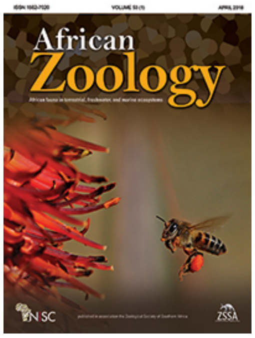

African Zoology

ISSN: 1562-7020 (Print) 2224-073X (Online) Journal homepage: http://www.tandfonline.com/loi/tafz20

Contrasting invasion patterns in intertidal and subtidal mussel communities

Lisa Skein, Mhairi Alexander & Tamara Robinson

To cite this article: Lisa Skein, Mhairi Alexander & Tamara Robinson (2018) Contrasting invasion patterns in intertidal and subtidal mussel communities, African Zoology, 53:1, 47-52, DOI: 10.1080/15627020.2018.1448720

To link to this article: https://doi.org/10.1080/15627020.2018.1448720

Published online: 20 Apr 2018.

African Zoology 2018, 53(1): 47–52
Printed in South Africa — All rights reserved

AFRICAN ZOOLOGY
ISSN 1562-7020 EISSN 2224-073X
https://doi.org/10.1080/15627020.2018.1448720

Short Communication

Contrasting invasion patterns in intertidal and subtidal mussel communities

Lisa Skein[1], Mhairi Alexander[2] and Tamara Robinson[1]*

[1] *Department of Botany and Zoology, Stellenbosch University, Stellenbosch, South Africa*
[2] *School of Science and Sport, University of the West of Scotland, Paisley, UK*
* *Corresponding author, email: trobins@sun.ac.za*

Two invasive mussel species are known from South Africa, *Mytilus galloprovincialis* and *Semimytilus algosus*. Most of the existing research on these invaders has focused on the intertidal zone, with little attention paid to subtidal habitats. This study addresses this knowledge gap by quantifying the relative abundance and size of native and alien mussels from the high-shore down to the subtidal zone, while accounting for the effects of wave exposure. This was achieved through extensive surveys along the west coast of South Africa and the Cape Peninsula. At all shore zones, mussel abundance varied among species and wave exposures. In intertidal habitats, invasive species were recorded in greatest abundances at wave-exposed sites. Specifically, *M. galloprovincialis* was dominant in the high-shore, but this pattern changed down the shore. In the mid-shore, the invaders were equally dominant over native mussels, while in the low-shore *S. algosus* became the most abundant. Notably, the native *Choromytilus meridionalis* was absent intertidally. In the subtidal zone *M. galloprovincialis* was rarely present, whereas *S. algosus* maintained a strong presence. The maximum size of native *Aulacomya atra* and invasive *S. algosus* in the subtidal zone was roughly double that recorded in the intertidal zone. Importantly, these results highlight that observations made from intertidal studies of mussel invasions cannot be used to infer subtidal patterns.

Keywords: alien species, marine invasions, *Mytilus galloprovincialis*, *Semimytilus algosus*

Introduction

The Mediterranean mussel *Mytilus galloprovincialis* (Lamarck, 1819) is a dominant invasive species along the South African coast occurring on rocky shores along approximately 2 800 km of the coastline between Namibia and East London (Assis et al. 2015). The impacts of *M. galloprovincialis* in this habitat are well studied (Alexander et al. 2016), which is likely attributable to it having been present along this coast for more than 30 years (Grant and Cherry 1985). On the west coast, these impacts include partial competitive displacement of native biota such as limpets (Steffani and Branch 2005) and mussels (Sadchatheeswaran et al. 2015), as well as changing habitat structure and subsequent community composition through the creation of complex novel habitats (Robinson et al. 2007; Sadchatheeswaran et al. 2015). On the south coast, partial habitat segregation between *M. galloprovincialis* and the native mussel *Perna perna* is maintained through differential recruitment patterns, post-settlement survival and adaptions to wave force (Bownes and McQuaid 2006; Zardi et al. 2006, 2008).

The Chilean mussel *Semimytilus algosus* (Gould, 1850) was first detected on the west coast of South Africa in 2009 (de Greef et al. 2013). Recent evidence suggests that this species arrived through larval dispersal from the alien population in Namibia (Zeeman 2016). In its native range, *S. algosus* exhibits strong competitive abilities through formation of dense beds capable of excluding competitors from primary rock space (Tokeshi and Romero 1995; Bigatti et al. 2014). In South Africa, *S. algosus* exerts similar impacts to *M. galloprovincialis*, through changes to community structure and species diversity (Sadchatheeswaran et al. 2015). In comparison to the well-studied distribution of *M. galloprovincialis* (Robinson et al. 2005; Assis et al. 2015), the distribution and spread of *S. algosus* along the coastline of South Africa has received far less attention. Nonetheless, as a species known to exert strong influences on rocky shore communities (Sadchatheeswaran et al. 2015), there is a need to monitor this invasion. The range of *S. algosus* in South Africa was documented as encompassing 500 km along the west coast in 2010 (de Greef et al. 2013) and in 2015 the prediction was made that, if *S. algosus* were to reach the south coast, the species would likely become established (Alexander et al. 2015). Since then such a range expansion onto the south coast has been documented (TR unpublished data).

In the intertidal zone, *S. algosus* has been recorded in highest abundance on the low-shore, whereas *M. galloprovincialis* dominates the mid- to high-shore (de Greef et al. 2013). However, there is a large gap in knowledge regarding the dynamics of subtidal mussel populations, and whether the invasive *M. galloprovincialis* and *S. algosus* are dominant in this habitat, as they are in the intertidal zone. In intertidal habitats, the upper

African Zoology is co-published by NISC (Pty) Ltd and Informa UK Limited (trading as Taylor & Francis Group)

Published online 20 Apr 2018

distributions of sessile species are determined predominantly by their physiological tolerances to desiccation, heat stress and wave exposure (Zardi et al. 2008; Erlandsson et al. 2011); while biotic interactions such as competition and predation become increasingly important low on the shore (Connell 1972; Menge 2002). However, factors such as desiccation and heat stress become irrelevant when organisms are permanently submerged and exposed to stable temperatures. Nonetheless, water movement remains as an important structuring force (Westerbom and Jattu 2006; von der Meden et al. 2008) and species occupying sites characterised by a high degree of water movement will require a stronger attachment strength compared with those that inhabit more sheltered sites (Steffani and Branch 2003a; von der Meden et al. 2008). Utilisation of resources such as food and space are also key determinants of subtidal mussel communities. Food intake in turn influences growth and reproduction (Xavier et al. 2007), and surplus energy can be invested into the production of byssus threads, shells and body tissues (Steffani and Branch 2003a).

Despite the knowledge base on the distribution and abundance of mussels within the intertidal zones of large sections of the South African west and south coasts (van Erkom Schurink and Griffiths 1993; Rius and McQuaid 2006; Branch et al. 2008; Erlandsson et al. 2011), information is presently lacking for subtidal habitats. As such, the aim of this study was to quantify and compare the abundance and size of intertidal and subtidal mussel species within the range shared by *M. galloprovincialis* and *S. algosus*. Based on intertidal trends, it was hypothesised that (1) the invasive mussels *M. galloprovincialis* and *S. algosus* would support populations in the subtidal zone, and (2) that the densities of invasive mussels would be greater than those of native mussels (*A. atra* and *C. meridionalis*) in both intertidal and subtidal communities.

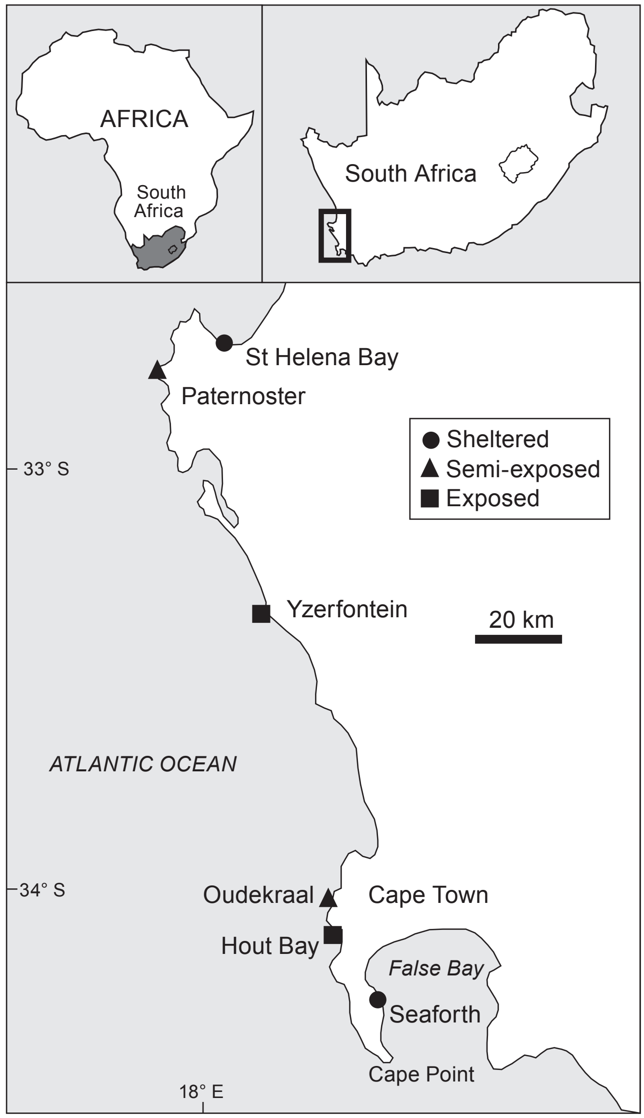

Figure 1: Sites that were surveyed during the winter months of 2016 along the west coast of South Africa and Cape Peninsula. These sites were categorised as either Sheltered (St Helena Bay, Seaforth), Semi-exposed (Paternoster, Oudekraal) or Exposed (Yzerfontein, Hout Bay)

Methods

Our survey was carried out in winter of 2016 along the west coast and Cape Peninsula, South Africa (Figure 1). Sites were chosen to cover the shared range of the two invasive mussels *Mytilus galloprovincialis* and *Semimytilus algosus*, and included sites exposed to different wave forces, i.e. sheltered ($n = 2$), semi-exposed ($n = 2$), and exposed sites ($n = 2$) (following Steffani and Branch 2003a).

At all sites, five 20 cm × 20 cm quadrat samples, separated by 1–10 m, were collected from each of the high-, mid- and low-shore zones. All mussels present were identified to species level and counted. At each site, 50 individuals per species where measured to the nearest millimetre, unless fewer individuals were detected. Subtidal surveys were conducted by divers. Surveys comprised four 50 m transects that were swum perpendicular to the shore in search of mussels. Along each transect, five quadrats (20 cm × 20 cm) were scraped from mussel beds and the samples returned to the laboratory where all mussels were identified to species level and individuals counted and measured.

As the appropriate statistical assumptions were met, mussel abundance was compared among species (*A. atra*, *C. meridionalis*, *M. galloprovincialis* and *S. algosus*) and wave exposure levels (sheltered, semi-exposed and exposed) using a two-way analysis of variance (ANOVA) followed by Tukey honestly significant difference *post-hoc* tests. Separate analyses were undertaken for each shore zone, including the subtidal zone. Mussels were absent from the intertidal on sheltered shores. As such, comparisons of abundance among species in the intertidal zone included only semi-exposed and exposed conditions. For each species, size was compared between intertidal and subtidal populations using a Mann–Whitney test. Additionally, Kolmogorov–Smirnov tests were used to compare size–frequency distributions of intertidal and subtidal mussels. All analyses were carried out in RStudio (R Development Core Team 2015).

Table 1: Results from two-way ANOVAs considering the effect of species and wave exposure on mussel abundance in the high-, mid- and low-shore zones as well as the subtidal zone

Factor	High-shore	Mid-shore	Low-shore	Subtidal
Species	$F_{2,45} = 33.43$, $p < 0.001$	$F_{2,54} = 104.4$, $p < 0.001$	$F_{3,72} = 101.57$, $p < 0.001$	$F_{2,306} = 5.536$, $p = 0.004$
Exposure	$F_{1,45} = 17.92$, $p < 0.001$	$F_{1,54} = 149.02$, $p < 0.001$	$F_{1,72} = 145.69$, $p < 0.001$	$F_{2,306} = 5.306$, $p = 0.005$
Species*Exposure	$F_{1,45} = 16.4$, $p < 0.001$	$F_{2,54} = 35.57$, $p < 0.001$	$F_{3,72} = 55.37$, $p < 0.001$	$F_{4,306} = 4.879$, $p < 0.001$

Results

Mussel abundance differed significantly among species and wave exposures, regardless of the shore zone considered (Table 1), with significant interactions between these factors.

In the high-shore of exposed and semi-exposed sites, invasive *Mytilus galloprovincialis* was the most abundant species (Figure 2). Both invasive species (*M. galloprovincialis* and *Semimytilus algosus*) attained highest abundance on the mid- and low-shore zones of exposed sites (Figure 2). At all sites, *M. galloprovincialis* and *S. algosus* were significantly more abundant than native species on the mid-shore. This general pattern was maintained under exposed conditions in the low-shore, but here *S. algosus* was dominant even over *M. galloprovincialis*. The native mussel *Choromytilus meridionalis* was absent from the high- and mid-shore, and first appeared in the low-shore, increasing in abundance in the subtidal zone, with the highest subtidal numbers of this species recorded at sheltered and exposed sites (Figure 2). Very low numbers of *M. galloprovincialis* were recorded in the subtidal zone, with only a few individuals recorded from a single exposed site (Hout Bay). In contrast, the recent invader *S. algosus* supported large populations in the subtidal zone, with highest numbers recorded at sheltered and exposed sites.

Mann–Whitney tests showed a significant difference in the sizes of intertidal and subtidal *Aulacomya atra* ($U = 541\ 080$, $p < 0.001$) and *S. algosus* ($U = 146\ 430$, $p < 0.001$) (Figure 3). Kolmogorov–Smirnov tests revealed a significant difference between the size frequency distributions of intertidal and subtidal populations of these species (*A. atra*: $D = 0.408$, $p < 0.001$; and *S. algosus*: $D = 0.225$, $p < 0.001$). For both species, intertidal populations supported few mussels > 25 mm, whereas larger mussels were common in subtidal populations. The intertidal size range of *A. atra* was 2–48 mm, whereas subtidal conspecifics ranged from 1 to 90 mm. *Semimytilus algosus* ranged from 3 to 54 mm in the intertidal, and from 1–128 mm in the subtidal zone. The absence of *C. meridionalis* and *M. galloprovincialis* from intertidal and subtidal sites, respectively, precluded comparisons between these habitats for these species.

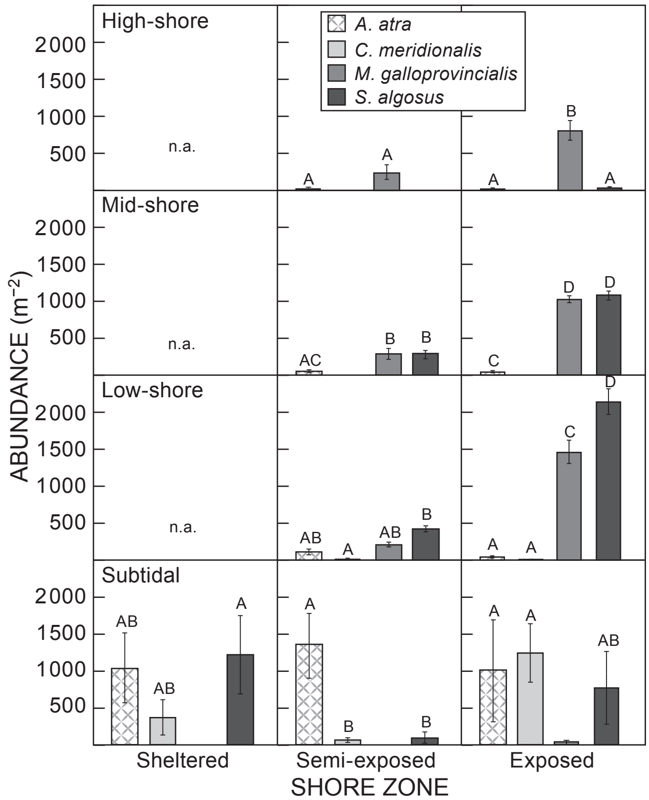

Figure 2: Abundance (mean ± SE) of native (*Aulacomya atra* and *Choromytilus meridionalis*) and invasive (*Mytilus galloprovincialis* and *Semimytilus algosus*) mussels in the various shore zones on sheltered, semi-exposed and exposed shores. Shared letters above bars indicate no statistical difference (Tukey's *post-hoc* test, $p > 0.05$). *Mytilus galloprovincialis* was not included in statistical comparisons in the subtidal zone as it only occurred at a single exposed site

Discussion

Invasive mussels supported greater densities than native mussels in intertidal communities, although this did not hold for the subtidal zone. In subtidal communities, native mussels were more abundant than intertidal conspecifics, and invasive *Semimytilus algosus* was present at densities comparable to that of native species. In contrast to intertidal communities, *Mytilus galloprovincialis* was the least abundant species in the subtidal zone. In intertidal habitats in the high-, mid- and low-shore, exposed sites supported a greater abundance of mussels than semi-exposed and sheltered sites, with no mussels present in the latter. While it is important to acknowledge that the sheltered sites in this study fell within St Helena Bay (an area well known for low oxygen conditions; Lamont et al. 2015) and along the Cape Peninsula in False Bay (which is adjacent to the biogeographic breakpoint that separates the south and west coasts; Sink et al. 2012), and that these two sheltered sites were the only sites to fall downstream of upwelling centres (Pfaff et al. 2011), the results obtained are considered a valid representation of sheltered shores. This is because (1) low oxygen conditions are focused in the bottom waters of St Helena Bay, with wind-driven mixing ventilating waters in the nearshore where this study was conducted (Lamont et al.

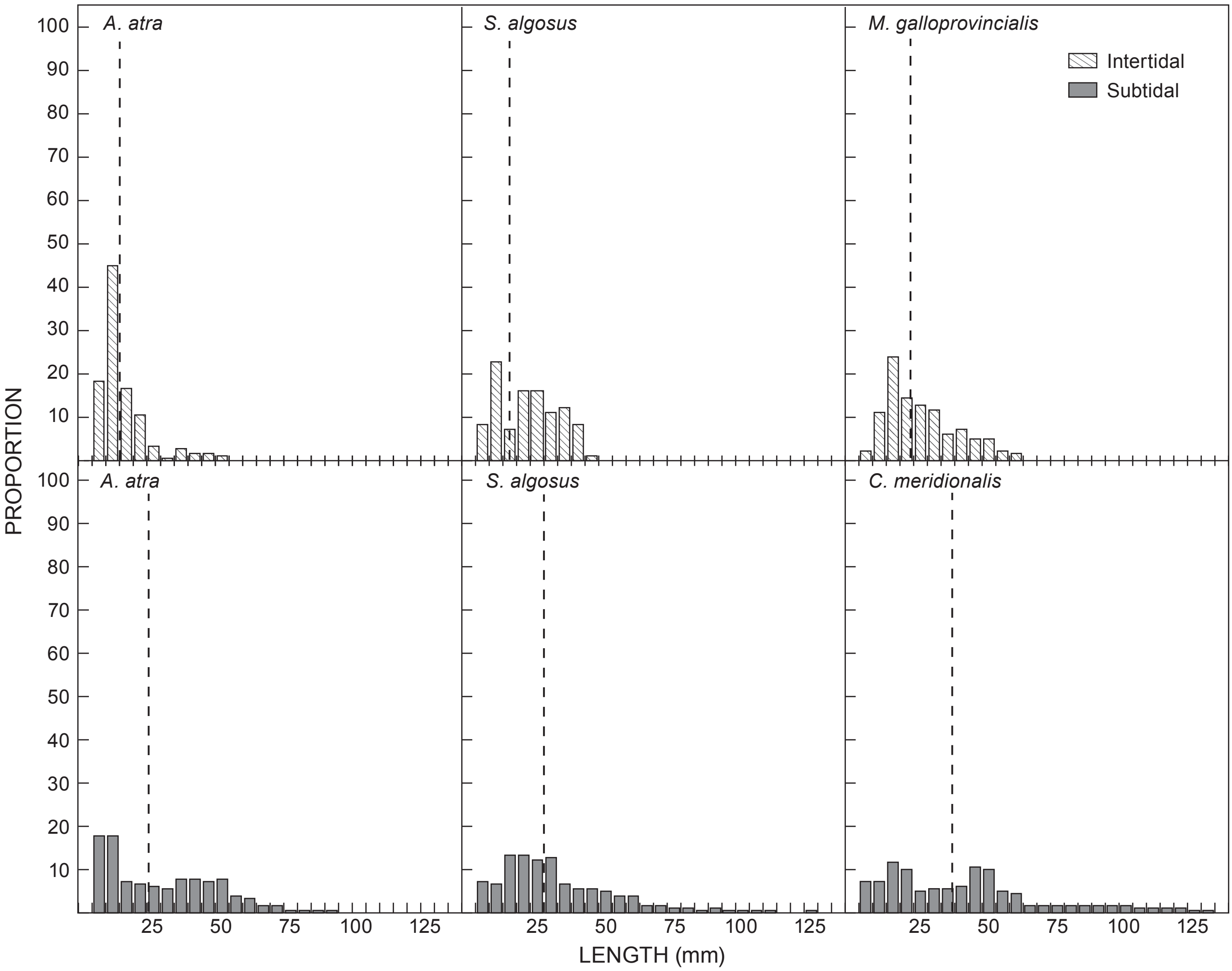

Figure 3: Proportional size frequency distributions of intertidal and subtidal mussels. Dotted lines represent medians. It was not possible to construct meaningful distributions for *Choromytilus meridionalis* in the intertidal or *Mytilus galloprovincialis* in the subtidal as fewer than 50 individuals were recorded for each of these species in these habitats

2015); (2) a previous study has demonstrated that mussels respond similarly to wave action along the Cape Peninsula as they do further up the west coast (Steffani and Branch 2003a); (3) intertidal recruitment of mussels is known to be greater downstream of upwelling centres (Pfaff et al. 2011), which suggests that if this factor affected our findings we should have recorded elevated abundances of mussels at our sheltered sites rather than their absence; and (4) the absence of mussels at sheltered sites has previously been documented along this coast (Steffani and Branch 2003b). Numerous studies considering the role of wave action have demonstrated its importance in determining the distribution and co-existence of sessile marine species. For example, it has been shown that *M. galloprovincialis* attains highest abundance in exposed sites (Branch et al. 2008), and that growth and condition index are highest on these shores (Steffani and Branch 2003a). It has been suggested that this is driven by an elevated food supply on more exposed shores resulting from greater water movement (Steffani and Branch 2005), and that the overall scarcity of mussels on sheltered shores is likely a result of an insufficient food supply for filter feeders such as mussels (Steffani and Branch 2003a, Branch and Steffani 2004).

The numerical dominance of *M. galloprovincialis* in the high- and mid-shore zones is supported by previous research (Branch and Steffani 2004; de Greef et al. 2013), and is most likely attributable to the high desiccation tolerance, high recruitment rates, and low tolerance to inundation by sand (van Erkom Schurink and Griffiths 1991; Hockey and van Erkom Schurink 1992; Zardi et al. 2008). In intertidal rocky shore communities on the west coast, the competitive superiority of *M. galloprovincialis* has been suggested to be an important driver of the decline of native *Aulacomya atra* (Robinson et al. 2007), and the overall scarcity of *C. meridionalis* (Sadchatheeswaran et al. 2015). However, with decreasing tidal elevation the abundance of *M. galloprovincialis* also decreased, with only a few individuals recorded at a single, exposed subtidal site (Hout Bay). This is surprising, especially considering the fact that this species is farmed subtidally in Saldanha Bay (Probyn et al. 2001). Intense predation by predators on sessile prey has been shown to limit, and in some cases even exclude, prey species (Rilov and Schiel 2005). It is thus possible that predation by native subtidal predators (e.g. whelks, lobsters, starfish and crabs) could be excluding *M. galloprovincialis* from this zone. However, recent research suggests that the rock lobster *Jasus lalandii* (H. Milne Edwards, 1837) and the starfish *Marthasterias africana* (Muller & Troschel, 1842) actively seek out native mussels over alien mussel prey (Skein et al. in press). This highlights the dynamic nature of biotic interactions and demonstrates the need for research into subtidal invasions.

The recently introduced *S. algosus* exhibited a strong presence in inter- and subtidal mussel communities. In its native range in Chile, *S. algosus* dominates the low-shore and is found subtidally (Tokeshi and Romero 1995). The dense beds of *S. algosus* formed in its native range have been ascribed to high recruitment rates and strong competitive abilities (Tokeshi and Romero 1995). On the South African coastline, a similar pattern is observed, with *S. algosus* outnumbering all co-occurring mussel species on the low-shore and native species in the mid-shore. Unlike *M. galloprovincialis*, this species attained high abundances subtidally, suggesting that *S. algosus* performs as well as native species in subtidal habitats. Notably, *S. algosus* was recorded in high numbers in intertidal and subtidal habitats at the edge of its current eastward distribution and, as such, monitoring of this species is recommended.

The large size attained by *S. algosus* and *A. atra* in the subtidal compared with the intertidal conspecifics is notable. Subtidally, *S. algosus* attained maximum sizes larger than 120 mm, in contrast to 54 mm in the intertidal. This is particularly surprising, as previous studies report that the maximum size of this species does not exceed 60 mm (de Greef et al. 2013). This is notable as the perceived small size of this species has underpinned the notion that *S. algosus* would remain within a window of vulnerability (5–60 mm) for mussel predators (de Greef et al. 2013). It is probable that the discrepancy in size between intertidal and subtidal habitats is the result of constant food supply for mussels in the latter (Westerbom and Jattu 2006). The scarcity of large mussels in intertidal zones is unlikely to be a result of selective harvesting, as the sites surveyed are not frequented by mussel harvesters. As such, it is suggested that while intertidal populations of *S. algosus* remain vulnerable to mussel predators, subtidal conspecifics may face reduced susceptibility due to their increased size. This has important implications for the future invasion of *S. algosus* as large mussels contribute proportionally more to the reproductive output of the population (van Erkom Schurink and Griffiths 1991) and can thus contribute to the spread of this invader. It would be useful for future studies to examine the mechanisms responsible for the size differences between inter- and subtidal mussels. For example, intertidal mussels might be facing trade-offs between energy invested in growth versus energy invested in attachment strength or desiccation tolerance, whereas subtidal mussels may invest more energy in growth as they are not exposed to the same environmental stressors as intertidal mussels.

In conclusion, the high densities supported by the invasive mussels *M. galloprovincialis* and *S. algosus* in the intertidal zone are not mirrored in the subtidal. Rather *M. galloprovincialis* is almost absent from natural subtidal habitats. Despite the relatively short timeframe that *S. algosus* has been present on South African shores, it has become a dominant invader both intertidally and subtidally. In light of the impacts associated with this invasion (de Greef et al. 2013; Sadchatheeswaran et al. 2015), it is recommended that monitoring of this incursion be undertaken in both intertidal and subtidal habitats.

Acknowledgement — The financial support of the DST-NRF Centre of Excellence for Invasion Biology is gratefully acknowledged.

ORCID

Tamara Robinson https://orcid.org/0000-0001-5515-1445

References

Alexander ME, Adams R, Dick JTA, Robinson TB. 2015. Forecasting invasions: resource use by mussels informs invasion patterns along the South African coast. *Marine Biology* 162: 2493–2500.

Alexander ME, Simon C, Griffiths CL, Peters K, Sibanda S, Miza S, Groenewald B, Majiedt P, Sink K, Robinson TB. 2016. Back to the future: reflections and directions of South African marine bioinvasion research. *African Journal of Marine Science* 38: 141–144.

Assis J, Zupan M, Nicastro KR, Zardi GI, McQuaid CD, Serrão EA. 2015. Oceanographic conditions limit the spread of a marine invader along southern African shores. *PLoS ONE* 10: e0128124.

Bigatti G, Signorelli JH, Schwindt E. 2014. Potential invasion of the Atlantic coast of South America by *Semimytilus algosus* (Gould, 1850). *BioInvasions Records* 3: 241–246.

Bownes SJ, McQuaid CD. 2006. Will the invasive mussel *Mytilus galloprovincialis* Lamarck replace the indigenous *Perna perna* L. on the south coast of South Africa? *Journal of Experimental Marine Biology and Ecology* 338: 140–151.

Branch GM, Odendaal F, Robinson TB. 2008. Long-term monitoring of the arrival, expansion and effects of the alien mussel *Mytilus galloprovincialis* relative to wave action. *Marine Ecology Progress Series* 370: 171–183.

Branch GM, Steffani CN. 2004. Can we predict the effects of alien species? A case-history of the invasion of South Africa by *Mytilus galloprovincialis* (Lamarck). *Journal of Experimental Marine Biology and Ecology* 300: 189–215.

Connell JH. 1972. Community interactions on marine rocky intertidal shores. *Annual Review of Ecology and Systematics* 3: 169–192.

de Greef K, Griffiths CL, Zeeman Z. 2013. Deja vu? A second mytilid mussel, *Semimytilus algosus*, invades South Africa's west coast. *African Journal of Marine Science* 35: 37–41.

Erlandsson J, McQuaid CD, Sköld M. 2011. Patchiness and co-existence of indigenous and invasive mussels at small spatial scales: the interaction of facilitation and competition. *PLoS ONE* 6: e26958.

Grant WS, Cherry MI 1985. *Mytilus galloprovincialis* Lmk. in southern Africa. *Journal of Experimental Marine Biology and Ecology* 90: 179–191.

Hockey PAR, van Erkom Schurink C. 1992. The invasive biology of the mussel *Mytilus galloprovincialis* on the southern African coast. *Transactions of the Royal Society of South Africa* 48: 123–139.

Lamont T, Hutchings L, van den Berg MA, Goschen WS, Barlow RG. 2015. Hydrographic variability in the St Helena Bay region of the southern Benguela ecosystem. *Journal of Geophysical Research* 120: 2920–2944.

Menge BA. 2002. Top-down and bottom-up community regulation in marine rocky intertidal habitats. *Journal of Experimental Marine Biology and Ecology* 250: 257–289.

Pfaff MC, Branch GM, Wieters EA, Branch RA, Broitman BR. 2011. Upwelling intensity and wave exposure determine recruitment of intertidal mussels and barnacles in the southern Benguela upwelling region. *Marine Ecology Progress Series* 425: 141–152.

Probyn T, Pitcher G, Pienaar R, Nuzzi R. 2001. Brown tides and mariculture in Saldanha Bay, South Africa. *Marine Pollution Bulletin* 42: 405–408.

R Development Core Team. 2015. R: a language and environment for statistical computing. Vienna: R Foundation for Statistical Computing.

Rilov G, Schiel DR. 2005. Trophic linkages across seascapes: subtidal predators limit effective mussel recruitment in rocky intertidal communities. *Marine Ecology Progress Series* 327: 83–93.

Rius M, McQuaid CD. 2006. Wave action and competitive interaction between the invasive mussel *Mytilus galloprovincialis* and the indigenous *Perna perna* in South Africa. *Marine Biology* 150: 69–78.

Robinson TB, Branch GM, Griffiths CL, Govender A, Hockey PAR. 2007. Changes in South African rocky intertidal invertebrate community structure associated with the invasion of the mussel *Mytilus galloprovincialis*. *Marine Ecology Progress Series* 340: 163–171.

Robinson TB, Griffiths CL, McQuaid C, Rius M. 2005. Marine alien species of South Africa — status and impacts. *African Journal of Marine Science* 27: 297–306.

Sadchatheeswaran S, Branch GM, Robinson TB. 2015. Changes in habitat complexity resulting from sequential invasions of a rocky shore: implications for community structure. *Biological Invasions* 17: 1799–1816.

Sink K, Holness S, Harris L, Majiedt P, Atkinson L, Robinson T, Kirkman S, Hutchings L, Leslie R, Lamberth S, Kerwath S, von der Heyden S, Lombard A, Attwood C, Branch G, Fairweather T, Taljaard S, Weerts S, Cowley P, Awad A, Halpern B, Grantham H, Wolf T. 2012. *National biodiversity assessment 2011: technical report*, vol. 4. Pretoria: South African National Biodiversity Institute.

Steffani CN, Branch GM. 2003a. Growth rate, condition, and shell shape of *Mytilus galloprovincialis*: responses to wave exposure. *Marine Ecology Progress Series* 246: 197–209.

Steffani CN, Branch GM. 2003b. Spatial comparisons of populations of an indigenous limpet *Scutellastra argenvillei* and an alien mussel *Mytilus galloprovincialis* along a gradient of wave energy. *African Journal of Marine Science* 25: 195–212.

Steffani CN, Branch GM. 2005. Mechanisms and consequences of competition between an alien mussel, *Mytilus galloprovincialis,* and an indigenous limpet, *Scutellastra argenvillei*. *Journal of Experimental Marine Biology and Ecology* 317: 127–142.

Tokeshi M, Romero L. 1995. Filling a gap: dynamics of space occupancy on a mussel-dominated subtropical rocky shore. *Marine Ecology Progress Series* 119: 167–176.

van Erkom Schurink C, Griffiths CL. 1991. A comparison of reproductive cycles and reproductive output in four southern African mussel species. *Marine Ecology Progress Series* 123–134.

van Erkom Schurink C, Griffiths CL. 1993. Factors affecting relative rates of growth in four South African mussel species. *Aquaculture* 109: 257–273.

von der Meden CEO, Porri F, Erlandsson J, McQuaid CD. 2008. Coastline topography affects the distribution of indigenous and invasive mussels. *Marine Ecology Progress Series* 372: 135–145.

Westerbom M, Jattu S. 2006. Effects of wave exposure on the sublittoral distribution of blue mussels *Mytilus edulis* in a heterogeneous archipelago. *Marine Ecology Progress Series* 306: 191–200.

Xavier BM, Branch GM, Wieters E. 2007. Abundance, growth and recruitment of *Mytilus galloprovincialis* on the west coast of South Africa in relation to upwelling. *Marine Ecology Progress Series* 346: 189–201.

Zardi GI, Nicastro KR, McQuaid CD, Erlandsson J. 2008. Sand and wave induced mortality in invasive (*Mytilus galloprovincialis*) and indigenous (*Perna perna*) mussels. *Marine Biology* 153: 853–858.

Zardi GI, Nicastro KR, McQuaid CD, Rius M, Porri F. 2006. Hydrodynamic stress and habitat partitioning between indigenous (*Perna perna*) and invasive (*Mytilus galloprovincialis*) mussels: constraints of an evolutionary strategy. *Marine Biology* 150: 79–88.

Zeeman Z. 2016. Genetics and ecosystem effects of the invasive mussel *Semimytilus algosus*, on the West Coast of South Africa. PhD thesis, University of Cape Town, South Africa.

Received 23 November 2017, revised 26 February 2018, accepted 2 March 2018
Associate Editor: Nicola James