

**TEMPORAL CHANGES IN AN INTERACTION BETWEEN AN INDIGENOUS
LIMPET *SCUTELLAstra ARGENVILLEI* AND AN ALIEN MUSSEL
MYTILUS GALLOPROVINCIALIS: EFFECTS OF WAVE EXPOSURE**

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A previous survey of 15 sites off the Namaqualand coast on the west coast of South Africa provided evidence of a competitive interaction between an alien mussel *Mytilus galloprovincialis* and an indigenous limpet *Scutellastra argenvillei*, and indicated that wave action mediates the strength of this interaction. In this study, the temporal persistence of these patterns was tested by selecting six sites, ranging from sheltered to very exposed, and monitoring them over a two-year period. The patterns remained consistent over time. Both *S. argenvillei* and *M. galloprovincialis* were perpetually absent from the most sheltered site. The limpet consistently dominated rock space at the semi-exposed site where mussel cover was always low. At exposed sites, *M. galloprovincialis* was dominant but its percentage cover varied temporally as a result of wave action, creating free space and allowing temporary expansion of limpet patches. However, with time the mussel recolonized the cleared rock space and repeatedly displaced the limpet from it. This provides additional observational evidence of competition for space between the alien invader and the indigenous limpet. It is concluded that *S. argenvillei* has a spatial refuge from *M. galloprovincialis* in areas with moderate wave action. However, the limpet is likely to become locally extinct on exposed shores because mussels outcompete it there and rapidly recolonize patches from which they have been temporarily eliminated by wave action.

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

Results from a once-off survey at 15 sites along the Namaqualand coast on the west coast of South Africa, which covered a wave-force regime from sheltered to extremely exposed, showed that an alien mussel *Mytilus galloprovincialis* has invaded much of the low shore, previously the habitat typically dominated by an indigenous limpet *Scutellastra argenvillei* (Steffani and Branch 2003). The study further suggested that the patterns of relative abundance and biomass of these two species could be attributable to competition for primary space between them, and that this interaction is influenced by the degree of wave force experienced at different sites. On semi-exposed shores, the limpet dominated much of the rock space, probably because wave action there is unfavourably low for *M. galloprovincialis*. However, at greater levels of wave force, spatial dominance by *M. galloprovincialis* increased, seemingly leading to competitive displacement of *S. argenvillei* from the primary space. On the other hand, the mussel bed provided a secondary substratum for limpet settlement, even if it did not support adult *S. argenvillei* because of their large size.

Such “snapshot” surveys can generate correlative evidence of interactions such as competition, but provide a static picture only. Spatial differences in interactions linked to variations in the physical environment may be revealed by such once-off observations. However,

the ultimate “winner” at any given site may not be revealed and modification of the strength of competition, or even reversals, should be anticipated (Paine 1994). Changes in competitive interactions can be related to seasonal migration (Race 1982), variable larval supply and recruitment rates (Dayton 1971, Hawkins and Hartnoll 1983, Underwood *et al.* 1983, Menge and Sutherland 1987, Menge *et al.* 1994, Gaines and Lafferty 1995, Robles 1997, Connolly and Roughgarden 1999), changes in predation intensity (Menge 1976, 1978, Underwood *et al.* 1983), seasonal or annual changes in abiotic factors (Hawkins 1981, Race 1982, Leonard 2000), catastrophic events (Branch *et al.* 1990) or physical disturbance (Dayton 1971, Sousa 1980, 1984, 1985, Paine and Levin 1981, Petraitis and Dudgeon 1999). Mussels are often very successful competitors for space (Paine 1974, Suchanek 1985, Seed and Suchanek 1992), and physical disturbance has been described as one of the primary mechanisms creating and/or maintaining open space, so preventing mussels from monopolizing the primary space on rocky shores and consequently preserving diversity (Levin and Paine 1974a, b, Paine and Levin 1981, Sousa 1984, 1985).

A common form of physical disturbance on rocky shores is the dislodgement of mussels by wave action. Dislodgements are sporadic events, and can occur

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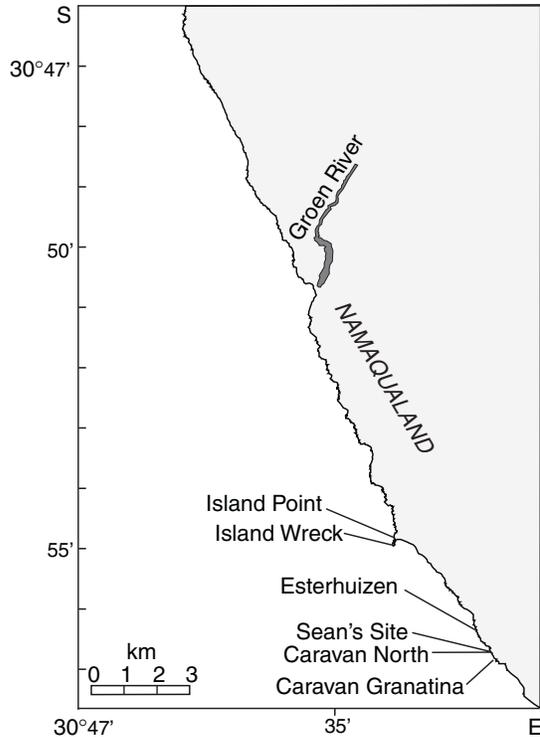


Fig. 1: Map of the Groen River region, showing the six sites selected from the 15 sites surveyed by Steffani and Branch (2003)

unpredictably during any time of the year on the west coast of South Africa. Strong storms during winter (Brundrit and Shannon 1989) render mussels particularly prone to disturbance then. The occurrences and effects of such disturbances can only be detected by temporal monitoring, which is crucial to interpreting patterns observed in once-off surveys, such as the apparent competition between *S. argenvillei* and *M. galloprovincialis* deduced from a large-scale comparative "snapshot" view (Steffani and Branch 2003).

The present study records interactions between *S. argenvillei* and *M. galloprovincialis* over a period of two years. For this purpose, six sites were selected to encompass sheltered, semi-exposed and exposed shores. The objectives were to test whether (1) the patterns observed during the once-off survey described in Steffani and Branch (2003) were consistent over time, (2) periods of high wave action clear patches among the mussel beds and thus provide a refuge in which *S. argenvillei* can establish populations, (3) these events

are more frequent in exposed areas, giving rise to greater temporal variability in the extent and composition of mussel beds there, and (4) succession after disturbance leads to the establishment of persistent limpet populations or to the re-establishment of a mussel-bed community and the exclusion of *S. argenvillei*. These questions are fundamental in answering whether alien invasives can lead to global extinction of indigenous species.

MATERIAL AND METHODS

Study sites

Six sites were selected from the 15 that were previously surveyed north and south of the Groen River mouth on the Namaqualand coast by Steffani and Branch (2003). The selection was designed to ensure a representative coverage of the wave exposure regime, from sheltered to highly exposed. Quantitative measurements of wave force were made on six randomly selected dates spanning two full years (1996 and 1997) at all 15 sites. This allowed a representative objective ranking of the sites in terms of wave action (for more details, see Steffani and Branch 2003). Neither of the two most exposed sites previously surveyed were chosen for the present study, because working conditions there were not conducive to regular sampling. The selected sites are shown in Figure 1. With their mean \pm SE maximum wave forces (expressed as $N\ m^{-2}$), they were Caravan Granatina ($2.7 \pm 0.3 \times 10^3\ N\ m^{-2}$), Caravan North ($7.2 \pm 0.4 \times 10^3$), Sean's Site ($10.2 \pm 0.6 \times 10^3$), Island Wreck ($10.9 \pm 0.6 \times 10^3$), Island Point ($12.3 \pm 0.7 \times 10^3$) and Esterhuizen ($12.7 \pm 0.8 \times 10^3$). The sites were classified as sheltered (Caravan Granatina), semi-exposed (Caravan North) and exposed (Sean's Site, Island Wreck, Island Point and Esterhuizen).

Transect monitoring

The emphasis in this study lay in monitoring temporal changes in the distribution and abundance of *S. argenvillei* and *M. galloprovincialis* at sites with different degrees of wave exposure, and the effects of periodic disturbances on these patterns. Instead of replicating a number of quadrats or smaller transects at each site, which might have obscured between-site differences because of patchiness caused by disturbance events, the entire site was monitored as one large transect. Underwood and Chapman (1996) defined scales of spatial variation with a variety of techniques and suggested that, for most species, an area of approximately $16\ m^2$ can adequately represent a site, because most

variation in density is found within an area of this dimension. Because the width of the Argenvillei Zone ranges from 1 to 3 m, each monitoring area was laid out in the form of a transect, 8 m long by 2 m wide, lying parallel to the shoreline within the zone normally occupied by *S. argenvillei* (between 15 and 55 cm above mean spring low water). The transects were permanently marked by screws drilled into the rock face. Starting in April 1997, immediately after completion of the one-off survey (Steffani and Branch 2003), these transects were surveyed on a three-monthly basis until April 1999. The monitoring programme followed the procedure described by Steffani and Branch (2003). In summary, at each monitoring event, the primary space covered by sessile organisms, the dimension of limpet patches occupied by *S. argenvillei* (see Steffani and Branch in 2003 for definition), the amount of bare rock outside the limpet patches and the area covered by mussel byssal threads were calculated from photographs taken during the surveys. Each transect was photographed as a series of 1 m² plots. Sessile organisms were classed as mussels, encrusting algae, upright corallines, foliose algae, colonial diatoms (recognizable on photographs by their colour and texture), the sea anemone *Aulactinia* (= *Bunodactis*) *reynaudi* or tubes of the sessile polychaete *Gunnarea capensis*. After dislodgement of mussels, byssal threads are often left behind and colonial diatoms are usually the first organisms to colonize them (Seed and Suchanek 1992). Thus, diatoms and byssus were grouped together as indicators of disturbance events.

This photographic method of estimating the areas covered by functional groups of organisms was coupled with an evaluation of percentage cover made directly in the field. The transects were divided into 16 squares of 1 m² each, and the cover by each group of sessile organisms, as well as by the bare rock space in each square, was estimated. This was facilitated by using a 1 × 1 m quadrat subdivided into 25 units of 4% each. Percentage cover for each group was then expressed as total cover for the entire 16 m² transect. Comparisons between the photographic and field-based measures of cover showed that they differed by only $7.8 \pm 8.4\%$ *SD*. (Hereafter all confidence limits are expressed as *SD* unless otherwise stated.) During the field estimations of mussel cover, the mussels were divided into four size-groups, which separated large adults (>70 mm long), medium-sized adults (35–70 mm), subadults (10–34 mm) and recruits (<10 mm). This differentiation proved to be difficult to derive from the photographs. Percentage cover of sessile organisms was therefore taken from the field data, whereas limpet patch dimensions and areas of bare rock were measured from the photographs.

In situ measurements of *S. argenvillei* densities and

size structures in the limpet patches or on mussel beds also followed the method described in Steffani and Branch (2003). The data from each limpet patch were kept separate. In cases where limpet patches were large (>2 m²), they were subsampled by using six 50 × 50-cm quadrats and the data were extrapolated. Smaller *S. argenvillei* are usually found on the shells of larger conspecifics in dense limpet stands (Branch 1971, Eekhout *et al.* 1992). The measurements of these juveniles were pooled with measurements of limpets from the rock surface (hereafter collectively referred to as “limpets on rock”), but their size-frequency distributions are depicted separately in graphs. Limpets <2 mm shell length were excluded from the measurements because they were impossible to identify to species in the field.

Definition of limpet density

Densities of *S. argenvillei* were expressed either as number per m² of total shoreline (referred to as “per m² of shore”) or as number per m² of habitat. Habitats comprised patches of *S. argenvillei* occupying the rock surface (referred to as “limpet patch”) and mussel beds. The first expression (per m² of shore) can also be calculated separately for limpets occurring on the rock surface or the mussel bed.

Statistical analyses

Data were tested for normality and homogeneity of variances by means of the Kolmogorov-Smirnov test and Levene’s test respectively. If necessary, data were log, square-root, root-root or arcsine transformed to meet the assumptions of parametric tests.

The proportional contributions of adults to the *S. argenvillei* rock-dwelling population were compared between sites by a one-way ANOVA, followed by Tukey HSD tests. The contribution of adults to the *S. argenvillei* population on mussel beds could not be analysed statistically because adults were often absent, which resulted in zero observations with no variability. The densities of *S. argenvillei* on rock (expressed per m² of limpet patch) versus those on mussel beds (per m² of mussel bed) were compared with a paired Student’s *t*-test. Limpet densities in each of these habitats were also analysed separately to compare between sites and times, using two-way Model I factorial-design ANOVA. For the analyses of limpet densities on mussel beds, sampling times April 1997 and April 1999 were excluded, because no limpets on mussel beds were recorded at these times at Caravan North, which resulted in zero values with no variability. To achieve equal sample sizes between limpet-patch

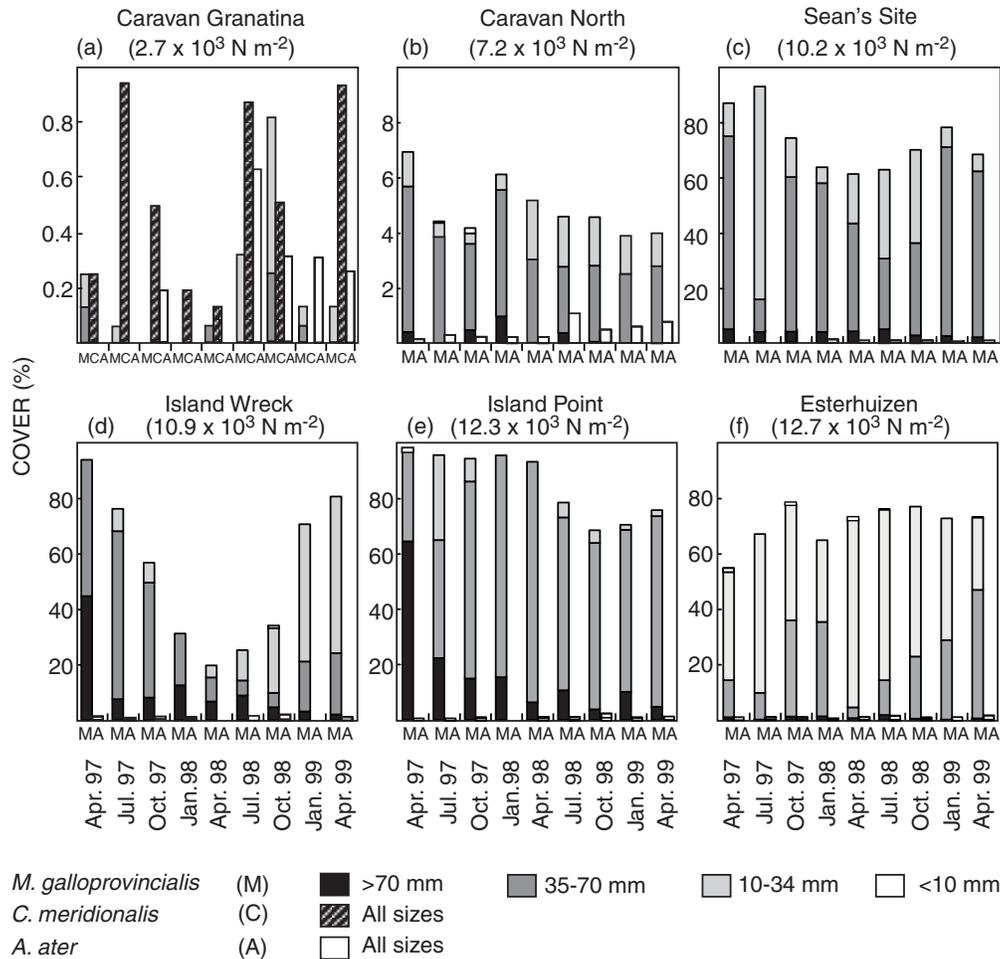


Fig. 2: Seasonality of percentage cover of the mussels *M. galloprovincialis* (in different size-classes), *C. meridionalis* and *A. ater* at the six sites. Mean wave forces are given in parenthesis. Note the different scales of the ordinates in (a) and (b) compared with (c–f) and that the key for (a) is different from that of (b–f)

counts, four limpet patches (or, where necessary, four subsamples) were randomly selected for each site and time using random tables, thereby ensuring independence of the samples and a balanced design. ANOVAs were followed by multiple-comparison Tukey tests.

In July 1998, no photographs could be taken at one of the sites (Esterhuizen), so there were no data on limpet patch sizes and density per m^2 of limpet patch for that time and site. The July 1998 data from all other sites were therefore not included in the analysis.

When ANOVA results show a significant interaction

between the factors, tests of the main effects are unreliable. Therefore, if interactions occurred, the means of one factor were compared separately at each level of the other factor and *vice versa* (Underwood 1997). Following these multiple-comparison Tukey tests, the probability of Type I error over the whole experiment was adjusted to compensate for the number of multiple-comparison tests conducted (Underwood 1997), by applying the sequential Bonferroni correction (Peres-Neto 1999). Statistical analyses were done using the software STATISTICA 5.5 for Windows,

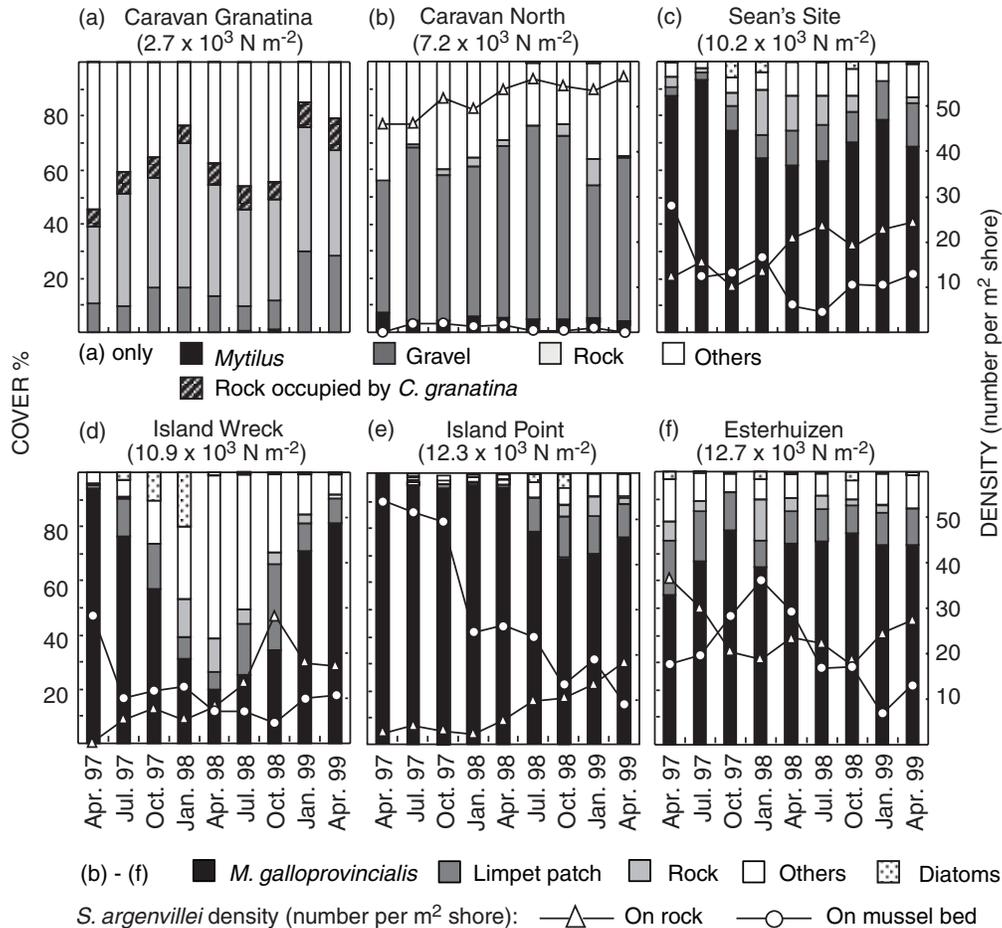


Fig. 3: Seasonality of percentage cover of *M. galloprovincialis*, limpet patches, other sessile organisms (including algae, *G. capensis* and *A. reynaudi*), and diatoms (including byssus threads). The lines depict the density of *S. argenvillei* per m^2 of shore, separating limpets on rock from those on mussel beds at the six sites. Mean wave forces are given in parenthesis. Note that Caravan Granatina has a separate key. No data were obtained for cover by limpet patches and bare rock in July 1998 at Esterhuizen, and values for the preceding month were inserted (but not used in any analyses)

StatSoft, Inc. (2000). The significance level for all analyses was $\alpha = 0.05$.

RESULTS

Coverage of primary space

Three species contributed to the mussel cover: two in-

igenous species, *Aulacomya ater* and *Choromytilus meridionalis*, and the alien mussel *M. galloprovincialis*. At the most sheltered site, Caravan Granatina (Fig. 2a), all three were recorded but all were scarce (total average cover by mussels of $0.9 \pm 0.6\%$, of which $0.19 \pm 0.25\%$ was *M. galloprovincialis*). At that site, *M. galloprovincialis* and *C. meridionalis* were all relatively large; individuals < 35 mm were never observed. This suggests that the *M. galloprovincialis* and *C. meridionalis* found there were individuals dislodged

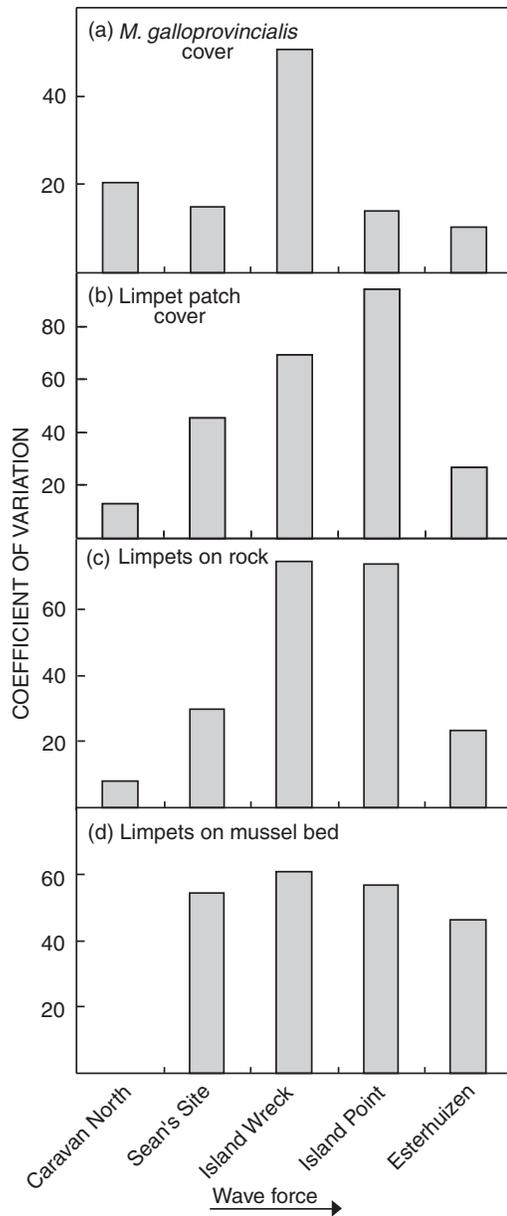


Fig. 4: Temporal coefficients of variation for (a) cover of *M. galloprovincialis*, (b) cover of limpet patches, (c) density of *S. argenvillei* (expressed per m² of shore) on rock and (d) on mussel beds. Sites are ranked in sequence from low (left) to high (right) wave forces. No calculation was done for limpets on mussels at Caravan North because virtually no limpets were found on mussels there. Caravan Granatina is excluded because mussels and limpets were absent or rare at that site

from elsewhere by storms and transported to that site. After a particularly strong storm, large numbers of very large *C. meridionalis* were found just next to the permanent transect, whereas three months earlier no mussels had been recorded there. They persisted, however, for only a short time and then died (CNS, pers. obs.). This suggests that, although they are capable of re-attaching, they did not thrive at this sheltered site. The only species of mussel that recruited to the sheltered site (and even then in low numbers) was *A. ater*, evidenced by their small shell length of <10 mm.

C. meridionalis was absent from all other sites. Of the other two species recorded, *A. ater* contributed only $3.0 \pm 3.9\%$ to the total mussel cover and only $0.7 \pm 0.3\%$ to the overall cover (Fig. 2b–f). Individual *A. ater* were also usually very small (<35 mm) and buried deeply in the *M. galloprovincialis* matrix. Their cover was therefore negligible and is not analysed further. The majority of cover by *M. galloprovincialis* consisted of medium-sized mussels (35–70 mm), except at Esterhuizen, where smaller mussels (<35 mm) dominated (Fig. 2).

Changes in the composition of rock cover over time are shown in Figure 3. At the most sheltered site (Caravan Granatina), the dominant limpet was *Cymbula granatina*, and *S. argenvillei* was not observed. Gravel, sand and pieces of broken shells often covered parts of the primary rock space (Fig. 3a). Sessile organisms other than mussels included *G. capensis*, *A. reynaudi*, foliose algae (mainly the red algae *Aeodes orbitosa* and *Gigartina radula* and the green alga *Ulva* sp.) and encrusting corallines, into which dense colonies of the black polychaete *Dodecaceria pulchra* and/or the colonial gastropod *Dendropoma corallinaceus* often burrowed. Because *M. galloprovincialis* did not seem to settle naturally at this site and *S. argenvillei* was never recorded there, data from Caravan Granatina were not included in the statistical analyses, although they are presented graphically.

At the other five study sites, cover of *M. galloprovincialis* and of *S. argenvillei* limpet patches varied over time, most dramatically at Island Wreck, but no consistent seasonal or long-term trends were apparent (Fig. 3b–f). In general, *M. galloprovincialis* cover was considerably lower at the semi-exposed site (Caravan North; $4.9 \pm 1.0\%$) than at the other four sites. In contrast, at the exposed sites of Sean's Site, Island Wreck and Island Point, a cover of >90% was temporarily achieved. At Esterhuizen, mussel cover was always <80%. The extent of limpet patches was greatest at Caravan North, averaging $60 \pm 8\%$. Cover by limpet patches at the other sites varied between 1 and 32% (Fig. 3). Bare rock outside the limpet patches was scarce but in some months reached about 10% (e.g. January 1998 at Sean's Site and April 1998 at Island Wreck). This increase in bare rock coincided with a decrease in mussel cover. At the same time,

diatoms and byssal threads were recorded. This suggests that mussels had been dislodged, presumably by storms, thus freeing more rock space. Subsequent to the decrease in mussel cover and the increase in bare rock, the area of limpet patches enlarged. However, over time the mussel cover increased again after the disturbance, and bare rock and limpet patches declined. This process of turnover of primary space coverage was most apparent at Island Wreck, where the mussel cover decreased from almost 100% in April 1997 to about 20% in April 1998 (Fig. 3d). This resulted in 13% bare rock becoming available in January 1998 and a maximum of 32% cover by limpet patches in October 1998. By April 1999, however, the situation had almost completely returned to the initial stage, with >80% mussel cover, 9% limpet patches and only 1% of bare rock. The most exposed site in this study (Esterhuizen), had a constant turnover of mussels, evidenced by the consistent presence of byssus and diatoms (Fig. 3f).

As a measure of temporal variability, coefficients of variation were calculated for cover of mussels and limpet patches at each site (Fig. 4). They showed that the temporal variability was greatest at sites in the middle of the wave-force scale (Sean's Site, Island Wreck and Island Point), whereas at both ends of the scale (Caravan North and Esterhuizen), variability was reduced.

Limpet density per m² of shore

The densities of *S. argenvillei* on rock and mussel beds per m² of shore are shown in Figure 3 to facilitate comparisons with temporal changes in cover of limpet patches and mussels. At almost all sites where *S. argenvillei* was present, it occupied both the rock surface and the mussel bed. The only exception was at Caravan North, where few or no limpets were found on mussels, reflecting the scarcity of mussels there. Over the entire study period, the density of limpets on rock was highest at Caravan North, with an average of 52.3 ± 4.1 m⁻² of shore – at least double the density at any of the other sites. The site with the next highest densities of limpets on rock was Esterhuizen (24.3 ± 5.7 m⁻²), followed by Sean's Site, Island Wreck and Island Point (18.0 ± 5.4 , 11.5 ± 8.5 and 7.9 ± 5.8 m⁻² respectively). Conversely, the densities of limpets on mussel bed (also expressed per m² of shore) were lowest at Caravan North and highest at Island Point (0.9 ± 0.8 m⁻² and 30.2 ± 17.1 m⁻², respectively) – a logical consequence of the relative mussel cover at these sites (Fig. 3).

There were few temporal changes in limpet density on rock or mussel bed at Caravan North, because the cover of mussels was always very low and the cover of limpet patches was relatively constant (Fig. 3b). The

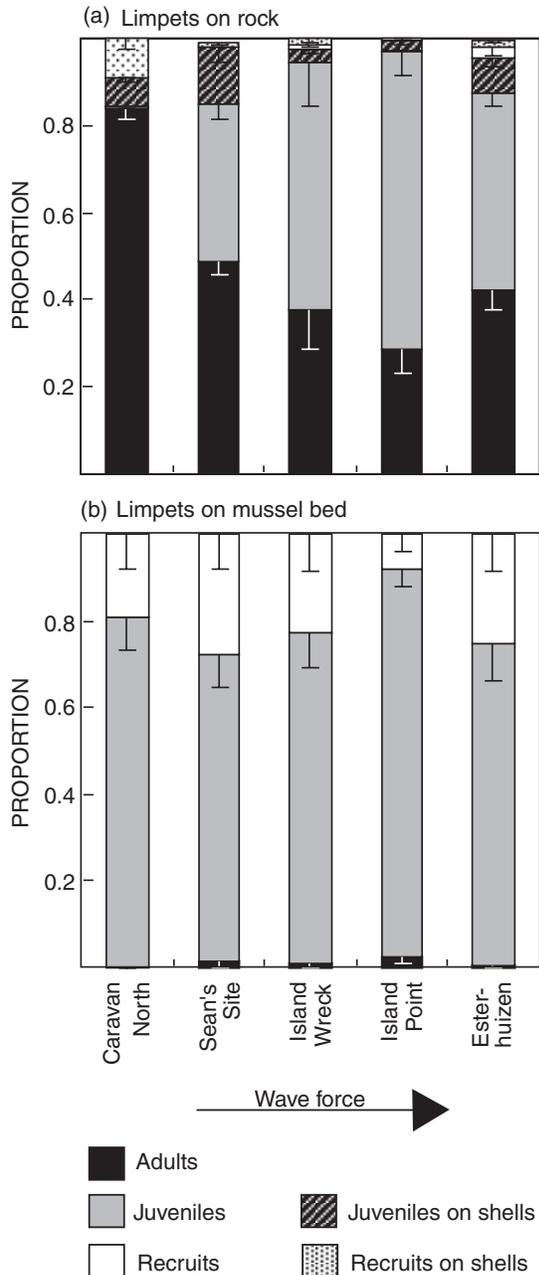


Fig. 5: Mean proportion (\pm SE) of adults, juveniles and recruits of *S. argenvillei* on (a) rock and (b) mussel beds, combined over the entire study period

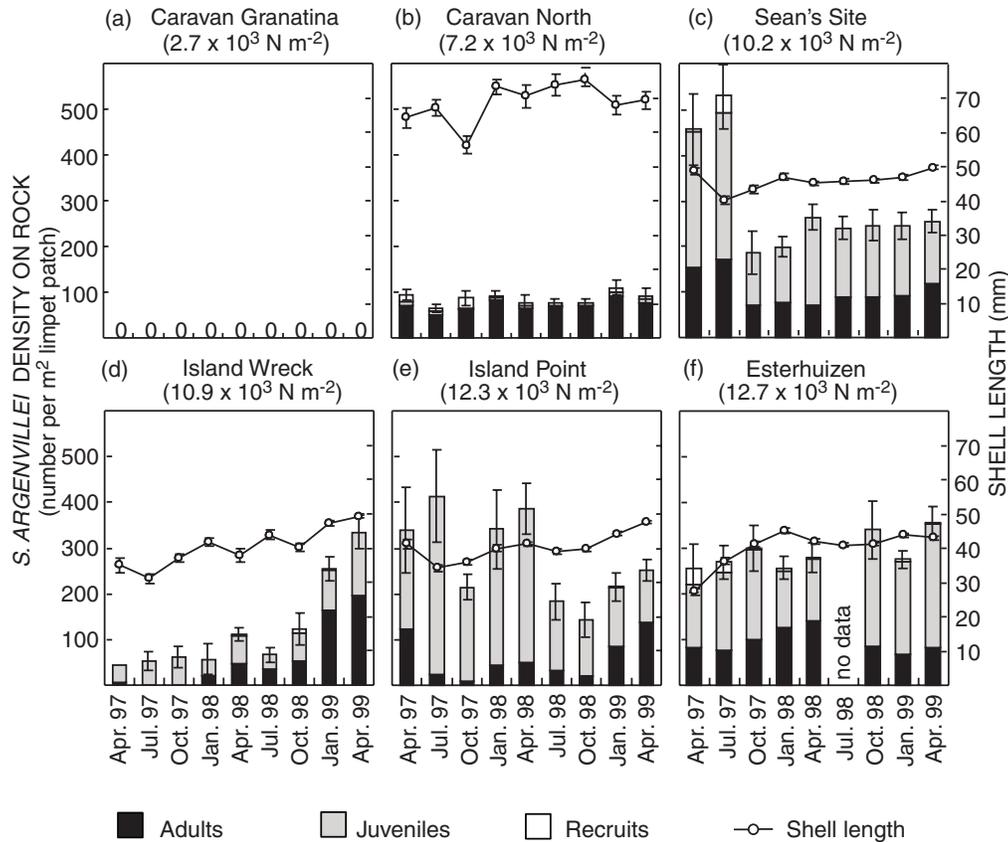


Fig. 6: Seasonality of mean densities (\pm SE) of adults, juveniles and recruits of *S. argenvillei* on rock, expressed per m^2 of limpet patch (\pm SE given for total density) at the six sites. Mean wave forces are indicated in parenthesis. Average shell lengths (\pm SE) are connected by lines to emphasize trends, not to imply interpolation

changes in limpet densities at the other sites mirrored the variations in cover exhibited by *M. galloprovincialis* and limpet patches at the sites. After mussels were dislodged, the extent of limpet patches increased and so did the limpet density on rock, whereas limpet density on mussel beds decreased. When mussels recovered from disturbances and their cover increased again, the density of limpets decreased on rock and increased on mussel beds (Fig. 3c–f).

Coefficients of variation showed that greatest temporal variability in limpet density was at sites with intermediate levels of exposure, coinciding with the greater variability in limpet patch and mussel cover exhibited there (Fig. 4c, d).

For the purpose of description and analysis, the populations of *S. argenvillei* were divided into adults

(>45 mm, the size at which they mature; Eekhout *et al.* 1992), juveniles (10–45 mm) and recruits (<10 mm). Adults made up substantial proportions of the limpet populations on rock, whereas the populations on mussel beds almost completely lacked adult limpets and were dominated by juveniles (Fig. 5b). A one-way ANOVA showed that the proportional contribution of adults to the limpet populations living on rock was significantly different among sites ($F_{4,40} = 15.086$, $p < 0.001$; data arcsine transformed). *Post hoc* tests showed that the adult portion of the rock population was significantly greater at the sheltered site at Caravan North than at any of the more exposed sites ($p < 0.001$ in all cases), none of which differed significantly ($p > 0.05$). The rest of the rock populations consisted mainly of juveniles, living primarily on the shells of larger con-

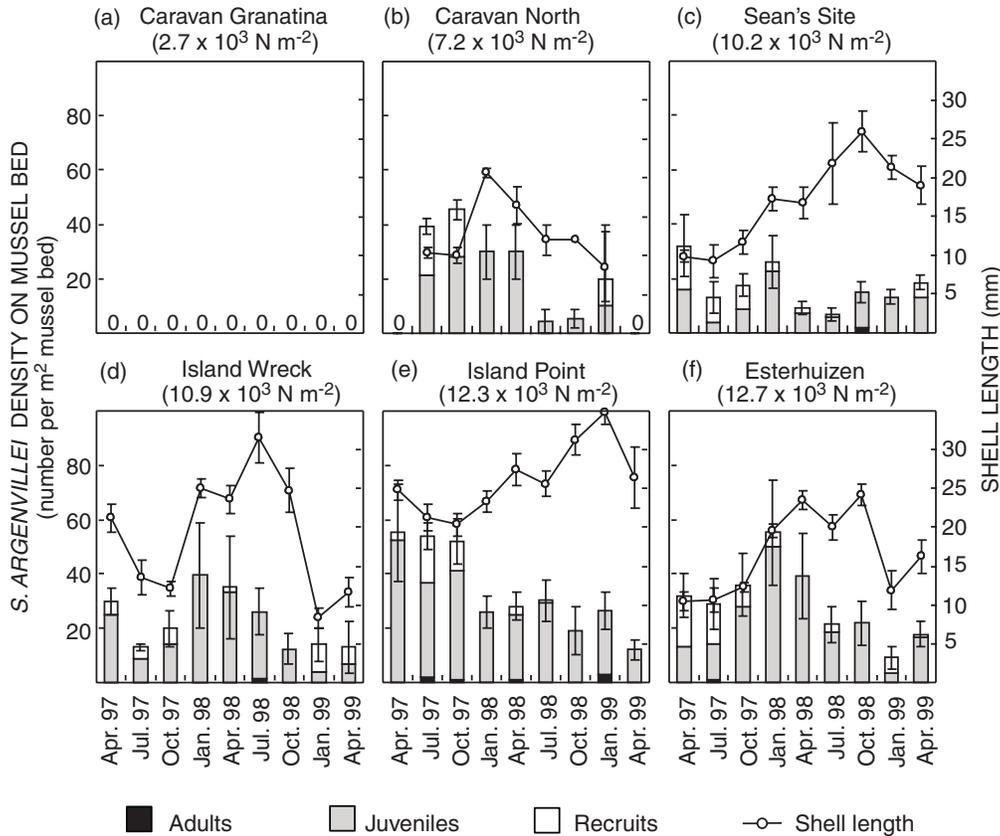


Fig. 7: Seasonality of mean densities (\pm SE) of adults, juveniles and recruits of *S. argenvillei* on mussel beds, expressed per m^2 of mussel bed at the six sites. Mean wave forces are given in parenthesis. Average shell lengths (\pm SE) are connected by lines to emphasize trends, not to imply interpolation

specifics. Recruits were scarce. The fraction of limpets living on the shells of other limpets decreased concomitantly with a decrease in the proportion of adults (Fig. 5a).

At all sites, adult limpets were absent or in low proportions (<2%) on the mussel bed (Fig. 5b), precluding rigorous statistical analysis of those data. Juvenile limpets were dominant, and recruits contributed between 10 and 25% to the population. No limpets were found on the shells of other limpets on the mussel bed, reflecting the lack of large individuals (Fig. 5b).

Limpet density per m^2 of habitat

A comparison of *S. argenvillei* densities between the

limpet patches and mussel beds was done by expressing the limpet density per m^2 of habitat (limpet patch or mussel bed). This revealed a nine-fold difference between the two habitats: a mean of 216.5 ± 196.4 per m^2 of limpet patch v. 25.4 ± 21.4 per m^2 of mussel bed (paired Student's *t*-test: $t_4 = 4.5$, $p < 0.02$).

A more detailed examination of *S. argenvillei* densities was also undertaken for each separate habitat (Fig. 6). A two-way ANOVA of densities per m^2 of limpet patch revealed that sites and times interacted in their effect on densities ($F_{28,120} = 3.866$, $p < 0.001$, data root-root transformed). For further *post hoc* tests, the means per site were first compared separately at each level of time. Overall, Caravan North had the lowest densities and Tukey tests showed that both that site and Island Wreck had significantly less dense

populations of *S. argenvillei* than did the other sites during the first three sampling dates ($p < 0.05$). No difference was found among the sites for the last five sampling dates ($p > 0.05$). The low densities at Island Wreck during the first 18 months of the study period (Fig. 6d) were probably a result of the initially high mussel cover coupled with the amount of time that elapsed before limpet densities rose in mussel-free patches created by storms that continuously dislodged mussels at that site. The increase in density at Island Wreck over the later period of observation was strongly biased towards increases in adult limpets (Fig. 6d). Tukey tests were further used to identify significant temporal differences within each site. Comparing sites, there was a clear pattern in temporal variability of limpet density. There were no significant differences over time at the sites representing the two extremes of the wave action occupied by *S. argenvillei*, i.e. Caravan North and Esterhuizen ($p > 0.05$). Greatest temporal change was at Island Wreck, which occupied the centre of the wave-action gradient. Viewing the sites in sequence in terms of increasing wave action, there were respectively 0, 1, 6, 2 and 0 occasions when the sites experienced significant temporal changes ($p < 0.05$).

On the mussel beds, limpet densities (per m² of mussel bed) varied over time but differed little between sites (Fig. 7). A two-way ANOVA revealed no interaction between sites and sampling times and no differences between the sites (interaction: $F_{24,105} = 1.068$, $p = 0.393$; site effect: $F_{4,105} = 2.394$, $p = 0.055$; data log-transformed). Time, however, had a significant effect on limpet densities ($F_{6,105} = 3.392$, $p = 0.004$). Tukey tests showed that the densities in October 1997 were significantly higher than in October 1998 ($p < 0.05$).

Limpet shell length

The mean shell lengths of rock-dwelling *S. argenvillei* (Fig. 6) were largest at Caravan North, averaging 67 ± 27 mm, and declined to 46 ± 14 mm at Sean's Site, 45 ± 13 mm at Island Wreck, 40 ± 9 mm at Island Point and 40 ± 16 mm at Esterhuizen. All size distributions were significantly different from each other (Kolmogorov-Smirnov two-sample test: $p < 0.001$, in all cases after sequential Bonferroni correction).

Figure 7 shows the mean shell lengths of limpets on mussel beds. Comparing the mean shell lengths of *S. argenvillei* in limpet patches (pooled mean for all sites, 47.1 ± 12.1 mm) with that of limpets on mussel shells (pooled mean for all sites, 18.3 ± 7.0), showed that the difference was highly significant (t -test: $t_{88} =$

14.881 , $p < 0.001$, data square-root transformed). Testing for differences among limpet sizes on the five mussel beds showed that limpets at Island Point were significantly larger (25 ± 11 mm) than those at the other sites (Kolmogorov-Smirnov two-sample test: $p < 0.001$, in all cases after sequential Bonferroni correction). This probably reflects the high percentage cover of mussels there and the high proportion of large mussels (Figs 2, 3). At the other sites, the overall mean shell length was 20 ± 10 mm at Island Wreck, 17 ± 8 mm at Esterhuizen, 16 ± 9 mm at Sean's Site and 13 ± 7 mm at Caravan North. No difference was found between the size distributions at Sean's Site and Caravan North, or Sean's Site and Esterhuizen ($p > 0.05$). The size distributions at all other sites differed significantly ($p < 0.001$, after Bonferroni correction).

Limpet recruitment on rock v. mussel beds

Recruits contributed up to 27% of the limpet populations on mussel beds, but never more than 10% of the rock-dwelling population (Fig. 5). However, if the densities of recruits are expressed per m² of habitat, their densities on rock (7.3 ± 1.7 m⁻²) were significantly greater than those on mussel bed (5.0 ± 0.6 m⁻²; Mann-Whitney U test: $Z_{160} = -2.541$, $p = 0.011$).

In both habitats, recruitment was highly variable over time and no clear seasonal pattern emerged. However, it was obvious that recruitment was higher in 1997 than in 1998. Only two measurements were made in 1999, but these suggested that recruitment had increased again (Fig. 8a, b).

Limpet patches

The densities of *S. argenvillei* in the limpet patches (expressed per m² of limpet patch) at Sean's Site, Island Wreck, Island Point and Esterhuizen were strongly and inversely related to the size of the patch (Fig. 9c-f). The increase in limpet density became particularly obvious as patch size fell below about 0.1 m². Caravan North had only one large limpet patch, but densities in this patch showed a similar trend (Fig. 9b).

DISCUSSION

Competitive interactions between species and the dominance of one species over another are not fixed but can vary over space and time. A once-off survey

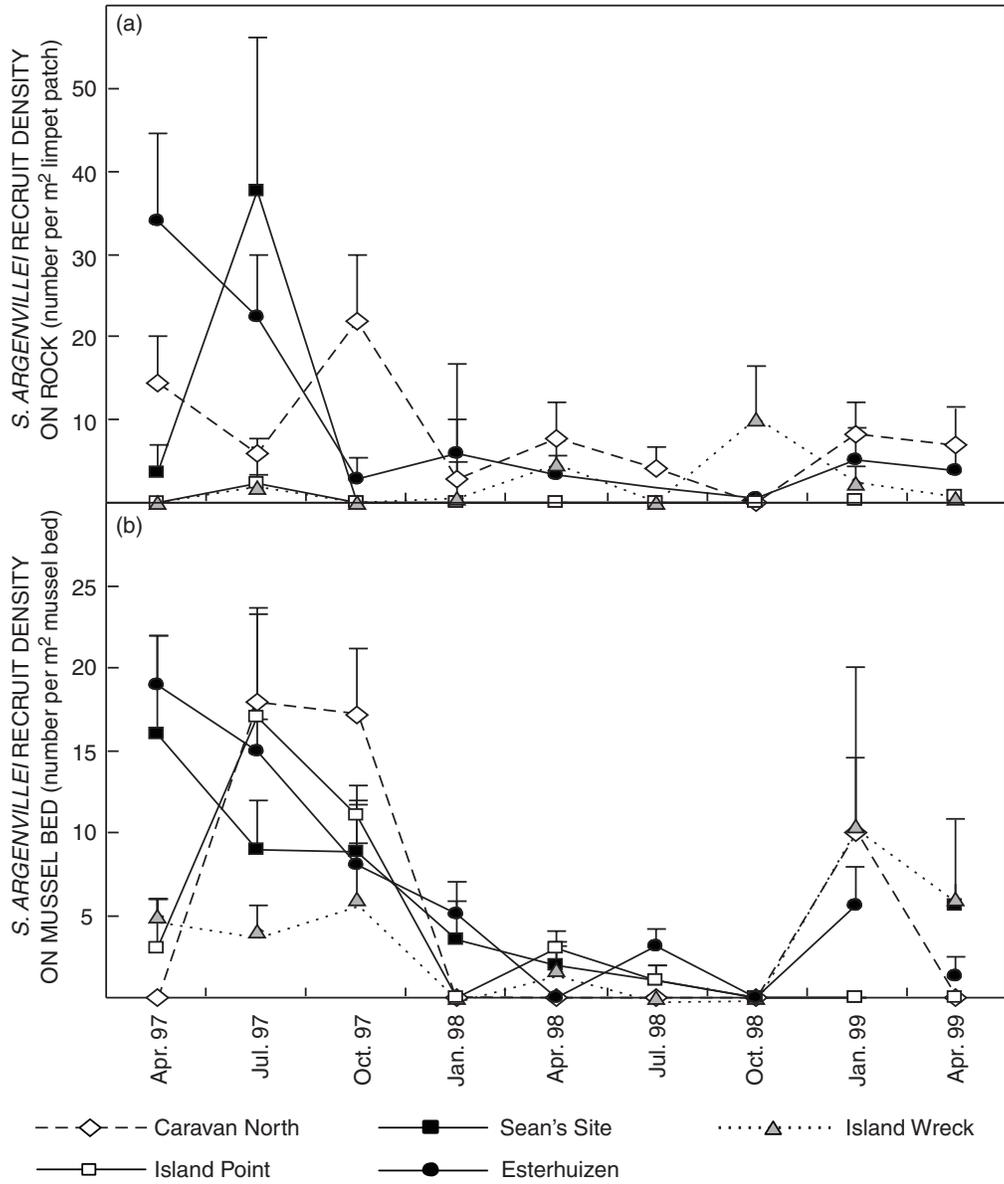


Fig. 8: Seasonality of mean densities (\pm SE) of *S. argenvillei* recruits on (a) rock and (b) mussel beds at five sites. Caravan Granatina is excluded because no *S. argenvillei* were recorded at that site. Note the differences in the scales of the y axes

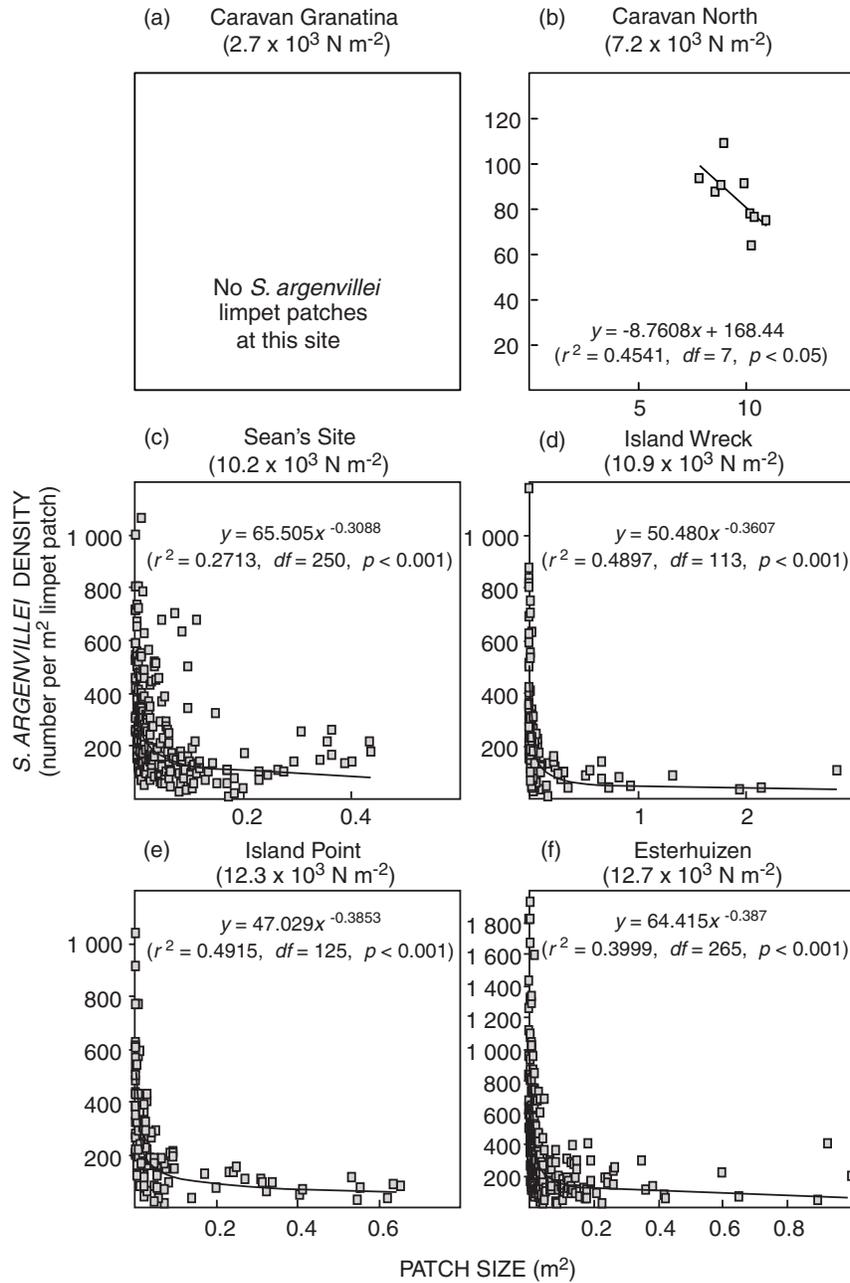


Fig. 9: Densities of *S. argenvillei* on rock in relation to patch size (m^2) at the six sites. Data are combined over time. Note differences in the scales of the x and y-axes

at 15 sites at the Groen Rivier mouth region provided the first circumstantial evidence suggesting that wave action mediates competition between *S. argenvillei* and *M. galloprovincialis* (Steffani and Branch 2003). However, biotic and abiotic factors may also change over time (continuously or sporadically), which can further affect interactions between competing species (Branch 1984). It was for this reason that six of the original 15 sites were selected and monitored over a period of two years.

Coverage of primary space and limpet density

The results showed that the patterns observed during the once-off survey persisted over time. Both *S. argenvillei* and *M. galloprovincialis* were always rare or absent at the most sheltered site (Caravan Granatina). It appeared that recruits of neither species ever settled there, although it must be recognized that settlement may not have been detected at the time intervals used for sampling. Whatever the cause, it seems that there is a threshold of wave action below which neither species can become established. A similar outcome was also described by Bustamante *et al.* (1995).

At the semi-exposed site of Caravan North, cover of the shore by *M. galloprovincialis* remained constantly low and the proportion of the shore occupied by limpet patches was consistently high. Rock-occupying *S. argenvillei* dominated the shore and maintained high densities per m² of shore. The scarcity of mussels at semi-exposed sites is likely attributable to slow growth and poor recruitment, factors that will be explored in further studies. If this is true, then *M. galloprovincialis* probably presents no competitive threat to *S. argenvillei* under these conditions and the limpet can persist at high densities.

At higher levels of wave action, however, mussel cover was high and limpet-patch cover reduced, but both varied over time. Periodic dislodgement of *M. galloprovincialis* intermittently created vacant patches in the mussel bed, so freeing space for *S. argenvillei*. This temporarily resulted in an increase in the area of limpet patches and the densities of rock-dwelling *S. argenvillei* (per m² of shore), whereas the densities of limpets on mussel bed (also expressed per m² of shore) decreased. However, these cleared patches were eventually recolonized by *M. galloprovincialis* and *S. argenvillei* was outcompeted from the primary space. This repeated exclusion strengthens the circumstantial evidence for the existence of competition and for the superior competitive ability of *M. galloprovincialis* over *S. argenvillei* at exposed sites.

At the three exposed sites (Sean's Site, Island Wreck and Island Point), there was substantial variability in

limpet densities per unit area of limpet patch. This variability resulted from the process of succession in disturbance patches. Dislodgement of mussels usually resulted in large gaps, within which the density of immigrant limpets was at first low and insufficient to prevent subsequent recolonization by *M. galloprovincialis*. As mussels encroached, the limpet patches became fragmented and decreased in size, as Paine and Levin (1981) and Sousa (1985) have observed elsewhere. The density of limpets per m² of limpet patch increased concomitantly. Several other investigations have also found that small patches in mussel beds contain higher densities of limpets than do larger ones (Suchanek 1978, Paine and Levin 1981, Sousa 1984).

In contrast, Esterhuizen, the most exposed site monitored, experienced more continuous disturbances that probably maintained a constant mixture of "young" and recovering gaps, so reducing the variability of *S. argenvillei* densities between sampling times (both per m² of shore and per m² of limpet patch). Moreover, the consequences of disturbances at Esterhuizen were not as severe as those of the single events at other sites (e.g. Island Wreck), probably because mussels at highly exposed sites develop stronger byssal threads, mono-layered mussel beds and other features that reduce the risk of dislodgement (Harger 1970, Price 1982, Witman and Suchanek 1984, Raubenheimer and Cook 1990, Seed and Suchanek 1992, Alvarado and Castilla 1996, Bell and Gosline 1997). This combination of factors maintained a relatively constant mussel cover that never exceeded 80%, compared to maximal values of >90% at the other sites, and this in turn resulted in relatively constant proportions of shore being occupied by limpet patches.

Dislodgement of mussels as a result of wave shear is likely on all mussel-dominated exposed rocky shores (Dayton 1971, Harger and Landenberger 1971, Paine and Levin 1981, Sousa 1985, Denny 1987, 1995). The recolonization of such disturbance gaps is dependent mainly on the size, shape and position of the gaps (Paine and Levin 1981, Keough 1984, Farrell 1989, Tokeshi and Romero 1995, Kim and DeWreede 1996), the length and intensity of disturbances and the time intervals between disturbance events (Paine and Levin 1981, Sousa 1980, 1984, 1985). Other important factors are the supply of larvae and the rate of recruitment of potential gap colonizers, which can be highly variable both temporally and spatially (Menge and Sutherland 1987, Petraitis 1991, Grosberg and Levitan 1992, Gaines and Bertness 1994, Reed *et al.* 2000). Many workers have monitored and described the successional recovery of disturbance gaps within mussel beds or beds of other dominant sessile species. Generally, early-succession opportunistic species colonize the patch, but the dominant competitor eventually recovers

the lost space and excludes inferior competitors from primary space, unless there is further disturbance (e.g. Dayton 1971, Sousa 1979a, 1984, Paine and Levin 1981, Keough 1984, Farrell 1989, Tokeshi and Romero 1995). For the maintenance of competitively inferior species, physical disturbance is therefore an important factor, especially at an intermediate level. Above this level, environmental conditions may be too harsh for some species, and below it the superior competitor may be too persistently dominant (Connell 1978, Paine and Levin 1981, Branch 1984, Sousa 1979b, 1985). This scenario is complicated by the fact that, as wave action increases, it may cause more dislodgement of mussels, but it also enhances their food supply and growth, and possibly the input of mussel larvae. The frequency and the magnitude of disturbance events are balanced against the biological response of the mussels, and the net effects will determine the intensity of mussel competition.

Limpet densities on mussel beds

The densities of mussel-dwelling *S. argenvillei* per m² of mussel bed varied little between sites and times. However, they were almost an order of magnitude lower than densities in limpet patches (expressed per m² of limpet patch). Limpets on mussel beds were also smaller than limpets on rock. The mussel-bed limpet populations consisted of up to 27% recruits but, nevertheless, the density of recruits per m² of habitat was higher on rock than on mussel beds. In dense stands of *S. argenvillei*, recruits and juveniles are usually found on shells of larger conspecifics (Branch 1971, Eekhout *et al.* 1992, Day *et al.* 2000). The same can be observed for another limpet, *Scutellastra cochlear*, which is abundant in the southern part of the west coast of South Africa. For this species, Branch (1971) suggested that larvae settle randomly on shells or rock, but that settlers on rock are bulldozed away by grazing limpets and that only those on the shells of others survive. However, Branch (1971) noted that, in mixed stands of *S. argenvillei* and *S. cochlear*, juvenile *S. cochlear* are also found on the shells of *S. argenvillei*, though the reverse seldom occurs. Perhaps settling larvae of *S. argenvillei* follow certain cues and thus select shells of conspecifics over other substrata, including mussel shells. However, more work is needed to substantiate this suggestion.

Overall, the evidence showing consistently lower densities, smaller sizes and lesser recruitment of *S. argenvillei* on mussel beds accords with the results reported by Steffani and Branch (2003). This further supports the suggestion that the mussel bed is not an

ideal secondary replacement substratum for *S. argenvillei* if it is displaced from the primary rocky substratum by *M. galloprovincialis*.

Timing of disturbance

The timing and the season of disturbance have often been considered to be critical in determining the type of successional community developing in disturbance gaps, because larvae of many potential colonizers are only seasonally available (Hawkins 1981, Sousa 1985, Dayton *et al.* 1992, Benedetti-Cecchi and Cinelli 1994, Blanchette 1996, Kim and DeWreede 1996). However, although the rate of successional replacement may vary because of seasonal recruitment, most evidence shows that patches created in different seasons eventually come to be re-occupied by the same dominant competitor (Sousa 1979a, Hawkins 1981, Blanchette 1996, Kim and DeWreede 1996).

S. argenvillei spawns during June and July (Branch 1974, Bosman *et al.* 1990, Eekhout *et al.* 1992). For the region near the Groen River mouth, Bosman *et al.* (1990) reported a pronounced annual cycle for *S. argenvillei* recruits, with peak densities from January to a maximum in March and decreasing to almost zero in July (see also Eekhout *et al.* 1992). Bosman *et al.* (1990) also described high variability between years. Strong annual variability was also found in the present study, but no clear seasonal pattern emerged, probably because recruitment was minimal during 1998. At the exposed sites of Sean's Site, Island Wreck and Island Point, there were single but strong disturbance events at the beginning of the austral winter between April and July, or just after July. This seemed to have been just after the peak recruitment season of *S. argenvillei*, so reducing the chances for recruits to colonize the disturbance gaps. Paine and Levin (1981) suggested that potentially long-lived species that are competitively inferior are geared to allow settling during the period when storms are most likely to provide fresh patches for colonization. In such patches, they would then be able to find temporal refuges, reach maturity and persist for one or more reproductive season until being overwhelmed again by the dominant competitor. However, at the study sites on the Washington coast, USA, researched by Paine and Levin (1981), the recovery of large disturbance gaps within *Mytilus californianus* beds began, on average, 26 months after the disturbance, and the rotation period was 7–8 years. Judging from the disturbance events documented here (see especially Island Wreck), the recovery period is clearly much shorter for *M. galloprovincialis* on the west coast of South Africa. *S. argenvillei* is a long-

lived species that matures at a size of 45 mm and at an age of approximately 3–4 years (Eekhout *et al.* 1992). This means that, even if *S. argenvillei* recruits colonize fresh disturbance gaps, they might not have enough time to grow to reach maturity and reproduce before the patch is closed over again by mussels. They are also unlikely to reach a size at which they are capable of inhibiting mussel settlement and encroachment. On the other hand, many of the limpets found in these disturbance gaps shortly after creation were juveniles or small adults, which suggest that they must have invaded the patches from the surrounding mussel beds rather than recruiting by way of larval settlement.

CONCLUSION

The patterns observed by Steffani and Branch (2003) in an initial once-off survey remained consistent over the two-year monitoring period. *S. argenvillei* and *M. galloprovincialis* were both continually absent from the most sheltered site. At a semi-exposed site, *M. galloprovincialis* cover remained low (<7%) throughout, whereas *S. argenvillei* commanded the majority of the rock space. At three exposed sites *M. galloprovincialis* dominated (at times >90% cover), but its percentage cover varied widely because wave action cleared gaps within the mussel beds. Patches of *S. argenvillei* were small, and densities in them were high as a result, but varied as patch size changed with mussel removal or encroachment. At the most exposed site studied, mussel cover was relatively constant, averaging 70% cover, and so was the cover of limpet patches (ca. 20%). Limpets on mussel beds had constant low densities and small sizes, and <3% reached the size of sexual maturity, rendering the mussel bed unsuitable as a replacement substratum for the limpet after its competitive exclusion from the rock face. Therefore, mussel beds may serve only as a temporary “holding” area that supports juvenile *S. argenvillei* until a mussel patch is dislodged and can be occupied by limpets moving from the adjacent mussel bed. Even then the limpets are unable to prevent subsequent invasion of the patch by mussels. In summary, the most obvious pattern was that mussel beds were periodically disturbed at the exposed sites, clearing space and allowing temporary expansion of the limpet patches. However, mussel domination returned cyclically as mussels settled or expanded laterally to encroach once again, so excluding the limpets from the primary space. This provides additional circumstantial evidence of competition for space between the alien

invader and the indigenous limpet that favours the former at high-exposure sites.

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