

# Comparisons of life-history traits of the alien invasive *Semimytilus algosus* and three other mytilid mussels on the West Coast of South Africa

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**ABSTRACT:** The invasive mytilid mussel *Semimytilus algosus* was first recorded on South African shores in 2009 and rapidly spread to occupy 500 km of the West Coast, where it dominates lower portions of the rocky shore. To identify mechanisms underlying the invasive success of *S. algosus*, the life-history parameters survivorship, reproductive output, recruitment, growth rate and shell and byssus strength were compared among *S. algosus* and another alien, *Mytilus galloprovincialis*, and the indigenous mussels *Aulacomya atra* and *Choromytilus meridionalis*. To standardise the effects of wave exposure and shore height on life history patterns, all observations and sampling were limited to the low shore at the research site, Bloubergstrand. The 4 mussel species employed very different means of maximising survival and/or space occupancy. *S. algosus* proved to be a typical *r*-selected species, with low survival due to its weak shell and byssal strength. Unexpectedly, it grew relatively slowly but had a high reproductive output and exceptionally high recruitment rate that largely account for its invasive success. This study therefore demonstrates how life-history traits influence the invasive success of alien species and allows predictions about their relative impacts on intertidal rocky shores.

**KEY WORDS:** Invasive species · Competition · Rocky shores · Recruitment · Growth · Reproduction

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## INTRODUCTION

Invasive species, which most authors define as aliens that have spread from their point of arrival (Robinson et al. 2016), have spread widely around the globe and many have significant effects on community composition and ecosystem functioning (Ruiz et al. 1997, Hockey & van Erkom Schurink 1992, Grosholz 2002, Thompson et al. 2002, Rilov & Crooks 2009).

Several studies have endeavoured to identify the characteristics of species that favour invasive success (Lodge 1993, Carlton 1996, Branch & Steffani 2004, Jaspers et al. 2018). Traits identified include high genetic variability (Stepien et al. 2005, Roman 2006, Rius et al. 2008), the ability to exploit resources (Dick et al. 2013, Alexander et al. 2015) and competitive strength (Branch & Steffani 2004). In the intertidal

zone in particular, predation and competition for space play a substantial role in determining zonation patterns, community structure and diversity (Connell 1961, Dayton 1971, Branch 1984, Menge & Branch 2001). Release from natural enemies may contribute to the success of invaders (Colautti et al. 2004), although native predators do restrict invasive species in some cases (Crooks 2002, Carlsson et al. 2009, Havel et al. 2015). In its native range, the mytilid mussel *Semimytilus algosus* is heavily predated upon by the indigenous whelk *Acanthina monodon* due to its thin shell and high caloric content (Soto et al. 2004). However, in South Africa, both the lobster *Jasus lalandii* and the starfish *Marthasterias africana* preferentially feed on the native *Choromytilus meridionalis* rather than on invasive *Mytilus galloprovincialis* or *S. algosus* (Skein et al. 2018).

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Life-history traits, such as growth rate, reproductive output and recruitment rate (Barkai & Branch 1989), shell strength (Caro et al. 2011) and byssus strength (Bell & Gosline 1996, 1997), influence the relative competitive abilities of intertidal species. For instance, the mussel *M. edulis* can experience 60% annual mortality without any reduction in percentage cover because it can double its size in 1 yr (Petraitis 1995). However, growth rate is influenced by both genetic differences among species and environmental factors, such as food availability and wave exposure (van Erkom Schurink & Griffiths 1993, Steffani & Branch 2003a,b). Additionally, mussels often dominate wave-exposed shores, largely due to their ability to attach to substratum and thus withstand wave action (Bell & Gosline 1996, Denny & Helmuth 2009), but also because they benefit from the greater food supply generated by wave action (Bustamante & Branch 1996a,b). Byssal threads are common to all mytilid bivalves and are used for post-larval attachment to the substratum (Pearce & LaBarbera 2009). Byssal strength is variable, as individual threads continually decay and new threads must be produced (Denny & Helmuth 2009).

Recruitment is another process that can allow rapid occupation of space. Recruitment comprises both settlement and early survival of settled larvae (Bownes & McQuaid 2009), and is affected by physical processes, tidal height, pelagic larval survival and larval behaviour (Rodríguez et al. 1993, Porri et al. 2007, Rilov et al. 2008, Pfaff et al. 2011).

Trade-offs between life-history traits—for example, between rapid growth and anti-predator defences—may promote invasion without necessarily sustaining large adult populations. For instance, this is true of the invasive Suminoe oyster *Crassostrea ariakensis*, which has a high growth rate and reaches maturity sooner than the indigenous eastern oyster *C. virginica*, but is more vulnerable to predation by the blue crab *Callinectes sapidus* due to its weaker shell strength (Bishop & Peterson 2006). Some mussels may also expend more energy on reproduction than on production of byssal threads, thereby reducing attachment strength (Zardi et al. 2007, Denny & Helmuth 2009).

On the South African coast, 89 alien species are currently known, of which 58 are invasive (Robinson et al. 2016). Until recently, only the Mediterranean mussel *M. galloprovincialis*, which originates from the North-Eastern Atlantic (Zardi et al. 2018), has had significant ecosystem effects over a large geographic scale on West Coast rocky shores (Branch & Steffani 2004, Robinson et al. 2005). Arrival of the

barnacle *Balanus glandula* has now added another species with similar invasive characteristics (Laird & Griffiths 2008). The mussel *S. algosus* was first detected on South African shores at Elands Bay in 2009, but within 4 yr had come to occupy 500 km of the West Coast, from Groenriviermond in the north to Bloubergstrand in the south, and now dominates the low intertidal (De Greef et al. 2013) and maintains a strong presence in the subtidal (Skein et al. 2018).

Native populations of *S. algosus* are found along the coast of South America from Ecuador to Chiloé Island in Chile, and recruit year-round with peaks in austral winter and summer (Navarrete et al. 2008). In its natural environment, *S. algosus* is outcompeted by *Perumytilus purpuratus*, which has a negative effect on the growth and survival of *S. algosus* (Caro 2009). However, *S. algosus* can co-exist with *P. purpuratus* because of its high recruitment rate. One of the attributes that gives *P. purpuratus* an advantage is that its shell is consistently thicker than that of *S. algosus*, although shell thickness of *S. algosus* does increase in response to predators, associated with a decrease in growth rate (Caro & Castilla 2004). On both mussel rafts and in aquarium experiments in Chile, *S. algosus* grows fast, in the range of 25–45 mm yr<sup>-1</sup> (González et al. 1980, Caro & Castilla 2004).

In South Africa, studies have shown that *M. galloprovincialis*, which exhibits high recruitment and growth rates (Branch & Steffani 2004), outcompetes several other mussel species (Steffani & Branch 2003a, Branch & Steffani 2004, Bownes & McQuaid 2006). The indigenous *Aulacomya atra* is slow-growing (Griffiths & King 1979, Barkai & Branch 1989, van Erkom Schurink & Griffiths 1993), and although *M. galloprovincialis* has a lower annual reproductive output than *A. atra* (van Erkom Schurink & Griffiths 1991), it still dominates exposed shores where its growth rate is highest (Steffani & Branch 2003a). Furthermore, even though *A. atra* spawns 3 times a year and *M. galloprovincialis* only once or twice a year (van Erkom Schurink & Griffiths 1991), settlement of *A. atra* larvae is intermittent (Griffiths & King 1979, Pollock 1979). In comparison with 3 indigenous mussels, *A. atra*, *C. meridionalis* and *P. perna*, survivorship for *M. galloprovincialis* is much higher than for the other species (Branch & Steffani 2004). However, environmental conditions may affect the physiological performance of mussels (Nicastro et al. 2010), and the geographic spread of *M. galloprovincialis* appears to have been halted by steep transitions to warmer waters on both the west and southeast African coasts (Assis et al. 2015).

To determine the underlying reasons why *S. alga* has become such a successful invader on intertidal shores in South Africa, we examined several of its life-history traits, namely growth rate, shell and byssal strength, survivorship, reproductive output and recruitment rate, relative to those of another invasive mussel, *M. galloprovincialis*, and 2 indigenous mussels, *C. meridionalis* and *A. atra*, all of which co-occur on the West Coast of South Africa.

Given (1) the rapidity with which *S. alga* has invaded the West Coast of South Africa, (2) its domination of the low shore at many localities (De Greef et al. 2013), (3) rapid growth rates recorded in Chile (González et al. 1980, Caro & Castilla 2004) and (4) the fact that on its native Chilean shores and in Namibia it exhibits high recruitment levels (Caro 2009, Reaugh-Flower et al. 2011), we anticipated that its life-history strategies will contribute to the competitive success of this mussel. Specifically, we tested the hypotheses that:

(1) *S. alga* and the alien mussel *M. galloprovincialis* have faster growth rates than the indigenous mussels *C. meridionalis* and *A. atra*.

(2) *S. alga* expends much of its energy in growth and reproduction, and therefore its shell and byssus strength will be low and, consequently, its survivorship will also be low.

(3) *S. alga* has a higher reproductive output and recruitment rate than the other 3 mussel species.

## MATERIALS AND METHODS

Various life-history parameters of *Semimytilus alga* were measured and compared with those of *Aulacomya atra*, *Choromytilus meridionalis* and *Mytilus galloprovincialis*. To standardise the effects of shore height, all observations, field measurements and sampling were limited to the low shore at Bloubergstrand (33° 48' 22" S, 18° 27' 50" E), a rocky shore 20 km north of Cape Town. As all 4 species co-occur there, and *S. alga* has established a dense population, this allowed us to compare the 4 mussel species under equivalent circumstances. The studies were conducted over 12–14 mo to span all 4 seasons, on dates specified below.

### Individual size, growth rate and survivorship

To measure absolute growth, 30 specimens of each species within areas of 100% cover by mussels in low-shore beds were labelled using Dymo tape glued

onto mussels with Pratley's clear glue. Sizes of individuals selected spanned the full range from the maximum observed shell lengths down to those that could be feasibly labelled and measured: 20–40 mm for *S. alga*; 15–50 mm for *C. meridionalis*; 18–62 mm for *M. galloprovincialis*; and 21–78 mm for *A. atra*. Total length, from umbo to the posterior margin, was measured monthly from May 2012 to May 2013, using Vernier callipers with an accuracy of 0.1 mm. Every 3 mo, additional mussels were labelled and measured to replace any lost to mortality.

For each species, Ford-Walford plots were drawn using the regression equation:

$$L_{t+3} = mL_t + i \quad (1)$$

where  $L_t$  is the length at the start and  $L_{t+3}$  is the length after 3 mo,  $m$  is the slope of the regression line, and  $i$  is the  $y$ -intercept. Constants derived from the Ford-Walford plots were thus based on 3 mo intervals, and were used to draw a von Bertalanffy growth curve using the equation:

$$L_t = L_\infty[1 - e^{-K(t-t_0)}] \quad (2)$$

where  $L_t$  is the length at time  $t$ ,  $L_\infty = i/(1 - m)$  and is the asymptotic length,  $K = -\log_e m$  and is the growth coefficient, and  $t_0$  is the theoretical age at the start of growth of settled larvae (assumed to be 0, see Blankley & Branch 1985).

Survival rates of the 4 species over the same 12 mo period were measured directly from the mussels labelled in the field for growth rate studies.

To determine whether growth rates differed significantly among species, the slopes and  $y$ -intercepts of the Ford-Walford plots were compared through analyses of covariance (ANCOVAs), with initial shell length ( $L_t$ ) as a covariate.

### Shell strength

Thirty individuals of each species were sampled once, during August 2015. Shell length, height, thickness and width of a single valve (Fig. 1) were measured using digital Vernier callipers, to 0.01 mm accuracy. Failure loads of shells were then measured using a Zwick 1484 universal tensile tester. Left valves of mussels were placed horizontally on the loading plate and compressive force applied to the highest part of the mussel shell at a rate of 2 mm s<sup>-1</sup>. Load displacement curves up to shell breaking point were obtained. Only shells without endoliths were used, as endolithic parasites negatively affect shell strength (Zardi et al. 2009).

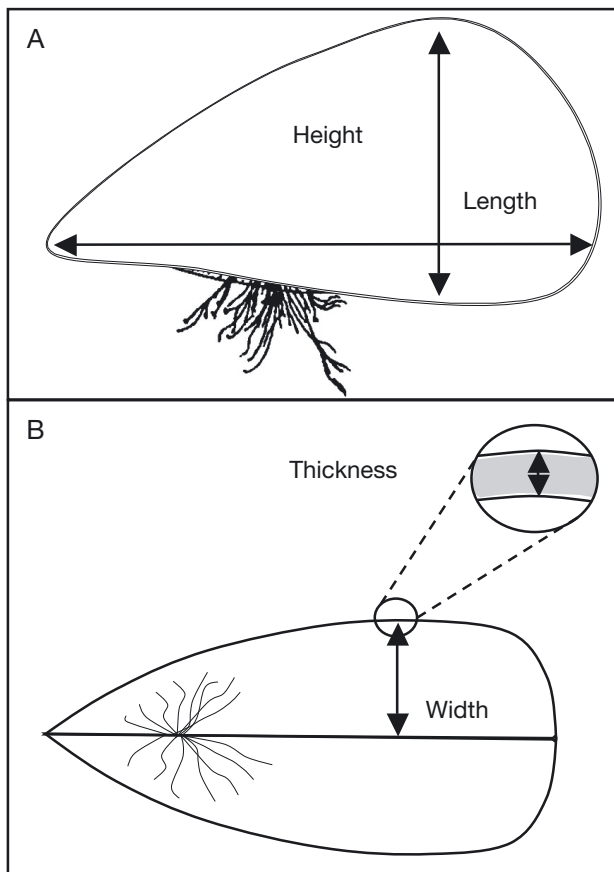


Fig. 1. Measurements taken of mussel shell morphology. (A) Lateral view: maximum shell length, and shell height (mm) measured at the tallest part of each shell. (B) Ventral view: valve width (mm) at the widest part of the left valve; and shell thickness (mm) at the widest part of the valve

Shell strength was taken as the maximum force required to fracture a shell. The different species spanned different ranges of shell length, and to account for this potential confounding factor, ANCOVAs were performed to test for differences in breaking force, shell thickness and the ratio between shell width and shell length for the 4 species, with length as a covariate. The width:length ratio was measured because of the possibility that more 'domed' shells with a high ratio might be stronger than 'flatter' shells with a low ratio. Multiple regressions were calculated to establish the relative contributions of these factors to shell strength. The assumptions of linearity, homoscedasticity, normality and independence of errors were tested using residual plots. Collinearity was assessed using Pearson's correlation. Best models were selected based on p-values ( $p < 0.05$ ). Length/breaking force and length/thickness regressions were calculated for each species and used to

estimate the breaking force and thickness of standard mussels 40 mm in length. This length fell within the range of specimens of all 4 mussel species.

### Byssus strength

Overall byssal strength was determined through tensile tests, which measured the vertical pull (in kg) required to break the byssus of specimens in the field. Tests were conducted once, during August 2015. Measurements were converted to Newtons. Fifty specimens of each species were selected randomly within mussel beds on the low shore at Bloubergstrand. Only individuals that were directly attached to the substratum were used. A retort clamp with a spring balance hooked to it was attached to each mussel and pulled steadily, perpendicular to the rock surface. Emulating Bell & Gosline (1997), tenacity ( $\text{N m}^{-2}$ ) was calculated as detachment/ $A_{\text{pl}}$ , where  $A_{\text{pl}}$  is the valve frontal planar area, calculated as an ellipse, using the following equation:

$$A_{\text{pl}} = \pi(\text{height}/2) \times (\text{width}/2) \quad (3)$$

The tensile strength of individual byssal threads ( $n = 3$  threads mussel $^{-1}$ ) was measured for 15 individuals of each species, as per Bell & Gosline (1996). Measurements were confined to the distal region of all threads, as different regions of a byssal thread behave differently under tension (Bell & Gosline 1996). Mussels were wet-weighed, shell length was measured, and the byssus was dissected out and wet-weighed. Byssal thread thickness was measured to an accuracy of  $0.01 \mu\text{m}$  using a digital micrometer. Breaking strengths of individual strands were measured using an Instron 5544 tensile tester with extensometer, applied at a rate of  $10 \text{ mm min}^{-1}$ .

Stress was calculated as breaking force/ $A_{\text{pl}}$ . Strain was calculated as extension/initial length. A stress-strain curve was drawn and the modulus calculated (Denny 1988). The ratio of stress to strain (modulus) is a measure of the resistance of a thread to deformation (stiffness) and contributes to its strength (Denny 1988).

One-way analyses of variance (ANOVAs) were performed on transformed values ( $\ln$ ), due to heteroscedasticity of the untransformed data, to test for differences among species in tenacity, single-thread tensile strength, modulus, number of byssal threads and the diameter of single byssal threads. As the assumption of normality could not be met for comparisons of tenacity among species, Kruskal-Wallis tests were applied in that instance. Multiple regressions

were also performed for each species, to establish the relative contributions of these factors to byssal tenacity.

### Reproductive output

Reproductive outputs of the 4 species were derived from dry flesh weight of mussels spanning a range of sizes above which sexual maturity is reached: 20–40 mm for *S. algosus* and *A. atra*, 30–50 mm for *M. galloprovincialis* and 35–70 mm for *C. meridionalis* (Steffani & Branch 2003a, Z. Zeeman pers. obs.). Thirty specimens of each species were collected randomly at monthly intervals for 14 mo from May 2012 to July 2013, from the low shore at Bloubergstrand.

In the laboratory, the byssus was removed, shell length, wet weight and sex were recorded, and the flesh was extracted and dried at 55°C for 48 h to achieve constant weight, then weighed. Regressions of dry flesh weight versus shell length were calculated for each species for each month and used to estimate the weights of standard 40 mm mussels. The estimated standard dry flesh weight was plotted against time to create an index showing cycles of weight gain and loss reflecting gonad accumulation and gamete release, following the approaches and methods of Griffiths (1977). To estimate annual reproductive output, differences between peaks in weight and ensuing troughs were taken as a measure of gonadal output and summed over the period of observation to account for the fact that >1 spawning took place. Relative reproductive output was calculated as the annual output divided by maximum body mass of each species, expressed as a percentage.

Interpretation of spawning periods was supported by histological analyses noting the change in gonad structure, by subjectively grading a gonadal smear from every female into 4 categories: (1) mature oocytes, (2) spawning with continuous oogenesis, (3) spent oocytes and (4) resorption (Griffiths 1977).

### Recruitment rate

Recruitment rates of the 4 species of mussels were determined by taking 5 replicate 10 × 10 cm scrapings monthly from the low shore at Bloubergstrand, from areas with 100% cover of each species. To compare the recruitment among shore heights at a time when all species were recruiting (March), scrapings within 5 replicate 10 × 10 cm quadrats were collected at 3 shore heights: low, mid and high.

Samples were sieved through a 1 mm mesh to remove sediment. Individual recruits were identified and counted under a dissecting microscope. Recruits were defined as individuals of 1–5 mm shell length (Reaugh-Flower et al. 2011).

Densities of recruits were plotted against time to provide a monthly rate of recruitment. Factorial ANOVAs were used to determine differences among species and months, and any interaction between species and month.

### Statistical analyses

All analyses mentioned above were performed using Statistica 12, Statsoft 2014. Normality was assessed by normality plots, and homogeneity of variances through Levene's test. To determine where differences lay, post-hoc Tukey's HSD tests were performed. The significance level was set at 0.05 for all analyses.

## RESULTS

### Growth and survivorship

Growth rates as determined from Ford-Walford plots (Fig. S1 in the Supplement at [www.int-res.com/articles/suppl/m607p113\\_supp.pdf](http://www.int-res.com/articles/suppl/m607p113_supp.pdf)) and von Bertalanffy growth curves derived from them (Fig. 2) showed that *Choromytilus meridionalis* had the highest growth rate (45.62 mm yr<sup>-1</sup> in the first year), followed by *Mytilus galloprovincialis* (30.72 mm yr<sup>-1</sup>), *Aulacomya atra* (25.69 mm yr<sup>-1</sup>) and *Semimytilus algosus* (11.98 mm yr<sup>-1</sup>). Constants for Ford-Walford plots and von Bertalanffy growth curves are recorded in Table 1.

One-way ANCOVA revealed significant differences among species in both the slopes and intercepts of the Ford-Walford plots. Initial length (*L*<sub>t</sub>) did not significantly affect slopes among species but did have a significant effect on the *y*-intercepts (Table 2). Tukey's HSD tests established that the slopes were significantly different (*p* < 0.05) between *C. meridionalis* and *M. galloprovincialis*, as well as between *C. meridionalis* and *A. atra*. The intercepts were significantly different among all species except between *S. algosus* and *A. atra*.

*M. galloprovincialis* exhibited the greatest survival rate, with 51% alive after 1 yr, and *S. algosus* the lowest, with only 6% survivors. *C. meridionalis* (43%) and *A. atra* (12%) were intermediate.



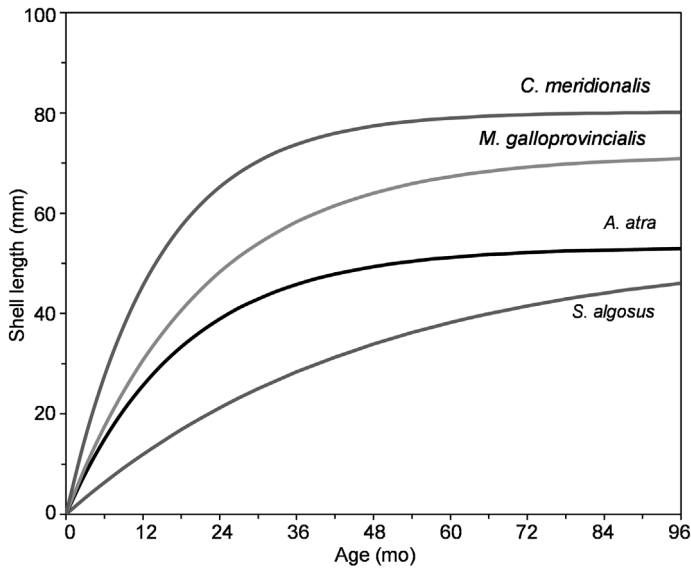


Fig. 2. Von Bertalanffy growth curves for *Semimytilus algosus*, *Aulacomya atra*, *Mytilus galloprovincialis* and *Choromytilus meridionalis*

**Shell strength**

*C. meridionalis* possessed the strongest shells, requiring a mean force of 256 N to break, with *M. galloprovincialis*, *A. atra* and *S. algosus* having mean breaking forces of 217, 160 and 54 N, respectively (Fig. 3A). ANCOVA detected significant differences in shell strength, thickness and the width:length ratio among species. Length (Fig. 3B) had a significant effect on breaking force and shell thickness, but not on the width:length ratio (Table 3). Tukey’s HSD tests revealed significant differences in breaking force among all species, except between *C. meridionalis* and *M. galloprovincialis* (Fig. 3A).

Shell thickness was significantly different among all species except *A. atra* and *C. meridionalis* (Fig. 3C), with *M. galloprovincialis* having the thickest shells, and *S. algosus* the thinnest. The ratio of

Table 1. Constants of the Ford-Walford and von Bertalanffy equations for the 4 mussel species: *m* is the slope of the line, *i* is the y-intercept, *R*<sup>2</sup> is the coefficient of determination, *L*<sub>∞</sub> is the asymptotic length, and *K* is the growth coefficient

Species	Ford-Walford			von Bertalanffy	
	<i>m</i>	<i>i</i>	<i>R</i> <sup>2</sup>	<i>L</i> <sub>∞</sub>	<i>K</i>
<i>Semimytilus algosus</i>	1.10	3.51	0.53	52.89	0.06
<i>Choromytilus meridionalis</i>	0.81	15.21	0.85	80.22	0.21
<i>Mytilus galloprovincialis</i>	0.87	9.36	0.91	71.71	0.14
<i>Aulacomya atra</i>	0.85	8.08	0.77	53.22	0.16

Table 2. Analysis of covariance comparing the slopes and intercepts of the Ford-Walford plots among species, with initial length (*L*<sub>0</sub>) as a covariate. Significant differences are indicated in **bold**

Variable	df	MS	<i>F</i>	<i>p</i>
<i>L</i> <sub>0</sub> (covariate)	1	2.18	2.21	0.14
Slope ( <i>m</i> )	3	4.86	4.92	<b>0.003</b>
<i>L</i> <sub>0</sub> (covariate)	1	3702.46	55.22	<b>&lt;0.001</b>
y-intercept ( <i>i</i> )	3	375.86	5.60	<b>0.001</b>

width:length was greatest for *A. atra* and was significantly different among all species (Fig. 3D). Multiple regressions (Table 4) showed that for *S. algosus*, thickness, length and the width:length ratio accounted for only 4% of the shell strength, with none of the factors contributing significantly (*F*<sub>3,46</sub> = 0.33, *p* = 0.80):

$$y = 5.41 + 0.10x_{\text{thick}} - 0.10x_{\text{length}} + 0.05x_{\text{W:L}} \quad (4)$$

$(R^2 = 0.04, p = 0.80, SE = 0.60)$

The multiple regression had the highest explanatory power for *C. meridionalis* (56% of variance), with thickness and length having significant effects on shell strength (*F*<sub>3,46</sub> = 21.88, *p* < 0.001):

$$y = 1.69 + 0.32x_{\text{thick}} + 0.53x_{\text{length}} + 0.10x_{\text{W:L}} \quad (5)$$

$(R^2 = 0.56, p < 0.001, SE = 0.36)$

For *M. galloprovincialis*, the multiple regression explained 42% of the variance, with only shell thickness significantly affecting shell strength (*F*<sub>3,46</sub> = 12.76, *p* < 0.001):

$$y = 4.42 + 0.63x_{\text{thick}} + 0.07x_{\text{length}} - 0.01x_{\text{W:L}} \quad (6)$$

$(R^2 = 0.42, p < 0.001, SE = 0.40)$

The multiple regression for *A. atra* accounted for 38% of the variance, with both length and the ratio of width:length being significant predictors of shell strength (*F*<sub>3,46</sub> = 11.05, *p* < 0.001):

$$y = 2.48 + 0.16x_{\text{thick}} + 0.44x_{\text{length}} + 0.33x_{\text{W:L}} \quad (7)$$

$(R^2 = 0.38, p < 0.001, SE = 0.48)$

Since length had a significant effect on breaking force in half the cases, regressions were calculated relating shell strength to length (Table S1), from which the breaking forces for standard-sized 40 mm mussels were calculated for each species. Standard-sized *A. atra* had the strongest shell, followed by *M. galloprovincialis* and *C. meridionalis*, whereas *S. algosus* had the weakest shell (Fig. 4). Although the estimated value for *S. algosus* should be treated with cau-

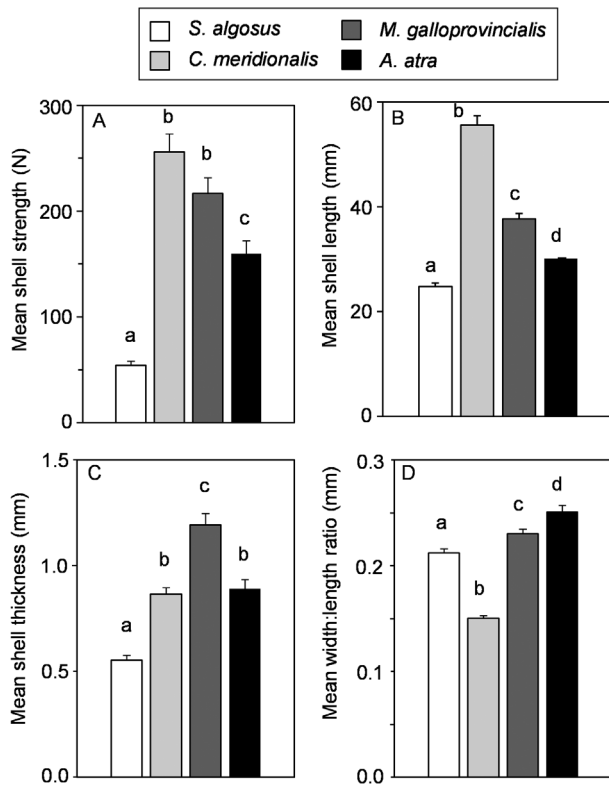


Fig. 3. (A) Mean shell strength, (B) shell length, (C) shell thickness and (D) width:length ratios of *Semimytilus algalosus*, *Aulacomya atra*, *Mytilus galloprovincialis* and *Choromytilus meridionalis*. Error bars are +1 SE. Lower-case letters indicate significant differences among species detected by post hoc tests ( $p < 0.05$ ). Statistical analyses were performed on log-transformed data, to meet the assumption of equality of variance

tion because of the non-significance of the regression, it is clear that its shell strength is decisively less than that of the other species. To establish whether shell thickness followed the same pattern as shell strength, the thicknesses of mussels 40 mm in length were also estimated from regressions (Table S1). The pattern was much the same: *A. atra* and *M. gallo-*

Table 3. Analysis of covariance comparing shell breaking force, shell thickness and the ratio of width:length among species, with shell length as a covariate. Significant differences are indicated in **bold**

Variable	df	MS	F	p
Length (covariate)	1	11.68	43.56	<b>&lt;0.001</b>
Breaking force	3	7.56	28.18	<b>&lt;0.001</b>
Length (covariate)	1	5.96	85.26	<b>&lt;0.001</b>
Thickness	3	3.68	52.60	<b>&lt;0.001</b>
Length (covariate)	1	0.04	2.43	0.12
Width:length ratio	3	1.40	77.89	<b>&lt;0.001</b>

*provincialis* had thick shells, while *S. algalosus* and *C. meridionalis* had comparable thinner shells (Fig. 4). Standard errors and statistical significance could not be calculated as the values for standard-sized mussels constituted single values.

### Byssus strength

*A. atra* exhibited the greatest tenacity, with a mean of  $16.38 \times 10^3 \text{ N mm}^{-2}$  required to break the byssus. Mean tenacities for *M. galloprovincialis*, *C. meridionalis* and *S. algalosus* were  $9.74$ ,  $5.45$  and  $6.49 \times 10^3 \text{ N mm}^{-2}$ , respectively (Fig. 5A). Kruskal-Wallis tests yielded significant differences in tenacity among all species ( $H_3 = 90.07$ ,  $p < 0.001$ ), except between *S. algalosus* and *C. meridionalis*.

Single-thread tensile strength (Fig. 5B) was marginally (but non-significantly) greater for *M. galloprovincialis* (1.41 N) than for *A. atra* (1.40 N) but significantly less for both *S. algalosus* (0.99 N) and *C. meridionalis* (0.82 N). Mean modulus was not significantly different among species due to high variance (Fig. 5C). The number of threads per byssus was significantly different among all 4 species (Fig. 5D), and resembled the pattern for tenacity with the notable difference that *S. algalosus* had significantly fewer threads than any of the other species. Mean thread diameter was significantly less between *S. algalosus* and both *M. galloprovincialis* and *A. atra*, and between *C. meridionalis* and *M. galloprovincialis* (Fig. 5E).

Table 4. Multiple regressions relating shell breaking force to shell thickness, length and width:length ratio, where *b* is the slope. Significant differences are indicated in **bold**

	<i>b</i>	SE	<i>t</i>	<i>p</i>
<b><i>Semimytilus algalosus</i></b>				
Thickness	0.10	0.18	0.58	0.57
Length	-0.10	0.17	-0.57	0.57
Width:length	0.05	0.17	0.33	0.74
<b><i>Choromytilus meridionalis</i></b>				
Thickness	0.32	0.15	2.20	<b>0.03</b>
Length	0.53	0.15	3.57	<b>&lt;0.001</b>
Width:length	0.10	0.12	0.80	0.43
<b><i>Mytilus galloprovincialis</i></b>				
Thickness	0.63	0.19	3.29	<b>0.002</b>
Length	0.07	0.17	0.40	0.69
Width:length	-0.01	0.13	-0.11	0.92
<b><i>Aulacomya atra</i></b>				
Thickness	0.16	0.16	0.98	0.33
Length	0.44	0.14	3.09	<b>0.003</b>
Width:length	0.33	0.14	2.29	<b>0.03</b>

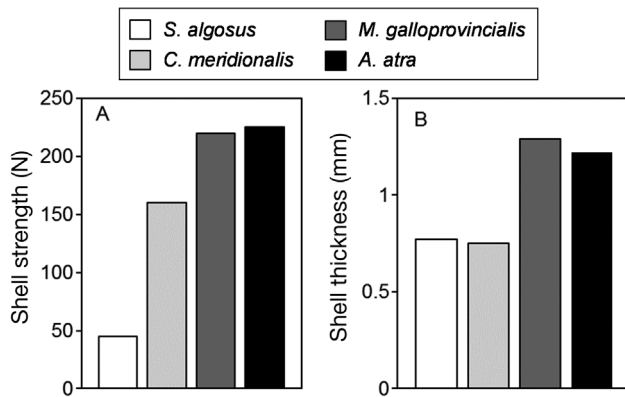


Fig. 4. (A) Shell strength and (B) shell thickness for standard-sized, 40 mm *Semimytilus algalosus*, *Aulacomya atra*, *Mytilus galloprovincialis* and *Choromytilus meridionalis* mussels

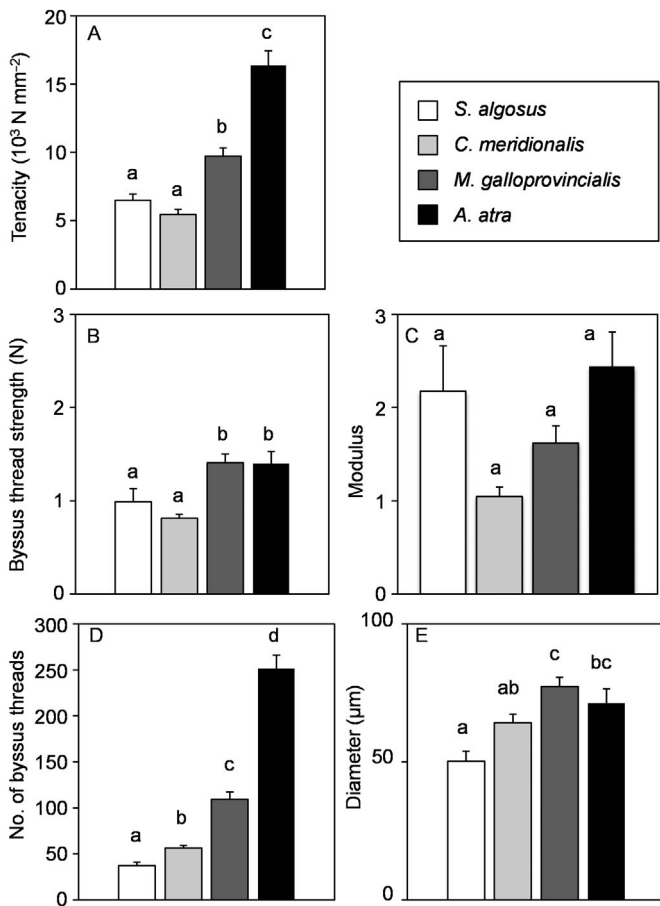


Fig. 5. (A) Overall tenacity, (B) single-thread tensile strength, (C) mean modulus (ratio of stress to strain), (D) number of byssus threads and (E) mean diameter of byssus threads in *Semimytilus algalosus*, *Aulacomya atra*, *Mytilus galloprovincialis* and *Choromytilus meridionalis*. Error bars are +1 SE. Lower-case letters indicate significant differences among species. Statistical analyses were performed on log-transformed data, to meet the assumption of equality of variance

Multiple regressions (Table 5) showed that for *S. algalosus*, 67% of the tensile strength of individual byssal threads was explained by the factors diameter and modulus. There was a particularly strong relationship between tensile strength and modulus:

$$y = -3.32 + 0.36x_{\text{dia}} + 0.72x_{\text{mod}} \quad (R^2 = 0.67, p < 0.001, SE = 0.32, df 2, 11) \quad (8)$$

Both diameter and modulus had significant effects for *C. meridionalis*:

$$y = -2.55 + 0.56x_{\text{dia}} + 0.39x_{\text{mod}} \quad (R^2 = 0.37, p < 0.001, SE = 0.26, df 2, 37) \quad (9)$$

For *M. galloprovincialis*, modulus was the only significant predictor of byssus strength:

$$y = -0.75 + 0.14x_{\text{dia}} + 0.85x_{\text{mod}} \quad (R^2 = 0.69, p < 0.001, SE = 0.26, df 2, 32) \quad (10)$$

For *A. atra*, 92% of byssus strength was explained by the 2 factors, with modulus being the greater and only significant predictor of tenacity:

$$y = -0.70 + 0.11x_{\text{dia}} + 0.98x_{\text{mod}} \quad (R^2 = 0.92, p < 0.001, SE = 0.13, df 2, 10) \quad (11)$$

### Reproductive output

All 4 species had 2 spawning events during the year, mostly in the austral late winter to early summer, with a smaller event during late autumn, although not during exactly the same months (Fig. 6). *A. atra* had the greatest fluctuations in dry weight of

Table 5. Multiple regressions relating single byssal thread breaking force to thread diameter and modulus (ratio of stress to strain, where *b* is the slope significant effects are indicated in **bold**)

	<i>b</i>	SE	<i>t</i>	<i>p</i>
<b><i>Semimytilus algalosus</i></b>				
Diameter	0.36	0.16	2.26	<b>0.03</b>
Modulus	0.72	0.16	4.46	<b>0.005</b>
<b><i>Choromytilus meridionalis</i></b>				
Diameter	0.56	0.13	4.35	<b>&lt;0.001</b>
Modulus	0.39	0.13	2.99	<b>0.005</b>
<b><i>Mytilus galloprovincialis</i></b>				
Diameter	0.14	0.10	1.44	0.16
Modulus	0.85	0.10	8.77	<b>&lt;0.001</b>
<b><i>Aulacomya atra</i></b>				
Diameter	0.11	0.08	1.39	0.19
Modulus	0.98	0.08	11.86	<b>&lt;0.001</b>



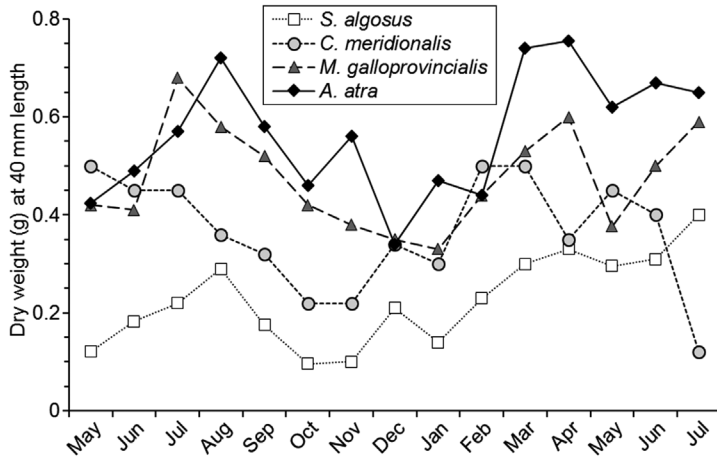


Fig. 6. Monthly dry flesh weight for standard mussels of 40 mm shell length, from May 2012 to July 2013, for *Semimytilus algosus*, *Aulacomya atra*, *Mytilus galloprovincialis* and *Choromytilus meridionalis*. Periods of weight loss reflect spawning

the 4 species. It also had the highest absolute reproductive output over 14 mo, at 0.72 g, with *C. meridionalis* yielding 0.66 g, *M. galloprovincialis* 0.57 g and *S. algosus* 0.47 g (Fig. 7A). Relative reproductive output was high for *S. algosus*, which achieved 118% output compared to its maximum body mass, exceeding the values for both but *M. galloprovincialis* (84%) and *A. atra* (96%), although *C. meridionalis* (132%) attained the highest value recorded (Fig. 7B). Overall male:female sex ratios were 49:51 for *C. meridionalis*, 59:41 for *A. atra* and 64:36 for *M. galloprovincialis*. As *S. algosus* is a simultaneous hermaphrodite, sex ratio was irrelevant.

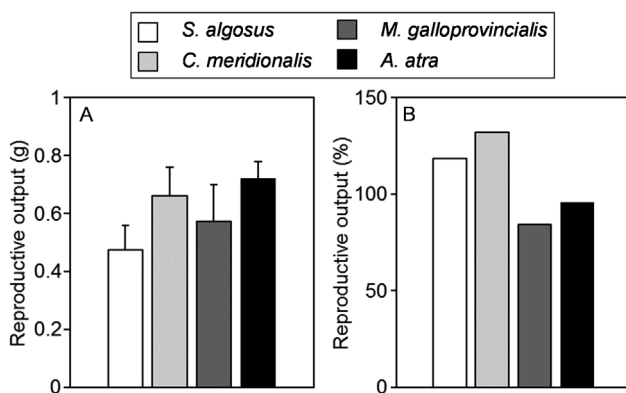


Fig. 7. (A) Absolute reproductive output and (B) relative reproductive output as a percentage of body mass, for standard-sized 40 mm *Semimytilus algosus*, *Aulacomya atra*, *Mytilus galloprovincialis* and *Choromytilus meridionalis* mussels, over the sampling period May 2012 to July 2013. Error bars are +1 SE

### Recruitment rate

The recruitment rate of *S. algosus* was substantially and significantly greater than that of any other species. Proportions of *S. algosus* recruits in patches formed by different mussel species were 98% in conspecific patches, 79% among *C. meridionalis*, 70% in *M. galloprovincialis* and 76% in *A. atra* patches (Fig. 8). All 4 species recruited in greatest numbers to patches of their own species. Mean recruitment within conspecific patches differed significantly among months, with a significant interaction between month and species because different species peaked in different months (Fig. S2, Table S2). Peaks in recruitment coincided with times when monthly dry mass attained low values, reflecting spawning periods (compare Fig. 6 and Fig. S2).

Mean numbers of recruits were also significantly different among shore heights, with a significant interaction between shore height and species arising from changes in the relative proportions of species at different shore heights (Table S3). *S. algosus* had significantly greater values than all other species on the low shore. On the mid-shore, its recruitment was lower, but still significantly greater than all species except *M. galloprovincialis*; but on

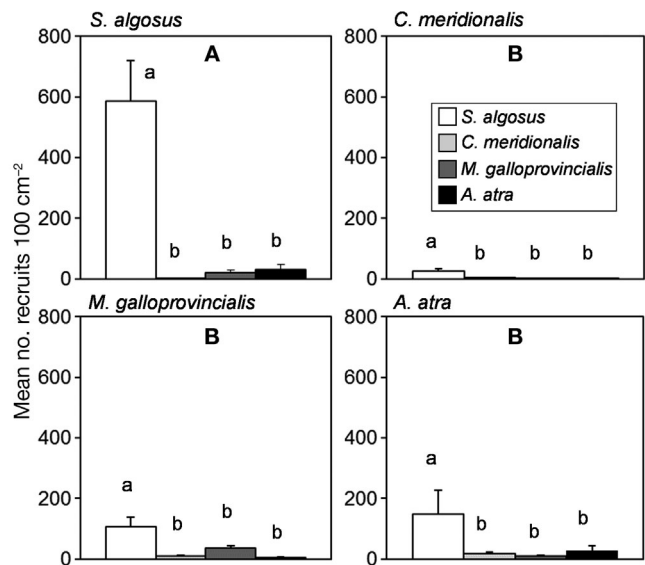


Fig. 8. Mean monthly number of recruits sampled within patches with 100% cover of each of the 4 mussel species (*Semimytilus algosus*, *Aulacomya atra*, *Mytilus galloprovincialis* and *Choromytilus meridionalis*). Error bars are +1 SE. Capitalised **bold** letters show significant differences among patches, and lower-case letters indicate differences among species within patches

the high shore there were no significant differences among species (Fig. 9). Recruitment of *S. algius* declined significantly up the shore, with a 3-fold reduction between the low shore and the mid-shore, and a further 3-fold reduction from there to the high shore. Recruitment of the other 3 species was relatively uniformly spread over the shore, with no significant differences among shore heights despite a peak mid-shore for *M. galloprovincialis*.

## DISCUSSION

Our first hypothesis predicted that *Semimytilus algius* would be fast-growing in South Africa because of its spatial dominance there, and because of its comparatively high growth rate in Chile (González et al. 1980, Caro & Castilla 2004, Caro et al. 2008). However, it had the slowest growth of the 4 species examined.

Our second hypothesis was that *S. algius* would have a weak shell and byssus strength and, indeed, it had the weakest byssus strength, and the thinnest, smallest and weakest shells overall. However, shell strength was influenced by shell length. Consequently, values of breaking force for standard-sized 40 mm mussels constituted a more valid comparison of relative strength. In those terms, shells of *S. algius* also proved to be the weakest of the 4 species. As predicted, the weak shell and byssal strength of this mussel explains the fact that it had the highest mortality rate.

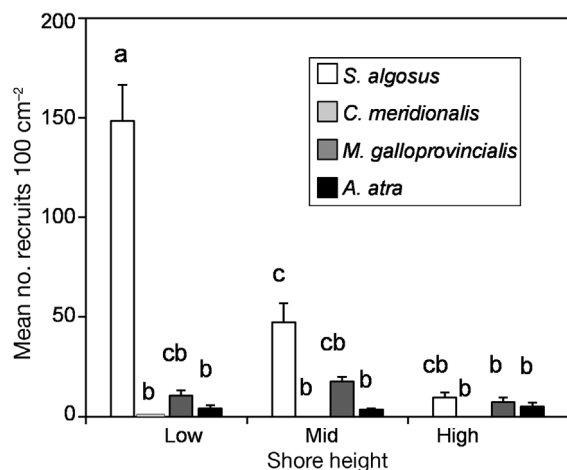


Fig. 9. Mean number of recruits for *Semimytilus algius*, *Aulacomya atra*, *Mytilus galloprovincialis* and *Choromytilus meridionalis* at different shore heights. Errors bars are +1 SE. Letters indicate significant differences among species and shore levels

The third hypothesis stated that *S. algius* would have the greatest reproductive output and recruitment rates of the 4 species. Relative to its body mass, *S. algius* proved to have the second-highest output, but in absolute terms, *Aulacomya atra* had the greatest reproductive output per individual, followed by *Choromytilus meridionalis* and *Mytilus galloprovincialis*, while *S. algius* had the lowest output, contradicting our expectations about reproductive output. Our most striking finding, however, was that the recruitment of *S. algius* was an order of magnitude greater than that of any of the other species, upholding that aspect of our third hypothesis.

## Growth rate

The growth rates we recorded for *M. galloprovincialis*, *C. meridionalis* and *A. atra* were all comparable to earlier measurements made in the same region (Barkai & Branch 1989, van Erkom Schurink & Griffiths 1993), but no previous measurements of growth have been made for *S. algius* in southern Africa. The comparatively high growth rate of *S. algius* in Chile led us to believe that it would be fast-growing in South Africa. In reality, it grew more slowly than the other 3 species examined.

Growth rate can influence competitive ability and the rapidity of colonisation (Wootton 1993). For example, in the US Pacific Northwest the high growth and recruitment rates of *M. galloprovincialis* allow it to outcompete *M. californianus* and *M. trossulus* (Shinen & Morgan 2009). Similarly, *S. algius* grows faster than *Perumytilus purpuratus* in its native range (A.U. Caro unpubl. data), which may contribute to its co-existence with that competitively superior species. Growth rate also influences predation resistance (Ehrlich 1986, van Erkom Schurink & Griffiths 1991, 1993, Lodge 1993, Branch & Steffani 2004).

## Shell strength and byssus attachment

Increased shell thickness and strength can increase the survival of mussels by protecting them from wave action and predators (Raubenheimer & Cook 1990, Steffani & Branch 2003a). However, this is energetically costly, since as much as 26% of energy intake can be expended on shell production (Griffiths & King 1979). Previous comparisons of *A. atra*, *C. meridionalis* and *M. galloprovincialis* showed that *A. atra* had the thickest and heaviest shells and *C. meridionalis* the thinnest and lightest shells (Grif-

fiths & Seiderer 1980, van Erkom Schurink & Griffiths 1993). We also found that *A. atra* and *M. galloprovincialis* had thick shells, while *C. meridionalis* (and *S. algius*) had thin shells. Shell strength is influenced by shell morphology, size and thickness (Griffiths & Seiderer 1980). West Coast rock lobsters *Jasus lalandii* can take larger *C. meridionalis* than *A. atra*, because *C. meridionalis* has weaker shell and attachment strengths (Griffiths & Seiderer 1980). Comparison of the shell morphology among the 4 species revealed that length followed the same pattern as mean shell strength. Shell thickness and breaking force for standard-sized mussels followed a similar pattern, so strength does not depend on size alone. Emanuel (2013) reported that shell thickness was the best predictor of shell strength for the 4 mussel species we examined. There may, however, be other factors that influence shell strength, including shell microtopographic texture and internal microstructure (Hiebenthal et al. 2013), as well as shell proportions. However, only in 1 instance (*A. atra*) did the ratio of shell height to length influence strength.

Among the species we examined, overall attachment strength (tenacity) and individual thread strength followed similar patterns, with *A. atra* and *M. galloprovincialis* having high values compared to *S. algius* and *C. meridionalis*. The same pattern emerged among species for the number of threads per byssus and the diameter of the threads. Only measures of modulus departed from this grouping, with *S. algius* having a relatively high value, and differences among species being non-significant, associated with high variances for this variable. Despite this, multiple regressions showed that modulus was the best predictor of single byssal thread strength for all 4 of the mussel species. Overall, the weak tenacity of *S. algius* could be ascribed to its weak, thin threads and the small number of threads it produces.

Trade-offs often exist between growth rate and shell and attachment strength. Thus, for example, *A. atra* grows slowly but has the strongest shell and attachment strength. However, *S. algius* was both slow growing and had a weak shell and byssus attachment. Other mechanisms must thus be sought to explain the spatial dominance on the low shore by this species.

### Reproductive output

One of the most important, though energetically costly, ways to colonise new areas is through high reproductive output. Mussels can spend up to 90 % of

their total energy on reproduction. Annual reproductive output is a function of the weight loss per spawning as well as the frequency of spawning. We considered spawning of all 4 species to be biennial, as described by van Erkom Schurink & Griffiths (1991), although the data for *M. galloprovincialis* reflected 3 troughs in mass that could be interpreted as 3 spawning events. Griffiths (1977) suggested that both *C. meridionalis* and *A. atra* may spawn up to 3 times  $\text{yr}^{-1}$ . In Chile, *S. algius* held on mussel-raft ropes had 2 peaks of reproduction per year (González et al. 1980).

Even though *S. algius* did not have the highest absolute annual reproductive output of the 4 species, there are other ways of considering its reproductive output. (1) It has the advantage of being a simultaneous hermaphrodite. Consequently, every individual is capable of producing larvae, in contrast to the other species, for which our data showed that females constituted 36–51 % of their populations. (2) Reproductive output can be expressed in relative terms as the proportional output compared with the maximum flesh mass. Standardised for 40 mm mussels, *S. algius* had a high relative output (118.5%), surpassed only by *C. meridionalis* (132%). (3) Reproductive output can be evaluated for the population as a whole. *S. algius* and *M. galloprovincialis* dominate wave-exposed shores on the West Coast of South Africa, contributing respectively 30–52 and 48–54 % of the mussel biomass. *A. atra* and *C. meridionalis*, by contrast, add trivial amounts of 0–5 and 0–9 % (De Greef et al. 2013). Accurate calculation of population reproductive output is not possible without a better knowledge of subtidal populations, but it is clear that overall intertidal reproductive outputs of *S. algius* and *M. galloprovincialis* will far exceed those of the indigenous species.

### Recruitment rate

Although the reproductive output for *S. algius* was not the highest of the 4 species, it translated into an exceptionally high recruitment rate—far greater than that of any of the other species. For all 4 species, recruitment was highest in conspecific beds. There is a strong small-scale correlation between adult densities of mussels and their recruitment (Robinson et al. 2007, Pfaff et al. 2011). However, even though the percentage of *S. algius* recruits was highest in conspecific beds (91.72 % of the recruits of all species combined), it still had significantly greater proportions of recruits than any other species within

patches of the other 3 species. The proportionally lower recruitment of *S. algalus* into beds of other species may reflect interspecific competition between species or preferential settlement among conspecifics—a distinction that cannot be resolved from our data. In its native range, *S. algalus* preferentially settles in conspecific beds, avoiding the beds of the dominant competitor, *P. purpuratus* (A. U. Caro unpubl. data), pointing to interspecific competition as the reason for the observed pattern.

In southern Africa, recruitment of mussels is most intense on the West Coast, diminishes on the South Coast, and is lowest on the East Coast (Reaugh-Flower et al. 2010, 2011). Retention–dispersion patterns may influence recruitment rates at small scales, but at a regional scale, recruitment is most likely to be affected by the gradient of increasing nutrient levels and pelagic primary production around the coast from east to west (Bustamante et al. 1995, Branch & Steffani 2004), presumably translating into greater food supplies for mussel larvae on the West Coast. This may contribute to the intense recruitment of *S. algalus* on the West Coast but would not explain the differences among mussel species there. Mussel recruitment varies among sites, and also among seasons and years (Reaugh-Flower et al. 2010). In our study, all 4 mussel species had 2 main recruitment peaks, in early summer and autumn to early winter, although not in the same months. Nevertheless, recruitment was still consistently higher for *S. algalus* than for the other mussel species in all months. In Namibia, *S. algalus* followed a similar seasonal pattern and always had the highest recruitment of 3 mussel species throughout the year (Reaugh-Flower et al. 2011). Our study was conducted over a period of 12 mo and at 1 site, so it is possible that the site and year examined provided particularly favourable recruitment for *S. algalus*. However, Reaugh-Flower et al. (2010, 2011) conducted a recruitment study over 5 yr (1995–1999) covering the entire coastline of southern Africa, and also established that *S. algalus* consistently had the highest recruitment rate of all mussel species across the span of its geographic distribution in the region.

Tidal height also affects recruitment rate (Porri et al. 2007, Bownes & McQuaid 2009). Recruitment of *S. algalus* was substantially greater than that of the other 3 species low on the shore but diminished up the shore to levels that were comparable to those of the other species at the top of the shore. *M. galloprovincialis* recruited in greatest abundance on the mid-shore. For both species, recruitment followed the pattern of adult tidal distribution (Zardi et al.

2006, De Greef et al. 2013), with *S. algalus* predominating in the low shore, and *M. galloprovincialis* in the mid- to high shore. Although small numbers of *S. algalus* did recruit to the high shore, surveys showed that adults were absent from the high shore, probably due to high recruit mortality there (Z. Zeeman pers. obs.).

The balance between growth and mortality rules spatial dominance, but where growth is insufficient to counter mortality, recruitment can offset mortality to maintain dominance (Petraitis 1995). *S. algalus* clearly dominates the low shore despite its high mortality and low growth rate, and relies on a high recruitment rate to maintain this spatial dominance. In addition, it does not follow a defensive strategy by investing in shell and attachment strength, but rather expends energy on reproduction. This leads to very high recruitment and rapid colonisation.

## COMPARISONS AND CONCLUSIONS

Our study shows that the 4 dominant mussel species that occupy South African West Coast rocky shores have adopted different life strategies. The native mussel *A. atra* expends most of its energy on predation resistance, as indicated by shell and byssus strength. *C. meridionalis* has a high growth rate and rapidly achieves a size large enough to escape most predation (Griffiths & Seiderer 1980, Griffiths & Hockey 1987). Conversely, the 2 invasive mussels allocate more energy to features associated with rapid colonisation to achieve spatial dominance. *M. galloprovincialis* possesses traits that allow it to occupy space by growing quickly and has a high reproductive output (Branch & Steffani 2004). *S. algalus* relies entirely on its exceptionally high recruitment rate to overcome the high mortality it experiences because of its weak shell and byssal attachment. However, its abundance is confined to the low shore, most likely because it is intolerant of physical stresses higher on the shore.

Life-history characteristics are affected by abiotic factors such as sea temperature, wave exposure and nutrient availability, and may vary among sites and seasons (Hickman 1979, Bayne et al. 1993, McQuaid & Lindsay 2000, Nicastro et al. 2010). We compared the life history patterns of the 4 mussel species at a single site and under circumstances that ensured comparability of data. It is possible that results might differ at other sites and shore heights. For example, *M. galloprovincialis* is the fastest-growing mussel in Algoa Bay on the warm South Coast of South Africa,



whereas *C. meridionalis* grows faster than *M. galloprovincialis* in the cooler, upwelled waters of Saldanha Bay on the West Coast (van Erkom Schurink & Griffiths 1993). However, our results concur with other life-history studies in this system. In particular, the studies of Reaugh-Flower et al. (2010, 2011) revealed that *S. algosus* consistently has the highest recruitment rates across the entire West Coast of southern Africa. Our central conclusion that high recruitment underpins the invasive success of *S. algosus* is therefore likely to be robust across the entire region.

It remains to be determined how the life-history characteristics of the mussels we examined will respond to variations in factors such as wave action, upwelling, food supply and local hydrography. It is well established that *M. galloprovincialis* dominates moderately exposed shores in southern Africa (Branch & Steffani 2004), largely because of the greater supplies of particulate food there (Bustamante & Branch 1996b), and it is likely that the same will be true of *S. algosus* (De Greef et al. 2013). What is abundantly clear is that *S. algosus* owes much of its success as an invader to its exceptionally high rates of recruitment, particularly low on the shore, which have now been recorded across almost 3000 km of the West Coast of southern Africa, from central Namibia (Reaugh-Flower et al. 2011) to the Bloubergstrand site we researched.

Although factors driving marine invasions are complex and varied (Bugnot et al. 2016), an understanding of these factors is important to inform management strategies. Our study shed light on the life-history characteristics that contribute to invasive success world-wide, and the circumstances under which species will become invasive and dominate invaded areas. Specifically, it highlights that the 2 alien mussels that have occupied large sections of the coast of southern Africa, *M. galloprovincialis* and *S. algosus*, achieve their dominance by reproductive characteristics that promote recruitment, rather than investment in means of resisting predators. Although *S. algosus* has not invaded other areas to date, it clearly has the capacity to become a global invader similar to *M. galloprovincialis*. Indeed, Bigatti et al. (2014) have warned of a potential invasion by *S. algosus* on the Atlantic coast of South America, after its detection in the ballast of a fishing vessel at Nuevo Gulf, Argentina.

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