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Complex interplays between limpets and alien species in South Africa: multispecies interactions, zonation and size effects

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Integrating observations and experiments, we address the progressive effects of three alien species, the mussels *Mytilus galloprovincialis* and *Semimytilus patagonicus*, and the barnacle *Balanus glandula*, on limpet species in South Africa. We describe four aspects: (1) Interactions among algae, the limpet *Scutellastra granularis* and *M. galloprovincialis*. (2) The influences of *B. glandula* on *S. granularis* and on the periwinkle *Afrolittorina knysnaensis*. (3) Transformation of the zonation of *S. granularis* by the successive arrival of these three aliens. (4) Assessment of how effective the published predictors of the effects of *M. galloprovincialis* have been when applied to *S. patagonicus*. We conclude: (a) *Scutellastra granularis* improves mussel survival and condition by regulating algae that would otherwise overgrow and smother the mussels. (b) *Balanus glandula* has largely occupied the upper half of rocky shores, and at high densities depletes or eliminates suitable bare-rock habitat for *S. granularis*. However, it has positive effects on another gastropod, *A. knysnaensis.* (c) *Mytilus galloprovincialis* dominates the midshore and has positive effects on the recruitment of *S. granularis*, but negatively influences adults of this limpet, so that its size composition, density, reproductive output and zonation are all altered by this mussel. (d) *Semimytilus patagonicus* presents different challenges to those created by *M. galloprovincialis*, settling at much greater densities, lower down the shore, and reaching smaller maximum sizes. Rather than generating a favourable habitat for epizootic *S. granularis* recruits and juveniles, it almost completely excludes that limpet. We conclude that the influences of alien species are not readily predictable, depending on the nature of the invader and recipient species, environmental conditions and complex interactions among species. Collectively, the three alien species now cover almost all zones on wave-exposed rocky shores, completing the ‘zonation squeeze’ on limpets, but are less influential on wave-sheltered shores and in years when recruitment is low.

KEYWORDS

barnacles, competition, facilitation, invasive, mussels, patellids, algae, rocky shores

1 Introduction

This paper deals with three of the alien species that have occupied the shores of southern Africa, namely *Mytilus galloprovincialis* (Mediterranean mussel), *Semimytilus patagonicus* (bisexual mussel) and *Balanus glandula* (Pacific barnacle), and their interactions with the indigenous limpets, particularly *Scutellastra granularis*, as well as the effects of *B. glandula* on the indigenous periwinkle *Afrolittorina knysnaensis*.

All of these alien species have become dominant on southern African rocky shores and have spread substantially from their points of origin. *Mytilus galloprovincialis* arrived in the late 1970s (Grant and Cherry, 1985) and now covers over 2000 km of the coast from northern Namibia to the south-east coast of South Africa. *Balanus glandula* was first formally recorded in South Africa in 2008 but probably arrived as early as 1992 (Jenkins et al., 2008; Laird and Griffiths, 2008; Simon-Blecher et al., 2008). It currently occurs over 500 km of the southern west coast. *Semimytilus patagonicus* (until recently known as *S. algosus*) originated from Chile, arrived in Namibia as early as 1930 and abruptly spread from there to South Africa in 2009, where it now occurs over almost the entire west coast and has penetrated to a limited extent on the south coast (De Greef et al., 2013; Alexander et al., 2015a; Ma et al., 2020a; Ma et al., 2020b; Zeeman et al., 2020).

The sequential arrival of these species at Marcus Island in Saldanha Bay on the West Coast is documented by Robinson et al. (2007) and Sadchatheeswaran et al. (2015; 2018), who showed that (a) after its arrival, *M. galloprovincialis* formed deep beds and increased habitat complexity, consequently augmenting community diversity; (b) *S. patagonicus* failed to have these effects, and (c) in zones where *B. glandula* later replaced *M. galloprovincialis*, the simpler monolayered structure of this barnacle substantially reduced complexity and diversity.

The interactions between *M. galloprovincialis* and the indigenous brown mussel *Perna perna* on the south coast of South Africa have attracted particular attention (Erlandsson et al., 2006; Zardi et al., 2006; Hanekom, 2007; Nicastro et al., 2007; Zardi et al., 2007; Nicastro et al., 2008; von der Meden et al., 2008; Nicastro et al., 2010a; Nicastro et al., 2010b; von der Meden et al., 2010; Lathlean et al., 2016; synthesized in Branch and Branch, 2018). In brief, survival of *M. galloprovincialis* is greater higher on the shore, and that of *P. perna* lower on the shore, hence their partial segregation and continued coexistence.

Interactions between *M. galloprovincialis* and the limpet *S. granularis* have also been explored (Griffiths et al., 1992; Hockey and van Erkom Schurink, 1992; Branch et al., 2010). In short, dense beds of the mussel provide a haven for recruits of the limpet, boosting its numbers; but adults of the limpet are crowded out when they become too large to occupy mussel shells (Supplementary Figure S1). The demographics and normal zonation pattern of the limpet have consequently been transformed. Before the arrival of *M. galloprovincialis*, the limpet was one of a group of limpets that Branch (1975; 1976) termed 'migratory', in the sense that they settle low on the shore and then progressively migrate upshore as their size and tolerance to physical to physical stresses increases. Arrival of *M. galloprovincialis* has overturned that, as we describe in this paper.

Alien species are one of the major threats to the integrity of marine systems, increasingly transforming and homogenizing the nature of ecosystems world-wide (Thompson et al., 2002; Robinson et al., 2007; Pyšek et al., 2020), being 'a potent driver of change with no sign of saturation' (Ros et al., 2023, p81). They are amply living up to the prognosis for the future made in 2008 that by 2025 their rate of spread would have radically increased (Branch et al., 2008a). In South Africa alone, the rate at which alien species have been recorded has escalated exponentially from just one in 1950 to 95 by 2023 (Robinson et al., 2005; Griffiths et al., 2009; 2010; Mead et al., 2011a; Mead et al., 2011b; Robinson et al., 2016; Robinson et al., 2020; Van Wilgen et al., 2023).

Jennsen (2015) expresses a pessimistic view: 'You have loosed a chaotic, unstable element into the Mosaic. They will destroy everything.' The effects of alien species are, however, not all unmitigatedly negative. Some, such as the ascidian *Pyura praepucialis* in Chile increase habitat complexity and enhance biodiversity as a result (Castilla et al., 2004). Arrival of the Mediterranean or blue mussel *Mytilus galloprovincialis* in South Africa has boosted the food supplies of the African Black Oystercatcher *Haematopus moquini*, improving its conservation status by trebling of the rate at which pairs of birds raise two chicks rather than one (Hockey and van Erkom Schurink, 1992; Coleman and Hockey, 2008).

A central focus of our paper is that alien species have complex and unpredictable effects on the structure and functioning of South African rocky shores. Part of the reason is that their effects of are moderated by a range of factors, including geographic distribution (Ma et al., 2023), zonation (Rius and McQuaid, 2006), wave action (Steffani and Branch, 2003a; Steffani and Branch, 2003b; Hampton and Griffiths, 2007; Branch et al., 2010), responses to predators (Alexander et al., 2015a), resistance to desiccation (Nicastro et al., 2010a), attachment strength (Zeeman et al., 2018), the effects of upwelling (Xavier et al., 2007), and the relative sizes of organisms (Branch and Steffani, 2004).

A second focus of the paper is the interplay of patellid limpets with alien species. Patellids are dominant grazers and can influence alien species either directly by removing them or indirectly by controlling other species such as algae that may influence them. Firth (2021, p30) describes limpets as 'the champion grazers of the rocky intertidal zone'. From the pioneering experimental removals of *Patella* spp. in Great Britain (Jones, 1946; Lodge, 1948) that demonstrated limpet grazing and not wave action was responsible for keeping algal growth in check, through multiple other experiments, removal of limpets has consistently resulted in algal proliferation (Southward, 1964; Branch, 1981; Hawkins and Hartnoll, 1983; Branch, 1985; Farrell, 1988; Dye, 1995; Jenkins et al., 1999; Lindegarth et al., 2001; Arrontes et al., 2004; Phillips and Hutchison, 2008; Maneveldt et al., 2009; Tejada-Martinez et al., 2016). A common pattern is that removal of limpets is followed sequentially by development of a film of diatoms and sporelings, then emphemeral algae such as *Ulva* spp., and finally slower-growing corticated algae (Hawkins, 1981).

Added to this, limpets can act is 'bulldozers', reducing the abundance of small settlers of species such as barnacles (Menge et al., 2010; Ellrich et al., 2020). The situation is even more complex when other members of the community indirectly influence the outcome of interactions. Barnacles may aid settlement and survival of algae, but algal settlement can increase the mortality rate of the barnacles and enhance recruitment of limpets that then deplete the algae (Hartnoll and Hawkins, 1985). Cycles may arise in which the abundances of algae and limpets alternate over roughly 10-year periods (Little et al., 2017).

Considering the multiplicity of factors influencing the effects of both alien species and grazers, it is not simple to forecast their precise interactions, which can range from competitive exclusion to facilitation (Miyamoto and Noda, 2004).

This paper addresses four aspects of interaction between alien species and limpets on South African shores. The first concerns a three-way interplay between *M. galloprovincialis*, algae and *S. granularis*. Grazing by the limpet on shells of the mussel may control algal growth, but the benefits (or otherwise) of this for the mussel are not easy to predict, as grazing on the mussel shells weakens them (Day et al., 2000) and may offset any benefits. Second, the influence of *B. glandula* on the abundances of both *S. granularis* and the periwinkle *Afrolittorina knysnaensis* is explored. The latter was selected because of previous correlative evidence of the influence of *B. glandula* on it (Laird and Griffiths, 2008), which we verify experimentally. Third, the influences of *M. galloprovincialis*, *S. patagonicus* and *B. glandula* on the zonation of *S. granularis* are described. Finally, we turn to predictions previously made about why *M. galloprovincialis* has successfully dominated large portions of the coast of southern Africa (Branch and Steffani, 2004) and, drawing on both our results and information in the literature, we consider the applicability of these predictions when applied to the later arrival and spread of *S. patagonicus*.

We address four specific hypotheses:

1. Grazing by the limpet *S. granularis* will benefit *M. galloprovincialis* by preventing algal overgrowth. Conversely, the mussel will support high densities of *S. granularis*, but only small individuals.
2. Dense settlements of the alien barnacle *B. glandula* will exclude *S. granularis* but will enhance densities of the periwinkle *A. knysnaensis*.
3. The 'normal' progressively upshore migration of *S. granularis* to establish an increasing gradient of size and a decreasing gradient of density will be interrupted by the arrival of *M. galloprovincialis* and further altered by *S. patagonicus* and *B. glandula*.
4. Factors that successfully predicted the invasive capabilities of *M. galloprovincialis* will not be the same as those applicable to *S. patagonicus*.

2 Materials and methods

2.1 Interactions among limpets, mussels and algae

Manipulative experiments were conducted at two sites just south of Groenriviermond on the west coast of South Africa (Figure 1), approximately 450 km north of Cape Town: Island Point (30°54.93´S; 17°36.17´E) and Nina's Site (30°54.88´S; 17° 36.28´E), from January to June 2000, after which the plots were destructively sampled, and measurement of the variables taken as described below. Steffani and Branch (2003a) class both sites as exposed, experiencing average wave forces of 10.0-12.0 × 10^3 N m^{-2}, and they fall in an area of active upwelling with high productivity (Andrews and Hutchings, 1980), and high algal, limpet and mussel biomass (Bustamante et al., 1995b). Tidal range was 1.9 m.

Five replicate plots per treatment of 30×30 cm were established at each site (five replicates × four treatments × two sites). These were installed at the mid-tide level (tidal height 0.9 m), where *M. galloprovincialis* comprised 97% of all mussels present, and the limpet *S. granularis* constituted 95% of all limpets present. Plots that were designed to exclude limpets were surrounded by 5-cm-wide band of lead oxide antifouling paint, to control ingress or egress of limpets. Undisturbed control plots and three treatments were employed, as visualized in Figure 2A: (1) Control plots that contained both mussels and limpets (+M+L). (2) Limpet removal plots from which all limpets were removed (+M–L) and exclusion maintained by ongoing monthly removals. (3) Mussel removal plots (–M+L) in which mussels were removed, but any limpets that entered were allowed to remain there. (4) Removal of both mussels and limpets (–M–L). Monitoring took place monthly, when plots were inspected and the required treatments maintained; but only data for the terminal sampling are presented, partly to avoid temporal pseudo-replication, but also because that was when the plots were sampled destructively to allow full assessment.

The outcomes of these treatments were assessed by measuring: (a) algal % cover and composition; (b) mussel condition and percentage survival relative to original densities at the start of the experiment; (c) limpet sizes, densities, reproductive output for the populations (wet g m^{-2}), and life-time reproductive output per individual (wet g $indivual^{-1}$). For all variables except condition and reproductive output, scoring was done *in situ* and (where feasible) a second estimate obtained using photographs of plots. The greater of these two values was accepted as being the most accurate. Population reproductive output was calculated from the counts and size composition of limpets measured per plot, converting sizes to ages using regressions taken from data in Branch (1975), and ages to wet-mass reproductive output per annum per plot, based on conversions derived from data in Branch (1974a). Life-time outputs per individual were calculated for standard individuals occupying mussels or rock, taking into account average survivorship per year, and outputs per annum summed over a lifespan, also based on survivorship and size-related annual reproductive outputs in

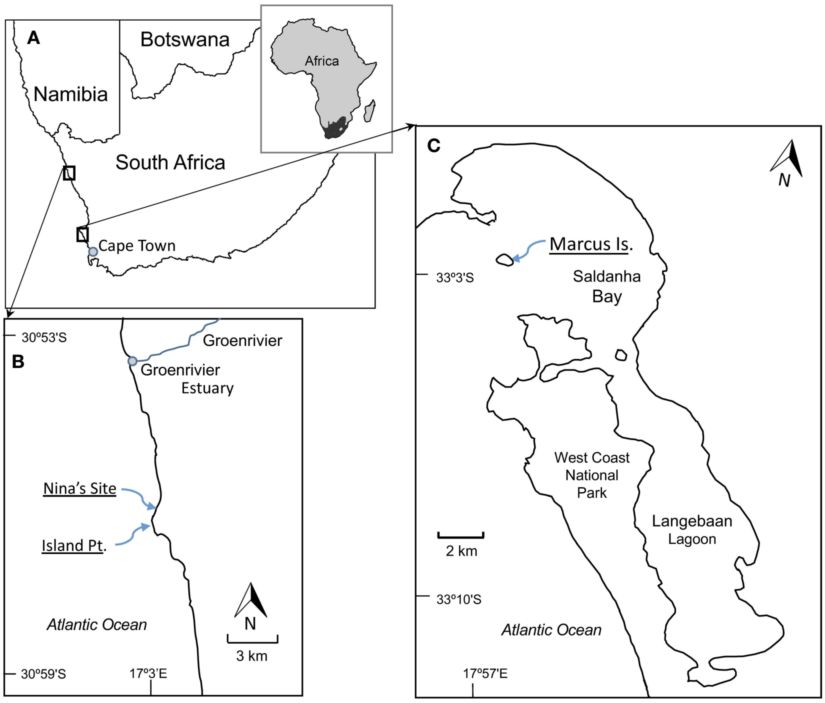

FIGURE 1
Maps of Africa and South Africa **(A)** and details **(B, C)** of the study sites (names underlined).

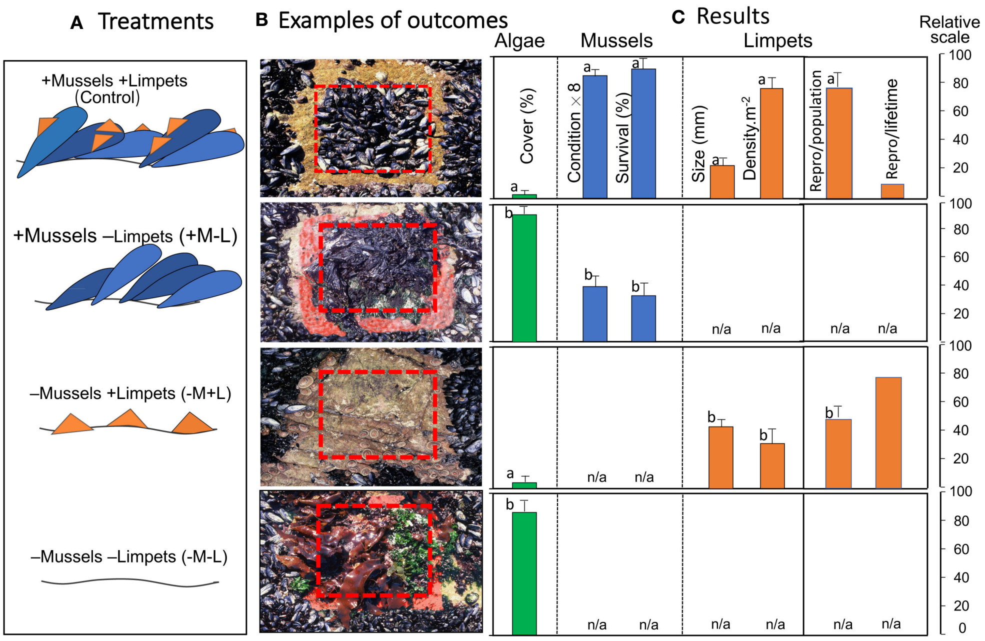

FIGURE 2
(A) Design of a field experiment to assess the interplay between the alien mussel *M. galloprovincialis*, the limpet *S. granularis* and algae. **(B)** Visual examples of outcomes. **(C)** Results showing the proliferation of algae in absence of limpets, better condition and survival of mussels in presence of limpets, and a drastic decline in lifetime reproductive output of (smaller) limpets that live on mussels versus rock, despite their greater densities. Data are mean values +1SD, n = 10; except for reproductive output per lifetime, which is a single calculated value. The data are standardised to the same scale of 0-100 in units specified for each variable, but values for condition have been multiplied by a factor of eight to improve visibility. Repro/population = the reproductive output (g wet mass m^{-2} yr^{-1}) of the population, calculated from replicate plots. Repro/lifetime = the reproductive outputs (g wet mass) per individual calculated over its lifetime, assuming individuals remain on shells or on rocks. No error term is attached to this value as it constitutes a single calculation. n/a, not applicable due to the absence or one or more taxa from the treatment. Lower case letters above bars differ if treatment were significantly different.

Branch (1974a; 1974b). These two measures are distinctly different and not necessarily correlated. The population reproductive output estimates the output per annum per unit area for each plot, so that a mean (and SD) value can be calculated for the population as a whole. The life-time reproduction is a single composite measure of what an individual (standard) limpet will achieve over its estimated lifespan. The former measure is relevant to population dynamics; the latter to the evolutionary reproductive success of individuals that remain on mussels or live on rocks. Both can be calculated for limpets on either mussels or rocks, making the assumption that individuals will remain there throughout their lives.

Mussel condition was determined from subsamples of 20 mussels (40-50 mm shell length) per plot taken at the end of the experiment and was measured as (dry) body mass divided by shell mass × 100 (Steffani and Branch, 2003a). For mussel survival, only mussels classed as adult, i.e., > 35 mm shell length, were counted, as those smaller than that were too difficult to score accurately at the start of the experiment. For the same reason, for limpet densities, only individuals > 10mm were counted.

To test for possible 'cage' (i.e., paint) effects on limpet presence or absence and algal growth, procedural controls with paint applied just at the corners of plots were established. We hypothesized entry of limpets would not be precluded by the paint, and that if limpets did enter the plots, they would control algal growth, but that if they did not, algal growth would proliferate to the same extent as in fully enclosed plots excluding limpets.

2.2 Barnacles, limpets and periwinkles

Interactions between *B. glandula* and *S. granularis*, and between *B. glandula* and the littorinid *Afrolittorina knysnaensis* were assessed at Marcus Island [33°02.59´S; 17°58.26´E; Figure 1)], starting April 2012, shortly after the barnacle was detected there, during a period when it covered extensive portions of the mid to high shore at tidal heights of 0.99 to 1.39 m above spring low-tide levels (SLT). Tidal range was 1.96 m and wave force rated as exposed, averaging 11.3×10^3 N m^{-2} (Sadchatheeswaran et al., 2015).

Interactions were assessed in two ways: (a) by first determining correlations between the numbers of barnacles and either limpets or littorinids, which provided information on natural patterns of relative abundance, and (b) by using manipulative experiments that followed immediately after the correlative data had been collected, to experimentally explore the responses of limpets or littorinids to barnacle cover, providing an independent cause-and-effect test of the relationship between barnacles and these species.

Correlations between the abundances *B. glandula* (% cover) and *S. granularis* and *A. knysnaensis* (counts) were determined from 50 randomly placed 14.1 × 14.1 cm quadrats, in the mid shore for *S. granularis*, and high shore for *A. knysnaensis*. Densities were converted to numbers m^{-2} for presentation.

For the manipulative experiment, six replicates of three treatments were established in plots of 20 × 20 cm at these two respective shore heights, in each of two areas separated by 50 m. Treatments comprised (a) control plots of in which *B. glandula* covered 95-100% of the substratum (Supplementary Figure S2), which were left unaltered (+*Balanus*), (b) removal plots of the same size in which 50% of the barnacles were removed, and (c) all barnacles were removed by scraping to bedrock (-*Balanus*). Numbers of any *S. granularis* that occupied plots were recorded after 1 month, and sizes estimated from either the total sample, or from a subsample of the first 50 individuals encountered per plot if numbers exceeded this. Subsampling was employed only after test sampling showed that 50 individuals were sufficient to secure a mean measure within 3% accuracy of that from total samples of up to 90 individuals.

2.3 Effects of alien species on zonation of *S. granularis*

To test the extent to which the arrival of *M. galloprovincialis*, *S. patagonicus and B. glandula* has altered the previously described progressive 'migratory' up-shore movement of *S. granularis* (Branch, 1975; see also Table 1, and hypothesis 3 in introduction), data on the densities and sizes of *S. granularis* were obtained from Marcus Island in April 1970 before the detection of any alien species; in April 2001 after *M. galloprovincialis* had become established and was at its peak abundance, and in April 2012 when *M. galloprovincialis* had diminished but *S. patagonicus* and *B. glandula* were established. On five replicate vertical transects up the shore and within quadrats of 1.0 × 0.5 m, five zones were surveyed, designated as Infratidal (0.0-0.1 m above SLT), Low (0.25-0.30 m), Mid (0.85-0.95 m), High (1.10-0.26 m) and Top (1.30-0.1.56 m). Densities were converted to numbers m^{-2}.

2.4 Predictors of the invasive success of *S. patagonicus*

To assess the features that could be used to predict successful invasions of respectively *M. galloprovincialis* and *S. patagonicus*, we integrated our results with published material (mainly Branch and Steffani, 2004; Zeeman et al., 2018, but also papers cited in Table 2), based on a literature search of journal articles in google and scholar.google.com for key words *Semimytilus algosus, Semimytilus patagonicus*, Mytilidae, mytilids, mussels.

2.5 Statistical analyses

For interactions among limpets, mussels and algae at Groenrivier, a two-way analysis of variance (ANOVA) with treatments nested in sites showed that differences between sites were non-significant for all variables: $ANOVA_{1,4}$, $p > 0.25$, so the data for the two sites were pooled (Quinn and Keough, 2002). In the case of algal cover, for which four treatment levels could be compared, the assumptions of normality and equality of variance for ANOVA could not be met even after transformations, so a non-parametric Kruskal-Wallis test was applied, followed by Dunn *post-hoc* comparisons among treatments. For the remaining variables

TABLE 1 (A) Summary of features characterising migratory and non-migratory limpets, derived from Branch (1975) and Lindberg (2007), and (B) how these have changed (bold entries) or not changed for *Scutellastra granularis* after the arrival of first *Mytilus galloprovincialis*, and later *Semimytilus patagonicus* and *Balanus glandula*.

(A)	Features of Migratory species	Features of Non-migratory species
	1. Settle low on shore, then shift upshore. Density drops but size increases upshore	1. Settles low on shore, remain there for life. Densities and sizes unrelated to zonation
	2. None are territorial	2. Many are territorial
	3. None 'garden' algal patches	3. Many 'garden' algal patches
	4. Diets are generalized and diverse	4. Diets specialised and narrow
	5. Growth often fast, gonad output high, longevity low	5. Growth usually slow, gonad output low, longevity high
	6. No differentiation between juveniles and adults	6. Strong differentiation between juveniles and adults
(B)	Features of *S. granularis* zonation in 2001, post-*Mytilus* arrival	Features of *S. granularis* in 2012 post-*Semimytilus* & *Balanus* arrival
	1. Settles mid- to high shore in *Mytilus* beds, shifts up and down with age	**1. Settles mid shore in *Mytilus* beds, shifts upshore; excluded from the low shore**
	2. Not territorial	2. Not territorial
	3. Does not 'garden' algal patches	3. Does not 'garden' algal patches
	4. Diet generalised and diverse	4. Diet generalised and diverse
	5. Growth slower in *Mytilus* beds, reproduction and longevity reduced there	**5. Growth slower in mussels; reproduction, density and longevity very low in *Semimytilus* zones**
	6. Strong differentiation between juveniles on *Mytilus* and adults on bare rock	**6. Juveniles on *Mytilus*; excluded from low shore by *Semimytilus*, Adults in top-shore**

where only two treatment levels existed (mussel condition/survival, limpet densities/sizes, population reproductive output), the assumptions of normality (assessed with normal probability plots) and of equal variances (accepted if ratios of variance did not differ by more than a factor of five; Quinn and Keough, 2002) were met without transformation, and Students t-tests applied. Life-time individual reproductive outputs were calculated for idealized individuals, thus yielding single values for limpets on mussels versus rocks, so no statistical tests of their difference were possible.

For the field-sampled relationship between *B. glandula* on the densities of respectively *S. granularis* and *A. knysnaensis*, Pearson's correlation coefficients were determined. For the manipulative experiment, differences between the two areas were again non-significant (ANOVA$_{1,5}$ P >0.25 in all cases) so the data were pooled for analysis. Densities of *S. granularis* could not be normalized and the variances remained unequal even after transformation because there were multiple zero values for the +*Balanus* treatment. We therefore applied Kruskal-Wallis tests followed by Dunn *post-hoc* comparisons among treatments. For *Afrolittorina knysnaensis* abundance, assumptions of equality of variance and normality (assessed as above) were met and the data analyzed without transformation. For sizes, normality and equality of variance were achieved by log-log transformations and one-way ANOVAs were applied to those data, followed by Tukey *post-hoc* tests of any significantly different data.

To test for differences in densities and for sizes of *S. granularis* amongst the five zones, the years (1970, 2001 and 2012) and their interaction, a two-way ANOVA was run with years and zones as fixed factors, using the aov function in R (R Core Team, 2019). For density, the data were log (x+1) transformed to meet assumptions of normality and equality of variance. The data for sizes did not require transformation, and were averaged for each quadrat (i.e., within each zone and transect) to achieve a balanced ANOVA design. No limpets were present in three of the five replicate samples in the infratidal zone and in these cases missing size data were substituted with dummy values without altering the mean and variance of the model cell. Tukey HSD was used for posthoc comparisons.

3 Results

3.1 Interactions among limpets, mussels and algae

There was no significant 'cage' (i.e., paint) effect. Limpets entered cage control plots in 7/10 cases, and inhibited algal growth, the abundance of which remined low and did not differ significantly from the respective +M+L and –M+L treatments (t-tests, df =8, p > 0.05 in all treatments). For the remaining control plots (3/10), limpets failed to enter, algae flourished and reached levels not significantly different from +M–L and –M–L treatments (t-tests, df =8, p > 0.05 in all treatments). In short, limpets were not inhibited from entering by partial 'cages', and algal growth depended on the presence or absence of limpets, not on the extent of the paint enclosure.

In the experimental plots that were fully enclosed with paint, the limpet *S. granularis* never entered plots from which they had been removed. In plots containing limpets, their densities remained within 85-100% of initial densities. Thus, the –L and +L conditions were effectively maintained.

In plots with the limpet *S. granularis* present (+M+L and -M+L), minimal amounts of algae became established, whereas plots from which the limpet was excluded (+M-L and -M-L) developed a prolific cover of close to 100% (Figure 2). The differences were significant (Kruskal-Wallis H = 29.95, df = 36; p < 0.0001), and Dunn *post-hoc* tests showed that significant differences (p < 0.05) were restricted to the two +L treatments versus the two -L treatments.

In plots that contained mussels, body condition and survivorship of mussels were both significantly lower in –L treatments, in which the mussels were covered by a dense algal growth, than in +L plots (Figure 2), with the differences being significant (t-tests = 20.18 and 28.58 respectively, df = 18, p < 0.0001 in both cases).

Limpet sizes were significantly smaller, and limpet densities significantly greater, in plots that contained mussels than in those lacking mussels (Figure 2; t-tests = 8.28 and 9.79 respectively, df =18, p < 0.0001 in both cases). Limpet reproductive output calculated per unit area for the population on mussels was about 1.33 times that of limpets on rocks in areas without mussels, the difference being significant (t-test = 2.58, df = 18, p = 0.018). Conversely, life-time reproductive output of those on rocks was about 7.9 times greater than that of limpets on mussels (Figure 2).

3.2 Barnacles, limpets and periwinkles

In the mid shore to high shore at Marcus Island, densities of *S. granularis* were significantly negatively correlated with those of the alien barnacle *B. glandula*, whereas those of the littorinid *Afrolittorina knysnaensis* were significantly positively correlated with *B. glandula* (Figure 3).

In the experimental plots in which the barnacles were left untouched, thinned by 50% or removed altogether (Figure 4A), the densities and sizes of *S. granularis* that became established were significantly different among all three treatments (Respectively Kruskal-Wallis H = 21.210, df = 2, n = 26, P < 0.0001, Dunn *post-hoc* tests P < 0.05 among all three treatment for sizes; and ANOVA $F_{2,27}$ = 66.807, P < 0.0001 and Tukey posthoc tests P < 0.05 among all treatments for densities).

For *A. knysnaensis* (Figure 4B), densities in the three treatments differed significantly (Kruskal-Wallis H = 25.865, df = 2, n = 30, P < 0.0001; Dunn *post-hoc* test P < 0.05 among all three treatments). Sizes did not, however, differ among treatments (ANOVA F = 0.059, df = 2,27, P = 0.94).

3.3 Effects of alien species on zonation of *S. granularis*

The densities of *S. granularis* on Marcus Island were significantly affected by an interaction between zones and years (ANOVA, F = 34.52, DF = 8,60, P <0.0001). *Post-hoc* Tukey tests showed that this was because of a shift from a progressive decrease in limpet density up the shore in 1970, to (a) a concentration in the mid and high shore, where the limpet increased from around 20 m^{-2} in 1970 to about 65 m^{-2} in 2001 when *M. galloprovincialis* had become dominant, and (b) declines in abundance of *S. granularis* in 2012 to about 2 m^{-2} in the infratidal and low-shore zones (Figure 5A) with the arrival and establishment of *S. patagonicus*, and to around 5-10 m^{-2} in the high zone associated with declines in *M. galloprovincialis* abundance and the range of its zonation, and the establishment of *B. glandula* in the high shore.

The sizes (shell lengths) of *S. granularis* (Figure 5B) also changed among years and zones with a significant interaction (ANOVA, F = 226.1, DF = 8,60, P <0.0001), which affected interpretation of the effects of year and zone. The interaction arose mainly from a reversal in of the 1970 pattern of an upshore increase in size, to one with smallest sizes in the mid and high shore, and then a restoration in 2012 to close to the original 1970 pattern of zonation. Tukey *post-hoc* tests showed this was attributable to (a) declines in the sizes of limpets in the mid to top-shore in 2001, associated with the occupation of *M. galloprovincialis* shells by limpet recruits and juveniles in the mid and high shore, and their

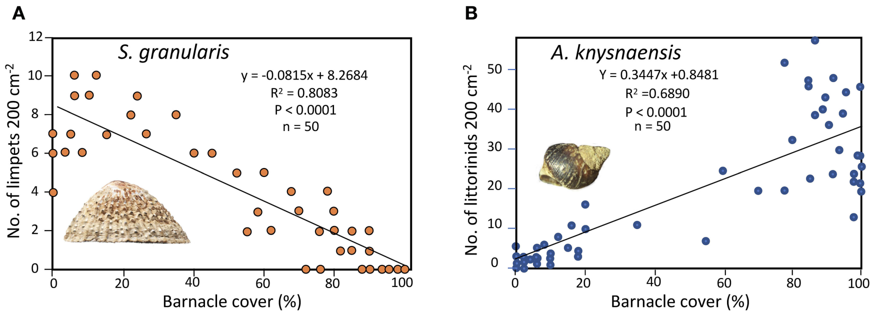

FIGURE 3
Densities of **(A)** the limpet *Scutellastra granularis* and **(B)** the littorinid *Afrolittorina knysnaensis* relative to the percentage cover of the alien barnacle *Balanus glandula* at Marcus Island, South Africa.

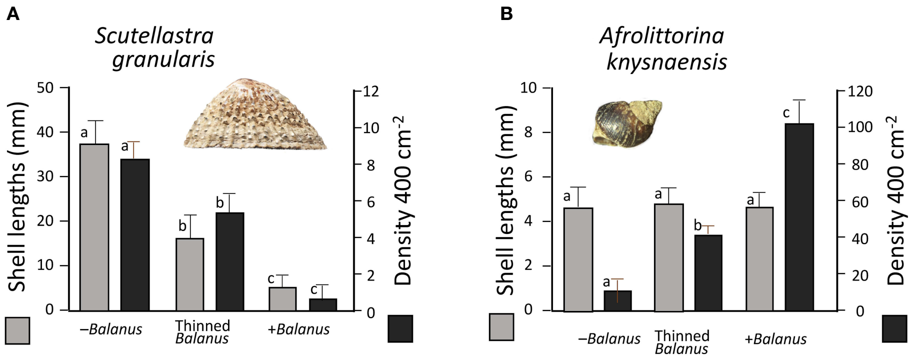

FIGURE 4
The sizes and densities of **(A)** *Scutellastra granularis* and **(B)** *A. knysnaensis* at Marcus Island, in relation to the three treatments of −Balanus (complete removal of barnacles), Thinned Balanus (removal of 50%) and +Balanus (natural density of barnacles close to 100%). Values are means +1SD; lowercase letters differ for treatments that were significantly different on *post-hoc* tests.

migration from there into both the infratidal and the top-shore zones, (b) radical reductions of sizes of the limpet in 2012 in the infratidal and lowshore, coinciding with the arrival of *S. patagonicus*, and (c) increases in size in the mid- to high shore with a reduction in the cover of *M. galloprovincialis* and arrival of *B. glandula* in the mid to high shore. Sizes in the top-shore, which was above the zonation range of any of the alien species, remained the highest or the second-highest values across all three periods.

In the context of classifying limpets as either migratory or non-migratory, Table 1A summarises the characteristics of these two groups, and Table 1B lists how the zonation patterns of *S. granularis* have changed from before to after the arrival of alien species.

3.4 Predictors of the invasive success of *S. patagonicus*

Table 2 synthesises nine potential predictors of invasion success. All proved applicable to *M. galloprovincialis*; but only seven were relevant for *S. patagonicus*, as we amplify in the discussion.

4 Discussion

As McQuaid and Arenas (2009, pp 316-317) note: ‘the effects of invasive species are highly dependent on their ecological context …

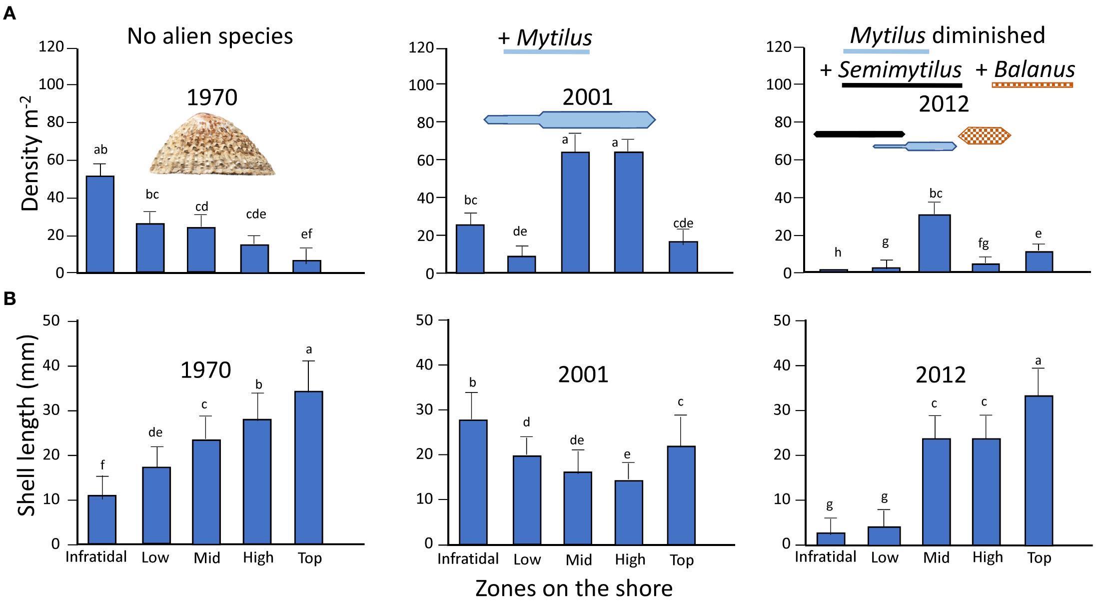

FIGURE 5
Densities **(A)** and sizes **(B)** of the limpet *S. granularis* in relation to zonation, in 1970 prior to arrival of alien species, in 2001 after arrival of *M. galloprovincialis* and in 2012 when *M. galloprovincialis* had diminished and *S. patagonicus* and *B. glandula* had arrived. Kite diagrams non-quantitatively show the relative zonation and abundance of alien species, coded by species. Values are means +1SD. Lower-case letters are shared if values are not significantly different.

TABLE 2 Efficacy of applying the characteristics of *Mytilus galloprovincialis* to predict its invasive capabilities and effects as an alien species, compared to their efficacy when applied to *Semimytilus patagonicus.*

Predictors of invasion success by features of the species	Applicability to *Mytilus*		Applicability to *Semimytilus*	
1. History of invasiveness	✓	Mediterranean and European NE Atlantic origin: now world-wide in temperate seas[1]	✗	Native to Ecuador, Peru, Chile. Arrival in Namibia 1931. Abrupt arrival and rapid spread in South Africa 2009[12]
2. Physiological superiority	✓	Rapid growth, desiccation-tolerant[2]; fast uptake of food[3]	✗	Slow growth, desiccation intolerant; moderate rate of food intake[14]
3. Reproduction, recruitment and dispersal	✓	High reproductive output, high settlement, fast dispersal[4]	✓✓	High reproductive output; exceptionally high recruitment; rapid spread[13]
4. Better performance at strong wave action	✓	Faster individual & population growth, greater abundance and greater settlement at strong but not extreme wave action[5]	✓	Densities and sizes greatest at localities with strong wave action[15]
5. Provide more food for predators	✓	Abundances of oystercatchers and whelks increased since arrival of mussel[6]	✓	Consumed by gulls[16]; but unlikely to affect gull numbers as they are increasing due to use of human sources of food[17]
6. Sizes of mussel and limpets affect interactions	✓	Large enough and sufficiently longlived to support small limpets but not large individuals or species[7]	✓	Too small and short-lived to support epibiotic limpets[18]
7. Zonation affects interaction with native species	✓	Dominates mid to high-shore zones; often excluded from lowshore by wave action due to weak attachment[8]	✓	Dominates low on the shore; excluded from higher zones by intolerance of physical stress[19]
8. Escape from predation	✓	Predation rates incapable of controlling mussel due to high recruitment rate[9]; individual whelks, lobsters and starfish prefer indigenous mussels, but conditioning changes the lobsters' preference to alien species, and in combination lobsters and whelks alter prey preferences[10]	✓	Heavily predated upon by gulls & oystercatchers; but predators incapable of limiting mussel populations[20]
9. Freedom from parasites	✓	Low rate of parasitism compared with *Perna*[11]	✓	Parasite load nil to extremely low[21]

[1] Branch and Steffani, 2004; Zardi et al., 2018; Lins et al., 2021.
[2] van Erkom Schurink and Griffiths, 1993; Branch and Branch, 2018; Zeeman et al., 2018.
[3] Alexander et al., 2015b.
[4] van Erkom Schurink and Griffiths, 1991; Reaugh-Flower et al., 2011; Branch and Branch, 2018; Zeeman et al., 2018.
[5] Steffani and Branch, 2003a; Steffani and Branch, 2003b; Steffani and Branch, 2003c; Branch and Steffani, 2004; Hammond and Griffiths, 2003; Rius and McQuaid, 2006; Branch et al., 2008b; Pfaff et al., 2011; Hoffmann et al., 2012; Skein et al., 2018a
[6] Hockey and van Erkom Schurink, 1992; Branch and Steffani, 2004.
[7] Griffiths et al., 1992; Hockey and van Erkom Schurink, 1992; Branch and Steffani, 2004.
[8] Bownes and McQuaid, 2006; Bownes and McQuaid, 2010; Rius and McQuaid, 2006; Rius and McQuaid, 2009; Zardi et al., 2007; Hoffmann et al., 2012.
[9] Branch and Steffani, 2004; Reaugh-Flower et al., 2011; unpublished experiments manipulating whelk densities.
[10] Alexander et al., 2015b; Robinson et al., 2015; Skein et al., 2018b; Skein et al., 2020; Alexander et al., 2022.
[11] Calvo-Ugarteburu and McQuaid, 1998a; Calvo-Ugarteburu and McQuaid, 1998b.
[12] De Greef et al., 2013; Ma et al., 2020a; Ma et al., 2020b; Zeeman et al., 2020.
[13] Branch and Branch, 2018; Zeeman et al., 2018.
[14] De Greef et al., 2013; Zeeman et al., 2020.
[15] De Greef et al., 2013; Zeeman et al., 2020.
[16] Personal observations.
[17] Steele, 1992.
[18] Current paper.
[19] De Greef et al., 2013; Zeeman, 2016; Skein et al., 2018a.
[20] Calculation based on per capita consumption and abundance.
[21] GMB and ZZ personal observations.
(Derived from Branch and Steffani, 2004, with two additional features.).
Tick = applicable; double tick = strongly so, and crosses = inapplicable.

difficult to predict … idiosyncratic and context-dependent'. Indeed, that was true in our results, with differences emerging even between the two invasive mussels, despite their being members of the same family, Mytilidae. Nevertheless, key principles emerged about the factors influencing the effects of the alien species:

1. The interactions were between organisms with very different trophic needs and lifestyles: sessile phototrophic algae, mobile herbivorous grazers, and sessile filter feeders. Space was the common resource over which competition took place. Space is an absolute requirement (Branch, 1984) and if it is insufficient, exclusion of subordinate competitors is likely. However, offsetting this, intertidal organisms can provide secondary space for epibionts even if they dominate primary space.
2. Size matters. Occupation of secondary space on shells depends on the relative size of the host and the epibiont.
3. Abundance powerfully affects competitive capability, and is influenced by settlement and recruitment rates, which can vary temporally and spatially, often with considerable vagaries (Underwood and Fairweather, 1989).
4. Ecological traits have proved valid predictors of the competitive advantages and invasive capabilities of *M. galloprovincialis* (Branch and Steffani, 2004). These include tolerance to thermal stress and desiccation, which can set differential vertical zonation patterns and potentially lead to spatial segregation that ameliorates competition. Differential adaptations to wave action and upwelling may determine horizontal differences in abundance, again moderating competition. In the concluding section of this discussion, we revisit the conclusions of Branch and Steffani (2004) to inquire how many of the successful predictions made about the invasive capability of *M. galloprovincialis* are applicable to *S. patagonicus*.

We explore these perspectives below, in the context of the four experimental and comparative cases we examined.

4.1 Interactions among limpets, mussels and algae

The capacity of limpets to control algal growth is amply demonstrated by a plethora of limpet removal experiments (see references in the introduction). In addition, evidence arises from marine protects areas (MPAs) in which protection from harvesting has increased limpet abundances and consequently decreased algal abundance (Micheli et al., 2005; Martins et al., 2010; Baliwe et al., 2022). In inaccessible areas such as islands, limpet numbers are often greater than in accessible mainland localities, increasing food supplies to predators such as oystercatchers which, in turn, reduce the numbers of limpets and confine them to vertical surfaces out of reach (Hockey and Branch, 1983; Branch, 1985; Branch et al., 1987; Lindberg et al., 1998). The effects of limpets on macroalgae cascade downwards to encrusting algae, which benefit because they would otherwise be overgrown (Steneck, 1982), and their speed of lateral growth – and, hence, ability to occupy space – is increased by grazing (Vanmari and Maneveldt, 2019). The ripple effects of grazers such as limpets thus extend up and down interaction chains.

Whereas the influence of *S. granularis* on macroalgal growth was predictable, the effects of algae on mussels were not. Others have reported that overgrowth by algae has detrimental effects on mussels, reducing growth and reproductive output (Dittman and Robles, 1991), density (Albrecht and Reise, 1994), productivity (Metri et al., 2002) and survivorship (O'Connor et al., 2006).

Our research on the three-way interaction between limpets, mussels and algae showed conclusively that *M. galloprovincialis* benefitted from the presence of limpets on their shells, improving their body condition and survival. The nearest parallel to our study is one by Miyamoto and Noda (2004), who tested the effects of grazers (two *Lottia* spp. and two littorinids) on algae growing on mussels. Unlike our study, they concluded that grazers had only minimal effects on the growth of algae. Grazing effects on host mussels are thus not universal.

Because *M. galloprovincialis* is relatively large, its shells provide secondary habitat for limpets, but limpets may use this only if they are sufficiently small. Miyamoto and Noda (2004) recorded densities of small (6-14 mm) *Lottia* spp. were 20 times greater on the mussel *Septifer virgatus* than on bare rock. Small (mostly juvenile, 3-25 mm) *S. granularis* reached much higher densities on mussels that on bare rock; but larger individuals (adults 25-65 mm) were excluded from the mussel beds and limited to bare rock, as previously reported (Griffiths et al., 1992; Hockey and van Erkom Schurink, 1992; Branch et al., 2008b).

While densities of *S. granularis* rise significantly on mussel beds, mean sizes are reduced. Individuals of < 0.8 g wet somatic mass (ca. 10-24 mm shell length) are pre-reproductive. At larger sizes, reproductive output per annum increases linearly with somatic mass and exponentially with shell length (Branch, 1974a; Branch, 1974b). Our results (Figure 2) show that taking into account densities and sizes and translating these to reproductive output yields two interesting facts. Firstly, reproductive output for the *population* (g yr^{-1} m^{-2}) is about 30% greater in mussel beds than that for limpets living on bare rock, with the greater densities of limpets in mussels more than offsetting their smaller sizes there. Secondly, and in contrast, from an evolutionary, life-time perspective, each *individual* limpet will achieve a much greater output – around seven times – if it spends its life on rock rather than in mussels, because it will achieve a much greater maximum size and greater longevity. This approximation is of course simplistic in that it assumes a given limpet will spend its whole life on mussels or on rock: but it is not unrealistic, given that the extensive cover of *M. galloprovincialis* in many parts of the west coast of South Africa (Supplementary Figure S1) leaves them no option but to occupy mussel shells, and the fact that prior to the arrival of this mussel (and in areas where it is sparse or absent), *S. granularis* spends its entire life on bare rock (Griffiths et al., 1992; Hockey and van Erkom Schurink, 1992).

Mytilus galloprovincialis has much worse effects on another co-occurring indigenous South African limpet, *Scutellastra argenvillei*, which is much larger (up to 95 mm) and matures sexually at about 47 mm. Dense mussel beds reduce its density, survivorship and homing fidelity (Ruiz Sebastián et al., 2002), confining it to small patches (Supplementary Figure S3), and no *S. argenvillei* ever reaches sexual maturity on mussel shells (Steffani and Branch, 2005).

Wave action does, however, moderate the effects of *M. galloprovincialis* on *S. argenvillei*. Abundance of *M. galloprovincialis* peaks at strong (but not extreme) levels of wave action, where food supply for the mussel is optimal (Bustamante and Branch, 1996); and the densities, sizes and reproductive potential of *S. argenvillei* are substantially reduced under those conditions. In contrast, at moderate levels of wave action the mussel settles and grows at lower rates, and the two species co-exist with minimal effects on each other (Steffani and Branch, 2003b; Steffani and Branch, 2003c; Branch and Steffani, 2004). Both the size of *S. argenvillei* and the intensity of wave action thus influence the outcome.

Various other factors influence the magnitude, speed and even direction of such interactions among mussels, barnacles, algae and limpet including geographic differences related to physical stress (Arrontes et al., 2004; Jenkins et al., 2005; Coleman et al., 2006; Crowe et al., 2011) and differences in mode of feeding. Not all limpets are conventional roam-and-scrape feeders. Some defend algal patches or garden specific algae (Stimson, 1973; Branch, 1975; Branch et al., 1992; McQuaid and Froneman, 1993), or trap drift algae (Bustamante et al., 1995a; Bustamante and Branch, 1996), and their effects on algal growth will be substantially less. The effects of limpet grazing on algae also depend on algal productivity. In New Zealand, limpet grazing has substantial effects at low-nutrient sites but not at upwelling sites (Guerry and Menge, 2017). Our study at Groenriver was, however, conducted in an area of active upwelling (Andrews and Hutchings, 1980) and high algal productivity (Bustamante et al., 1995b), yet the effects of limpet exclusion were decisive.

4.2 Barnacles, limpets and periwinkles

Our results show that the barnacle *B. glandula* has negative effects on *S. granularis* but positive effects on littorinids. There are many other examples of negative barnacle-limpet interactions (Dayton, 1971; Branch, 1976; Hawkins, 1983; Dungan, 1986; Santini et al., 2019; Ellrich et al., 2020), but in New South Wales, Creese (1982) showed that a small species of limpet, *Patelloida latistrigata*, benefits from the presence of barnacles that provide a refuge from competition with a larger species of limpet, *Cellana tramoserica*, which is excluded because it cannot move over and feed effectively on barnacles. Again, size matters.

The effects of *B. glandula* on *S. granularis* are particularly severe for two reasons. First, indigenous barnacles are generally scarce on the west coast of South Africa (Boland, 1997). In particular, there is a large gap in distribution of the native high-shore *Chthamalus dentatus* between Namibia and the south coast of South Africa (with genetic differences between the two populations of *C. dentatus* suggesting they are separate species; Motro et al., 2023). This gap is now filled by *B. glandula*. Second, *B. glandula* predominates in the high shore where there was previously a void in occupation of the shore by barnacles. Our demonstrations that the barnacle *B. glandula* has negative effects on *S. granularis* but positive effects on littorinids, support previous findings by respectively Griffiths et al. (1992) and Laird and Griffiths (2008).

4.3 Effects of alien species on zonation of *S. granularis*

The successive advents of *M. galloprovincialis*, *S. patagonicus* and *B. glandula* have radically altered the zonation patterns of *S. granularis*. Prior to their arrival, *S. granularis* was recognized as a typical member of a group of 'migratory' limpets that Branch (1975; 1976) distinguished on the grounds that they settle low on the shore and then migrate progressively upwards as they age, in contrast to 'non-migratory' species that remain in the same zone as they settle throughout their lives. Table 1A summarises the features of migratory and non-migratory southern African species of patellid limpets. Hobday (1995) has demonstrated for the limpet *Lottia digitalis* that this zonation pattern is maintained by migration. Arrival of *M. galloprovincialis* changed those patterns (Table 1B). Most notably, recruits and juveniles of *S. granularis* became concentrated in beds of *M. galloprovincialis* and then shifted both up and down the shore with an increase in size (and age). The advent of *S. patagonicus* and *B. glandula* brought further changes. Low on the shore where *S. patagonicus* predominates, *S. granularis* is virtually excluded and no individuals over 8 mm recorded were recorded there. Upwards migration of *S. granularis* from the (diminished) recruitment beds of *M. galloprovincialis* into the top zone did restore a semblance of the size-zonation pattern originally present, but high densities of *B. glandula* in the high zones largely exclude the limpet. Both *S. patagonicus* and *B. glandula* constitute a poor substratum for the limpet: the former because of its small size and short life, which make it an unsuitable host, and the latter because its rough texture makes attachment and feeding problematic – both difficulties that Creese (1982) suggests large limpets will experience among barnacles.

4.4 Predictors of the invasive success of *S. patagonicus*

Ros et al. (2023) bemoan that little research has compared whether the ecosystem impacts of alien species are related to their life-history traits. Based on comparisons of such traits among South African mussels, Branch and Steffani (2004) advanced seven predictors of whether the characteristics of *M. galloprovincialis* influence its capacity to invade. With subsequent research, including the results reported in this paper, it is possible to extend the list of predictors for *M. galloprovincialis* to nine (Table 2), and to then use those traits to explore the extent to which they have proven valid predictors of the invasions recorded for *S. patagonicus*.

The almost world-wide invasion of temperate waters by *M. galloprovincialis* made it an obvious predictor that it would invade South Africa (Table 2, item 1). It was not, however a useful predictor of the arrival of *S. patagonicus*, which was first described from material in Argentina (d´Orbigny, 1842, p 647), but has not been recorded there since (Signorelli and Pastorino, 2021), apart from transient records of it on fishing-boat hulls in 2013 (Bigatti et al., 2014). Thus, there was no evidence of it invading other parts of the world before its arrival in Namibia in 1931. Its subsequent spread in that country, abrupt and dense settlement in South Africa in 2009 and recent rapid range expansion there (Zeeman et al., 2018; Ma et al., 2020a; Ma et al., 2020b) were therefore not events predictable by any history of invasions elsewhere. Likewise, the physiological superiority exhibited by *M. galloprovincialis* in terms of its rapid growth, desiccation tolerance, shell strength and food uptake rate (Alexander et al., 2015b; Zeeman et al., 2018) associated with its invasion capabilities was not evident in *S. patagonicus* (Table 2, item 2).

The most successful predictor of the capacity of *S. patagonicus* to invade and spread in Namibia and South Africa was its astounding rate of recruitment (Table 2, item 3), reaching around 2-5 million recruits m^{-2} in the low shore, orders of magnitude greater than that of any of the indigenous mussels (Reaugh-Flower et al., 2011). The remaining predictors of invasion capability (Table 2, items 4-9) serve as well for *M. galloprovincialis* as for *S. patagonicus*, both of which reach greatest densities (and maximal effects) on shores with strong wave action, and provide additional food for predators, although none of the known predators provide any predator-driven resistance to invasion by *S. patagonicus* (Robinson et al., 2015; Skein et al., 2020). The brief lifespan, high densities and particularly the small size of *S. patagonicus* are firm predictors of its almost complete exclusion of limpets. This accords with other limpet-mussel interactions in South Africa. For example, the relatively tiny (20-30-mm) *Scutellastra aphanes* lives almost its entire live on shells of *Perna perna* (Robson, 1986) whereas the large (80-100 mm) *S. argenvillei* is largely excluded by dense beds of *M. galloprovincialis* (Steffani and Branch, 2003a; Steffani and Branch, 2003b; Steffani and Branch, 2003c; Branch and Steffani, 2004).

Skein et al. (2021) have broadened the consideration of characteristics that influence the invasion success of alien species to include features of both prey and predator. For prey, they list gregarious behaviour, high fecundity, high recruitment, dispersal potential and refuge from predation; for predators, preference for alien over native species, high feeding rate and high abundance feature. All the features listed for prey are applicable to *M. galloprovincialis*, *S. patagonicus* and *B. glandula*. High reproductive capacity and high to exceptionally high settlement and recruitment are important features for *M. galloprovincialis* and *S. patagonicus*, and Skein et al. (2021) make the point that this may overwhelm any predatory biotic resistance to alien species. The same is true for *B. glandula* (Robinson et al., 2015). In short, although there are several know predators of the two alien mussels, none seem positioned to provide effective biotic resistance to them. Both *M. galloprovincialis* (Calvo-Ugarteburu and McQuaid, 1998a; Calvo-Ugarteburu and McQuaid, 1998b) and *S. patagonicus* (personal observations) are relatively free of parasites, which is likely to increase their invasive capabilities.

Four factors are, however, likely to ameliorate the effects of the alien mussels and barnacle: wave action, upwelling, zonation and recruitment. All three alien species predominate on wave-exposed shores and are less abundant at upwelling headlands than downstream bays (Pfaff et al., 2011). Their recruitment is diminished on sheltered shores and at upwelling headlands and, correlated with this, adult abundances are reduced (Hoffmann et al., 2012), reducing their competitive capability.

The three alien species are also differentially zoned: *B. glandula* is concentrated in the high shore (Hoffmann et al., 2012; Supplementary Figure S2), *M. galloprovincialis* predominates in the mid to high shore, although it can extend to cover the low shore (Hoffmann et al., 2012; De Greef et al., 2013) and *S. algosus* is strictly a low-shore species (De Greef et al., 2013) that extends well into the subtidal zone (Skein et al., 2018a). However, in combination, *S. patagonicus*, *M. galloprovincialis* and *B. glandula* now exert a ‘zonation squeeze’ that covers all but the highest (top) zone on the shore (Sadchatheeswaran et al., 2015; Supplementary Figure S4).

Finally, recruitment of many marine organisms is patchy, both spatially and temporally (Underwood and Fairweather, 1989). For mussels and barnacles, concentration of settlement and recruitment at bays downstream of upwelling headland and on wave-exposed shore focuses their effects there (Pfaff et al., 2011). More importantly, periodic ‘sweepstake’ settlements take place, with periods of several years between which settlement and recruitment are very low to absent (Reaugh-Flower et al., 2011). Maximal effects are felt when settlement is dense, but between such events mussel and barnacle populations diminish in vertical extent and abundance, as we recorded for *M. galloprovincialis* between 2001 and 2012.

5 Conclusions

Returning to the hypotheses outlined in the introduction:

(1) Grazing by the limpet *S granularis* did benefit *M. galloprovincialis* by preventing algal overgrowth, improving survivorship and condition of the mussel. In turn, the mussel supported high densities of small individuals of *S. granularis*; but excluded large ones.
(2) Dense settlements of the alien barnacle *B. glandula* in the high shore excluded *S. granularis* but enhanced densities of the periwinkle *A. knysnaensis*.
(3) The previously described progressively upshore migration of *S. granularis* was disrupted by the arrival of *M. galloprovincialis*, which concentrated recruits of the limpet in the mid to high shore; and further altered by *S. patagonicus* and *B. glandula*, which largely excluded the limpet from respectively the low- and high-shore zones.
(4) Factors that predicted the invasive success of *M. galloprovincialis* were largely applicable to *S. patagonicus*, with the most important departures being (a) the absence of an invasive history that would have forecast its arrival in Namibia, and thence South Africa; and (b) the slow growth, intolerance of physical stresses and relatively low rate of food uptake in *S. patagonicus* that are at odds with its successful invasions and spread. Pivotal to its success is its astonishingly high rate of recruitment.

Factors mitigating the negative effects of the alien species were (a) differences in their zonation, response to wave action and upwelling that partially separate species; (b) differences among species in their relative sizes, which determined whether the alien species could provide a secondary substratum for native species; and (c) fluctuations in recruitment that grant respite between periods of heavy settlement of alien species. Generalities did, thus emerge, but each alien was sufficiently different from the others to be unique in its interactions. As Silverberg (2015) says: 'The main thing about aliens is that they are alien. They feel no responsibility for fulfilling any of your expectations'.

Data availability statement

The raw data supporting the conclusions of this article will be made available by the authors, without undue reservation.

Author contributions

GB conceived and supervised the research, undertook data collection, analysis and writing. NS was responsible for the work on limpet-mussel-algae interaction including the experiments, data collection and revision of that section of the paper. MP and NB were mainly involved with work on changing zonation patterns, including data gathering, analysis and revision of the text. ZZ was responsible for work on *Semimytilus* and helped revise that section of the paper. All authors contributed to the article and approved the submitted version.

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Conflict of interest

Publisher's note

Supplementary material

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fmars.2023.1190456/full#supplementary-material

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