which *S. argenvillei* was present, it occurred on both the primary substratum of rock and the secondary substratum provided by mussel beds. The densities of *S. argenvillei* found on rock were calculated for each entire transect and expressed per m^2 of shore. Adult limpets on rock were most dense on semi-exposed shores ($7-10 \times 10^3$ N m^{-2}), where mussel cover was low. However, with increasing wave force, mussel cover increased and adult limpet density on rocks decreased considerably (Fig. 3). The transition from a limpet-dominated to a chiefly mussel-dominated shore was at exposed sites with wave forces of approximately 10×10^3 N m^{-2} (see Fig. 2 for wave forces at the sites). Mussel cover peaked at exposed sites but decreased slightly with extreme wave forces over 15×10^3 N m^{-2}, resulting in a significant polynomial relationship between mussel cover (y) and wave force (x):

$$y = -1.60x^2 + 47.76x - 273.16 \ (r^2 = 0.475, df = 11, p < 0.01) \ .$$

Densities of adult *S. argenvillei* (y) declined with increasing wave force (x, at least at wave forces $>7 \times 10^3$ N m^{-2}):

$$y-1 = 1.6 \times 10^3 x^{-5.10} \ (r^2 = 0.620, df = 11, p < 0.002) \ .$$

Because adults of *S. argenvillei* (y) and *M. galloprovincialis* (z) responded oppositely to wave action, there was a negative relationship between the two species:

$$y = -0.574z + 48.038 \ (r^2 = 0.688, df = 11, p < 0.001) \ .$$

Juvenile limpets, and to a lesser extent recruits, were present at semi-exposed sites at intermediate densities, mainly on shells of larger conspecifics, but their densities reduced with increasing wave forces and concomitantly higher mussel cover (Fig. 3). However, at very exposed sites, where the mussel cover diminished, the densities of limpet juveniles and recruits were highest. Adult limpets were absent at those sites and most of the juveniles and recruits were on the rock, although some were on the shells of larger juveniles (35–40 mm). There was no significant relationship between densities of either juveniles or recruits of *S. argenvillei* and wave action ($r^2 = 0.266, df = 11, p > 0.05$ and $r^2 = 0.248, df = 11, p > 0.05$ respectively).

The area in the transects occupied by limpet patches was 30–60% at semi-exposed sites (Fig. 4). This was reduced to <8% at the sites with the greatest mussel cover, but increased again slightly at very exposed sites, concomitant with a decrease in mussel cover. Within the limpet patches, up to 38% of the space was occupied by *S. argenvillei*. The amount of bare rock outside the patches was always <5%, except at the two most sheltered sites where both *S. argenvillei* and *M. galloprovincialis* were absent (Fig. 4). At all other sites the rest of the shore was covered by mussels and, at moderately exposed sites, with a substantial proportion of other sessile organisms (Fig. 4) including foliose algae (mainly *Champia lumbricalis*), kelps (*Ecklonia maxima, Laminaria pallida*), the sea anemone *Aulactinia* (=*Bunodactis*) *reynaudi* and the sessile polychaete *G. capensis*.

S. argenvillei was also present on the mussel beds and its densities there were calculated for each entire transect (Fig. 5). Adult *S. argenvillei* were absent from mussel beds at all sites. The densities of juveniles and recruits increased at more strongly exposed sites as a consequence of the greater mussel cover there. Recruits were particularly abundant at the most exposed site. *S. argenvillei* was not found on the shells of conspecifics on the mussel beds. The densities of juvenile (y) and recruit (z) *S. argenvillei* on mussel bed (per m^2 of shore) were positively related to wave exposure (x):

$$y = 3.684x - 26.455 \ (r^2 = 0.484, df = 11, p < 0.01)$$
$$z = 5.4 \times 10^{-6} \ x^{5.48} \ (r^2 = 0.608, df = 11, p < 0.002) \ .$$

Limpet size structure

The size structures of limpets on rock shifted from being dominated by large individuals at moderate wave forces to exclusively small individuals at higher wave forces (Fig. 6). In contrast, the size compositions of *S. argenvillei* on mussel bed consisted of relatively small limpets at all wave exposures, comparable with those found on rock at very high wave forces. The proportion of limpets on the shells of conspecifics tended to be greatest at intermediate levels of wave action where limpet densities on rock where high, and were largely confined to animals <40 mm in length.

Density of limpets

Increases in the cover of mussels reduced primary space for *S. argenvillei* and confined adults to limpet patches within the mussel beds. Within these patches,
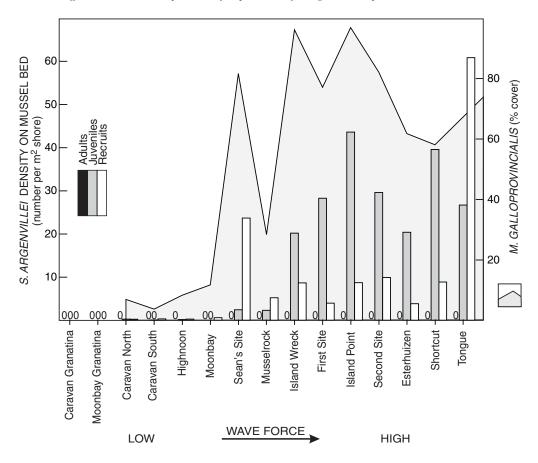
Fig. 5: Densities of adults, juveniles and recruits of *S. argenvillei* on mussel beds and percentage cover of *M. galloprovincialis*. Zeros indicate an absence of *S. argenvillei* of any particular size-class and the line shows *M. galloprovincialis* cover. Note that adult *S. argenvillei* were absent

limpet density (expressed as numbers per m² of limpet patch) reached very high values, and increased significantly with intensifying wave force (Fig. 7a). The average shell length, however, decreased as wave force rose (Fig. 7a). Splitting the limpet populations into size groups demonstrated that adult and juvenile densities responded in opposite ways to wave force (Fig. 7c). Adult density decreased, whereas juvenile density increased significantly with rising wave exposure. No significant trend was detected for recruits ($r^2 = 0.272$, $df = 11$, $p > 0.05$).

Results were similar for limpets on mussel beds, depicted as density per m² of mussel bed. Overall densities also increased with increasing wave force, although they were in general an order of magnitude lower than in limpet patches. However, the average size of limpets on mussels showed no relationship with wave force, a reflection of the absence of adult limpets from the mussel beds (Fig. 7b). Averaged over all sites, the mean shell length of limpets on mussel bed was small (16.8 ± 6.3 mm *SD*). Division of the limpets into juveniles and recruits revealed a significant increase in juvenile densities with wave force (Fig. 7d), but no relationship was found for recruits ($r^2 = 0.036$, $df = 11$, $p > 0.5$). Adults were absent from the mussel bed.
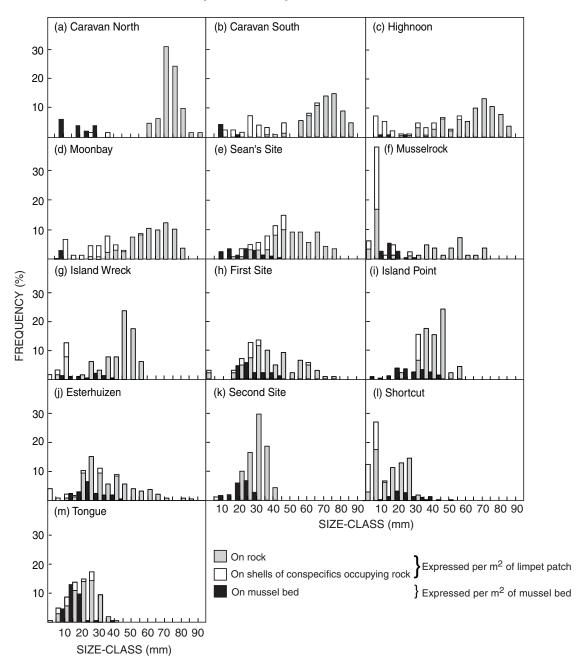
Fig. 6: Size structure of *S. argenvillei* on rock and on mussel bed at the study sites at which limpets were present. Sites are arranged from low to high wave forces in rows from left to right (sequentially a–m)

(a) Length: $y = -4.6404x + 95.512$
($r^2 = 0.688$, $df = 11$, $p < 0.001$)
Density: $y = 76.289x - 564.2$
($r^2 = 0.586$, $df = 11$, $p < 0.005$)

■ Density
△ Shell length

(b) Density: $y = 10.369x - 83.012$
($r^2 = 0.858$, $df = 11$, $p < 0.001$)

(c) Adults: $y = -11.677x + 203.78$
($r^2 = 0.413$, $df = 11$, $p < 0.02$)
Juveniles: $y = 61.448x - 523.53$
($r^2 = 0.821$, $df = 11$, $p < 0.001$)

■ Adults
◇ Juveniles
○ Recruits

(d) Juveniles: $y = 9.991x - 84.561$
($r^2 = 0.890$, $df = 11$, $p < 0.001$)

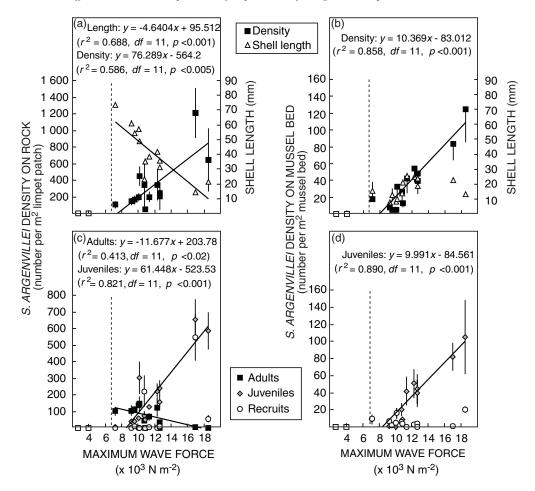MAXIMUM WAVE FORCE
(x 10^3 N m^{-2})

Fig. 7: Effects of wave force on density and mean shell length of all *S. argenvillei* in (a) limpet patches within the mussel bed and (b) on mussel beds. In (c) and (d) the data for densities are treated separately for adults, juveniles and recruits in limpet patches and on mussel beds respectively. Data are means ± *SE*. The dotted line and the two empty squares indicate the wave force below which no *S. argenvillei* were found. Statistical analyses were restricted to sites with higher wave forces. Note the differences in the scales of the ordinate. Regressions are provided only for relationships that were significant ($p < 0.05$)

Biomass of limpets and mussels

In terms of biomass, the decrease in density of adult *S. argenvillei* on rock with rising wave force and increasing mussel cover, coupled with the strong decrease in size of rock-dwelling limpets (Fig. 7a, c), resulted in a significant reduction of biomass of limpets on rock per m^2 of limpet patch with increasing wave exposure (Fig. 8a). The biomass dropped from around 500 g m^{-2} of limpet patch at sites with wave forces between 7 and 10×10^3 N m^{-2} to around 200 g m^{-2} at exposures $>11 \times 10^3$ N m^{-2} and to <100 g m^{-2} at wave forces over 15×10^3 N m^{-2}. Contrary to this, the biomass of limpets on mussel beds increased with wave force (Fig. 8b). This increase reflects the fact that limpet densities on mussel beds increased and their sizes remained constant (Fig. 7b). However, at moderate wave forces ($7-10 \times 10^3$ N m^{-2}), the biomass supported by
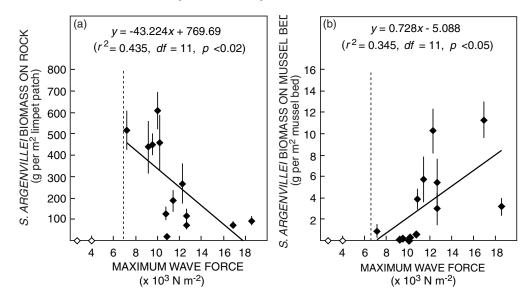
Fig. 8: *S. argenvillei* dry somatic biomass per m² of substratum in (a) limpet patches and (b) on mussel bed in relation to wave force. Data points are means ± *SE*. The dotted line and the two empty diamonds indicate the wave force below which no *S. argenvillei* were found. Statistical analyses were restricted to sites with higher wave forces. Note the different scales of the ordinate

1 m² of primary rock surface was approximately 230 times greater than that on 1 m² of mussel bed. Even at very high wave forces, there was a 19-fold difference.

The biomass of *M. galloprovincialis* per m² of shore peaked at exposed wave forces and was reduced at extremely exposed sites with wave forces >15 × 10³ N m⁻², resulting in a significant polynomial relationship between mussel biomass (y) and wave force (x):

$$y = -26.21x^2 + 731.61x - 4081.9 \ (r^2 = 0.368, df = 11, p < 0.05) \ .$$

However, the mussel biomass per m² of mussel bed was unrelated to wave force ($r^2 = 0.003$, $df = 11$, $p > 0.5$).

Mussel shell length

The average shell length of *M. galloprovincialis* ranged from 26.3 ± 1.1 mm *SD* to 48.2 ± 4.0 mm *SD*. Only animals >10 mm were included in the calculations of mean shell length because they are the major contributors to the cover of mussels on the shore. The shell length of *M. galloprovincialis* did not vary pre-

dictably with wave force ($r^2 = 0.062$, $df = 11$, $p > 0.2$). Furthermore, the densities and the average shell lengths of *S. argenvillei* living on mussel beds were unrelated to the mean length of *M. galloprovincialis* ($r^2 = 0.045$, $df = 11$, $p > 0.5$ and $r^2 = 0.033$, $df = 11$, $p > 0.5$ respectively).

DISCUSSION

Wave force

An important element structuring communities of rocky coasts is the degree of exposure to wave action. Denny (1987, 1988, 1995) and Denny and Shibata (1989) stressed the significance of hydrodynamic forces exerted on organisms in wave-swept environments, their role in supplying resources (e.g. food, larvae), and the importance of measuring these forces. The device chosen for measuring wave force in this study generates only one datum per deployment, but is easily constructed and inexpensive, and can objectively measure wave forces at a substantial number of sites. The results show that the sites at both ends

of the scale were significantly different from sites in the middle of the scale, whereas the majority of sites spanned a continuum from moderately exposed to exposed sites, with only gradual increases in wave force. This highlights the difficulty of reliably ranking sites based on subjective evaluation.

Interaction between the alien mussel and the native limpet

When resources are in short supply, the stage is set for interspecific (and intraspecific) competition. Because *M. galloprovincialis* and *S. argenvillei* have different feeding guilds, competition will be for primary space.

The survey showed that both *M. galloprovincialis* and *S. argenvillei* were absent from very sheltered sites. At the more exposed sites, the mussel invaded the Argenvillei Zone and co-occurred with *S. argenvillei*. However, the relative abundance and biomass of the mussel and the limpet at these sites varied markedly along the gradient of wave energy. At semi-exposed sites ($7–10 \times 10^3$ N m^{-2}), mussel cover was low and adults of *S. argenvillei* were abundant on rock, where they attained large sizes. At exposed sites ($>10–15 \times 10^3$ N m^{-2}), mussel cover increased considerably and the density of adult *S. argenvillei* on rock dropped sharply. Bare rock was always in short supply ($<5\%$), indicating that this resource was limiting.

Studies in South Africa and elsewhere have shown that *M. galloprovincialis* occurs on both relatively sheltered and exposed shores (Hosomi 1980, Dalla Via *et al.* 1987, Cáceres-Martínez *et al.* 1994, Raubenheimer and Cook 1990, Hockey and van Erkom Schurink 1992), but is more abundant at semi-exposed and exposed sites (Willis and Skibinski 1992, Cáceres-Martínez *et al.* 1993, van Erkom Schurink and Griffiths 1993, Bustamante and Branch 1996a, Bustamante *et al.* 1997). The present study supports this observation; *M. galloprovincialis* was absent from the two very sheltered sites and present at all other sites, from semi-exposed to extremely exposed, but with highest cover at exposed sites. Several reasons could explain this phenomenon, including faster growth, higher settlement rate and less predation at sites with greater wave action. Greater delivery of food and better feeding opportunities as a result of high water flow and more "splash" are believed to be responsible for the better growth performances and enhanced nutritional status of filter-feeders at exposed sites (Menge 1978, Denny 1988, Bertness *et al.* 1991, van Erkom Schurink and Griffiths 1993, Dahlhoff and Menge 1996). On the South African west coast, particulate organic matter (65% of which is kelp-derived detritus) is high all year round, particularly on exposed shores, and water turnover is seven times greater there than on sheltered shores. This could explain the greater biomass of filter-feeders found on exposed shores (Bustamante and Branch 1996b). Higher settlement rates at exposed sites are at least partly attributable to an increase in larval supply with increasing water flux (Cáceres-Martínez *et al.* 1993, Hunt and Scheibling 1996).

It has also been suggested that predation is likely to be less intense at exposed sites, because high wave energy restricts foraging time and efficiency (Menge 1978, Menge and Sutherland 1987, Brown and Quinn 1988, Etter 1996). However, a recent study near the Groen River found no reduction in the predation intensity of the whelk *Nucella cingulatus* on *M. galloprovincialis* at exposed compared with sheltered shores (Griffin 2000). Nevertheless, apart from whelks, *M. galloprovincialis* is preyed upon by African black oystercatchers *Haematopus moquini* and Cape gulls *Larus dominicanus* (Hockey and van Erkom Schurink 1992), which may be hindered on wave-exposed shores. In the case of the black mussel *Choromytilus meridionalis*, competition for space is of primary importance in populations where settlement is high and growth is fast. In slow-growing populations, such as those higher on the shore or on sheltered shores, competition is less important and predation becomes the major density-regulating factor (Griffiths and Hockey 1987). It is possible that this principle also applies to *M. galloprovincialis*, further suggesting that predation is relatively unimportant at exposed sites but important at sheltered sites, where growth may be slower. All these factors collectively suggest that high wave action favours *M. galloprovincialis*. On the other hand, extremely high wave action may be detrimental, potentially hindering feeding, increasing sand scour, physically damaging or detaching mussels, or causing the diversion of energy to attachment devices or shell strength rather than growth and reproduction (Seed and Suchanek 1992).

In contrast, *S. argenvillei* depends to a great extent on subtidal kelp as a food resource and its density correlates with that of accessible nearby live kelp (Bustamante *et al.* 1995). Sheltered shores are usually devoid of live kelp and this species was rarely found there. Similarly, adults, which feed on kelp, were virtually absent from the two most exposed sites, where kelp was also absent.

Only a few predators have been described for *S. argenvillei*, the African black oystercatcher (Hockey and Branch 1984, Hockey and Underhill 1984) and the giant clingfish *Chorisochismus dentex*, a specialist limpet-eater, but which rarely consumes *S. argenvillei* (Lechanteur and Prochazka 2001). The modal

size of the oystercatcher's prey is 30–40 mm (Hockey and Underhill 1984) and the clingfish seldom attacks limpets >45 mm in length (Bustamante *et al.* 1995, Lechanteur and Prochazka 2001). Predation is therefore probably not a major controlling factor for adult *S. argenvillei*. Dislodgement by hydrodynamic forces is unlikely to be a threat because the tenacity of *S. argenvillei* is among the highest recorded for limpets (Branch and Marsh 1978). Limpets (including *S. argenvillei*) sometimes suffer mass mortalities from episodic extreme events such as river floods (Branch *et al.* 1990) and red tides that lead to anoxia (Matthews and Pitcher 1996), but no such catastrophic losses of limpets have been recorded in the study area.

Overall, the distribution of high-density populations of *S. argenvillei* seems to be most likely dependent on the availability of primary space and the accessibility of live kelp fronds (Bustamante *et al.* 1995), and the limpet is most abundant at sites bordered by kelp forests, which also buffer the shore from waves. The range of *S. argenvillei* therefore encompasses sites with accessible kelp: in this study, all sites apart from the two most sheltered (Caravan Granatina and Moonbay Granatina) and the two most exposed (Shortcut and Tongue).

However, the present results showed that adult limpet density decreased with increasing wave force, but juvenile density increased. Concomitantly, mean limpet size decreased sharply at higher wave forces. This decline in size, despite the high density of juveniles, resulted in a marked decrease in biomass. These decreases in limpet biomass and adult density were accompanied by an increase in the abundance and biomass of mussels.

Two alternative hypotheses could explain this pattern. First, differences in the relative abundances of the mussels and limpets may be a reflection of the amount of wave energy they experience at different sites. According to this hypothesis, *S. argenvillei* may experience optimal conditions at semi-exposed sites where kelp is readily accessible. With increasing wave force, adult density may decrease despite the presence of kelp, because trapping of kelp becomes increasingly difficult and/or risky. However, environmental conditions may be optimal for *M. galloprovincialis* at exposed sites (e.g. high food and/or larval supply), whereas it may be restricted at either end of the wave-force range. This hypothesis would mean that *M. galloprovincialis* and *S. argenvillei* have virtually no overlapping habitat requirements and the pattern observed for each species would therefore also occur in the absence of the other species.

Second, the observed pattern may involve competitive interaction between the two species. Sites with moderate degrees of exposure apparently favour *S.*

argenvillei, and there the limpet may be capable of preventing *M. galloprovincialis* from dominating the shore. Lower supplies of mussel larvae might enable the limpets to bulldoze away newly settled mussels. Slower rates of growth of mussels might also slow the lateral spread of mussel beds. However, at higher levels of wave force, the environment may still be favourable for limpets, but provide optimal conditions for mussels. This may in turn give mussels a competitive advantage over *S. argenvillei*, so confining limpets to small gaps within the mussel bed and reducing the density of adult limpets. Comparison with previous work suggests that exposed sites currently almost completely covered by mussels were previously dominated by *S. argenvillei*, which supports the hypothesis of competitive displacement. For example, Bustamante *et al.* (1995), working in the late 1980s and early 1990s, described well-established, almost continuous Argenvillei Zones with very dense stands of *S. argenvillei* (averaging >200 individuals m^{-2}) on semi-exposed to exposed shores in Namaqualand. More specifically, surveys conducted by GMB (unpublished data) at Sean's Site in 1987, about 10–15 years after the invasion of South African shores by *M. galloprovincialis*, revealed a conspicuous Argenvillei Zone with high cover of *S. argenvillei* (mean percentage cover 42.2 ± 22.7% *SD*) and moderate cover of *M. galloprovincialis* (34.5 ± 21.2%). In 1996, during the present study, percentage cover for the mussel had risen to 81.5% in the Argenvillei Zone, whereas the *S. argenvillei* population on rock had been reduced to small patches within the mussel bed, with a cover of 5.5% and densities of 13 individuals per m^2 of shore (see Fig. 3).

At extremely exposed sites, the mussel cover was slightly less than at sites with exposed wave forces, increasing the rock space available for limpets. Although density of *S. argenvillei* increased at these sites, the population consisted almost entirely of juveniles and recruits. Adults were absent or very rare, probably attributable to the lack of accessible kelp; limpets >40 mm depend on kelp as their major food source (Bustamante *et al.* 1995). The biogeographical range of *S. argenvillei* only slightly exceeds the distributional limits of kelp, and at sites without kelp the density, biomass and sizes of limpets are considerably reduced (Bustamante *et al.* 1995). It seems that, although there is high recruitment of *S. argenvillei* even where wave force is very high, these recruits do not grow to adulthood. *S. argenvillei* was not found at the most sheltered sites. The absence of adults may be attributable to the absence of kelp, but this cannot explain the absence of juveniles and recruits because they do not feed on kelp. Possibly the larvae of *S. argenvillei* do not settle at sheltered sites because of the low wave

action (larval choice), or perhaps they do settle but are eliminated by *C. granatina*, which reaches high densities there. These explanations are, however, speculative and need further study.

Several studies have reported modifications of interspecific competition along gradients of physical factors. The Eastern Pacific alga *Hedophyllum sessile* experiences its physiological optimum at sites subject to high degrees of wave action. Nevertheless, it is the competitive dominant only in moderately exposed areas, and it loses its dominance at exposed sites to the competitively superior kelp *Lessoniopsis littoralis* (Dayton 1975). In central Chile, the competitive interaction between the brown algae *Lessonia nigrescens* and *Durvillaea antarctica* also depends on the degree of wave impact (Santelices *et al.* 1980). Several other studies on the community structure of marine systems invaded by alien species have shown that differences in tolerances of physical factors may prevent total exclusion of natives by competitively superior invaders (e.g. Race 1982, Brenchley and Carlton 1983, Vallarino and Elias 1997). Safriel and Sasson-Frostig (1988) found that the alien Red Sea mussel *Brachidontes variabilis* competes by interference with the local mytilid *Mytilaster minimus* in the Mediterranean. However, the outcome of competition depended on the degree of wave exposure.

The results here suggest that peak abundances of *M. galloprovincialis* on exposed shores have reduced primary space available for *S. argenvillei*. This poses the question of whether *S. argenvillei* can become established on mussel beds, and the degree to which mussel beds act as a substitute secondary substratum for the limpet if it is displaced from primary rock space.

Mussel bed as a secondary substratum

Studies on competition for space have often focused on the displacement of an inferior competitor from primary space by a superior competitor (Dayton 1971, Paine 1966, 1974, Sousa 1979, Underwood and Denley 1984). However, another type of interspecific "competitive" interaction, termed "substrate displacement" (*sensu* Lee and Ambrose 1989), can take place and is defined as the colonization of secondary space provided by the superior competitor after competitive exclusion from primary space. Lohse (1993a) reported that, on rocky shores dominated by *Mytilus californianus*, virtually all species that can live on rock also live on mussel shells.

The beds of the alien mussel *M. galloprovincialis* serve as a secondary substratum for many rocky shore organisms, including *S. argenvillei*. The density of the limpet on mussel beds (expressed per m² of shore) increased with rising wave force, as a logical consequence of the greater mussel cover at more exposed sites. However, no adult limpets occurred on mussel shells. The average shell length of limpets on mussel beds was consistently low, averaging only 16.8 ± 6.3 mm *SD*. The density of limpets on mussel beds was lower than in limpet patches; their overall average density (per m²) on mussel beds was only 40 ± 34 *SD*, compared to 328 ± 307 *SD* on limpet patch. Comparison of limpet biomasses further illustrates the marked differences between the two habitats. At semi-exposed to exposed sites, the biomass in limpet patches was approximately 230 times greater than on mussel beds. Even at extremely exposed sites, the ratio was 19:1. Clearly, the mussel bed is unfavourable for *S. argenvillei*, particularly in the case of adults.

This contrasts with other studies that have shown that populations of inferior competitors can end up being enhanced as a result of the secondary space provided by a dominant spatial competitor. For example, barnacles that are inferior competitors to *Mytilus californianus* for primary space have higher densities and better survivorship on *M. californianus* shells than on rock (Lee and Ambrose 1989, Lohse 1993b). Many limpet species live on both rock and mussel beds (Lohse 1993a, b, Minchinton and Ross 1999) and often achieve higher densities on the secondary substratum (Lewis and Bowman 1975). For example, *Scutellastra granularis* has higher densities, recruitment and total reproductive output on *M. galloprovincialis* beds than on rock, although it achieves lower maximum sizes and individual reproductive output on mussels (Hockey and van Erkom Schurink 1992). Some of the advantages that mussel beds offer include refuge from competition (Lohse 1993b) and protection from desiccation and wave action (Lewis and Bowman 1975, Hockey and van Erkom Schurink 1992, Seed and Suchanek 1992).

The reason why *S. argenvillei* does not thrive on mussel beds is probably because of its large size (up to 100 mm). This view is borne out by the absence of large individuals on mussel shells. The body size of a species in relation to its host seems to determine whether or not it can utilize secondary space provided by the host. Tokeshi and Romero (1995) found that two small barnacles, *Jehlius cirratus* and *Notochthamalus scabrosus*, are able to live on beds of the mussel *Semimytilus algosus*, although competitively excluded from primary space. However, the larger barnacle *Balanus laevis* rarely occurs on shells of *S. algosus*. Limpet species that have been reported to succeed on bivalve beds are much smaller than their hosts (Lohse 1993b, Minchinton and Ross 1999). Larger species of limpets usually reach smaller maximum sizes when they

occur on mussel beds. For instance, the limpet *Scutellastra aphanes* exists as a small ecomorph living on the mussel *Perna perna* and a larger ecomorph on rock (Robson 1986). Reaching a size of almost 100 mm and becoming sexually mature at 45 mm, *S. argenvillei* is incapable of achieving reproduction on mussel beds. Limpets confined to mussel beds therefore represent sinks to the population.

CONCLUSIONS

Spatial comparisons of populations of *S. argenvillei* and *M. galloprovincialis* among the four different wave actions categorized in the study area are as follows:

(i) On very sheltered shores, *S. argenvillei* was absent, most likely because of the absence of kelp there. *M. galloprovincialis* was also absent, perhaps because supplies of food or larvae were inadequate.

(ii) At semi-exposed sites, *M. galloprovincialis* cover was relatively low, probably as a result of low productivity. On rock, *S. argenvillei* reached high densities, large sizes and biomasses; the equivalent values for limpets on mussels were very low.

(iii) At exposed sites, *M. galloprovincialis* dominated primary space, most likely because of favourable environmental conditions. *S. argenvillei* densities, sizes and biomass decreased on rock. Densities on mussels were higher, but consisted of small individuals with low biomass; adults were absent.

(iv) At extremely exposed sites, *M. galloprovincialis* cover dropped slightly and *S. argenvillei* densities increased, but adult limpets were not found there, despite recruits being abundant. This is probably because the lack of accessible kelp and physical stress made it impossible for adult limpets to survive.

The results of this study are correlative and the patterns observed can be explained either by differences in the optimal conditions required by the mussels and limpets, or as a result of competitive encroachment by the alien mussel. Support for the latter hypothesis is strengthened by comparisons with previous surveys, which showed that exposed sites now largely covered by the alien mussel were once dominated by dense populations of the limpet. Therefore, the results provide the first evidence that, on a broad spatial scale, there is competition between *S. argenvillei* and *M. galloprovincialis*, but it is mediated by the effects of wave exposure. The outcome of competition will be influenced by periodic disturbance and will depend on the

frequency and severity of such events (see Steffani and Branch 2003), the relative rate of recruitment of mussels and the ability of *S. argenvillei* to utilize space created by disturbance.

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