African Journal of Marine Science

ISSN: (Print) (Online) Journal homepage: https://www.tandfonline.com/loi/tams20

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To cite this article: KCK Ma , CD McQuaid , A Pulfrich & TB Robinson (2020) Status of a decennial marine invasion by the bisexual mussel *Semimytilus algosus* (Gould, 1850) in South Africa, African Journal of Marine Science, 42:4, 507-515, DOI: 10.2989/1814232X.2020.1820376

To link to this article: https://doi.org/10.2989/1814232X.2020.1820376

African Journal of Marine Science 2020, 42(4): 507–515
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AFRICAN JOURNAL OF
MARINE SCIENCE
ISSN 1814-232X EISSN 1814-2338
https://doi.org/10.2989/1814232X.2020.1820376

Short communication

Status of a decennial marine invasion by the bisexual mussel *Semimytilus algosus* (Gould, 1850) in South Africa

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The invasion history and current distribution of the alien marine mussel, the bisexual mussel *Semimytilus algosus*, on rocky shores of South Africa is described in this study. The eastern edge of its distribution has been monitored since 2014, and the most-recent observations were made between January and March of 2020, at 16 sites between Hondeklipbaai on the west coast and Nature's Valley on the south coast. From these 2020 records, the species ranged across approximately 840 km along the coast, from Hondeklipbaai to Hermanus. The species' invasion history and distribution suggests that this mussel has persisted on the west coast over the past decade, and spread along the coast in both northward and south–southeastward directions. Since 2010, the species has spread predominantly in a southerly and then easterly direction, extending its range by ~270 km into the Agulhas ecoregion. In contrast, its spread has been slower to the north, with a range extension of only ~75 km. Long-term, routine monitoring of the coast to track the spread of *S. algosus* and other invasive marine species, and to identify new incursions, is recommended to support evidence-based management of biological invasions.

Keywords: biological invasion, bivalve, invasive species, monitoring, Mytilidae, Namibia, rocky shore, southern Africa

Online supplementary material: Additional records of *Semimytilus algosus* observed in Namibia can be found in Supplementary Table S1, available at https://doi.org/10.2989/1814232X.2020.1820376

Introduction

Three marine alien mussels—namely the Mediterranean mussel *Mytilus galloprovincialis* Lamarck, 1819, Asian green mussel *Perna viridis* (Linnaeus, 1758), and bisexual mussel *Semimytilus algosus* (Gould, 1850)—have been introduced to South Africa (Mead et al. 2011a; Robinson et al. 2016). Two of these, *M. galloprovincialis* and *S. algosus*, are considered invasive as they have spread from their points of introduction, rapidly colonising and establishing populations in wave-swept rocky-shore communities along the coast (Branch and Steffani 2004; de Greef et al. 2013; Skein et al. 2018a). Furthermore, both invasive species interact with native marine mussels by competing with native species for food and space on rocky shores (Rius and McQuaid 2006, 2009; Alexander et al. 2015a, 2015b). Although less is known about the potential for *P. viridis* to spread within South Africa (de Greef et al. 2013; Micklem et al. 2016), it has become widespread in other regions where it has been introduced (Wells 2017) and could compete or hybridise with the native brown mussel *Perna perna* (Linnaeus, 1758) (Mead et al. 2011b; Micklem et al. 2016).

Invasive mussels have a substantial effect on the structure and maintenance of intertidal and subtidal rocky-shore communities across South Africa (Branch and Steffani 2004). In particular, *M. galloprovincialis* has modified intertidal rocky shores and has impacted native mussel species. For example, on the west coast, it reduces the abundance of the ribbed mussel *Aulacomya atra* in intertidal habitats, and it restricts the distribution of the black mussel *Choromytilus meridionalis* (F. Krauss, 1848) (Griffiths et al. 1992; Hockey and van Erkom Schurink 1992; Branch and Steffani 2004; Robinson et al. 2007; Reimers et al. 2014; Alexander et al. 2015b; Sadchatheeswaran et al. 2018). On the south coast, *M. galloprovincialis* interacts intensely with the native *P. perna*, and the two species exhibit partial habitat segregation based on differences in settlement, recruitment and adult growth rates (Bownes and McQuaid 2006, 2009) as well as complex interactions including competition and facilitation (McQuaid et al. 2015). In subtidal habitats, predation has the potential to facilitate or resist invasions by the alien mussels *M. galloprovincialis* and *S. algosus*, but the outcome depends on whether predators (e.g. lobsters and whelks) co-occur or not (Skein et al. 2018b, 2020).

Considered native to the Pacific coast of South America (Soot-Ryen 1955), *S. algosus* had been introduced to

Published online 16 Dec 2020

Namibia by the late 1920s (Lamy 1931; Mead et al. 2011b), and was first noted in South Africa in 2009 (Mead et al. 2011a; de Greef et al. 2013) and along the Atlantic coast of South America in 2013 (Bigatti et al. 2014). In both its native and non-native ranges, recruitment can occur year-round, peaking during the (austral) summer in Chile and Namibia (Navarrete et al. 2008; Reaugh-Flower et al. 2011), and peaking bimodally in summer and again in autumn in South Africa (Zeeman et al. 2018). Hull-fouling and contaminated aquaculture products (e.g. transport of oyster spat) have been implicated as vectors for the introduction of *S. algosus* (Mead et al. 2011a; de Greef et al. 2013; Bigatti et al. 2014). Although molecular evidence, coupled with a pattern of rapid geographic spread, suggests that this mussel was introduced from Namibia to South Africa via long-distance larval transport, the importation of oyster spat remains a contender as a possible vector (Zeeman 2016; Zeeman et al. 2020).

In South Africa, *S. algosus* was first reported from Elandsbaai on the west coast in 2009 (Mead et al. 2011a; de Greef et al. 2013) but may have been introduced at an earlier date—although no earlier than 1988–1992, because the species was not detected during large-scale regional surveys over that period (Bustamante 1994). Also, the species was not observed at either Groenriviermond or the Cape Peninsula between 1995 and 1999 (ReaughFlower et al. 2011). The certainty of the absence of *S. algosus* from sites sampled by Bustamante (1994) and Reaugh-Flower et al. (2011) is bolstered by the fact that these investigators were familiar with the species from Namibian sites. Moreover, the lack of mention of *S. algosus* in studies spanning 1988–1993, 2001–2003 and 2006–2007 suggests that it was generally absent from the region prior to the first formal record in Elandsbaai (Wieters 2006; Branch et al. 2008, 2010; Blamey and Branch 2009).

In 2010 the distribution of *S. algosus* ranged approximately 500 km between Groenriviermond and Bloubergstrand on the west coast (de Greef et al. 2013). In the years immediately following its discovery, the range of this species expanded only in a southerly direction, reaching Hout Bay in 2012. However, by 2016 it had spread in a southeasterly direction, around Cape Point, to Seaforth in False Bay (Zeeman 2016; Skein et al. 2018a). This pattern of spread is consistent with the expectation that this species would become established along the south coast (Alexander et al. 2015a).

Unlike *M. galloprovincialis*, the distribution of which is believed to have reached a temporary equilibrium over 2 050 km of shore after approximately 25 years of its 40-year invasion history (Robinson et al. 2005; Assis et al. 2015), *S. algosus* may still be spreading in South Africa. The South African National Biodiversity Institute (SANBI) is mandated by law to monitor and report on the status of biological invasions in South Africa. To fulfill this mandate, SANBI requires up-to-date information on the status and distribution of alien taxa. This study provides such information for *S. algosus*. Specifically, we present: (i) the invasion history of *S. algosus* since its discovery on the west coast of South Africa in 2009; and (ii) an update on its current distribution, which can serve as a time-stamp on this ongoing invasion in South Africa.

Materials and methods

Invasion history and monitoring

Occurrence records from the literature (de Greef et al. 2013; Alexander et al. 2015a, 2015b; Sadchatheeswaran et al. 2015, 2018; Zeeman 2016; Pulfrich 2018; Skein et al. 2018a; Zeeman et al. 2018; Emanuel et al. 2020) and from monitoring of rocky shores (present study) were combined to reconstruct the invasion history of *S. algosus* in South Africa. Monitoring for this species was done annually, from 2014 to 2019, and was geographically focused at sites at the eastern edge of its distribution. At each site, the species was reported as either present or not detected. By identifying the sites that represented the limits of distribution in a given year and using the first year of detection at a site, we could track changes in these limits in time. This allowed us to estimate rates of spread by computing the alongshore distances between sites representing the distributional limits divided by the number of years that had elapsed between the observations

Current distribution

To assess the current distribution of *S. algosus* in South Africa, 16 rocky-shore sites, from Hondeklipbaai to Nature's Valley, were surveyed in January and March of 2020, during spring low tides (Table 1). Suspected specimens of *S. algosus* (*n* = 1 to 6 individuals per site) were collected and examined live to confirm the species identity based on morphology (see below). Shell length was measured using calipers, and the resilial ridge in the shell of each individual was examined under a stereomicroscope. Note that finding even a single specimen was sufficient to record the species as present at a site.

Morphological examination

Mussel specimens were dissected by severing the posterior adductor muscle, using a scalpel to open the shell to visually inspect the gonads, because in a majority of individuals *S. algosus* can be distinguished from other mytilid mussels by being hermaphroditic, possessing both male and female gonads concurrently (Bigatti et al. 2014; Oyarzún et al. 2020). After gonads were inspected, the soft body tissues were removed to examine the shell for the following features: (a) elongate, brownish green or brownish pink shells; (b) a bulge below the apex; (c) an undivided posterior foot retractor-muscle scar; (d) an anterior byssus retractor-muscle scar divided into two parts; (e) a narrow resilial ridge; and (f) absence of pits in the resilial ridge (Soot-Ryen 1955; Kensley and Penrith 1970).

Results

Historical occurrence data from the literature and our recent monitoring efforts were tabulated (Tables 1 and 2) and then mapped (Figure 1). On the west coast, at the northern distributional limit in South Africa, the species was initially detected at Groenriviermond in 2010 (and again in 2012) and at Hondeklipbaai in 2020, indicating a northward range extension of ~75 km (Table 3). On the south coast, at the southern and eastern distributional limits, the species was detected for the first time at the following sites: (i) Bloubergstrand in 2010; (ii) Hout Bay in 2012 (and

Table 1: Occurrence records of *Semimytilus algosus* from 16 rocky-shore sites in South Africa in 2020

Site	Latitude (°S)	Longitude (°E)	Date	Occurrence
Hondeklipbaai	30.31341	17.27383	6 February	Present
Doringbaai	31.81317	18.23491	7 February	Present
Elandsbaai	32.35310	18.31483	9 January	Present
Paternoster	32.80704	17.88643	9 February	Present
Jacobsbaai	32.94307	17.88526	8 February	Present
Yzerfontein	33.35424	18.15079	9 February	Present
Bloubergstrand	33.80519	18.46248	11 January	Present
Three Anchor Bay	33.90837	18.39328	10 February	Not detected
Fish Hoek	34.14197	18.43353	11 February	Not detected
Muizenberg	34.10971	18.46866	12 January	Present
Gordons Bay	34.15993	18.86976	13 January	Present
Hermanus	34.40920	19.27048	12 February	Present
Cape Agulhas	34.81411	20.05056	13 February	Not detected
Mosselbaai	34.18121	22.15809	26 March	Not detected
Groot-Brakrivier	34.06488	22.21037	1 January	Not detected
Nature’s Valley	33.98637	23.54832	25 March	Not detected

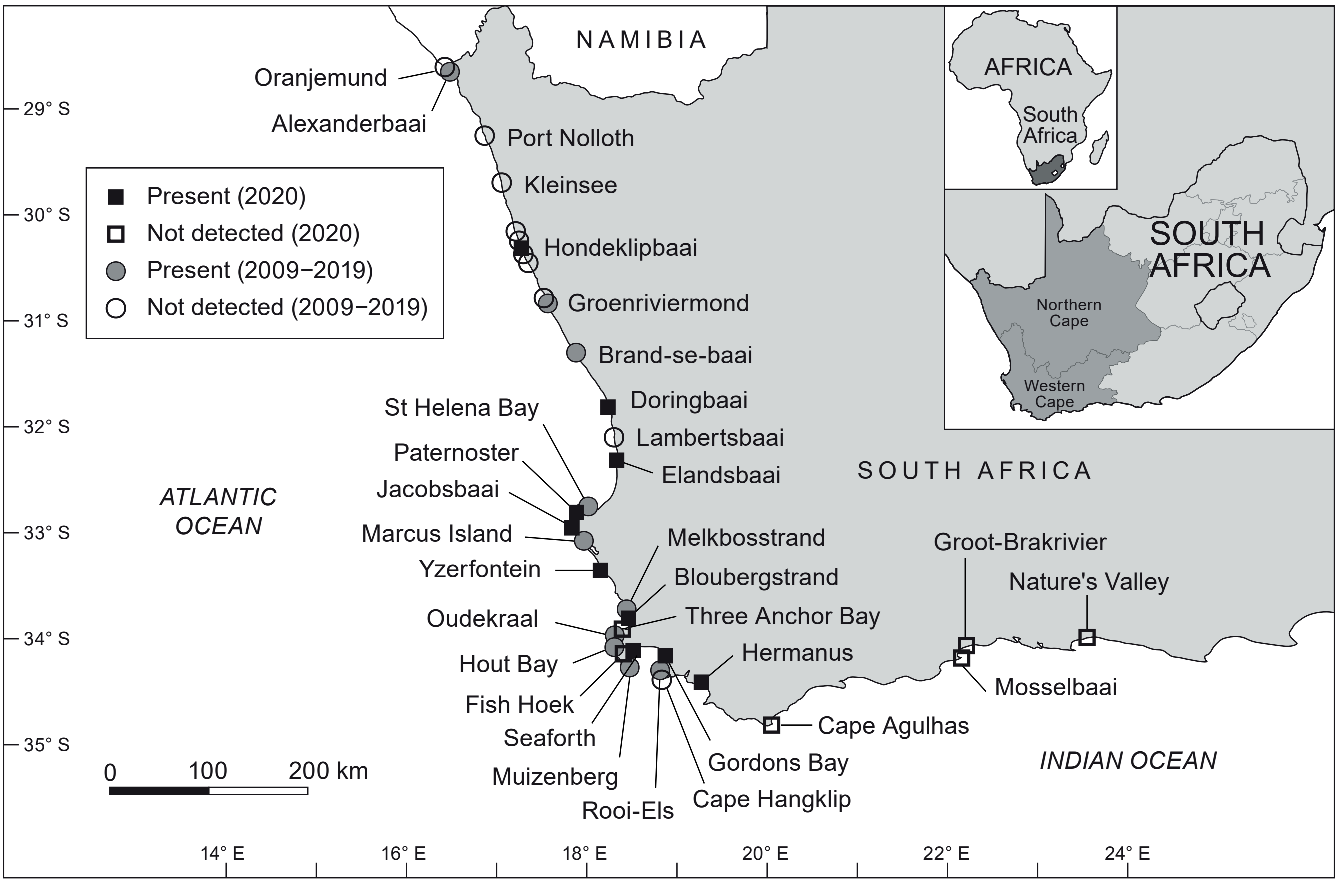

Figure 1: Overall distribution of *Semimytilus algosus* in South Africa, based on occurrence records from the present study and the literature (see Tables 1 and 2)

again in 2014), extending the range by 50 km; (iii) Seaforth in 2015 – a 70-km extension; (iv) Muizenberg in 2016 – 12 km; (v) Gordons Bay in 2017 – 40 km; (vi) Rooi-Els in 2018 (and again in 2019) – 25 km; and (vii) Hermanus in 2020 – 70 km (Table 3).

From 2014 to 2017, a new section of the African west coast in southern Namibia (from Mittag to Hostel) was gradually invaded by *Semimytilus algosus* (Supplementary Table S1). Although the species was generally spreading northwards from Mittag, it was observed at Alexanderbaai in July 2017 (Table 2), immediately south of the border between Namibia and South Africa. This observation, together with the data from our 2020 survey, indicated that the spatial gap between the invasions originating from southern Namibia and South Africa has decreased to a distance of ~305 km, between Alexanderbaai and Groenriviermond (in 2017), to only 230 km, between Alexanderbaai and Hondeklipbaai (in 2020).

Based on the two available occurrence records anchored in space and time (i.e. 2010 and 2020), the estimated rate of the species' northward spread, from Groenriviermond to Hondeklipbaai, was approximately 7.5 km y^{-1} (Table 3). Over the same period, the average rate of south–southeastward spread, from Bloubergstrand to Hermanus, was approximately 26.7 km y^{-1}. More specifically, the rate of southward spread was 25 km y^{-1}, and, later, the rate of easterly spread ranged from 12 to 40 km y^{-1} (Table 3).

Suspected specimens of *S. algosus* that were collected in 2020 were confirmed based on morphology (Figures 2–4). Of the 16 sites surveyed, this species was observed at 10 waveswept rocky-shore sites, spanning a distance of about 842 km of coast (Table 1; Figure 1). The detection and, subsequently, the collection of mussel specimens were likely biased towards larger individuals; nevertheless, the overall average shell length ranged from 17 mm (SD 3) to 29 mm (SD 4), depending on the site (Appendix).

Discussion

A substantial number of geo- and time-referenced records going back more than 10 years, presented in this study, coupled with molecular data compared among native and non-native populations of *Semimytilus algosus* from Chile, Namibia, and South Africa (e.g. Zeeman 2016), allow for a sound understanding of this species' invasion history in South Africa. In contrast, published records of *Mytilus galloprovincialis* dating from the first decade of its invasion of southern Africa are limited in terms of spatial

Table 2: Occurrence records of *Semimytilus algosus* in South Africa, from 2009 to 2019. See Table 1 for records from 2020

Year	Site	Occurrence	Source*
2009	Elandsbaai	Present	[1]
2010	Port Nolloth	Not detected	[1]
	Kleinsee	Not detected	[1]
	Hondeklipbaai	Not detected	[1]
	Groenriviermond	Present	[1]
	Brand-se-baai	Present	[1]
	Doringbaai	Present	[1]
	Elandsbaai	Present	[1]
	Yzerfontein	Present	[1]
	Melkbosstrand	Present	[1]
	Bloubergstrand	Present	[1]
	Fish Hoek	Not detected	[1]
2012	Oranjemund	Not detected	[2]
	Port Nolloth	Not detected	[2]
	Groenriviermond	Present	[2]
	Brand-se-baai	Present	[2]
	Elandsbaai	Present	[2]
	Marcus Island	Present	[3], [4]
	Yzerfontein	Present	[2]
	Bloubergstrand	Present	[2], [5], [6]
	Hout Bay	Present	[2]
2013	Bloubergstrand	Present	[5]
2014	Lambertsbaai	Not detected	[7]
	Elandsbaai	Present	[7]
	Marcus Island	Present	[4], [7], [8]
	Bloubergstrand	Present	[7]
	Hout Bay	Present	[7]
	Seaforth	Not detected	Present study
	Gordons Bay	Not detected	Present study
	Cape Hangklip	Not detected	[7]
	Hermanus	Not detected	[7]
2015	Marcus Island	Present	[4]
	Seaforth	Present	Present study
	Muizenberg	Not detected	Present study
	Gordons Bay	Not detected	Present study
	Hermanus	Not detected	Present study
2016	St Helena Bay	Present	[9]
	Paternoster	Present	[9]
	Marcus Island	Present	[4]
	Yzerfontein	Present	[9]
	Oudekraal	Present	[9]
	Hout Bay	Present	[9]
	Seaforth	Present	[9]
	Fish Hoek	Not detected	Present study
	Muizenberg	Present	Present study
	Gordons Bay	Not detected	Present study
	Hermanus	Not detected	Present study
2017	Alexanderbaai	Present	Present study
	Seaforth	Present	Present study
	Muizenberg	Present	Present study
	Gordons Bay	Present	Present study
	Rooi-Els	Not detected	Present study
2018	21 km north of Hondeklipbaai	Not detected	[10]
	9 km north of Hondeklipbaai	Not detected	[10]
	9 km south of Hondeklipbaai	Not detected	[10]
	20 km south of Hondeklipbaai	Not detected	[10]
	5 km north of Groenriviermond	Not detected	[10]
	Seaforth	Present	Present study
	Muizenberg	Present	Present study
	Gordons Bay	Present	Present study
	Rooi-Els	Present	Present study
2019	Seaforth	Present	Present study
	Muizenberg	Present	Present study
	Gordons Bay	Present	Present study
	Rooi-Els	Present	Present study

*Sources: [1] de Greef et al. (2013); [2] Zeeman (2016); [3] Sadchatheeswaran et al. (2015); [4] Sadchatheeswaran et al. (2018); [5] Zeeman et al. (2018); [6] Emanuel et al. (2020); [7] Alexander et al. (2015a); [8] Alexander et al. (2015b); [9] Skein et al. (2018a); [10] Pulfrich (2018)

Table 3: Increase in the distributional range (spread) and the estimated rate of spread of *Semimytilus algosus* in South Africa. E = eastern range limit; N = northern range limit

Year	Observed spread (km)	Range (km)	Rate of spread (km y^{-1})	Cumulative rate of spread (km y^{-1})	Remarks
2009					First report from Elandsbaai
2010	–	500	–	–	From Groenriviermond to Bloubergstrand
2011					No new occurrence data
2012	50	550	25	25	From Groenriviermond to Hout Bay
2013					No new occurrence data
2014					Not detected from Seaforth
2015	70	620	23.3	24	Reported from Seaforth
2016	12	632	12	22	Reported from Muizenberg
2017	40	672	40	24.6	Reported from Gordons Bay
2018	25	697	25	24.6	Reported from Rooi-Els
2019					Reported again from Rooi-Els
2020	75 (N), 70 (E)	842	7.5 (N), 35 (E)	7.5 (N), 26.7 (E)	From Hondeklipbaai to Hermanus

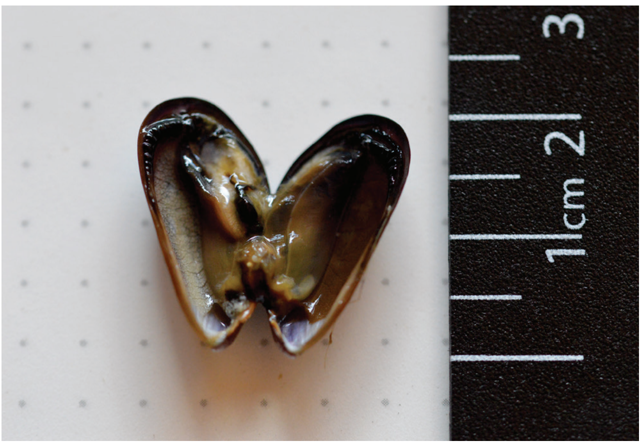

Figure 2: Soft tissues of *Semimytilus algosus* collected from Jacobsbaai, South Africa. Male and female gonads are on opposite sides. In most mytilid mussels, gonad tissues are creamy white in males and orange in females, although determining sex based on colour may not always be accurate (Petes et al. 2008). Photograph: AJ Dievart

extent and resolution (e.g. Grant and Cherry 1985; Griffiths et al. 1992; McQuaid and Phillips 2000; Branch et al. 2008; Reimers et al. 2014; Sparks et al. 2014; Branch and Branch 2018). Perhaps because of a paucity of records, the known range of *M. galloprovincialis* in 1984 was reported to be only from Saldanha Bay to Hermanus about five years after its discovery in South Africa (Grant et al. 1984). It was not until 1988, almost a decade after its discovery, that studies with greater spatial coverage revealed that the distribution of this species had expanded rapidly northwards, as far as Lüderitz in southern Namibia, with a small population at Port Elizabeth on the south coast of South Africa, which was introduced for aquaculture purposes (van Erkom Schurink 1991; Griffiths et al. 1992; McQuaid and Phillips 2000). For the older biological invasion by *S. algosus* in Namibia, there were even fewer records dating from the earlier years of the invasion (Lamy 1931; Kensley and Penrith 1970; Mead et al. 2011b). Reconstructing this invasion history would be challenging, and details of the initial regional spread of *S. algosus* in Namibia may never be known with a high degree of certainty, given the lack of occurrence (and/or abundance) data anchored in time and space.

After its discovery in South Africa, at Elandsbaai on the west coast in 2009, a large-scale survey for *S. algosus* in 2010 revealed an extensive distribution over a distance of 500 km of shore within the cool-temperate Benguela ecoregion (de Greef et al. 2013; Robinson et al. 2020). Subsequent surveys indicate that the northern limit of its range remained unchanged until 2020, when the species was detected in Hondeklipbaai. However, during the same time-period, from 2010 to 2020, the south–southeastern limit of its range extended beyond the Benguela ecoregion and crossed a (transitional) biogeographic boundary. Notably, the species was first reported east of Cape Point in 2015. By 2020, *S. algosus* was detected at Hermanus, indicating that the species is well established in the Agulhas ecoregion (Robinson et al. 2020). Throughout this range, the abundance (i.e. density and biomass) of this species varied geographically, peaking near the middle of its distribution from Elandsbaai to Hout Bay, being relatively rarer at northerly sites north of Elandsbaai, and spatially patchy at sites east of Cape Point (de Greef et al. 2013; Alexander et al. 2015a; Zeeman 2016).

As noted for another widespread invader of rocky shores, the Pacific barnacle *Balanus glandula* Darwin, 1854 (Robinson et al. 2015), the rate of spread of *S. algosus* was expected to decrease as the species approached the biogeographic transition at Cape Point and to increase once the species crossed this boundary. As the species approached the boundary, the observed rate of spread was ~23 km y^{-1} and increased slightly to ~29 km y^{-1} in the transitional zone (Seaforth to Hermanus); however, rates were as high as 35 and 40 km y^{-1} during some years. Nevertheless, these rates are lower than the rate of *M. galloprovincialis* spread northwards during the early stages of its invasion of the west coast (~115 km y^{-1}: Branch and Steffani 2004) and of the south coast (between 55 and 97 km y^{-1} going eastwards: Branch and Branch 2018; McQuaid and Phillips 2000).

Semimytilus algosus, like other established marine invasive species (e.g. *B. glandula*), has been extending its South

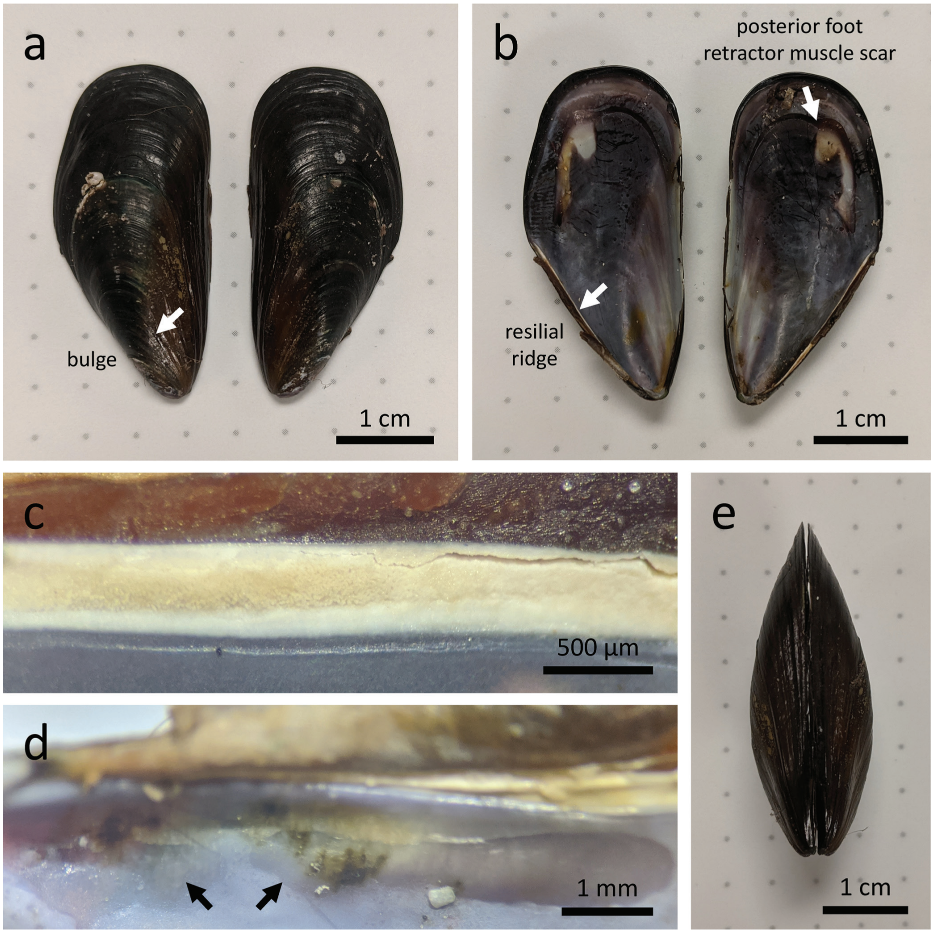

Figure 3: *Semimytilus algosus* collected from Hermanus, South Africa: (a) Exterior view of valves and view of the bulge below the apex; (b) interior view of valves and view of the posterior foot retractor-muscle scar; (c) narrow resilial ridge, notably with an absence of pits; (d) two-part anterior byssus retractor-muscle scar (indicated by arrows; also see Figure 4d for a clearer example); (e) ventral view. Photographs: KCKM

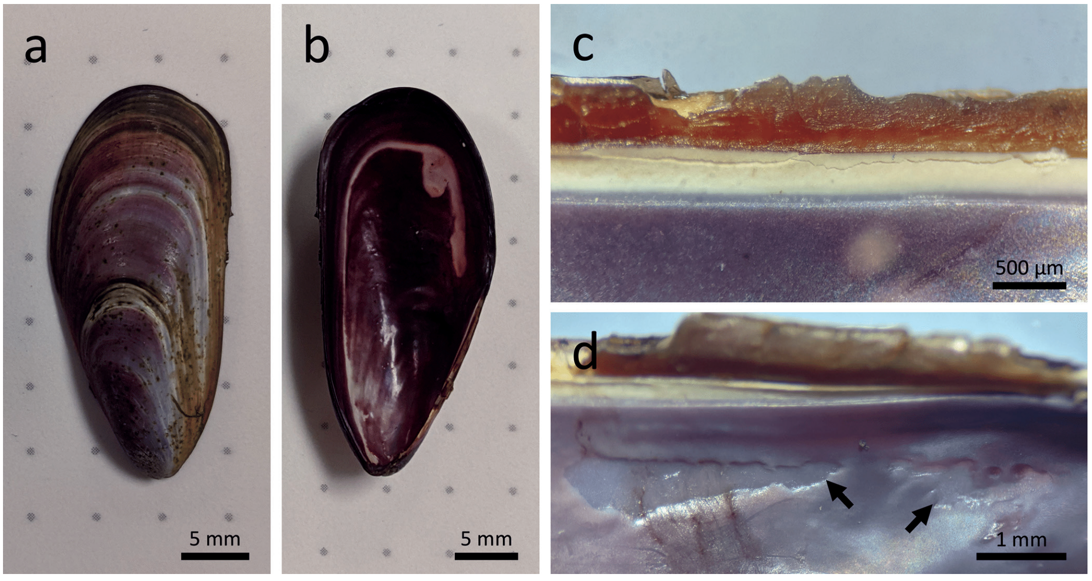

Figure 4: *Semimytilus algosus* collected from Yzerfontein, South Africa: (a) exterior view of valve and view of the bulge below the apex; (b) interior view of valve and view of the posterior foot retractor-muscle scar; (c) narrow resilial ridge; (d) two-part anterior byssus retractor-muscle scar (indicated by arrows). Photographs: KCKM

African distribution both north and south (Robinson et al. 2015). Furthermore, the distance between the Namibian and the South African *S. algosus* populations on the west coast appears to be decreasing, with recent observations from the southern areas of the Namibian coast (Zeeman 2016; Zeeman et al. 2020) and from just south of the border with South Africa (Figure 1), which suggest that the species has been undergoing a southward spread in that region. Also, until recently, the geographic extent of *M. galloprovincialis* in South Africa had exhibited a temporal equilibrium since 2005 (Robinson et al. 2005; Assis et al. 2015), but new populations in 2020 were observed at localities approximately 150 km east of what was originally thought to be the easternmost limit (KCKM pers. obs.), which suggests ongoing eastward spread. In the long-term, changes in climate may destabilise current biogeographic boundaries and result in the further spread of invasive and native species (Blamey and Branch 2012; Bolton et al. 2012). In the case of *S. algosus*, it is uncertain how far east this species will spread in South Africa.

A better understanding of range expansion (and, equally important, retreat) of biological invasions may reveal processes facilitating and limiting their spread (e.g. Assis et al. 2015), but this requires monitoring of not only ongoing invasions but also those at apparent equilibrium (e.g. *M. galloprovincialis*). Presently, there are 95 marine alien species (of which 56 are considered invasive) and 39 cryptogenic species representing a broad range of taxonomic groups in South Africa (Robinson et al. 2016, 2020). In South African coastal systems, detecting new biological invasions and assessing the impacts of these invasions can be challenging (e.g. Robinson et al. 2020); therefore, long-term, routine, and large-scale monitoring is recommended to track the expanding distributions of marine invasive species (e.g. *B. glandula*, *S. algosus*) and to detect new incursions. Occurrence records resulting from such monitoring efforts can provide invaluable baseline information and support evidence-based management.

Acknowledgements — We thank Jaqueline Trassierra, Alexia Dievart, Adam Wyness, and Mhairi Alexander for logistic and field assistance. This project was supported by the South African Research Chairs Initiative of the Department of Science and Technology and the National Research Foundation (grant no. 64801) and the DSI-NRF Centre of Excellence for Invasion Biology. We wish to express our enormous gratitude to George Branch and an anonymous reviewer for their editorial suggestions and for drawing our attention to further species records, both of which have greatly improved this manuscript.

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Manuscript received April 2020 / revised June 2020 / accepted June 2020

Appendix: Average shell lengths of *Semimytilus algosus* collected from six rocky-shore sites in South Africa between 6 and 12 February 2020. SD = standard deviation

Site	Average length (SD) (mm)	*n*
Hondeklipbaai	20	1
Doringbaai	23	1
Paternoster	26 (8)	4
Jacobsbaai	17 (3)	6
Yzerfontein	29 (4)	5
Hermanus	23 (6)	5