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Biogeographic drivers of distribution and abundance in an alien ecosystem engineer: Transboundary range expansion, barriers to spread, and spatial structure

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Abstract

Aim: Biogeographic boundaries can act as either weak or strong barriers to the spread of species undergoing distributional change. Once a novel species spreads across a boundary, it can have a substantial impact on the ecosystem, for instance by competing with local species, and, over the long-term, re-engineer the ecosystem. Marine biogeographic regions are clearly defined on the coast of southern Africa and we tested the influence of their boundaries on the spread and spatial structure of an alien ecosystem engineer.

Location: Southern Africa.

Taxon: An invasive mussel, Mytilus galloprovincialis.

Methods: Records of M. galloprovincialis were compiled into a database to determine its decadal patterns of spread across multiple bioregions. Distribution and abundance (estimated using density and semi-quantitative abundance scale [ACFOR]) of this mussel were surveyed to determine patterns in spatial structure across bioregions. In addition, we compared the size structure of populations at the eastern margins of its range with those of larger populations nearer the range centre.

Results: Initial breaching of biogeographic boundaries was associated with rapid spread, but other boundaries encountered decades later acted as barriers to further spread. Across >2,800 km of coast, spatial autocorrelation was observed in densities (low and mid shore levels) and in ACFOR abundances. Repeating spatial patterns in densities and ACFOR abundance were detected at scales of 120–160 km and of 400–990 km. Considerable effort was required to detect populations at the absolute eastern limits of its range with those of larger populations nearer the range centre.

Main conclusion: Detection of spatial structures at multiple scales suggests that ecologically determined processes regulate abundance at both intra-bioregional and inter-bioregional scales, which may help tease apart the historic and contemporary consequences of interspecific interactions on the structure of rocky shore communities. This study demonstrates the influence of biogeography in driving temporal patterns of spread and spatial structure on the distribution and abundance of an invasive species.
1 | INTRODUCTION

Patterns of species distribution at local and biogeographic scales are dynamic and the scale-dependent processes regulating them are complex and wide-ranging, including population dynamics, species interactions, and climatic variation (Byers & Noonburg, 2003; Farnsworth & Ellison, 1996; Reaugh-Flower et al., 2011; Rius et al., 2014; Whitlatch et al., 1998). In marine systems, large-scale processes including climate and oceanographic currents influence dispersal, connectivity, and survival of many species, resulting in observed distributional patterns (Assis et al., 2015; Galarza et al., 2009; Quinteiro et al., 2007). Identifying how biogeography influences the spread of native and introduced species can help us better understand these large-scale processes and design conservation units such as marine protected areas to protect biodiversity (Awad et al., 2002; Emanuel et al., 1992; Harrison, 2002; Spalding et al., 2007; Waters et al., 2010).

Biogeographic boundaries or transitional zones are areas of abrupt, extensive changes in the species composition of a community, occurring within a limited geographic area (Wieters et al., 2012). They are defined based on the basis of changes in overall species composition, so that some species may be found on both sides of a given boundary. Thus, biogeographic boundaries are not absolute and can act as either weak or strong limits to the distribution of species in, and in the case of introduced species, as weak or strong barriers to their spread. Our understanding of the mechanisms controlling how species interact with such boundaries is still unclear. For instance, life history traits, such as dispersal ability (planktonic larvae vs. direct developers), do not predict whether a particular species will be constrained by biogeographic barriers (Hidas et al., 2007). Rather, the ability of an organism to use a variety of habitats (e.g., both wave-exposed and wave-sheltered rocky shores) within a bioregion better explain distributions across barriers (Ayre et al., 2009). Oceanographic conditions, such as seawater temperature and prevailing currents, have been shown to regulate the distribution of biological invasives even in the case of highly invasive species with the capacity for long-distance dispersal (Aronson et al., 2007; Assis et al., 2015; Fraser et al., 2018). On evolutionary timescales, the emergence and disappearance of biogeographic barriers can give rise to new species through geographic isolation or result in species extinction due to climate change (Neiva et al., 2014; Teske et al., 2013). In addition, climate change may de-stabilise biogeographic boundaries by facilitating shifts in species distributions (Bolton et al., 2012; Chan et al., 2019; Jones et al., 2010; but see Fraser et al., 2018; Poloczanska et al., 2011).

In the case of rocky shore assemblages, biogeographic barriers to species distribution have been linked to sharp transitions in seawater temperature (Bolton & Anderson, 1990; Schils & Wilson, 2006), regions of persistent upwelling (Teske et al., 2011), and the influence of ocean currents (Assis et al., 2015; Nicastro et al., 2019; Teske et al., 2008; Zardi et al., 2011). At coarse spatial scales, maintenance of these barriers could give rise to patterns such as increasing abundance and shifts in size-frequencies towards the centre of the range (Brown, 1984; Brown et al., 1995; Guo et al., 2005; but see Hidas et al., 2010; Sagarin & Gaines, 2002) but, at finer scales, other factors (e.g., wave exposure) can contribute to local variations in distribution and abundance (Bustamante et al., 1997), while at still finer spatial scales, biological interactions become important (McGill, 2010). Given that biogeographic boundaries are associated with environmental discontinuities, or sharp abiotic clines, there are several possibilities for a species that is extending its range towards such a boundary. If environmental factors characterising the boundary are ones that directly affect the species, it may slow or even stop its spread. Even if this is not the case, it will encounter new biotic interactions as it enters what is effectively a novel biogeographic region. Again, these interactions may be expected to slow or prevent its spread. If the species is able to tolerate both the altered environmental conditions and any associated biotic resistance, then spread may continue, possibly following a temporary check. For example, this pattern of slow advance followed by rapid spread has been observed for an alien barnacle (Balanus glandula) approaching and, eventually, breaching a biogeographic boundary in southern Africa (i.e., spreading from the Southwest Cape to the Agulhas bioregion; Robinson et al., 2015). Even in the absence of clear biogeographic discontinuities, saltatory spread is common among marine invasive species (Lyons & Scheibling, 2009; Mineur et al., 2010).

Biogeographic boundaries are essentially the geographic interface between two given bioregions, which is certainly the case for coastal inshore bioregions (Spalding et al., 2007). Of course, there are substantial featural differences among biogeographic boundaries, such as, for instance, differences in the size of transitional zones and coastal geometry (Jooset et al., 2018). The global biogeographic framework developed by Spalding et al. (2007) divides the nearshore coasts of southern Africa into five marine bioregions (from west to east, the Namib, Namaqua, Agulhas, Natal, and Delagoa bioregions). With additional understanding of local marine biodiversity and input from experts, Spalding et al.’s Namaqua bioregion can be further divided into two, referred to as Namaqua to the north and Southwest Cape (Griffiths et al., 2010; Lombard et al., 2004; also see ‘ecozones’ in Sink et al., 2012). Assessments of these bioregions generally support this biogeographic framework, but biogeographic features of transitional zones remain an area of active research (Bolton et al., 2004; Emanuel et al., 1992; Jooset et al., 2018; Sink et al., 2005).

To date, 95 marine alien species have been reported across the South African bioregions, three of which are dominant intertidal invaders (a barnacle, Balanus glandula, and two mussels, Mytilus galloprovincialis and Semimytilus algosus) due to their high abundance and
competitive dominance in their invaded habitats (Robinson et al., 2020). The oldest of these three invaders is the Mediterranean mussel, *M. galloprovincialis*, which was discovered in the 1970s and has since spread 1,000 s of km along the coasts from its two successful introduction points: one in the Southwest Cape bioregion and the other in the Agulhas bioregion (Assis et al., 2015; Grant & Cherry, 1985). In invaded coastal habitats, *M. galloprovincialis* is an ecosystem engineering species, which can substantially alter the structure of rocky shore communities by interacting (e.g., competition) with other mussel species (Bownes & McQuaid, 2006, 2009; Griffiths et al., 1992; McQuaid et al., 2015; Sadchatheeswaran et al., 2015, 2020). High levels of endolithic infestations on mussel shells have been hypothesised to be detrimental (e.g., death or reduced growth) to the host through shell collapse or by requiring the organism to re-allocate somatic and reproductive energy to shell maintenance (Kaehler, 1999; Kaehler & McQuaid, 1999; Ndhlovu et al., 2019; Zardi et al., 2009). These adverse biotic interactions, coupled with other stressors, could regulate invasive mussel populations (Zardi et al., 2009), especially at their range edge, where they are likely to experience sub-optimal conditions. Degradation of the shell through endolithic infestation can facilitate the settlement of epibionts, which can either positively or negatively affect the fitness and survival of a mussel, for example by reducing its capacity for filter-feeding or the probability of being attacked by a predator (Lesser et al., 1992; Marquet et al., 2013; Wahl, 2008).

Because the geographic spread of *M. galloprovincialis* along the coast has been essentially one-dimensional (e.g., Sagarin & Gaines, 2002), across multiple inshore bioregions in succession, and over decadal timescales, we can use this species as a model and ask: (1) if the rate of spread decreased or halted as the species approached a biogeographic boundary; (2) if the rate of spread increased immediately or shortly after breaching a biogeographic boundary; (3) if any along-shore spatial structure in its abundance can be detected at biogeographic scales; and (4) if populations at the margins of the range are dissimilar to populations nearer to the centre of the range in terms of abundance (standardised by search effort), size-frequencies, degree of endolithic infestation, and proportion of the population overgrown by epibionts, with the expectation that abundance will decrease, frequencies will shift to smaller sized mussels for populations closer to the range edge as predicted by the abundant-centre hypothesis (Brown, 1984; Brown et al., 1995; Guo et al., 2005) and the severity of endolithic infestation and the level of epibiosis will increase for range edge populations approaching a biogeographic barrier due to underlying abiotic stressors present at or near such a barrier.

2 | MATERIALS AND METHODS

2.1 | Temporal patterns

2.1.1 | Database of occurrence records

Time- and geo-referenced records of *M. galloprovincialis* occurrence (i.e., ‘present’ and ‘not detected’) from southern Africa—from Angola in the west to Mozambique in the east—were compiled into a database (see Appendix S1 in Supporting Information). These records were extracted from the scientific literature (n = 109), postgraduate theses (n = 23), technical reports (n = 7), online datasets (n = 4) from the Ocean Biogeographic Information System (OBIS; https://obis.org/), and our own field observations from two separate projects (described below) to evaluate decadal patterns of spread (e.g., range expansion, rate of spread) across bioregions. Years associated with each record were either based on the date of collection or observation (DOC) or the date of publication (DOP) if DOC was not available. In some cases, missing DOCs and additional records were made available via personal communication. The precision of GPS coordinates varied among the records depending on how they were reported. In published sources, coordinates were extracted from figures using a semi-automated software (Rohatgi, 2019), tables (including supplementary lists), and the text.

2.1.2 | Temporal analyses

The distance between the most distant sites (cumulative distance over time and interannual fluctuations in the known range based on sampled sites within a given year) and the rate of spread (omnidirectional spread and directional spread from introduction points) of *M. galloprovincialis* were calculated. Also, the timing of when the species crossed from one bioregion to another was determined to detect any temporal patterns of spread in relation to biogeographic boundaries. Fluctuations in the known range based on sampled sites within a given year serve as a proxy of interannual variation in the spatial extent of sampling effort of this species in southern Africa. Given that sampling effort likely varied interannually, a wavelet analysis was used to determine any repeating patterns in the spatial extent of sampling (Fortin & Dale, 2005). The wavelet power spectrum was computed using the Morlet wavelet (n = 100 simulations) and summarised by taking the wavelet power for each period.

2.2 | Spatial patterns

2.2.1 | 2018–2019 field survey

Sixty-two rocky shore sites were visited and surveyed between October 2018 and April 2019. These intertidal sites ranged over 3,025 km of coast from Port Nolloth in the west (29.29°S; 16.87°E) to Mabibi in the east (27.39°S; 32.73°E), South Africa (Figure 1a). At each site, digital photographs of 25 × 25 cm quadrats were taken at four different shore levels (subtidal fringe, low shore, mid shore, and high shore). The subtidal fringe corresponded to the zone between the infralittoral and the lower balanoid, the lower shore to the lower balanoid zone, the mid shore to the zone between the lower and upper balanoid, and the high shore to the upper balanoid zone (Branch & Branch, 2018). Quadrats were placed haphazardly on the shore. The number of replicates differed among sites. The
mean numbers of replicates (±SD) at each shore level were: (i) the subtidal fringe, 3.5 ± 3.1, (ii) the low shore, 3.0 ± 2.5, (iii) the mid shore, 2.9 ± 2.4, and (iv) the high shore, 5.1 ± 4.0. From each photograph, *M. galloprovincialis* was identified and counted to provide a calculation of density (i.e., number of individuals per m$^2$).

### 2.2.2 | 2019–2020 field survey

The occurrence and abundance of *M. galloprovincialis* were determined and estimated from 109 rocky shore sites between September 2019 and March 2020. Surveyed sites ranged over 2,849 km of coast from Alexanderbaai in the west (28.65°S; 16.48°E) and Zinkwazi Beach in the east (29.29°S; 31.44°E), South Africa (Figure 1a). Mussel abundance at each intertidal site was assigned a semi-quantitative category using an adapted ACFOR scale with six categories: abundant, common, frequent, occasional, rare, and not detected (Firth et al., 2015; Simkanin et al., 2005). Specifically, ‘rare’ was the condition when there were <20 individuals were found per 1 man-hour of search, ‘occasional’ when there were scattered individuals that were not aggregated in mono-specific mussel patches, ‘frequent’ when there were many scattered individuals with some aggregated in small patches, ‘common’ when there were large patches that were localised in some areas along-shore, and ‘abundant’ when there were large patches that were widespread along-shore. This approach is generally considered to be standardised with minimal observer bias because a majority of observations (n = 107) were made by the same experienced observer with only two other observations that were made by another observer who is also experienced in identifying mussel species (Fitzpatrick et al., 2009).

### 2.2.3 | Spatial analyses

Global spatial statistics (Moran’s I) were employed to measure spatial autocorrelation of (1) the densities of *M. galloprovincialis* at different shore levels across 3,025 km coast of South Africa, (2) the densities at different shore levels of each of the bioregions where the species was present (namely, the Namib, the Southwest Cape, and the Agulhas bioregions), and (3) semi-quantitative ACFOR abundances along 2,849 km of the coast of South Africa. Prior to analyses, all GPS co-ordinates (i.e., in Cartesian space) were re-configured along a straight line based on their along-shore distances (in kilometres) among sites. This ensures that calculations of distances do not pass through any landmasses due to the geometry of the coastline.

Variograms were used to graphically evaluate variability in mussel abundance (densities and ACFOR abundance) among sites as a function of distance and wavelet analyses were used to examine the spatial structure (scale(s) of repeating patterns) of mussel abundance in South Africa (Fortin & Dale, 2005). For both variographic and wavelet analyses, the adapted ACFOR scales were converted into numeric values (i.e., not detected = 0, rare = 1, occasional = 2, frequent = 3, common = 4, and abundant = 5). The largest lag intervals used in variographic analyses were 80% of the maximum lag intervals because variograms decompose at large lag intervals (e.g., Pérez-Castañeda & Defeo, 2004). We computed wavelet power spectra using the Morlet wavelet (n = 100 simulations) and summarised this by taking the average wavelet power for each period to represent the relevant range of spatial scales. Additionally, the correlation (1) among densities at different shore levels and (2) between the densities at different shore levels (2018–2019 survey) and ACFOR abundances (2019–2020 survey) for 55 sites common to both surveys, were evaluated using Pearson product-moment correlation coefficient. Figures were plotted and spatial (and temporal) analyses were performed in the R programming environment (R Core Team, 2020). In R, analyses were also carried out using ‘ape’, ‘geoR’, and ‘WaveletComp’ packages (Paradis & Schliep, 2019; Ribeiro Jr & Diggle, 2020; Roesch & Schmidbauer, 2018).

### 2.3 | Populations at the range edge

To determine the easternmost limit of the distribution of *M. galloprovincialis* in southern Africa, 18 rocky shore sites from Mosselbaai in the west (34.18°S; 22.16°E) to Port Edward in the east (31.08°S; 30.21°E), South Africa, were searched for the target species between December 2019 and March 2020 (Figure 1a,b). We emphasised greater search effort in the coastal regions of the Ciskei and Transkei (Figure 1b) because the last known confirmed and unconfirmed sightings prior to this study came from this area. The search terminated once the species was no longer detected from more than three consecutive sites east of its last recorded occurrence. At each of these sites, the search continued for at least 2.75 man-hours until the species was considered locally ‘not detected’.

At sites where the species was rare in abundance, all located specimens were collected for species identification in the laboratory, measured (shell length to the nearest 0.1 cm), examined for endolithic infestation (present or absent) and epibionts (present or absent). At sites where the species was more abundant, a 25 × 25 cm quadrat (n = 3–6 replicates per site) was placed in a mono-specific mussel bed in the low shore zone and all mussels were removed and collected for identification, measured and evaluated for endoliths and epibionts as above. Furthermore, the level of endolithic infestation on mussel shells was estimated for each individual (level categories: 0, >0 to 25, >25 to 50, >50 to 75, >75 to <100, and 100% of total shell area).

### 3 | RESULTS

#### 3.1 | Range expansion

In southern Africa, *M. galloprovincialis* was introduced multiple times (including a failed population in Durban in 1972; Knudsen, 1980), experienced rapid spread, and, by the 2000s, was widely
FIGURE 1  (a) Sampling extent of the field surveys of Mytilus galloprovincialis in South Africa: the 2018–2019 survey of mussel densities at different shore levels from Port Nolloth to Mabibi (3,025 km of coast), the 2019–2020 survey of mussel ACFOR abundance from Alexanderbaai to Zinkwazi Beach (2,849 km), and the 2019–2020 survey from Mosselbaai to Port Edward (1,082 km) to delimit the eastern range edge of its distribution. Locations of inshore bioregions and their biogeographic boundaries in southern Africa are drawn according to Lombard et al., (2004) and Kirkman and Nsingi (2019). (b) Locations of 18 rocky shore sites that were surveyed in 2019 and 2020, with emphasis in sampling the coastal regions of the Ciskei and Transkei, to determine the easternmost limit of the distribution of M. galloprovincialis in southern Africa and the presence of small range-edge populations (i.e., <10 individuals per man-hour of search) and larger non-range-edge populations nearer to the range centre (i.e., 50 individuals per man-hour of search). Map projection = equirectangular
established across three bioregions (Table 1 and Figure 2). Rapid spread originating from two successful introduction points—namely, Saldanha Bay in 1979 and Port Elizabeth in 1988—were documented in the proceeding years (Table 1; Figure 2). Despite the rapid spread from these introduction points, a disjunct distribution on the south coast was evident for several years between 1988 and 1991 (Figure 2). On three occasions, the species moved across bioregions: (1) southward then eastward from the Southwest Cape to the Agulhas bioregion in 1980 (record from Dalebrook), (2) northward from the Southwest Cape to the Namaqua bioregion in 1981 (record from the vicinity of Lambert’s Bay), and (3) northward from the Namaqua to the Namib bioregion in 1993 (record from Walvis Bay; Figures 2 and 3). These three events were each associated with a sudden marked increase in the rate of spread (i.e., >90 km/year) and, correspondingly, an increase in the species’ range (Table 1; Figure 3). The interannual fluctuations in the known range based on sampled sites within a given year (Figure 3) exhibited significant repeating temporal patterns approximately every 2.2 years (Appendix S2).

More recently, the distribution of *M. galloprovincialis* appears to have reached temporal equilibrium for the past 19 years with a range of at least 3,707 km of coast from Portuguese Lorry in northern Namibia to Kidd’s Beach in South Africa (Figure 2). Since 2002, at the northermost range edge, the species has been observed only 215 km south of the boundary between the Namib and Angolan bioregions, which, according to Kirkman and Nsungi (2019), is located at or near Tømbua in southern Angola (Figure 1a). Between 2002 and 2020, the species has spread slowly at the easternmost range edge (i.e., about 150 km over this period) towards the boundary between the Agulhas and Natal bioregions, located at or near the mouth of Mbashe River (see Lombard et al., 2004) in southeastern South Africa (Figure 1a). By 2020, the species had a range of 3,860 km of coast from Portuguese Lorry in the west to Tenza Beach in the east, which was only 20–25 km west of the biogeographic boundary in the vicinity of Mbashe River (Figure 1b).

### 3.2 Spatial structure

Densities at all shore levels and ACFOR abundances of *M. galloprovincialis* varied substantially across space (Figure 4). Furthermore, mussel densities tended to be greater in the low and mid shore levels and centred at and near the Southwest Cape bioregion (Figure 4). Overall, a lack of correlation was found in mussel densities among shore levels except between: (1) subtidal fringe and mid shore densities (Pearson’s *r* = 0.36, *p* = 0.028) and (2) subtidal fringe and high shore densities (*r* = 0.43, *p* = 0.004). These two relationships were statistically significant, but the correlation coefficients were low. We found that there were positive correlations between densities at different shore levels and ACFOR abundance. These relationships were stronger when the density data were log <sub>10</sub>(*x* + 1) transformed, that is, (i) *r* = 0.51 (*p* < 0.001) between subtidal fringe densities and ACFOR abundance, (ii) *r* = 0.72 (*p* < 0.001) between low shore densities and ACFOR abundance, (iii) *r* = 0.68 (*p* < 0.001) between mid shore densities and ACFOR abundance, and (iv) *r* = 0.58 (*p* < 0.001) between high shore densities and ACFOR abundance.

Spatial autocorrelation was detected in low and mid shore densities (but not in subtidal fringe and high shore) and in ACFOR abundance of *M. galloprovincialis* in South Africa (Table 2). When the dataset of mussel fringe and high shore densities was partitioned into bioregions, spatial autocorrelation was only detected in mussels distributed in the mid shore in the Namib bioregion and in the low shore of the Agulhas bioregion (Table 2). Consistent with the results from the global spatial statistics, variability in low and mid shore densities (but not in subtidal fringe and high shore) and ACFOR abundances of the species increased as a function of distance, that is, sites that are closer together were more similar than those separated by greater distances (Figure 5). Significant repeating patterns in density were detected for mussels at the subtidal fringe (spatial scale = c. 134 km), low shore (c. 419 km), and mid shore (c. 121 km) levels but not at high shore level (Figure 6a). Similarly, significant repeating patterns in ACFOR abundance were detected at multiple scales, that is, 157, 405, and 988 km (Figure 6b).

#### 3.3 Populations at the range edge

After extensive search effort (mean of 2.40 man-hours of search per site) from Mosselbaai to Port Edward, our surveys of rocky shores revealed small (i.e., <10 individuals per man-hour of search; Table 3) range-edge populations of *M. galloprovincialis* at eight sites east from Glen Gariff with the easternmost limit of distribution likely to occur between Tenza Beach and Folokwe (Figure 1b). The mean shell length of mussels collected from these range-edge populations (namely, Tenza Beach, Mazeppa Bay, Seagulls, Kei Mouth, Morgans Bay, Haga Haga, Cintsa West, and Glen Gariff) was 2.2 cm, which is comparable to the mean length of 2.4 cm from larger (i.e., >50 individuals per man-hour of search; Table 3) range-edge populations in South Africa (Table 2). When *M. galloprovincialis* data were subdivided into bioregions (Table 2), the range of >25 to 75 and >75 to 100 percent cover of the shell, respectively.
**TABLE 1** Estimated rate of spread of *Mytilus galloprovincialis* in southern Africa from four directions: (i) north from Saldanha Bay (1979 to present), (ii) south then east from Saldanha Bay (1979 to 1991), (iii) west from Port Elizabeth (1988 to 1991), and (iv) east from Port Elizabeth (1988 to present)

| Year | North from Saldanha Bay | South then east from Saldanha Bay | West from Port Elizabeth | East from Port Elizabeth | Remarks | Source*
|------|-------------------------|----------------------------------|--------------------------|--------------------------|---------|------
| 1972 | Record from Durban [1], [2] | | 36.0 | | |
| 1979 | | Record from Saldanha Bay [2], [3] | | | |
| 1980 | | 251.0 | | | |
| 1981 | 103.5 | | | Record from the vicinity of Lambert’s Bay [5] | |
| 1982 | 136.0 | | | Record from the vicinity of Groenriviermond [5] | |
| 1983 | | | Records within known range | | |
| 1984 | 114.5 | 36.0 | | Records from Port Nolloth and Hermanus [3], [5] | |
| 1985 | | | Records within known range | | |
| 1986 | 167.5 | | | Record from the south of Lüderitz [5] | |
| 1987 | | 8.3 | | | |
| 1988 | 40.3 | | | Records from Lüderitz and Port Elizabeth [4], [4], [8] | |
| 1989 | | 109.3 | 24.0 | 151.0 | Records from Cape Infanta, Chelsea Point, and Rufanes [5], [9] |
| 1990 | | 323.0 | | 9.0 | Records from Plettenberg Bay and Three Sisters [5], [8], [9] |
| 1991 | | 19.5 | 13.0 | | Records from Maitland River Mouth and Fish River [8], [9] |
| 1992 | | | Records within known range | | |
| 1993 | 98.0 | | | Record from Walvis Bay [5] | |
| 1994 | 32.5 | | | Record from Swakopmund [5] | |
| 1995 | 5.0 | | | Record from Mile 4 [10], [11] | |
| 1996–1997 | | | Records within known range | | |
| 1998 | 6.1 | | | Record from Hamburg [12] | |
| 1999 | | | Records within known range | | |
| 2000 | | | 14.0 | Record from Kidd’s Beach [12] | |
| 2001 | | | | Records within known range | |
| 2002 | 94.0 | | | Record from Portuguese Lorry [13] | |
| 2003–2006 | | | | Records within known range | |
| 2007 | | | 4.9 | Record from Bonza Beach [14] | |
| 2008–2009 | | | | Records within known range | |
| 2010 | | | 19.3 | Record from Kei Mouth (near Morgans Bay) [15] | |
| 2011–2018 | | | | Records within known range | |
| 2019 | | | 0.4 | Record from Kei Mouth Present study | |
| 2020 | | | 57.0 | Record from Tenza Beach Present study | |

FIGURE 2  Occurrence and decadal spread of *Mytilus galloprovincialis* in southern Africa in the (a) 1970s, (b) 1980s, (c) 1990s, (d) 2000s, (e) 2010s, and (f) year 2020. Records extending the species’ distribution from Saldanha Bay and Port Elizabeth are annotated. Map projection = equirectangular
Epibionts (algae and invertebrates) on mussel shells were found in a high proportion of mussel populations at all surveyed sites, with the lowest proportions at Nature's Valley (48%; Table 3). Although the level of epibiosis was relatively greater in small range-edge populations than in large non-range-edge populations (Table 3), the type of epibionts (taxa) differed among sites. We documented the following taxa associated with *M. galloprovincialis* (in descending order of frequency): encrusting coralline algae (34.7% of examined specimens), *Chthamalus dentatus* (barnacle; 20.3%), spirorbid worm (12.6%), *Ralfsia verrucosa* (encrusting brown alga; 10.9%), *Gelidium* sp. (thalloid red alga; 6.9%), *Spirobranchus krausii* (sabellid tube worm; 5.8%), *Tetraclita serrata* (barnacle; 2.8%), *Ulva* spp. (green alga; 2.8%), *Bunodosoma capensis* (sea anemone; 2.5%), *Arthrocystis* spp. (articulated coralline algae; 1.7%), *Scutellastra* sp. (patellid limpet; 1.7%), unidentified red alga (1.1%), *Amphibalanus amphitrite* (barnacle; 0.9%), *Gunnarea gaimardi* (sabellid tube worm; 0.8%), unidentified encrusting bryozoan (0.8%), small unidentified bivalve (0.7%), *Celleporella hyalina* (encrusting bryozoan; 0.4%), *Helcion* sp. (patellid limpet; 0.4%), *Siphonaria* sp. (pulmonate limpet; 0.3%), *Acanthochitonidae* sp. (chinon; 0.1%), *Caulerpa racemosa* (green alga; 0.1%), *Hymeniacidon perlevis* (sea sponge; 0.1%), and *Notomegabalanus algicola* (barnacle; 0.1%).

**4 | DISCUSSION**

**4.1 | Biogeographic barriers to spread**

Biogeographic boundaries are conventionally viewed as acting as natural barriers limiting dispersal and the expansion of species’ ranges (Assis et al., 2015; Glor & Warren, 2010). The removal of natural barriers (e.g., the opening of the Suez Canal) and the de-stabilisation of ecological processes regulating biogeographic regimes (e.g., poleward range shifts) support the notion that geographic or climatic conditions are required to change before spread can occur (Chan et al., 2019; Rilov & Galil, 2009). Our findings revealed that breaching a natural boundary can also be associated with rapid spread (in the new bioregion) without the removal or destabilisation of the barrier. This pattern suggests that a spreading species does not necessarily spread at a constant rate in a contiguous seascape encompassing multiple bioregions (i.e., transboundary spread) and is consistent with saltatory range expansion exhibited in other marine invasions (Lyons & Scheibling, 2009; Mineur et al., 2010). One explanation for this pattern could be a scenario in which boundaries represent a transitional region of unfavourable habitat dividing two suitable habitats (Glor & Warren, 2010). By overcoming the barrier to spread presented by the unfavourable conditions of such boundaries, for example through natural or human-aided dispersion (Avila et al., 2020; Carlton et al., 2017; Lee & Chown, 2007), some species can continue spreading in the novel habitat or bioregion (e.g., *Mytilus* sp. in the Antarctic; Cárdenas et al., 2020). This process is akin to re-initiating the invasion process (i.e., from introduction to establishment to geographic spread; Williamson, 2006) each time the species breaches a boundary. In this case, sufficient propague pressure may be required to overcome any demographic and physiological barriers to the establishment of populations in the new bioregion.

In southern Africa, boundaries encountered by *M. galloprovincialis* earlier in its invasion history (i.e., 1993 and earlier) were breached within 10 years of arrival in a novel bioregion, which was likely facilitated by the availability of suitable habitats and favourable environmental conditions. However, boundaries encountered later in its invasion history presented a more permanent barrier to further advances due to a suite of processes such as hydrodynamic barriers to larval dispersal and physiological barriers to growth and survival (Assis et al., 2015; Branch & Branch, 2018; Zardi et al., 2007). Similarly, several species of invasive ascidians in South Africa exhibited exceptionally high rates of spread during the first decade or so after their respective discoveries but whether the timing of these increases in rates correlated with breaches of boundaries is uncertain (Rius et al., 2014). In terms of the total number of alien species in South Africa, the most invaded regions have been the Southwest Cape and the western portion of the Agulhas bioregions, which likely indicates that bioregions, coupled with high levels of anthropogenic activities, shape patterns of biological invasions (Mead et al., 2011). For marine alien species that have spread into natural habitats, the vast majority...
(69%) have spread across at least one South African biogeographic boundary (Robinson et al., 2020).

Of the several occasions that were detected in this study when rates of spread exceeded 90 km/year (see Table 1), three events (1980, 1981, and 1993) were associated with *M. galloprovincialis* breaching a biogeographic boundary. On the west coast, rapid colonisation events in 1982, 1984, 1986 and 2002 suggest that the species experienced favourable environmental conditions and relatively low biotic resistance in the Namaqua and Namib bioregions (compared to other neighbouring bioregions), although the rate of spread decreased in 1988 as the species approached the biogeographic boundary between the Namaqua and Namib bioregions at or near Sylvia Hill in southern Namibia (Figure 1a). Additionally, this region around Sylvia (i.e., the Lüderitz cell) is associated with the most extreme and powerful upwelling conditions in southern Africa, which probably contributed to this temporary barrier to spread (Lutjeharms & Meeuwis, 1987). Perhaps due to a favourable climate and lack of biotic resistance, spread continued rapidly in 2002 as the species approached the boundary between the Namib and Angolan bioregions, which is an area associated with low numbers of endemic species due to the influence of the northern Benguela upwelling system (Awad et al., 2002; Branch & Branch, 2018; Scott et al., 2012). On the south coast, rapid colonisation events occurred in 1989 and 1990 as the species spread eastward from Gansbaai (Figure 2b) to Plettenberg Bay (Figure 2c), which is a region associated with the range expansion of the kelp *Ecklonia maxima* due to a sharp change in inshore temperature regime (Bolton et al., 2012), and in 1989 as *M. galloprovincialis* spread eastwards from Port Elizabeth in the year immediately after its introduction for aquaculture, but at slower rates thereafter.

After spreading across multiple boundaries between temperate bioregions in southern Africa (namely, the Namib, Namaqua, Southwest Cape, and Agulhas bioregions), the biogeographic boundaries between these temperate bioregions and subtropical bioregions (Angolan in the west and Natal in the east) appear to constitute stronger barriers to the dispersal and survival of *M. galloprovincialis*. The barrier between temperate and subtropical bioregions for *M. galloprovincialis* matches a scenario in which boundaries represent a transitional region of unfavourable habitat dividing suitable habitat on one side and unsuitable habitat on the other side.

**TABLE 2** Global spatial autocorrelation (observed Moran’s *I* coefficient) of the densities of *Mytilus galloprovincialis* at different shore levels of (i) South Africa (*n* = 62 sites), (ii) the Namib bioregion (*n* = 11 sites), (iii) the Southwest Cape bioregion (*n* = 6 sites), and (iv) the Agulhas bioregion (*n* = 17 sites). **NS** = not statistically significant.
of the boundary (Glor & Warren, 2010). At the eastern range limit of the species, the presence of sub-optimal conditions associated with the barrier was indicated by the progressive decrease in abundance (standardised by search effort) with increasing proximity to the boundary region between the Agulhas and Natal bioregions. Our examinations of range-edge and (larger) non-range-edge populations indicated that size-frequencies appeared to be relatively comparable across all populations. Although large proportions of mussels were parasitised across all sampled populations, parasitised individuals from non-range-edge populations exhibited a greater severity of endolithic infestation. Also, the proportion of the mussel individuals from non-range-edge populations exhibited a greater sensibility (Hall, 2014).

Disentangling the processes that drive observed patterns in nature (e.g., spatial and temporal patterns of a spreading species) is a primary problem in ecology and detecting and distinguishing ecologically determined patterns from stochastic patterns can be a valuable approach. Here, *M. galloprovincialis* densities (at low and mid shore levels) and, more broadly, ACFOR abundance values exhibited spatial autocorrelation (i.e., spatial dependence) across the species’ South African range, which is consistent with past observations from the Agulhas bioregion (von der Meden et al., 2008). In contrast to our study, where the species was more abundant in the low and mid shore zones, spatial analysis performed by von der Meden et al. (2008) used percent cover data sampled from the high shore as the species was more abundant at that shore level. Furthermore, the contrast between the random distribution patterns observed for the native mussel, *Perna perna*, and the non-random patterns of the invasive mussel, *M. galloprovincialis*, in South Africa suggests that the geographic factors (e.g., coastal topography) differentially affect the distribution and abundance of native and alien mussel species at scales of 10 and 100 s of km (von der Meden et al., 2008). Yet, at smaller scales, adult densities of *P. perna* exhibited spatial dependence, which indicates that factors such as variations in habitat topography and population dynamics may drive mussel distribution patterns at 10 s of m (Erlandsson & McQuaid, 2004).

The spatial scales at which ecologically determined processes were likely to drive the observed patterns in *M. galloprovincialis* depended on the intertidal zone, that is, we observed zone-dependent spatial structure. Spatial structure in mussel abundance was detected at shore levels from the subtidal fringe to the mid shore but not on the high shore. Spatial structure (i.e., the dominant spatial scale with detectable repeating patterns) increased from a scale of 130 km for subtidal fringe abundance patterns to a scale of 420 km for low shore patterns and decreased to a scale of 120 km for mid shore patterns, which is about the same magnitude as for the subtidal fringe. Separately, results based on ACFOR abundance values also revealed spatial structure (i.e., dominant, repeating patterns) at comparable scales of 160 km and between 400 and 990 km. The detection of spatial structure at spatial scales of both 120–160 km and 400–990 km indicates that a combination of local and biogeographic processes influence abundance of this invasive mussel across its South African range.

A massive surveillance effort allowed us to delimit the easternmost range edge of *M. galloprovincialis* with some precision and to
identify a decrease in abundance approaching the biogeographic boundary at or near the mouth of the Mbashe River, which roughly separates the Agulhas and Natal bioregions in southeast South Africa (Figure 1b). Data collected from the eastern range edge region (Table 3) show that this pattern is consistent with the assumption of the abundant-centre hypothesis (Brown, 1984; Brown et al., 1995; Guo et al., 2005). Using the full complement of data and notwithstanding substantial spatial variation, higher mussel abundances were centred around the Southwest Cape bioregion (Figure 4a), which was also where the species was initially successfully introduced (i.e., 1979 in Saldanha Bay). However, visually, no peak in abundance can be ascertained from the 1988 translocation event at Port Elizabeth, which demonstrates the limitations of applying the abundant-centre hypothesis to the interpretation of distribution patterns without more information on the species’ ecology, physiology, and habitat.

4.3 | Invasion history

Compilation of time- and geo-referenced occurrence records for this quadragenarian marine invasion was a daunting task. Of course, additional records of *M. galloprovincialis* from the grey literature that we may have missed could further improve our data set. In our database, the vast majority of records (about 90%) extracted from the primary literature were dated only a decade after the first successful introduction (1979 in Saldanha Bay), which probably obscures our understanding of early fine-scale patterns of spread.

To the best of our knowledge, *M. galloprovincialis* likely arrived in southern Africa in the late 1970s, which can be deduced from its absence from the archaeological deposits, museum collections, and the primary literature (Branch & Steffani, 2004; Griffiths et al., 1992; Hockey & van Erkom Schurink, 1992). The species was not found in any Koi-San shell middens pre-dating European contact (Grant & Cherry, 1985) or entered into any museum records prior to the 1970s (de Moor & Bruton, 1988; Griffiths et al., 1992; Knudsen, 1980). In the older literature, the species was conspicuously absent from the rocky shores of South Africa before the 1970s (Barnard, 1964; Day, 1969; Stephenson, 1939, 1944, 1948) and Angola and Namibia before the 1980s (Kensley & Penrith, 1973, 1980; Penrith & Kensley, 1970a, 1970b).

The first record of *M. galloprovincialis* came from Durban in 1972 (Knudsen, 1980). The specimen was dredged c. 40 km offshore at a depth of 420 m. Later, it was examined and mis-identified as *Mytilus edulis* by Knudsen (1980). The photographs and drawings of the specimen published by Knudsen (1980) were re-examined and identified as *M. galloprovincialis* by Grant and Cherry (1985). The species was not detected from subsequent surveys of Durban and vicinity (Sink et al., 2005; van Erkom Schurink & Griffiths, 1990). Unsurprisingly for this temperate-adapted species, the arrival of this species to the subtropical Natal bioregion failed to establish any viable populations.

Introduced for aquaculture purposes, the second record of *M. galloprovincialis* from Saldanha Bay in 1979 represents the first known successful introduction of the species to southern Africa (Branch & Branch, 2018; van Erkom Schurink, 1991). A closer examination of data collected from two islands in the bay, Malgas Island and Jutten Island, in 1979 also supported the presence of the species (Griffiths et al., 1992; Hockey & van Erkom Schurink, 1992). In the bay, studies on Marcus Island reported the species as absent in 1980 and 1981 (Reimers et al., 2014; Robinson, 2005) and present in 1983 (Alexander et al., 2015).

Historical photographs placed *M. galloprovincialis* in Dalebrook in Cape Town in 1980 (Reimers et al., 2014), which represented the first major southern then eastern range expansion of about 250 km, with an estimated rate of spread from Saldanha Bay of c. 250 km/
TABLE 3  Summary of (i) distances between sites, (ii) occurrence and search effort, (iii) abundance, (iv) mean shell length, (v) proportion of specimens with endolithic infestation, and (vi) proportion of specimens in epibiotic association of eastern populations of *Mytilus galloprovincialis* surveyed from December 2019 and March 2020. ND = not determined

<table>
<thead>
<tr>
<th>Site</th>
<th>Latitude (°S)</th>
<th>Longitude (°E)</th>
<th>Distance to the next site (km)</th>
<th>Occurrence [man-hours of search]</th>
<th>Abundance (no. of individuals man-hour⁻¹)</th>
<th>Mean shell length (cm) [no. of specimens]</th>
<th>Proportion of specimens with endolithic infestation</th>
<th>Proportion of specimens in epibiotic association</th>
</tr>
</thead>
<tbody>
<tr>
<td>Port Edward</td>
<td>31.07572</td>
<td>30.20534</td>
<td>107.5</td>
<td>Not detected [3.47]</td>
<td>0</td>
<td>—</td>
<td>—</td>
<td>—</td>
</tr>
<tr>
<td>Port Saint John’s</td>
<td>31.64882</td>
<td>29.52168</td>
<td>43</td>
<td>Not detected [1.18]</td>
<td>0</td>
<td>0</td>
<td>—</td>
<td>—</td>
</tr>
<tr>
<td>Presley Bay</td>
<td>31.88182</td>
<td>29.26346</td>
<td>19</td>
<td>Not detected [3.15]</td>
<td>0</td>
<td>0</td>
<td>—</td>
<td>—</td>
</tr>
<tr>
<td>Coffee Bay</td>
<td>31.98704</td>
<td>29.15329</td>
<td>8</td>
<td>Not detected [3.15]</td>
<td>0</td>
<td>0</td>
<td>—</td>
<td>—</td>
</tr>
<tr>
<td>Hole-in-the-Wall</td>
<td>32.03749</td>
<td>29.11266</td>
<td>17.5</td>
<td>Not detected [2.75]</td>
<td>0</td>
<td>0</td>
<td>—</td>
<td>—</td>
</tr>
<tr>
<td>Folokwe</td>
<td>32.14286</td>
<td>29.01123</td>
<td>40.5</td>
<td>Not detected [3.65]</td>
<td>0</td>
<td>0</td>
<td>—</td>
<td>—</td>
</tr>
<tr>
<td>Tenza Beach</td>
<td>32.37717</td>
<td>28.75172</td>
<td>17</td>
<td>Present [2.27]</td>
<td>0.4</td>
<td>3.5 [1]</td>
<td>1</td>
<td>1</td>
</tr>
<tr>
<td>Mazeppa Bay</td>
<td>32.47361</td>
<td>28.65708</td>
<td>33</td>
<td>Present [1.97]</td>
<td>1.0</td>
<td>2.7 [2]</td>
<td>1</td>
<td>0.50</td>
</tr>
<tr>
<td>Seagulls</td>
<td>32.64195</td>
<td>28.42819</td>
<td>9</td>
<td>Present [2.30]</td>
<td>0.9</td>
<td>3.1 [2]</td>
<td>1</td>
<td>1</td>
</tr>
<tr>
<td>Kei Mouth</td>
<td>32.69769</td>
<td>28.37331</td>
<td>4.5</td>
<td>Present [3.48]</td>
<td>5.5</td>
<td>2.3 [19]</td>
<td>0.95</td>
<td>1</td>
</tr>
<tr>
<td>Morgans Bay</td>
<td>32.71141</td>
<td>28.33936</td>
<td>12</td>
<td>Present [2.63]</td>
<td>8.4</td>
<td>2.2 [22]</td>
<td>1</td>
<td>0.95</td>
</tr>
<tr>
<td>Haga Haga</td>
<td>32.76393</td>
<td>28.25188</td>
<td>16</td>
<td>Present [2.27]</td>
<td>9.3</td>
<td>2.3 [21]</td>
<td>1</td>
<td>0.90</td>
</tr>
<tr>
<td>Cintsa West</td>
<td>32.84500</td>
<td>28.11946</td>
<td>7.5</td>
<td>Present [0.73]</td>
<td>4.1</td>
<td>1.6 [3]</td>
<td>0.67</td>
<td>1</td>
</tr>
<tr>
<td>Glen Gariff</td>
<td>32.89307</td>
<td>28.09136</td>
<td>54</td>
<td>Present [3.40]</td>
<td>9.7</td>
<td>2.0 [33]</td>
<td>0.85</td>
<td>0.88</td>
</tr>
<tr>
<td>Kidd’s Beach</td>
<td>33.14925</td>
<td>27.70255</td>
<td>67</td>
<td>Present [2.85]</td>
<td>50.3</td>
<td>2.6 [169]</td>
<td>0.98</td>
<td>0.83</td>
</tr>
<tr>
<td>Old Woman’s River</td>
<td>33.48270</td>
<td>27.15211</td>
<td>441</td>
<td>Present [1.61]</td>
<td>ND⁵</td>
<td>2.8 [80]</td>
<td>0.94</td>
<td>0.65</td>
</tr>
<tr>
<td>Nature’s Valley</td>
<td>33.98637</td>
<td>23.54832</td>
<td>185.5</td>
<td>Present [1.27]</td>
<td>ND⁵</td>
<td>2.0 [234]</td>
<td>0.82</td>
<td>0.48</td>
</tr>
<tr>
<td>Mosselbaai</td>
<td>34.18121</td>
<td>22.15809</td>
<td>—</td>
<td>Present [1.02]</td>
<td>ND⁵</td>
<td>2.4 [167]</td>
<td>0.83</td>
<td>0.65</td>
</tr>
</tbody>
</table>

⁵Abundance at these sites surpassed 100 individuals per man-hour of search effort.
year that included the breaching of the biogeographic boundary at or near Cape Point between the Southwest Cape and Agulhas bioregions in southwest South Africa (Figure 1a). The range of the species eventually reached Cape Infanta in 1989, which added c. 700 km to its range east of Saldanha Bay (Robinson, 2005).

In the 1980s, sites from Lüderitz in Namibia to the Transkei on the south coast of South Africa were surveyed (Branch & Branch, 2018; Hockey & Erkom Schurink, 1992; Robinson, 2005; van Erkom Schurink, 1991). On the west coast, the northward spread from Saldanha Bay was monitored with observations of the species breaching the biogeographic boundary around Cape Columbine between the Southwest Cape and Namaqua bioregions in western South Africa (Figure 1a) in 1981 (record from the vicinity of Lambert’s Bay) and eventually reaching Lüderitz in Namibia in 1988 (Branch & Branch, 2018; Robinson, 2005). The presence of *M. galloprovincialis* in Lüderitz corresponded to a range expansion of about 990 km and a conservative estimated rate of spread of c. 110 km/year. Our estimated rate of spread corresponds closely with the northern spread of 115 km/year calculated by Branch and Steffani (2004). Although the spatial resolution of sampling was relatively coarse in the 1980s compared to the present study, the presence of the species in Port Nolloth and Groenvrijermond (Branch & Branch, 2018; Branch et al., 2008; Branch & Steffani, 2004; Hockey & Erkom Schurink, 1992; Robinson, 2005) and the lack of any absence records suggest that the distribution was continuous across the range north of Saldanha Bay.

In 1988, *M. galloprovincialis* was translocated from aquaculture operations in Saldanha Bay to a facility in Port Elizabeth (Branch & Steffani, 2004; Hockey & Erkom Schurink, 1992; McQuaid & Phillips, 2000). The species was reported as being absent at Plettenberg Bay and Tsitsikamma in 1988, which are sites between Gansbaai and Port Elizabeth (Hockey & Erkom Schurink, 1992). This gap of about 825 km in 1988 represented a disjunct distribution of *M. galloprovincialis* on the south coast of South Africa. When the species was detected at Cape Infanta and Chelsea Point in 1989, the gap decreased to c. 580 km (Phillips, 1994; Robinson, 2005).

Range expansion from Port Elizabeth was monitored annually between 1988 and 1992, which provided a finer spatial and temporal resolution of the local spread of *M. galloprovincialis* (McQuaid & Phillips, 2000; Phillips, 1994). A year after its arrival in Port Elizabeth in 1988, the species’ range in 1989 expanded 24 km west to Chelsea Point and 151 km east to Rufenes (Phillips, 1994; but not reported in McQuaid & Phillips, 2000). The range expanded further 9 km east to Three Sisters in 1990, 13 km east to Fish River in 1991, and 39 km west to Maitland River Mouth in 1991 (McQuaid & Phillips, 2000; Phillips, 1994).

In 1992, the disjunct distribution of *M. galloprovincialis* on the south coast disappeared with the species detected at multiple sites—notably from Cape Agulhas, Arniston, Cape Infanta, Mosselbaai, Plettenberg Bay, and Cape St. Francis (Phillips, 1994). However, surveys in the same year failed to detect the species from Cape Infanta, Mosselbaai, and Tsitsikamma (Bustamante, 1994). Regardless, the total distance of the species’ distribution in early 1990s was about 2,450 km from Lüderitz in the Namaqua bioregion (in Namibia) to Fish River in the eastern portion of the Agulhas bioregion.

On the west coast, in Namibia, *M. galloprovincialis* expanded its range about 490 km north of Lüderitz to Walvis Bay in 1993 (Robinson, 2005), which corresponded to an estimated rate of spread from Saldanha Bay of c. 105 km/year including the breaching of the biogeographic boundary at or near Sylvia Hill (southern Namibia) between the Namaqua and Namib bioregions (Figure 1a), giving a total species range of about 2,940 km in southern Africa. Spreading c. 695 km north at a rate of 77.3 km/year, the species was eventually observed in 2002 from Portuguese Lorry in northern Namibia (George M. Branch, pers. comm.), which is located about 215 km away from the neighbouring Angolan bioregion, which is characterised by nutrient-poor subtropical waters (Lass et al., 2000).

From 1998 to 2019, the range of *M. galloprovincialis* on the south-east coast expanded incrementally by about 40 km east to Hamburg (Rius Viladomi, 2004), another 28 km to Kidd’s Beach (Rius Viladomi, 2004), 34 km to Bonza Beach (NaGISA Project, 2018), 58 km to Kei Mouth near Morgans Bay (Hall, 2014), and 4 km to Kei Mouth. During this period, the rate of eastward spread remained slow and ranged between 0.4 and 19.3 km/year. However, increased search effort in 2020 detected a single individual in Tenza Beach, which substantially increased the range by 57 km east and caused an artificial uptick in the estimated rate of spread. Tenza Beach is located only 22.5 km from the neighbouring Natal bioregion, which is characterised by warmer, subtropical waters (Jooset et al., 2018; Lombard et al., 2004). Although no adults were detected, dispersion of larvae may reach as far east as Coffee Bay, approximately 65 km east of Tenza Beach (Hall, 2014). This realised dispersal ability suggests that survival of post-settlement individuals may limit the establishment of self-sustaining populations at the margins of its distribution. Given its low abundance at the range edge, we expect that future observations of the eastern limits of this species may oscillate among several sites between Kei Mouth and Tenza Beach, which is also a region where mussels and limpets were heavily exploited at an artisanal level (Rius et al., 2006; Siegfried et al., 1985) and continue to be harvested (Appendix S5). These small-scale fisheries may further reduce the likelihood that *M. galloprovincialis* will maintain population sizes above the detection threshold at the margins of its distributional range.

The detection and description of range-edge populations provide an insight into the effort required to detect and monitor range-edge mussel populations. For *M. galloprovincialis*, detection required substantial search effort targeting a single species. In range-edge populations, east of Kidd’s Beach, the mussels occurred individually on open rock—typically in association with barnacles (*Octomeris angulosa*) and other mussel species (*Perna*; also see Hall, 2014) or embedded in reef-building worms (*Gunnarea gaimardi*) on the low shore (Appendix S6). The conspicuous absence from the mid shore zone indicates that surveillance of this mussel species at its range edge must be done at low tide when the lower intertidal zones are exposed.
At present, the range of *M. galloprovincialis* in southern Africa spans four temperate bioregions across a total distance of about 3,860 km (1,510 km in Namibia and 2,350 km in South Africa) and bounded to west and east by two subtropical bioregions. Although the distribution is likely to be continuous, there are two unsampled regions in northern Namibia consisting of more than 200 km of shore: between Students Bay (20.13°S; 13.13°E) and Henties Bay (22.15°S; 14.29°E) and between Walvis Bay (22.94°S; 14.50°E) and Meob Bay (24.54°S; 16.60°E).

### 4.4 Main conclusions

This study documents the interaction between a biological invasion and multiple biogeographic barriers in a contiguous seascape. The discrete timing of rapid spread of *M. galloprovincialis* (a temperate-adapted species) associated with breaching biogeographic boundaries in southern Africa supports the notion that boundaries are barriers dividing suitable habitats (Glor & Warren, 2010). This transboundary pattern of spread ended after invasion of all four connected temperate bioregions (Namib, Namaqua, Southwest Cape, and Agulhas). As the species approached the subtropical Angolan and Natal bioregions on the west and east coasts of southern Africa, respectively, the rate of spread either slowed substantially or ceased over the past two decades, giving rise to a distribution that appears to be at temporal equilibrium (Assis et al., 2015; McQuaid et al., 2015). This pattern suggests that the biogeographic barriers between temperate and subtropical bioregions divide suitable from unsuitable habitats (Glor & Warren, 2010) so that further spread into adjacent bioregions is unlikely.

Furthermore, we detected that ecologically determined processes are involved in driving the spatial structure of mussel abundance at local and regional scales. Although the nature of local ecological processes was not explicitly investigated, we can speculate that a suite of biogeographic processes (e.g., thermal regimes, ocean currents) likely influence large-scale patterns of mussel abundance coupled with abiotic and biotic drivers at smaller scales (e.g., wave action, sand inundation, and possibly competition; Branch et al., 2008; McQuaid et al., 2015; Zardi et al., 2006; Zardi et al., 2008). The combined analyses of transboundary range expansion, barriers to spread and spatial structure demonstrate that biogeography influences the distribution and abundance of *M. galloprovincialis* over decadal timescales and across multiple bioregions.

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### DATA AVAILABILITY STATEMENT

Data generated from this study are deposited online in Dryad under http://doi.org/10.5061/dryad.crjdfnn33n.

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### REFERENCES


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Author contributions: KCKM and CDM conceived the ideas; KCKM and MNCG co-ordinated field work; KCKM, MNCG, GIZ, KRN, and JRM curated the data; KCKM analysed the data; KCKM and CDM prepared the manuscript; and all authors edited and reviewed the manuscript.

**SUPPORTING INFORMATION**

Additional supporting information may be found online in the Supporting Information section.