DISTRIBUTION AND PREDICTORS OF NON-INDIGENOUS MARINE SPECIES WITHIN SOUTH AFRICA’S MPA NETWORK

By

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January 2016

Minor dissertation in partial fulfillment of the requirements for the degree of Masters of Science in Applied Marine Science

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ACKNOWLEDGEMENTS

Firstly, thanks to my supervisors, Tammy Robinson and Coleen Moloney for their support and wise comments. Special thanks to Tammy Robinson, without whom I wouldn't have been able to complete this project; and who always extended guidance to me amidst her busy schedule and has been awesome. Thanks to SANBI who provided me with the funding to do this extensive project and for being a great proactive organisation. Thanks also to the Ma-Re Institute and Centre of Excellence for Invasion Biology for providing funding. Thanks to everyone who helped me in the field, Jenna Keightley, Donovan Martin, Jennifer Angoh, Josh Brooker, Koebraa Peters Abbas and more from the previous years' work. A special thanks to Boets Chris Waspe and Paul Juby, exceptional okes and exceptionally handsome. K2B, GGWP. Big thanks to my parents Colin and Sandy Brooker for always supporting me with what I try out in life. Lastly, thanks to the lovely Rachel Gebers, for actually being my girlfriend because, let's face it, you are too pretty for me. Thank you for the constant support and encouragement you provide.

ABSTRACT

Considering the continual dissemination of marine non-indigenous (NIS) species across biogeographic borders, little is known about the status of these species within the network of South African marine protected areas (MPAs). Using the most recent data, a target list of NIS was set up for each MPA. Nineteen of the 23 South African MPAs were surveyed intertidally for alien and invasive species. The intertidal zone was divided into high-, mid- and low-shore and surveys were conducted during spring low tide. The presence and location in the intertidal zone of alien and invasive species were recorded. Additionally, invasive species' biomasses were quantified at sites at which they were found. Classification and regression tree (CART) analysis was used to assess which factors result in high numbers of NISs within MPAs. The invasive Mediterranean mussel, *Mytilus galloprovincialis*, was the most widespread species, occurring in 13 of the 19 sampled MPAs. It was most prominent on the island MPAs of the West Coast National Parks and had an overall highest biomass in the mid-shore. The bryozoan, *Bugula dentata,* was also widespread - present in MPAs across all three ecoregions. The invasive acorn barnacle, *Balanus glandula*, and bisexual mussel, *Semimytilus algosus*, both exhibited high levels of invasion in MPAs on the west coast. Extensions of known ranges were recorded for a number of species: the bryozoans *Bugula dentata*, *Watersipora subtorquata* and *Cryptosula pallasiana*, the polychaete *Neodexiospira brasiliensis*, the amphipod *Orchestia gammarellus* and the hydrozoan *Obelia dichotoma*. Certain species were recorded outside of harbours for the first time: the hydrozoans *Obelia dichotoma* and *Obelia geniculata*, the bryozoan *Cryptosula pallasiana* and the ascidians *Microcosmus squamgiger* and *Diplosoma listerianum*. CART analysis indicated that the size of the nearest port was an important indicator of the number of alien species in an MPA. When the nearest port is bigger than 0.4 km^2, more alien species are likely to occur within that MPA. For invasive species, the distance to the nearest yacht marina was the most important factor, with MPAs within 3.7 km of a yacht marina being more likely to have more invasive species in their borders. For all NISs, the highest numbers in an MPA were expected when the nearest port was greater than 2.1 km^2 and the nearest yacht marina was within 3.7 km of that MPA. Using these findings, spatial planning of future MPAs can further be prioritised to minimise the risk of introduction and spread of NIS therein. MPAs at risk as defined by these findings require structured monitoring regimes. A proactive measure would be establishing an interdisciplinary forum between relevant management authorities in order to enable dissemination of information on NIS. While controlling established NIS is difficult, the creation of task groups to act as rapid response teams for NIS, and the possibility of small-scale fisheries from edible invasive species are practical avenues that could be explored as mitigation efforts.

1. INTRODUCTION

With the expansion over time of the human population around the world, species have been intentionally and unintentionally transported across their natural biogeographic boundaries, resulting in a slow process of globalisation of the earth's biota (Vitousek *et al.,* 1997; Canning-Clode, 2016). As technology has provided modern methods of trade and transport, the pace of this introduction of biota to novel regions has increased through time (Meyerson and Mooney, 2007; Canning-Clode, 2016). As few of the species that are transported establish in the new environment into which they are released (Kolar and Lodge, 2001), common characteristics that allow successful species to settle are not easy to identify (Parker *et al.,* 1999). Nonetheless, the invasion process has been observed to follow the same series of stages regardless of the taxonomic grouping of the species: 1) uptake of the species by a human transport vector and transport to its destination location outside of its natural range, 2) the introduction of the species into the new environment via captivity or quarantine, cultivation, or direct release into the new environment, 3) the establishment of the non-native species in the novel region where the potential for further spread depends on the populations' ability to reproduce and be self-sustaining and 4) the expansion stage characterised by populations surviving and reproducing a significant distance from the point of introduction (Kolar and Lodge, 2001; Floerl and Inglis, 2005; Arim *et al.,* 2006, Blackburn *et al.,* 2011).

There has been much disparity within the literature regarding the terms "non-indigenous", "alien" and "invasive" (Colautti and MacIsaac, 2004; Falk-Petersen *et al.,* 2006). This is problematic in that it hinders the comparison of pattern and process in invasions and may lead to multiple terms for a specific definition and vice-versa (Blackburn *et al.,* 2011). Robinson *et al.* (2016) have offered a rational terminology for use in South African marine invasion biology research so as to standardise definitions and support the uptake of research by managers and policy makers. These will be used as the framework of the definitions in this study. It is important to note that definitions for marine alien and invasive species were updated during the course of this study, and as such certain species classifications changed. The study was carried out on the definitions and classifications that were available when it commenced. Alien species can be indigenous or non-indigenous, but for the purpose of this study we focus only on non-indigenous species. An alien species is thus defined as "a non-indigenous species translocated via a human-mediated vector to a place outside its natural distribution range, which exhibits no apparent potential or actual ecological, social or economic impacts, to the best of scientific knowledge". An invasive species is defined as "a non-indigenous species translocated via a human-mediated vector to a place outside its natural distribution range, whose establishment and spread has actual or potential ecological, social or economic impacts". Non-indigenous species (NIS) will be used as an umbrella term for both alien and invasive species.

1.1. VECTORS OF MARINE NON-INDIGENOUS SPECIES

Humans have been intentionally and unintentionally transporting species from their natural biogeographic ranges since ocean travel began (Mead *et al.,* 2013). With trade and global connectivity increasing at unprecedented levels (Mack *et al.,* 2000), indigenous biota face the greatest ever risk of invasion by non-indigenous species (Vitousek *et al.,* 1997).

Historically, ocean-going vessels were made of wood and dry ballast was loaded onto ships to control buoyancy and trim. Wooden hulls were suitable habitat for species that bore into wood, while the dry ballast that was collected from coastal areas of the source port supported a variety of intertidal and driftline meiofauna and infauna (species living in the sediment or substratum of a marine environment), coastal plants, seeds and insects (Minchin *et al.,* 2009). Carlton (1999) estimated that in 1750 a vessel could contain up to 120 species that had bored into or fouled the hull, and an extra 30 present as a result of cargo or dry ballast. The introduction of wood borers such as the isopods *Limnoria* spp. and the bivalve *Teredo navalis* are likely a result of historical shipping routes (Griffiths *et al.,* 2009a). Species associated with wood boring and dry ballast were replaced by an entirely new suite of organisms between 1880 and 1950, during the transition to steel hulled ships and ballast water (Hewitt *et al.,* 2009a).

Ship ballast water is considered the most significant vector in movement of species between biogeographical barriers, with Carlton (1999) estimating that, at any given moment, up to 10 000 species could be in transit around the globe in ballast water tanks. Species associated with ballast water are primarily planktonic, being holo- (entire life cycle), tycho- (accidentally caught up) or mero-planktonic (spend a portion of the life cycle in the water column). Additionally, the sediment that builds up in ballast tanks can host a variety of assemblages made up different infaunal species that exist in the sediment and substratum that is created by it (Hewitt *et al.,* 2009a). Potential non-indigenous species would have struggled in the early days of ballast water tanks to make the long trans-oceanic journey. However, with the subsequent increase in technology resulting in cleaner ballast tanks and faster ships, species associated with ballast water have an increased chance of surviving journeys along shipping routes (Bax *et al.,* 2003). Indeed, sedimentation occurs within almost all ballast tanks and infauna present in the sediment have been known to survive for months in a resting state in unsuitable conditions (Hewitt *et al.,* 2009a).

The International Maritime Organisation first assessed the issue of ballast water in the 1980s and concluded that shipping and specifically ballast water were indeed contributing to the transfer of non-indigenous species, including those that could be harmful to humans. The Ballast Water Working Group was thus established to facilitate an appropriate regulatory framework (Hewitt *et al.,* 2009b). In 2004 the International Convention on the Control and Management of Ships' Ballast Water and Sediments was adopted with the aim of minimising and, where possible, eliminating the risks posed to human health and resources arising from the transfer of detrimental marine organisms (Ballast Water Management Convention, 2005). It included a ballast water exchange regulation that required ships to exchange port water for oceanic water in an effort to purge the ballast tanks of any viable species unintentionally taken up during ballasting. While there are concerns that military and small vessels are not covered, and that short shipping routes (within 200 nautical miles) are not long enough for ballast exchange to take place without delaying the vessel, the Ballast Water Management Convention is a step in the right direction towards providing international standards by which ballast water discharges can be regulated (Hewitt *et al.,* 2009b).

While there is some regulation of ballast water management, the vector of hull fouling is not dealt with directly in any body of legislation, but is indirectly affected by the Convention on the Control of Harmful Anti-Fouling on Ships (2001). The fouling of hulls increases drag and thus operating costs of vessels. These costs were mitigated by the effectiveness of early anti-fouling coatings applied to vessel hulls. Anti-fouling paints using organotins, including tributyltin, were very effective at mitigating fouling species (Minchin, 2006). However, tributyltin paints had deleterious effects on biotic communities near ports as they act as endocrine disruptors (Hewitt *et al.,* 2009a). Organotin anti-fouling paints were therefore discontinued through the Convention on the Control of Harmful Anti-Fouling on Ships. Present day vessels, being large, fast and constructed from steel, are likely to play host to a different suite of fouling organisms than those of old days (Griffiths *et al.,* 2009b). Organisms such as hydroids, bivalves, tubeworms, barnacles, bryozoans and ascidians make up the majority of these organisms. However, small mobile species such as amphipods, isopods and polychaetes are able to survive among the fouling organisms with increasing community complexity (Griffiths *et al.,* 2009a). Evidence is growing that suggests that fouling of oil platforms and drilling ships may be an important vector in the transport of species around the globe (Ferreira *et al.,* 2006; Yeo *et al.,* 2009), with the associated faunal richness equivalent to an array of species synonymous with a subtropical reef community due to towing of rigs across biogeographic barriers (Wanless *et al.,* 2010). The Convention on the Control of Harmful Anti-Fouling on Ships, coupled with increased propagule pressure from ships, is thought to have caused ports to become even more susceptible to invasions (ICES, 2001).

Introduction of non-indigenous species through aquaculture occurs via both the intentional transport of the target species and the unintentional transport of associated epibiota (organisms existing on the surface of others) and infauna (Haupt *et al.,* 2010). Oysters are particularly problematic organisms in this regard (Ruesink *et al.,* 2005) as their hardiness and resistance to desiccation have enabled them to be transported since early oceanic travel (Haupt *et al.,* 2010). Shells provide suitable substratum for fouling organisms, as oysters do not bury into the sediment (Ruesink *et al.,* 2005). The nature of farming practices differs, ranging from wild accumulations, whereby species are collected prior to sale and may be fed, to quarantine practices, where cultivation occurs under strict control of all access and waste, as well as having decontamination measures in place with sterility control (Minchin, 2007). Farming practices may provide a means of infestation to regions other than the original area of introduction owing to transport of the market organism, especially when the farmed organism has a variety of life stages (e.g. oyster spat being imported from Chile to South Africa) (Haupt *et al.,* 2010). Additional associate species may be transported with the market organism and spread before they are identified (Minchin, 2007). A particular concern is the threat of parasite organisms which, if introduced to indigenous species that have no resistance, could have serious negative effects on these species (Torchin *et al.,* 2002). The spread of diseases and pests thought to be related to the imports of cultivation species resulted in development of the ICES Code of Practice on the introduction and transfer of marine organisms (ICES, 2005).

Another vector of marine invasions, which has been underestimated, is that of the live bait trade. Fowler *et al.,* (2016) recently showed that this vector transports a plethora of organisms: up to 17798 macro organisms ranging across 58 taxa in the Maine baitworm trade alone. These species are often exposed to environments outside of their natural distribution range as the bait is intended for use while alive. The lack of management consideration on this activity despite the risk posed by the diversity of organisms that are transported is a red flag that must be urgently mitigated.

While ballast water and hull fouling are thought to contribute to the majority of alien and invasive species introductions, additional vectors exist that play a role in the transport of species. Canals facilitate the transfer of organisms between different biogeographic regions. For example, many marine species are recorded to have extended their range from the Red Sea to the Mediterranean Sea through the Suez Canal (Galil *et al.,* 2015). Intentional imports of aquarium species and live foods for human consumption are distributed to respective stores, markets and restaurants (Chapman *et al.,* 2003). Subsequent intentional or unintentional release may lead to establishment of the species. For example, on the Atlantic coast of North America the Pacific lionfish, *Pterois volitans,* was introduced via aquarium releases (Whitfield *et al.,* 2002). Research efforts that result in the escape, discarding or purposeful planting or release of experimental organisms contribute towards introductions of alien and invasive species. In San Diego, California, the New Zealand mangrove *Avicennia marina* was planted for physiological research and it subsequently invaded the region (Callaway and Zedler, 2004).

1.2. IMPACTS ASSOCIATED WITH MARINE INVASIONS

The potential impact of invasive species spans the economic, social and ecological spheres (Molnar *et al.,* 2008). This can make management of invasions difficult as different species' effects may interact with each of these spheres on different spatial and temporal scales (Parker *et al.,* 1999).

1.2.1. Economic impacts

Economic effects are felt primarily in industries based on marine resources such as fisheries, aquaculture, tourism and marine infrastructure (Bax *et al.,* 2003; Reaser *et al.,* 2007). In Saldanha Bay the ropes of *Mytilus galloprovincialis* mussel rafts become extensively fouled by the invasive ascidian *Ciona intestinalis* and wild spat of the same mussel species. *Ciona* *intestinalis* reaches densities of 800 000 individuals per mussel raft whereas *M. galloprovincialis* spat has been shown to reach 1.7 million individuals per mussel raft. This inhibits the ability of farmed mussels to grow, reduces efficiency when handling the ropes due to excess weight and reduces efficiency when sorting mussels into size classes. This causes heavy economic cost to the mariculture companies (Rius *et al.,* 2011). Robinson *et al.* (2005a) estimated that the cost of removal of *C. intestinalis* is up to R100 000 per annum. Another example is that of the highly invasive zebra mussel, *Dreissena polymorpha*, in North America. It has had major impacts on infrastructure, particularly power stations, by fouling intake pipes, with bits of shell breaking loose and blocking filters, valves and smaller pipes. The estimate is that the cost of removal and mitigation was US $1 billion between 1988 and 2000 (Elliot *et al.,* 2005).

1.2.2. Social and health impacts

Introduced species disturb ecosystem services that support human wellbeing, such as food provision, regulation of diseases and providing aesthetic value. This may have a direct or indirect impact on human health and social wellbeing (Pyšek and Richardson, 2010). Social and economic effects are not mutually exclusive and may act in synergy. An example of direct human health threats through disease or ailment can be seen in the invasive ascidian *Styela clava* which, when contact is made, can spray a respiratory-inhibiting substance that can damage tissue (Pyšek and Richardson, 2010). Additionally, unicellular organisms such as the dinoflagellate *Alexandrium catenella* can cause harmful algal blooms, which can result in paralytic shellfish poisoning (Lilly *et al.,* 2002). Decrease in human health can lower productivity of an employee, or cripple a workforce by diminishing attendance numbers. This in turn affects the business through slowed productivity and the workers' families through decreased income. Alternatively, if an invasive species impacts an industry by affecting the resource directly, this could result in retrenchment if the business is failing (Bax *et al.,* 2003).

1.2.3. Ecological impacts

Ecological interactions resulting from the introduction of alien and invasive species may manifest as impacts on the native species and communities, as well as on ecosystem processes and function (Katsanevakis *et al.,* 2014). These impacts can be measured at five levels (Parker *et al.,* 1999): 1) individual effects, 2) genetic effects, 3) population dynamic effects, 4) community effects and 5) ecosystem process effects.

Effects on individuals:

Effects of invasive species on individuals of a native species are manifested primarily in predation and competition interactions (Parker *et al.,* 1999). Native individuals can alter habitat use or activity patterns as a behavioural response to an invasive species. For example in California's Eel River, several fish species changed microhabitat use owing to the introduction of a predatory pikeminnow, *Ptychocheilus grandis* (Brown and Moyle, 1991). Additionally, species can suffer reduced growth and reproduction rates (Byers, 2000) and changes in morphology in response to a new competitor or predator (Busch and Smith, 1995).

Genetic influences:

The pressures exerted by an invasive species on native biota can cause altered patterns of natural selection or gene flow within the native population (Parker *et al.,* 1999). In addition to affecting natural selection of the native species through competitive pressures, hybridisation can occur between an invasive and a native species (Parker *et al.,* 1999, Huxel, 1999). The formation of a new hybrid genotype can often produce a high-impact fertile invasive species, for example when the cordgrass *Spartina alterniflora* hybridised with the European *Spartina maritima* to produce *S. anglica* (Katsanevakis *et al.,* 2014). Mass reproduction of the hybrid species and widespread introgression in the population results in genetic pollution and potential extinction of the native species (Rhymer and Simberloff, 1996). This production and spread of a hybrid species can be a rapid process. In the northwest Atlantic, mitochondrial introgression spread faster than larval dispersal during an increase in range of the invasive European shore crab, *Carcinus maenas* (Darling *et al.,* 2014).

Effects on population dynamics:

Measures such as change in abundance, range, distribution and age or size class are used to quantify the direct and indirect effects of invasive species on native species populations (Parker *et al.,* 1999). The bisexual mussel, *Semimytilus algosus,* is a recent invader of South Africa's west coast. It is thought to exclude the native limpet *Scutellastra granularis* completely from the primary rock space where it is present (de Greef *et al.,* 2013), despite the limpets being able to persist on the shells of the invasive Mediterranean mussel *Mytilus galloprovincialis* adjacent to *S. algosus* (Branch and Steffani, 2004). This is due to the large surface area of *M. galloprovincialis* shells. The result is that the population structure of *S. granularis* has changed, with local exclusion at *S. algosus* beds and with limpets on *M. galloprovincialis* beds being smaller than those on bare rock (Sadchatheeswaran *et al*., 2015).

Community level effects:

Community level effects are evident in changes of species richness and total species number. The invasive alga *Caulerpa taxifolia* altered meiofaunal structure along the coast of New South Wales in Australia, facilitating an overall increase of nematode species that were absent from the native environment (Gallucci *et al.,* 2012). Locally, *S. algosus* is thought to exclude all organisms owing to very small interstitial spaces. In contrast, *M. galloprovincialis* beds support a rich and diverse infaunal assemblage. A change in habitat complexity linked to these species over time in the intertidal zone on the west coast has caused associated fluctuations of native species abundances (Sadchatheeswaran *et al.,* 2015).

Ecosystem level effects:

By altering abiotic factors (such as substratum, light intensity, pH and nutrient flow) and biotic factors (such as species abundance and community composition), invasive species can act as ecosystem engineers. This can have knock-on effects that change the natural processes of the ecosystem, such as disturbance regimes and nutrient cycling (Wallentinus and Nyberg, 2007).

1.3. MANAGEMENT OF INVASIVE SPECIES

When mitigating introductions and subsequent invasion, action needs to be swift and efficient. Management focus on individual potential invaders is impossible due to the vast pool of species and uncertainty in ascertaining the risk species. Therefore, prevention is considered the most efficient management action (Pyšek and Richardson, 2010). Preventative protocols are effective and cheap in comparison to control measures (Bax *et al.,* 2003). This method of combating the threat of marine alien and invasive species is, however, reliant on legislative frameworks being upheld at a regional and global scale. While prevention may be able to reduce inoculation in the short term at a national level, without regional co-operation invasion mitigation will be impossible due to the high relative number of inoculation events and adaptation abilities of marine alien and invasive species (Bax *et al.,* 2003). Proportionally few NISs have been evaluated for impacts, which has created a stumbling block among many management authorities. Often species that are classed as "data-deficient" receive no more attention by management, whereas a true precautionary approach would be to class them as high risk. Impacts of the species could become clear long after the invasion, in which case it is too late for any meaningful management action (Ojaveer *et al.,* 2015). The same is true when a study fails to detect an impact. It is often assumed that the species does not pose a risk to the recipient region, whereas it may be that, in a different context, the recipient region does indeed incur negative impacts (Ojaveer *et al.,* 2015). Effective prevention of all non-native introductions is impossible to achieve and thus must be strengthened by efficient reactive measures, which are put in place by information gained from comprehensive risk assessments. Risk assessments are tools that enable management to identify consequences of invasion by species and their respective likelihoods, and provide a robust and systematic action to combat these (Hewitt and Campbell, 2007). Among other uses, risk assessments can facilitate the identification of vectors of concern and prioritisation of localities that are likely to be vulnerable to invasion. GloBallast has made progress by initiating port surveys (Hewitt and Campbell, 2007). Risk assessments allow effective implementation of rapid response protocols. In Darwin Harbour Estuary, routine monitoring identified *Mytilopsis sallei* as an introduction. Subsequent quarantine and eradication efforts enabled the new invader to be eradicated within a year (Bax *et al.,* 2002).

1.4. MARINE PROTECTED AREAS AND THE THREAT OF INVASIVE SPECIES

Although not created for the mediation of non-native species introductions and spread, MPAs are significant management tools for the preservation of marine resources and need to be managed with the potential threats of alien and invasive species in mind (Simberloff, 2000). According to the IUCN (Dudley, 2008, p.8) “A protected area is a clearly defined geographical space, recognised, dedicated and managed, through legal or other effective means, to achieve the long-term conservation of nature, associated ecosystem services and cultural values”. MPAs were initially implemented to combat the declining global fish stocks (Halpern, 2003). When MPAs were first acknowledged as successful management tools, there was focus on the strategic design and implementation of MPAs (Ward *et al.,* 1999; Sala *et al.,* 2002; Halpern *et al.,* 2003). The aim was to benefit a range of different objectives, for example the preservation of rare or endemic species, habitat heterogeneity, sensitive life stages of regional species, the provision of fish stocks to adjacent areas, provision of research and education opportunities and the provision of recreational areas (Norse, 1993; Hockey and Branch, 1997). An area that has received little consideration in management of MPAs when compared to terrestrial systems is that of introduced species (Simberloff, 2000). Together, the Center for Marine Conservation, the World Conservation Union, the United Nations Environment Programme, the WWF and the World Bank produced a Global Marine Biological Diversity Strategy (Norse, 1993) and outlined the following broad primary objectives of MPAs: 1) To ensure protection of representative sections of the marine environment in all major biogeographic regions, 2) To maximise habitat diversity (thus species and community diversity) within the MPAs, 3) To ensure protection of rare, localised or endemic species through ensuring protection of their habitat and 4) To protect areas essential for the completion of vulnerable life-history stages of coastal species.

There have been various studies on how to best conserve ecological systems within an MPA and marine reserves were run on the same principles as terrestrial protected areas for some time (Meffe and Carroll, 1994; Simberloff, 2000). Processes such as nutrient cycling, propagule dispersal and species interactions differ fundamentally between the marine and terrestrial systems, however, and threats to the marine environment do not align with those of the terrestrial environment (Hockey and Branch, 1994; Carr *et al.,* 2003). For example, there is less human-induced habitat fragmentation in the ocean compared to land (Hockey and Branch, 1994), there is a greater mean range of biota and dispersal of propagules (Kinlan and Gaines, 2003) and there is limited local endemism but higher phyletic diversity when compared to land (Carr *et al.,* 2003). The oceanographic processes of the marine environment that facilitate large range and dispersal of organisms are key aspects indicating that marine invasive species require consideration in the design and implementation of MPAs (Simberloff, 2000). The invasion of the alga *C. taxifolia* in the Mediterranean is evidence that a single marine invader is able to disrupt a prolific MPA network (Meinesz, 1999) and disrupt community structure over a vast area.

1.5. MARINE INTRODUCTIONS IN SOUTH AFRICA

South Africa has been a component of a significant trade route between Europe and Asia since colonial times. It is thus almost certain that species introductions have been ongoing since European settlers arrived over 400 years ago (Griffiths *et al.,* 2009b). This has created historical data gaps, as data were not collected on marine invasions in South Africa until recently (Griffiths *et al.,* 1992). Large areas of South Africa's coastal environment are unexplored with regards to marine invasions (Robinson *et al.,* 2005a; Griffiths *et al.,* 2009b). In addition, coastal habitat types have not been surveyed equally, and some not at all (Mead *et al.,* 2011a; Mead *et al.,* 2013). South Africa is thus a region where much work is needed in the field of marine invasions (Mead *et al.,* 2011a). Mead *et al.* (2011b) addressed these issues and provided the most recent published list of introduced and cryptogenic (unknown origin) marine species in South Africa. The study recorded 86 introductions and 39 cryptogenic species, covering 22 taxonomic groups (Mead *et al.,* 2011a,b). This is, however, considered an underestimate and new recordings of introductions continue (Bolton *et al.,* 2011; Clark and Griffiths, 2012; Peters *et al.,* 2014). Carlton (2009) estimates that the number of introductions in South Africa could be as high as 220.

Of the introductions into South Africa, 48% are attributed to hull fouling and 38% to ballast water, making these the most important vectors of introductions (Mead *et al.,* 2011a). Mariculture is recognised as a growing pathway in South Korea and South Africa (Seo and Lee, 2009). The highest numbers of introductions were recorded along the west coast in the cool temperate Benguela ecoregion (as defined in Sink *et al.,* 2012), with species originating from the northern hemisphere being prominent in that region and the temperate southeast coast. Concurrently, species originating in the southern hemisphere appear to establish more successfully on the east and north east coasts (Mead *et al.,* 2011a). Oceanographic and climatic factors dictate the biogeography of the regions (Sink *et al.*, 2005). Despite this, there is a large number of alien and invasive species that are shared across the temperate regions of the coastline, which is indicative of the high levels of plasticity that marine alien and invasive species exhibit (Occhipinti-Ambrogi, 2007).

1.6. SOUTH AFRICAN MARINE PROTECTED AREAS AND THE RESEARCH GAP

South Africa's 3650 km long coastline is unique in that it spans two oceans. The west coast (Atlantic Ocean) is a productive system influenced by the cold Benguela current, with the coastal regions exhibiting upwelling. This system falls into the Southern Benguela ecoregion. The east coast (Indian Ocean) experiences the warm Agulhas current's nutrient poor equatorial waters (Lutjeharms*,* 1998). The Agulhas ecoregion comprises the south and southeast coasts of the country, where productivity is lower than on the west coast (Griffiths *et al.,* 2010). The warm subtropical Natal ecoregion extends north from the east coast until it transitions into the tropical Delagoa ecoregion in the far northeast of the coastline.

South Africa has 23 MPAs along its coastline, which span all four ecoregions and collectively make up 23% of the coastal length (Sink *et al.,* 2012) (Figure 1). However, only three of these have been surveyed for marine alien species. Robinson *et al.* (2004) surveyed Marcus Island and Langebaan Lagoon MPAs for alien and invasive species. The Mediterranean mussel *M. galloprovincialis* was recorded on wave-exposed rocky shores but was absent from most of the lagoon. This mussel had highest biomass in the mid-shore on Marcus Island (25.4 ± 18.7 SD kg.m^{-2}). In contrast the invasive gastropod *Littorina saxatilis* was restricted to sheltered *S. maritima* beds in the high-shore within the lagoon. Population estimates suggest 2.4 million individuals within the lagoon at a highest density of 433 ± 123 SD individuals.m^{-2}. Lastly, an invasive anemone *Sagartia ornata* was restricted to habitats in the lagoon containing rocky substratum covered by sandy sediment, occurring at a maximum density of 508.4 ± 69.1 SE individuals.m^{-2}.

Malherbe and Samways (2014) undertook a comparative survey of the Betty's Bay MPA, contrasting the presence of marine alien species inside and outside the MPA. *M. galloprovincialis* was more abundant outside of the MPA than inside, where no individuals

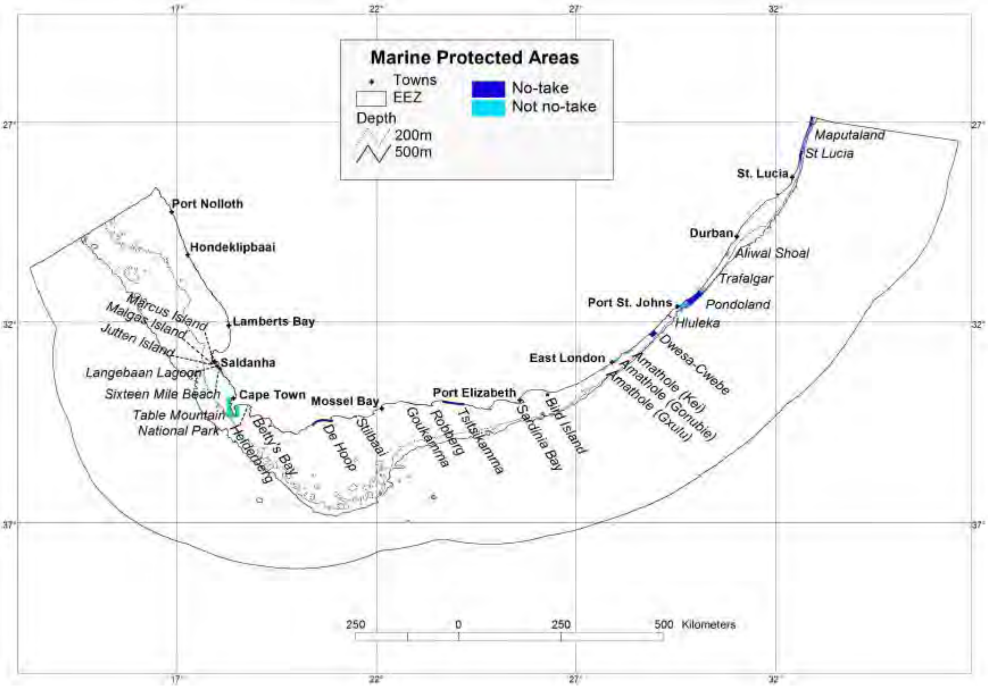

Figure 1. The distribution and take (extraction of resources controlled) or no take (no extractive activities permitted) status of MPAs around South Africa's coast. Obtained from Sink *et al.* (2012).

were recorded, apparently owing to the sheltered nature of most of the intertidal habitat. One other alien species was found, namely the Red Rust bryozoan, *Watersipora subtorquata*. In contrast to the mussel, this bryozoan was more abundant inside the MPA than outside. This was also likely due to the sheltered conditions of the intertidal zone of the MPA.

Whereas these studies provide baselines for the three respective MPAs, 86% of the South African MPA network remains unsurveyed for marine alien and invasive species. In addition, these studies were undertaken before Mead *et al.* (2011b) produced the most recent list of 86 introduced and 39 cryptogenic species known from the region. This study aims to addresses this significant gap in knowledge by:

1) Undertaking the first systematic survey of 19 of South Africa's 23 MPAs for alien and invasive species.
2) Identifying factors that are likely to be driving the number of alien and invasive species present in these conservation areas. This in turn will provide support to management authorities tasked with prioritising monitoring within MPAs.

2. METHODS AND MATERIALS

2.1. STUDY SITES

Data were collected from 19 of the 23 MPAs on the South African coastline (Table 1, Figure 1). MPAs not included due to time and logistical constraints were the Hluleka, Dwesa-Cwebe, Pondoland and Maputaland MPAs.

2.2. DATA COLLECTION

2.2.1. Field surveys

Using the most recent publication on the marine alien and invasive species of South Africa (Mead *et al.,* 2011b), a target list of these species was drawn up for each MPA (APPENDIX I). Although many of the species on this list have previously been recorded subtidally or in

Table 1. The MPAs surveyed, their abbreviations and responsible management authority.

MPA	Abbreviation	Managing authority
Langebaan Lagoon	LL	South African National Parks (SANParks)
Marcus Island	MAR	SANParks
Malgas Island	MAL	SANParks
Jutten Island	JUT	SANParks
Sixteen Mile Beach	SMB	SANParks
Table Mountain National Park	TBMNP	SANParks
Helderberg	HB	City of Cape Town and Department of Envrionmental Affairs
Betty's Bay	BB	Cape Nature
De Hoop	DH	Cape Nature
Still Bay	SB	Cape Nature
Goukamma	GOU	Cape Nature
Robberg	ROB	Cape Nature
Tsitsikamma	TK	SANParks
Sardinia Bay	SAR	SANParks
Bird Island	BI	SANParks
Amathole	AMA	Eastern Cape Parks and Tourism Agency
Trafalgar	TRA	Ezemvelo KZN Wildlife
Aliwal	ALI	Ezemvelo KZN Wildlife
St Lucia	STL	Ezemvelo KZN Wildlife

harbour environments, they were included to make the target list as inclusive as possible. This was done to ensure that species that can occur in the extreme low shore or that recently might have spread from harbours would be detected if they were present. Active searches were undertaken to locate the target species. Owing to time constraints, target species included only invertebrate macrofauna or macroflora. This "target list approach” unavoidably did not detect any unrecorded NIS but enabled a strategic and focused sampling approach that used time and resources efficiently.

Fieldwork took place between March 2013 and December 2014. In each MPA the shoreline was divided into high-, mid-, and low-shore zones and each was searched for the targeted species. Observer bias was minimised by having one searcher who was constant over all MPAs and was accompanied by an assistant on each survey. The surveys took place from one and a half hours before spring low tide until one and a half hours after spring low tide and the number of target species located per hour was recorded. At least 20% of the length of each protected area was searched apart from De Hoop, Tsitsikamma and St Lucia, because of their large size and time constraints. For De Hoop and Tsitsikamma, at least 10% of the coast was searched, whereas for St Lucia at least 5% of the coastline was searched. The searches included all intertidal habitat types present in the MPAs. The location of each alien and invasive species was recorded. For invasive species, biomass was also estimated except for the ascidians *Botryllus schlosseri* and *Ciona intestinalis*, and the bryozoan *Watersipora subtorquata*. The classification of *B. schlosseri* and *W. subtorquata* was recently updated to invasive and they were considered alien when they were documented in the field. The observation of *C. intestinalis* was an isolated one of a few individuals on a pontoon and thus was not quantified. Once an invasive species was located, ten 0.5m x 0.5m quadrats were randomly placed within each shore zone and density was estimated as percentage cover for sessile species, and counts of individuals for mobile organisms. These measures were later converted to a common unit of whole wet biomass.m^{-2} based on weighed subsamples of either five scraped areas of 0.1 m^2 or a minimum of 50 individuals per species.

2.2.2. Desktop study

In order to identify factors influencing invasions in MPAs, data about the nature of the MPAs and activities that take place within their borders and in surrounding areas were compiled (Table 2). Care was taken to not include variables that may be co-dependent on one another, as is cautioned in Spear *et al.* (2013). Fundamental characteristics of the MPAs such as age and area are important to include because they enable immediate flagging of vulnerable MPAs according to these parameters. Broad ecological characteristics such as number of habitat types in MPAs, ecoregion and regional species richness will likely play a role in in the occurrence of NIS in a given MPA. The regional richness was obtained from Awad *et al.,* (2002), who used distribution data from species records on the 11 of the most well recorded taxonomic groups, dividing the coastline into 100km units. The question of whether local species richness facilitates NIS establishment or provides biotic resistance has been the subject of debate in the literature and is termed the ‘invasion paradox’ (Fridley *et al.,* 2007). Variables that consider potential nodes of human exploitation are important, thus the broad level of access was considered under access control, whether the MPA was take or no take and whether there was recreational diving which takes place within the MPA. Lastly, well-known nodes of introduction were considered in relation to MPAs under the distance to nearest yacht basin, distance to nearest port, size of nearest port and distance to nearest aquaculture facility (Table 2).

Table 2. Predictor variables from each MPA used in CART analyses, the levels at which they were measured and the relevant source used to obtain information for each MPA.

Predictors	Levels / Units	Source
Age of MPA	Age in years	Government gazettes
MPA area	km^2	MPAtlas database (www.mpatlas.org)
Number of habitat types	Count	Jackson *et al.* (1984)
Ecoregion	Benguela/Agulhas/Natal	Sink *et al.* (2012)
Regional species richness	Number of species per 100km coastline	Awad *et al.* (2002)
Access control	Yes/No/Partly	Government gazettes
Distance to nearest aquaculture facility	km	Google Earth
Distance to nearest yacht basin	km	Google Earth
Distance to nearest port	km	Google Earth
Nearest port size	km^2	Ports and Ships website (www.ports.co.za)
Take or no-take	Take/no-take	Sink *et al.* (2012)
Recreational diving	Yes/No	www.skaphandrus.com

2.3. STATISTICAL ANALYSIS

2.3.1. Biomass data analysis

Univariate analyses on biomass were undertaken using the statistical software R (R Core Team, 2013). Prior to univariate tests, data were tested for normality using Shapiro-Wilk's tests. Homogeneity of variances was tested by investigating the spread of residuals around the mean of a general linear model of the data. A two-factor generalized linear model (GLM) was undertaken for each invasive species to investigate the effects of shore zone (three levels: high-, mid- and low-shore) and MPA (*M. galloprovincialis*: 13 levels; *S. algosus*: four levels; *B. glandula*: five levels) on respective species' biomass. Overdispersion was present in all cases and thus quasipoisson GLMs were implemented.

2.3.2. Classification and Regression Tree Analysis

CART$^{®}$ analysis was performed using Salford Systems. This method was used to create easily interpretable regression tree models that provide information on likely predictors of the number of alien and invasive species recorded per hour in the various MPAs (Floerl and Inglis, 2005). CART analysis uses recursive partitioning to categorise any combination of categorical and continuous predictor variables in order to best account for the variability in a response variable (Breiman *et al.,* 1984). It uses an index of information gain to "prune" the trees, thus differentiating the target variable using the best explanatory variables for the data pattern by splitting the data into terminal and non-terminal nodes. Trees were pruned using the Gini Index, which uses information gain as the measure by which splits in the trees are made (Breiman *et al.,* 1984). Three trees were developed, one for each response variable: number of alien species, number of invasive species and number of NIS located per hour. These were used as proxies for the level of invasion. The regression model was run concurrently with V-fold cross validation to prevent overfitting of the data, due to the small size of the sample dataset (Breiman *et al.,* 1984). Each tree has an associated cross validation (CV) cost. The tree chosen was the one deemed most appropriate by minimising the CV error but still being interpretable in the output (Breiman *et al.,* 1984).

3. RESULTS

Twenty-two non-indigenous species were found within the intertidal zone of South Africa's MPAs (Table 3), representing 43% of the species on the target lists. Langebaan Lagoon MPA supported the most invasive species (six), as well as three alien species (Figure 2). There were two MPAs (Sixteen Mile Beach and Helderberg) in which no non-indigenous species were recorded. Invasive species were found in all MPAs apart from these two. MPAs on the southeast coast, from Still Bay to Bird Island, all supported one invasive species, the Mediterranean mussel *M. galloprovincialis* (Figure 2). The largest number of alien species was found in Betty's Bay and Amathole MPAs, both supporting five. Alien species were absent from Malgas Island, Jutten Island, Still Bay, Goukamma and Robberg MPAs.

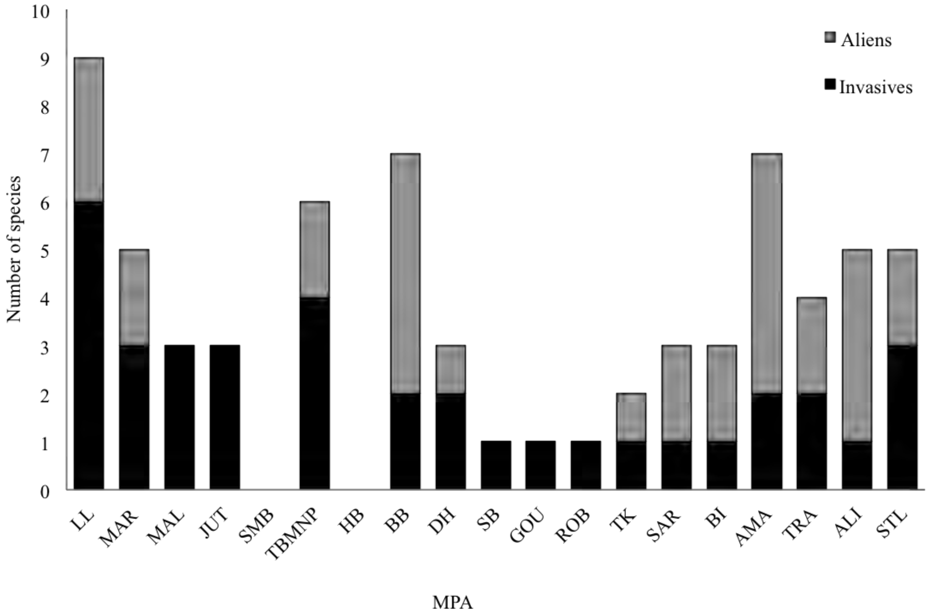

Figure 2. Number of alien and invasive species observed in each MPA. MPAs are ordered along the coastline from west to east.

3.1. TAXONOMIC BREAKDOWN OF NIS IN SOUTH AFRICA'S MPAS

Non-indigenous species belonged to a variety of taxa (Table 3, Figure 3). Bryozoa and Ascidiacea, both well-known fouling taxa, had the most non-indigenous species (two alien and two invasive species each). Bivalvia, Rhodophyta and Chlorophyta contained only invasive species, whereas Anthozoa, Hydrozoa, Polychaeta and Amphipoda contained only alien species. Cirripedia and Gastropoda both contained one alien and one invasive species (Figure 3).

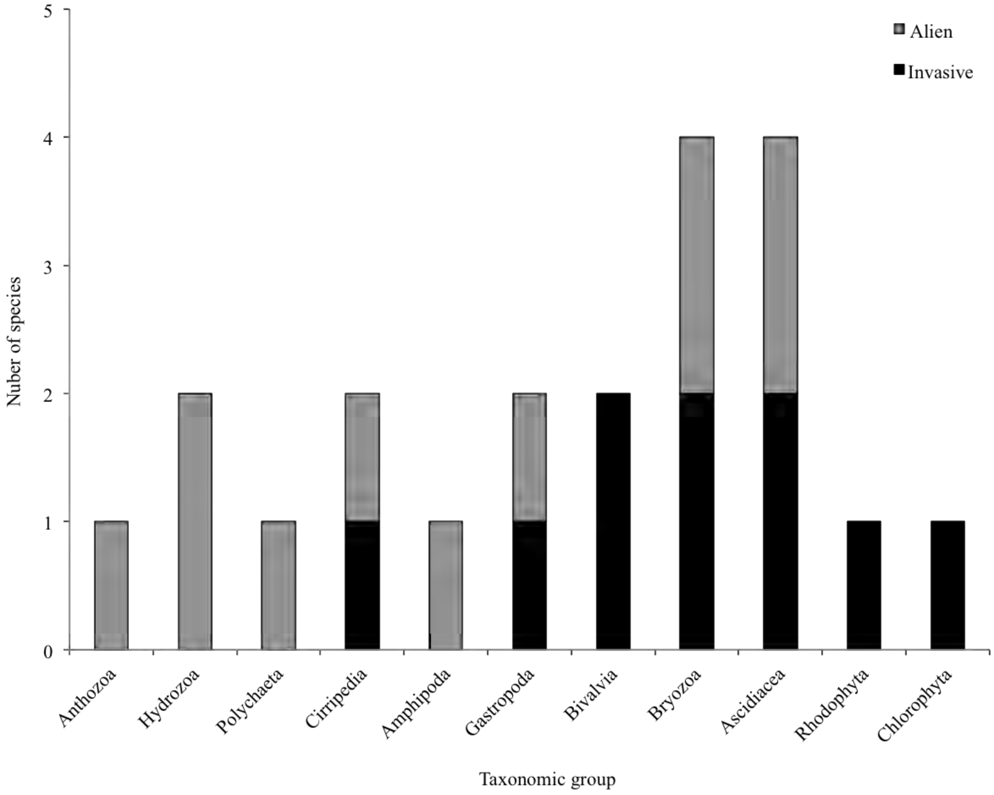

Figure 3. Number of alien and invasive species recorded from each broad taxonomic group.

When the broad taxonomic groups were considered per MPA, Bivalvia were the most widespread occurring in 13 of the 19 MPAs (Figure 4) but not on the east or northeast coasts. Bryozoa species were found in nine, Cirripedia in eight and Ascidiacea in seven MPAs. Polychaeta were present in only four MPAs (Figure 4).

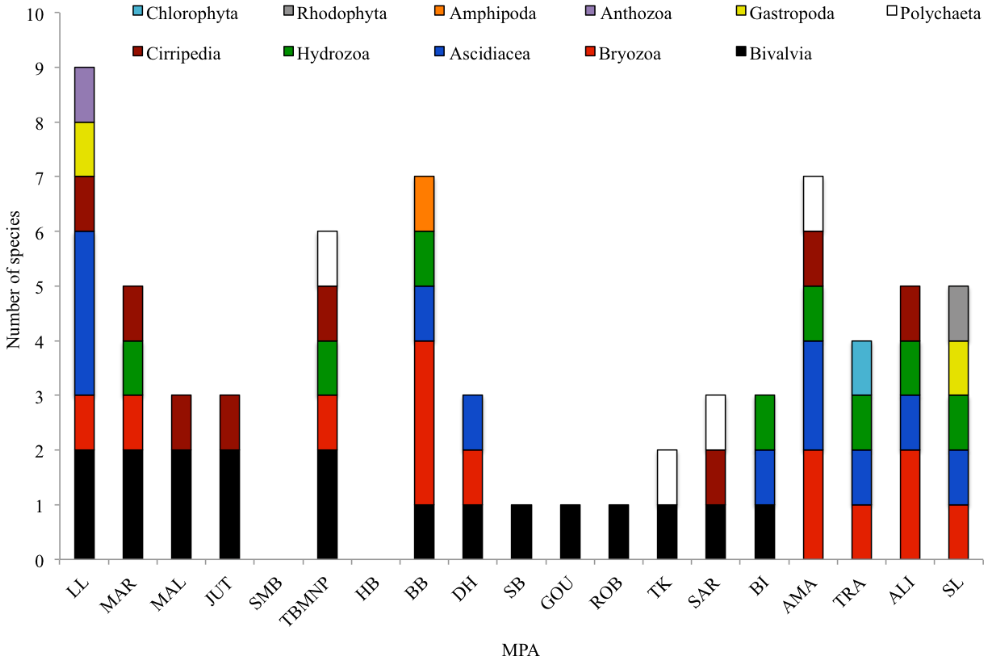

Figure 4. A taxonomic breakdown of the non-indigenous species occurring in South African MPAs.

3.2. THE DISTRIBUTION OF NIS ACROSS SOUTH AFRICA'S MPAS

Langebaan Lagoon, which had the most non-indigenous species recorded in an individual MPA, also had the most invasive species (Table 3), the majority of which were recorded from Langebaan Yacht Club, which falls within the borders of the MPA.

The bivalve *M. galloprovincialis* occurred in all MPAs containing rocky shores along the west and south coasts until Bird Island in Algoa Bay (Table 3). It was even noted as being present on a fencepost on the border of Helderberg MPA. Additional widespread organisms included the alien hydrozoan *Obelia dichotoma*, the alien bryozoan *Bugula neritina*, and the invasive *Bugula dentata*, all of which spanned the cold southern Benguela ecoregion, the warmer temperate Agulhas ecoregion and the warm subtropical Natal ecoregion (Table 3).

Table 3. Alien (○) and invasive (■) species recorded in the South African MPAs.

	LL	MAR	MAL	JUT	SMB	TBMNP	HB	BB	DH	SB	GOU	ROB	TK	SAR	BI	AMA	TRA	ALI	STL
Cnidaria																			
Anthozoa																			
Sagartia ornata	○																		
Hydrozoa																			
Obelia dichotoma						○		○							○	○	○	○	
Obelia geniculata		○																	
Pennaria disticha																			○
Annelida																			
Polychaeta																			
Neodexiospira brasiliensis						○							○	○		○			
Crustaceae																			
Cirripedia																			
Amphibalanus venustus														○		○		○	
Balanus glandula	■	■	■	■		■													
Amphipoda																			
Orchestia gammarellus								○											
Mollusca																			
Gastropoda																			
Littorina saxatilis	○																		
Tarebia granifera																			■
Bivalvia																			
Mytilus galloprovincialis	■	■	■	■		■		■	■	■	■	■	■	■	■				
Semimytilus algosus	■	■	■	■		■													

	LL	MAR	MAL	JUT	SMB	TBMNP	HB	BB	DH	SB	GOU	ROB	TK	SAR	BI	AMA	TRA	ALI	STL
Bryozoa																			
Bugula dentata						■			■							■	■	■	■
Bugula neritina		○						○										○	
Cryptosula pallasiana								○											
Watersipora subtorquata	■							■								■			
Chordata																			
Ascidiacea																			
Botryllus schlosseri	■																		
Ciona intestinalis	■																		
Diplosoma listerianum	○							○	○						○	○			
Microcosmus squamiger																○	○	○	○
Rhodophyta																			
Asparagopsis taxiformis																			■
Chlorophyta																			
Cladophora prolifera																	■		

Conversely, the invasive barnacle *Balanus glandula* and the mussel *S. algosus* were not recorded in MPAs outside of the southern Benguela ecoregion. The alien barnacle *Amphibalanus venustus* and the alien ascidian *Microcosmus squamiger* were both found only in MPAs on the east and northeast coasts (Table 3).

3.2.1. Mytilus galloprovincialis

The mussel *M. galloprovincialis* was the most widespread invasive organism in this study, occurring in 13 of the surveyed MPAs. Shore zone was found to be a significant factor in determining the biomass of this species ($F_{2;1950} = 281.24$, $p < 0.001$; Table 4a, Figure 5), with the high-shore supporting a lower biomass than both the mid- and low- shore in all MPAs. The interaction between the shore-zone and MPA variables was significant ($F_{24;1950} = 9.45$, $p < 0.001$; Table 4a), with *M. galloprovincialis* having greater low-shore than mid-shore biomass in MPAs on the west coast and a greater mid-shore than low-shore biomass in MPAs on the southeast coast (Figure 5). In particular, the low biomass in the low-shore on the southeast coast means that the mid-shore supported the greatest overall mean biomass of the mussel. The output further indicated a significant effect of MPA on biomass ($F_{12;1950} = 67.67$, $p < 0.001$; Table 4a). The island MPAs of West Coast National Parks exhibited the highest overall mean biomasses of *M. galloprovincialis*, with Marcus Island supporting the highest biomass in the study (2925.35 ± 359.96 SE $g.m^{-2}$). The lowest biomasses were supported in De Hoop (110.89 ± 76.77 SE $g.m^{-2}$) and Still Bay (140.85 ± 22.47 SE $g.m^{-2}$) MPAs.

Table 4. GLM outputs for invasive species biomass with regards to shore zone (SZ), MPA and the interaction between shore zone and MPA.

	df	Deviance	Residual df	Residual deviance	F	P
a.) *M. galloprovincialis*						
SZ	2	1011788	1947	4750866	281.24	< 0.001
MPA	12	1460640	1935	3290226	67.67	< 0.001
SZ:MPA	24	408141	1911	2882084	9.45	< 0.001
b.) *S. algosus*						
SZ	2	43319	297	227659	30.91	< 0.001
MPA	3	10959	294	216700	5.21	<0.01
SZ:MPA	6	25162	288	191538	5.98	< 0.001
c.) *B. glandula*						
SZ	2	169258	447	501613	84.24	< 0.001
MPA	4	85634	443	415980	21.32	< 0.001
SZ:MPA	8	92257	435	323722	11.46	< 0.001

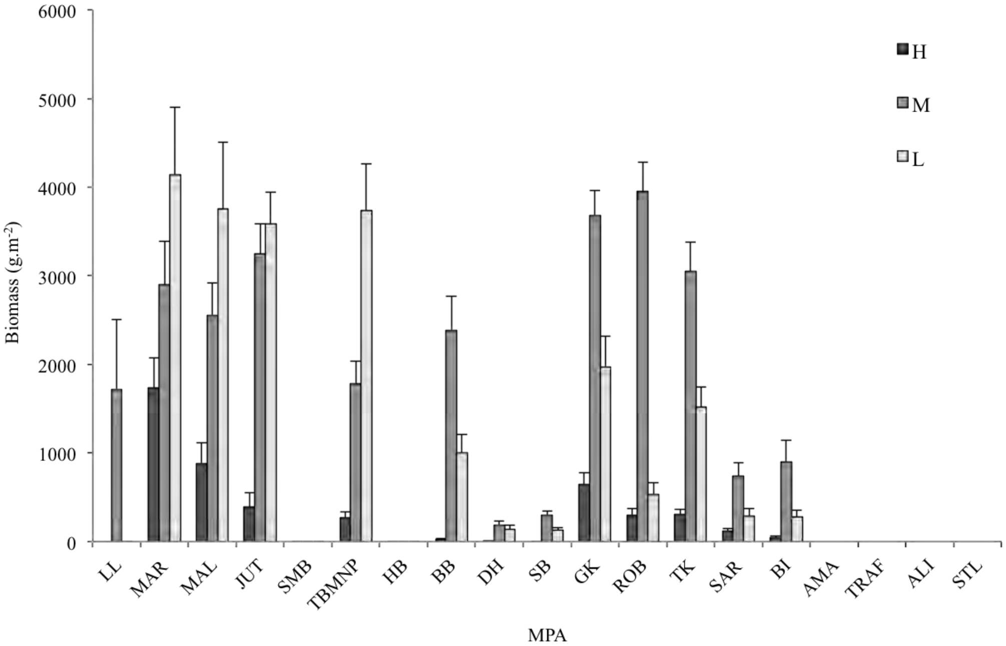

Figure 5. Mean biomass (+ SE) of the mussel *Mytilus galloprovincialis* in the high-, mid- and low-shores of South Africa's MPAs.

3.2.2. Semimytilus algosus

The bisexual mussel *Semimytilus algosus* was observed from all the MPAs on the west coast that contained a rocky shore intertidal habitat. Both shore zone ($F_{2;300} = 30.91$, $p < 0.001$) and MPA ($F_{3;300} = 5.21$, $p < 0.01$) had a significant effect on biomass (Table 4b, Figure 6). The high-shore always supported a lower biomass than the mid- and low-shore. The MPA with the greatest biomass of *S. algosus* was Marcus Island (872.75 ± 92.31 SE g.m^{-2}), while Table Mountain National Park supported a reduced biomass in comparison to that of West Coast National Parks (415.41 ± 86.61 SE g.m^{-2}). There was a strong interactive effect of shore zone and MPA ($F_{6;300} = 5.98$, $p < 0.001$; Table 4b). This is likely driven by the mid-shore biomass being greater than that of the low-shore in the West Coast National Parks island MPAs, but decreasing in Table Mountain National Park, where the low-shore biomass exceeded that of the mid-shore (Figure 6).

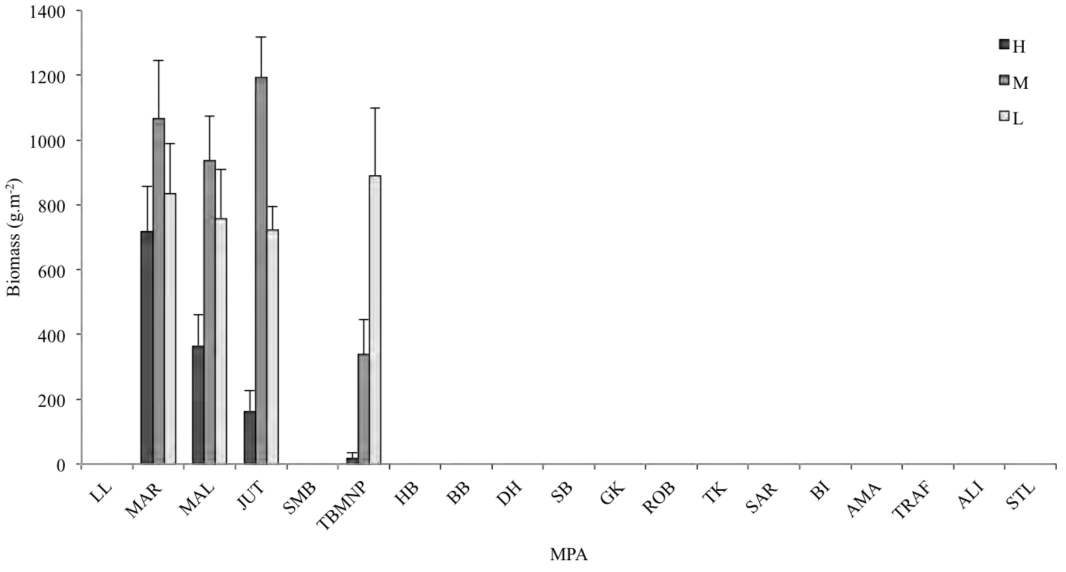

Figure 6. Mean biomass (+ SE) of the mussel *Semimytilus algosus* in the high-, mid- and low-shore of each MPA.

3.2.3. Balanus glandula

The Pacific barnacle occurred in all MPAs on the west coast that contained rocky shore habitat and was prominent in the mid- and high-shore. As such, shore zone had a significant effect on the biomass of *B. glandula* ($F_{2;450} = 84.24$, $p < 0.001$; Table 4c), with the mussel being virtually absent from the low-shore and most prominent in the mid- and high-shore in all MPAs (Figure 7). MPA was also a significant factor in the determination of *B. glandula* biomass ($F_{4;450} = 21.32$, $p < 0.001$; Table 4c). Langebaan Lagoon supported the highest mean biomass (1072.10 ± 247.06 SE g.m^{-2}) and Jutten Island the lowest mean biomass (116.50 ±

30.30 SE $g.m^{-2}$) of the barnacle. There was a significant interaction factor between the MPA and shore zone factors ($F_{8;450} = 11.46$, $p < 0.001$; Table 4c). This is likely due to site-specific factors which caused *B. glandula* to be dominant in the mid-shore in some MPAs and in the high-shore in others (Figure 7). Recently noted as spreading east of Cape Point by Robinson *et al.,* (2015), *B. glandula* is not yet known to occur east of Table Mountain National Park MPA.

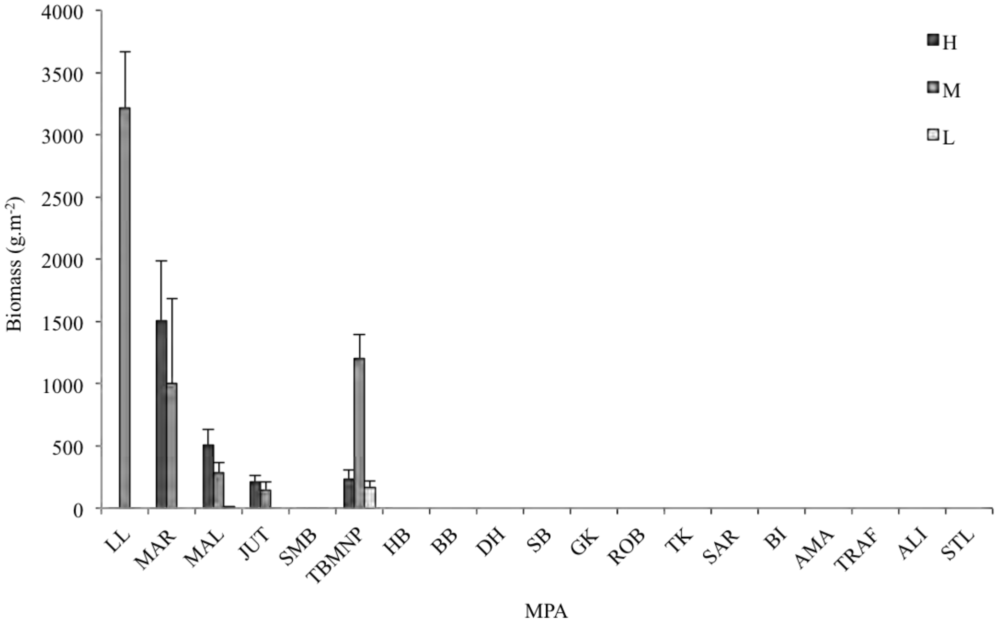

Figure 7. Mean *Balanus glandula* biomass (+ SE) for the high-, mid- and low-shores of all MPAs.

3.2.4. *Sagartia ornata*

Although this anthozoan is no longer listed as invasive because of evidence of declining populations and range restriction (Swart and Robinson, 2015), when sampling was undertaken in Langebaan Lagoon it was listed as invasive and was recorded, adding to the existing data for this alien anemone. *Sagartia ornata* was recorded solely in Langebaan Lagoon MPA, in communities, with many individuals occurring in a small area. The anemones occurred primarily attached to rocky substrata under a thin layer of sediment, with the oral disk protruding the surface. This situation is present on sandy shores of the lagoon as well as in *Spartina maritima* beds. A novel situation was recorded, where *S. ornata* was attached to crevices of a fossilised oyster bed entirely inundated with sand. The mean biomass of *S. ornata* for sites sampled in Langebaan Lagoon was relatively low (208.23 ± 37.46 SE g.m^{-2}).

3.2.5. Littorina saxatilis

In a similar situation to *S. ornata*, *L. saxatilis* was listed as invasive when data collection took place in Langebaan Lagoon MPA and was thus quantified. It has subsequently been listed as a non-invasive alien. This species was only noted from Langebaan Lagoon MPA and occurred in sheltered habitats, primarily towards the head of the lagoon in the cordgrass *S. maritima* beds, as well as amongst *Nanozostera capensis* beds. The mean biomass was low (75.81 ± 12.37 SE g.m^{-2}) and individuals were sparsely distributed within these habitats, despite *N. capensis* being a patchy resource.

3.2.6. Bugula dentata

The dentate moss animal *Bugula dentata* was recorded from MPAs that spread over all three ecoregions covered in this study (Figure 8). In all cases this species was located in the low shore. In Table Mountain National Park, De Hoop and Amathole MPAs it was observed from a very low-shore rocky wall or gully, while in Trafalgar, Aliwal and St Lucia MPAs on the northeast coast, it was found higher in the low-shore, being attached to boulders, rocky walls and overhangs. All biomass recordings were relatively low as it occurred sparsely. However, the frequency with which it was noted increased in the MPAs of the northeast coast. The lowest mean recorded biomass was in Table Mountain National Park at 5.3 ± 5.3 SE g.m^{-2}, whereas the greatest biomass recorded was in Aliwal MPA at 25.5 ± 7.6 g.m^{-2} (Figure 8).

3.2.7. Cladophora prolifera

The invasive green alga *C. prolifera* was noted only in Trafalgar MPA in this study. It occurred in the low-shore, growing on a wave cut rocky platform. The observation consisted of a few individual organisms in the area and the mean biomass was low (70.7 ± 41.2 SE g.m^{-2}).

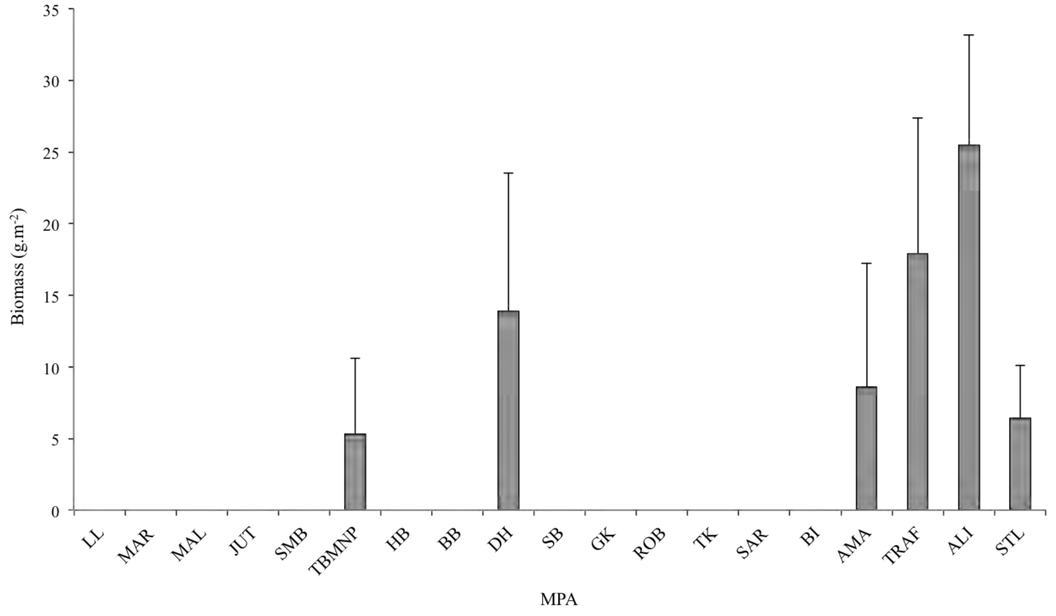

Figure 8. Mean biomass (+ SE) of *Bugula dentata* in the low-shore of all MPAs.

3.2.8. *Tarebia granifera*

This invasive gastropod was recorded from the Mgobezeleni River mouth in Sodwana Bay, St Lucia. It was present on the surface of sandy sediment of the river mouth, as well as buried in the sediment, in high numbers. The highest density recorded was 840 individuals.m^{-2}, with a mean of 155.6 ± 65.97 SE individuals.m^{-2}. This translates to a mean biomass of 202.3 ± 60.6 SE g.m^{-2}.

3.2.9. *Asparagopsis taxiformis*

The plumose red alga *A. taxiformis* was recorded from a low-shore rocky pool at Jesser Point in St Lucia. This species was dominant on much of the shallow subtidal rocky substratum in the area. The mean recorded biomass was 1956.9 ± 604 SE g.m^{-2}.

3.3. EXPANSION OF KNOWN SPECIES RANGES

A number of species exhibited expansion of their known ranges in this study. Four alien species and two invasive species were recorded outside of their known ranges. The hydrozoan *Obelia dichotoma* was described by Millard (1975) as having a range from Lambert's Bay on the west coast to Algoa Bay on the southeast coast. In this study it was found beyond Algoa Bay in the Amathole MPA complex on the east coast and Trafalgar and Aliwal MPAs on the northeast coast.

Knight-Jones and Knight-Jones (1974) recorded the range of the tubeworm *N. brasiliensis* as Cape Town to Port Elizabeth; the present study observed it in Sardinia Bay MPA, but also further up the coast in the Amathole MPA complex, particularly in Gxulu MPA. This was the first recording of the species since that of Knight-Jones and Knight-Jones (1974).

The European shore hopper *Orchestia gammarellus* was recorded from Betty's Bay MPA, amongst driftline kelp. Its previous distribution was Langebaan Lagoon (Barnard, 1951), Table Bay (Mead *et al.,* 2011b) and Knysna Estuary (Griffiths, 1974).

The encrusting bryozoan *Cryptosula pallasiana* was also observed from Betty's Bay MPA. Awad *et al.* (2005) recorded it from Saldanha Bay, while Henschel *et al.* (1990) recorded it from the west of False Bay. It was recorded growing in the microhabitat provided by kelp holdfasts. Prior to this the species had only been recorded from artificial substrata.

Two invasive bryozoans were also recorded in new regions for the first time. The red-rust bryozoan *Watersipora subtorquata* was described by Florence *et al.* (2007) to have a range from Saldanha Bay to False Bay. Malherbe and Samways (2014) recorded it in Betty's Bay MPA, which concurred with this study. The present study also found this species in the Amathole MPA complex, particularly Gxulu MPA, at Kidd's Beach. This is the second record of this species occurring on a natural substratum, and the first that describes the habitat in which the species was observed: with *W. subtorquata* growing on low-shore boulders and amongst kelp holdfasts in Betty's Bay and encrusting low-shore boulders and barnacles in Amathole. The dentate moss animal *Bugula dentata* was recorded over three ecoregions in this study. This species was described as ranging from Cape Point to Durban. Here it was recorded within that range, but also north of Durban, in St Lucia MPA, at Jesser Point.

Addtional species that were recorded in a natural habitat for the first time are *Bugula neritina*, *Diplosoma listerianum* and *Microcosmus squamiger*.

3.4. PREDICTORS OF ALIEN AND INVASIVE SPECIES IN MPAS

3.4.1. Alien species

The optimal tree from the CART analysis contained three terminal nodes and two non-terminal nodes, with a CV error of 0.96. This tree indicated that the factor that plays the biggest role in the prediction of alien species numbers is the size of the port nearest to the MPA (Figure 9). The tree indicates that MPAs with a nearest port that is larger than 0.4 km^2 support more alien species than those near ports that are small. In MPAs close to large ports, regional richness is the next most important factor in predicting the number of alien species. If the regional richness is greater than 951 species per 100km unit of coastline, more alien species are expected (Figure 9).

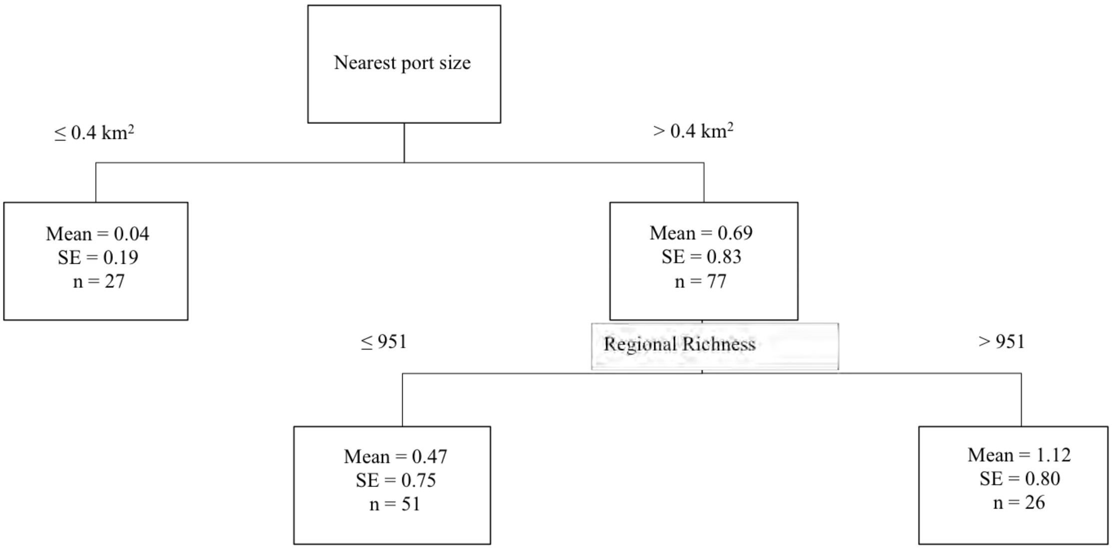

Figure 9. Resultant regression tree of the CART analysis showing the explanatory variables to predict different observation rates of alien species (species found per hour).

3.4.2. Invasive species

The CART analysis produced a tree that contained three terminal and two non-terminal nodes for invasive species. The CV error was 0.84. This tree illustrates the importance of distance to yacht basins for the occurrence of invasive species in MPAs. Greater numbers of invasive species are likely to be found when an MPA is within 3.7 km of a yacht basin. In those MPAs further than 3.7 km from yacht basins, the regional species richness becomes an important indicator of the presence of invasive species. Where the richness per 100 km units of coastline (for benthic invertebrates) is less than 743 species, more invasive species can be expected (Figure 10).

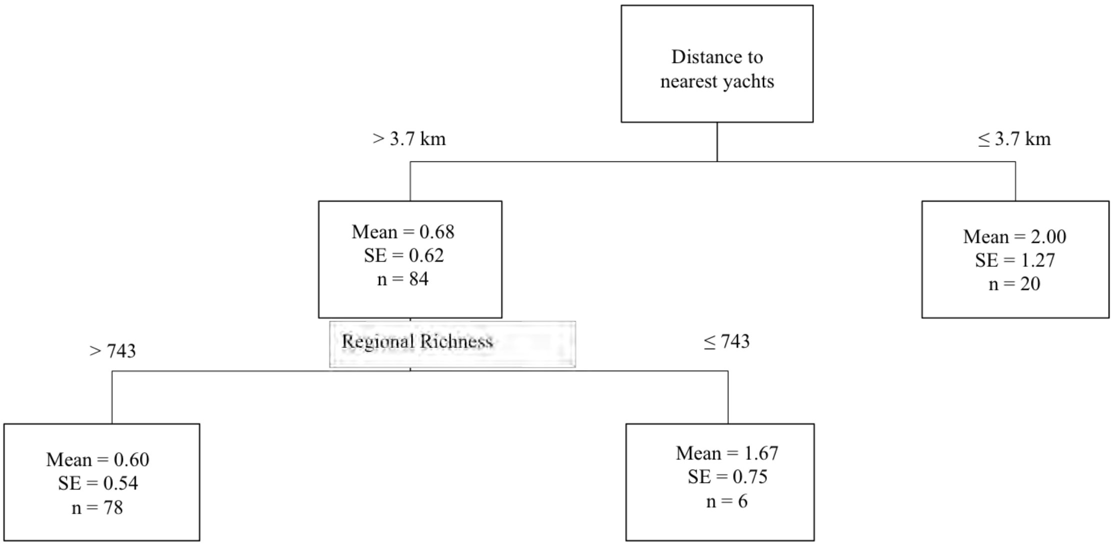

Figure 10. Resultant regression tree of the CART analysis showing the explanatory variables to predict different observation rates of invasive species (species found per hour).

3.4.3. Non-indigenous species

The CART tree that was produced considering all alien and invasive species together indicated that a tree with four terminal nodes and three non-terminal nodes was most suited to the data, with a CV error of 1.03 (Figure 11). The model indicates that when the nearest port to a given MPA is greater than 2.1 km^2 in size and the distance to the nearest yacht basin is less than or equal to 3.7 km, the MPA is likely to contain the most non-indigenous species. Where the nearest port size is smaller than 2.1 km^2, regional richness becomes a predictor, with more NIS expected when regional richness is greater than 1016 species per 100 km coastal unit.

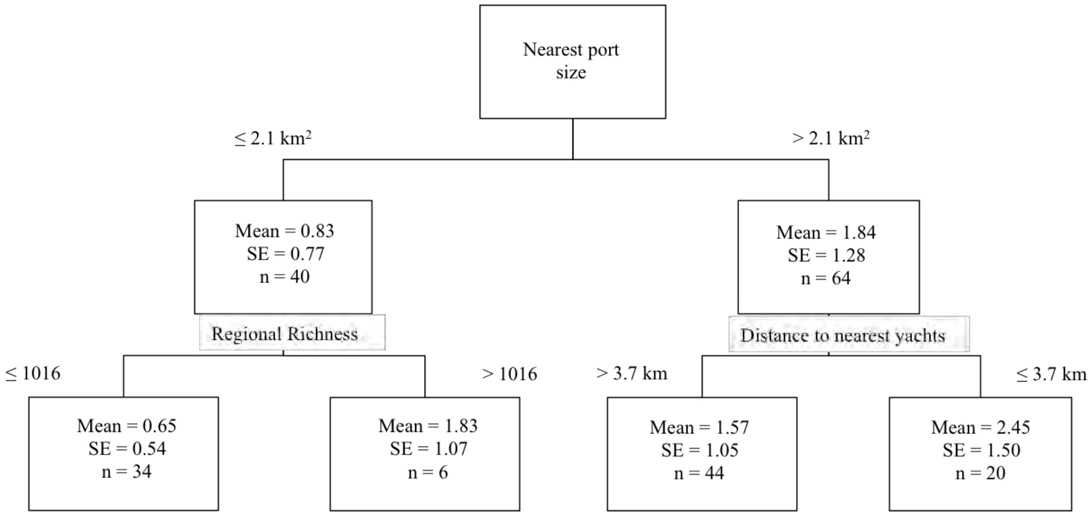

Figure 11. Resultant regression tree of the CART analysis showing the explanatory variables to predict different observation rates of alien and invasive species (species found per hour).

4. DISCUSSION

Marine Protected Areas play a vital role in protecting marine living resources and as such management efforts need to be focused on ensuring that MPAs do not become adverse environments to native biota. Various threats are pertinent to marine biodiversity (Mead *et al.,* 2013), but one that is little documented is that of alien and invasive species in MPAs (Simberloff, 2001). The impacts of alien species on native biota are able to hinder an entire ecosystem's ability to function as it would under natural conditions (Meinesz, 1999) and as such mitigating effects of NIS needs to be made a priority in MPA management plans. This study has addressed the area of marine bioinvasions in MPAs in South Africa by providing baseline information on the presence and distribution of non-indigenous marine species and on the biomass of invasive species in MPAs. Factors that are likely to influence the spread of marine alien and invasive species to MPAs were also identified, thus allowing for the development of guidelines for management authorities with regard to spatial planning of MPAs around the coast.

4.1. MPA SURVEYS

Just over one quarter of the species listed as introduced in Mead *et al.* (2011b) were recorded in the intertidal zone within South Africa's MPA network. This is slightly under half of the species present on the target list (22 out of 52 species). A relatively large proportion of NIS thus occurs within the borders of South Africa's MPAs. Many of the species occur subtidally, and many NIS are found exclusively in harbour environments. Of the 52 species on the target list, 23 had previously been recorded only on artificial substrata in South Africa. During this study, six of these species were recorded on the open coast for the first time. It is also worth noting that seven species on the target list were last recorded over 20 years ago and four species were only recorded once. The fact that these species were not detected during this study could be because they no longer occur along South Africa's coast.

4.1.1. Invasive species not recorded

Certain species that are known as invasive to many regions of the globe were not observed in this study, although they were present on the target list. These include the Japanese oyster *Crassostrea gigas*, the European green crab *Carcinus maenas*, and the lightbulb ascidian *Clavelina lepadiformis*. The location of 23 of the 51 target species exclusively on artificial substrata could be because the majority of species introduced into a new region are not able to spread readily onto the adjacent open coast (Kolar and Lodge, 2001). Port infrastructure provides a variety of novel conditions to biota within the region. The artificial substratum may have a direct effect on the suitability for settlement of sessile organisms (Bulleri and Chapman, 2010). Additionally, the gradient of the substratum is in most cases vertical, such as for jetties, seawalls, pilings and moorings. This is in contrast to the natural rocky geology of the coastline. Fouling assemblages in ports are thus different to those occurring in a natural environment (Bulleri *et al.,* 2005), which allows introductions of opportunists into the area, as there is relatively little competition for space on the substratum. The sheltered conditions provided by harbours can change abiotic conditions such as water temperature, turbidity, sedimentation, shading and oxygen availability. Over time, these conditions can cause species that have settled to undergo physical changes in an adaptive process (Bulleri and Chapman, 2010). For example, the mussel *Mytilus trossulus* is known to reach larger sizes inside than outside harbours but has lower shell mass and weaker byssal threads (Kirk *et al.*, 2007). Adaptations of this nature could be detrimental to species sustainability on the recipient coast. The failure of species to establish along the open coast in South Africa is often attributed to the nature of the country's coastline, which is rugged and exposed to much wave action, with few sheltered bays (Griffiths *et al,* 2009a) and thus limited in habitat mimicking a harbour environment.

Crassostrea gigas

The Japanese oyster *C. gigas* was introduced for aquaculture in 1955. It was not until 2001 that wild populations were recorded (Robinson *et al.,* 2005b). Currently, *C. gigas* is known to have populations in the Breede, Swartkops and Kaaimans estuaries (Keightley *et al.,* 2015). *C. gigas* was not recorded on the open coast in MPAs in this study and is thought to be absent from fully marine environments (Keightley *et al.,* 2015). This has been the case since it was first noted in the wild, probably because of the effect of wave action along the coast, which plays a mediating role in many invasive species' establishment on the coast (Robinson *et al.,* 2005b). Additionally, *C. gigas* populations are thought to have undergone population bottlenecks, attributed to flooding conditions and human exploitation or lack of genetic diversity due to few introduction events, or both (Keightley *et al.,* 2015). Despite the decline in certain populations, estuaries that have previously supported or are supporting oyster mariculture and wild populations are priority areas for monitoring efforts (Robinson *et al.,* 2005b).

Carcinus maenas

The invasive European green crab was first noted in South African waters in 1983 (Griffiths *et al.,* 2009a) and is known to be a voracious predator of various intertidal organisms in regions other than South Africa (Le Roux *et al.,* 1990). Despite being recorded in seven intertidal sites by 1990, it has not extended its intertidal range (Robinson *et al.* 2005a; Griffiths *et al.,* 2009a) and is restricted to sheltered areas such as Table Bay and Hout Bay harbours, where it reaches high densities (Robinson *et al.,* 2005a). Hampton and Griffiths (2007) conducted a study that illustrated *C. maenas'* limited ability to maintain its vertical position on a rocky substratum in flowing water in comparison to the native *Plagusia chabrus*. Furthermore, its limbs are lighter and smoother than those of *P. chabrus* and it appears to be maladapted to wave-exposed environments (Hampton and Griffiths, 2007). There is however concern that this species could spread and invade more sheltered areas, particularly Saldanha Bay and False Bay (Hampton and Griffiths, 2007). Thus *C. maenas* currently appears to be absent from the intertidal zones of South African MPAs but it is known to be present subtidally in Hout Bay and Table Bay harbours and thus is present in the Table Mountain National Park MPA.

Ficopomatus enigmaticus

The tubeworm *F. enigmaticus* is known to construct extensive reefs in estuaries and harbours and, as such, is known as an ecosystem engineer (Schwindt *et al.,* 2004). Its introduction was a result of hull fouling, and has subsequently resulted in its South African distribution extending from Milnerton Lagoon in Table Bay to Kosi Bay (Mead *et al.* 2011a,b). This species is primarily estuarine and has not been observed on the open coast in prior studies or this study. However, it reaches depths of up to 33m in estuaries (Blaber *et al.,* 1974). McQuaid and Griffiths (2014) noted that it provides shelter for infaunal species and has driven a large increase in invertebrate biomass in recent decades in Zandvlei estuary in Table Bay. The lack of record of *F. enigmaticus* in this study is likely due to limited suitable habitat in respective MPAs.

Clavelina lepadiformis

The lightbulb ascidian *C. lepadiformis* naturally occurs in Europe, with an extensive range from Norway to the Mediterranean (Reinhardt and Hudson, 2012). It occurs in harbours and estuaries all around the coast of South Africa (Rius *et al.,* 2014). This species' salinity tolerance is one of the characteristics that have propelled its expansion in recent decades (Millar, 1971; Reinhardt and Hudson, 2012). Narnajo *et al.* (1996) described *C. lepadiformis* as a species that is likely dominant in harbours or areas with transformed substrata, a low rate of water cycling, and excess silting and suspended matter. As such, it is likely that the absence of this species is caused by the unsuitable nature of most of the open coastline around the country, even though populations can be high in number in suitable estuaries and on artificial substrata within harbours.

Discinisca tenuis

Discinisca tenuis, a brachiopod native to Namibia, was first noted in South Africa in Saldanha Bay on cultured *C. gigas* oysters (Haupt *et al.,* 2010). It is yet to have been observed occurring on a natural substratum, but it has reportedly been found on oysters sourced from cultures in Algoa Bay (Mead *et al.,* 2011b). This species was thought to be confined to mariculture facilities but Peters *et al.* (2014) recorded it from St Helena Bay and Saldanha Bay habours, indicating that it is able to settle outside of mariculture facilities. All localities in which it has been found are subtidal and support calm conditions. This suggests that it would not occur in the intertidal zone in wave-exposed environments.

Perna viridis

The Asian green mussel *P. viridis* was first recorded in South Africa from East London harbour (Mead *et al.,* 2011b). This was found to be a misidentification by Micklem *et al.* (in prep) and the species is known now only from Durban harbour. It is native to the indo-pacific region, particularly India and Southeast Asia. *Perna viridis* is widely distributed globally, exhibiting a tolerance of broad environmental conditions and a fast growth rate (Rajagopal *et al.,* 2003). The Asian green mussel is known to coexist with *Perna perna*, but may well be able to outcompete the native species. However, further research is needed on the two species' coexistence (Micklem *et al.,* in prep). Another threat, if this species is able to spread, is the potential for hybridisation with the native *P. perna* (Rajagopal *et al.,* 2006). It is also a potential pest organism in harbours, as it fouls ropes, pylons, hulls and other artificial structures (Rao *et al.*, 1990). This species can be confused with *P. perna*, which ranges in colouration from brown to bright green, whereas *P. viridis* is green. Monitoring personnel will thus need to be trained to distinguish between the two species. The population in Durban harbour is thought to be small, as the native *P. perna* is already established within the harbour (Micklem *et al.,* in prep). This may be preventing *P. viridis* from increasing in number and spreading onto the coast. However, monitoring for *P. viridis* is vital due to its notoriety as a successful invasive species.

4.1.2. MPAs

Langebaan Lagoon, Marcus, Malgas and Jutten Islands (West Coast National Parks)

The MPAs on the west coast of South Africa, which are characterised by the cool temperate conditions of the Benguela ecoregion, had a markedly greater number and higher biomass of invasive species than either the Agulhas or the Natal ecoregions. West Coast National Park includes five MPAs within its boundaries, Marcus, Jutten and Malgas Islands, Langebaan Lagoon and Sixteen Mile Beach. The intertidal zones of the islands are exposed or semi-exposed rocky shores, Langebaan Lagoon MPA contains sheltered sandy habitat and Sixteen Mile Beach is characterised by exposed sandy shores. Saldanha Bay, which houses the three island-associated MPAs and is adjacent to Langebaan Lagoon, is South Africa's only natural sheltered bay, with the vast majority of the coastline being exposed to strong wave action. This is a potential explanation for the lack of spread of otherwise threatening invasive species, such as the green crab *Carcinus maenas* (Hampton and Griffiths, 2007). The calm nature of Saldanha Bay thus makes the translocation between the commercial port, the bay and Langebaan Lagoon viable for introduced species, with Saldanha Bay thought to contain 62 of the 86 introductions in Mead *et al.* (2011b) (Clark and Griffiths*,* 2012). Langebaan Lagoon MPA is a Ramsar site, and thus a wetland of global biodiversity significance

(Robinson *et al.,* 2005a), containing various sensitive biota such as the endangered gastropod *Siphonaria compressa*, which is localised in *Nanozostera capensis* beds (Herbert, 1999). It contained the highest number of alien and invasive species (nine) in this study.

The ability of introduced species to spread from the site of introduction and settle in this region is illustrated by *Sagartia ornata* and *Littorina saxatilis,* which were present in Langebaan Lagoon. The brooding anemone occurred in relatively clumped distributions which is thought to reflect the life history characteristic of birthing live young that brood in the coelenteron (Acuña *et al.,* 2004). In Britain, *S. ornata* is known to occur on rocky shores as well as on kelp holdfasts (Gibson *et al.,* 2001) and thus monitoring of current *S. ornata* populations is essential, given the ideal conditions of South Africa’s cold west coast and kelp forest habitats (Robinson *et al.,* 2004; Swart and Robinson, 2015). The role that *S. ornata* plays as a predator in the environment of Langebaan Lagoon is of interest, as it affects the species assemblage in the immediate vicinity. Polychaetes and amphipods make up the majority of the anemone’s diet in the region (Swart and Robinson, 2015), which makes it unlikely that the endangered mollusc *Siphonaria compressa* will be a component of the feeding regime of *S. ornata*, despite both species occurring in *Nanozostera capensis* beds.

Littorina saxatilis was restricted to sheltered sites at the head of the lagoon where *Spartina maritima* beds occurred. Robinson *et al.* (2004) similarly recorded highest densities in these areas of the lagoon, but with higher densities than found here, with a mean of 433 individuals.m^{-2}. Population numbers appear to be waning, and ecological effects are thus difficult to quantify. The gastropod may be a suitable food source for wading birds that frequent the lagoon. In Britain it is found to occur high on the rocky shore (Gibson *et al.,* 2001) and thus if it were to translocate onto the shores of the west coast it could compete with native *Afrolittorina* species. Both *L. saxatilis* and *S. ornata* occurred inside *N. capensis* beds, which have been in steady decline since 1960 (Pillay *et al.,* 2010). Considering the co-occurrence of *L. saxatilis* and *S. compressa* in the declining *N. capensis* habitat, competition could arise between the two grazers, which would potentially be deleterious to the critically endangered *S. compressa*.

Ciona intestinalis, an ascidian originating in the northern Atlantic, favours settling in dark, calm conditions (Howes *et al.,* 2007). It is a subtidal species that is prominent in harbours around the coast and sheltered bays such as Saldanha Bay, where it has the ability to massively foul harbour ropes, pylons, kelp and mussel farm rafts (Rius *et al.,* 2011). It was recorded in Langebaan Lagoon yacht club, the only recording of this species in this study. Fouling by this species has severe economic implications to mariculture operations within Saldanha Bay (Robinson *et al.,* 2005a). *C. intestinalis* is thought to be widespread in the temperate regions of the globe (Howes *et al.,* 2007). Its presence in Langebaan Lagoon MPA is likely due to the sheltered nature of the MPA, which provides the calm conditions preferred by *C. intestinalis*. Langebaan Lagoon MPA was the only MPA where a yacht club within the borders of the MPA was searched. Most MPAs do not contain yacht marinas within their harbours, but for those that do, one can expect to find *C. intestinalis*. Peters *et al.* (2014) reported that, according to scrape samples taken, *C. intestinalis* supported the highest biomass from the group ascidiacea within Hout Bay harbour. This means that, although this study did not locate the species in Table Mountain National Park MPA, it is present within the MPA borders. The natural intertidal zone is not optimal habitat for the subtidal *C. intestinalis*, but the species can be found all along the coastline in harbours (Mead *et al.,* 2011b) and, as such, monitoring efforts must take *C. intestinalis* into consideration.

Botryllus schlosseri is a colonial ascidian with characteristic star-shaped zooids. It is thought to be confined to harbours and lagoonal areas in South Africa (Griffiths *et al.,* 2009a), ranging from Alexander Bay to Port Elizabeth (Mead *et al.,* 2011b). This species is listed as invasive and, like *C. intestinalis*, was recorded once from Langebaan Lagoon yacht club, but in no other MPAs. However, it must be included in monitoring efforts of MPA authorities. It is of particular risk to the declining *N. capensis* beds in Langebaan Lagoon, as in its natural range it is known to foul eelgrass (Griffiths *et al.,* 2009a).

The intertidal zones of Marcus, Malgas and Jutten Islands within Saldanha Bay were dominated by three invasive species: *M. galloprovincialis*, *S. algosus* and *B. glandula.* The high wave action experienced on these islands may be a factor in the occurrence of fewer alien species here than in Langebaan Lagoon. However, the invasive species that have been able to establish on the west coast have altered the fundamental community composition along the rocky shore (Sadchatheeswaran *et al.,* 2015).

Mytilus galloprovincialis, first noted in 1979 and confirmed in 1984 by Grant and Cherry (1984), has become the dominant bivalve on the west coast through larval spreading by surface currents (Branch and Steffani, 2004). The propagule pressure has been sustained by the cultivation activities in the bay. Traits such as high resistance to desiccation and aeration, fast growth rates and the broadcast of propagules make it an efficient invader, having settled in at least nine regions beyond its native range (Branch and Steffani, 2004). The Mediterranean mussel has spatially transformed the rocky shores by outcompeting the slow-growing ribbed mussel, *Aulacomya atra*, and the black mussel *Choromytilus meridionalis* (Sadchatheeswaran *et al.,* 2015). Individuals of the limpet *Scutellastra granularis* have been recorded as being smaller when settling on the surface of the mussel than when settling on rocky substratum, since displacement from primary rock space means the mussel beds become the only suitable substratum for juveniles to settle on, until they grow too big and are excluded (Branch and Steffani, 2004). Additionally, in exposed areas, *M. galloprovincialis* is a superior competitor to *Scutellastra argenvillei* and outcompetes the native limpet, whereas on semi-exposed and extremely exposed shores there appears to be little competition between the two because of suboptimal conditions (Branch and Steffani, 2004). Positive effects have also been noted as breeding pairs of the near-threatened African Black Oystercatcher, *Haematopus moquini*, have increased because of the plentiful food resource (Griffiths *et al.,* 1992).

The Pacific barnacle *Balanus glandula* was confirmed as present in South Africa in 2007 (Simon-Blecher *et al.,* 2008) and is a species that originates from the northeastern Pacific, preferring cold waters. It has established on three continents, and in two localities outside of South Africa, namely Argentina (Rico and Lopez-Gappa, 2006) and Japan (Kado, 2003). Despite it being noted only in 2007, photographic evidence from Hout Bay harbour confirms that the species has been present since at least 1992 (Laird and Griffiths, 2008). However, it had been confused with the native and similar *Cthalamnus dentata. Balanus glandula* is known to be abundant in the mid- and high-shore on the west coast of North America (Hui and Moyse, 1987), and its prominence in the mid- and high-shore was reflected in this study, with the barnacle being almost absent from the low-shore zone. It has a fast skeletal growth rate, efficient feeding mechanism and high reproductive rate (Simon-Blecher *et al.,* 2008), that allow it to readily establish in any available space in a new environment (Robinson *et al.,* 2015).

de Greef *et al.* (2013) recorded the invasion of another Mytilid bivalve, *Semimytilus algosus*. Populations are thought to have been introduced either from Chile along with oyster spat, or from the extension of the range of the Namibian population of *S. algosus*, which has been present since as far back as 1930 (Lamy, 1931). This small mussel has been recorded to exhibit high levels of recruitment and has been found growing among *M. galloprovincialis*, both in the mariculture ropes and on the rocky shore (de Greef *et al.,* 2013). Its growth among the ropes of mussel rafts inhibits productivity on farms due to their having to be manually removed from the ropes. This also disrupts the grading process of the mussels (de Greef *et al.,* 2013). On the shore, *S. algosus* is thought to exclude all infauna from the beds it creates due to its small interstitial spaces (de Greef *et al.,* 2013).

A contributing factor to the levels of introduction presented by these sites is the spatial location of the MPAs of West Coast National Parks within or adjacent to Saldanha Bay, which contains many vectors of introduced species. The port is South Africa's second-most commercially active, and contains several mariculture operations, including the farming of the invasive Mediterranean mussel *M. galloprovincialis,* and the invasive oyster *C. gigas*. Additionally, within the bay there are three separate yacht basins, one of which falls within the MPA boundaries of Langebaan Lagoon. At Langebaan Yacht Club alone, one alien and six invasive species were observed.

Table Mountain National Park

This situation in Table Mountain National Park is similar to that of West Coast National Parks MPAs, with the MPA being adjacent to the port of Cape Town, and three significant harbours existing in the MPA (Hout Bay, Simon's Town and Kalk Bay) which facilitates intra-regional transfer of species. Table Mountain National Park contained the three dominant west coast rocky shore invaders, as well as the bryozoan *B. dentata* that was recently classified as an invasive species (Robinson *et al.,* in review). This bryozoan is primarily a low-shore and subtidal species, first recorded in South Africa by Busk (1852), and is thought to have been introduced by ballast water or hull fouling (Mead *et al.,* 2011a). *Bugula dentata* has an Indo-Pacific distribution that spans temperate and tropical regions and has been reported from Australia and New Zealand, Japan, Madeira, Brazil and South Africa. This widespread distribution is typical of a species that has long been transported via shipping-related vectors (Mead *et al.,* 2011b). Its presence in the cold waters of the Benguela ecoregion likely indicates the historic prevalence of *B. dentata* as a fouling species introduced through shipping and subsequent intra-regional transfer that has taken place for many years.

Table Mountain National Park had the second most invasive species in the MPAs searched, indicating the expansive distribution of invasive species on the Benguela coast. de Greef *et al.*

(2013) reported a significant spatial segregation between the two invasive bivalves, with *M. galloprovincialis* being present in the mid-shore and *S. algosus* dominating the low-shore zones. This pattern is not apparent from the results here, which record the two species as having similar distributions across the mid- and low-shore, albeit with *M. galloprovincialis* having a higher overall biomass. Whereas the specific effects of *S. algosus* have not been tested, the implication of invasion by two mussel species is that the two naturally-occurring mussels on the west coast, *C. meridionalis* and *A. atra*, will remain restricted to sand-inundated and subtidal areas respectively. Additionally, it is thought that shellfish predator richness could increase due to the new availability of the smaller *S. algosus*.

Balanus glandula was almost exclusively found in the mid- and high- shore zones throughout all MPAs on the Benguela coast, clearly avoiding the lower shore. This was also observed by Laird and Griffiths (2008). *Balanus glandula* and *M. galloprovincialis* could compete directly in the mid-shore zone as they are both primarily mid-shore species, and the result is that *B. glandula* is forced to occur in highest densities in the upper mid and high shore zones. This invasive barnacle has recently spread around Cape Point for the first time and has been observed in False Bay (Robinson *et al.,* 2015), which is cause for concern as it has demonstrated the physiological ability to establish in different conditions. Whereas effects on the native *C. dentata* barnacle on the west coast were limited, this was likely to be only because the native barnacle's distribution was sparse west of Cape Point (Laird and Griffiths, 2008).

The two alien species recorded in Table Mountain National Park were the hydroid *O. dichotoma* and the polychaete worm *N. brasiliensis*. *Obelia dichotoma* is thought to occur all around South Africa's coast (Branch *et al.,* 2010), and is a part of a suite of hydroids that are common fouling species (Mead *et al.,* 2011b). Genetic confirmation is needed to ensure that the species found around the coast is synonymous with that of harbour specimens (Mead *et al.,* 2011b). *Neodexiospira brasiliensis* was originally misidentified as *Spirorbis foraminosus* by Day in 1953 (Mead *et al.,* 2011b). Whereas Knight-Jones *et al.* (1975) reported the distribution of *N. brasiliensis* from Cape Town to Port Elizabeth, this study reports the eastern boundary of this species as the Amathole MPA complex. The effects of this species have not been measured in South Africa. However, in the Netherlands it is an alien species found on *Zostera marina* seagrass and has been found to weigh the leaf blades down into the sediment and inhibit photosynthetic capabilities of the grass (Critchley and Thorpe, 1985; Eno *et al.,* 1997).

Betty's Bay

The Agulhas ecoregion comprises the south and east coasts until where the continental shelf deviates from the coastline. Betty's Bay MPA, part of the UNESCO Kogelberg Biosphere Reserve, has a range of habitats and relatively sheltered areas within the MPA (Tunley, 2009). Two invasive species, *Mytilus galloprovincialis* and *Watersipora subtorquata*, were recorded within the protected area. On the south coast the biomass of *M. galloprovincialis* decreased drastically from that of Table Mountain National Park and West Coast National Park.Shore differences in the biomass of *M. galloprovincialis* in Betty's Bay MPA were apparent, with the mussel appearing to favour settlement in the mid-shore. The native mussel *P. perna* covered the majority of the low shore, likely because of its stronger byssal attachments and thus tolerance to hydraulic stress (Erlandsson *et al.,* 2006). However, *M. galloprovincialis* is able to settle in the mid-shore because of its increased resistance to desiccation (Branch and Steffani, 2004).

Watersipora subtorquata is a species that is cosmopolitan in distribution and is common in harbours on artificial substrata. It is Caribbean in origin and is known to be a highly invasive organism in California, New Zealand and Australia (Floerl *et al.,* 2004; Mackie *et al.,* 2006). In this case it was found under low-shore boulders as well as on *Laminaria pallida* holdfasts within sheltered microhabitats. Malherbe and Samways (2014) reported that *W. subtorquata* occurred in the MPA at higher densities than outside of the MPA. *Watersipora subtorquata* is known to be resistant to a number of biocide paints and is thus a prominent fouling organism. Additionally it is believed to act as a non-toxic refuge for multiple species, exaggerating the risk of hitchhiker introductions or regional transferrals (Floerl *et al.,* 2004).

Betty's Bay and Amathole both supported the highest number of alien species (five). The bryozoan *Bugula neritina* was present in the intertidal zone. This species is also an important fouling organism, and is thought to have its origins in shipping. This species is of some importance in that it produces a secondary metabolite known as bryostatin, which exhibits anti-cancer properties (Mcgovern and Hellberg, 2003). *Bugula neritina* is a globally distributed species because of its fouling tendencies (Ryland and Hayward, 1977). This fouling species could become a cause for concern was it to undergo a change in conditions that facilitated an increase in density of this organism. Alien and invasive species can often remain present in a non-natural range for a long time before undergoing rapid spread and increase in numbers. If this were the case for *B. neritina*, a cause for concern would be the unpalatable nature of its larvae to many generalists (Mcgovern and Hellberg, 2003).

Another early introduction, thought to have occurred via solid ballast (Mead *et al.,* 2011a,b) is the European shore hopper, *Orchestia gammarellus*. It has been noted as common along the driftline in areas of historical introduction (Langebaan Lagoon, Table Bay docks and Knysna estuary). This is the first recording of this species occurring in Betty's Bay. This species has not been evaluated for potential impacts, however they may compete with native shore hoppers for detritus as food and habitat around the driftline. Additional alien species recorded for the first time in Betty's Bay were: *Cryptosula pallasiana*, which was recorded encrusting algae species in the low-shore, *Diplosoma listerianum*, which was recorded as growing on *Ecklonia* holdfasts and *Obelia dichotoma*, which was attached to algae in the low-shore.

De Hoop and Still Bay

De Hoop Nature Reserve is situated 60 km east of Cape Agulhas on the southern coast, with the protected coastline spanning 46 km. The MPA is a no-take zone, which allows no extractive activities, and as such is an important region in conserving the subtidal and intertidal assemblages found in it. *Mytilus galloprovincialis* and *B. dentata* were the two invasive species observed, with *M. galloprovincialis* biomass being markedly lower than elsewhere where it was found. This is a surprising result due to the wavecut rocky platform habitat present in De Hoop MPA (Jackson *et al.*, 1984). The observations from De Hoop's wave-exposed intertidal zone could indicate that the life-history strategy adopted by *P. perna* allows it to be the dominant bivalve in that particular habitat of De Hoop MPA. *Perna perna* invests more energy into producing stronger byssal attachments, while *M. galloporvincialis* invests more energy into reproductive output, which may limit its ability to displace *P. perna* in wave-exposed shores such as De Hoop (Zardi *et al.,* 2007). Biomass is similarly low in Still Bay MPA. However, this is likely due to the majority of the MPA habitat being estuarine and sandy shore. The alien ascidian *D. listerianum* was also present in the low shore of De Hoop MPA. Originally a European species, *D. listerianum* now has a cosmopolitan distribution (Lambert, 2001) and covers a variety of sessile organisms such as mussels, algae and other ascidians. The South African population is thought be made up of multiple clades, with exact origins for different regions unknown (Pérez-Portela *et al.,* 2013). The occurrence of *D. listerianum* in a natural environment is important, due to the fact that it is yet to have been recorded on the open coast. The spread of this species is undoubtedly due to its ability to foul a variety of organisms, including bivalves, algae, bryozoans and other ascidians (Branch *et al.,* 2010). It is possible that this species could occur in other areas not yet surveyed.

Goukamma, Robberg, Tsitsikamma, Sardinia Bay and Bird Island

The pattern of competitive exclusion, as demonstrated by Bownes and McQuaid (2006), between *M. galloprovincialis* and *P. perna* was observed along the south coast until Bird Island MPA. The biomass of *M. galloprovincialis* increased markedly in Goukamma, Robberg and Tsitsikamma MPAs compared to De Hoop and Still Bay. This is likely due to a prevalence of semi-exposed rocky habitat upon which the invasive mussel is able to settle. *Mytilus galloprovincialis* biomass was lower in Sardinia Bay and Bird Island, near the eastern boundary of its range. In 1988 a population of *M. galloprovincialis* was introduced to Port Elizabeth harbour for mariculture purposes (Branch and Steffani, 2004). McQuaid and Phillips (2000) investigated the spread dynamics of *M. galloprovincialis* from Port Elizabeth harbour. The annual average range expansion of *M. galloprovincialis* between 1988 and 1992 was between 55 and 97km northeasterly, and between 12 and 29km southwesterly. It was concluded that wind-driven surface currents transport the larvae. Around Port Elizabeth the winds are predominantly southwesterly and there is thus a net north-easterly movement of propagules. This is likely the means by which the species reached Bird Island in the northeast of Algoa Bay, after propagules were transported from the mussel farm in the bay (McQuaid and Phillips, 2000).

Neodexiospira brasiliensis was the only other non-indigenous species observed in Tsitsikamma, South Africa's oldest MPA. It was found in mid- to high-shore pools growing on blades of the algae *Sargassum incisifolium*.

Likely an introduction resulting from hull fouling, *A. venustus* is a species native to the tropical and subtropical North Atlantic (Mead *et al.,* 2011a,b). It was found to be relatively common under low shore boulders in this study in MPAs from Sardinia Bay northwards to Aliwal, spanning the Agulhas and Natal ecoregions. It occurred together with the indigenous species *Amphibalanus amphitrite* and *Notomegabalanus algicola*, as well as on *P. perna* and

Thais shells. *Amphibalanus venustus* has been introduced to the Mediterranean, the Persian Gulf and much of the Indian Ocean (Biccard, 2012). It is known from harbours around the coast from Cape Town to Mozambique (Biccard, 2012). Studies quantifying its potential impacts have not yet been undertaken.

Amathole

The Amathole MPA complex is made up of the Gxulu, Gonubie and Kei Mouth MPAs, around East London. The MPA spans a variety of habitats, from fine grain sandy beaches to coarse grain sandy beaches, wavecut rocky platforms and rocky headlands (Jackson *et al*., 1984). The proximity to East London harbour of the Gonubie and Gxulu MPAs provides a possible rationalisation for the high number of alien species found within the Amathole complex (five), which was joint highest with Betty's Bay. This harbour contains a yacht marina, and hosts around 1250 ships annually (http://www.ports.co.za).

The dentate moss animal *B. dentata* was only observed once in Gxulu, in a low shore gully. *Watersipora subtorquata* was recorded in this area on the southeast coast for the first time, previously being described as occurring from Saldanha to False Bay (Mead *et al.,* 2011b) and later being found in Betty's Bay (Malherbe and Samways, 2014). This study has found it to occur in Betty's Bay and in Amathole. This species requires monitoring efforts, as it has the potential to be highly invasive, having spread to many cool-temperate regions of the globe since 1980 (Ryland *et al.,* 2009).

Amphibalanus venustus and *N. brasiliensis* exhibited similar patterns to Sardinia Bay, occurring under low-shore boulders and in mid-shore pools on *Sargassum* algae respectively. *Neodexiospira brasiliensis* was found only at Kidd's Beach of Gxulu MPA, while *A. venustus* was relatively common across Gxulu, Gonubie and Kei Mouth MPAs.

Microcosmus squamiger is a species that was observed in Amathole and extended further north to St Lucia, occurring in each MPA surveyed along the way. This species tends to occur in monospecific clumps, and can be difficult to notice as it is covered in an array of fouling epibionts. It is a common harbour species known to settle in natural envrionments in its introduced range (Mead *et al.,* 2011b). The presence of *M. squamiger* in Amathole and the other subtropical MPAs can be explained by the success of certain ascidian species in reproducing and settling in warm water (Stachowicz, 2002). Rius *et al.* (2014) studied four non-native ascidian species and illustrated that all have extended their range regardless of the optimal temperature range of the species. Temperatures of 15 to 25°C, however, favoured *M. squamiger*, with high survival of larvae, stage two and adult individuals, indicating rapid growth and high reproduction potential. The northeasterly MPAs' abiotic conditions appear to favour *M. squamiger*, which explains the ascidian's presence along the east and northeast coasts.

Trafalgar

The short shoreline of the Trafalgar MPA (4.8km) contained more observations of *Bugula dentata* than previous MPAs, but at a low biomass. Additionally, an invasive green alga, *Cladophora prolifera*, was noted from this MPA. This species is thought to have been introduced from the Mediterranean into the southern hemisphere (Hewitt *et al.,* 2004). It is locally common in the low shore of KwaZulu-Natal (Branch *et al.,* 2010) and was observed in the low- and mid-shore zones in Trafalgar MPA.

Aliwal

The warm subtropical conditions appeared to provide optimal abiotic conditions for the invasive *B. dentata*, with the number of observations increasing in Aliwal and St Lucia MPAs. *Bugula dentata* was present on low-shore rocks in Aliwal and on rocky pool walls and overhangs in St Lucia. This species was found slightly higher up in the low-shore zone in the MPAs of the Natal ecoregion and was much more common than in the other ecoregions. In Aliwal it was found in several localities, supporting the highest biomass of this species in this study.

Microcosmus squamiger individuals were recorded occurring in the low shore in rocky environments as well as washed up on the shore. This species was recorded from the east coast Amathole MPA complex to St Lucia on the northeast coast. The potential facilitative effect that warm temperatures may have in the expansion process of certain ascidians by allowing for earlier reproduction provides a rationale for close monitoring of alien and invasive ascidians, particularly within the Natal ecoregion (Stachowicsz, 2002; Rius *et al.,* 2014).

Amphibalanus venustus was found under low shore boulders in the MPA, exhibiting commonality along the east to northeast coasts. This species has not been assessed for potential impacts on native biota, but monitoring is necessary, due to the shared habitat type with species such as *Notomegabalanus algicola* and *Amphibalanus amphitrite*.

Bugula neritina was recorded growing on a sheltered rocky overhang formation of a wavecut platform in Scottburgh, indicating the extensive range of environments that it is able to grow in. Despite having been observed only in a few MPAs, these MPAs are located on the west coast, south coast and northeast coasts, spanning the southern Benguela, Agulhas and Natal ecoregions.

St Lucia

The alien hydrozoan *Pennaria disticha*, which was first observed in 1906 by Warren (1906), was relatively common in the lower littoral rocky pools. It is also thought to occur on ships' hulls (Millard, 1975). The origin of this species is unknown. However, it is widespread globally and genetic analyses are required to determine its native range (Mead *et al.,* 2011b).

The invasive plumose red alga *Asparagopsis taxiformis* in the Natal ecoregion has Atlantic-Mediterranean origins. Gametophyte plants were commonly noted at Jesser Point in low-shore pools attached to rocky substrate at a high biomass, which is similar to the findings of Bolton *et al.* (2011). This species has been recorded as having a large gap in distribution around the coast, with a population in Knysna Lagoon's Leisure Isle boat harbour and specimens being recorded south of Durban some 1000km away at Reunion Rocks and Scottburgh (Bolton *et al.,* 2011). This recent invader could pose a threat to native intertidal and shallow subtidal biota, as it forms dense mats on rocky substrata (De Clerck *et al.,* 2005).

Tarebia granifera is a freshwater gastropod originating from Southeast Asia that has become invasive on three continents, with the first report from Africa in 1999 in northern KwaZulu-Natal (Appleton and Nadasan, 2002). It has since moved northward and is distributed along the eastern half of South Africa, particularly KwaZulu-Natal and Mpumalanga (Appleton *et al.,* 2009). It is a parthenogenetic species that gives birth to fully developed juveniles (Miranda *et al.,* 2011). This, coupled with its temperature (0 – 45°C) and salinity (30 psu for 65-75 days) tolerances is thought to be key to its establishment and spread (Miranda *et al.,* 2010). It was not recorded on the coast, but in the mouth of the Mgobezeleni River, with individuals being either on the sandy substrate or buried under a layer of sandy sediment. The population of the Mgobezeleni estuary experiences variability due to the stochastic environment associated with coastal estuarine environments. However, the adundance (up to 21000 individuals.m^{-2}) (Appleton *et al.,* 2009) and density of *T. granifera* ensures its persistence in these regions (Miranda *et al.,* 2011). The abundance of these organisms may pose a large risk to the nature of the benthos of a variety of waterbodies, and the array of microhabitats it is able to colonise makes it a species that is almost certainly going to spread further north into Zimbabwe and Mozambique (Appleton *et al.,* 2009). In this study the maximum observed number of indviduals was 840 per m^2. This species plays host to the eyefluke, *Philopthalmus gralli* and appears to be replacing the native gastropod *Melanoides tuberculata*, which is the traditional host (Appleton *et al.,* 2009). This eyefluke has been implicated in outbreaks on ostrich farms in Zimbabwe (Mukaratirwa *et al.,* 2005), and the dominance of *T. granifera* as a suitable host could cause the problem to worsen.

4.2. PREDICTORS OF NON-INDIGENOUS SPECIES IN MPAS

Human-mediated spread of alien and invasive species depends on certain factors: 1) the presence of suitable vectors; 2) the frequency of vector movements between invaded and uninvaded areas; 3) the number of propagules released; 4) the congruence of the propagule release and the species' life history; and 5) the availability of resources in uninvaded locations (Buchan and Padilla 1999; Davis *et al.,* 2000; Verling *et al.,* 2005; Floerl *et al.,* 2009). The invasion process is thus stochastic and not easily predictable. Predictions are, however, needed to support management in mitigating invasion events, by focusing on sources of introductions for a given region. This strategy emphasises the importance of managing the relevant vectors and pathways of introduction.

The transition between ports and the open coast is clearly one that not all introduced species are able to make. Peters *et al.* (2014) investigated the assemblages of NIS within harbours of the Western Cape. When compared to the species found in the MPAs of the Western Cape in this study, there is clear overlap in eight species, whereas ten species were found to be unique to harbours and seven unique to the coast. Species that are able to transition between MPAs and the open coast need to be adapted to the highly altered conditions of the harbour environment, as well as to the often more extreme conditions created by the rugged nature of the South African coastline. This, in turn, could mean that the species adapt negatively for settlement on the open coast, particularly in South Africa, where most of the coastline is highly exposed. Thus, species that are able to transition from harbours to natural habitats show strong tolerance of environmental conditions and can be flagged as species that are important in risk assessments in MPAs.

4.2.1. Nearest port size to the MPA

Nearest port size was the most pertinent factor in explaining the observation rates of alien as well as NIS. Floerl and Inglis (2003) suggest that small sheltered harbours are susceptible to fouling by alien and invasive species because of the relatively high concentration of propagules within the harbour. This was also suggested to be the case for harbours of the Western Cape of South Africa by Peters *et al.* (2014). Conversely, Floerl *et al.* (2009) suggested that it is not necessarily the size of the harbour or port that influences the fouling, but rather how busy that harbour or port is, with busier ports being 75% more likely to become invaded than quieter ports. In the case of South Africa, smaller-sized ports are very busy, thus the threshold size of nearest port size need only be greater than 0.4 km^2 when predicting alien species and 2.1 km^2 when predicting all NIS. Floerl *et al.* (2009) suggested that even small, quiet ports played an unexpectedly important role in NIS propagation. In predicting for alien species, nearest port size is followed by regional richness, whereas for both alien and invasive species it is followed by the distance to nearest yacht marina

4.2.2. Nearest yacht basin

Yachts create a suitable habitat for fouling species by often having long layover times, which facilitates the spread of communities within a given harbour (Hewitt *et al.,* 2009). The CART analysis indicated that the highest numbers of NIS could be expected in an MPA when the nearest port size is not small (> 2.1 km^2), and the nearest yacht basin is a short distance away (≤ 3.7 km). The propensity that MPAs close to ports and yacht basins have for alien and invasive species reflects what is known in the literature regarding these factors as drivers of NIS introductions (Floerl & Inglis, 2003; Floerl *et al.,* 2004; Floerl and Inglis, 2005; Floerl *et al.,* 2009; Jurk, 2011; Peters *et al.,* 2014). Given that the connectivity of transport hubs along the coast is a significant factor in the spread of NIS, as outlined by this study as well as Floerl *et al.* (2009), South Africa's coastline is at high risk of the propagation of satellite populations of introduced species; the MPAs that were nearest to yacht basins (i.e. the West Coast National Park MPAs, specifically Langebaan Lagoon MPA, and Table Mountain National Park MPAs) supported more invasive species.

4.2.3. Regional richness

Along the coast of South Africa, regional richness is lowest in the west, and spikes in the transition area at False Bay, staying relatively high until Durban, before decreasing towards the northeastern border of the country (Awad *et al.,* 2002). The maximum regional richness occurred in Port Elizabeth, with 1141 species. The hypothesis of biotic resistance states that ecosystems with a high biodiversity are more resistant against invasion by non-native species than ecosystems of low biodiversity (Jeschke *et al.,* 2012) and species richness is used as a measure of ecosystem biodiversity in many related studies (Jeschke *et al.,* 2012). Decreased invasion success with increasing native species richness has been reported by studies (Stachowicz *et al.,* 1999; Kennedy *et al.,* 2002), as has increased invasion success with increasing native richness (Stohlgren *et al.,* 1999; Dunstan and Johnson, 2004). This has been termed the 'invasion paradox' (Fridley *et al.,* 2007), with experimental studies of this phenomenon being biased towards the former and observational studies being biased towards the latter. For marine benthic invertebrates there is more evidence for the former hypothesis – decreased invasion success with increasing native species richness (Jeschke *et al.,* 2012). There is evidence that, at large scales, many extrinsic and covarying environmental factors play a role, not accounted for in localised experimental studies. These factors cause the observed positive relationship between native and invader richness (Stachowicz and Byrnes, 2006).

Space is seen as the most important resource for sessile marine invertebrates (Stachowicz *et al.,* 1999; Stachowicz *et al.,* 2002), and the relationship between open space and invasion success is a strongly positive one (Stachowicz and Byrnes, 2006). This is supported by the CART analysis of invasive species in MPAs, which identifies areas of low regional richness that are close to yacht basins as priority areas, as they are likely to have high numbers of invasive species. CART outputs further indicated that MPAs with areas of high regional richness supported elevated numbers of alien species and NIS. Areas of inoculation of NIS, such as harbours and ports, are prevalent in both species-rich and species-poor regions around the coast. The success of NIS in both regions is highlighted by the fact that nearest port size and distance to nearest yachts preceded regional richness as factors predicting for NIS in the CART analysis.

Drake and Lodge (2004) conducted a study that considered the role that transport hubs play as inoculation hotspots in the spread of alien and invasive species. They found that decreasing the per-ship chance of causing inoculation of NIS had more impact on decreasing biotic homogenisation than removal of important ports that are key centres for the global spread of NIS. The primary area for effective management response is thus that at which non-native species are introduced, such as busy international ports. In order to do this, effective and ongoing monitoring strategies need to be implemented so that early detection is possible and the option to quarantine an area and carry out a local eradication is open (Bax *et al.,* 2002). Subsequent inter-regional monitoring is vital. The practical implications for MPA management are that MPAs should be constructed far away from ports, and never with a yacht marina within their borders or adjacent to the MPA. MPAs that do not currently fulfill these conditions are priority for monitoring efforts. Future declarations of MPAs need to include these issues as restrictions. A proactive approach is needed to set up monitoring programmes for each MPA in order to maintain good knowledge of the biotic status of the respective MPA.

5. CONCLUSION

This has been the first systematic assessment of NIS within the MPAs of South Africa, with 17 of 19 MPAs sampled containing NIS in their borders. This study offers the first record of six alien species occurring in a natural environment outside of a harbour, as well as recording range expansions for six NIS species along the coast. Despite the baseline nature of this intertidal survey, all MPAs were found to be invaded to some extent, apart from Sixteen Mile Beach and Helderberg MPAs. This is likely caused by the fact that the majority of the target species inhabit rocky substrata and these MPAs consist of sandy shore habitats. This study thus forms a knowledge base of NIS within MPAs in South Africa, supporting management action by allowing prioritisation of species for monitoring efforts.

There appears to be a variety of different factors influencing the spread of alien and invasive species to MPAs, but the most important concept to emerge from this study is the facilitative role of transport hubs (i.e. ports/harbours and yacht marinas) in the introduction of NIS. As such, a primary consideration in diminishing NIS spread in MPAs is the spatial location of the MPA relative to the nearest port and yacht marina. Monitoring efforts should prioritise MPAs that contain or are close to large harbours and ports, especially those that contain yachts, because of their increased risk of invasion by NIS. MPAs to be declared in the future should be situated as far away from large ports and yacht marinas as reasonably possible.

To prevent the spread of NIS into MPAs, it is imperative that mitigation action is taken. This could entail exerting restrictions on gear used by vessels that could contribute to the spread of NIS. For example, in certain French MPAs authorities provide floating, anchored buoys for recreational and commercial craft, and restrict the use of fishing nets that are known to spread the invasive alga *C. taxifolia* (Simberloff, 2000). Publicity in these areas is also a plausible management option, such as emphasising the importance of correct practice for use of nets and hull cleaning and anti-fouling procedures.

National authorities need to adopt a cooperative approach that includes port surveys and subsequent risk assessments to mitigate the threat of marine NIS. Further research efforts are important in ensuring that risk assessments are effective, as proportionally few NIS have been assessed for their potential impacts (15 out of 89 NIS). This is information that is essential for the efficacy of risk assessments. Continuous dissemination of information gained from port surveys and risk assessments among researchers, management authorities and MPA staff is required as new findings come to light. The risk assessment protocol should be expanded and implemented for each MPA for NIS once thorough surveys are completed, as this is an effective tool for quantifying and combating the threat of NIS. An important step in the success of the above is enabling an accessible flow of information related to NIS. The South African Biodiversity Institute is currently the primary curator and management body of marine NIS. Within MPAs, this falls to the relevant provincial authority (i.e. Cape Nature, Eastern Cape Parks and Tourism Agency, Ezemvelo KZN Wildlife). There is much dissemination of information and training that is needed from the top. For example, rangers in the MPAs need to be trained in the threats and identification of NIS. This is challenging, as there is a lack of taxonomic expertise in South Africa, however it is an important step. While iSpot can be a very useful tool for monitoring species ranges, this should be prioritised, before relying on open source databases such as iSpot.

Managing areas where invasive species have already become well established is a difficult, yet important challenge that needs to be considered holistically by governmental, conservation and MPA authorities. In a country such as South Africa where there are high levels of unemployment and an excess of able-bodied working class citizens, governmental initiatives that require high numbers of people to do physical labour are plausible management options, such as the Working for Water and Working on Fire initiatives in terrestrial invasion biology. This has never been attempted explicitly in marine invasion biology, however the opportunity for this exists. This sort of task team establishment will not only facilitate a means by which we can attempt to tackle highly invaded areas, but also provide us with a rapid response option if a new invader is discovered or if a current NIS is discovered to be expanding its range. If such an effort is to be an efficient use of precious financial resources, it will have to be carried out in a responsible manner, whereby the employees share an understanding of marine invasions and an appreciation for the coastal ecology. The management of a programme such as this is in itself a vital step, so as to ensure the work is carried out correctly and efficiently.

For certain edible species, a potential harvesting programme might be considered. Rural communities along the east coast of South Africa have harvested the indigenous brown mussel as a food source for hundreds of years. Certain communities, with the help of conservation and governmental initiatives and funding, have even used this as a baseline for creating a sustainable blue economy, from which community empowerment and alternative livelihoods have stemmed (Harris *et al.,* 2003; Napier *et al.,* 2005). The abundance of edible invasive mussel presents an opportunity to establish a comparable programme along the coast in the range of invasive species such as *Mytilus galloprovincialis*, whereby communities are educated through focus groups on the subject of marine invasions, and the harvesting of these species for food and alternative livelihood options. This has been considered by Robinson *et al.,* (2007) for three areas in the Northern Cape and could be explored along the entire range of *M. galloprovincialis*, as site specificity may render it viable in certain areas but not in others.

The findings of this study have bearing on spatial planning of future MPAs and extension projects of current MPAs. Whereas MPA borders can restrict anthropogenic activities, these borders do not restrict alien and invasive species. As such, the proximity of risk activities to MPAs is an important consideration in curbing the effects of invasion within MPAs. By using the baseline provided by this study and further monitoring efforts, MPA management should work with relevant authorities to prevent unnecessary introduction of harmful NIS into these vital areas of conservation.

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APPENDIX I

Table 5. Target list of species for MPA surveys.

Species name and broad taxonomic group	Origin	SA Distribution
Porifera		
Suberites ficus	NE Atlantic and Mediterranean	W Coast
Cnidaria		
Anthozoa		
Sagartia ornata	Europe, Mediterranean	Saldanha Bay
Hydrozoa		
Obelia dichomata	Unknown	Table Bay harbour, Durban
Obelia bidentata	Unknown	Lambert's Bay to Algoa Bay
Obelia geniculata	Europe, Mediterranean	Entire coast
Coryne eximia	N Atlantic, Pacific	Table Bay harbour
Pachycordyle navis	Europe, Mediterranean	Table Bay harbour
Pennaria disticha	Unknown	Durban to Mozambique border
Annelida		
Polychaeta		
Dodecaceria fewski	Pacific N America	Table Bay docks
Ficopomatus engimaticus	Australia	Cape Town to Kosi Bay
Janua pagenstecheri	Europe	Cape Town to Durban
Alitta succinea	Europe	Mossel Bay to Durban
Neodexiospira brasiliensis	West Indies, Brazil	Cape Town to Port Elizabeth
Polydora hoplura	Europe, Mediterranean	Saldanha Bay to Plettenberg Bay
Crustacea		
Cirripedia		
Amphibalanus venustus	Tropical N Atlantic	Hermanus to Mozambique
Balanus glandula	Pacific N America	W Coast
Isopoda		
Dynamene bidentata	Europe	Port Elizabeth
Paracerceis sculpta	NE Pacific	Port Elizabeth
Sphaeroma serratum	Europe	Durban Bay
Sphaeroma walkeri	N Indian Ocean	KZN
Amphipoda		
Orchestia gammarellus	Europe, Mediterranean	Langebaan Lagoon, Table Bay, Betty's Bay, Knysna Lagoon
Platorchestia platensis	Unknown	Gansbaai
Decapoda		
Carcinus maenas	Europe, Mediterranean	Saldanha Bay, Table Bay harbour, Hout Bay harbour
Xantho inicus	Europe, Mediterranean	Kleinsee

Mollusca		
Gastropoda		
Littorina saxatilis	N Atlantic	Langebaan Lagoon, Berg River Eastuary, Knysna Lagoon
Tarebia granifera	SE Asia	KZN
Thais blanfordi	Tropical Indo-Pacific	Durban
Thais tissoti	Tropical Indo-Pacific	Durban
Bivalvia		
Crassostrea gigas	Japan, NW Pacific	S Cape estuaries
Mytilus galloprovincialis	Atlantic	Alexander Bay to East London
Ostrea edulis	Europe, Mediterranean	Alexander Bay
Perna viridus	SE Asia	East London harbour
Semimytilus algosus	Pacific S America	Alexander Bay to Cape Town
Brachiopoda		
Discinisca tenuis	Namibia	St Helena Bay, Saldahna Bay, Algoa Bay
Bryozoa		
Bugula dentata	Indo-Pacific	Cape Town to Sodwana Bay
Bugula flabellata	Unknown	Port Nolloth to Plettenberg Bay
Bugula neritina	Unknown	Port Nolloth to Durban
Conopeum seurati	Europe	Saldanha Bay, False Bay
Cryptosula pallasiana	Europe	Saldanha Bay, Table Bay harbour, False Bay, Betty's Bay
Watersipora subtorquata	Caribbean	Saldanha Bay to False Bay, Betty's Bay, Christmas Rock
Echinodermata		
Tetrapygus niger	W Coast S America	Alexander Bay
Ophiactis savignyi	Indo-west Pacific	Durban Bay
Chordata		
Ascidiacea		
Botryllus schlosseri	Europe	Alexander Bay to Port Elizabeth
Ciona intestinalis	N Atlantic	Entire coast
Clavelina lepadiformis	NE Atlantic and Mediterranean	Saldanha Bay to Durban
Diplosoma listerianum	Europe	Alexander Bay to Durban
Microcosmus squamiger	Australia	Mossel Bay to Sodwana Bay
Styela plicata	W Pacific	Mossel Bay to Durban
Rhodophyta		
Schottera nicaeensis	Europe	S KZN
Asparagopsis armata	Australia and New Zealand	Cape Town to Port St Johns
Asparagopsis taxiformis	N Atlantic and Mediterranean	Cape Town to Sodwana Bay
Chlorophyta		
Cladophora prolifera	Mediterranean	Trafalgar, Kosi Bay