Chapter 9
Coastal Invasions: The South African Context

Tamara B. Robinson, Koebraa Peters, and Ben Brooker

Abstract In total, 95 marine alien species are known from the South African coast, of which 56 have spread from their points of introduction to become invasive. While just over half of these alien species are restricted to harbours, 45 invasive species have been recorded in natural habitats. The association between marine alien species and harbours reflects the importance of shipping as a pathway for introducing novel marine biota. In the South African context, 91% of introductions have been linked to this mode of transport, with the majority originating from the North Atlantic Ocean. The most invaded region is the Southern Benguela ecoregion along the west coast, where 67 alien species have been detected, with the number declining towards the east. The drivers of this spatial pattern are not yet fully understood, although an interaction between vector strength and compatibility of climate between recipient and donor harbours is likely to play a role. Three species, the Mediterranean Mussel *Mytilus galloprovincialis*, the Chilean Mussel *Semimytilus algosus* and the Pacific Barnacle *Balanus glandula*, have become abundant and widespread along the open coast, and are dominant on wave-exposed rocky shores along the west coast. Here, their sequential invasions have altered intertidal community structure, predominantly through their high abundance and resultant alteration of habitat complexity. Furthermore, the potential threat posed by alien biota to the effectiveness of marine protected areas (MPAs) is increasingly being recognised. Baseline surveys of 19 South African MPAs have revealed the presence of 22 alien species from eight phyla. The highest number of alien species (9) has been noted in Langebaan Lagoon (along the west coast), while Sixteen Mile Beach and Helderberg MPAs (along the west and south coasts, respectively) remain the only MPAs free of alien species. Dedicated research effort in the last two decades has undoubtedly provided valuable

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baseline knowledge on the status of marine invasions in this region. This is expected to provide a solid basis upon which effective evidence-based management will be developed in the future.

9.1 Introduction

Marine alien species were likely first introduced to southern Africa with the arrival of European settlers in the early 1600s (Mead et al. 2011a). Despite this long history of human-associated introductions, the dedicated study of marine invasions along the South African coast only began in 1992 when the first list of alien species was produced (Griffiths et al. 1992), detailing the presence of just 15 species. Over the next decade this list was refined, with some species being removed as initial mis-identifications were uncovered, while others were removed as local extinctions were recorded (Griffiths 2000; Awad 2002). Following international trends, the subsequent decade saw numerous updates to the list of alien species known from the region (Robinson et al. 2005; Griffiths et al. 2009; Mead et al. 2011a). Notably, the list was expanded to include cryptogenic species (Robinson et al. 2005) and historical introductions (Mead et al. 2011a). In keeping with international best practice, the most recent listing of alien marine biota differentiated between alien species (those whose presence in a region is attributable to human actions) and invasive species (those alien species that have self-replacing populations over several generations and have spread from their point of introduction) (Richardson et al. 2011). This saw the recognition of 89 alien species of which 53 were considered to be invasive (Robinson et al. 2016). Nonetheless, historic invasions continue to be recognised and new invasions continue to occur. Reflecting this, an additional five alien species [the intertidal isopod *Ligia exotica* (Greenan et al. 2018), the Chilean Stone Crab *Homalaspis plana* (Peters and Robinson 2018), the South American Sunstar *Heliaster helianthus* (Peters and Robinson 2018), the Maritime Earwig *Anisolabis maritima* (Griffiths 2018) and the barnacle *Perforatus perforatus* (CL Griffiths pers. comm)], as well as two invasive species [the amphipod *Caprella mutica* (Peters and Robinson 2017) and the porcelain crab *Porcellana africana* (Griffiths et al. 2018)] have been recorded since 2016.

While this increasing trend is typical of many marine ecosystems (Wonham and Carlton 2005; Galil et al. 2014), the number of alien species known from South Africa still appears to be much lower than in other well-studied sites. For example, over 680 alien species are known from the Mediterranean Sea (Galil et al. 2014), while 180 have been recorded in the restricted area of Port Philip Bay, Australia (Hewitt et al. 2004). Although presently comparatively low, the number of alien species recognised from along the South African coast is expected to keep rising. This increasing trend is likely to be sustained by new incursions, but also by the study of previously under-studied habitats (e.g. kelp beds and temperate reefs), regions (e.g. large stretches of the East coast) and taxa (especially taxa such as nematodes and ostracods). Nonetheless, the value of such increased research effort will depend largely on the availability of taxonomic experts to correctly identify alien taxa. This key skill is presently underrepresented within the marine research community in South Africa (Griffiths et al. 2010) and the shortage of specialist taxonomists has been highlighted as an impediment to the development of a comprehensive list of alien marine species for the region (Griffiths et al. 2009). Despite this obstacle, marine invasion biology in South Africa is a growing field of study. This is reflected most clearly in the publication of 36 peer-reviewed papers in the decade ending 2008, followed by an almost doubling to 70 publications in the decade ending 2018. Pre-2000 most studies considered the establishment and spread of alien taxa in easily accessed habitats such as rocky shores and reported the results of field surveys (Alexander et al. 2016). Since that time there has been an increased focus on experimental studies (both laboratory and field-based) and an emphasis on understanding biological interactions (e.g. Steffani and Branch 2003; Zardi et al. 2006; Branch et al. 2008, 2010; Bownes and McQuaid 2010) and intra-regional spread (Peters et al. 2017).

9.2 Status of Marine Alien Species

In total 95 alien species are known from South Africa, with an additional 39 species being reported as cryptogenic (Table 9.1). These species represent a variety of taxonomic groups, including micro-organisms such as protists (*Mirofolliculina limnoriae*) and dinoflagellates (e.g. *Alexandrium minutum*), polychaete worms (e.g. *Polydora hoplura*), starfish (*Heliaster helianthus*) and even algae (e.g. *Codium fragile*). The majority of species are crustaceans (including barnacles, copepods, amphipods, isopods and crabs), which account for 32% of recognised alien species (Fig. 9.1). Cnidarians (including anemones and hydrozoans) and molluscs (including gastropods and bivalves) account for 14% and 13%, respectively, while 12 different taxonomic groups account for the remaining species.

Of the 95 alien species, 56 are considered to be invasive. It is notable that 80% of these invasive species have been recorded in natural habitats although only three, the Mediterranean Mussel *Mytilus galloprovincialis*, the Chilean Mussel *Semimytilus algosus* and the Pacific Barnacle *Balanus glandula* have become abundant and widespread along the open coast. Table 9.1 lists all of these species, including the ecoregions that they have invaded in South Africa (see Sink et al. 2012). Six of the remaining 39 alien species are considered naturalised (i.e. they support self-sustaining populations) but have not yet spread from their points of introduction.

Tracking changes in numbers of alien species can be difficult, especially in marine habitats, where they can remain unobserved for many years after their introduction. In addition, temporal patterns of introductions can be masked by changing research effort through time. Nonetheless, some clear patterns emerge when considering the number of marine alien species known from the South African coast through time. The earliest record dates back to 1852, when the bryozoan *Virididentula dentata* (previously known as *Bugula dentata*) was first noted (Mead et al. 2011b). In total, only four alien species were recorded in the 1800s. This is in contrast with the 1900s, when 65 species were noted, giving a

Table 9.1 List of 45 invasive species that have spread into natural habitats, along the South African coastline and the ecoregions in which they occur

Taxonomic group	Species	Ecoregion Southern Benguela	Agulhas	Natal	Delagoa
PORIFERA	*Suberites ficus*	√			
CNIDARIA					
Hydrozoa	*Coryne eximia*	√			
	Obelia dichotoma	√	√	√	
	Odessia maeotica			√	√
	Pennaria disticha			√	√
ANNELIDA					
Polychaeta	*Alitta succinea*		√	√	
	Boccardia proboscidea	√	√		
	Ficopomatus enigmaticus	√	√	√	
	Neodexiospira brasiliensis	√	√	√	
	Polydora hoplura	√	√		
CRUSTACEA					
Cirripedia	*Amphibalanus venustus*		√	√	√
	Balanus glandula	√	√		
Isopoda	*Sphaeroma walkeri*			√	
Amphipoda	*Caprella mutica*	√	√		
	Ericthonius brasiliensis	√	√	√	√
	Jassa morinoi	√	√	√	
	Jassa slatteryi	√	√		
	Orchestia gammarellus	√	√		
	Platorchestia platensis		√		
Decapoda	*Carcinus maenas*	√			
	Pinnixa occidentalis	√			
	Porcellana africana	√			
INSECTA					
Coleoptera	*Cafius xantholoma*	√			
Dermaptera	*Anisolabis maritima*			√	
MOLLUSCA					
Gastropoda	*Littorina saxatilis*	√	√		
	Myosotella myosotis		√		
	Tarebia granifera			√	√
	Indothais blanfordi		√	√	
	Semiricinula tissoti			√	
Bivalvia	*Crassostrea gigas*		√		
	Mytilus galloprovincialis	√	√		
	Semimytilus algosus	√	√		
	Teredo navalis	√			
BRYOZOA					
	Bugula neritina	√	√	√	
	Bugulina flabellata	√	√	√	
	Conopeum seurati	√	√		
	Cryptosula pallasiana	√	√		
	Virididentula dentata	√	√	√	
	Watersipora subtorquata	√	√		

(continued)

Table 9.1 (continued)

Taxonomic group	Species	Ecoregion Southern Benguela	Agulhas	Natal	Delagoa
CHORDATA					
Ascidiacea	*Diplosoma listerianum*	√	√	√	
	Microcosmus squamiger		√	√	
RHODOPHYTA					
	Antithamnionella spirographidis	√	√		
	Asparagopsis armata	√	√	√	
	Asparagopsis taxiformis		√	√	
CHLOROPHYTA					
	Cladophora prolifera				√
	Codium fragile	√	√		

discovery rate of 6.5 species per decade. Notably, since 2000, 27 further new species have been recognised, a discovery rate of 15 species per decade. While increased attention to marine invasions has undoubtedly contributed to the accelerating trend in recognised introductions, the fact that new introductions continue to be noted in historically well-studied and frequently-surveyed regions such as Saldanha Bay (Peters and Robinson 2018) suggests an increase in the rate of new introductions.

A large proportion of species (44%) introduced to the coast of South Africa originate from the North Atlantic Ocean (Fig. 9.2) with most being native to the coasts of Europe, the United Kingdom and northern Africa. Interestingly, only 15% of introduced species have their origins in the southern hemisphere. This pattern is

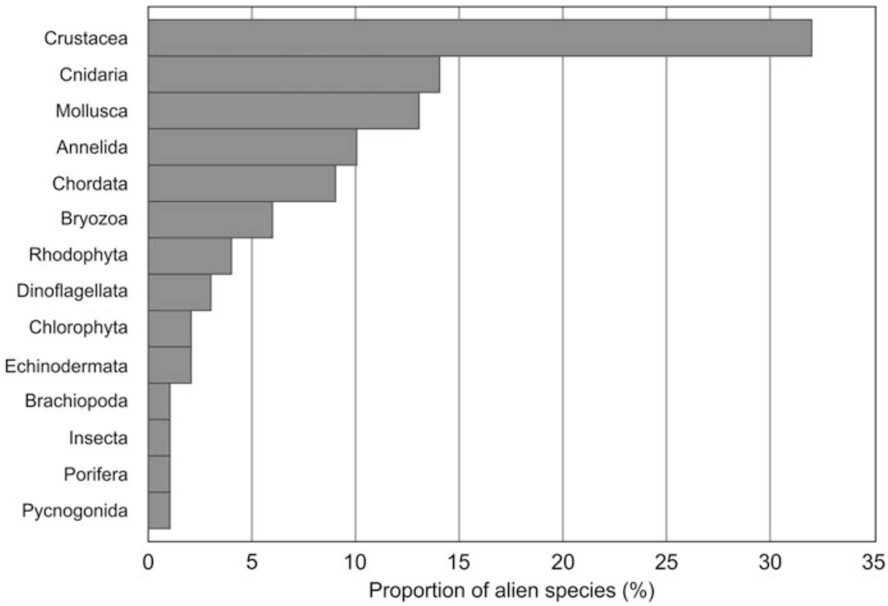

Fig. 9.1 The taxonomic breakdown of alien taxa known from along the South African coast

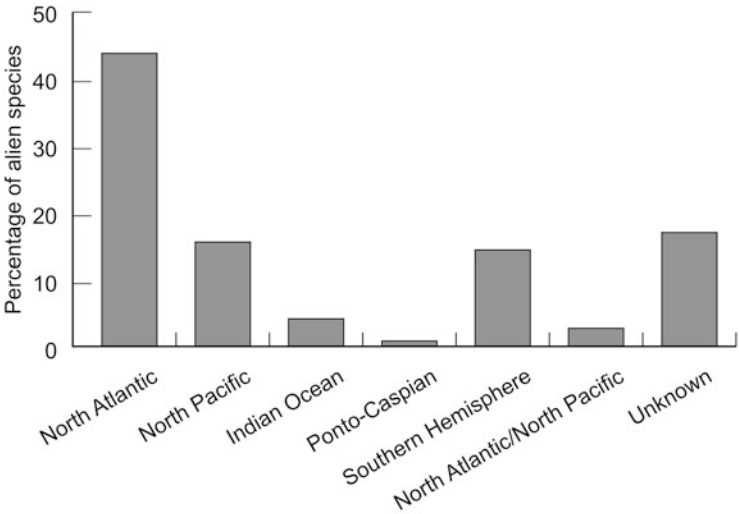

Fig. 9.2 The percentage of South African marine introductions from the different regions of origin

likely due to a combination of shipping patterns and the fact that the west coast of South Africa offers cool temperate conditions that match those of the North Atlantic Ocean (Griffiths et al. 2009).

9.3 Geographic Patterns Around a Variable Coast

Five ecoregions are recognised along the South African coast (Sink et al. 2012). The majority of alien species (n = 67) occur in the Southern Benguela ecoregion on the west coast. The numbers of alien species gradually decline eastward along the coast (Fig. 9.3). It is notable that 43 alien species are present in only one ecoregion, and only three alien species occur in all four ecoregions along the coast; all three are amphipods (*Cerapus tubularis*, *Ericthonius brasiliensis* and *Ischyrocerus anguipes*).

The observed patterns in alien species distributions could be explained in several ways. Alien species numbers may reflect a gradient of research effort around the coast (Robinson et al. 2005), as much of the research undertaken on marine alien species has been focused on the Western Cape (Griffiths et al. 2009). Nonetheless, extensive research on rocky shores in KwaZulu-Natal (e.g. Sink et al. 2005), and recent surveys of harbours between Mossel Bay and Richards Bay (Peters et al. 2017) failed to detect new marine alien species, suggesting that other factors may be at play. A second explanation may relate to differential vector strength along the coast. Shipping is the oldest and most important vector for the transfer of marine alien species and one of the oldest harbours (Table Bay) is situated in the Southern Benguela ecoregion. It is likely that the long history of shipping there is linked to the high numbers of alien species observed in this ecoregion, at least for historical introductions. Interestingly, Durban

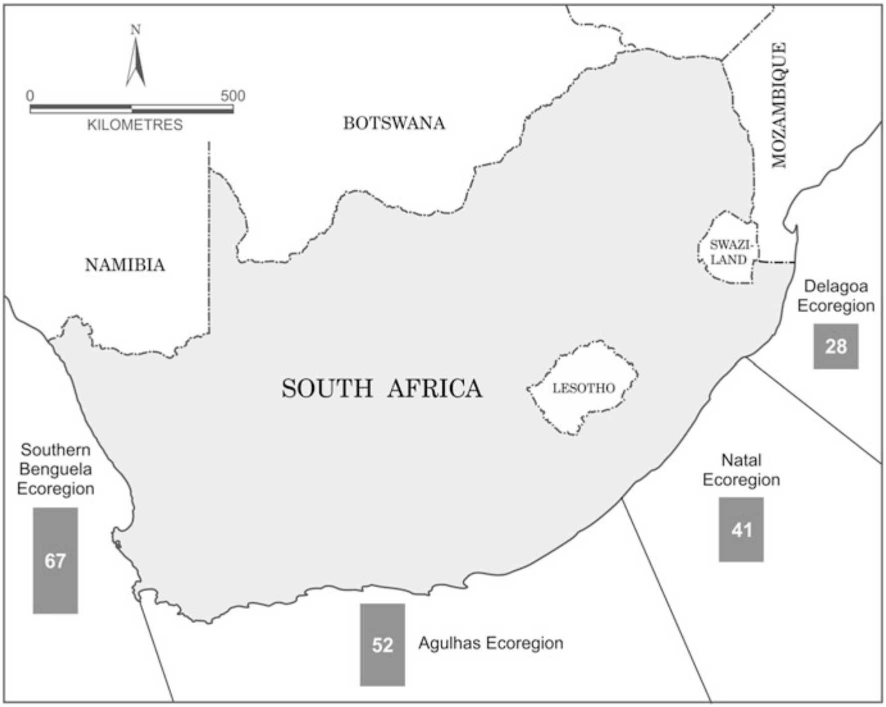

Fig. 9.3 Marine ecoregions in South Africa, with bars representing the total numbers of alien species present in each coastal ecoregion. Note the the lines demarcating the ecoregions are extended offshore for illustrative purposes only

harbour, in the Natal ecoregion, has received the highest number of international vessels in recent times (Faulkner et al. 2017), demonstrating that vector strength alone does not explain the observed numbers of alien species. In fact, relative similarity of climate between donor and recipient regions may moderate invasion success of arriving species (Ashton 2006). This has been highlighted in Saldanha Bay, where six new alien species have been recorded since 2004, 50% of which come from Chile and Peru (Peters and Robinson 2018). The temperate upwelling nature of that region very closely matches the environmental conditions of Saldanha Bay (Branch and Griffiths 1988; Arntz et al. 1991), highlighting the importance of climatic matching in explaining spatial invasion patterns.

9.4 Vectors Driving Marine Invasions

The vectors responsible for marine introductions to South Africa have changed considerably through time (Faulkner et al. 2020, Chap. 12). Initially, wooden sailing ships carried wood-boring and fouling species on their hulls, as well as species associated with their dry ballasts (Griffiths et al. 2009). Dry ballast consisted of rocks and sand placed in the hull to maintain stability and trim and was offloaded when vessels filled their hulls with cargo, depositing associated species in new regions. With the development of steel ships, the suite of species being transported changed. While wood-boring species were no longer transported, hull fouling remained as an important vector for the transfer of alien species, particularly fouling in the niche areas (such as the rudder, propeller, propeller shafts and sea chests). The transition to steel ships also saw a change in the type of ballast used, with ballast water replacing solid ballast. This resulted in an important shift in the types of species that were associated with shipping. Notably, species associated with dry ballast were no longer inadvertently moved, but planktonic species, and those with planktonic life stages, were taken up along with ballast water and released into novel ranges (Griffiths et al. 2009). Additionally, benthic species associated with sediment taken up along with ballast water could be translocated (Hewitt et al. 2009). Furthermore, the change from using sails to using steam and then oil increased the speed at which vessels could travel. The speed, size and number of vessels has increased dramatically since the 1970s (UNCTAD 2007), and with this it is expected that the number of successful invasions has increased as well (Hulme 2009). Moreover, the increased speed resulted in shorter transit times which in turn resulted in increased likelihood of survival and likelihood of introduction of associated species.

The recognition of the dominant role that shipping plays in marine introductions resulted in international efforts to regulate ballast water through the International Convention for the Control and Management of Ships' Ballast Water and Sediments (BWM Convention). The aim of this convention is to prevent, minimise and eliminate the risks associated with transferring harmful organisms in ballast water (IMO 2004) and in 2017 the Convention entered into force (IMO 2017). Since the initial development of this Convention, the role of ballast water in transporting marine species is likely to have been reduced and although hull fouling was always present, this has emerged as the dominant vector for marine species transfer (Hewitt et al. 2009; Williams et al. 2013). Shipping is responsible for approximately 91% of marine introductions to South Africa, but it is extremely difficult to associate particular introductions with ballast water or hull fouling, as many species can be introduced via either vector. Nonetheless, this separation has been possible for some introductions to South Africa, with 23% of introductions being due to fouling only and 5% associated with ballast water only (Fig. 9.4). Two other vectors have been responsible for introductions to this coast, these being mariculture (Haupt et al. 2012) and oil and gas infrastructure (Sink et al. 2010). To date, mariculture has been linked to the introduction of only five species to the region. Whilst this number may appear low, three of the five species (the polychaete *Boccardia proboscidea*, the oyster *Crassostrea gigas* and the brachiopod *Discinisca tenuis*) have become invasive. Oil and gas infrastructure is an emerging vector in the region and while it has potentially been responsible for only one introduction to date (the European shore crab *Carcinus maenas*), efforts by the South African government to establish South African ports as a premier destination for oil rig maintenance suggest that this vector may become more important in the future. Although it has not yet introduced any marine alien species to South Africa, the aquarium and pet trade is

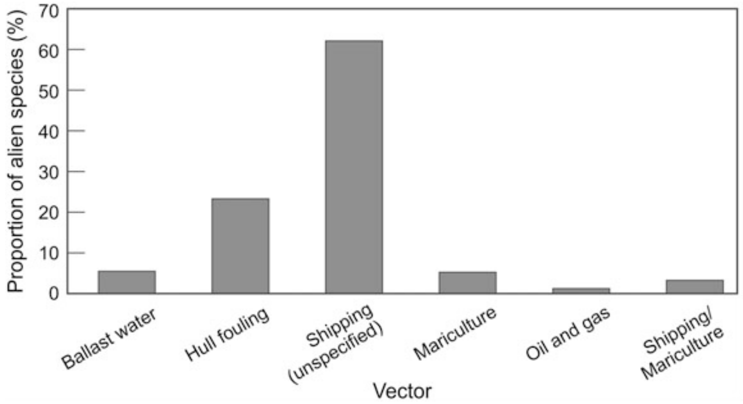

Fig. 9.4 The proportion of marine alien species introduced through a number of vectors, along the South African coastline

a vector that has been linked to introductions elsewhere (Hayes et al. 2002; Holmberg et al. 2015; Faulkner et al 2020, Chap. 12; Measey et al 2020, Chap. 27). Although the risk posed by this vector has not been quantified, the active trading of aquarium species online and through aquarium shops highlights the potential for introductions via this mechanism.

While the above section has highlighted primary vectors responsible for the introduction of biota into South African waters, the role of vectors in intra-regional spread is equally important. Although shipping can also be responsible for secondary spread, the pathway takes on a slightly different nature at a regional scale, as large commercial vessels become less important, and small and recreational vessels become more important (Clarke-Murray et al. 2011). In South Africa, fouling on recreational yachts was recently linked to the regional spread of marine alien species (Peters et al. 2014, 2017), with the Japanese Skeleton Shrimp, *Caprella mutica* offering an example of a newly-introduced species that has been moved at a regional scale (Peters and Robinson 2017). Although only recreational yachts have been investigated as a mechanism of intra-regional species transfer, it is likely that other regional vessels such as tour boats and fishing boats also play a role, but this remains to be quantified. Furthermore, aquaculture has been linked to the secondary spread of species associated with oysters, as these are moved among farms (Haupt et al. 2010, 2012).

9.5 Alien Species in Marine Protected Areas

Marine Protected Areas (MPAs) have wide-ranging objectives not only as an important mechanism for the conservation of living marine resources, but also for preservation of rare or endemic species, maintenance of habitat heterogeneity, protection of sensitive life stages of species under threat, supplementation of fish stocks in adjacent areas, and provision of research and education opportunities

(Norse 1993; Hockey and Branch 1997). With the continuous proliferation of marine invasions, the ability of MPAs to meet these conservation objectives is likely to be challenged (for example see Robinson et al. 2007a).

South Africa has a network of 23 coastal MPAs with an additional 20 offshore MPAs that are expected to be proclaimed in 2019. The coastal network (Table 9.2) accounts for 23% of the South African coastline (Sink et al. 2012), although only about 10% is fully protected. Despite the conservation imperative for MPAs and the recognition of the potential threat posed by marine alien species, by 2010 only three of the coastal MPAs had been surveyed for alien species. In 2003, three alien species were recorded in Langebaan Lagoon and Marcus Island on the west coast (Robinson et al. 2004). The Mediterranean Mussel *Mytilus galloprovincialis* was the most widespread and abundant species, supporting an estimated biomass of 117 tonnes on Marcus Island and just less than 1 tonne in Langebaan Lagoon (Robinson et al. 2004), but it has since disappeared from the lagoon. An additional two species were noted within the lagoon, the anemone *Sagartia ornata* and the intertidal periwinkle *Littorina saxatilis*. The distribution and abundance of *S. ornata* was reassessed in 2013 when it was found to alter the community structure of invaded sandy shores (Robinson and Swart 2015). Betty's Bay MPA was surveyed for the first time in 2010, and the only alien species recorded was the bryozoan *Watersipora subtorquata* (Malherbe and Samways 2014).

Table 9.2 A list of all South African Marine Protected Areas and the years in which they were surveyed for marine alien species

MPA	Years in which surveys have been conducted
Langebaan Lagoon	2003, 2013
Marcus Island	2003, 2013
Malgas Island	2013
Jutten Island	2013
Sixteen Mile Beach	2013
Table Mountain National Park	2013
Helderberg	2013
Betty's Bay	2010, 2013
De Hoop	2014
Still Bay	2014
Goukamma	2014
Robberg	2014
Tsitsikamma	2014
Sardinia Bay	2014
Bird Island	2014
Amathole	2014
Trafalgar	2014
Dwesa-Cwebe	Unsurveyed
Hluleka	Unsurveyed
Pondoland	Unsurveyed
Aliwal Shoal	2014
St Lucia	2014

In response to the lack of knowledge about the status of invasions in MPAs, baseline surveys of the intertidal and shallow sub-tidal zones were undertaken for 19 of the 23 MPAs by Brooker (2016). In total, 22 alien species from eight phyla were recorded across the MPA network. The highest number of alien species was noted in Langebaan Lagoon, with the next most invaded MPAs being Betty's Bay and Amathole, each supporting seven species (Fig. 9.5). Notably, only two MPAs remained uninvaded (Sixteen Mile Beach and Helderberg). This absence of alien

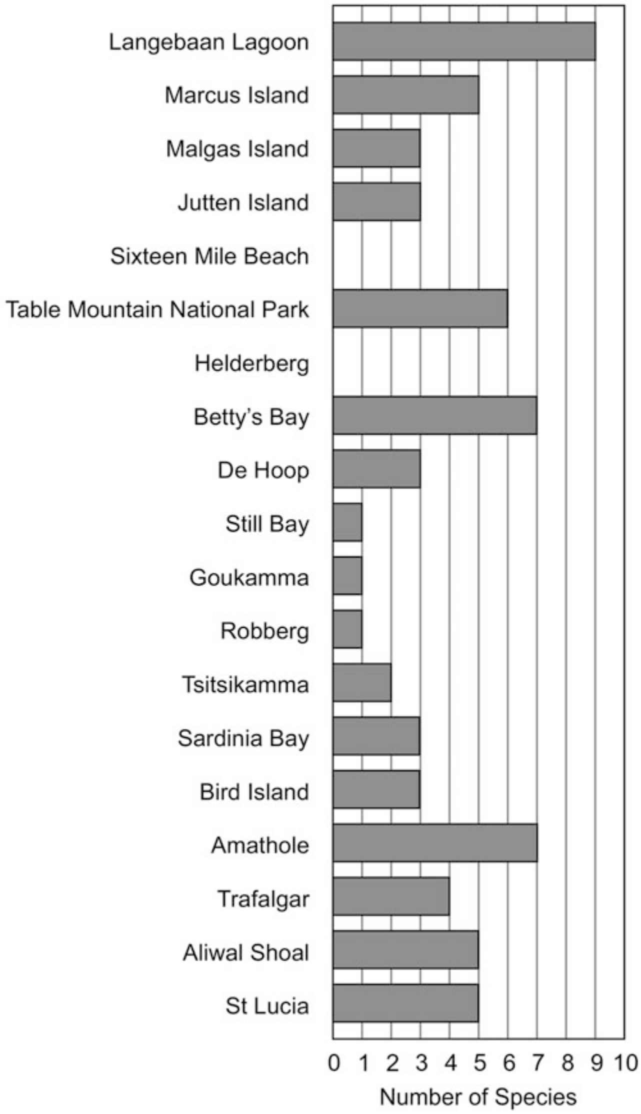

Fig. 9.5 The number of alien species recorded in each of the surveyed MPAs along the South African coast

species likely reflects the lack of rocky shores in these sandy protected areas, as most alien species known from South Africa require hard substrata like rocks or artificial infrastructure for attachment (Mead et al. 2011a). The most widespread species was *M. galloprovincialis*, which occurred in 13 of the protected areas spanning the region between Langebaan Lagoon on the west coast and Bird Island on the south coast. Other notable occurrences included the first reports of the ascidians *Microcosmus squamiger* and *Diplosoma listerianum*, the hydrozoans *Obelia dichotoma* and *Obelia geniculata* and the bryozoan *Cryptosula pallasiana* in natural habitats. This highlights that although most marine alien species are known from harbours, natural habitats are susceptible to regional spread. This may be of particular conservation concern in protected areas. A strong link exists between yachts and the local spread of alien species along the South African coast (Peters et al. 2017). As such, MPAs that are situated close to harbours, or that are visited by yachts, may be at elevated risk of invasion by alien species and should be prioritised for monitoring.

9.6 Impacts of Dominant Intertidal Invaders

Because they are easily accessed and offer habitat to spatially dominant alien species, the ecological impacts of non-native biota on rocky shores have been well studied in South Africa. Three species have extensively invaded rocky shores along the open coast, *M. galloprovincialis*, *Semimytilus algosus* and *Balanus glandula* (Fig. 9.6). It is notable that all three invasions emanated on the west coast, with species spreading south before crossing the biogeographic break of Cape Point and dispersing onto the south coast.

Mytilus galloprovincialis was first noted in Saldanha Bay in the late 1980s. It is now the dominant intertidal species between northern Namibia and East London on the south coast (Assis et al. 2015). This accounts for approximately 2800 km of the South African coast. Within this range, it has proliferated at the expense of various native taxa (Branch and Steffani 2004; Robinson et al. 2007b). Along the west coast, this dominance has been driven primarily by the alien mussel's superior growth rate, reproductive output and tolerance to desiccation when compared to the native mussels *Choromytilus meridionalis* and *Aulacomya atra* (van Erkom Schurink and Griffiths 1991, 1993; Hockey and van Erkom Schurink 1992). As a result, since the arrival of *M. galloprovincialis*, mussel beds in this region have extended further up shore (Hockey and van Erkom Schurink 1992). Along the south coast *M. galloprovincialis* co-exists with the native mussel *Perna perna*, through partial habitat segregation that sees the alien mussel excluded from the low-shore by a combination of wave exposure and interspecific competition with *P. perna* (Rius and McQuaid 2006). Through its ability to preclude other species from occupying primary rock space, *M. galloprovincialis* has also displaced native limpets. Through this mechanism the abundance of the Granular Limpet *Scutellastra granularis* has declined on bare rock but, interestingly, overall abundance has increased as *M. galloprovincialis* shells offer a favourable recruitment substratum for juvenile limpets (Hockey and van Erkom Schurink 1992; Branch et al. 2010). Thus, the mean

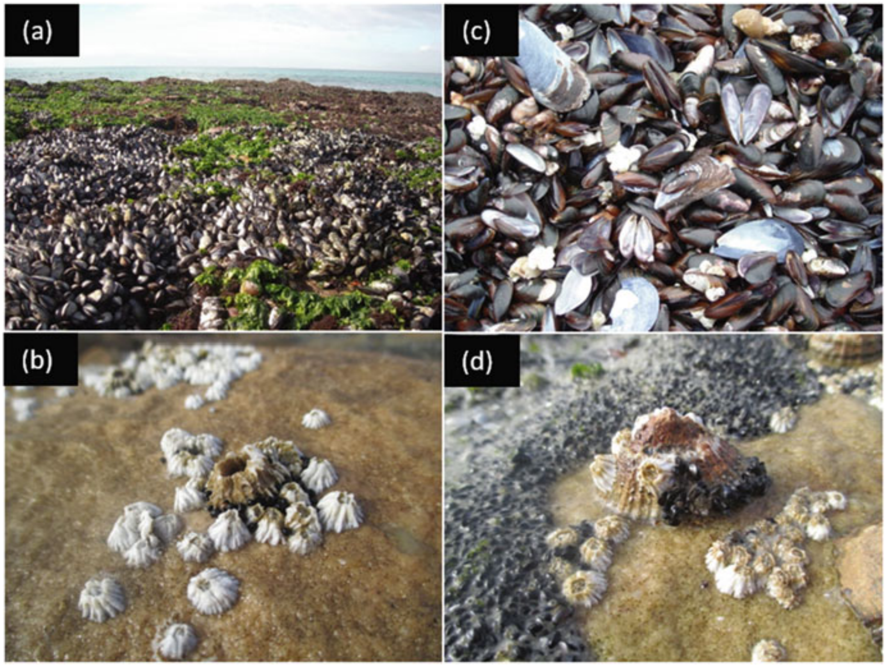

Fig. 9.6 (**a**) Extensive beds of the Mediterranean mussel *Mytilus galloprovincialis* in False Bay. (**b**) The density of the high-shore gastropod *Afrolittorina knysnaensis* is raised in areas invaded by the Pacific barnacle *Balanus glandula*. The gastropods nestle between the barnacles in search of shelter. (**c**) A washout of mussels in St Helena Bay along the west coast. The majority of mussels are the alien *Semimytilus algosus* but native *Choromytilus meridionalis* are also present. (**d**) A granular limpet *Scutellastra granularis* attempts to maintain open rock space despite inundation by *M. galloprovincialis* recruits and settlement of *B. glandula*. Both alien species have even recruited onto the limpets shell. Photographs courtesy of Tammy Robinson

size of this limpet has declined as the maximum size that individuals can reach is now limited by the size of the mussel shell upon which they settle (Griffiths et al. 1992). While *Scutellastra argenvillei* has also been impacted by the *M. galloprovincialis* invasion, the impact of the alien mussel on this limpet is moderated by wave action (Steffani and Branch 2003). At high levels of wave action the mussel has displaced the limpet, but at moderate wave exposures the limpet persists and retains dominance of open rock. Maybe one of the most notable effects of this invasive mussel has been its positive impact on the African Black Oyster-catcher *Haematopus moquini*. Before the mussel invasion, the oystercatcher fed predominantly on limpets and the native ribbed mussel *Aulacomya atra*, but following invasion the birds were presented with an abundant new food source (Branch and Steffani 2004). This resulted in increased breeding success and ultimately increased population size of *H. moquini* along the west coast (Coleman and Hockey 2008). It is notable that *M. galloprovincialis* is nearly free of internal parasites in South Africa, unlike the endemic *Perna perna*, which has a 15–70% incidence of infection, slowing growth, reducing body condition and even causing parasitic castration (Calvo-

Ugarteburu and McQuaid 1998). This places *P. perna* at a disadvantage relative to the alien. However, the external surfaces of *M. galloprovincialis* shells are heavily eroded by endolithic lichens and cyanobacteria (Zardi et al. 2009), making them brittle and fragile compared with the shells of the endemic *Choromytilus meridionalis*.

In 2009 a second alien mussel, *S. algosus*, was recorded in Elands Bay on the west coast (de Greef et al. 2013). This invader has subsequently spread south and around Cape Point, and now occurs throughout False Bay (TB Robinson pers. obs). Within the intertidal zone, this South American mussel is dominant in the low-shore, especially under exposed conditions (Skein et al. 2018a). It does not extend as high on the shore as *M. galloprovincialis* because of its relative intolerance of desiccation (Zeeman 2016). Also in contrast to *M. galloprovincialis*, which is virtually absent from the subtidal zone, *S. algosus* also occurs in large numbers in this habitat (Skein et al. 2018a). It appears to owe much of its success and rapid rates of spread to an exceptionally high recruitment rate (Reaugh-Flower et al. 2011; Zeeman et al. 2018). Many of the impacts associated with *S. algosus* are similar to those of *M. galloprovincialis*, as both species dominate previously open rocky surfaces. Notably, both species elevate the structural complexity of invaded rocky shores (Sadchatheeswaran et al. 2015), ultimately elevating diversity and altering community structure (Robinson et al. 2007b; Sadchatheeswaran et al. 2018). As they also form an abundant prey resource, these alien mussels have also altered the foraging landscape of native predators. While some, such as the whelk *Trochia cingulata* (Alexander et al. 2015) have incorporated the alien mussels into their diet, others such as the West Coast Rock Lobster *Jasus lalandii* and the starfish *Marthasterias africana* (Skein et al. 2018b), have not. These findings have highlighted that native predators may not necessarily regulate invasive prey, even when predators are known to be generalist feeders. In fact, when predators preferentially feed on native species and avoid alien prey, they may facilitate the invasion by removing native comparators that might have offered resistance via inter-specific competition. It remains to be investigated if this process will play out in relation to mussel invasions in South Africa.

Although first recognised as an invasive species in South Africa in 2007 (Simon-Blecher et al. 2008), the barnacle *B. glandula* is likely to have been present along the west coast since the mid-1990s (Laird and Griffiths 2008). Since its introduction, it has become the dominant intertidal barnacle on the west coast at the expense of the native barnacle *Chthamalus dentatus* (Laird and Griffiths 2008; Robinson et al. 2015). *Balanus glandula* now occurs on the south coast as far as Cape Hangklip (TB Robinson pers. obs). Although not to the same extent as the invasive mussels, this barnacle also elevates structural complexity on invaded shores (Sadchatheeswaran et al. 2015). In particular the high-shore gastropod *Afrolittorina knysnaensis* benefits from the presence of *B. glandula* (Laird and Griffiths 2008). The abundance of this native species is raised by more than an order of magnitude as individuals nestle between the barnacles, presumably gaining protection from wave action (Sadchatheeswaran et al. 2015).

Together, these three alien intertidal species now dominate west coast rocky shores. While *M. galloprovincialis* appears to have reached its maximum range on the south coast (Assis et al. 2015), *S. algosus* and *B. glandula* have only recently spread into this region (Robinson et al. 2015; Skein et al. 2018a). Notably, laboratory studies suggest that *S. algosus* will continue to spread along the south coast but that *M. galloprovincialis* is likely to maintain dominance (Alexander et al. 2015). In contrast, feeding experiments predict that *B. glandula* could hold an even greater advantage on the south coast (Pope et al. 2016). While the extent to which the *S. algosus* and *B. glandula* will continue to spread, and the impacts that will result, remain to be seen, it is clear that together with *M. galloprovincialis* they have already altered large stretches of the South African coast.

9.7 Conclusion

Substantial progress has been made in establishing the status and distribution of marine alien species along the South African coast. As the number of alien taxa continues to rise, the need to prevent incursions and manage problematic species is becoming more pressing. In an country with limited biosecurity resources, it is vital that research be strategically undertaken so as to support evidence-based management that is both effective and efficient.

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