Effects of protection and environmental factors on rock lobster, abalone, and giant periwinkle abundances in the Table Mountain National Park Marine Protected Area

Kathryn Gardner
Supervisors: Prof Colin Attwood and Dr Alison Kock

DST/NRF Centre of Excellence at the
Percy Fitzpatrick Institute of African Ornithology
University of Cape Town
Rondebosch 7701
South Africa

August 2021

Submitted in partial fulfillment of the requirements for the degree of
Master of Science in Conservation Biology
in coursework and dissertation

Plagiarism Declaration

1. I know that plagiarism is wrong. Plagiarism is using another's work and to pretend that it is ones own.
2. I have used the Conservation Biology Journal format as the convention for citation and referencing. Each significant contribution to, and quotation in, this project from the work, or works of other people has been attributed and has cited and referenced.
3. This project is my own work. I have not allowed, and will not allow, anyone to copy my work with the intention of passing it off as his or her own work.
4. I acknowledge that copying someone else's assignment or essay, or part of it, is wrong, and declare that this is my own work.

Signed:
Kathryn Gardner

Signed by candidate

Date: 01/08/2021

Acknowledgements

I am immeasurably grateful to my supervisors Prof Colin Atwood and Dr. Alison Kock. Thank you Colin for your support and guidance with the design of my research questions and the statistical analysis. Thank you Alison for allowing me the opportunity to do this study. Thank you for your support and guidance with my writing and for the encouragement when the data seemed too floored to get the best of me. Thank you to both of you for your patience and understanding through the extended process of writing this dissertation. Thank you to Barry Clark and Ken Hutchings for your intellectual input and to the team of Anchor Environmental for the data collection in 2019, and to Yves Lechanteur for use of the baseline survey data from 2000 and 2003. Thank you to South African National Parks (SANParks) for allowing me access to the data collected in 2019 and to The WWF Table Mountain Fund for financing the data collection through a grant to Dr Alison Kock for the project, "Re-assessing the status of biodiversity, exploited marine species and resource use in the Table Mountain National Park marine protected area".

I am grateful to Dr. Susie Cunningham for your leadership, motivation and care throughout the course. You did not hesitate to go out of your way to inspire and assist. Thank you to Claire Spottiswoode for your guidance and words of reassurance during the proposal planning. To Prof. Peter Ryan and the other conservation biology course leaders, thank you for allowing me this opportunity to learn and for your investment in my education and future. To Hilary Buchanan, thank you for being the proverbial 'fairy godmother' of the CB class. You were always available to enquire over, arrange and sort out our affairs. Thank you in particular for your help with the administration processes of this extended degree. To the CB class of 2019/2020, thank you for an amazing year and engaging with me so passionately on so many topics, I look forward to watching you change the world.

To Louise and Mark; thank you for your endless faith in my capabilities and your deep care. You are a source of inspiration and comfort to me and I truly treasure your friendship. Kate and Ceci, thank you. Your passion, sound judgment and wise advice have inspired and motivated me in both completing this degree and life in general. Thank you for sticking by me through many a crisis.

Pier, Thank you for supporting me through the final stages of the write up.

Dad and Ally. If I had asked you to read 100 drafts, I know you would have. Thank you dad for your understanding, patience, and unwavering support. Thank you for my stellar education that has opened doors and lead me here. This manuscript is as much your accomplishment as it is mine. Ally, you have been an irreplaceable source of joy and companionship. Your determination and humanity humble me.

To my friends and family, without you, this manuscript, or my sanity, would not exist; thank you

Abstract

The Table Mountain National Park Marine Protected Area (TMNP-MPA) was established in 2004 to restore and protect the Cape Peninsula's biodiversity, including the populations of exploited macro-invertebrate species. Scientific publications on MPAs support the idea that biodiversity protection is well served by MPAs, particularly no-take MPAs. Focusing on west coast rock lobster, abalone and giant periwinkle, historically the three most important invertebrate resources of the region, this study assesses the effectiveness of spatial regulations in the TMNP-MPA. Three comprehensive peninsula-wide SCUBA surveys were conducted in 2000, 2003 and 2019. Patterns in the abundance of the three species were analyzed using generalized-linear models (GLM) to explore the effects of the TMNP-MPA and no-take zones within, whilst accounting for habitat, depth, species interactions, and the physical protection offered by False Bay. Overall, the rock lobster abundance around the Cape Peninsula decreased since the implementation of the TMNP-MPA, however, to a lesser degree than the dramatic overall decline of the rock lobster population in South Africa over this time. This decrease is possibly due to increased illegal harvesting of adults and juveniles and increased predation from recovering fish populations within TMNP-MPA. However, rock lobster abundance did respond positively to the length of protection in no-take zones, suggesting that the enforcement of no-take zones within the MPA was effective. The beneficial effects of the no-take zones are likely insufficient to compensate for increased harvesting in adjacent areas within the MPA but prevented a greater decline in rock lobster. No change in abalone abundance was detected over the years in the TMNP-MPA or within no-take protected zones. The regional abalone population has declined drastically over a similar period due to poaching. Effective policing has likely prevented the abalone within the MPA from following suit. Giant periwinkle abundance increased since the establishment of TMNP-MPA. However, it is unknown if this pattern reflects the regional giant periwinkle population, so it cannot be determined if the increase is a direct result of the MPA. However, the giant periwinkle abundance had not benefited from the no-take zones, suggesting general harvest restrictions in TMNP-MPA are affording them sufficient protection, or that the greater population is increasing. A combination of environmental factors, such as warmer water temperatures and reduced nutrients, could explain the decreased abundance of rock lobster in False Bay, compared to those along the Peninsula's west coast. Predation by rock lobster could explain the opposite pattern found in both the giant periwinkle and abalone that were more common in False Bay. Expected abundance patterns based on the habitat preferences of each species, associated with water depth, the presence of sand, and kelp and urchin density were found. The creation of the TMNP-MPA, with its many and varied no-take and harvest zones provided an excellent opportunity to test the effectiveness of no-take spatial protection in a complex marine community and in the vicinity of a heavily exploited coastal zone near a metropolitan setting. This is especially valuable for macro-invertebrates, which are not commonly the focus of MPA studies in South Africa. This study supports the use of MPAs as a protection measure for over-exploited macro-invertebrates. The extent of the success of this protection is evident by way of comparison with the magnitude of declines elsewhere. As both rock lobster and abalone fisheries are heavily plagued by poaching, the impact of no-take zones and the enhanced policing brought by the TMNP-MPA as a whole, likely helped to buffer the declines of rock lobster and abalone, respectively.

Key words

Marine invertebrates, Marine Protected Area, Abalone, Rock lobster, Giant periwinkle, Table Mountain National Park, Harvesting, Poaching

Introduction

Cape marine resources

The Cape Peninsula in South Africa is renowned for its exceptional biodiversity (Awad et al. 2002; Griffiths et al. 2010). This marvel is extended from the land into the surrounding marine environment. Two great oceans, the Atlantic and Indian, unite at the tip of South Africa (Figure 1), forming two distinct marine ecoregions, the Southern Benguela Ecoregion to the west and the Agulhas Ecoregion to the south-east (Sink et al. 2012). The Southern Benguela Ecoregion is characterized by cool, nutrient-rich waters, and the Agulhas Ecoregion by warmer nutrient-poor waters (Griffiths et al. 2010; Sink et al. 2012). The overlap between the two marine provinces is positioned between Cape Point and Cape Agulhas (Hockey & Buxton 1989). This distinctive setting supports numerous species, many of which are endemic to the region (Centre for Marine Studies 2001; Scott et al. 2012).

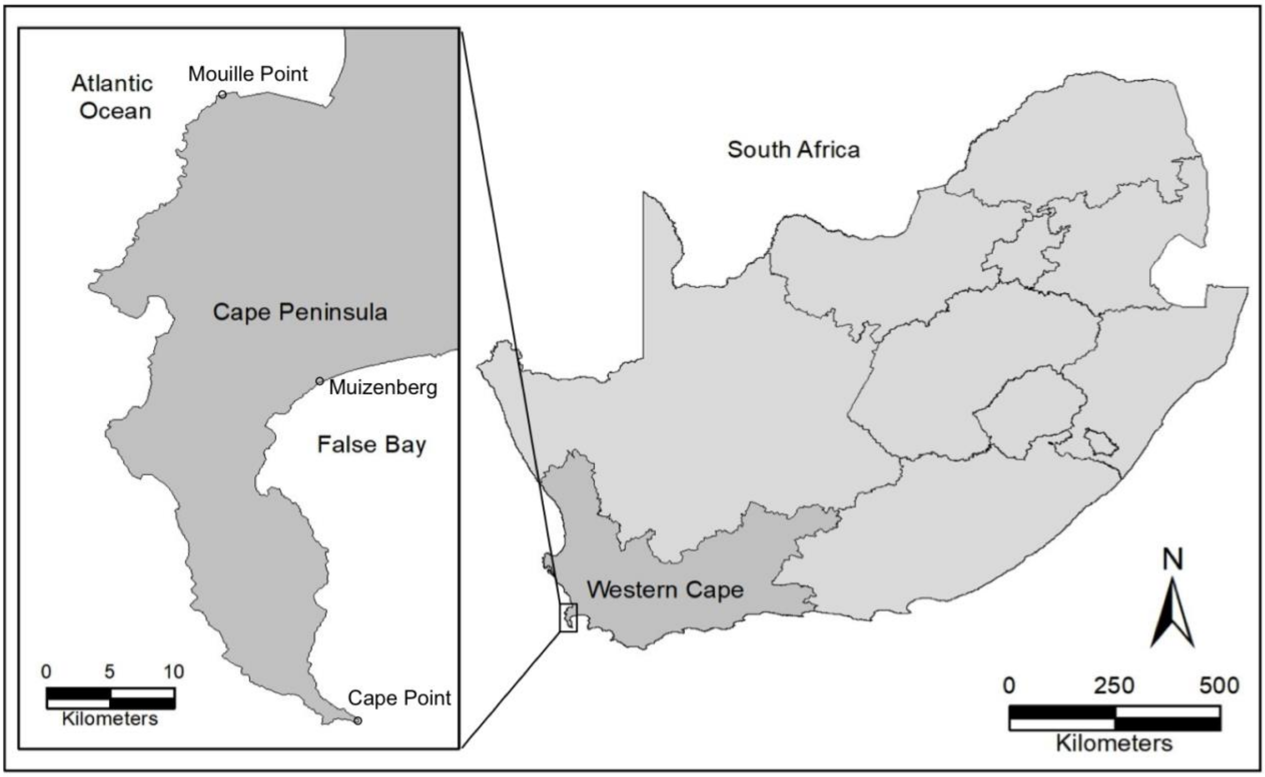

Figure 1. This study was conducted along the Cape Peninsula in the Western Cape province of South Africa from Mouille Point to Muizenberg.

Many recreational, subsistence, and commercial fishers harvest natural resources around the Cape Peninsula for food or livelihoods (Griffiths et al. 2004; Pfaff et al. 2019). The most commonly targeted marine invertebrate species around the Cape Peninsula are the South African abalone (*Haliotis midae*), West Coast rock lobster (*Jasus lalandii)*, giant periwinkle (*Turbo sarmaticu*s), the Cape Hope squid (*Loligo reynaudii*), the common octopus (*Octopus vulgaris*), white mussels (*Donax serra*), and the Cape rock oyster (*Striostrea margaritacea*), all to varying degrees (Pfaff et al. 2019; DFFE 2020). Rock lobster, abalone and giant periwinkle are the most abundant herbivore species found within the kelp forests around South Africa (Anderson et al. 1997). Kelp species (*Ecklonia maxima, Macrocystis pyrifera,* and *Laminaria pallida*) and the Cape sea urchin (*Parechinus angulosus)* are two other important elements of the coastal invertebrate communities which are harvested (Anderson et al. 1997).

Study Species and Harvesting Histories

Rock Lobster

The West Coast rock lobster, referred to as rock lobster hereafter, is a marine crustacean with a range extending from Walvis Bay, Namibia, to Port Elizabeth, South Africa, where they are prevalent in subtidal zones at depths less than 30 m (Jones 2008) . They can reach 300 mm in carapace length and are slow growing (Jones 2008). Found in groups, they feed on urchins, mussels and barnacles (Mayfield & Branch 2000; Mayfield et al. 2001) and are preyed on by fish, small sharks, octopus, and seals (Jones 2008). Rock lobsters with a carapaces of 80 mm are five to seven years of age if male and 12 years of age if female (Jones 2008). The current minimum legal size for harvesting is a carapace length of 75 mm (Jones 2008).

Rock lobsters are under heavy harvesting pressure in South Africa, and their population is considered heavily depleted (DFFE 2020). Harvesting began in the late 1800s and peaked at 18 000 tonnes in the 1950s (DFFE 2020). Within a decade, due to more efficient traps and motorboats, this yield decreased to 10 000 tonnes and has continued to decrease since (DFFE 2020). Two rock lobster sanctuaries were established along the Cape Peninsula before 1976 to mitigate declining stocks: namely Table Bay and Kommetjie rock lobster sanctuary. However, their efficacy has been questioned (Centre for Marine Studies 2001). A minimum size limit (carapace length of 89 mm) was implemented in 1979, and in the 1980s, a total allowable catch (TAC) system was implemented (Figure 2; DEFF 2020). In 2001, their harvestable biomass was estimated to be only 4% of its pre-exploitation levels (Centre for Marine Studies 2001). Commercial yield has not exceeded 3 000 tonnes since 2005 (Figure 2; DEFF 2020). Although the rock lobster population is estimated to be only 1.8% of pre-fished levels, this species continues to support a fishing industry worth R500 million per annum (DFFE 2020). The rock lobster range is divided into five fishing super-zones (DFFE 2020). According to catch per unit effort (CPUE) data from the fishery-independent monitoring survey (FIMS) and commercial catch-statistics, the population in the two southern-most super-zones, closest to the TMNP-MPA, has decreased by 55% between 2000 and 2016 (DFFE 2020). Apart from the commercial, recreational and subsistence harvest, it is the illegal harvest of rock lobster that is of concern to managers (Brill & Raemaekers 2013; Okes et al. 2018; DFFE 2020). For recreational and subsistence fishing, there is a bag limit of four rock lobsters per person per day, which may only be harvested from 8am to 4pm, only during the summer months on specific days and without the use of traps or SCUBA. The minimum legal harvest size is set as 80 mm carapace length for recreational and subsistence harvesting.

Abalone

The South African abalone, commonly referred to by its Afrikaans name perlemoen, is a species of marine gastropod endemic to South Africa (Rhode et al. 2017). They have a disjunct distribution between St Helena Bay on the West Coast to just north of Port St Johns on the East Coast of South Africa, divided into a western and eastern population (DFFE 2020). They favour rocky reefs and kelp beds in water less than 5 m deep but occur down to 20 m (DFFE 2020). As broadcast spawners, they aggregate in large groups (Jones 2008). Abalone species have a maximum dispersal distance of several kilometers (Morgan & Shepherd 2006).They feed on drift algae and kelp (Jones 2008; Zeeman et al. 2014). This species is the largest of its South African counterparts, growing up to 230 mm (van der Merwe 2009). Living up to 30 years (DFFE 2020), they reach sexual maturity after seven years and minimum legal size for harvest only after eight to nine years (DFFE 2020).

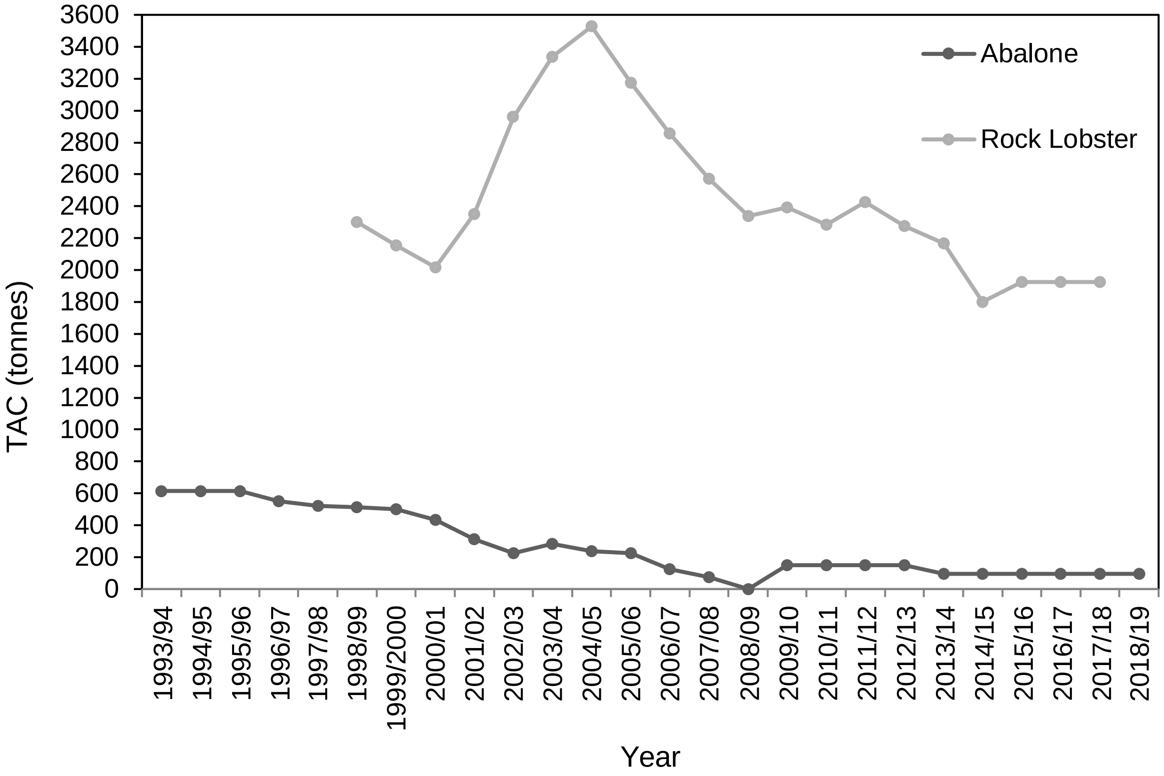

Figure 2. Annual total allowable catches (TAC) for the commercial abalone fishery and the commercial and recreational west coast rock lobster fishery in South Africa (Adapted from DEFF 2020)

Abalone meat is an expensive delicacy, and an abalone conservation crisis has ensued (Raemaekers et al. 2011; Zeeman et al. 2014). Of the five species of abalone found in South Africa, *H. midae* is one of two edible species and targeted for commercial harvest (Steinberg 2005). In South Africa, abalone supported a robust commercial fishery for six decades (1953-2018/19; DEFF 2020); and abalone is currently the most exported species in South African aquaculture, contributing considerably to the country's international trade (DFFE 2020). Unrestricted commercial harvesting began in 1949, but due to concerns about the declining stock, seasonal restrictions were implemented in 1968 (Raemaekers et al. 2011). The total annual catch remained stable until the mid-1990s, after which abalone poaching and the illegal trade boomed in South Africa, causing continuous declines in commercial catches (Figure 2; Steinberg 2005; Raemaekers et al. 2011; DEFF 2020). The illegal trade is driven by demand from East-Asian markets (DFFE 2020), with Hong Kong receiving 90% of exports (Okes et al. 2018). Within a decade, the species was threatened with commercial extinction. In 2001 an estimated 10% of the pre-exploited population remained (Centre for Marine Studies 2001). All recreational harvesting was banned in 2004 (DFFE 2020). Additionally, in 2004, abalone was listed on the CITES Appendix 3 and the National Environmental Management: Biodiversity

Act 10 (NEMBA). Each year the commercial total allowable catch was decreased until 2008 when a complete and controversial fishery closure was implemented (Figure 2; Raemaekers et al. 2011; DEFF 2020). However, due to pressure from the fishing industry and the listing having little effect on the illegal trade, they were removed from CITES in 2010, and the commercial fishery was reopened. According to a linear trend analysis on the fishery-independent abalone surveys (FIAS) counts, from 2000 to 2016, the western abalone population decreased by 87% (DAFF 2016). These declines in the abalone populations were also attributed to the southern migration of rock lobster as they indirectly reduce abalone recruitment (Raemaekers et al. 2011). Recreational harvesting is still prohibited (Raemaekers et al. 2011; DFFE 2020). Today illegal harvesting continues to extents far greater than historical legal quotas (Raemaekers et al. 2011; Okes et al. 2018). An average of 2 174 tonnes of abalone were poached annually, between 2000 and 2016, estimated to be worth R628 million each year (Okes et al. 2018). Poaching is increasing, demonstrated by the 47% increase in illegal catch from 2017-2018 (DFFE 2020). A South African abalone ranching industry developed in the 1990s, providing legal abalone for export and offering restocking opportunities for the wild populations (Troell et al. 2006; Raemaekers et al. 2011).

Giant periwinkle

The giant periwinkle (*T. sarmaticus*), commonly referred to by its Afrikaans name, alikreukel, is a gastropod (Jones 2008). Their range is from the Cape Peninsula to Port St Johns, where they can be found in the intertidal zone to a depth of 10 m (Jones 2008). They feed on kelp (Jones 2008). Thus being restricted to kelp forests in their range around the Cape Peninsula (Pulfrich & Branch 2002). Being slow growing, giant periwinkles of three to four years old are 60 mm in length, although they can reach 120 mm (Jones 2008).

The giant periwinkle is harvested for recreational and subsistence purposes. However, until the start of the 21st century the species was not considered over exploited and there is no updated data on their current status (Pulfrich & Branch 2002). There is a minimum harvest size limit of 63.5 mm shell diameter and a maximum bag limit of five individuals per person per day (Pulfrich & Branch 2002). Although there is no commercial fishery for this species, an estimated sustainable yield for giant periwinkle in 2002 was 77 tonnes annually (Pulfrich & Branch 2002).

Kelp

Kelps are brown seaweeds of the order Laminariales (Bolton et al. 2012). *Ecklonia maxima* and *Laminaria Pallida* are the dominant kelp species along the west coast of South Africa (Rothman 2015). *Ecklonia maxima* form dense stands to depths of 10 m, and *L. pallida* form a subcanopy from about 6 m down to 30 m (Anderson et al. 1997). *E. maxima* form extensive kelp beds from Luderitz, Namibia, to De Hoop, South Africa (Bolton et al. 2012). The *E. maxima* forests around the Western Cape appear to be increasing in density and expanding their ranges eastwards (DFFE 2020). This change has been attributed to cooling inshore water temperatures due to climate change (DFFE 2020). *L. pallida* ranges from Kunene, Namibia, to Danger Point, South Africa (Rothman 2015). *E. maxima* is gradually replaced by *L. pallida* as the dominant species northwards into Namibian shores (Rothman 2015). *Macrocystis pyrifera* is present in isolated patches along the southern part of the west coast (Rothman 2015).

Kelp harvesting is less intense on the Cape Peninsula than for the macro-invertebrate species but sustains a valuable industry. The kelp fishery is valued at R40 million per year (DFFE 2020). Most extracted kelps are traded internationally, however, 5000 tonnes of fresh kelp are extracted annually in the Western Cape for the abalone ranching industry (DFFE 2020). There is a maximum bag limit of 10 kg per permit per day for recreational and subsistence fishing. The stock status and fishing pressure of kelp are currently considered optimal (DFFE 2020).

Urchins

The Cape Urchin (*P. angulosus*) is an endemic species of echinoderm found in the intertidal zone to 98 m depth, ranging from Luderitz, Namibia, to Durban, South Africa (Jones 2008). They are common on rocky shores and reefs in the Western Cape, where they graze on kelp and other algae (Jones 2008). They are prey to rock lobsters and offer abalone recruits protection from predators (Tarr et al. 1996; Day & Branch 2000a, 2002a; Mayfield et al. 2001; Jones 2008).

Species interactions

The rock lobster, abalone, giant periwinkle, kelp, and urchin, along with other species, exist in a complex community comprised of predator-prey relationships, competition, and commensalism (Breen & Mann 1976; Tegner & Dayton 1981; Tarr et al. 1996; Pinnegar et al. 2000; Estes & Duggins 2019). Rock lobsters are key predators of other invertebrates, and can severely alter community structure (Barkai & Branch 1988; Mayfield 1998; Barrett et al. 2009;

Haley et al. 2011; Blamey & Branch 2012). Variation in rock lobster density can mediate a switch between predator or herbivore dominated systems (Barkai & Branch 1988; Blamey & Branch 2012). Through urchin predation, increases in rock lobster have been linked with decreases in abalone in several kelp communities across the world (Mayfield & Branch 2000; Blamey & Branch 2012; Zeeman et al. 2014). In the 1980s-1990s, the range of rock lobster shifted from the western coast southward, invading naïve communities (Tarr et al. 1996; Mayfield & Branch 2000; Blamey & Branch 2012). Populations of already overexploited abalone have faced further threat by the increase in density of rock lobster in those areas (Mayfield & Branch 2000; Zeeman et al. 2014). This interaction has been attributed to the indirect effects of urchin predation by the rock lobster (Tarr et al. 1996; Mayfield & Branch 2000). Urchins act as protective nurseries to juvenile abalone, who shelter beneath urchin's spines until they reach a shell length of 18 mm (Tarr et al. 1996). The increase in urchin predation by rock lobsters reduces successful abalone recruitment (Tarr et al. 1996; Day & Branch 2000b; Mayfield & Branch 2000; Day & Branch 2002b). Thus, the persistence of abalone populations is tightly linked to the presence of urchins (Day & Branch 2000b).

Kelp populations are dependant on the regulation of urchin populations via predation. Urchins feed on macroalgae, and declines in kelp forests resulting from increased urchin abundance have been recorded (Breen & Mann 1976; Estes & Duggins 2019). The absence of otters, a primary predator of urchins in the North Pacific, resulted in reduced and less variable kelp populations, but in the presence of the otters, the urchin density was lower and less variable, allowing kelp to increase (Estes & Duggins 2019). Two stable states exist in these intertidal communities, namely, kelp dominated or urchin dominated (Estes & Duggins 2019). Abalone are also important herbivores in kelp forest systems, however, as they feed only on drift kelp, kelp and benthic community composition are not affected by fluctuations in abalone abundance (Barrett et al. 2009; Zeeman et al. 2014). However, abalone could outcompete other species for space and thus affect other rock-dwelling species, such as giant periwinkle (Jenkins 2004).

Marine Protected Areas

Marine protected areas (MPAs) are widely accepted as an effective way to conserve marine life (Law 2000; Halpern 2003; Jones 2007; Sciberras et al. 2013; Kirkman et al. 2021). Unlike terrestrial ecosystems, marine ecosystems exist mostly as open systems (Attwood et al. 1997b). This restricts privatization, and thus the oceans are traditionally open access. The tragedy of the commons (Hardin 1968) applies across most of the world's oceans in the absence of private property rights. A corresponding lack of ownership and resource husbandry has contributed enormously to the over exploitation of fish stocks (Luypaert et al. 2018). In addition, harvesting of wild populations targets individuals that are old and large; unlike captive breeding, this actively removes beneficial genetic material from the population's gene pool; therefore fishing selects for weaker genes (Law 2000). Harvesting decreases the health of the populations over time and their ability to recover from exploitation (Law 2000). MPAs may allow for genetically stronger individuals to persist and maintain the genetic diversity and integrity of the population (Attwood et al. 1997a). In theory, one function of MPAs is to regulate resource extraction from an area and create a sanctuary for marine life (Sciberras et al. 2013). This management instrument allows more individuals to grow and potentially reproduce (Attwood et al. 1997a; Jones 2007). Supporting evidence for this effect is seen through increased levels of species biomass, increases in the density and average size of some species within MPAs over time than unprotected areas (Halpern 2003; Sale et al. 2005; Sciberras et al. 2013). MPAs can take the form of complete no-take reserves, where all harvesting of any species is restricted, or partially protected areas where harvesting is restricted to certain species, times or bag and size limits (Sciberras et al. 2013).

Populations of targeted species within MPAs often increase positively with the length of their protection status (Sciberras et al. 2013; Gillespie & Vincent 2019). The increase in biomass of target populations within the MPA will, in theory, result in excess production, which will then 'spill over' into unprotected areas, benefiting the fisheries (Sale et al. 2005; Jones 2007; Gillespie & Vincent 2019). For sessile species, this is beneficial to the entire population as dispersal results in restocking of populations outside of the MPA (Quinn et al. 1993; Branch & Branch 2018). Highly mobile target species can also benefit from MPAs as only a proportion of their population will be under threat of harvest at any one time (Branch & Branch 2018). Invertebrates can respond differently to fish species, thus both groups need to be monitored for comprehensive assessment (Gillespie & Vincent 2019). In ideal cases, MPAs will cover areas that host important life stages of a species, such as spawning areas or nurseries, to protect the population's production (Sale et al. 2005). Non-target species can also benefit from MPA refugia (Sciberras et al. 2013). Specific fishing methods, such as trawling, are highly destructive to habitats and sessile species, and MPAs can offer protection from such activities (Attwood et al. 1997a). A MPA is also an insurance that over-harvesting will be prevented in the future due to formal governmental gazettes (Attwood et al. 1997a; Sale et al. 2005).

Furthermore, MPA objectives also consider other pressures and threats to marine life and habitats, that don't come from extraction of natural resources, such as mining, seismic surveying, pollution, and aquaculture. Thus, MPAs can mitigate against various pressures on the ecosystem (Attwood et al. 1997a; Sale et al. 2005).

One argument against MPAs is that they will not decrease fishing pressure but rather displace it into smaller areas; thus, causing a greater decline of the stocks in these areas and creating a trap, pulling in more biomass from the MPA (Willis et al. 2003; Jones 2007). Displacement may increase fishing pressures in other areas or MPAs that are less regulated. Marine protected areas also do not prevent illegal fishing (Hilborn & Sinclair 2021). Some argue that MPAs detract from other potential solutions and that stricter and better-monitored fishing regulations are the answer to prevent stock declines and not MPAs (Sale et al. 2005; Hilborn & Sinclair 2021). However, these arguments do not take into account the holistic protection MPAs afford marine ecosystems.

MPAs and Species Interactions

If the establishment of a MPA affects the populations of one species, there may be secondary effects experienced by other species (Pinnegar et al. 2000). Species interactions should be considered when assessing the overall effects of a MPA. Over time trophic and competitive interactions, which are usually altered due to over-extraction, can be restored as populations recover (Pinnegar et al. 2000; Edgar et al. 2007; Edgar & Barrett 2012). This can further influence species' response to MPAs, in addition to their population recovery, and some species may decline if competition or predation is increased (Shears & Babcock 2003; Barrett et al. 2009). A study on the effect of MPAs on invertebrate populations in Tasmania found that the rock lobster populations increased; however, the abalone populations did not (Barrett et al. 2009). The authors attributed this result to an increase in predation on abalone by the increasing rock lobster population and an increase in cryptic behaviour by the abalone to avoid the increasing abundance of predators. The predator theory is substantiated by the decrease in juvenile abalone and the maintenance of the size of above-legal-harvest size population (Barrett et al. 2009). Barrett et al. (2009) also reported a substantial decrease in urchins within the reserves, again attributed to rock lobster predation. Abalone mortality was also attributed to interspecific competition by other herbivore populations recovering within the MPA (Barrett et al. 2009). MPAs can also result in the change of the age structure of populations; Barrett et al. (2009) found that decreases in abalone within a MPA could be attributed to a significant decline in the number of smaller or juvenile individuals, which again could be the result of an increase in predators.

Untangling which population changes are causal, which are responses to other con-specific population changes, and which are a result of human extraction is important in deciphering the causes of community structure shifts. It can be hypothesised that, in the communities around the Cape Peninsula, an increase in rock lobster would result in a decline in urchins and thus an increase in kelp and a decrease in abalone, and vice versa. An increase in abalone would unlikely be reflected in the changes in the abundance of the other species, except for space competitors such as giant periwinkle. Figure 3 outlines a simple hypothesised web of the interactions between all five study organisms.

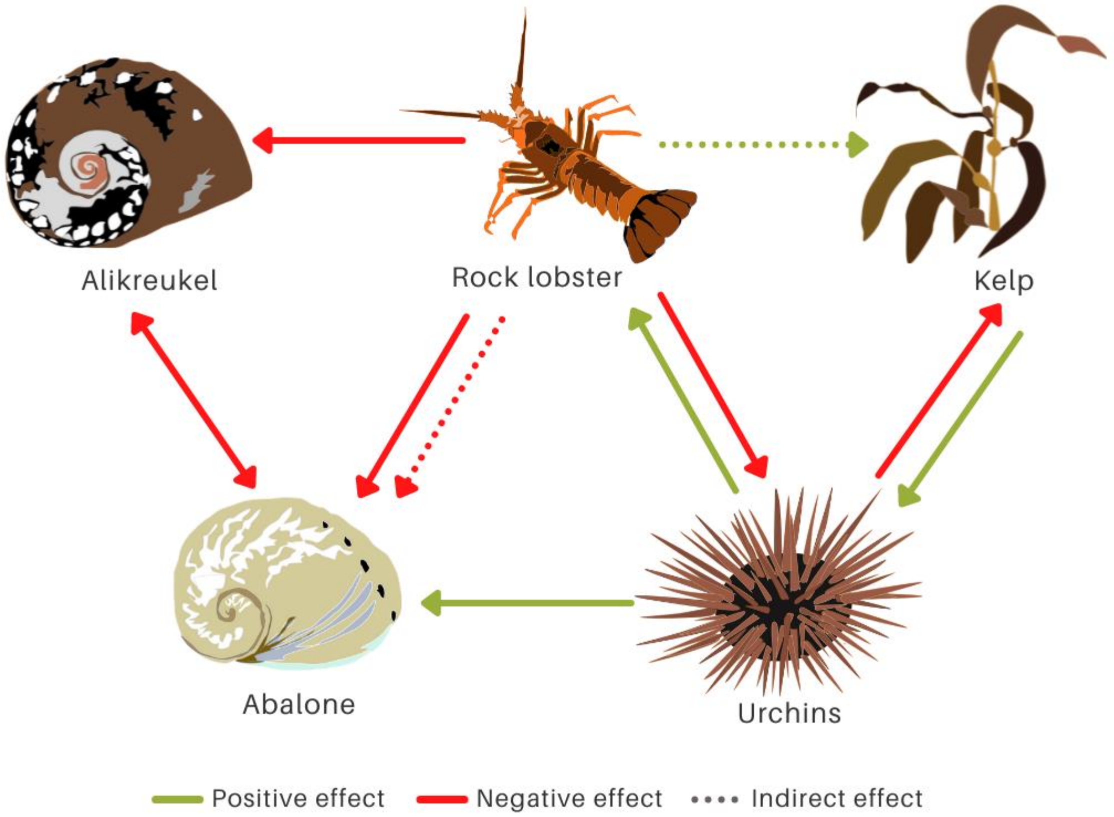

Figure 3. A Diagram of expected species interactions across trophic levels within kelp forests of select species. Interactions include predation, competition and indirect relationships.

Table Mountain National Park Marine Protected Area

In 1979, a series of discrete marine reserves existed along the Cape Peninsula (Figure 4), consisting of two rock lobster sanctuaries and four reserves with limited harvesting restrictions

(Centre for Marine Studies 2001). The regulations in these reserves varied from strict no-take zones to the allowance of shore fishing. Later reports by Attwood et al. (1997b) and Mayfield et al. (2005) suggested that these reserves were not positioned to cover an adequate representation of the biodiversity found in this area, nor were they able to protect biodiversity from the high levels of fishing pressure (Centre for Marine Studies 2001). A new marine park, Table Mountain National Park Marine Protected Area (TMNP-MPA), was proposed and established in 2004. It surrounds the entire peninsula, extending from Mouille Point on the Atlantic Seaboard to Muizenberg in False Bay, consolidating the discreet historical reserves. The main objectives of the MPA were to:

1. *Protect the marine environment and the marine biodiversity*
2. *Allow over-exploited and commercially collapsed species of fish a sanctuary in which to recover and breed.*
3. *Promote and regulate eco-tourism activities and scientific research in a way that does not adversely affect the marine environment and to prescribe penalties for contraventions*

(DEFF 2004:695)

Within the TMNP-MPA there are six ‘no-take’ zones, where all harvesting (except for snoek *Thyrsites atun* in one of the no-take zones) is prohibited (Figure 4). The remaining areas are managed as controlled zones where regulated harvesting is permitted. Inside the controlled zones, fisheries regulations in the form of bag and size limits are enforced. There are also minimum size limits for each harvested individual for abalone, rock lobster and giant periwinkle, as previously described.

Before establishment of the new MPA, two sets of SCUBA surveys were conducted in 2000 and 2003 to establish the status and distribution of invertebrate populations along the peninsula. Since then, the populations have not been assessed at an MPA level. It is currently unknown if they have changed or if the MPA fulfills its goals of conserving biodiversity and the sustainable use of marine resources. Both legal and illegal harvesting have continued throughout TMNP-MPA. It is a large area, making comprehensive monitoring difficult, and abalone trade is linked with other dangerous and powerful illegal trades. The success of conservation areas is affected by the monitoring of the conservation efforts (Attwood et al. 1997b). Effective adaptive management and best practice are informed by real-time monitoring. A newer set of SCUBA surveys were conducted in 2019, offering the opportunity to report on population changes since the establishment of TMNP-MPA and the effectiveness of the zones.

Aims

Many scientific publications on MPAs (Stander 1990; Law 2000; Halpern 2003; Jones 2007; Sciberras et al. 2013) support the idea that biodiversity protection is well served by MPAs and particularly no-take MPAs. However, there are some compelling arguments suggesting that biodiversity conservation in the oceans would be achieved more effectively using other methods (Hilborn & Sinclair 2021). The creation of the TMNP-MPA, with its many and varied no-take and harvest zones, provides an excellent opportunity to test the effectiveness of no-take spatial protection in a complex marine community and in the vicinity of a heavily exploited coastal zone near a metropolitan setting. This is especially valuable for macro-invertebrates, which are not commonly the focus of MPA studies in South Africa. Poaching of marine resources, particularly those that form the subject of this study is rife in and around Cape Town, allowing the claim that no-take MPAs are not an effective strategy against illegal fishing to be tested.

Rock lobster, abalone, and giant periwinkle are historically among the region's three most important invertebrate resources. Kelp and urchins also play an important role in ecosystem dynamics but, in South Africa, these two species do not present a conservation concern. All five species are part of a complex coastal ecosystem in which the abundances of each species are potentially as much dependent on each other as they are on human stressors and environmental factors. The effect of the removal of fishing from several zones in the TMNP will be directly tested after accounting for the effects of habitat, depth, the physical protection offered by False Bay, and, most importantly, species interactions.

This study aims to use data from three surveys of invertebrate abundance in the TMNP conducted over a 19 year period to evaluate (a) whether the MPA as a whole had a positive effect on the abundances of rock lobster and abalone relative to their larger population and (b) whether the no-take zones within the MPA resulted in greater abundances of these targeted species than in the adjacent harvested zones. The responses of a third harvested species, the giant periwinkle, can be tested only for the effect of the no-take zones, given an absence of a population wide assessment.

Methods

Study site

The study was conducted along the inshore waters of the Cape Peninsula, in the Western Cape Province of South Africa, extending from Mouille Point on the Atlantic Seaboard (33° 53' 48.3612"S, 18° 24' 33.5988'E) to Muizenberg beach in False Bay (34° 6' 52.3188" S, 18° 28' 7.5" E; Figure 1). The sampling sites to the west of Cape Point fall within the Southern Benguela Ecoregion, henceforth considered to be on the Atlantic seaboard side, and those to the east, henceforth considered to be on the False Bay side, are within the Agulhas Ecoregion (Sink et al. 2012).

SCUBA Surveys

Selected sites around the Cape Peninsula were surveyed using underwater visual census (UVC) three times, in 2000, 2003 and 2019 (Table 1). At each site, two SCUBA divers independently surveyed three to six separate 10 m long transects. Transects were positioned over reef substrate in depths of three to 10 meters. At each site, the date, time, GPS coordinates, visibility and diver details were recorded. In 2000, surveys were conducted at 163 sites, and an additional site was added in 2003. In 2019, due to resource constraints, only 84 of the original sites were selected, and six transects were completed at each site. A table indicating which sites were surveyed in each year can be found in Appendix 1. A map of the location of each site can be found in Appendix 2.

At the start of each transect, the water depth was recorded. The presence of sand on the floor of each transect was also recorded. Each SCUBA diver scored (0-3) the number of urchins and kelp fronds present (Table 2). Along the 10 m transect, the SCUBA diver counted the numbers of rock lobster, abalone, and giant periwinkle within an area of 0.5 m on either side of each transect. An estimate was given to the proportion of rock lobster and abalone recorded below legal-harvest size, i.e. 80 mm carapace length for rock lobster and 114 mm for abalone. A total of 1498 SCUBA surveys were completed over the three years (Table 1).

Table 1: The years, dates, number of sites and transects per site recorded for the SCUBA surveys.

Variable	**Year**		
	2000	**2003**	**2019**
Date	16/12/2000 – 2/01/2001	21/12/2002 – 3/11/2003	26/02/2019 – 21/05/2019
Number of sites	163	164	84
Transects per site	3	3	6
Number of surveys	489	492	504

Table 2. The categorical scoring system used in the SCUBA surveys to represent the estimated number of urchins and kelp fronds found within a 1 m^2 area.

Score	**Number of individuals**	
	Urchins (m^{-2})	**Kelp (m^{-2})**
0	0	0
1	1-9	1-2
2	10-50	3-5
3	More than 50	More than 5

Table 3. A list of marine conservation areas along the Cape Peninsula, past and present, that have existed since 1976, their year of establishment and year of closure, and the range of site numbers in each.

Conservation Area	**Included sites**	**Established**	**Closed 2004**	**Reference**
Table Bay Rock Lobster Sanctuary	1-55	1976	Yes	(Stander 1990)*
Kommetjie rock lobster sanctuary	59-64	1976	Yes	(Stander 1990)*
Karbonkelberg Marine Reserve	18-48	2004	-	(Stander 1990)
Cape of Good Hope Marine Reserve	77-96	1976	No	(Stander 1990)*
Paulsberg Marine Reserve	122-126	2004	-	
Castle Rock Marine Reserve	132-137	1979	No	(Stander 1990)
Boulders Marine Reserve	142-148	2004	-	
Glencairn Marine Reserve	153-156	Pre-1979	Yes	(Stander 1990)*
Kalk Bay Marine Reserve (Kalk bay - St James)	160-162	1986	No	(Branch et al. 1988)
Kalk Bay Marine Reserve (St James - Muizenberg)	164	1986	Yes	(Branch et al. 1988)

* Protected areas mentioned in Stander (1990) as already in existence in 1979.

Survey sites and harvested species around the Cape Peninsula have had varying degrees of protection levels over the survey years (Table 3 and Figure 4). Consequently, this needed to be accounted for in the data analysis. Therefore, the protection level for each species at each site for each survey year was considered. This information was included as a continuous variable, namely the number of years under formal protection (Table 4 and 5). This was calculated by considering the length of time from the establishment year of each discreet marine reserve to the year of the survey.

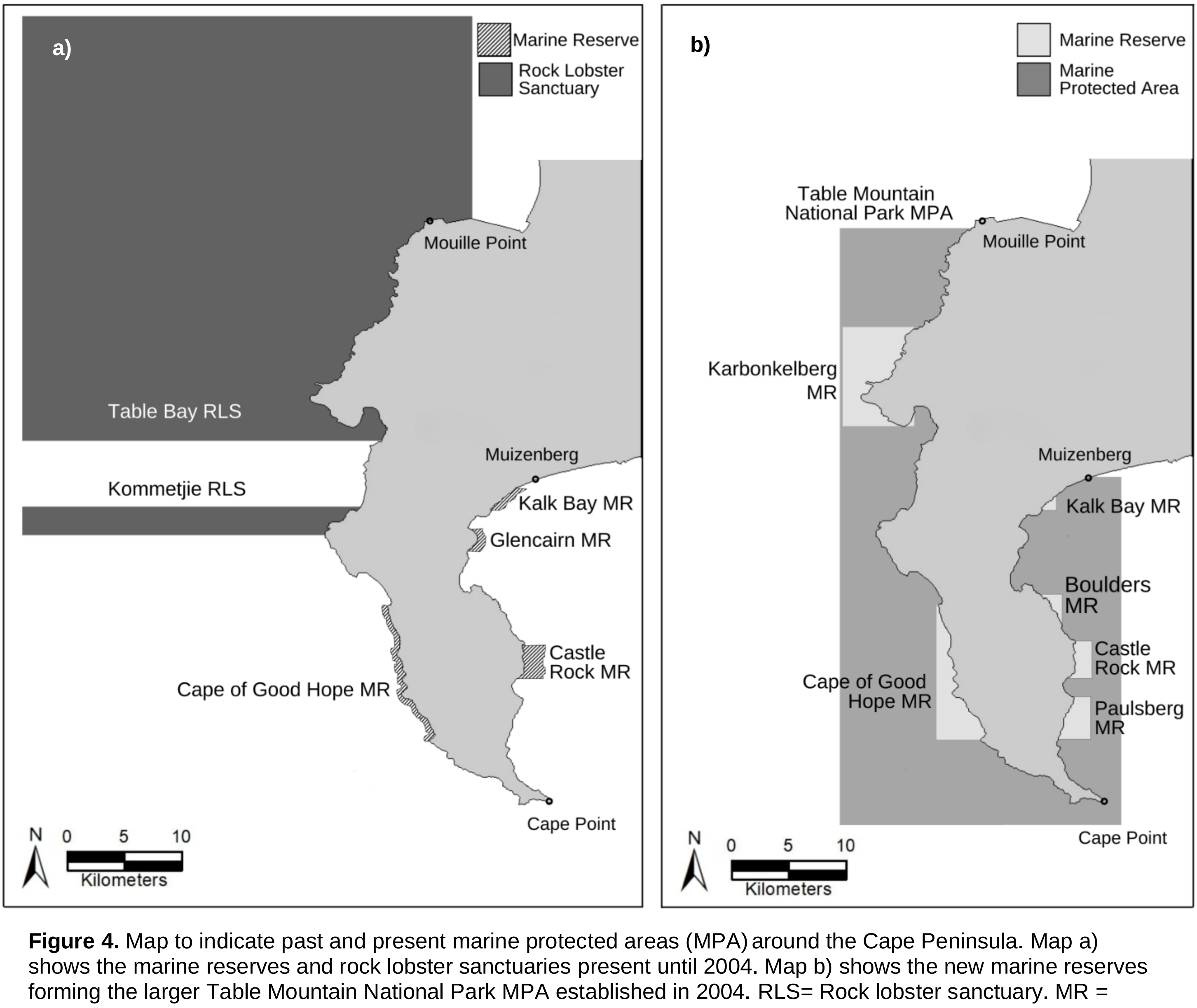

Figure 4. Map to indicate past and present marine protected areas (MPA) around the Cape Peninsula. Map a) shows the marine reserves and rock lobster sanctuaries present until 2004. Map b) shows the new marine reserves forming the larger Table Mountain National Park MPA established in 2004. RLS= Rock lobster sanctuary. MR = Marine reserve.

Table 4. The name of the reserve and length of formal protection, in years, for rock lobster at each study site, across all three survey years. If a site remains protected across time intervals then the years are accumulated. However, if the site is not protected in that specific year, regardless of its history, then the entry is zero. All sites in 2019 with protection length = 0 lost protection in 2003TMNP-MPA = Table Mountain National Park Marine protected area. RLS= Rock lobster sanctuary. MR= Marine reserve.

	Conservation Area			**Protection length**		
Survey Site	**2000**	**2003**	**2019**	**2000**	**2003**	**2019**
1-17	Table Bay RLS	Table Bay RLS	TMNP-MPA	24	27	0
18-48	Table Bay RLS	Table Bay RLS	Karbonkelberg MR	24	27	43
49-55	Table Bay RLS	Table Bay RLS	TMNP-MPA	24	27	0
56-57	No protection	No protection	TMNP-MPA	0	0	0
59-64	Kommetjie RLS	Kommetjie RLS	TMNP-MPA	24	27	0
65-77	No protection	No protection	TMNP-MPA	0	0	0
77-96	Cape of Good Hope MR	Cape of Good Hope MR	Cape of Good Hope MR	24	27	43
97-121	No protection	No protection	TMNP-MPA	0	0	0
122-126	No protection	No protection	Paulsberg MR	0	0	16
127-131	No protection	No protection	TMNP-MPA	0	0	0
132-137	Castle Rock MR	Castle Rock MR	Castle Rock MR	21	24	40
138	Castle Rock MR	Castle Rock MR	TMNP-MPA	21	24	0
139-142	No protection	No protection	TMNP-MPA	0	0	0
142-148	No protection	No protection	Boulders MR	0	0	16
149-153	No protection	No protection	TMNP-MPA	0	0	0
154-156	Glencairn MR	Glencairn MR	TMNP-MPA	14	17	0
157-159	No protection	No protection	TMNP-MPA	0	0	0
160-162	Kalk Bay MR (Kalk bay - St James)	Kalk Bay MR (Kalk bay - St James)	Kalk Bay MR	14	17	33
164	Kalk Bay Marine Reserve (St James - Muizenberg)	No protection	TMNP-MPA	14	0	0

Table 5. The name of the reserve and length of formal protection, in years, for giant periwinkle and abalone at each study site, across all three survey years. If a site remains protected across time intervals then the years are accumulated. However, if the site is not protected in that specific year, regardless of its history, then the entry is zero. All sites in 2019 with protection length = 0 lost protection in 2003. TMNP-MPA = Table Mountain National Park Marine Protected Area. RLS = Rock lobster sanctuary; MR = Marine reserve.

	Conservation Area			**Protection length**		
Survey Site	**2000**	**2003**	**2019**	**2000**	**2003**	**2019**
1-17	Table Bay RLS	Table Bay RLS	TMNP-MPA	0	0	0
18-48	Table Bay RLS	Table Bay RLS	Karbonkelberg MR	0	0	16
49-55	Table Bay RLS	Table Bay RLS	TMNP-MPA	0	0	0
56-57	No protection	No protection	TMNP-MPA	0	0	0
59-64	Kommetjie RLS	Kommetjie RLS	TMNP-MPA	0	0	0
65-77	No protection	No protection	TMNP-MPA	0	0	0
77-96	Cape of Good Hope MR	Cape of Good Hope MR	Cape of Good Hope MR	24	27	43
97-121	No protection	No protection	TMNP-MPA	0	0	0
122-126	No protection	No protection	Paulsberg MR	0	0	16
127-131	No protection	No protection	TMNP-MPA	0	0	0
132-137	Castle Rock MR	Castle Rock MR	Castle Rock MR	21	24	40
138	Castle Rock MR	Castle Rock MR	TMNP-MPA	21	24	0
139-142	No protection	No protection	TMNP-MPA	0	0	0
142-148	No protection	No protection	Boulders MR	0	0	16
149-153	No protection	No protection	TMNP-MPA	0	0	0
154-156	Glencairn MR	Glencairn MR	TMNP-MPA	14	17	0
157-159	No protection	No protection	TMNP-MPA	0	0	0
160-162	Kalk Bay MR (Kalk bay - St James)	Kalk Bay MR (Kalk bay - St James)	Kalk Bay MR	14	17	33
164	Kalk Bay Marine Reserve (St James - Muizenberg)	No protection	TMNP-MPA	14	0	0

Statistical Analysis

All statistical analyses were conducted in R v3.6.1 (R Core Team 2019).

To avoid confounding factors in the statistical analysis, a Pearson's correlation test was run between all continuous explanatory variables. Variables with correlation values smaller than -0.6 or greater than 0.6 were considered strongly correlated (Mukaka 2012). A Cramer's V-test was run between all categorical variables, and those with a Cramer's V-value above 0.30 were considered strongly correlated. The variable considered to be a better predictor of the response variable from a correlated pair was chosen to be included as a proxy for both.

To find the patterns for each species' abundance and the effects of environmental factors and protection status, a set of three generalized linear models (GLMs) was run using the *Stats* package (R Core Team 2019). The abundance of rock lobster, abalone and giant periwinkle were used as the response variables in each model. The models investigated the overall differences in species abundance considering the year of the survey, the side of the peninsula on which each site was positioned (Atlantic seaboard or False Bay), the water depth (Shallow = < 3 m; Moderate = 3 – 7 m; Deep = > 7 m), the presence of sand, the density of kelp and urchins, and the length of formal protection afforded to that species.

The abundance of rock lobster, giant periwinkle, and abalone followed an over-dispersed Poisson distribution, so the quassipoisson family of GLMs was used. For each GLM, a saturated model was created, and a backward stepwise regression was performed using the significance values produced by the *Anova* function in the *car* package (Fox & Weisberg 2019) to find a reduced model that best explains the data. Variables with significance scores lower than 0.1 were retained in the final models. To interpret the parameter estimates, the estimates on the original scale were obtained by inversing the log link function of the Poisson distribution (exp(estimate)). All pairwise post-hoc tests on multi-level factors were conducted using Tukey contrasts with the *glht* function in the *multcomp* package (Hothorn et al. 2008).

Where the effect of survey year was significant in the previous set of models for rock lobster and abalone, a second GLM was run with the species divided into two size classes: above legal-harvest size and sub-legal-harvest size. This was done to further interpret the changes in abundance of the populations. Only rock lobster qualified for this analysis.

Where variables of particular interest (survey year and protection length) were removed from the models due to the lack of a significant effect, a post-hoc power analysis for linear regressions was conducted using the *pwr.f2.test* function from the *pwr* package (Champely 2020). This analysis was done to determine the theoretical effect size that could have been detected with the given survey effort (sample size).

Results

Rock lobster

The number of rock lobster counted were highest in 2003 and lowest in 2019 and the average number of rock lobster per transect mirrored this trend (Table 6). The number of transects containing rock lobsters decreased with every survey year (Table 6).

Table 6. The total count, maximum count per transect, the average count, and the percentage of transects with zero counts of west coast rock lobsters recorded during SCUBA surveys along 10 m transects over the three survey years.

Year	Total count	Maximum count per transect	Average per transect (+SE)	% Transects with zero rock lobster
2000	2362	100	4.83 (+0.42)	41.7
2003	2937	92	5.97 (+0.50)	38.4
2019	1315	79	2.55 (+0.29)	55.6

For rock lobster abundance in the first set of GLMs, all of the initial eight explanatory variables were maintained in the model (Table 7).

Overall, the effect of the survey year was significant, caused by a difference between 2019 and the first two survey years, 2000 and 2003 (Figure 5). There was a 29.8% decrease in rock lobster abundance from 2000 to 2019 and a 44.0% decrease from 2003 to 2019. There was no difference between 2000 and 2003 (Table 7). On which side of the peninsula the survey was conducted had a substantial effect on rock lobster abundance; 59.5% less rock lobster occurred in False Bay than on the Atlantic coast (Figure 6). Depth had an overall effect on abundance; however, only a difference between shallow and deep-water depth was significant. Rock lobster decreased by 60.5% from shallow to deep water (Figure 7). In the presence of sand, rock lobster abundance decreased by 31.9% (Figure 8).

Kelp density had a significant positive relationship with rock lobster abundance (Figure 9). The rock lobster increased significantly with every increase in kelp density level, except between the absence of kelp and density level 1 (1-2 fronds/m^2). At a kelp density level of 3 (>5 fronds/m^2), the abundance of rock lobster increased by more than three times from that in the absence of kelp. This factor had the greatest effect on rock lobster abundance (Figure 9).

Urchin density had a negative relationship with rock lobster abundance; rock lobster abundance was highest where urchins were absent, and the presence of urchins alone corresponded with a 42.5% decrease in rock lobster (Figure 10). Rock lobster abundance did not differ significantly depending on the level of urchin density after they were present. The highest recorded density of urchins (>50 individuals/m^2) corresponded with a 61.9% decrease in rock lobster abundance compared to the absence of urchins.

The length of formal protection had a positive effect on rock lobster abundance; with every year of protection, the abundance of rock lobster increased by 1.1% (Figure 11).

Table 7. Results from generalized linear model assessing the differences in rock lobster abundance per 10 m^2 across multiple variables. Results from the *Anova* function analyses for each variable presented. Estimate and SE results from the Tukey *summary* analyses for the mutli-leveled variables presented. (*p < = .05, **p < = .01, ***p < = .001).

Response	**Explanatory**	**X^2**	**df**	**Estimate (β_1)**	**SE**	**p-value**	**Interpreted estimate exp(β_1)**
Rock Lobster	Year	21.893	2			<0.001***	
	2000 - 2003			0.225	0.101	0.068	1.252
	2003 - 2019			-0.579	0.128	<0.001***	0.560
	2000 - 2019			-0.354	0.135	0.023*	0.702
	Side	42.164	1	-0.879	0.144	<0.001***	0.415
	Depth	7.624	2			0.022*	
	Shallow-Moderate			-0.809	0.384	0.077	0.445
	Moderate-Deep			-0.122	0.103	0.436	0.885
	Shallow-Deep			-0.930	0.391	0.039*	0.395
	Sand substrate	5.001	1	-0.247	0.113	0.029*	0.781
	Kelp density	47.181	3			<0.001***	
	0-1			0.479	0.299	0.354	1.614
	0-2			0.905	0.292	0.009**	2.472
	0-3			1.210	0.293	<0.001***	3.353
	1-2			0.425	0.120	0.002**	1.530
	1-3			0.731	0.127	<0.001***	2.077
	2-3			0.306	0.104	0.015*	1.358
	Urchin density	41.464	3			<0.001***	
	0-1			-0.554	0.164	0.004**	0.575
	0-2			-0.909	0.204	<0.001***	0.403
	0-3			-0.965	0.271	0.002**	0.381
	1-2			-0.355	0.237	0.423	0.701
	1-3			-0.411	0.304	0.512	0.663
	2-3			-0.056	0.325	0.998	0.946
	Protection length	9.984	1	0.011	0.003	0.002**	1.011

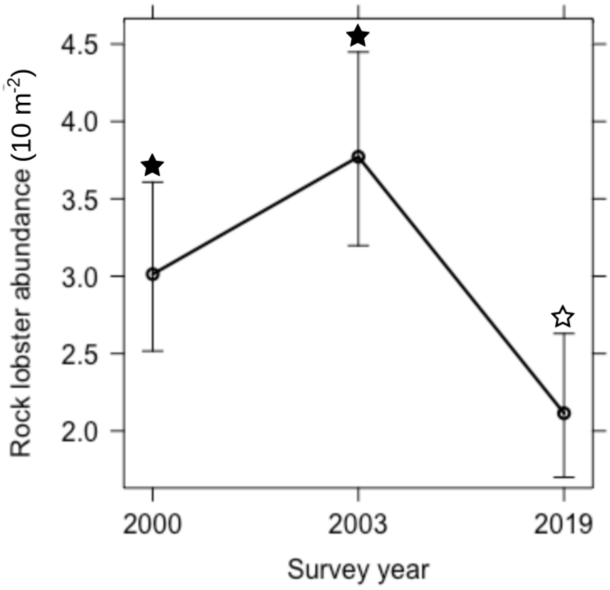

Figure 5. The effect of survey year on the abundance of rock lobster (10 m^{-2}) around the Cape Peninsula is shown with 95% confidence intervals. Years not sharing a star colour differ significantly. Significance at p-value < 0.05.

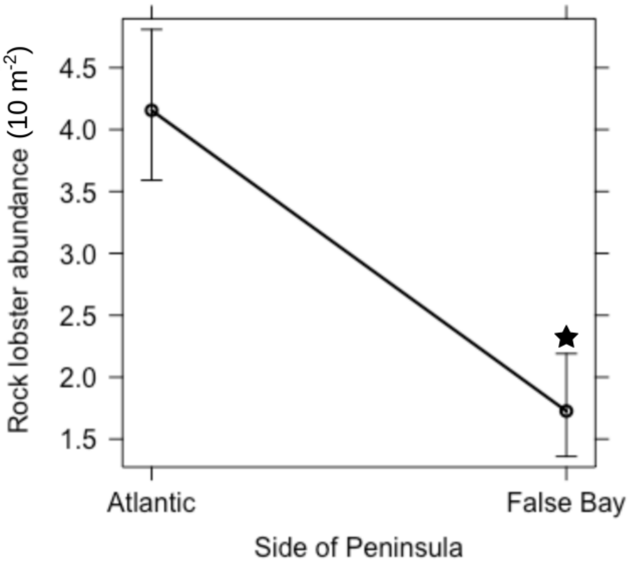

Figure 6. The effect of the side of the Cape Peninsula on the abundance of rock lobster (10 m^{-2}) is shown with 95% confidence intervals. The star indicates that the difference between abundances in False Bay and the Atlantic is significant. Abundances measured in 2000, 2003 and 2019. Significance at p-value < 0.05.

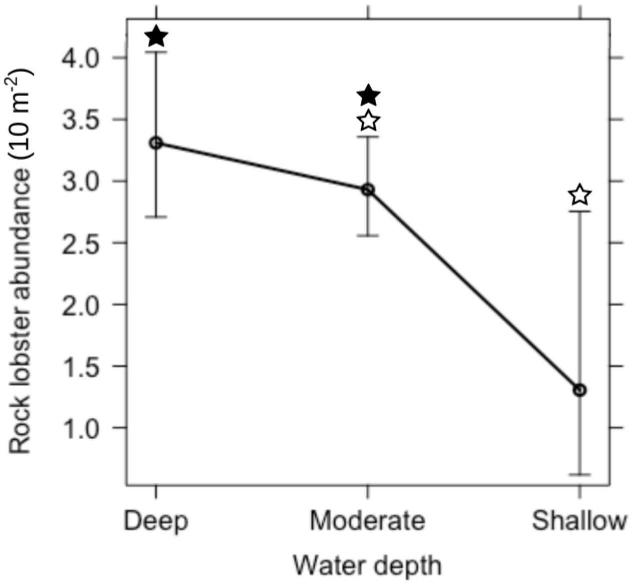

Figure 7. The effect of water depth on the abundance of rock lobster (10 m^{-2}), around the Cape Peninsula is shown with with 95% confidence intervals. Shallow = < 3 m; Moderate = 3 – 7 m; Deep = > 7 m. Abundances measured in 2000, 2003 and 2019. The rock lobster abundances at depths sharing a star colour do not differ significantly. Significance at p-value < 0.05.

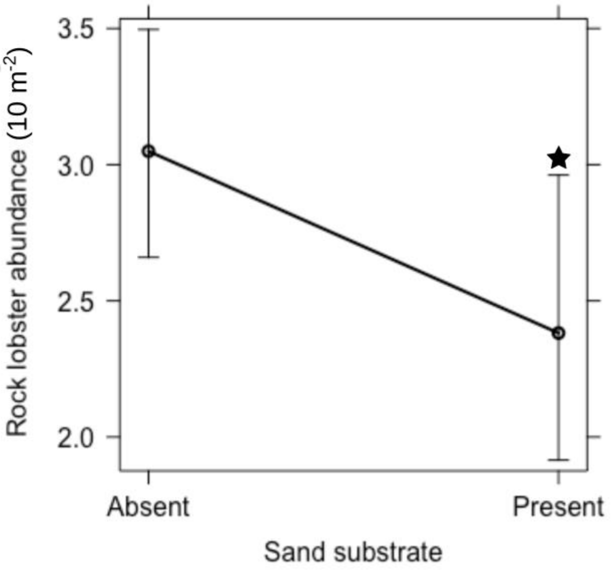

Figure 8. The effect of the presence and absence of sand on the abundance of rock lobster (10 m^{-2}), around the Cape Peninsula is shown with 95% confidence intervals. Abundances measured in 2000, 2003 and 2019. The star indicates that the difference between abundaces in the absence and presence of sand is significant. Significance at p-value < 0.05. Significance at p-value < 0.05.

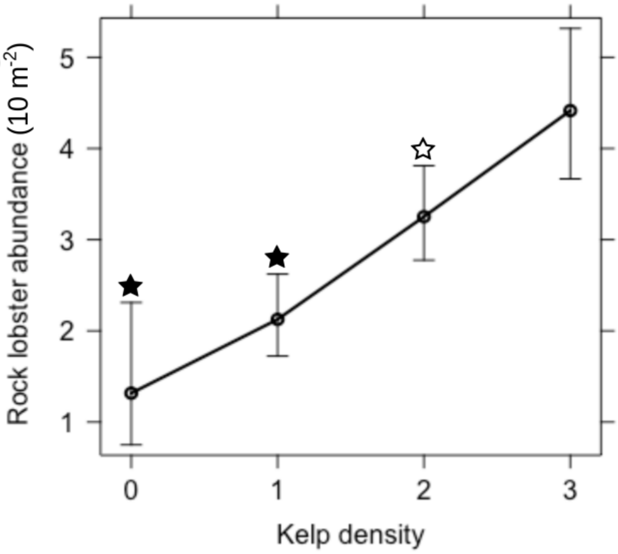

Figure 9. The relationship between kelp density and rock lobster abundance (10 m^{-2}), around the Cape Peninsula is shown with with 95% confidence intervals. Kelp density: 0 = 0 fronds/m^2; 1 = 1-2 fronds/m^2; 2 = 3-5 fronds/m^2; >5 fronds/m^2. Abundances measured in 2000, 2003 and 2019. The rock lobster abundances at kelp densities sharing a star colour do not differ significantly. Significance at p-value < 0.05.

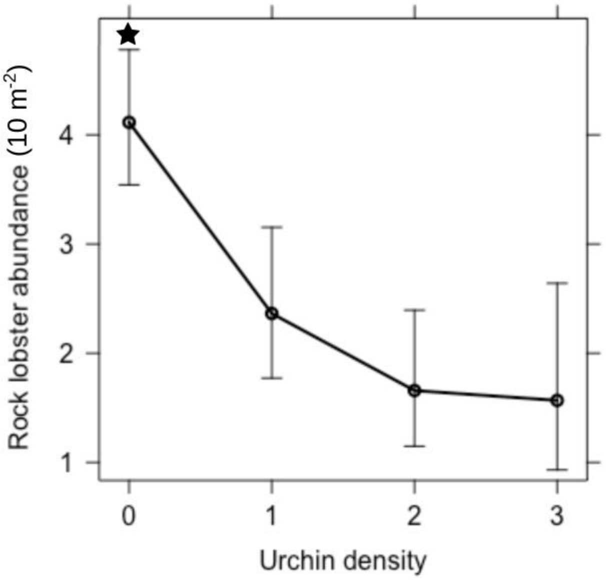

Figure 10. The relationship between urchin density and rock lobster abundance (10 m^{-2}) around the Cape Peninsula is shown with with 95% confidence intervals. Urchin density: 0 = 0 individuals/m^2; 1 = 1-9 individuals/m^2; 2 = 10-50 individuals/m^2; >50 individuals/m^2. Abundances measured in 2000, 2003 and 2019. The star indicates that the rock lobster abundance at urchin density 1 differs significantly from the rest of the density levels. Significance at p-value < 0.05.

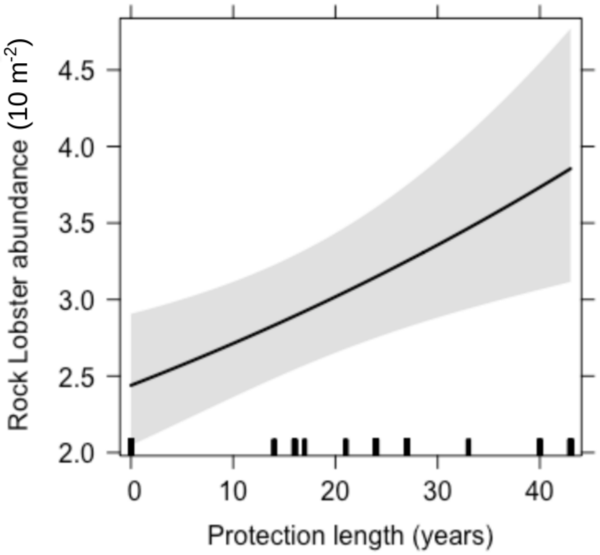

Figure 11. The effect of protection length on the abundance of rock lobster (10 m^{-2}), around the Cape Peninsula is shown with a 95% confidence interval. Abundances measured in 2000, 2003 and 2019. This relationship is significant. Significance at p-value < 0.05.

Size classes

The difference in abundance between years was significant for both the sub-legal and above-legal classes (Table 8). The abundance of sub-legal-harvest size rock lobster increased from 2000 to 2003 by 71.9% and then decreased from 2003 to 2019 by 31.1% (Figure 12). The above-legal-harvest size rock lobster abundance decreased from 2000 to 2003 by 36.9% and then again from 2003 to 2019 by 87.6% (Figure 13).

Table 8. Results from generalized linear models assessing the differences in rock lobster abundance per 10 m^2 across multiple variables across three years, sub-classed by size group: Sub-legal = <80 mm carapace length. Above-legal = >80 mm carapace length. Results from the *Anova* function analyses for each variable presented. Estimate and SE results from the Tukey *summary* analyses for the mutli-leveled variables presented. (*p < = .05, **p < = .01, ***p < = .001)

Size	**Explanatory**	**X^2**	**df**	**Estimate (β_1)**	**SE**	**p-value**	**Interpreted estimate exp(β_1)**
Sub-legal	Year	24.097	2			<0.001***	
	2000 - 2003			0.542	0.116	<0.001***	1.719
	2003 - 2019			-0.373	0.128	0.010**	0.689
	2000 - 2019			0.169	0.143	0.461	1.184
Above-legal	Year	104.905	2			<0.001***	
	2000 - 2003			-0.461	0.123	<0.001***	0.631
	2003 - 2019			-1.495	0.240	<0.001***	0.224
	2000 - 2019			-1.956	0.234	<0.001***	0.141

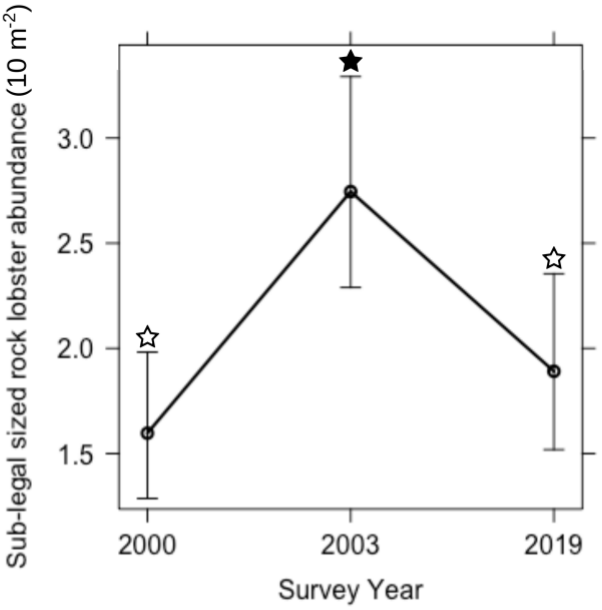

Figure 12. The effect of year on the abundance of sub-legal-harvest size rock lobster (10 m^{-2}), around the Cape Peninsula is shown with with 95% confidence intervals. Years not sharing a star differ significantly. Significance at p-value < 0.05.

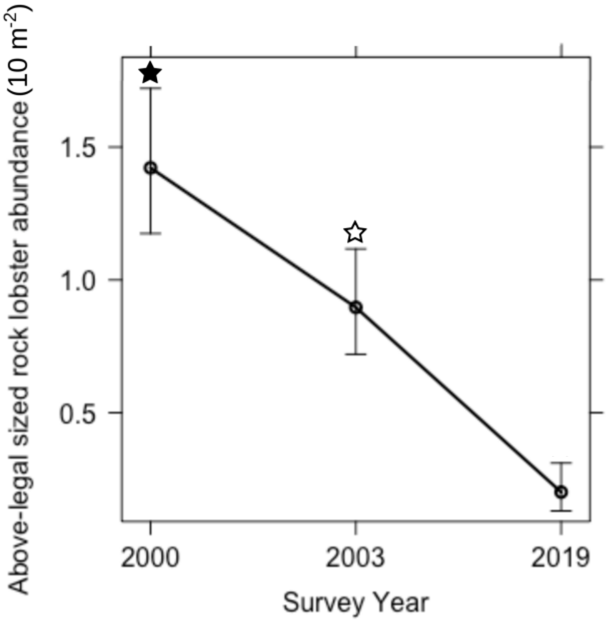

Figure 13. The effect of year on the abundance of above-legal-harvest size rock lobster (10 m^{-2}), around the Cape Peninsula is shown with with 95% confidence intervals. Years not sharing a star differ significantly. Significance at p-value < 0.05.

Abalone

The number of abalone counted were lowest in 2000 and highest in 2019, and the average number of abalone per transect mirrored this trend (Table 9). The number of transects containing abalone decreased with every survey year (Table 9).

Table 9. The total count, maximum count per transect, the average count, and the percentage of transects with zero counts of abalone recorded during SCUBA surveys along 10 m transects over the three survey years.

Year	**Total count**	**Maximum count per transect**	**Average per transect (+SE)**	**% Transects with zero abalone**
2000	293	18	0.60 (+0.08)	80.0
2003	349	30	0.71 (+0.12)	78.0
2019	462	18	0.90 (+0.08)	65.7

In the analysis of abalone abundance, the effects of the survey year, the presence of sand substrate, and the length of protection were removed from the final model, suggesting that the abalone abundance did not respond significantly to these variables (Table 10). The effect of the peninsula side had a substantial effect on abalone abundance (Table 10). Two and half times more abalone occurred in False Bay than along the Atlantic coast of the study area (Figure 14). Overall, the water depth affected the abalone abundance (Table 10); however, no significant differences were detected between the shallow, moderate and deep waters (Figure 15). A similar pattern was found with kelp density; overall kelp density had a significant relationship with abalone abundance (Table 10), the most influential of all the factors; however, no difference between density levels was detected in the Tukey post-hoc test (Figure 16).

Significantly fewer abalone were found in the absence of urchins; the abalone abundance almost doubled in the presence of even the lowest urchin density level (1-9 individuals/m^2), compared to the absence of urchins (Figure 17). The difference in abalone abundance did not differ significantly depending on the level of present urchin density thereafter (Figure 17).

According to the posteriori power analysis, to detect a significant difference in abalone abundance between survey years, a change of 0.6% or more in the abundances would be required between years. Therefore, a sample size of 482 abalone was required to detect a 2% change in abundance between survey years. An effect size of 0.5% per year is needed to determine differences in abalone abundance caused by protection length. Therefore, a sample size of 392 abalone was required to detect a 2% change in abundance with each added year of protection. The over-dispersion and zero-inflation of the abundance data means the calculated power and effect size was likely overestimated (Doyle 2009).

Table 10. Results from the generalized linear model assessing the differences in abalone abundance per 10m^2 across multiple variables. Results from the *Anova* function analyses for each variable presented. Estimate and SE results from the Tukey *summary* analyses for the mutli-leveled variables presented. (*p < = .05, **p < = .01, ***p < = .001).
Variables at the bottom of the table and marked with a "<" were removed from the model via backward stepwise regression when significance scores were greater than 0.1.

Response	**Explanatory**	**X^2**	**df**	**Estimate (β_1)**	**SE**	**p-value**	**Interpreted estimate exp(β_1)**
Abalone	Side	30.095	1	0.950	0.181	<0.001***	2.586
	Depth	6.668	2			0.036*	
	Shallow-Moderate			-0.515	0.338	0.268	0.598
	Moderate-Deep			0.457	0.226	0.102	1.579
	Shallow-Deep			-0.059	0.394	0.987	0.943
	Kelp density	8.747	3			0.033*	
	0-1			1.774	0.874	0.150	5.894
	0-2			1.749	0.872	0.158	5.749
	0-3			1.501	0.886	0.290	4.486
	1-2			-0.025	0.149	0.998	0.975
	1-3			-0.273	0.228	0.593	0.761
	2-3			-0.248	0.220	0.638	0.780
	Urchin density	15.431	3			0.001**	
	0-1			0.644	0.204	0.008**	1.904
	0-2			0.708	0.203	0.003**	2.030
	0-3			0.674	0.262	0.047*	1.962
	1-2			0.634	0.171	0.982	1.885
	1-3			0.031	0.250	0.999	1.031
	2-3			-0.033	0.248	0.999	0.968
	>Year	0.333	2			0.564	
	>Sand substrate	0.319	1			0.573	
	>Protection length	0.105	1			0.746	

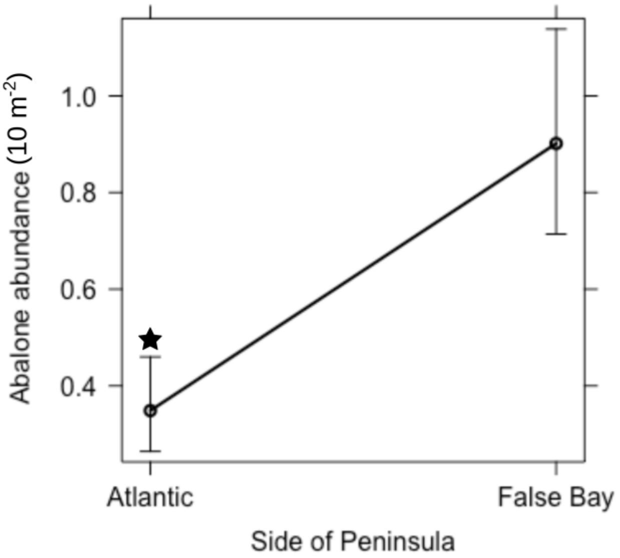

Figure 14. The effect of the side of the Cape Peninsula on the abundance of abalone per (10 m^{-2}), around the Cape Peninsula is shown with with 95% confidence intervals. Abundances measured in 2000, 2003 and 2019. The star indicates that the difference between abundaces in False Bay and the Atlantic is significant. Significance at p-value < 0.05.

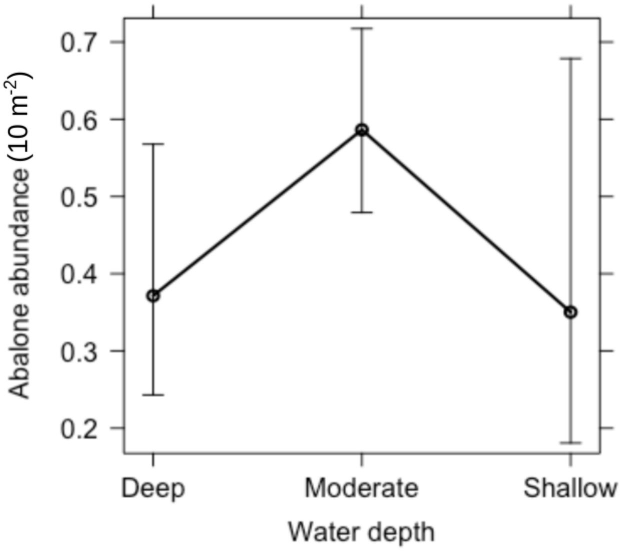

Figure 15. The effect of water depth on the abundance of abalone (10 m^{-2}), around the Cape Peninsula is shown with with 95% confidence intervals. Shallow = < 3 m; Moderate = 3 – 7 m; Deep = > 7 m. Abundances measured in 2000, 2003 and 2019. The rock lobster abundnaces differ significantly between depth levels. Significance at p-value < 0.05.

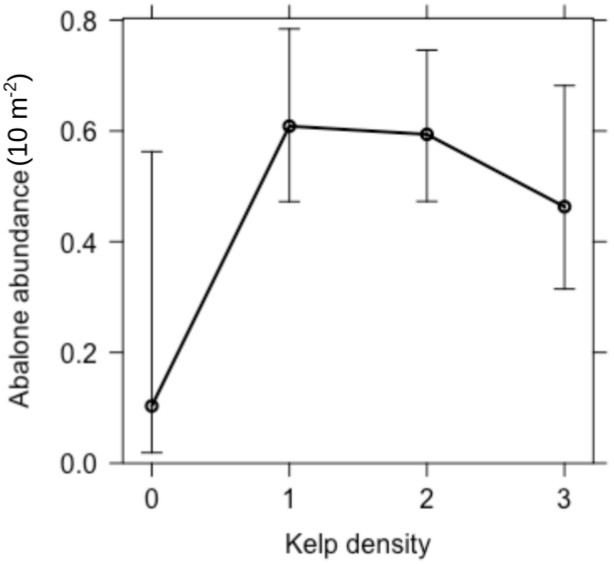

Figure 16. The relationship between kelp density and abalone abundance (10 m^{-2}), around the Cape Peninsula is shown with with 95% confidence intervals. Kelp density: 0 = 0 fronds/m^2; 1 = 1-2 fronds/m^2; 2 = 3-5 fronds/m^2; >5 fronds/m^2. Abundances measured in 2000, 2003 and 2019. The abalone abundances do not differ significantly at different kelp densities. Significance at p-value < 0.05.

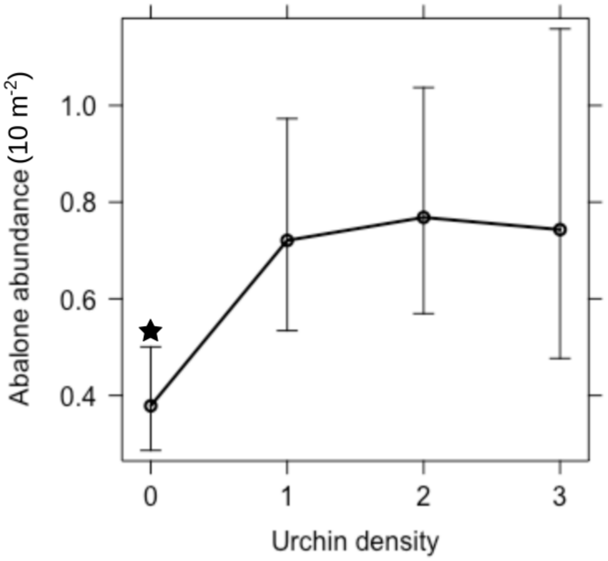

Figure 17. The relationship between urchin density and abalone abundance (10 m^{-2}), around the Cape Peninsula is shown with with 95% confidence intervals. Urchin density: 0 = 0 individuals/m^2; 1 = 1-9 individuals/m^2; 2 = 10-50 individuals/m^2; >50 individuals/m^2. The star indicates that the abalone abundace at urchin density 1 differs significantly to the rest of the density levels. Significance at p-value < 0.05.

Giant Periwinkle

The total number of giant periwinkle counted were lowest in 2003 and highest in 2019, and the average number of giant periwinkle per transect mirrored this trend (Table 11). The number of transects containing giant periwinkle increased from 2000 to 2009 and then decreased again in 2019 (Table 11).

Table 11. The total count, maximum count per transect, the average count, and the percentage of transects with zero counts of giant periwinkle recorded during SCUBA surveys along 10 m transects over the three survey years.

Year	Total count	Maximum count per transect	Average per transect (+SE)	% Transects with zero giant periwinkle
2000	158	25	0.32 (+0.07)	85.3
2003	112	10	0.23 (+0.04)	89.0
2019	385	26	0.75 (+0.09)	74.8

In the analysis of giant periwinkle abundance, all explanatory variables were retained in the model (Table 12). The overall effect of the survey year had a significant relationship with giant periwinkle abundance (Table 12). In the post-hoc analysis, only the difference between 2003 and 2019 was significant; the mean abundance in 2019 was more than twice that in 2003 (Figure 18). The giant periwinkle abundance was more than five times higher in False Bay than on the Atlantic coast of the Peninsula (Figure 19). Water depth also had a significant effect; 66.5% more giant periwinkle occurred in moderate depths than shallow water (Figure 20). Deep depths affected abundance more positively than shallow depths and more negatively than moderate depths; however, neither of these effects was significant. The presence of sand correlated to a 48.2% decrease in giant periwinkle abundance compared to the absence of sand (Figure 21).

Kelp density was negatively correlated with giant periwinkle abundance; giant periwinkle decreased by 72.9% in the presence of even the lowest density of kelp (Figure 22). When present the density of kelp did not affect the giant periwinkle abundance. In the presence of urchin density levels one and two, giant periwinkle abundance increased by 280.4% and 286.6%, respectively, compared to the absence of urchins. At level-three urchin density, the giant periwinkle abundance increased by 217.9% compared to no urchins; however, this result was not significant. The difference in giant periwinkle abundance did not differ significantly depending on the density of present urchins (Figure 23).

Table 12. Results from generalized linear model assessing the differences in giant periwinkle abundance per 10 m^2 across multiple variables. Results from the *Anova* function analyses for each variable presented. Estimate and SE results from the Tukey *summary* analyses for the mutli-leveled variables presented. (*p < = .05, **p < = .01, ***p < = .001).

Response	**Explanatory**	**X^2**	**df**	**Estimate (β_1)**	**SE**	**p-value**	**Interpreted estimate exp(β_1)**
Giant periwinkle	Year	17.288	2			<0.001***	
	2000 - 2003			-0.444	0.234	0.139	0.641
	2003 - 2019			0.832	0.212	<0.001***	2.298
	2000 - 2019			0.388	0.200	0.128	1.474
	Side	63.001	1	1.651	0.238	<0.001***	5.212
	Depth	10.385	2			0.006**	
	Shallow-Moderate			-0.833	0.309	0.018*	0.435
	Moderate-Deep			0.383	0.244	0.249	1.467
	Shallow-Deep			-0.450	0.376	0.444	0.638
	Sand substrate	8.942	1	-0.658	0.232	0.005**	0.518
	Kelp density	12.735	3			0.005**	
	0-1			-1.307	0.351	<0.001***	0.271
	0-2			-1.302	0.343	<0.001***	0.272
	0-3			-1.415	0.382	0.001**	0.243
	1-2			0.004	0.164	0.999	1.004
	1-3			-0.108	0.255	0.973	0.898
	2-3			-0.112	0.243	0.965	0.894
	Urchin density	22.405	3			<0.001***	
	0-1			1.031	0.254	<0.001***	2.804
	0-2			1.053	0.254	<0.001***	2.866
	0-3			0.779	0.316	0.063	2.179
	1-2			0.023	0.173	0.999	1.023
	1-3			-0.252	0.263	0.765	0.777
	2-3			-0.275	0.252	0.688	0.760
	Protection length	11.467	1	-0.023	0.007	0.001**	0.977

The length of formal protection had a negative effect on giant periwinkle abundance; with every year of protection, the abundance of giant periwinkle decreased by 2.3% (Figure 24). Size data were not recorded consistently for the giant periwinkle across all three years, and thus an analysis of the size structure across years was not conducted.

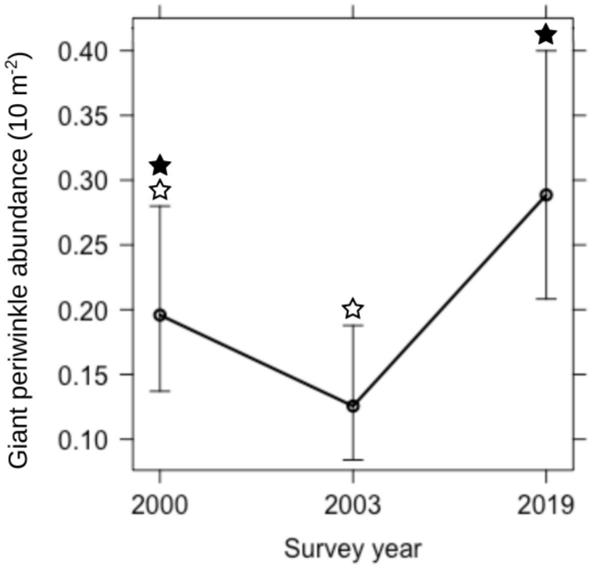

Figure 18. The effect of year on the abundance of giant periwinkle (10 m^{-2}), around the Cape Peninsula is shown with with 95% confidence intervals. Years not sharing a star differ significantly. Significance at p-value < 0.05.

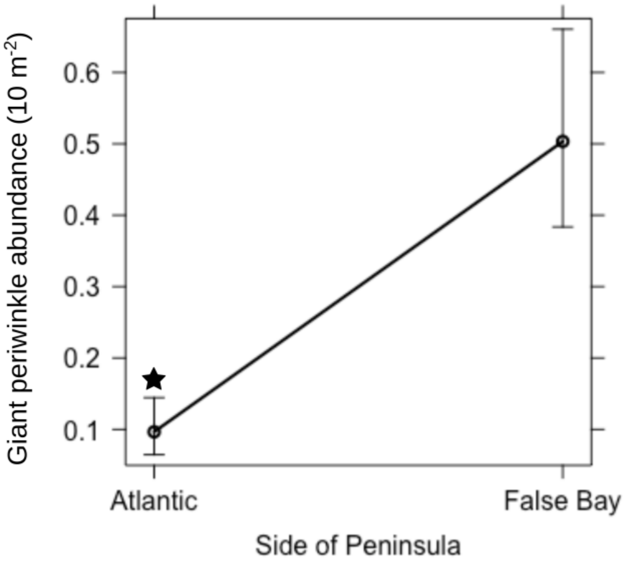

Figure 19. The effect of side of the peninsula on the abundance of giant periwinkle (10 m^{-2}), around the Cape Peninsula is shown with with 95% confidence intervals. Abundances measured in 2000, 2003 and 2019. The star indicates that the difference between abundances in False Bay and the Atlantic is significant. Significance at p-value < 0.05.

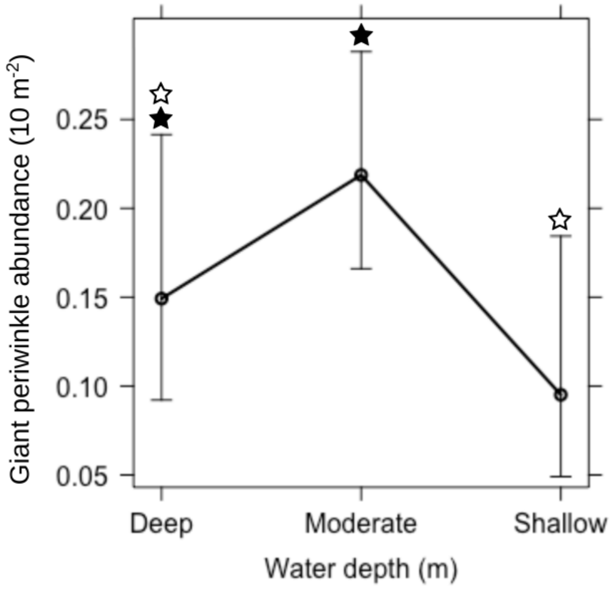

Figure 20. The effect of water depth on the abundance of giant periwinkle (10 m^{-2}), around the Cape Peninsula is shown with with 95% confidence intervals. Shallow = < 3 m; Moderate = 3 – 7 m; Deep = > 7 m. Abundances measured in 2000, 2003 and 2019. The giant periwinkle abundnaces at depths sharing a star do not differ significantly. Significance at p-value < 0.05.

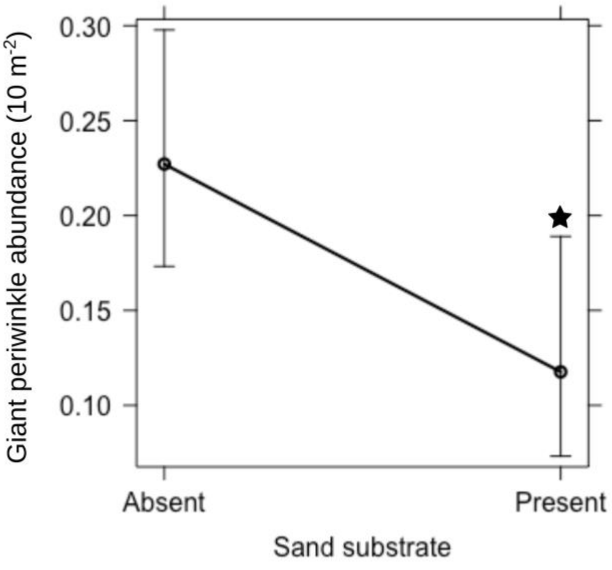

Figure 21. The effect of the presence and absence of sand on the abundance of giant periwinkle (10 m^{-2}), around the Cape Peninsula is shown with with 95% confidence intervals. Abundances measured in 2000, 2003 and 2019. The star indicates that the difference between abundaces in the absence and presence of sand is significant. Significance at p-value < 0.05.

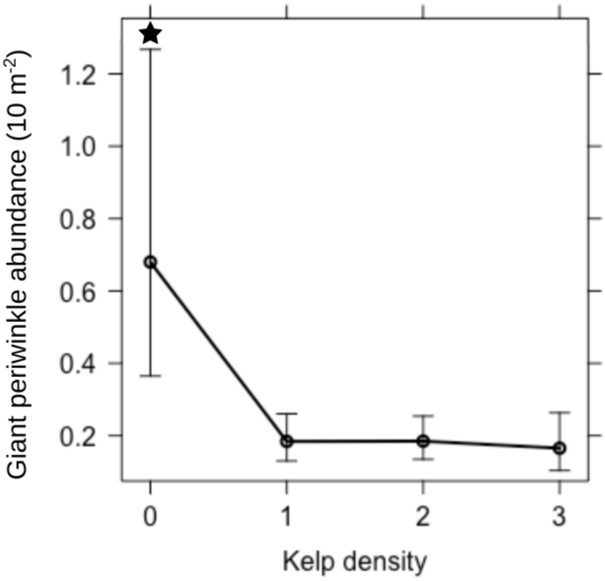

Figure 22. The relationship between kelp density and giant periwinkle abundance (10 m^{-2}), around the Cape Peninsula is shown with with 95% confidence intervals. Kelp density: 0 = 0 fronds/m^2; 1 = 1-2 fronds/m^2; 2 = 3-5 fronds/m^2; >5 fronds/m^2. Abundances measured in 2000, 2003 and 2019. The star indicates that the giant perwinkle abundance at kelp density 1 differs significantly from the rest of the density levels. Significance at p-value < 0.05.

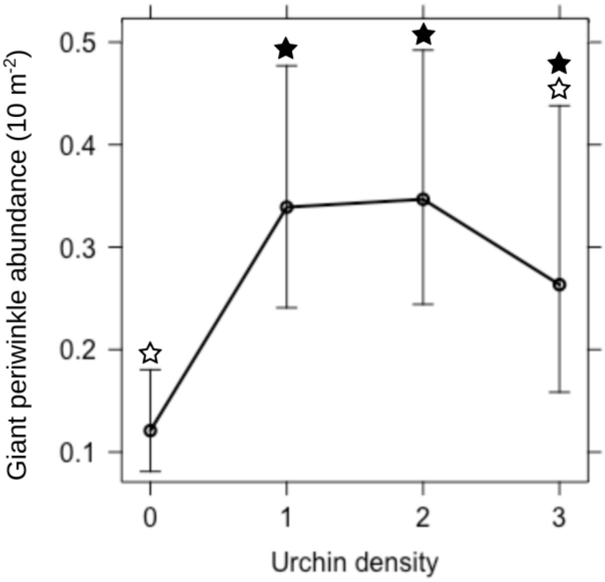

Figure 23. The relationship between urchin density and giant periwinkle abundance per (10 m^{-2}), around the Cape Peninsula is shown with with 95% confidence intervals. Urchin density: 0 = 0 individuals/m^2; 1 = 1-9 individuals/m^2; 2 = 10-50 individuals/m^2; >50 individuals/m^2. Abundances measured in 2000, 2003 and 2019. The giant periwinkle abundances at urchin densities sharing a star do not differ significantly. Significance at p-value < 0.05.

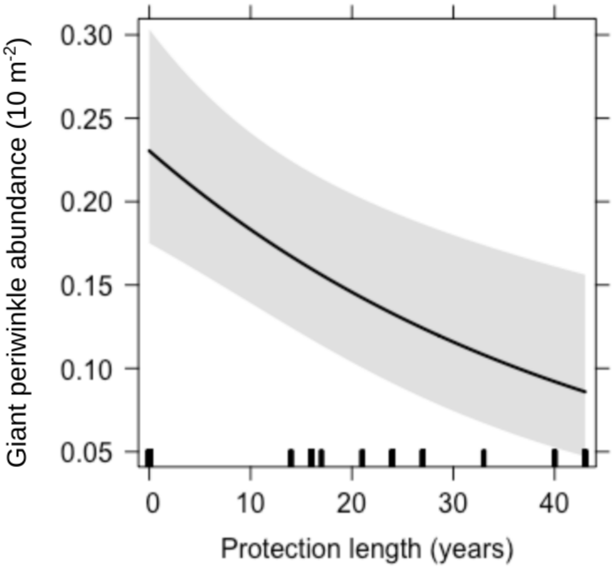

Figure 24. The effect of protection length on the abundance of giant periwinkle (10 m^{-2}), around the Cape Peninsula is shown with a 95% confidence interval. Abundances measured in 2000, 2003 and 2019. This relationship is significant. Significance at p-value < 0.05.

Discussion

Marine protected areas are widely accepted as pertinent conservation measures for restoring and protecting exploited species (Law 2000; Halpern 2003; Jones 2007; Sciberras et al. 2013). In this study, the abundances of three harvested marine invertebrate species from three different years, spanning 19 years, at sites located around the Cape Peninsula were analyzed to determine their relationship with formal protection and environmental variables. Overall, a decrease in rock lobster abundance, no change in abalone and an increase in giant periwinkle following the implementation of harvesting regulations was found. I found a positive effect of no-take zonation on rock lobster, no effect on abalone, and a negative effect for giant periwinkle, which was measured as the length of time each species was under formal no-take protection.

Rock lobster abundance benefited from the no-take zonation; however, this increase in abundance was not extended to the whole TMNP-MPA. In 2019 the abundance was lower than in both 2000 and 2003. Despite the positive effect of protection length in a combination of five no-take zones, there were fewer rock lobster in 2019, across the entire TMNP-MPA than before the establishment of the MPA. To determine the cause of this pattern, patterns in adult and juvenile abundances were analysed separately. The abundance of rock lobster below the legal harvest size (juveniles) mirrored that of the combined abundances, as they increased by more than half from 2000 to 2003. Conversely, the above-legal sized, or adult, rock lobster abundance decreased between these two years by almost 40%. When these results are considered together, they point towards increased recruitment success between 2000 and 2003 despite a reduction in the adult abundance. This could be evidence for a prior recruitment peak. Subsequent increases in the harvest of adults, particularly by way of poaching (Brill & Raemaekers 2013), likely drove the reduction in abundance in the years that followed, and reduced subsequent recruitment. Juvenile abundance decreased by 2019 to similar levels as surveyed in 2000.

The adult abundance also plummeted, with only 14.1% of the abundance recorded in the year 2000 present in 2019. The decreasing adult abundance seen between 2000 and 2003 could have continuously reduced recruitment success, thus reducing adult and juvenile numbers (Miller & Kendall 2009). However, the parallel increase in juveniles between 2000 and 2003 discounts this theory. Instead, juvenile harvesting likely increased from 2003 due to poaching, despite the implementation of the TMNP-MPA. Reducing juvenile abundance would have led to reductions in adults; thus, less recruitment, creating a positive feedback loop between reduced rates of recruitment success and reductions in the population (Botsford et al. 2019). The decreased juvenile abundance could also be attributed to an increase in predation (Pinnegar et al. 2000). If the TMNP-MPA successfully reduced harvesting pressure on fish stocks, then the recovering fish populations could have applied more predation pressure on the rock lobsters, especially the juveniles (Edgar & Barrett 2012).

The greater population surrounding the TMNP-MPA decreased by an average of 7.6% per annum between 2000 and 2016, equating to a 55% decrease in the rock lobster population overall (DFFE 2020). The decrease in rock lobster abundance within the TMNP-MPA between 2000 and 2019 was 28.9%, or 1.5% per annum. It is probable that the smaller decrease within the TMNP-MPA is not due to harvesting solely within this area but rather of the population as a whole. This suggests that the MPA still had a positive effect, although it was not protected from the overall trend. The overall decline might have acted as a sink (Sale et al. 2005) drawing out the otherwise increasing or stable numbers of rock lobster within the MPA. This reasoning is supported by the positive influence of the no-take zones within the MPA. The TMNP-MPA may have allowed the rock lobster abundance to grow, mitigating some of the harvesting pressure on the population outside of the MPA. Although rock lobster abundance did not increase around the Cape Peninsula, policing with the TMNP-MPA likely prevented further declines.

No changes in abalone abundance were detected between 2000, 2003 and 2019, nor with the length of formal no-take zonation. According to Cohen (1988), an effect size for linear regressions of 2% is considered small, 15% is medium, and 35% is large. Based on this interpretation, the difference needed in abalone abundance to detect effects of survey years and with each year of no-take protection is considerably small. To detect a 2% change in abalone abundance between survey years, a sample size of 482 was needed, and to detect the same difference with each year of protection, a sample size of 392 was needed. These numbers are far below the actual 1498 transects surveyed. This leads to the conclusion that the low p-values associated with these two variables reflect a genuine similarity (within 0.6%) in the abundance of abalone between survey years and the length of time under no-take protection. It is worth noting that because the abalone count data were over-dispersed and zero-inflated, the power and effect size calculated from the post-hoc analysis was likely over-estimated (Doyle 2009).

However, the effect sizes calculated here were small enough that this difference between the calculated and real estimates are likely negligible (Doyle 2009).

The greater abalone population is far below its historical levels, and the level that delivers optimal production (DFFE 2020). Therefore, it was expected that their abundance would have increased between 2003 and 2019 with the implementation of the TMNP-MPA. Additionally, the ban on recreational harvesting of abalone in 2004 should have further reduced harvesting pressure on the abalone population. This stable abundance could be evidence of continued abalone poaching undermining any positive population growth that the TMNP-MPA could have otherwise afforded the species. The lack of growth in the abundance, if not poaching related, could be attributed to changes in environmental carrying capacity, insufficient recruitment, or interspecies interactions (Pinnegar et al. 2000; Barrett et al. 2009; Miller & Kendall 2009). For example, the rock lobster population could have responded more rapidly to the implementation of the MPA, thus decreasing the urchin population and consequently preventing the abalone population from recovering to its previous size (Barrett et al. 2009). However, the reduction in the rock lobster abundance, since creating the TMNP-MPA opposes this theory. If the corresponding urchin abundance was recorded more explicitly, further conclusions could have been made about this interaction. If poaching occurs, it is unlikely to respect the formal boundaries of the no-take zone, so the result supports this theory that the abalone abundance within the no-take zones have not increased as seen in the TMNP-MPA as a whole.

The greater western abalone population yielded average annual declines of 1.5% across four management zones from 2000 to 2016 (DAFF 2016). Overall, the population decline over the period of 2000 to 2016 was 87%. This decline is a stark contrast to the findings in this study of a stable abundance within the TMNP-MPA. Although poaching is likely to have continued, the protection afforded to the abalone within the TMNP-MPA, regardless of zonation, was beneficial compared to that of the rest of the population. Even if the abalone abundance in the MPA did not recover, the MPA helped prevent the dramatic declines evident elsewhere. In a more mobile species a source-sink dynamic could draw individuals out of the MPA into the adjacent areas (Sale et al. 2005). Abalone are a slow growing species with limited motility (Jones 2008), with a dispersal distance limited to several kilometers (Morgan & Shepherd 2006), therefore the abundance in the MPA was protected to a degree not seen with the more mobile rock lobster.

The giant periwinkle abundance had increased considerably from 2003 to 2019, but there was no difference in 2019 from 2000. This suggests that high harvest rates before the establishment of the TMNP-MPA, coupled with the success of the TMNP-MPA in preventing giant periwinkle extraction, allowed their population to increase. The negative relationship between giant periwinkle abundance and the number of years of formal protection support this theory; the establishment of the TMNP-MPA has benefited giant periwinkle populations, but not inside the no-take zones. The increased giant periwinkle population could also be linked to an improvement in other favourable factors, such as the reduction in predators, namely the rock lobsters, or the lack of competition from abalone populations (Jenkins 2004). Giant periwinkle poaching may still have been present in the TMNP-MPA but sufficiently counteracted by decreased predation and increased recruitment success as has been recorded for similar taxa (eg. Quinn et al. 1993). There is a lack of population-wide data in the literature, so it cannot be concluded that this increase results from the protection afforded by the TMNP-MPA and not as a consequence of a greater population increase.

Despite the varied results, this study provides support for the use of MPAs as a protection measure for over-exploited macro-invertebrates. The extent of the success of this protection is evident by way of comparison with the magnitude of declines elsewhere. For the rock lobster and abalone, the decline in the MPA was less than that seen elsewhere. As both fisheries are heavily plagued by poaching, the MPA does appear to play a positive role in retarding the decline. The impact of no-take zones, and the enhanced policing brought by the TMNP-MPA as a whole, helped to buffer the declines of rock lobster and abalone, respectively.

Whether the site was on the west coast of the Cape Peninsula or eastward within False Bay had a substantial effect on all three species abundances. Previous studies comparing the composition of herbivorous invertebrates at sites on the west coast of the peninsula to sites in False Bay reported that abalone and giant periwinkle were almost absent at west coast sites, with stark increases at False Bay sites (Anderson et al. 1997; Pulfrich & Branch 2002). These findings are corroborated here. Giant periwinkle abundance was most influenced by this factor. Giant periwinkle were five times more abundant False Bay than on the Atlantic coast. In line with previous studies (Pulfrich & Branch 2002), rock lobster abundance was higher along the west coast. These patterns are likely caused by differences in environmental factors between the two marine ecoregions. The temperatures along the west coast are lower than those in False

Bay by about 2 °C (Smit et al. 2013). There is also a difference in nutrients between the two coasts as False Bay is sheltered from the southeasterly winds that cause the nutrient upwelling on the west coast (Griffiths et al. 2010; Sink et al. 2012). The warmer waters of False Bay could be a deterrent to the rock lobster, thus allowing the abalone and giant periwinkle protection from rock lobster predation (Mayfield & Branch 2000; Zeeman et al. 2014).

Rock lobster abundance increased with increasing water depths; deeper waters could provide more protection from poaching. This pattern is also in line with the natural range; they inhabit waters up to 30 m deep (Jones 2008), and our study only recorded abundance in depths up to 11 m, thus capturing only the first third of what is likely a normal distribution. Although depth did affect abalone abundance, no distinction between the different depth categories could be determined. This could be due to insufficient power when the abalone abundance is divided into smaller groupings (Cohen 1992). Giant periwinkle abundance was highest in moderate depths (3-7 m) and lower in shallow and deep water. This distribution of abundance among the three different water depth categories is inline with their range that extends to 10 m (Jones 2008).

Rock lobster and abalone abundance had a positive relationship with kelp density. The rock lobster abundances increased significantly with each increase in kelp density. The effect of different kelp densities on abalone abundance cannot be deciphered as there are not any significant effects between the levels, despite a very significant p-value overall. Again, like the water depth effect, insufficient data would explain why the power of the analysis deteriorated when the abalone abundance was divided into smaller groupings. The giant periwinkle had a negative relationship with kelp, with a significant increase in giant periwinkle in the absence of kelp. The kelp forests act as shelter for the animals living within them, protecting them from the force of wave action and predation, and provide food in the case of herbivores, like the abalone and giant periwinkle (Jones 2008; Zeeman et al. 2014). It was expected that the giant periwinkle would exhibit a positive relationship with kelp and have been reported to be restricted to kelp forests (Pulfrich & Branch 2002).

The rock lobster abundance and urchin density had a negative relationship, likely due to the predation of the urchins by the rock lobster (Mayfield & Branch 2000; Mayfield et al. 2001). The abalone and urchin abundances had a positive relationship, likely due to the reliance of the juvenile abalone on the urchins for shelter from predation (Tarr et al. 1996). These relationships reflect those reported by Mayfield and Branch (2000). This suggests a negative relationship between the rock lobster and abalone as an indirect interaction mediated by the urchins (Tarr et al. 1996; Mayfield & Branch 2000). The giant periwinkle abundance increases in the presence of urchins excepting the highest level of urchin density. However, the p-value associated with this relationship is borderline significant (Table 10). There is no evidence suggesting that the giant periwinkle relies on the urchins for survival in a similar way to the abalone, so perhaps this positive relationship reflects their parallel prey relationship with rock lobster. Like the alternative herbivore or predator dominated systems found by many studies (Breen & Mann 1976; Tegner & Dayton 1981; Pinnegar et al. 2000; Blamey & Branch 2012; Estes & Duggins 2019), my findings illustrate a predator dominated system, comprising more rock lobster, on the Atlantic seaboard, and a prey dominated system, comprising more abalone, giant periwinkle and urchins in False Bay.

Conclusions

The rock lobster abundance around the Cape Peninsula have decreased since the implementation of TMNP-MPA, which is in line with the overall decline of the rock lobster population in South Africa over this time. This decrease is likely due to increased harvesting of adults and juveniles above what regulations permit and potentially increased predation from recovering fish populations within TMNP-MPA. However, the enforcement of no-take zones within the MPA benefited the rock lobster abundance, despite the greater population reduction. The beneficial effects of the no-take zones are insufficient to compensate for harvesting in adjacent areas within the MPA, but could have prevented a greater decline in rock lobster. No change in abalone abundance was detected over the years in the TMNP-MPA or with no-take protection. The greater abalone population declined drastically over a similar period. Better policing than outside the MPA likely prevented the abalone abundance in the MPA from following suit. Giant periwinkle abundance had increased since the establishment of TMNP-MPA. It is unknown if this pattern reflects that of the regional giant periwinkle population, and so we cannot say the increase is a direct result of the MPA. However, the giant periwinkle abundance did not benefit from the no-take zones, suggesting that general harvest restrictions have allowed the population to increase as a whole. This study supports the use of MPAs as a protection measure for over-exploited macro-invertebrates, although on its own the TMNP-MPA is clearly unsuccessful in reversing population-wide trends. The causes of the declines, most likely rampant poaching, will still need to be addressed.

A combination of environmental factors could explain the decreased abundance of rock lobster in False Bay compared to those along the west coast of the peninsula. Predation by rock lobster on giant periwinkle and abalone could explain the opposite pattern found in both the giant periwinkle and abalone distributions. Expected abundance patterns based on the habitat preferences of each species, associated with water depth, the presence of sand, and kelp and urchin density were found.

Caveats

The composition of kelp bed communities is determined by multiple factors, environmental and ecological (Dayton et al. 1998; Rothman 2015). Water temperature is the main environmental factor that influencing marine communities (Barry & Dayton 1991), but wave action, substrata, disturbance, depth, nutrients and tides are also influencing factors (Dayton et al. 1998; Rothman 2015). In this study, only depth and substrata were included as factors in the models, and thus the conclusions drawn about these influences and the protection length, year, and species interactions are limited. The other environmental factors mentioned above should ideally have been included in this study to make conclusions about all the factors influencing the abundance and composition of the study species.

The time of year of the surveys was also not consistent, with some survey periods falling over multiple seasons. Rock lobster, for one, shifts from inshore to offshore depending on the season (Mayfield & Branch 2000). Not accounting for the time of year or not confining the surveys to a constant season may have created confounding factors. The extended break in monitoring between 2003 and 2019 does limit the ability to interpret the observed patterns; the reduced juvenile population in 2019 could have been a result of one year of unsuccessful recruitment. More consistent monitoring would have made for more certain conclusions.

There were two levels of site specific dependency that were not taken into account in the analysis. Firstly, each site had multiple transects which could have resulted in more similar variables and species abundances to each other than adjacent and nearby sites. Secondly, in each survey year the same sites were revisited, so site specific phenomena might have influenced the results.

Incorporating poaching pressure as a variable to better determine the causes of the observed abundance patterns could enhance the conclusions of this study. More measures of poaching such as reports from tip-lines, law-enforcement seizure data, distances of each site from human settlements, or the accessibility to each site from the shore could be useful in further analyses of the data.

References

Anderson RJ, Carrick P, Levitt GJ, Share A. 1997. Holdfasts of adult kelp Ecklonia maxima provide refuges from grazing for recruitment of juvenile kelps. Marine Ecology Progress Series **159**:265–273.

Attwood CG, Harris JM, Williams AJ. 1997a. International experience of marine protected areas and their relevance to South Africa. South African Journal of Marine Science **18**:311–332.

Attwood CG, Mann BQ, Beaumont J, Harris JM. 1997b. Review of the state of marine protected areas in South Africa. South African Journal of Marine Science **18**:341–367.

Awad AA, Griffiths CL, Turpie JK. 2002. Distribution of South African marine benthic invertebrates applied to the selection of priority conservation areas. Diversity and Distributions **8**:129–145.

Barkai A, Branch GM. 1988. Contrasts between the benthic communities of subtidal hard substrata at Marcus and Malgas Islands: A case of alternative stable states? South African Journal of Marine Science **7**:117–137.

Barrett NS, Buxton C, Barrett NS, Buxton CD, Edgar GJ. 2009. Changes in invertebrate and macroalgal populations in Tasmanian marine reserves in the decade following protection. Journal of Experimental Marine Biology and Ecology **370**:104–119.

Barry JP, Dayton PK. 1991. Physical Heterogeneity and the Organization of Marine Communities BT - Ecological Heterogeneity. Pages 270–320 in J. Kolasa and S. T. A. Pickett, editors. Springer New York, New York, NY.

Blamey LK, Branch GM. 2012. Regime shift of a kelp-forest benthic community induced by an ‘invasion’ of the rock lobster Jasus lalandii. Journal of Experimental Marine Biology and Ecology **420–421**:100–109.

Bolton JJ, Anderson RJ, Smit AJ, Rothman MD. 2012. South African Kelp Moving Eastwards: The Discovery of Ecklonia Maxima (Osbeck) Papenfuss at De Hoop Nature Reserve on the South Coast of South Africa. African Journal of Marine Science **34**:147–151.

Botsford LW, White JW, Hastings A. 2019. Population Dynamics for Conservation. Oxford University Press, Oxford.

Branch G, Branch M. 2018. Marine Protected Areas. Pages 299–307 Living ShoresRevised ed. Penguin Random House South Africa, Cape Town.

Branch GM, Griffiths CL, Field JG. 1988. Progress report to SEREF - December 1988: Monitoring the effects of new conservation areas in False Bay. Rondebosch, Cape Town.

Breen PA, Mann KH. 1976. Changing lobster abundance and the destruction of kelp beds by sea urchins. Marine Biology **34**:137–142.

Brill GC, Raemaekers SJPN. 2013. A decade of illegal fishing in Table Mountain National Park (2000-2009): trends in the illicit harvest of abalone Haliotis midae and West Coast rock lobster Jasus lalandii. African Journal of Marine Science **35**:491–500.

Centre for Marine Studies. 2001. Stock assessment of exploited invertebrate subtidal reef species and characterisation of habitat types along the coast of the Cape Peninsula National Park ZA 5027. Cape Town.

Champely S. 2020. pwr: Basic Functions for Power Analysis.

Cohen J. 1988. Statistical power analysis for the behavioral sciences. L. Erlbaum Associates, Hillsdale, N.J.

Cohen J. 1992. Statistical Power Analysis. Current Directions in Psychological Science **1**:98–101. SAGE Publications Inc.

DAFF (Department of Agriculture, Forestry and Fisheries). 2016. Status of the South African marine fishery resources 2016. Cape Town.

Day E, Branch GM. 2000a. Evidence for a positve relationship between juvenile abalone Halitosis midae and the sea urchin Parenchinus angulosus in the South-western Cape, South Africa. South African Journal of Marine Science **22**:145–156.

Day E, Branch GM. 2000b. Relationships between recruits of abalone Haliotis midae, encrusting corallines and the sea urchin Parechinus angulosus. South African Journal of Marine Science **7615**:137–144.

Day E, Branch GM. 2002a. Effects of sea urchins (Parechinus angulosus) on recruits and juveniles of abalone (Haliotis midae). Ecological Monographs **72**:133–149.

Day EG, Branch GM. 2002b. Influences of the sea urchin Parechinus angulosus (Leske) on the feeding behaviour and activity rhythms of juveniles of the South African abalone Haliotis midae Linn. Journal of Experimental Marine Biology and Ecology **276**:1–17.

Dayton PK, Tegner MJ, Edwards PB, Riser KL. 1998. Sliding Baselines , Ghosts , and Reduced Expectations in Kelp Forest Communities. Ecological Society of America **8**:309–322.

DFFE (Department of Forestry, Fisheries and Environment). 2004. Marine Living Resource Act ,1998 (Act no. 18 of 1998): Declaration of the Table Mountain National Park Marine Protected Area. (Notice 695). Government Gazette, 26431, 4 June.

DFFE (Department of Forestry, Fisheries and Environment). 2020. Status of the South African marine fishery resources 2020. Cape Town.

Doyle SR. 2009. Examples of computing power for zero-inflated and overdispersed count data. Journal of Modern Applied Statistical Methods **8**:360–376.

Edgar G J, Russ G R, Babcock R C. 2007. Marine protected areas. Pages 534-565 In Marine Ecology S.D. Connell and B.M. Gillanders, editors. Oxford University Press.

Edgar GJ, Barrett NS. 2012. An assessment of population responses of common inshore fishes and invertebrates following declaration of five Australian marine protected areas. Environmental Conservation **39**:271–281.

Estes JA, Duggins DO. 2019. Sea Otters and Kelp Forests in Alaska : Generality and Variation in a Community Ecological Paradigm. Ecological Society of America **65**:75–100.

Fox J, Weisberg S. 2019. An {R} Companion to Applied RegressionThird. Sage, Thousand Oaks, CA.

Gillespie KM, Vincent ACJ. 2019. Tropical invertebrate response to marine reserves varies with protection duration, habitat type, and exploitation history. Aquatic Conservation: Marine and

Freshwater Ecosystems **29**:511–520.

Griffiths CL et al. 2004. Impacts of human activities on marine animal life in the Benguela: A historical overview. Oceanography and Marine Biology: An Annual Review **42**:303–389.

Griffiths CL, Robinson TB, Lange L, Mead A. 2010. Marine biodiversity in south africa: An evaluation of current states of knowledge. PLoS ONE **5**.

Haley CN, Blamey LK, Atkinson LJ, Branch GM. 2011. Dietary change of the rock lobster Jasus lalandii after an ‘invasive’ geographic shift: Effects of size, density and food availability. Estuarine, Coastal and Shelf Science **93**:160–170.

Halpern BS. 2003. The impact of marine reserves: Do reserves work and does reserve size matter? Ecological Applications **13**:117–137.

Hardin G. 1968. Tradegy of the commons. Science **162**:1243–1248.

Hilborn R, Sinclair ARE. 2021. Biodiversity protection in the 21st century needs intact habitat and protection from overexploitation whether inside or outside parks. Conservation Letters **e12830**:1–4.

Hockey P, Buxton C. 1989. Conserving biotic diversity on southern Africa’s coastline. Pages 289–309 in B. J. Huntley, editor. Biotic diversity in southern Africa: concepts and conservation. Oxford University Press, Cape Town.

Hothorn T, Bretz F, Westfall P. 2008. Simultaneous Inference in General Parametric Models. Biometrical Journal **50**:346–363.

Jones G. 2008. A feild guide to the marine animals of the Cape Peninsula. Southern Underwater Research Group Press, Hout Bay, Cape Town.

Jones PJS. 2007. Point-of-View: Arguments for conventional fisheries management and against no-take marine protected areas: Only half of the story? Reviews in Fish Biology and Fisheries **17**:31–43.

Kirkman SP et al. 2021. Evaluating the evidence for ecological effectiveness of South Africa’s marine protected areas. African Journal of Marine Science **43**:389–412. Taylor & Francis.

Law R. 2000. Fishing, selection, and phenotypic evolution. ICES Journal of Marine Science **57**:659–668.

Luypaert T, Hagan JG, McCarthy ML, Poti M. 2018. Status of Marine Biodiversity in the Anthropocene. Pages 57–82 in S. Jungblut, V. Liebich, and M. Bode-Dalby, editors. YOUMARES 9 - The Oceans: Our Research, Our Future. Springer Open, Oldenburg, Germany.

Mayfield S. 1998. Assessment of predation by the West Coast rock lobster (Jasus lalandii) : relationships among growth rate, diet and benthic community composition, with implications for the survival of juvenile abalone (Haliotis midae). University of Cape Town.

Mayfield S, Branch GM. 2000. Interrelations among rock lobsters, sea urchins, and juvenile abalone: implications for community management. Canadian Journal of Fisheries and Aquatic Sciences **57**:2175–2185.

Mayfield S, De Beer E, Branch GM. 2001. Prey preference and the consumption of sea urchins and juvenile abalone by captive rock lobsters (Jasus lalandii). Marine and Freshwater Research

52:773–780.

Miller B, Kendall AW. 2009. Population Dynamics and Recruitment. Pages 181–228 Early Life History of Marine Fishes. University of California Press.

Morgan LE, Shepherd SA. 2006. Chapter 6 - Population and Spatial Structure of Two Common Temperate Reef Herbivores: Abalone and Sea Urchins. Pages 205–246 in J. P. Kritzer and P. F. Sale, editors. Marine Metapopulations. Academic Press, Burlington.

Mukaka MM. 2012. Statistics corner: A guide to appropriate use of correlation coefficient in medical research. Malawi medical journal : the journal of Medical Association of Malawi **24**:69–71. The Medical Association Of Malawi.

Okes N, Burgener M, Moneron S, Rademeyer J. 2018. Empty Shells: An assessment of abalone poaching and trade from Southern Africa.

Pfaff MC et al. 2019. A synthesis of three decades of socio-ecological change in False Bay, South Africa: Setting the scene for multidisciplinary research and management. Elementa Science of the Anthropocene **7**.

Pinnegar JK et al. 2000. Trophic cascades in benthic marine ecosystems: Lessons for fisheries and protected-area management. Environmental Conservation **27**:179–200. UCT University of Cape Town Libraries.

Pulfrich A, Branch TA. 2002. Giant winkles in the Western Cape, South Africa. South African Journal of Marine Science **24**:161–183.

Quinn J, Wing SR, Botsford LW. 1993. Harvest Refugia in Marine Invertebrate Fisheries : American Zoologists **33**:537–550.

R Core Team. 2019. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria.

Raemaekers S, Hauck M, Bürgener M, Mackenzie A, Maharaj G, Plagányi ÉE, Britz PJ. 2011. Review of the causes of the rise of the illegal South African abalone fishery and consequent closure of the rights-based fishery. Ocean and Coastal Management **54**:433–445.

Rhode C, der Merwe AEB, Roodt-Wilding R. 2017. An assessment of spatio-temporal genetic variation in the South African abalone (Haliotis midae), using SNPs: implications for conservation management. Conservation Genetics **18**:17–31.

Rothman M. 2015. The phylogeny, biology and biogeography of the Southern African kelps Ecklonia maxima and Laminaria pallida. University of Cape Town.

Sale PF et al. 2005. Critical science gaps impede use of no-take fishery reserves. Trends in Ecology and Evolution **20**:74–80.

Sciberras M, Jenkins SR, Kaiser MJ, Hawkins SJ, Pullin AS. 2013. Evaluating the biological effectiveness of fully and partially protected marine areas. Environmental Evidence **2**:1–31.

Scott RJ, Griffiths CL, Robinson TB. 2012. Patterns of endemicity and range restriction among southern African coastal marine invertebrates. African Journal of Marine Science **34**:341–347.

Shears NT, Babcock RC. 2003. Continuing trophic cascade effects after 25 years of no-take marine reserve protection. Marine Ecology Progress Series **246**:1–16.

Sink KJ et al. 2012. National Biodiversity Assessment 2011: Technical Report. Volume 4: Marine and Coastal Component. Pretoria.

Smit AJ, Roberts M, Anderson RJ, Dufois F, Dudley SF, Bornman TG, Olbers J, Bolton JJ. 2013. A coastal seawater temperature dataset for biogeographical studies: Large biases between in situ and remotely-sensed data sets around the coast of South Africa. PLoS ONE **8**.

Stander GH. 1990. Aspekte van de beskerming en benutting van Valsbaai. Cape Towm.

Steinberg J. 2005. The illicit abalone trade in South Africa.

Tarr RJQ, Williams PVG, MacKenzie AJ. 1996. Abalone, sea urchins and rock lobster: A possible ecological shift that may affect traditional fisheries. South African Journal of Marine Science **17**:319–323.

Tegner MJ, Dayton PK. 1981. Population structure, recruitment and mortality of two sea urchins (Strongylocentrotus franciscanus and S. purpuratus) in a kelp forest. Marine Ecology Progress Series **5**:255–268.

Troell M, Robertson-Andersson D, Anderson RJ, Bolton JJ, Maneveldt G, Halling C, Probyn T. 2006. Abalone farming in South Africa: An overview with perspectives on kelp resources, abalone feed, potential for on-farm seaweed production and socio-economic importance. Aquaculture **257**:266–281.

van der Merwe E. 2009. Toward best management practices for the growth of the abalone Haliotis midae Linnaeus on a commercial South African abalone farm. University of the Western Cape.

Willis TJ, Millar RB, Babcock RC, Tolimieri N. 2003. Burdens of evidence and the benefits of marine reserves : putting Descartes before des horse ? Environmental Conservation **30**:1–14.

Zeeman Z, Branch GM, Pillay D, Jarre A. 2014. An experimental test of the effect of the abalone Haliotis midae on benthic community composition. Marine Biology **161**:329–337.

Appendix 1: Surveys carried out in each year by site. An “x” indicates a site was sampled by and a dark grey cell indicates the site was not sampled. The red line separates sites on the west coast from sites in False Bay.

Site	Year		
	2000	2003	2019
1	X	X	
2	X	X	
3	X	X	
4	X	X	
5	X	X	
6	X	X	
7	X	X	
8	X	X	
9	X	X	
10	X	X	
11	X	X	
12	X	X	X
13	X	X	X
14	X	X	X
15	X	X	X
16	X	X	X
17	X	X	X
18	X	X	X
19	X	X	
20	X	X	
21	X	X	
22	X	X	X
23	X	X	
23A		X	
24	X	X	X
25	X	X	
26	X	X	
27	X	X	X
28	X	X	
29	X	X	
30	X	X	X
31	X	X	
32	X	X	
33	X	X	X
34	X	X	
35	X	X	
36	X	X	X
37	X	X	
38	X	X	X
39	X	X	
40	X	X	
41	X	X	
42	X	X	X
43	X	X	
44	X	X	
45	X	X	X
46	X	X	
47	X	X	
48	X	X	X
49	X	X	
50A	X	X	
50B	X	X	X
50C	X	X	X
51	X	X	X
52	X	X	X
53	X	X	X
53A	X	X	
54	X	X	
55	X	X	
56	X	X	
57	X	X	
58	X	X	
59	X	X	
60	X	X	
62	X	X	
63	X	X	
64	X	X	
65	X	X	
66	X	X	X
67	X	X	X
68	X	X	X
69	X	X	X
70	X	X	
71	X	X	
73	X	X	
74	X	X	
75	X	X	
76	X	X	
77	X	X	
77A	X	X	X
78	X	X	
79	X	X	X
80	X	X	
81	X	X	X
82	X	X	
83	X	X	X
84	X	X	
85	X	X	X
86	X	X	
87	X	X	
88	X	X	X
89	X	X	X
91	X	X	
92	X	X	X
93	X	X	
94	X	X	X
95	X	X	
96	X	X	X
97	X	X	X
98	X	X	X
99	X	X	X
100	X	X	X
101	X	X	X
102	X	X	
103	X	X	
104	X	X	
105	X	X	
106	X	X	
107	X	X	
109	X	X	
110	X	X	
111	X	X	
112	X	X	
113	X	X	
114	X	X	
115	X	X	
116	X	X	
117	X	X	
118	X	X	
119	X	X	X
120	X	X	X
121	X	X	X
122	X	X	X
123	X	X	X
124	X	X	X
125	X	X	X
126	X	X	X
127	X	X	X
128	X	X	X
129	X	X	X
130	X	X	X
131	X	X	X
132	X	X	X
133	X	X	X
134	X	X	X
135	X	X	X
136	X	X	X
137	X	X	X
138	X	X	X
139	X	X	X
140	X	X	X
141	X	X	X
142	X	X	X
143	X	X	X
144	X	X	X
145	X	X	X
146	X	X	X
147	X	X	X
148	X	X	X
149	X	X	X
150	X	X	X
151	X	X	X
152	X	X	X
153	X	X	X
154	X	X	X
155	X	X	X
156	X	X	X
157	X	X	X
158	X	X	X
159	X	X	X
160	X	X	X
161	X	X	X
162	X	X	X
164	X	X	X

Appendix 2: Map of the Cape Peninsula and the locations of the sites where the abundance of abalone, rock lobster and alikreukel were surveyed.