

***Ecklonia maxima* kelp forests along a thermal gradient: community composition and recovery from disturbance**

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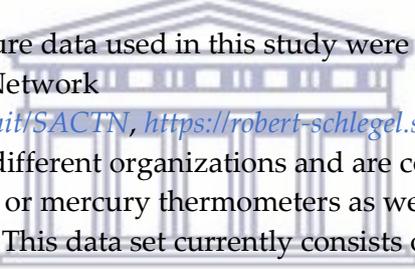
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Declaration

I declare that '*Ecklonia maxima* kelp forests along a thermal gradient: community composition and recovery from disturbance' is my own work, that it has not been submitted before for any degree or examination in any other university, and that all the sources I have used or quoted have been indicated and acknowledged as complete references.

Date: 19th April 2017

Signed:



Ross Mark Coppin



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Abstract

Climate change will influence species distributions, survival and ecosystem functioning, mostly through changes in sea surface temperatures and storm disturbance. Species are expected to shift poleward in response to ocean warming, which will increase species interaction strength, and cause tropicalisation of temperate ecosystems. Furthermore, if storm frequency and magnitude increases, this could have detrimental effects for species already on their thermal limits. One such group of coastal species is kelp. Kelp are ecosystem engineers that rely on cool-temperate water for survival, and which support an array of fauna and flora. Kelp-based ecosystems are also highly productive, and provide important inorganic input into coastal food webs, largely through detritus. Temperature and disturbance have been shown to be important drivers of kelp ecosystems globally, and we expect that local changes in these drivers may affect kelp ecosystem composition and functioning along the south-western Cape coastline where they form extensive habitats.

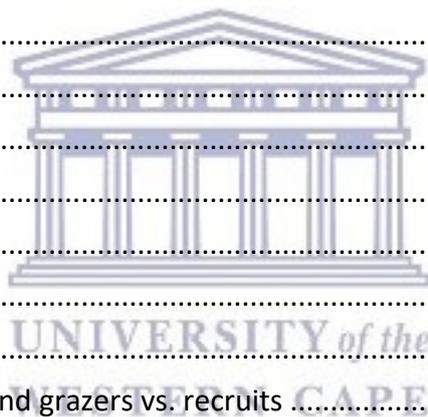
This project aimed to determine if kelp forest structure and recovery, through manipulation experiments, differed between study sites (Oudekraal, Bordjies Reef, and Betty's Bay) along the South African coastline, and whether these differences could be attributed to the sites' contrasting environmental regimes. The results showed that the sites in this study differed significantly in terms of benthic species composition and kelp population structure composition. Differences in the benthic species composition were most evident for the flora, while faunal species composition overlapped more. In terms of kelp population structure, the number of adults did not differ between sites; however, there were differences in recruit abundance between sites. The higher recruit abundance was attributed to heat wave events which took place during the study, which may have caused increases in spore release because of thermal stress. These differences were further linked to *in situ* characteristics such as the temperature climatology and presence/absence of important grazers. To a lesser extent, wave exposure, light, competition and space could conceivably also explain some of the differences observed. No differences in recovery were found between study sites, and both sites recovered to a similar state as before the kelp clearance experiment was initiated. There was some variation in benthic cover during the experiment, but no significant differences were found between the start and the end of the experiment. It was difficult to separate out direct effects of temperature, grazing, and other site characteristics. However, the consensus in the literature point to temperature as the main mechanism. Kelp ecosystems and their drivers are complex, and future studies should take a multi-factorial approach to be able to tease apart the direct effects of these important drivers.

Key words: Climate change, kelp, temperature, grazing, disturbance, top-down, bottom-up, species composition, temperate reef, ecology, benthos, kelp population.

Contents

Chapter 1 – Introduction	8
1.1 Global change: temperature and storminess as agents of change	9
1.2 Kelp ecosystems.....	10
1.3 Drivers of algae population structure	11
1.3.1 Temperature	11
1.3.2 Substratum type	12
1.3.3 Water motion.....	12
1.3.4 Canopy structure.....	13
1.3.5 Algal turf cover.....	13
1.3.6 Grazing	13
1.3.7 Kelp growth rate and size	14
1.3.8 Germination times	14
1.4 Climate change impacts on kelp ecosystems	14
1.4.1 Temperature	14
1.4.2 Disturbance	17
1.4.3 Upwelling and nutrients	19
1.5 An overview of South African kelp ecosystems.....	20
1.6 Structure of the thesis	22
1.6.1 Aims.....	22
1.6.2 Objectives.....	22
1.6.3 Null hypotheses	23
Chapter 2 – Benthic species composition of South African kelp forests between contrasting sites	24
2.1 Introduction	25
2.1.1 Kelp ecosystems.....	25
2.1.2 The South African context	25
2.1.3 Aim and objectives.....	27
2.1.3.1 Aim	27
2.2 Methods.....	27
2.2.1 Study sites	27
2.2.2 Data collection	29
2.2.3 Data analysis	30
2.2.3.1 Community analysis	30
2.2.3.2 Diversity and benthic cover	30
2.2.3.3 Abalone and rock lobster	30

2.2.3.4 Correlations.....	30
2.3 Results.....	31
2.3.1 Community analysis.....	31
2.3.2 Benthic cover.....	34
2.3.3 Abalone and rock lobster.....	35
2.3.4 Correlations.....	36
2.4 Discussion.....	37
2.4.1 Benthic community.....	37
2.4.2 Conclusion.....	40
Chapter 3 – Population structure of <i>E. maxima</i> along contrasting sites.....	42
3.1. Introduction.....	43
3.1.1 Global context.....	43
3.1.2 The South African context.....	44
3.1.3 Aim and objectives.....	44
3.1.3.1 Aims.....	44
3.2 Methods.....	45
3.2.1 Study sites.....	45
3.2.2 Data collection.....	45
3.2.3 Data analysis.....	45
3.3 Results.....	46
3.3.1 Kelp abundance.....	46
3.3.2 Adults vs. recruits and grazers vs. recruits.....	46
3.3.3 Stipe lengths.....	47
3.3.4 Temperature regime analysis.....	47
3.4 Discussion.....	49
3.5 Conclusion.....	51
Chapter 4 – Recovery of kelp population and associated benthos after a pulse disturbance event.....	53
4.1. Introduction.....	54
4.1.1 Temperature.....	54
4.1.2 Storm disturbance.....	54
4.1.3 The South African context.....	54
4.1.4 Aims and objectives.....	56
4.2 Methods.....	56
4.2.1 Study sites.....	56
4.2.2 Data collection.....	56



4.2.3 Data analyses	57
4.3 Results	57
4.3.1 Benthic community	57
4.3.2 Kelp population	60
4.4 Discussion.....	61
4.4.1 Benthic community	62
4.4.2 Kelp population recovery	63
4.4.3 Conclusion.....	64
Chapter 5 – Synthesis.....	65
Appendix: List of figures	86
List of abbreviations.....	87



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Chapter 1 – Introduction

1.1 Global change: temperature and storminess as agents of change

Marine ecosystems are maintained by a variety of complex interactions between abiotic and biotic variables such as temperature, pH, competition, and processes such as top-down and bottom-up control, predator-prey relationships and phenology (Doney et al. 2012). These abiotic and biotic variables, the interactions between them, and the various ecological processes, ultimately determine the community composition and ecological functioning of all ecosystems. Climate change directly and indirectly affects the way in which abiotic and biotic variables interact, but is often compounded by other impacts such as habitat destruction, pollution, and over-fishing (Blamey et al. 2015a). Temperature and storminess have been recognised as important variables with regards to climate-driven changes within the ocean. Mounting evidence shows that direct and indirect effects – in particular those that involve seawater temperature – can play important roles in determining species composition and ecosystem function (Walther et al. 2002; Doney et al. 2012). For instance, warming of the ocean may increase the stratification within the water column, and if this stratification is too intense, and if wind action is not great enough, it may prevent upwelling of important nutrients that may limit the overall primary productivity of coastal ecosystems (Doney et al. 2012). Increasing temperature is also expected to push species that are already at their thermal limit past their physiological ability to acclimatise to changing environmental conditions, which would lead to their extirpation or possible extinction (Wernberg et al. 2010, Doney et al. 2012). In general, species are expected to shift poleward under future climate scenarios, which would change species interactions and facilitate the ‘invasion’ of species into environmentally suitable regions from which they were previously absent (Walther et al. 2002; Doney et al. 2012). Climate change may also act in a facilitative manner with regards to species interactions. For example, temperature may increase grazing rates of herbivores, such as sea urchins, which may reduce the competition for space thereby facilitating settlement of macroalgae spores by reducing the competition for space. These possible changes may further lead to local shifts in species dominance and composition, and therefore the structure and spatial range of populations with subsequent alterations to ecosystem function.

Storm frequency and magnitude are also expected to increase due to larger atmospheric pressure gradients over the sea’s surface and the adjacent land, and this ultimately determines the strength of prevailing winds (Doney et al. 2012). On the other hand, it may also be argued that increases in strength of prevailing winds may in fact favour upwelling regimes, thereby increasing the frequency and magnitude of upwelling and subsequent nutrient delivery to the euphotic zone, where primary productivity would be enhanced (García-Reyes et al. 2015). However, a main and direct consequence of increased storminess concerns some of the important habitat-forming species, which are prone to be damaged by an intensification of waves and storm surges that would decrease habitat heterogeneity and reduce the resilience of associated ecosystems. Others may argue that disturbance may increase habitat heterogeneity, increase species richness, and increase resilience to disturbance (Chapman 1974, Thrush et al. 2008, McClain and Barry 2010). Habitat-forming species structure the environment around them, and processes that increase their rate of loss past a certain threshold could conceivably cause a shift to an alternative ecosystem state that may not provide the same ecosystem goods and services as in the unperturbed state

(Walther et al. 2002). An example of such an important ecosystem engineer is kelp, and these ecosystems are the focus of the rest of this chapter and thesis.

1.2 Kelp ecosystems

Kelps dominate approximately 25% of global, shallow, rocky reef ecosystems and play a significant role in the functioning of these ecosystems. Kelps are 'ecosystem engineers' that provide a critical 3-dimensional habitat for fauna and various flora, and they are also highly productive organisms (Ojeda and Santelices 1984, Dayton 1985, Steneck et al. 2002). The high productivity of kelps allows important nutrients to be exported to adjacent and distant habitats as allochthonous production, and therefore their role in the food web is not limited to the shallow subtidal zone; instead they are the base for many connected coastal food webs (Stuart et al. 1982, Dayton 1985, Bustamante and Branch 1996, Duggins and Eckman 1997, Kelly 2005, Miller and Page 2012, Krumhansl et al. 2014). Environmental factors such as nutrients (Jackson 1977, Field et al. 1980b, Fram et al. 2008), turbidity, light (Reed and Foster, 1984; Graham, 1997; Toohey et al., 2004; Wernberg et al., 2005; Bennett et al., 2015), sedimentation (Kennelly 1983, Vadas et al. 1992, Madsen et al. 2001, Schiel et al. 2006), temperature (Novaczek 1984, Wiencke 1989, Rothäusler et al. 2009, Wernberg et al. 2010, Bolton et al. 2012, Vergés et al. 2014, 2016, Basford et al. 2016) and hydrodynamics (Seymour et al., 1989; Dayton et al., 1992; Utter and Denny, 1996; Kawamata, 2001; Taylor and Schiel, 2003; Fowler-Walke et al., 2006) have been shown to affect the growth, recruitment and recovery of kelps (Wernberg et al. 2010, Mohring et al. 2014).

Kelps are also economically important as they are harvested for alginate production, fertilizer supplement and feed for abalone in aquaculture settings (Troell et al. 2006, Bolton et al. 2009). In addition, they provide habitat for other economically important species, such as reef fish, rock lobster and abalone. Kelps are dependent on cold or cool-temperate water for their survival, which means that changes in ocean temperature could affect the physiological and ecological well-being of kelp species, including the ecosystems they 'engineer' (Dayton et al. 1992, Wernberg et al. 2010, Doney et al. 2012). Since a whole host of interconnected environmental variables can affect the distribution of kelp, it is often difficult to identify the main environmental driver and to separate the direct effects from the indirect effects. However, most of the literature points towards temperature as being one of the main drivers of kelp ecosystems, and temperature stress may compound the effects of other variables.

The warming of oceans because of climate change will significantly affect the physiological functioning of kelps and their ecosystems more broadly. For example, a change in the ocean temperature may alter the ability of kelps to endure or recover from strong, local, short-term physical disturbances (Dayton et al. 1999), and if kelps are less resilient to such disturbance events, this may cause a shift to an alternative ecosystem state such as sea urchin barrens (Ebeling et al. 1985), algal turfs (Benedetti-Cecchi et al. 2015), communities of sessile suspension feeders (Jones 1973, Rossi and Snyder 2001, Etter and Miller 2008, Gorman and Connell 2009, Wernberg et al. 2016) and other community structures (Carr 1989, Dayton et al. 1998, Steneck et al. 2002, Provost et al. 2016). These alternative states have been shown to be less productive than the preceding kelp forests, and therefore, even though these states may be stable, they are not able to provide the necessary energy to adjacent or other

distant marine ecosystems and be able to maintain complex coastal food webs (Bustamante et al. 1995, Kelly 2005).

Kelps have been shown to react in one of three ways to climate change; they migrate, adapt or die. A study by Wernberg et al. (2010) showed that *Ecklonia radiata* (C. Agardh) J. Agardh can acclimatise to changing temperature conditions, but that this is done at a cost and only to a certain limit, which when exceeded, may drive the kelp past its physiological limits of persistence and recovery. Also, pulse events of high temperatures have been shown to cause reduction in kelp biomass and distribution (Smale and Wernberg 2013). These types of events are expected to increase in frequency and magnitude in future climate scenarios (Schlegel et al. 2017). In South Africa, the dominant kelp *Ecklonia maxima* (Osbeck) Papenfuss has shifted its distribution further east along the South African coastline. This shift in distribution is significant as this kelp population has been stable along the west coast for at least approximately 70 years prior to this (Bolton et al. 2012). This shift in distribution has been linked to a cooling of waters around the south-west coast (Rouault et al. 2010), allowing for kelps to move to these new environmentally suitable areas. Since kelps are habitat-forming organisms, the relatively recent shift in their distribution will more than likely have significant affects for temperate reef ecosystems along the South African coastline.

Climate change will ultimately affect the main drivers of kelp ecosystems, which include temperature, as well as disturbance (wave exposure, grazer intensity), and the frequency and magnitude of upwelling (nutrients). These factors have been investigated in the literature; however, local studies are lacking and more research is needed to fill the gaps in understanding how kelp forests will respond to climate change within the South African context.

1.3 Drivers of algae population structure

1.3.1 Temperature

Temperature is an important factor for developmental stages of macroalgae (Dayton 1985, Vadas et al. 1992). For young stages of kelps, optimal temperatures combined with the availability of nutrients create a 'window of opportunity' for gametogenesis (Deysher and Dean 1986). Optimal conditions differ from species to species as well as between different stages of kelp development (Vadas et al. 1992). For instance, the temperature optima for *Macrocystis pyrifera* (Linnaeus) C. Agardh gametogenesis, was defined as a range between 15–16°C (Deysher and Dean 1986, Gaitán-Espitia et al. 2014), while Bolton and Levitt (1985) showed that the growth rate of *E. maxima* gametophytes is optimal between 17.5–22.5°C. Temperature alone has also been negatively correlated with kelp recruitment, suggesting that temperature is important in the early stages of kelp development (Vadas et al. 1992, Connell and Russell 2010). Temperature may also determine the physiological functioning of individual kelp species, which in turn may affect growth rates, of recruits and sporophytes, as more energy is required for acclimatisation (Wernberg et al. 2010; Wernberg et al. 2011; Vergés et al. 2014, 2016). Temperature may act in combination with other abiotic or biotic variables. For instance, a study by Gaitán-Espitia et al. (2014) investigated the interactive effects of dissolved carbon dioxide and temperature on germination, dormancy and mortality of *M. pyrifera* zoospores. The results showed that the combination of increased

temperature and pCO₂ can significantly decrease germination rates and increase spore mortality. In their study, spore mortality only occurred under higher temperature and pCO₂ treatments. Temperature may also act synergistically with grazing. A study by Rothäusler et al. (2009) investigated the effects of temperature and grazing on growth, reproduction and survival of *M. pyrifera* and *Macrocystis integrifolia* Bory sporophytes. The grazer considered in this study was an amphipod *Peramphithoe femorata* Kroyer. Rothäusler et al. (2009) showed that at temperatures between 15–20°C (considered moderate), survival depended upon the presence or absence of grazers, but that survival increased under lower temperatures (below 15°C) due to lower degradation rates and increased growth rates, the latter compensating for loss of biomass from grazing.

1.3.2 Substratum type

Substratum type can affect the settlement of algae in various direct and indirect ways. The stability and nature of the surface itself plays an important role (Devlinny and Volse 1978; Vadas et al. 1992). For example, if the substratum is unstable it may affect the settlement as well as other early stages of algal recruitment, while the presence or absence of crustose algae may also have an effect (Gunnill 1986, Schiel et al. 2006). The nature of the surface also refers to if the surface is irregular or fairly 'smooth'; i.e. depressions in the surface area may act as ideal sites for attachment and settlement for certain species (Vadas et al. 1992). Sedimentation, which also affects the substratum characteristics, has also been shown to cause significant mortality for early stages of algae. Schiel et al. (2006a) investigated the effects of sedimentation on the recruitment of habitat-forming species and concluded that along with the effects of grazing, and results showed sedimentation had the largest effect on settlement of spores.

1.3.3 Water motion

Water motion affects settlement, attachment and survival of algal propagules and sporophytes (Vadas et al. 1992, Bettignies et al. 2013). In high water motion environments, settlement of algae is reduced unless depressions or uneven settlement surfaces exist (Vadas et al. 1992). Settlement of algae may occur in low flow niches; however, consequent growth is dependent on the assimilation of nutrients from the water column, which is enhanced by increased water motion (Hurd 2000). Mechanical dislodgement of individuals may occur in high water motion environments; however, some kelp species can adapt to the *in situ* hydrodynamic environment. A study by Kawamata (2001) showed an adaptive holdfast strategy of the kelp *Saccharina japonica* (Areschoug) C. E. Lane, C. Mayes, Druehl & G. W. Saunders *Laminaria japonica* to different wave environments, as well as different morphology based on wave exposure. Another study by Wernberg (2005) showed that *E. radiata* exhibited patterns of increased holdfast aggregation in wave exposed compared to wave-sheltered sites. Morphological plasticity was identified as an adaptive strategy to reduce mortality of individuals from intense wave exposure. Wave exposure (in combination with substratum) was also the main cause for kelp mortality in high wave energy environments in a study by Wernberg and Kendrick (2004). These latter authors showed that morphological attributes, such as thallus size, interacted with the hydrodynamic environment. Therefore, different stages of kelp development may perform better in different wave motion environments.

1.3.4 Canopy structure

The canopy structure of kelp forests may affect the early stages of algal settlement and recruitment through altering the light environment (Vadas et al. 1992, Bennett et al. 2015). There are obvious patterns with regards to recruit abundance and canopy cover, and therefore more quantitative approaches are needed in future studies (Vadas et al. 1992). The various mechanisms that have been inferred are competition for space (Wernberg and Goldberg 2008, Arkema et al. 2009), competition for light (Deysher and Dean 1986a, Edwards 1998), dislodgement by sweeping fronds (Velimirov and Griffiths 1979, Velimirov 1983, Denny 2014) and reduced light (Vadas et al. 1992, Bennett et al. 2015). Kelp canopies may also structure the physical environment around them. Wernberg et al. (2005) investigated the effects of *E. radiata* canopies on associated foliose algae. They showed that *E. radiata* canopies modify the physical environment by reducing light and sedimentation. However, other studies show that canopy effects do not reflect any changes in kelp abundance. For example, a local study by Rothman et al. (2006) showed that different harvesting techniques of kelp, which affected canopy structure and ultimately the light environment, did not have any significant effects on recruit abundance. Based on their results, the authors concluded that factors other than light are responsible for controlling the recruitment of understory algae. It is likely that the effects of canopy cover on early stages of algae development are site specific, and due to the lack of quantitative data on the mechanisms involved, they must be inferred. Furthermore, it is often difficult to separate the direct effects of canopy cover on algae populations from indirect effects.

1.3.5 Algal turf cover

Algal turf cover tends to affect recruitment of algae through limitation on space and the sweeping action of low lying turf, foliose or canopy algae (Velimirov 1983, Dayton 1985, Vadas et al. 1992, Connell and Russell 2010). Algal turf cover has been shown to reduce recruitment of *Macrocystis* spp., through reduction in space (Kennelly 1987, Vadas et al. 1992). However, in contrast (Brawley and Johnson 1992) showed that long-term survival of artificially recruited zygotes of *Pelvetia* was highest in dense algal turfs. This indicates that algal turf coverage has differing effects on recruitment of different kelp species. Invertebrates may also reduce space for settlement, therefore also playing a role in kelp recruitment. A study by Dayton (1973) showed a strong negative effect of mussels on the recruitment of *Postelsia* sp.

1.3.6 Grazing

Grazing is the main mechanism of mortality of young stages/juveniles of most algal species (Fricke 1979, Dayton 1985, Vadas et al. 1992, Andrew 1993, Sjøtun et al. 2006). Experiments by Dean et al. (1989) showed reduced survival of juvenile *M. pyrifera* in the presence of the white sea urchin, *Lytechinus anamesus* Clark, suggesting grazing effects. In extreme cases, grazing by sea urchins may cause a phase-shift. For instance, Ebeling et al. (1985) investigated the effects of storm disturbances on community structure in a southern California kelp forest. The loss of kelps after winter storms resulted in a loss of 'drift kelp', which is the primary food source for sea urchins *Strongylocentrotus franciscanus* Agassiz and *Strongylocentrotus purpuratus* Stimpson; predatory fish, which shelter in the kelp forests, also declined in abundance (Ebeling et al. 1985). The sea urchins were then released from

predation pressure and grazed down most of the understory kelps, shifting the system from a kelp-dominated system to an urchin 'barren' system, dominated primarily by urchins, crustose algae and patches of low turf algae (Ebeling et al. 1985). Grazing effects may also act in combination with other variables. For instance, Sjøtun et al. (2006) investigated the effects of sea urchin grazing and canopy-shading on recruitment of the kelp *Laminaria hyperborea* (Gunnerus) Foslie. The study showed that grazing by the sea urchin *Echinus esculentus* Mortensen, and canopy-shading (reduction in light environment) contributed significantly to the mortality of young kelps.

1.3.7 Kelp growth rate and size

Growth rate and size are important factors for mortality of kelp recruits. Some species of algae are capable of increasing cell division in the early stages of pre-recruitment processes, which allows for rapid growth rates. For example, in some species of Rhodophyta spores have multiple nuclei and therefore large amounts of DNA, which allows for almost unlimited cell division and DNA replication (Goff and Coleman 1986). This in turn allows species of algae to grow rapidly to a size that may preclude them from grazing, thereby decreasing mortality (Vadas et al. 1992). It is assumed that early stages of algal development are more vulnerable to predation than adult stages, and kelp is no exception (Vadas et al. 1992). A local study by Fricke (1979) noted that the abundant sea urchin *Parechinus angulosus* Leske, is unable to attach to adult *E. maxima* due to the sea urchin's small size and the local turbulent water conditions; instead the urchins only grazes juvenile kelp or younger stages.

1.3.8 Germination times

Species that have longer germination times often suffer greater mortality due to grazing, as an appropriate 'refuge size' cannot be achieved in time. However, spore viability may allow settled spores to begin germination during environmentally suitable times or 'recruitment windows', which may increase the likelihood of survival in some species; although, this differs between species (Vadas et al. 1992). For example, the spores of *Nereocystis* and *Agarum* spp. remain viable for over 16 years (Vadas et al. 1992), while those of *Sargassum muticum* (Yendo) Fensholt lose their viability after 2-3 weeks (Norton 1983).

1.4 Climate change impacts on kelp ecosystems

1.4.1 Temperature

The effect of temperature on the physiology of macroalgae may reduce their ability to recover after large storms or heat waves (Wernberg et al. 2010, 2013, Caputi et al. 2014). Temperature may directly affect macroalgae physiology through changes in growth and photosynthetic carbon uptake (Brown et al. 2014). Under warmer ocean temperatures these important functions may be reduced, making macroalgae more vulnerable to disturbance under future climate scenarios. Using long-term data sets, a study by Tegner et al. (1996) investigated if climate change had caused changes in Californian kelp forests. Their results showed a strong correlation between sea surface temperature and total kelp harvested, i.e. during periods of warming biomass of kelp was low resulting in a lower harvest.

Other factors acting with temperature may also play a role. Ling et al. (2009) for instance showed that over-fishing of an important predators, coupled with ocean warming, resulted

in overgrazing of macroalgae, and in severe cases can cause a switch to an urchin barren. Similarly, Steneck et al. (2004) showed that kelp forests in the Northern Atlantic have switched back and forth between alternative ecosystem states as a consequence of over-fishing of important apex predators. Macroalgae, such as kelps, can react to an increase in ocean temperatures in one of three ways: they can migrate, adapt or die (Biskup et al. 2014).

1.4.1.1. Migration

Biogeographical distributions of marine species, including kelps, are largely temperature dependent (Dayton 1985, Jeffree and Jeffree 1994, Schils and Wilson 2006, Sorte et al. 2010, Anderson et al. 2012) and changes in ocean temperature, through global warming are likely to impact these distributions (Ling and Johnson 2009, Krumhansl et al. 2016). Smale and Wernberg (2013) present evidence to show that extreme warming events, which are expected to increase in frequency and magnitude with climate change, can cause changes to species distributions. Biogeographical shifts of kelp species can already be seen in areas where ocean warming is occurring (see e.g. Müller et al. 2009, Bolton et al. 2012). Most kelp species are arctic and/or temperate organisms, and the warming of ocean temperatures is expected to cause a poleward shift in these species due to climate change (Bolton and Anderson 2012).

The South African kelp, *E. maxima*, has expanded its distribution along the south-west coast to just east of Cape Agulhus. This shift in distribution has been attributed to a cooling trend along the coast of South Africa (Bolton et al. 2012; Smit and Schlegel, 2017). This would support the more general observations on kelps globally, which tend to migrate poleward as they try to stay ahead of the body of warm water expanding meridionally away from the equator. This shift in kelp forest distribution probably also had a significant effect on the associated benthic community.

Range extensions of grazing herbivores and fish are causing phase-shifts in warming hotspots around the world (Vergés et al. 2014). For instance, Fodrie et al. (2010) has shown a warming induced increase in abundance of herbivorous fish, such as the parrotfish *Nicholsina usta* Valenciennes, in the northern Gulf of Mexico. The increase in grazing rates and the colonization by other algal species into these areas can reduce the ability of kelps to recover (Wernberg et al. 2010). Migration of other species may occur as well because of changing environmental conditions. For instance, in the early 1990s, *Jasus lalandii* Edwards, a well-known predator of grazers typically associated with kelp beds in the Western Cape, expanded its distribution south-eastwards along the South African coast (Cockcroft et al. 2008), radically transforming benthic reefs in this region (Blamey et al. 2010, Blamey and Branch 2012). Kelp forests once dominated by urchins, abalone and encrusting corallines are now dominated by understory algae, sessile species such as sponges and ascidians, and rock lobsters (Blamey et al. 2010); these beds are significantly different to adjacent kelp forests where rock lobsters are scarce (Blamey and Branch 2012). This example of invasion may be true for other organisms that may migrate to areas where they can exploit ecological niches and possibly outcompete other species resulting in localised extinctions or regime-shifts. However, more research is needed to better understand how climate change may affect these types of mechanisms within the South African context.

1.4.1.2. Acclimitisation

With climate change expected to increase ocean temperatures, kelp populations must acclimatise to survive, grow and reproduce. The ability of kelp to adapt to local conditions is well-known. For instance, a study by Biskup et al. (2014) investigated the functional response (primary production, metabolic rates, and rate of photosynthesis) of two kelp species to rising sea surface temperatures. The authors found that *Laminaria ochroleuca* Bachelot de la Pylaie exhibited a poor ability to acclimatise which was dependent on the kelp's life history traits. On the other hand, intertidal *Saccorhiza polyschides* (Lightfoot) Batters showed a higher physiological flexibility to changing temperature conditions compared to subtidal individuals. This may be because the intertidal experiences a wider range of temperature conditions compared to those in the subtidal, and therefore kelps in the intertidal are forced to adapt to harsher conditions where fluctuations in temperature, sunlight, turbidity and water motion are common. Although kelps may be able to acclimatise to changing environmental conditions, this acclimatisation is done at a cost. This was investigated by Wernberg et al. (2010), who looked at resilience of kelp beds along a latitudinal temperature gradient. They found that kelp abundance is likely to decline with the predicted warming of ocean waters, and although kelps can acclimatise and adjust their metabolic performance, which in turn allows them to change their physiological performance to mitigate the seasonal fluctuations in temperature, this is done at a great energy cost. The study showed that kelp beds in the northern regions had a lower resilience to perturbations, such as physical and biological disturbance, disease, competition from invasive species and decreasing water quality. This was as a result of low abundance of recruits, reduced physiological responsiveness and reliance on mature adult kelp for net recruitment, growth of recruits and recovery of canopy loss (Wernberg et al. 2010). Despite the difficulties in excluding the influences of other environmental parameters (sunlight, nutrients and wave exposure), Wernberg et al. (2010) found that temperature was most likely the main environmental driver of these effects. While kelps may be able to maintain populations in the warmer upper limits of their distributions, the cost of acclimation will make them more susceptible to other stressors such as disturbance from anthropogenic sources, disease, competition, grazing and decreasing water quality.

1.4.1.3 Extirpation/extinction

The effects of temperature on macroalgae may manifest themselves over short periods of time, which often leads to local extinction. Once macroalgae have been pushed passed their physiological ability to recover, and if environmental conditions causing the physiological stress continues, this may lead to local extinction. The work by Smale and Wernberg (2013) mentioned previously also showed that an important habitat-forming kelp species, *Scytothalia dorycarpa* (Turner) Greville, was eliminated from an area in Western Australia during a heat wave event. This population of *S. dorycarpa* was already located at the warmer end of its distribution and after the heat wave caused the population to be pushed past its physiological threshold, which lead to death. Other research by Wernberg et al. (2013) investigated the heat wave affects to overall community structure, and found significant differences before and after the heat wave in terms of macroalgae, sessile invertebrates and benthic fish communities. If the frequency and magnitude of heat waves are expected to increase, this would ultimately lead to more local extinctions and phase-shifts for species that are already on the edge of their distributional range.

1.4.2 Disturbance

Disturbance is another factor that can affect both the consumer and producer biomass, and therefore can alter top-down and bottom-up processes (Reed et al. 2014). Disturbance structures kelp communities, the term encompassing various mechanisms i.e. wave disturbance, grazer disturbance, and harvesting disturbance. As mentioned previously, the frequency and magnitude of storms are expected to increase under future climate models (Doney et al. 2012). If this were indeed the case, which increasing amounts of evidence confirms (Wendland 1977, Harley et al. 2006, Merzouk and Johnson 2011, Lionello et al. 2012, Voerman et al 2013, Sydeman et al. 2014, Blamey et al. 2015, García-Reyes et al. 2015), it would ultimately mean an increase in frequency of wave disturbance to kelp ecosystems.

Wave disturbance affects kelp through mechanical removal of kelp sporophytes due to high wave energy, and ultimately determines the standing biomass of kelp. For example a study by Cavanaugh et al. (2011) showed that wave motion was the main determining factor in determining *M. pyrifera* biomass in exposed regions, compared to sheltered regions. Another study by Britton-Simmons et al. (2008) used aerial photography to estimate the size of *Nereocystis luetkeana* (K. Mertens) Postels & Ruprecht beds, at sites adjacent to San Juan Island in Washington, in relation to tidal height. Tidal height data was collected every 10 minutes to quantify tidal height over the 2-year study period. The results showed that *N. luetkeana* beds decreased in visible bed size as current velocity and consequently tidal level increased. In high wave energy environments, wave disturbance may overwhelm other important physical and biological processes. For instance, a study by Reed et al. (2011) showed that in Central California, the excessive wave energy experienced by those kelp communities, was ultimately the main driver of structuring *M. pyrifera* communities in Central California. If storm frequency and magnitude does increase, it may lead to the failure of kelps to recover to its original state in terms of abundance; this may also be compounded by other climate change factors such as the effect of warming on kelp physiological functioning.

Kelp canopies act as important habitats for certain apex predators that control herbivore abundance as well as species seeking refuge from predators (Bodkin 1986, Anderson 2001). The failure of kelps to recover after storms could cause a shift in species composition or a phase-shift to a less productive system, such as algal turfs. The drop, in productivity could also have significant knock-on effects on other ecosystems reliant on organic input from kelp forests. A study by Bustamante et al. (1995) demonstrated this connectivity. They showed that intertidal temperate species rely on organic matter for survival, of which approximately 66% is derived from kelp forests. Furthermore, kelp forests support unique species assemblages compared to surrounding marine ecosystems, and therefore declines in kelp forests may threaten associated species and reduce the overall biodiversity of coastal ecosystems. Work by Ebeling et al. (1985) investigated the effects of storm disturbances on community structure in a southern California kelp forest. The loss of kelps due to winter storms resulted in the loss of drift kelp from the ecosystem, the primary food source for the sea urchins *S. franciscanus* and *S. purpuratus*. In addition, the loss of the giant kelps caused most predators to vanish from this system resulting in a trophic cascade as urchins were released from predation pressure and consequently were forced to graze down most of the understory kelps, which now served as an alternate food source (Ebeling et al. 1985). This shifted the system from a kelp-dominated system to an urchin barren, a system which is dominated primarily by urchins, crustose algae and patches of low turf algae. The impacts

on the detritus-based food web, which is an integral part in these ecosystems for fish and sea urchin populations, were severe (Ebeling et al. 1985). However, a subsequent storm removed grazing sea urchins from the newly formed barren, allowing the giant kelp and the understory kelp to regrow, which in turn allowed drift kelp to once again accumulate on the bottom, restoring the detritus food chain, increasing secondary production and fish densities (Ebeling et al. 1985). This study is one of many that reveal sea urchins as a major role player in structuring kelp ecosystems; other examples are given by Breen and Mann (1976), Lang and Mann (1976), Kenner (1992), Tegner and Dayton (2000), and Brown et al. (2014).

Alteration of primary production through consumer pressure is known as 'top-down' control. This generally occurs when trophic interactions between grazers and their associated predators are strong, which ultimately determines the type and amount of plant biomass available (Reed et al. 2014). A well-known example of top-down control comes from Duggins (1980) who investigated the role of sea otters *Enhydra lutris* Linnaeus, in structuring kelp forests through experimental manipulations in Alaska. Experimental removal of sea urchins resulted in development of macroalgae in areas where it was not previously present. These results were further verified by monitoring areas where sea otters had recently been translocated. The results showed a marked increase in kelp biomass following the return of sea otters and the authors attributed this to a reduction in grazing pressure because of sea otter predation on the urchins. A similar example is described by Estes and Duggins (1995) who described a higher kelp abundance where herbivore abundance was low and sea otters were present. Salomon et al. (2000) demonstrated top-down control of community structure on temperate reefs in New Zealand, through experimental removal of the dominant sea urchin *Evechinus chloroticus* Valenciennes from urchin barrens. Their results showed that over a 12-month period, the habitat changed from a crustose coralline algal dominated habitat to a macroalgal dominated habitat.

While urchin barrens are common in most parts of the world (Watanabe 1984, Vanderklift et al. 2009), they are not common along the South African coast, likely due to turbulent waters, the small size of the urchin *P. angulosus* and the abundance of kelp detritus that are the primary food source for *P. angulosus* (Anderson et al. 1997). However, *P. angulosus* can still graze on kelp recruits (Anderson et al. 1997). Climate change may alter grazing pressure through range shifts of organisms that can exert a top-down influence on kelps. For instance, a study by Vergés et al. (2014) showed that increased grazing rates, or phase-shifts, are as a result of tropical organisms extending into ranges that were once temperate. Other work by Ling et al. (2009) showed that warming along the eastern coast of Tasmania has allowed the range extension of *Centrostephanus rodgersii* Agassiz, which has overgrazed local kelp forests leading to a loss of biodiversity. This, coupled with over-fishing of an important predator of *C. rodgersii*, led to a phase-shift into urchin barrens. These types of phase-shifts increases grazing pressure in macroalgal systems that are already stressed physiologically and therefore abiotic factors may act synergistically with biotic factors to compound the effect of climate change in these systems.

In South Africa, because of the economic importance of *E. maxima*, much research has focused on the effects of harvesting on kelp populations, as harvesting may be regarded as a type of disturbance. For instance, a study by Levitt et al. (2002) looked at the effects of harvesting methods on the recovery of kelp and the benthic understory biota. Their results showed recovery of kelp after two years, with no notable differences in the understory

communities. Rothman et al. (2006) investigated the effects of different harvesting techniques on *E. maxima* population structure, growth rate, and recruitment. Even though the different harvesting techniques essentially altered the light environment (through changes in canopy cover), the authors found no differences between the treatments and concluded that factors other than light played a role in kelp recruitment. Another example by Anderson et al. (2006) investigated the effects of kelp harvesting on three obligate, red algal epiphytes. The results of their field manipulation experiments showed that epiphyte communities only fully recovered ~4.5 years later.

1.4.3 Upwelling and nutrients

The roles that abiotic factors and primary productivity have in structuring communities is known as 'bottom-up control' (Reed et al. 2014). In the context of kelp forests and associated reefs, bottom-up refers predominantly to nutrients as a limiting factor, that, if limiting, will impair the productivity of the entire ecosystem. Jackson (1977) investigated the production of the giant kelp *M. pyrifera* in southern California and concluded that the most limiting factor to productivity of this species was nitrogenous nutrients.

The importance of nutrients in sustaining the productivity of kelps is well understood (Dayton 1985, Gaylord et al. 2012). Dissolved nitrogen and nitrate is important. However, research has also placed emphasis on phosphate for the optimal physiological functioning of kelps (Dayton 1985). Some kelps have the ability to store inorganic nitrogen in order to compensate for periods of low nutrient availability through the process of luxury consumption – this has been observed for *Laminaria* and *Macrocystis* species (Dayton 1985, Gaylord et al. 2012). Nutrient stratification is also an important factor, particularly for canopy-forming kelps. The concentration of nutrients at the surface is important to the functioning and maintenance of the canopy. For instance, kelp canopies in California often deteriorate in the summer months when surface nitrate levels are low (Jackson 1977). Water motion is important in the assimilation of nutrients from the water column and kelp have been shown to adapt blade morphology in order to create more turbulence around the boundary layer of the frond to enhance nutrient assimilation (Wheeler 1980).

Temperature is closely linked with nutrient concentrations (Sydeman et al. 2014). Nutrients are often in higher concentrations in the water column during low temperature events. This is often an indication of upwelling, which brings cold and nutrient rich waters from subsurface layers to the surface of the water column (Waldron and Probyn 1992).

Temperature can also play a direct role in the uptake of nutrients through its effects on algal metabolism although this may vary from species to species (Raven and Geider 1988, Raikar et al. 2001). Most studies investigate multiple environmental factors (i.e. temperature, light and water motion), while studies investigating the direct role of temperature in nutrient assimilation in marine algae are lacking. Work by Rouault et al. (2010) showed that the South African coastline is exhibiting a cooling trend, which may be because of increased upwelling events. Following that, García-Reyes et al. (2015) showed that future climate scenarios may favour upwelling, although thermal stratification in the water column may hinder upwelling in the Eastern Boundary Upwelling Systems. A review by Blamey et al. (2015) showed an increase in upwelling frequency during the mid-1990s that coincided with an increase in southerly winds. Although future climate scenarios for South Africa are

difficult to predict, changes are still expected. These changes could have important implications for ecosystems, particularly habitat-forming organisms such as kelp.

Changes in upwelling regimes can have profound effects on the productivity of marine systems and variations in upwelling are expected in future climate scenarios (García-Reyes et al. 2015). For example, a study by Snyder et al. (2003) investigated the possible future changes in upwelling along the Californian coast. The authors projected an increase in upwelling due to an increase in the ocean-land temperature gradient because of global warming, and predicted that this will have impacts on ecosystem structure. A change in productivity could result in changes in bottom-up processes, which may lead to changes in ecosystem structure. There is consensus in the literature that upwelling regimes will in general increase, accompanied by a change in seasonality of upwelling regimes (Snyder et al. 2003, Doney et al. 2012).

1.5 An overview of South African kelp ecosystems

The South African coastline can be divided into three bioregions: the cool-temperate west coast; the warm-temperate south coast; and the sub-tropical east coast (Bolton 1986, Bolton and Stegenga 2002). Each region supports a different array of fauna and flora, with some overlap in terms of species composition at transition zones. The tip of the Cape Peninsula through to Cape Agulhas (Figure 2.1) acts as one such transition zone between the cold-temperate west coast and warm-temperate south coast (Bolton and Stegenga 2002). This transition allows for some striking differences in temperature regimes between the different coasts. South African kelp forests extend along the entire west coast to just east of Cape Agulhas on the south coast (Bolton and Stegenga 2002, Bolton et al. 2012). They are dominated by two species of kelp, *E. maxima* and *Laminaria pallida*, although two other less abundant species of kelp, *E. radiata* and *M. pyrifera*, are also found along the coastline.

Ecklonia maxima is a canopy-forming species that dominates the southern part of the west and south-west coasts (Branch and Griffiths 1988). In contrast, *L. pallida* is a sub-canopy species that replaces *E. maxima* in deeper waters. This latter species also dominates kelp beds further north along the west coast into Namibia (Branch and Griffiths 1988). Kelp forests along the west coast are characterised by large beds of red understory algae, filter-feeders (such as the ribbed mussel *Aulacomya ater* Molina and black mussel *Choromytilus meridionalis* Krauss) and the predatory west coast rock lobster *J. lalandii* (Field et al. 1980). East of Cape Point, in the transition zone, kelp forests are dominated by benthic herbivores and encrusting corallines, while understory algae are less abundant (Field et al. 1980; Anderson et al. 1997). In this region, the Cape sea urchin *P. angulosus* and the South African abalone *Haliotis midae* are the dominant herbivores, but others include the gastropods *Turbo sarmaticus* Linnaeus, *T. cidaris* Gmelin, and *Oxystele* spp. (Field et al. 1980, Tarr et al. 1996). A study by Velimirov et al. (1977) aimed to determine the faunal and floral boundaries, and biomass of kelp communities in South Africa. Oudekraal was the site used in this study. The results showed solar radiation, with wave and wind action being supplementary drivers. Wave action is important in assimilation of nutrients, and prevents grazers from climbing and attaching to kelp, as well as bending kelp over so that the abalone *H. midae* can trap fronds underneath their foot. The authors also concluded the small standing crop of grazers at the site (*Turbo*, *Haliotis* and the limpet *Patella compressa* Linnaeus – which lives on kelp stipes), suggests that little kelp production is passed on by means of grazing.

The economic importance of *E. maxima* has led to studies investigating the effects of harvesting on kelp populations, and their associated benthic community. For example, a study by Rothman et al. (2006) investigated the effects of three different harvesting techniques on *E. maxima* population structure, growth rate, and recruitment. The authors found no differences between the treatments and concluded that factors other than light may play a role in kelp recruitment, particularly at Bordjies Reef, False Bay. Levitt et al. (2002), investigated the effects of harvesting on re-growth and the understory benthic community at Danger Point, South Africa. The results showed a recovery time of 2 years in terms of associated benthos, biomass and density of kelp. Anderson et al. (2006), investigated the effects of kelp harvesting on three obligate, red algal epiphytes. The results of field manipulation experiments showed that epiphyte communities only fully recovered ~4.5 years later.

The role of upwelling on the west coast of South Africa, as a result of frequent and strong south-westerly winds during the summer months, has been shown to be an important driver of nearshore kelp ecosystems (Field et al. 1980; Newell et al. 1982). This seasonal upwelling brings nutrient rich waters to the surface and plays an important role in the productivity of kelps (Field et al. 1980). Under future climate scenarios, the upwelling regimes are expected to increase due to a change in wind intensity which alters temperature stratification within the water column. Models and predictions exist for areas such as California, however, there is a lack of literature on how the upwelling regimes along the coastline of South Africa may be affected. A review by Cury & Shannon (2004) investigated changes in pelagic fisheries with regards to the west coast upwelling cell. The authors showed by using satellite data and historical fisheries records that during periods of cool sea surface temperatures (SST), upwelling is stronger and this is reflected in phytoplankton and zooplankton biomass, while during warm events upwelling decreases due to the deepening of thermal stratification in the water column. These warm events coincided with a phase-shift in lower trophic levels of the food chain, which ultimately affects higher trophic levels. There is a trend of cooling around the South African coastline, which may be due to changes in wind intensity, which in turn favour upwelling regimes (Schlegel et al. 2017).

Primary productivity in kelp forests also supply important organic material to surrounding ecosystems. A local study by Bustamante et al. (1995) demonstrated this connectivity. They showed that intertidal species rely on organic matter for survival, of which approximately 66% is derived from kelp forests. Furthermore, kelp forests support unique species assemblages compared to surrounding marine ecosystems, and therefore declines in kelp forests may threaten associated species and reduce the overall biodiversity of coastal ecosystems. Another study by Stuart et al. (1982) using a modified $^{51}\text{Cr}:^{14}\text{C}$ twin-labelling technique showed that a large portion of the west coast ribbed mussel *A. ater*'s diet is obtained from kelp detrital material.

Jasus lalandii is a major predator in South African kelp ecosystems and other temperate reefs, and feeds on a wide variety of prey (Pollock 1979, Mayfield et al. 2000, 2001, van Zyl et al. 2003), although it does show preference for mussels, sea urchins and juvenile abalone (van Zyl et al. 1998, Mayfield and Branch 2000). Given their preference for certain prey, and their ability to scavenge (Barkai and McQuaid 1988), *J. lalandii* plays a powerful role in structuring benthic communities (Barkai and McQuaid 1988). The sea urchin, *P. angulosus*, is a conspicuous organism along the South African Cape coast and occurs in both the intertidal

and subtidal. Despite its abundance, *P. angulosus* is not considered an active grazer and instead tends to feed mainly on drift kelp (Day and Branch 2002); it may, however, feed on kelp sporophytes (Fricke 1979, Anderson et al. 1997). Direct grazing pressure by *P. angulosus* on kelp is therefore not at the same magnitude as their northern hemisphere counterparts (*S. franciscanus* and *S. purpuratus*) that are able to feed on both juvenile and adult kelps (Brown et al. 2014). Instead, *P. angulosus* plays a more facilitative role in which it provides shelter for juvenile abalone that seek shelter beneath its spines (Day and Branch 2000a, 2002) and nourishment from the trapped drift kelp (Day and Branch 2002). In addition, *P. angulosus* exhibits preferential feeding for certain types of species (Anderson and Velimirov 1982).

The direct mechanisms in which climate change would affect top-down control in South African kelp forests is unclear. However, climate change may expand range distributions of some species (e.g. *J. lalandii*) that may alter species composition through top-down mechanisms. In this way climate change may alter species compositions indirectly through range shifts in certain important predators. Furthermore, temperature may negatively affected kelp populations, which in turn, may have impacts on associated benthos, some of which are economically important.

1.6 Structure of the thesis

I have argued that temperature and disturbance are the main drivers of kelp forest ecosystem structure. Changes in climate will drive changes in these two important abiotic drivers of kelp forest ecology. However, there are gaps in knowledge within the South African context with regards to how temperature may affect species composition, as well as the recovery of kelp and its associated benthos from a disturbance event. If kelp ecosystems are not able to recover from disturbance events under future scenarios, this may lead to a regime shift to alternative ecosystem states that may be less productive, such as a turf-dominated system or a sea urchin communities. This would also have broader impact on surrounding ecosystems, as much of the energy produced in kelp forests sustains complex coastal food webs. Furthermore, it would also mean a decline in economically important species such as the west coast rock lobster and abalone, which may lead to broader socio-economic impacts. Therefore, given the economic and ecological significance of *E. maxima* in South Africa, it is important to elucidate the effects that temperature and disturbance may have on local kelp ecosystems.

1.6.1 Aims

Given that South African kelp forests are distributed across a temperature gradient (cold-temperate west coast and warm-temperate south-west coast), this project aims to investigate: (1) the structure of kelp forest communities across this gradient in the presence and absence of rock lobsters as the dominant predators: and (2) how kelps and the associated benthic species in the system will respond to a pulsed disturbance event along the temperature gradient.

1.6.2 Objectives

These aims were achieved through the following objectives:

1. To determine the diversity of benthic invertebrates and understory algae across sites.

2. To determine the kelp population structure at the selected sites.
3. To determine the recovery of benthic understory and kelp populations at these sites following a pulsed disturbance event.

1.6.3 Null hypotheses

1. H₀: Species composition and diversity of benthic invertebrates and understory algae will not differ between the three sites.
2. H₀: Kelp population structure will not differ between contrasting study sites.
3. H₀: Recovery of kelps and associated benthos following a pulsed disturbance event will not differ between sites.

The thesis is structured around five chapters: an introduction (this Chapter) wherein the justification and rationale for the research is made clear; three data chapters that address each of the hypotheses separately; and finally, a summary chapter.

Chapter 2 investigates the differences in species composition of *E. maxima* forests among three sites that capture the thermal gradient around False Bay and the Cape Peninsula. The sites also differ in the presence or absence of an important predator, *J. lalandii*. I show that there are differences in species composition between all three sites with regards to fauna and flora, which may be differences attributed to temperature, grazing and sedimentation.

In Chapter 3 I ask whether there are differences in the kelp population structure across the study sites. Inferences on kelp population structure are made on stipe length data, and abundance of adult and juvenile kelp. I find differences in kelp population structure among all three sites, and attribute these differences possibly to temperature and some other site specific characteristics such as grazing and sedimentation.

In Chapter 4 I investigate how kelp forests recover after an artificially-induced disturbance event. Kelp forest recovery was measured by following the change in kelp population abundance and size class distribution with time after impact; simultaneously, changes in the community composition of the associated benthos was also traced. This experiment was conducted over a 13-month period, with monitoring of sites before removal, 3-months, 6-months and 13-months after removal. I find no significant differences in change of the benthos during this time, but there are differences in kelp population recovery between sites over the 13 months.

In Chapter 5 I provide a synthesis of all the work completed, and highlight important aspects highlighted in this study, which future studies should investigate.

**Chapter 2 – Benthic species composition of South African kelp forests
between contrasting sites**



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2.1 Introduction

Kelps are a cold-water species of large brown algae, belonging to the order Laminariales (Kelly 2005). They are regarded as ecosystem engineers, providing a 3-dimensional habitat for a variety of fauna and flora. In addition, kelp ecosystems host a number of economically important species such as lobster, abalone and fish (Dayton 1985, Steneck et al. 2002).

Various abiotic (e.g. light, wave exposure, sedimentation) and biotic (e.g. grazing) factors structure kelp forests (Devlinny and Volse 1978, Dayton et al. 1992, Utter and Denny 1996, Toohey et al. 2004, Rothman et al. 2006, Sjøtun et al. 2006, Wernberg and Goldberg 2008, Pedersen et al. 2012). Variations in these factors ultimately affects the way kelp-associated benthos communities are structured (Dayton 1985, Guimaraes and Coutinho 1996, Wernberg and Goldberg 2008, Wernberg 2009).

2.1.1 Kelp ecosystems

Temperature is recognised as the main abiotic driver of marine species distributions (Dayton et al. 1992, Hiscock et al. 2004, Wernberg et al. 2011, 2013, 2016, Mabin et al. 2013). Given kelp's preference for cold-temperate waters, ocean warming poses a serious threat to these ecosystems (Wernberg et al. 2010, 2011, Vergés et al. 2016). In the absence of kelp, other types of systems may persist, for example algal turf, coralline reefs or urchin barrens (Vergés et al. 2016). These other systems support a different array of fauna and flora and are considered less diverse and less productive than kelp forests (Dayton 1985, Connell et al. 2008, Byrnes et al. 2011). In future climate scenarios, species distributions are expected to shift poleward in response to changing ocean temperatures. Given kelps are cold-water species, changes in ocean temperatures, particularly warming, could have detrimental effects on their growth, survival, reproduction and recruitment.

Other abiotic drivers such as light (Dayton et al. 1984, Bolton and Levitt 1985, Dieck 1993, Sjøtun et al. 2006, Wernberg and Goldberg 2008), sedimentation (Duggins et al. 1990, Vadas et al. 1992, Schiel and Foster 2006, Schiel et al. 2006) and water motion (Hurd 2000, Kawamata 2001, Mudge and Scrosati 2003, Scrosati and Mudge 2004, Wernberg and Goldberg 2008, Pedersen et al. 2012) have been shown to be important in the settlement, growth, and survival of kelp and biotic variables (e.g. see Black 1976, Kennelly 1983, Dayton et al. 1984, Harris et al. 1984, Carpenter 1990, Sivertsen 2006, Harley et al. 2012) play an equally important role in structuring kelp communities, through alteration in top-down and bottom-up control mechanisms (Breen and Mann 1976, Duggins 1980, Harris et al. 1984, Estes and Duggins 1995, Shears and Babcock 2002, Arkema et al. 2009, Blamey and Branch 2012)

2.1.2 The South African context

Ecklonia maxima a large canopy-forming kelp that dominates shallow temperate reefs off South Africa, particularly along the southern part of the west and the south-west coasts (Bolton and Stegenga 2002). The south-west coast is considered a transition zone between the cool-temperate west coast and warm-temperate south coast and is characteristic of a rapid change in ocean temperature as well as an overlap in species composition between the two coasts (Bolton and Stegenga 2002). Kelp forests on the west coast north of Cape Point are largely dominated by rock lobsters *Jasus lalandii*, filter-feeders (including the mussels *Choromytilus meridionalis* Krauss, and *Aulomya ater* Molina) and red understory seaweeds

(Field and Clark 1976, Field et al. 1980a, Leliaert et al. 2000, Levitt et al. 2002). Kelp forests east of Cape Point are grazer dominated (Anderson et al. 1997, 2006, Leliaert et al. 2000) and understory algae include a mixture of Ochrophyta, Chlorophyta and to a lesser extent Rhodophyta. These differences have been attributed largely to temperature but factors such as light, water motion, depth and grazer abundance may also play a role (Velimirov et al. 1977, Field et al. 1980, Leliaert et al. 2000, Bolton and Stegenga 2002, Levitt et al. 2002). East of False Bay, kelp ecosystems have recently undergone a shift in benthic communities because of an increase in abundance of *J. lalandii*, a well-known predator of benthic herbivores including the urchin *Parechinus angulosus* (Blamey et al. 2010, Blamey and Branch 2012).

The sea urchin *P. angulosus* is the dominant herbivore in South African kelp forests along the south-west coast (Velimirov et al. 1977, Field et al. 1980, Leliaert et al. 2000) however, turbulent waters and its small size prevent it from feeding on adult kelps. Instead the urchin is restricted to feeding mostly on kelp detritus, but also on juvenile kelps (Fricke 1979, Day and Branch 2002). The abalone *Haliotis midae* is also a notable herbivore in this ecosystem, but it too feeds predominantly on kelp detritus (Tarr et al. 1996, Mayfield and Branch 2000). This abalone is closely associated with *P. angulosus*, whereby juvenile abalone take refuge beneath urchin spines (Day and Branch 2000a, 2000b, Mayfield and Branch 2000).

The west coast rock lobster *J. lalandii* is known for its role in maintaining alternative stable states (Barkai and Branch 1988) and is a major predator of both *P. angulosus* and juvenile *H. midae* (Mayfield et al. 2001, Blamey and Branch 2012), particularly east of Cape Point where subtidal mussel beds are scarce. In the early 1990s, *J. lalandii* expanded its distribution east of False Bay (Cockcroft et al. 2008). Following the 'invasion' of rock lobsters, herbivore numbers declined significantly, most likely as a result of direct lobster predation, which resulted in an increased abundance of macroalgae and sessile invertebrates (Blamey et al. 2010, Blamey and Branch 2012). This suggests that the invasion of *J. lalandii* into these areas has resulted in the establishment of an alternative stable-state (Blamey and Branch 2012) and is an excellent example of the role that predators can play in transforming the structure and functioning of ecosystems, without directly disturbing kelp themselves.

Much of the past research on South African kelps has focused on kelp population dynamics in relation to different harvesting techniques, and the effects of temperature on physiology, growth, function and distribution. Research on kelp ecosystems have focused on understanding energy flow in this system and associated benthic community structures, as well as species interactions between key species. However, there is no recent work investigating differences in benthic species composition between kelp beds presenting contrasting temperature regimes and presence/absence of key predators. Given that temperature is a major driver of species distributions, this study offers a unique opportunity to investigate if kelp forest benthic species composition differs between cooler and warmer areas, and in the presence/absence of *J. lalandii*.

2.1.3 Aim and objectives

2.1.3.1 Aim

The aim of this research was to investigate the benthic species composition of kelp forests between sites that differ in their thermal climatology and absence/presence of a predator, *J. lalandii*, and to relate these findings to those of similar studies reported in the scientific literature.

Objectives

1. To assess the benthic community composition at three representative sites.
2. To examine the similarities and differences in the diversity of the benthic communities and cover types across the sites using an array of uni-and multivariate analyses.
3. To discuss the findings of my study in relation to similar research reported in the literature where effects have been attributed to temperature and grazers as drivers of community composition.

Null hypothesis

H₀: Species composition and diversity of benthic invertebrates and understory algae will not differ between the three sites.

2.2 Methods

2.2.1 Study sites

The South African coastline has been categorised into three marine provinces. These marine provinces are determined by temperature regimes and the resulting distribution of benthic fauna and flora. The west coast is characterised by cool water which extends as far north as Namibia, and is often referred to as the Benguela Marine Province with its southern limit around Cape Point. The annual mean temperature for areas along the west coast are generally between 12–14°C. However, there are rapid and wide temperature changes during periods of upwelling that may persist for days at a time. Due to the upwelling, nutrient concentrations are also more abundant in this region compared to regions outside of the influence of the Benguela Current. The west coast region has been termed as ‘cool-temperate’ region, which is defined as a region where mean monthly temperatures are always above 10°C and always below 15°C (Smit et al. 2013). East of Cape Point marks the beginning of an overlap or transition area, which is also referred to as the Benguela-Agulhas Transition Zone (Smit et al. 2013). This area is comprised of seaweed species representative of the Benguela Marine Province and the Agulhas Marine Province, which starts east of Cape Agulhas (Smit et al. 2013). The Agulhas Marine Province is characterised by a wide temperature range of up to 7°C difference between mean monthly temperatures between summer and winter (Smit et al. 2013). The study sites selected for this research are present within the Benguela Marine Province and the Benguela-Agulhas Transition Zone.



Oudekraal (Figure 2.1) is within the Benguela Marine Province and experiences the cold ocean temperatures and a higher nutrient flux typical of upwelling systems (Blamey et al. 2015a, Smit et al. 2016). Max temperatures of 18°C and 12°C are experienced in the summer and winter months respectively (Figure 2.2) (Schlegel et al. 2017). Bordjies Reef is just north of Cape Point, inside False Bay, and falls within the transition zone between the cool-temperate west and warm-temperate south coasts. This latter site is substantially warmer because it is characterised by reduced upwelling as well as a greater annual thermal variability (max of 22.5°C and 18°C in the summer and winter months respectively) by virtue of it being influenced by upwelling from the Benguela Current and the warming influence of the Agulhas Current (Smit et al. 2016, Schlegel et al. 2017). Betty's Bay is east of False Bay, but still within the transition zone and is now characterised by a greater abundance of rock lobster and fewer grazers, following the lobster invasion in the early 1990s (Blamey et al. 2010). It has a maximum temperature of 21°C and 18°C in summer and winter respectively and is thus like that of Bordjies Reef in terms of its thermal regime (Schlegel et al. 2017).

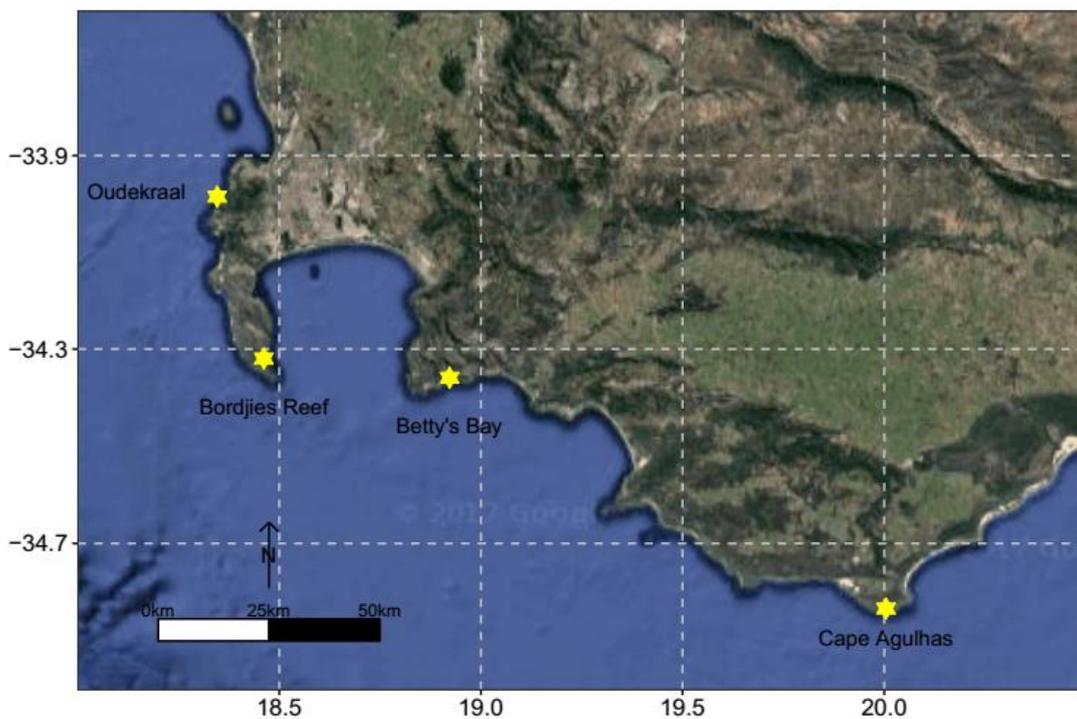


Figure 2.1: Map of South African coastline, and study sites

In terms of the topography, Oudekraal has a very heterogeneous topography due to the presence of large granite boulders. Bordjies Reef is a flat with small occasional rocky outcrops, while at Betty's Bay the kelps are located on reefs that are separated by kelp-free gullies.

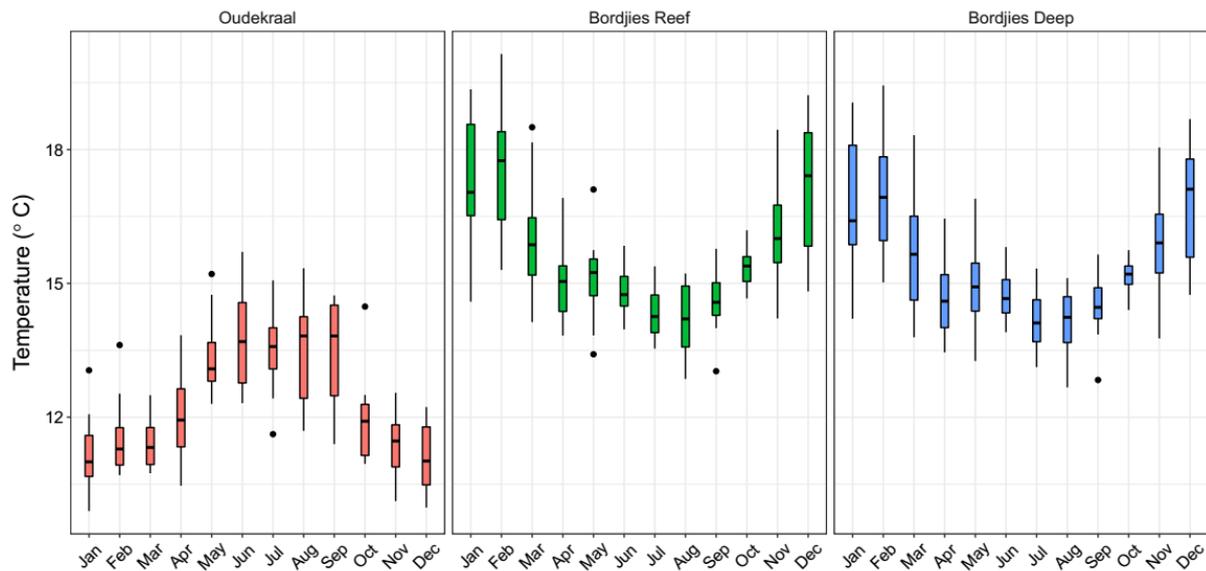


Figure 2.2: Monthly temperature data showing the yearly trend at each site for 2015. The black line represents the mean. The lower and upper 'hinges' correspond to the first and third quartiles, and the 'whiskers' are the 5th and 95th percentiles (SACTN 2017).

2.2.2 Data collection

At each site, two 16m diameter circular plots within the middle of the kelp beds were selected. Each plot was approximately 200m² in area. Long-term temperature loggers (StarOddi: Starmon mini) are located nearby at each site.

Each plot was permanently marked with a 0.5 m railway bar placed in the center of the plot and a GPS position recorded. Sampling of the plots involved SCUBA divers attaching a transect line to the railway bar at the center of the plot and swimming out 8m along predetermined compass bearings. Rock lobsters and abalone were counted within 1m either side of the transect. On the return swim towards the center of the plot 0.5 × 0.5m quadrats were sampled at 1m and 4m along the transect. The percentage cover of sand, rock, foliose algae, encrusting coralline algae, sponge, mussel and silt were estimated and recorded. Larger invertebrates such as abalone and rock lobster were counted and recorded 1m either side of the transect line. All other species encountered within the quadrats, except adult kelp and larger invertebrates mentioned above, were then scraped off, placed in collecting bags, and taken back to the laboratory where they were identified and weighed (wet and dry mass in grams). These steps were repeated on four different compass bearings giving: (1) a total of eight (0.5 × 0.5m) quadrats sampled for each of the two plot (i.e. 16 quadrats per site); and (2) a total of four 8m transects for each of the two plots for the rock lobster and abalone counts. Given the abundance of urchins at some sites, a mean biomass estimate was obtained for this species. This was achieved through collecting 50 individuals of *P. angulosus*, which were then oven dried, weighed and mean biomass calculated. Biological material in collecting bags, taken from the quadrats, were transferred to plastic sample bags. Back in the laboratory all samples were frozen at -20°C for later identification. All biological material were identified as far as possible to species and their wet and oven dry mass were measured and recorded.

2.2.3 Data analysis

All data analyses were done using the R software (R Core Team, 2016), and the vegan package (Oksanen et al. 2016) and ggplot2 (Wickham 2009). The Shapiro-Wilk normality test was run before any analyses to investigate the distribution of the data. All benthic data were first 4th root transformed before any analyses were run to down-weight species that had high biomass values and low abundance values, as this may have affected the ordination analysis. The transformed data was then used to generate a Bray-Curtis similarity matrix.

2.2.3.1 Community analysis

An analysis of similarity (ANOSIM) was run on 4th root transformed biomass data (macroalgae and invertebrates) to reveal if there were any differences in community composition between sites. A Similarity percentage (SIMPER) analysis was then run on the same data to confirm findings from the ANOSIM, as well as to identify the species contributing the most to any similarities/differences. A scatter graph was produced for species present at each site. This allowed for visual representation of similarities/differences in species present between sites. The Bray-Curtis similarity matrix was then analysed using non-metric multidimensional scaling (nMDS) and plotted. Hierarchical clustering using Ward's method (Ward 1963), was also used to aid in investigating any overall differences in community structure. Separate dendrograms were created for fauna and flora.

2.2.3.2 Diversity and benthic cover

Percentage cover data were pooled for each site to create averages, which were then plotted in the form of a bar graph. A SIMPER analysis was run on raw percentage cover data to determine what cover types were contributing most to the similarity/differences. A non-parametric Kruskal-Wallis test was used to investigate differences between sites. Boxplots were used to compare percentage cover between sites. These assessments served to verify results from the SIMPER analysis.

2.2.3.3 Abalone and rock lobster

A Kruskal-Wallis test was used to test for differences in abundances between sites. A combination of a boxplot with data points was used to visualise any differences in abundance of abalone and rock lobster between sites.

2.2.3.4 Correlations

Pearson correlations were performed for all cover data, as well as to data on the abundance of kelp recruits, kelp adults and sea urchins. Before any correlations were performed, the kelp data (recruits and adults) were first divided by a factor of four to scale the data to be comparable with percentage cover and sea urchin data. Correlations were visualised with the aid of a heatmap showing the correlation coefficient.

For all analyses performed, differences were considered statistically significant at $p < 0.05$.

2.3 Results

2.3.1 Community analysis

There was a clear distinction in benthic species composition between all three sites ($r = 0.795$, $p = 0.001$) (Figure 2.3). Further analysis supported this finding by revealing a 97.6% dissimilarity between Oudekraal and Bordjies Reef, a 90.1% dissimilarity between Oudekraal and Betty's Bay and a 94.5% dissimilarity between Bordjies Reef and Betty's Bay. Bordjies Reef was characterised by the dominance of the Cape sea urchin *P. angulosus*, while Oudekraal was characterised by abundance of Rhodophyta (red algae), and the ribbed mussel *A. ater*. Betty's Bay had a mixture of red and green algae, however, most of the species that occurred in Betty's Bay did not occur at the other two sites. Also, sponges dominated the benthic community at Betty's Bay; Bordjies Reef and Oudekraal had relatively low sponge biomass. The red seaweeds, particularly *Pachymenia carnosa* (J. Agardh) J. Agardh and *Pachymenia cornea* (Kützting) Chiang, had a high biomass at Oudekraal, were comparatively low at Betty's Bay and non-existent at Bordjies Reef (Figure 2.6). Species contributing most to the dissimilarity between Bordjies Reef and Oudekraal included the Cape sea urchin *P. angulosus*, the red seaweed *P. carnosa* and the brown seaweed *Bifurcariopsis capensis* (Areschoug) Papenfuss. Between Bordjies Reef and Betty's Bay important contrasting species were *P. angulosus*, various species of sponge and *B. capensis*. Finally, between Oudekraal and Betty's Bay, organisms contributing most to the dissimilarity, were sponges, *P. carnosa* and the west coast ribbed mussel *A. ater*.

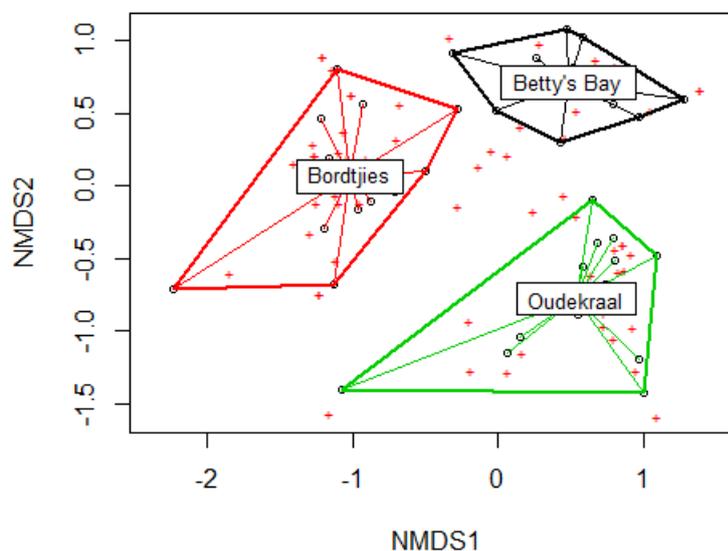


Figure 2.3: nMDS plot of all samples across the three sites, based on standardized fourth-root transformed biomass data for species. Black circles represent site scores, and red '+' signs represent species scores.

Hierarchical clustering was used to further clarify the distinction between sites, firstly for all species combined, and then for fauna and flora separately (Figure 2.4). The dendrogram showed a similar pattern to the nMDS plot, with clear dissimilarity between all three sites,

further indicating a clear distinction between macrobenthic community structures (Figure 2.4). The first group to cluster out comprised data mainly from Betty's Bay, followed by two separate clusters comprising data mainly from Oudekraal and Bordjies Reef respectively (Figure 2.4). When looking only at floral species composition, Bordjies Reef was more distinct from the other two sites and clustered out first (Figure 2.4), while there was more similarity between Oudekraal and Betty's Bay. In terms of faunal species composition, Oudekraal overlaps with both Bordjies Reef and Betty's Bay, but there is little overlap between Bordjies Reef and Betty's Bay (Figure 2.4).

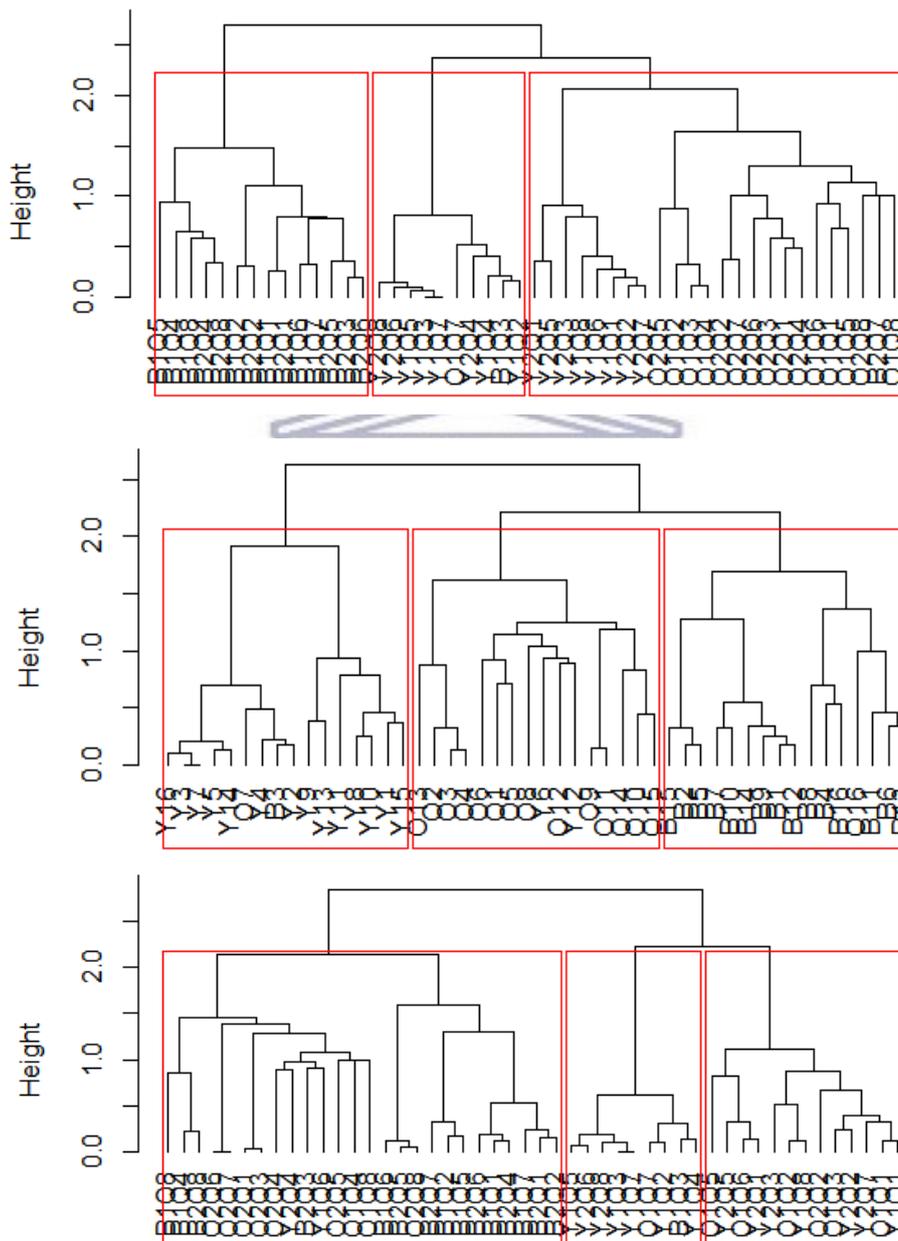


Figure 2.4: Hierarchical clustering of the quadrats across all sites for both flora and fauna (top), flora only (middle) and fauna only (bottom) using Ward's agglomeration method. B: Bordjies Reef; O: Oudekraal; Y: Betty's Bay.

Species richness was greatest at Bordjies Reef ($S = 40$), followed by Oudekraal ($S = 32$) and then Betty's Bay ($S = 19$). Shapiro-Wilk's normality test showed that diversity was normally distributed across sites ($w = 0.956$, $p < 0.05$). An ANOVA revealed a significant difference in diversity between sites ($p < 0.05$, Figure. 2.5). The *post-hoc* Tukey's multiple comparison procedure showed that the diversity was not significantly different between Oudekraal and Bordjies Reef ($p > 0.05$, Figure. 2.5) or Oudekraal and Betty's Bay ($p > 0.05$, Figure. 2.5). However, there was a significant difference between Bordjies Reef and Betty's Bay ($p < 0.003$, Figure. 2.5). Figure 2.5 shows the average species diversity for each site. Bordjies Reef had the highest average diversity, followed by Oudekraal, and Betty's Bay with the lowest value (Figure. 2.5). A complete species list for all sites is represented in Figure 2.6.

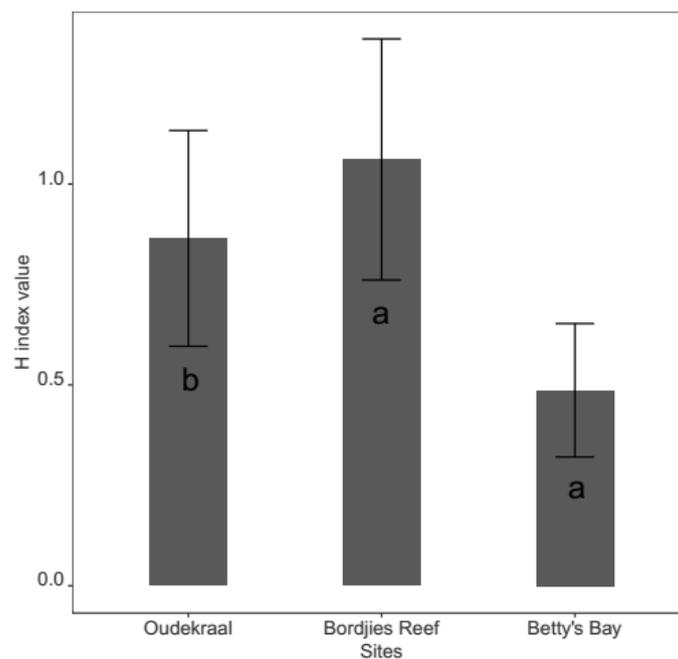


Figure 2.5: Shannon-Wiener index of diversity averaged over all replicates within each site. Error bars represent the 95% confidence interval. The symbols indicate significance; if bars share the same letter they are significantly different.

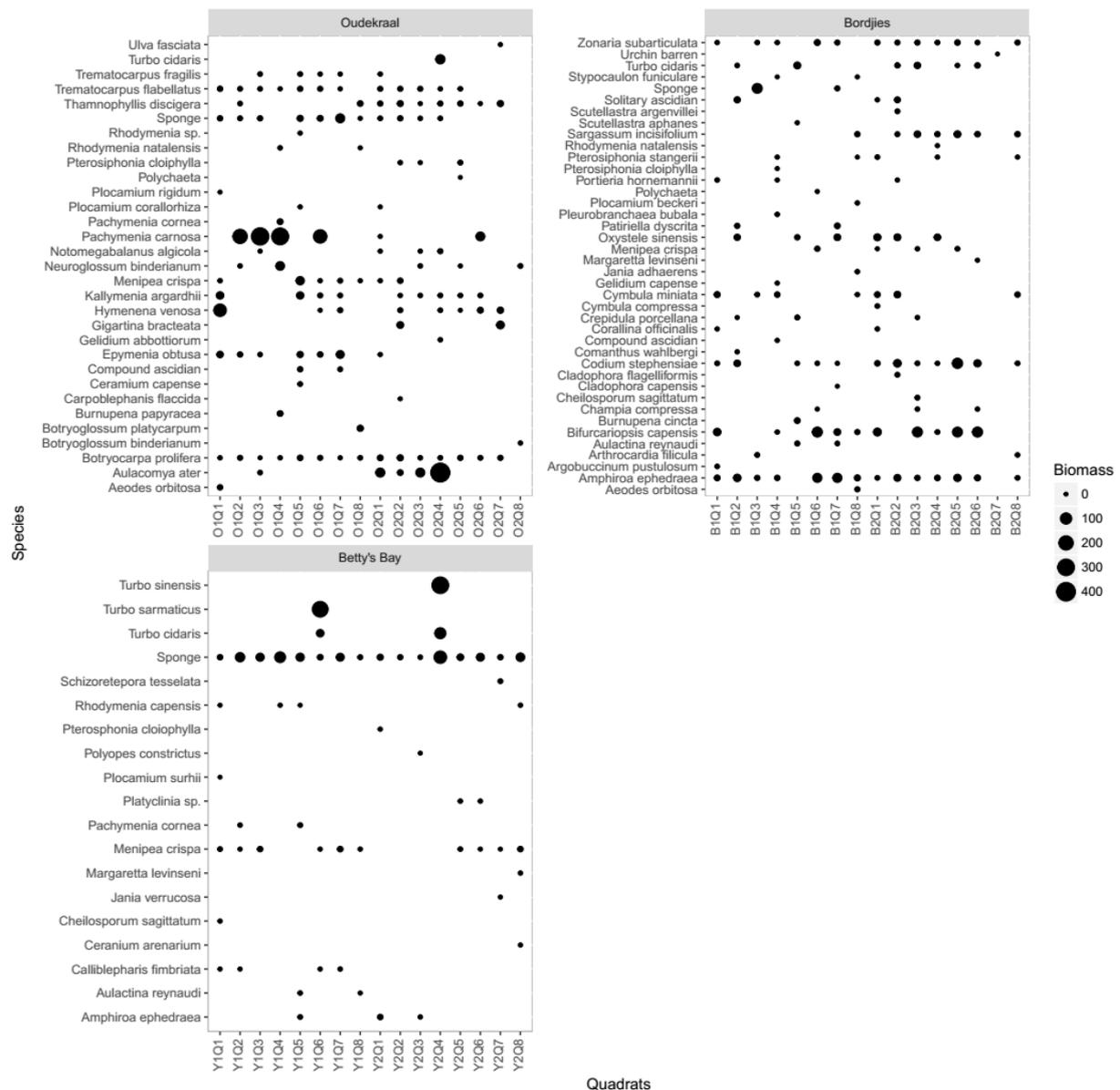


Figure 2.6: Presence/Absence scatter graph for quadrats across all sites for both fauna and flora. B: Bordjies Reef; O: Oudekraal; Y: Betty's Bay.

2.3.2 Benthic cover

Oudekraal had a greater percentage cover of foliose algae compared to Bordjies Reef and Betty's Bay, as well as a greater percentage cover of the ribbed mussel *A. ater*. Bordjies Reef had a high percentage cover of encrusting coralline algae, and Betty's Bay was characterised by large amounts of sponge and silt, while *A. ater* was absent from both Bordjies Reef and Betty's Bay. A SIMPER analysis revealed encrusting coralline algae, foliose algae and silt cover as distinguishing features between Bordjies Reef and Oudekraal, with over 75% of the cover dominated by encrusting corallines at Bordjies Reef, which was significantly more than the 28% cover at Oudekraal ($p < 0.05$, Figure 2.7). Foliose algae had a mean of 43% cover at Oudekraal compared to less than 25% at both Bordjies Reef and Betty's Bay (Figure 2.7). Between Bordjies Reef and Betty's Bay the defining features were encrusting coralline, silt and sponge, and between Oudekraal and Betty's Bay it was silt, foliose and sponge cover.

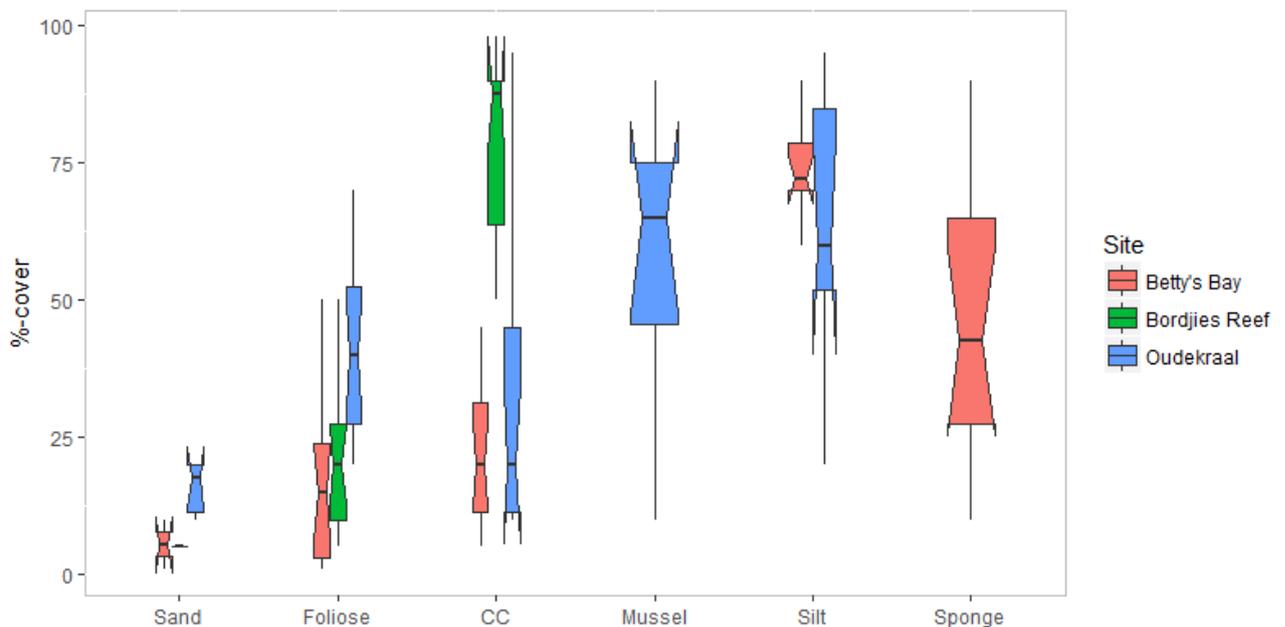


Figure 2.7: Boxplots comparing percentage cover types across sites. If 'notches' do not overlap, the medians are considered to be significantly different. The lower and upper "hinges" correspond to the first and third quartiles. Box widths are proportional to the square-roots of the number of observations in the groups.

Encrusting coralline dominates the benthic environment at Bordjies Reef of over 80%, compared to 24% at Betty's Bay, which is significantly lower ($p < 0.05$, Figure 2.7). Instead, sponge dominated the benthic environment at Betty's Bay with a significantly higher percentage (34%, $p < 0.05$, Figure 2.7) compared to Bordjies Reef's (0%). The silt cover at Betty's Bay of 45% was significantly higher than Bordjies Reef's 0%. Other defining features between Oudekraal and Bordjies Reef was silt, foliose and sponge cover. Silt cover at Betty's Bay was significantly higher than at Oudekraal ($p < 0.05$, Figure 2.7), with 44% and 28% respectively. This was also true with sponge cover ($p < 0.05$, Figure 2.7) with Betty's Bay's 34%, compared to Oudekraal's 0%. Foliose cover was significantly greater at Oudekraal ($p < 0.05$, Figure 2.7) with a mean of 43% compared to Betty's Bay which had a mean of 15%.

2.3.3 Abalone and rock lobster

There was a significant difference in the number of rock lobsters ($p < 0.05$) and abalone ($p < 0.05$) between sites (Figure 2.8) with Bordjies Reef having the greatest abundance of abalone (mean = 1), which was significantly more than that recorded at Betty's Bay and Oudekraal (mean = 0.25 and 0 respectively). Rock lobster were significantly more abundant at Betty's Bay (mean = 8.125), compared to Bordjies Reef (mean = 0) and Oudekraal (mean = 1.25) (Figure 2.8).

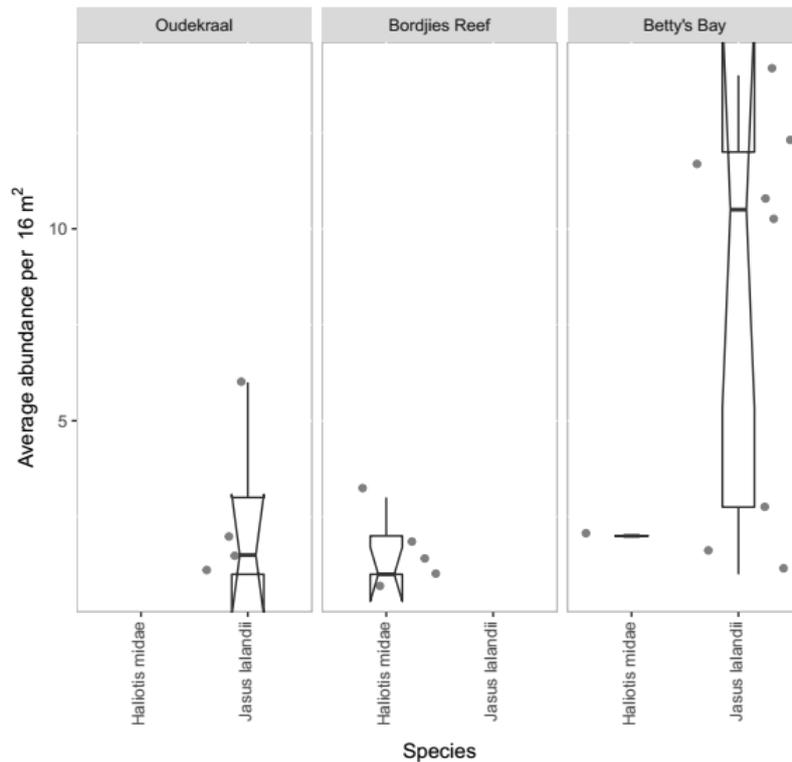
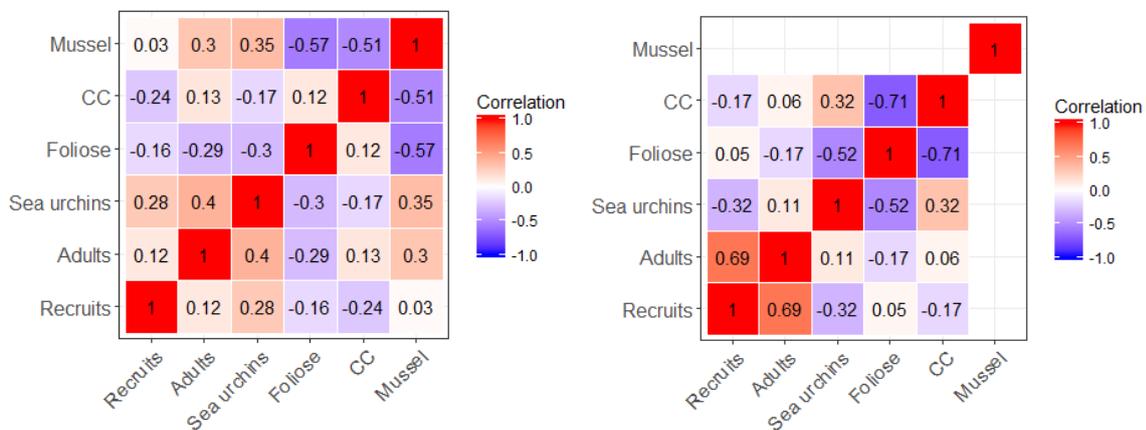


Figure 2.8: Boxplot showing abundance (averaged over all 16 m²) of abalone *Haliotis midae* and rock lobster *Jasus lalandii* between sites. Each point represents a total measure of *H. midae* and *J. lalandii* respectively. The lower and upper 'hinges' correspond to the first and third quartiles. Box widths proportional to the square-roots of the number of observations in the groups.

2.3.4 Correlations

Figure 2.9 shows the significant correlations between community components found for each site. At Bordjies Reef, a significant positive correlation was found between kelp adults and kelp recruits ($p < 0.003$, $r = 0.69$; Figure 2.9). Significant negative correlations were found between foliose cover and sea urchins ($p < 0.05$, $r = -0.52$, Figure 2.9), and between encrusting coralline and foliose cover ($p < 0.05$, $r = -0.71$; Figure 2.9), at Bordjies Reef. No significant correlations were found for either Oudekraal or Betty's Bay.



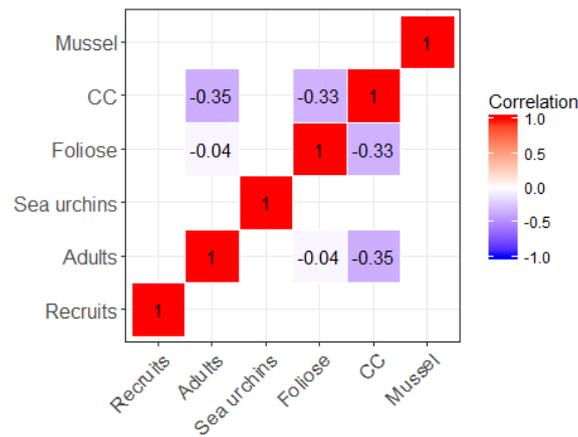


Figure 2.9: Heatmaps for correlations for each site. In the top-left is Oudekraal, top-right is Bordjies Reef, and bottom is Betty’s Bay. Values within block represent the r – value. Red represents a ‘+’ correlation coefficient and blue a ‘-’ correlation coefficient.

2.4 Discussion

2.4.1 Benthic community

Various abiotic and biotic factors play a role in structuring kelp forests, and its associated benthos. These variables (such as grazing intensity, wave exposure, sedimentation, temperature ect.) are often site specific. However, which variables are the main drivers in systems are often difficult to determine due to the complexity of kelp ecosystems. Therefore, it is important that insight is provided into which variables may be structuring kelp ecosystems, as this is lacking in the South African context.

In this study, there were significant differences in benthic species composition with regards to fauna and flora between sites. In this study, Oudekraal was characterised by a low abundance of grazers, high percentage cover of foliose algae, and the presence of filter-feeders. Bordjies Reef is characterised by the high abundance of the sea urchin *P. angulosus*, and encrusting coralline dominated the benthic environment. Very little foliose cover was present. Betty’s Bay was characterised by the high abundance of rock lobster *J. lalandii*, and a high percentage cover of silt/sediment. Temperature regimes differed between sites, however, *in situ* characteristics, such as grazing pressure, sedimentation, competition for space, may also play a role in determining species composition of sites in this study.

Bordjies Reef had a mixture of Chlorophyta, Ochrophyta and Rhodophyta, which is in line with what Leliaert et al. (2000) found in their study. Bordjies Reef was dominated mainly by brown algae, such as *B. capensis*, whereas Oudekraal was occupied mostly by Rhodophyta species, with certain species such as *P. carnosa* and *P. cornea* dominating. *P. carnosa* and *P. cornea* are large foliose species which may scour the bottom and reduce bottom irradiance making it difficult for other species to persist. While there was a clear distinction between sites in terms of flora, there was overlap in faunal species composition between Oudekraal and Betty’s Bay, with Bordjies Reef remaining distinct. This was surprising due to the large differences in temperature regimes between Oudekraal and Betty’s Bay and one would expect Bordjies Reef and Betty’s Bay to be more similar in terms of faunal species

composition, however it may be due to the shared presence of certain gastropods (see below), and absence of other grazers (sea urchins).

Grazers, particularly the sea urchin *P. angulosus*, were abundant at Bordjies Reef relative to the other sites, and this was a defining feature of Bordjies Reef in this study, given transition zone kelp beds are known for their grazer abundance (Field et al. 1980, Anderson et al. 1997). The high abundance of grazers, and in particular *P. angulosus*, may partly be due to the low numbers of predatory rock lobster at the study site; in addition, could also be the reason why Bordjies Reef had the greatest *H. midae* counts relative to the other sites, as juveniles of *H. midae* use sea urchins as a refuge from predation by hiding underneath them, allowing them to grow to a size that may preclude them from predation in later stages of their development (Day & Branch 2000a, 2000b). It is also possible however, that illegal fishing of abalone has not been as intense at Bordjies Reef given its location within the Cape Point Nature Reserve.

Grazing pressure may induce a form of disturbance, which has been shown to increase overall diversity in kelp forests. For instance, an experimental study by Vance (2011) showed that grazed sites showed an overall higher diversity compared to un-grazed sites. The author concluded that this was because grazing created new environmental patches for other species of fauna and flora. The collective grazing pressure of mesoherbivores at Bordjies Reef, particularly the sea urchin *P. angulosus*, may allow for more open areas for settlement and growth of algal species. False Bay has historically had a high diversity of various types of gastropods, limpets and other fauna, which may be adding to the slightly higher overall diversity at Bordjies Reef. However, the lack of significant difference in overall diversity between Oudekraal and Bordjies Reef may be due to *P. angulosus*' feeding methods or preferential feeding by *P. angulosus*, at Bordjies Reef. *Parechinus angulosus* is well-known for passive grazing, in which individuals remain rather sedentary and instead of actively grazing, they trap pieces of drift weed (Fricke 1979, Day and Branch 2002). However, in the absence of drift seaweed, they are likely to switch to active grazing, as has been seen in for example in southern California (Harrold and Reed 1985), and to graze preferentially on certain species of algae. A study by Anderson & Velimirov (1982) investigated the palatability of 13 common seaweeds to the sea urchin *P. angulosus*. The results of three different feeding experiments showed that palatability of seaweeds can be categorised into 'preferred', 'intermediate', and 'non-preferred'. Preferred species were *P. cornea* and *Carradoria virgata* (C. Agardh) Kylin, and non-preferred species were *Desmarestia firma* (C. Agardh) Skottsberg, and *Botryocarpa prolifera* Greville (Anderson and Velimirov 1982). Sea urchins at Bordjies Reef may similarly be targeting certain species of benthic algae, allowing other less palatable species such as *B. capensis* to dominate. Grazing may also be acting in combination with temperature to structure macroalgal communities. For instance, experimental work by Rothäusler et al. (2009) suggest that survival of floating *Macrocystis* spp. is dependent on a combination of temperature and grazing. Furthermore, their results showed that at moderate temperatures (+4°C ambient temperature) the survival of *Macrocystis* spp. was determined by the presence or absence of associated grazers.

The lack of foliose cover at Bordjies Reef is most likely due to the high grazer abundance. The opposite is probably true for Oudekraal, where the greater cover of foliose algae is most likely due to a lack of grazers, as has been reported for reef systems elsewhere in the world (Sturner 1986, Vanderklift et al. 2009, Vergés et al. 2016). The lack of foliose cover probably

accounts for the higher encrusting coralline cover, as foliose algae are better competitors and can overgrow encrusting coralline algae (Field et al. 1980).

The ribbed mussel *A. ater* was present at Oudekraal but not at the other sites. This was not surprising given that filter-feeders, such as these mussels, are considered characteristic of the west coast (Field et al. 1980), where they thrive due to seasonal upwelling. Oudekraal is likely a suitable environment due to it being positioned within an upwelling cell. *Aulacomya ater* is an important prey item for *J. lalandii* populations along the west coast (Mayfield et al. 2001), but in recent decades these lobster populations have undergone a serious decline and are now estimated at ca. 2.5% of pre-exploitation biomass (Johnson and Butterworth 2016), which may explain the relatively low abundance at Oudekraal. The lower overall diversity at Oudekraal may be due to the lack of grazers, which might make space a more limiting factor through release in grazing pressure. Sea urchin abundance at Oudekraal was low, and the sea urchins that were recorded, were limited to confined crevices within the study plots and the extreme shallows (pers. obs.). Also, if certain species of benthic algae can outcompete one another, such as *P. cornea* and *P. carnosa*, this may lead to certain benthic seaweeds dominating. This seems to be the case for Oudekraal, which has mostly Rhodophyta dominating the benthic environment. There is evidence to suggest that some species of Rhodophyta can undergo rapid growth, which allows them to outcompete other species (Goff and Coleman 1986, Vadas et al. 1992). The dense kelp canopy cover that is present at Oudekraal reduces the underwater irradiance, with less light penetrating to the bottom reef when compared to that at Bordjies Reef (pers. obs.). Rhodophyta are able to cope better in light stressed environments than other types of seaweeds (Vadas et al. 2000, Raikar et al. 2001). Different irradiance levels have been shown to affect macroalgae growth (Bearham et al. 2013, Tait 2014). This would allow Rhodophyta species to possibly outcompete other algae for light, as well as space. The inter-specific competition for light and space may therefore be lower at Bordjies Reef than at Oudekraal. There was a significant difference in overall species diversity between Bordjies Reef and Betty's Bay however, these may still be comprised of similar species, but the floral community shows distinction, while there is overlap in terms of fauna. These findings were similar to past research (Field et al. 1980; Leliaert et al. 2000; Wernberg et al. 2003).

The high biomass of turban snails at Betty's Bay (eg. *Turbo cidaris* and *Turbo sarmaticus*), compared to the other sites, is likely due to the large size of individuals recorded there and not their abundance. Rock lobsters feed on a wide variety of prey, including gastropods such as turban snails (van Zyl et al. 1998). However, lobsters are restricted to a certain size of gastropod, as they are with other prey (Mayfield et al. 2001), and those gastropods that manage to attain a large enough size will then escape predation by rock lobsters. This appears to be the case at Betty's Bay. The low number of fauna and flora species recorded at Betty's Bay is most likely due to the presence of the predatory lobster *J. lalandii*, as well as a large amount of silt recorded on the reef. Fauna species present at Betty's Bay consisted mainly of sponges, ascidians and large gastropods. The ascidians may be a low energetic food source for the rock lobsters at Betty's Bay due to elimination of preferred food items (e.g. sea urchins and small gastropods) by direct intensive rock lobster predation (Haley et al. 2011). Blamey and Branch (2012) found that faunal species diversity was low at lobster-invaded sites such as Betty's Bay, compared to adjacent non-invaded sites, while floral species diversity was higher. In this study, both faunal and floral species diversity were low,

most likely because of increased siltation on the reef and the absence of mobile grazers to clear it away, as has been suggested by Day (1998). The detailed effects of silt at Betty's Bay is discussed later. At Betty's Bay sponge dominates the benthic environment. A high percentage cover of foliose algae at Betty's Bay was expected due to the lack of grazing pressure and based on what was recorded by Blamey et al. 2010 and Blamey and Branch 2012; however, this was not the case. This may be as a result of the large amounts of silt cover found in the quadrats. Schiel et al. (2006) showed the potential of sedimentation as a driver of settlement and survival of kelp gametophytes. The sedimentation could also be having a negative effect on irradiance through 'choking' the growth and settlement of algal spores and invertebrate larvae. Furthermore, an area located further out from the plots sampled contained a mixture of Rhodophyta, Chlorophyta and Ochrophyta seaweeds and a higher foliose cover, and less silt cover (pers. obs.) suggesting that Betty's Bay may have a similar benthic environment to Oudekraal. Therefore, the low percentage of foliose algal cover at Betty's Bay is due to localised siltation.

The high abundance of rock lobster at Betty's Bay was expected, due to the recent 'invasion' into the area (Blamey and Branch 2012). Rock lobsters feed primarily on sea urchins and therefore the lack of sea urchins at Betty's Bay is probably largely due to predation by *J. lalandii* (Blamey and Branch 2012). The rock lobster—sea urchin—abalone interaction can also explain the relative densities of abalone and rock lobsters recorded at the other sites. Sea urchins provide shelter for juvenile abalone, as well as nourishment, and therefore act in a facilitative role in abalone recruitment (Day and Branch 2000a, Mayfield and Branch 2000). Since rock lobsters predate largely on sea urchins, one can expect that in areas where rock lobster abundance is high, one would find fewer urchins and therefore fewer abalone. Reasons for lack of foliose cover are unclear and are beyond the scope of this study. A significant difference in abalone counts between Bordjies Reef and Oudekraal was found, which may be due the variable abundance of *P. angulosus* and their relationship with abalone and rock lobster. Due to the high presence of rock lobster at Betty's Bay a significant difference in abalone counts were expected, however, this was not the case. Once again, reasons are unclear, but poaching and over-fishing may be contributing to the low number of abalone at Betty's Bay.

2.4.2 Conclusion

There are clear differences in community composition between the three sites. The results of this study support the findings by Leliaert et al. (2000) and strongly suggest that temperature and grazing are the drivers influencing kelp ecosystem community composition and diversity between the west and south-west coasts of South Africa. However, whether the causal influence is temperature only or also grazers remains unclear. The most plausible explanation for the differences between sites appears to be grazing pressure from *P. angulosus*.

Therefore, in this study the differences in overall community structure may be due to a combination of temperature and *in situ* site characteristics. Additional factors such as light, wave action, sedimentation may also be playing a role as suggested by other studies (Gerard 1982, Graham et al. 1997b, Stevens et al. 2001, Taylor and Schiel 2003, Scrosati and Mudge 2004, Schiel et al. 2006, Bearham et al. 2013). The null hypothesis that species composition and diversity of benthic invertebrates and understory algae will not differ between the three

sites is therefore rejected. Future studies should undertake a multi-factorial approach, investigating how these act in combination with one another in order to determine which factors are the most important drivers. Furthermore, additional studies are needed to investigate the effects of wave motion, light and sedimentation, as studies on these factors are lacking in the South African context.



Chapter 3 – Population structure of *E. maxima* along contrasting sites



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3.1. Introduction

Research has shown that both abiotic (e.g. temperature, nutrients, wave exposure, light, substrate, ect.) and biotic (e.g. competition and grazing) factors play a major role in the distribution and physiological functioning of species, with kelp being no exception. Abiotic and biotic factors may play a role in structuring kelp communities through physiological mechanisms that determine recruitment patterns both spatially and temporally, which will ultimately determine abundance and cohort structure. Grazing intensity has also been shown to be a key mechanism of mortality for kelp recruits (Ebeling et al. 1985, Watanabe and Harrold 1991, Dayton et al. 1992, Vadas et al. 1992, Hagen 1995, Villouta et al. 2001, Sivertsen 2006, Sjøtun et al. 2006), which is the only stage that the local sea urchin *Parechinus angulosus* can feed on kelp successfully (Fricke 1979, Anderson et al. 1997).

3.1.1 Global context

Kelp forest structure can be influenced by a variety of factors that ultimately determine the size frequency distribution of individuals and their spatially and temporarily variability. Much of the past research on kelp population structure focuses on the different variables that may affect kelp recruitment. It is generally accepted that most kelps rely on a 'recruitment window'; a time when environmental factors are favourable for spore release and growth (Deysher and Dean 1986); however, other factors such as temperature, nutrients, light, wave motion, substratum, sedimentation, grazing etc. may also be important in the settlement and growth of spores, even during optimal recruiting conditions (Devinny and Volse 1978, Dayton 1985, Deysher and Dean 1986a, 1986b, Vadas et al. 1992, Kawamata 2001, Taylor and Schiel 2003, Schiel et al. 2006, Rothäusler et al. 2009, Staehr and Wernberg 2009, Wernberg et al. 2011, Gaitán-Espitia et al. 2014, Franco et al. 2015).

Temperature is recognised as the main driver of species distributions, and kelp is no exception (Bolton and Levitt 1985, Vadas et al. 1992, Wernberg et al. 2010). Temperature may also affect the physiological functioning of kelps, which in turn may reduce their resilience from storm disturbance, or warming (Wernberg et al. 2010, 2013). Warming of the ocean has resulted in kelp loss, and topicalization of what were once temperate ecosystems. This has also allowed the range extension of tropical herbivores into these regions which has resulted in destructive grazing of macroalgae communities, and regime-shifts into turfs or algal barrens (Harris et al. 1984, Vergés et al. 2014). Other abiotic factors may also drive kelp population dynamics through settlement patterns of kelp gametophytes. Nutrients are important in growth and survival of kelp, and some species of kelp are able to store nutrients (Deysher and Dean 1986b, Vadas et al. 1992). Wave action is important for uptake of nutrients of kelp sporophytes, however in higher wave energy environments the settlement of gametophytes may be reduced. Wave energy may also cause scour the bottom further reducing settlement. Light is also important for growth and survival of kelp, and ideal light conditions differ from species to species (Gagnon et al. 2003; Utter & Denny 1996; Vadas et al. 1992). Canopy-forming kelp has been shown to structure the light environment, and greatly reducing bottom irradiance (Gerard 1984, Clark et al. 2004). Space, and substratum are important in the settlement of kelp gametophytes, which alters the population through variation on cohorts over time (Vadas et al. 1992). The mechanism

driving kelp population dynamics is complex, and is often difficult to quantify the effects. Recent work regarding kelp forests has investigated the combined effects of certain abiotic and biotic factors, which has shown that certain important drivers (temperature and grazing) may act synergistically to drive kelp population dynamics (Sjøtun et al. 2006, Connell and Russell 2010).

3.1.2 The South African context

South African kelp forests extend along the entire west coast to just east of Cape Agulhas on the south coast. They are dominated by two species of kelp, *Ecklonia maxima* and *Laminaria pallida*, although two other less abundant species of kelp, *Ecklonia radiata* and *Macrocystis pyrifera* are also found along the coastline. The kelp *E. maxima* is the most conspicuous organism in the subtidal along the South African coastline, as the kelp 'heads' are often visible from the surface, particularly during low-tide.

Population structure of *E. maxima* may depend on a variety of factors such as temperature (Lee and Brinkhuis 1988, Raven and Geider 1988, Wiencke 1989, Dieck 1993, Connell and Russell 2010, Bartsch et al. 2012, Mabin et al. 2013), light (Lee and Brinkhuis 1988, Altamirano and Murakami 2004, Wernberg and Goldberg 2008, Arkema et al. 2009, Tait 2014), wave motion (Graham et al. 1997a, Kawamata 2001, Wernberg 2005, Fowler-Walker et al. 2006, Pedersen et al. 2012) and nutrients (Jackson 1977, Andrews and Hutchings 1980, Field et al. 1980b, Probyn and McQuaid 1985, Guimaraes and Coutinho 1996, Edwards and Estes 2006). At shallow depths (2–3m), the canopy tends to reach the surface; however, the structure changes to a mixture of sub-canopy and canopy at greater depths (5–10m), with eventual transition into *L. pallida* dominated canopy (>10m) (Rothman et al. 2006, 2010). Therefore, from the surface it may appear that there is a change in biomass due to reduction in canopy cover with depth; however, due to the presence of sub-canopy kelps at deeper depths the biomass changes insignificantly (Rothman et al. 2006). Populations of *E. maxima* dominate the west coast, but more recently have increased in density in False Bay and further east (Reimers 2012), extending their range by 70km along the south coast (Bolton et al. 2012). The range extension of *E. maxima* has been associated with a possible cooling and increased nutrient supply in the nearshore around the South African south-west coast (Moloney et al. 2005, Blamey et al. 2015b).

In South African kelp forests the effects of grazing on macroalgal communities may be considered insignificant relative to northern hemisphere regions, given that the urchin *P. angulosus* feeds mostly on drift kelp, but is known to also feed on juvenile or early developmental stages of kelp (Fricke 1979), which have been shown to obtain refuge in kelp holdfasts (Anderson et al. 1997). Studies by Day and Branch (2000; 2002) have shown the importance of *P. angulosus* in sheltering juvenile *Haliotis midae* and have shown the urchin to be a selective forager (Anderson and Velimirov 1982).

3.1.3 Aim and objectives

3.1.3.1 Aims

This chapter aims to compare the population structure of *E. maxima* across contrasting study sites in the Western Cape, and in doing so, hopes to shed light on the abiotic and biotic

factors driving the differences that might exist. In this study, the variability in adult kelp and recruit abundances across sites were used to infer characteristics of the kelp populations.

3.1.3.2 Objectives

1. To assess kelp population structure at three representative sites.

3.1.3.3 Null hypothesis

H₀: Kelp population structure will not differ between the three contrasting sites in terms of temperature and grazer presence/absence.

3.2 Methods

3.2.1 Study sites

See Chapter 2, section 2.2.1, page 26).

3.2.2 Data collection

At each site, two 16 m diameter circular plots within the middle of the kelps beds were marked. Each plot was approximately 200 m² in area. Long-term temperature loggers (StarOddi: Starmon mini), are located nearby each site.

Each plot was permanently marked with a 0.5 m railway bar placed in the center of the plot and a GPS position recorded. Sampling of the plots involved SCUBA divers. Four transects, each on a different compass bearing from the center of the plot, were swum out. Two 1 × 1 m quadrats were sampled at 1 m and 4 m along each transect. In each quadrat, the number of adult (>50 cm) and juvenile (≤50 cm) kelps were recorded, and the stipe length of each adult was then measured using a tape measure.

3.2.3 Data analysis

All data analyses were done using the R software (R Core Team, 2016) and the vegan package (Oksanen et al. 2016) and ggplot2 (Wickham 2009). Before any analyses were conducted, data were first checked for normality using the Shapiro-Wilk normality test.

For data that were not normally distributed, a Kruskal-Wallis test was used to test for significant differences in adult and recruit kelp abundance between sites. A combination of boxplots and scatterplots were used to visually represent adult and recruit abundance differences between sites. One again, a Kruskal-Wallis test was used to investigate differences in stipe length. These assessments were verified visually using a combination of a boxplot and scatterplot to aid in visual representation of possible differences between sites. The individuals for each site were then categorised into juvenile (<50 cm), sub-canopy and canopy (reaches the surface), in order to further investigate kelp population structure. This was done per each site's depth profile (Bordjies Reef 5 m, Oudekraal 7 m and Betty's Bay 8 m), and any stipe length 1m below the maximum depth was allocated to the sub-canopy category.

Correlations from Chapter 2 (section 2.3.4, page 28) are referred to in this chapter, and were used to investigate the link between recruit abundance and grazing intensity.

Temperature regimes were calculated and represented as a graph for each site. This allowed investigation into frequency and magnitude of thermal extremes over the duration of the experiment, and any possible links to adult and recruit abundance structure between sites.

3.3 Results

3.3.1 Kelp abundance

Significant difference in recruit kelp abundance was found between sites ($\chi^2 = 6.892$, d.f. = 1, $p < 0.05$, Figure 3.1). Differences in recruit abundance were between Bordjies Reef and Oudekraal, with medians of 24 and 3.5 of kelp recruits respectively, as well as Betty's Bay which had no kelp recruits. There were no significant differences in adult kelp abundance between sites ($\chi^2 = 5.539$, d.f. = 2, $p > 0.05$, Figure 3.1).

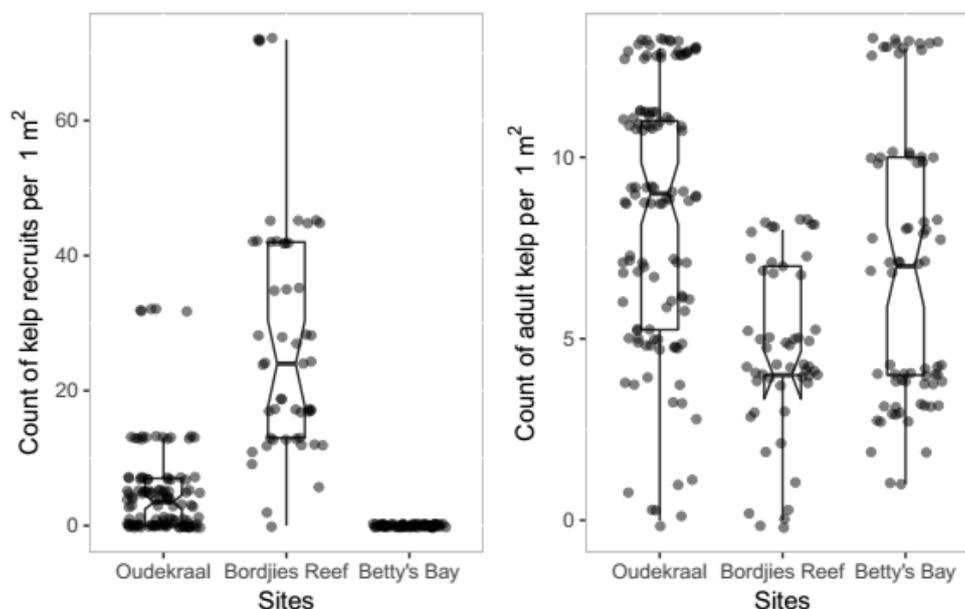


Figure 3.1: Box plot with data points comparison of the median recruit (left plot) and adult (right plot) kelp abundance within 1 m² quadrats across sites. Each point represents the count of recruits or adults recorded per quadrat and horizontal black lines represent the median. The lower and upper 'hinges' correspond to the first and third quartiles, and the 'whiskers' are the 5th and 95th percentiles. Box widths are proportional to the square-roots of the number of observations in the groups.

3.3.2 Adults *vs.* recruits and grazers *vs.* recruits

A Pearson's correlation between the number of kelp recruits relative to the adults for Bordjies Reef showed a positive correlation between these two variables ($r = 0.69$, $p < 0.001$), while no correlation was found for Oudekraal ($r = 0.12$, $p < 0.05$). No significant correlation was found between sea urchins and kelp recruits at Bordjies Reef ($r = 0.28$, $p > 0.05$), or at Oudekraal ($r = 0.28$, $p > 0.05$). No significant correlation was found between sea urchins and adult kelp at Bordjies Reef ($r = 0.11$, $p > 0.05$), or at Oudekraal ($r = 0.40$, $p > 0.05$). No sea urchins were recorded at the Betty's Bay site.

3.3.3 Stipe lengths

Significant differences in stipe length was found between sites ($\chi^2 = 135.06$, d.f. = 2, $p < 0.05$) (Figure 3.2). For all three sites the notches do not overlap, and therefore all three sites were significantly different in terms of overall stipe length. Betty's Bay had the greatest median stipe length of 620 cm, followed by Bordjies Reef with 310cm, and Oudekraal with the lowest median of 170 cm.

Stipe length variability was greatest at Oudekraal, with Bordjies Reef showing intermediate variability and Betty's Bay showing the least variability in stipe length (Figure 3.2). This was also reflected in the canopy-type, which shows Oudekraal to have the most sub-canopy kelps, followed by Bordjies Reef and then Betty's Bay. Betty's Bay was a combination of sub-canopy and canopy kelps, with no recruits recorded. All sites had canopy kelps.



Figure 3.2: Box plot comparison of stipe lengths across sites. Each point represents a length of an individual kelp, which is colour coded by canopy-type. The label 'None' indicates a quadrat where no kelp was recorded. The lower and upper 'hinges' correspond to the first and third quartiles. Box widths proportional to the square-roots of the number of observations in the groups.

3.3.4 Temperature regime analysis

Bordjies Reef was the warmer of the three sites, with a similar but slightly higher temperature regime compared to Betty's Bay, while Oudekraal was the colder site due to its location within an upwelling cell. A heat wave is defined as any temperature that goes above the threshold (Schlegel et al. 2017) and is indicated in Figure 3.3. At Bordjies Reef, heat waves took place in January 2015, February 2015, and December/January 2016 (Figure 3.3). The heat waves in 2015 and 2016 did not go above 21°C. The control plot for Bordjies Reef was sampled in February 2015, which falls between the 2015 heat waves. Betty's Bay also experienced a heat wave in January 2015, and again in October/November and December 2016 (Figure 3.3). The heat wave in 2015 did not go above 20°C, while the 2016 events lasted longer, but also did not go above 20°C. The control plots at Betty's Bay were sampled in

April of 2015. Heat waves at Oudekraal manifested themselves in December/ January of 2015, and another one in March 2015, with maximum temperature of approximately 15°C and 17.5°C respectively (Figure 3.3). Heat wave events took place at similar times in 2016, with maximums of approximately 15°C and 16°C respectively. The control plots were sampled in March of 2015, which fell during a heat wave event.

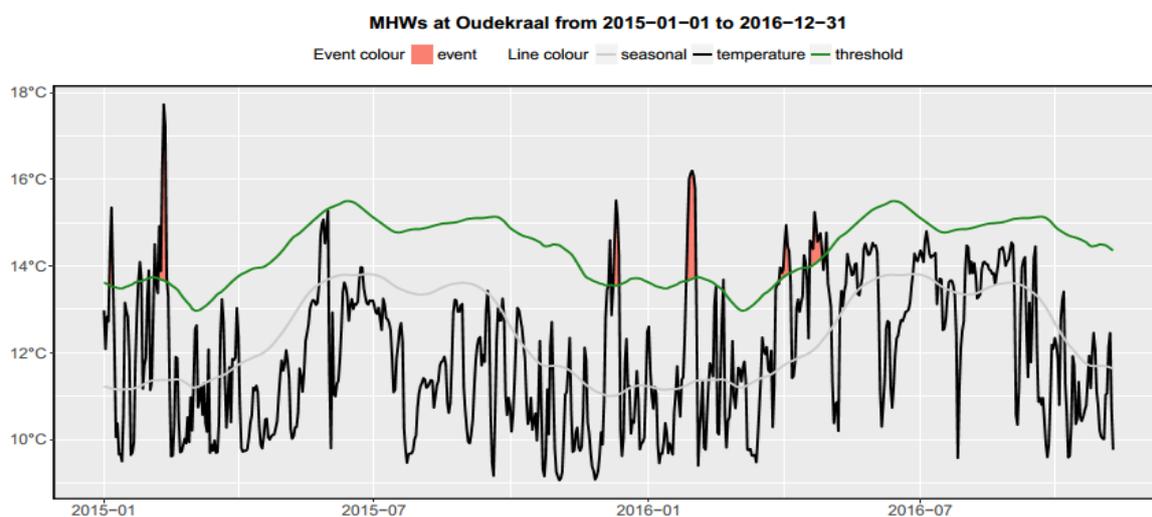
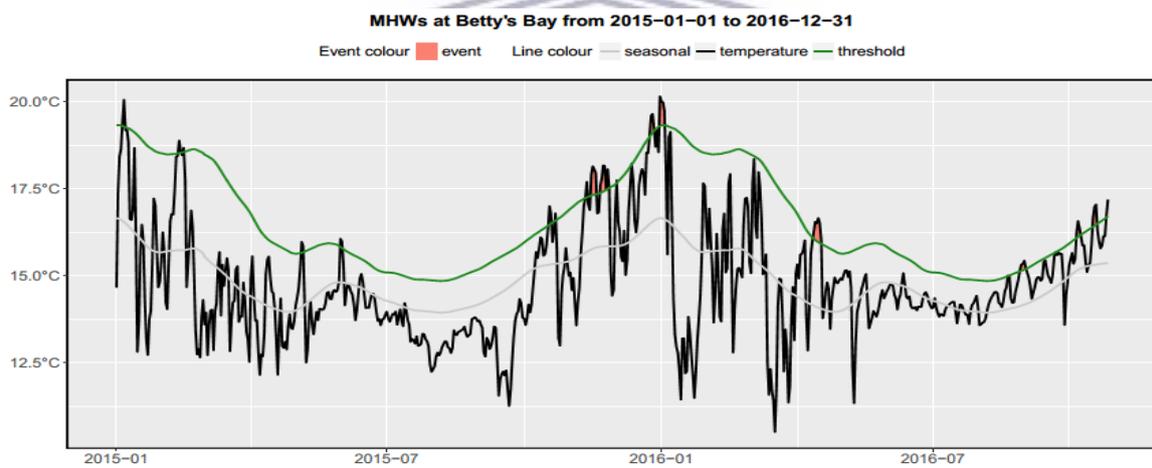
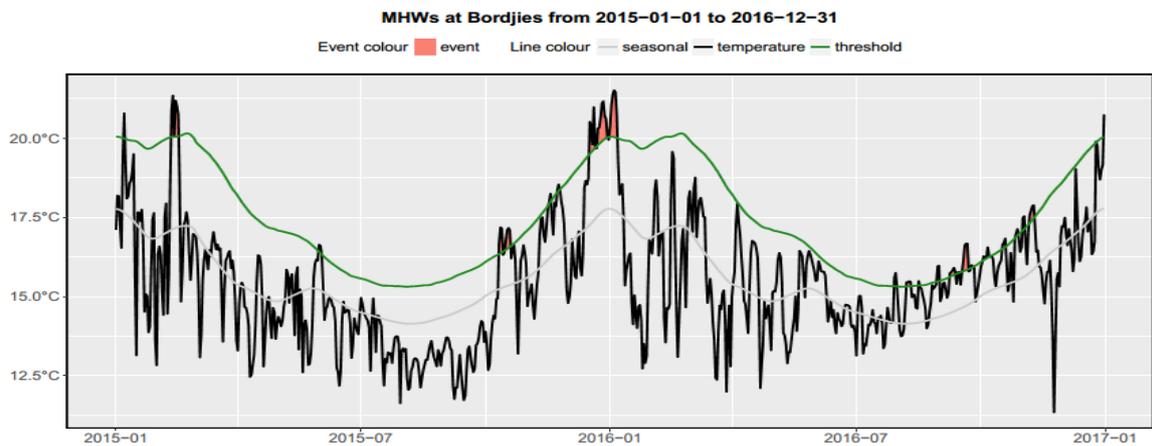


Figure 3.3: Temperature regimes for each site, showing extremes and their duration. The measured temperature series is indicated by solid black line, the seasonal climatology is represented by the grey line, the thermal threshold is indicated by the green line and heat extremes are indicated in pink.

3.4 Discussion

This study aimed to provide information about how the *E. maxima* populations at three sites, Bordjies Reef, Oudekraal and Betties Bay may be influenced by two important drivers of kelp population dynamics, viz., temperature and grazing. These two drivers were discussed in Chapter 1, which summarised numerous international and local studies on kelp population dynamics (e.g. Dayton 1985; Vadas et al. 1992; Deysher & Dean 1986; Franco et al. 2015; Staehr & Wernberg 2009; Wernberg et al. 2011; Gaitán-Espitia et al. 2014; Rothäusler et al. 2009; Devinsky & Volse 1978; Schiel et al. 2006; Taylor & Schiel 2003; Kawamata 2001), as being highly influential in structuring kelp beds at local and regional scales.

Temperature data and potential grazing pressure (see Chapter 2) differ between the study sites. Bordjies Reef is characterised by a high abundance of *P. angulosus*, while abundances at Oudekraal and Betty's Bay are low. Data extracted from a data base of coastal temperatures along the South African shore show that the temperature profiles at the sites differ in annual temperature regime, as well as in the maximum and minimum temperatures (Schlegel et al. 2017). This offers the opportunity to investigate kelp population structure between contrasting study sites in terms of thermal regime, and grazer absence/presence.

The lack of differences in adult abundance is interesting, as the significantly higher recruit abundance at Bordjies Reef could lead to a significantly higher adult kelp abundance compared to Oudekraal. This points to a possible 'thinning' mechanism on the kelp population. Different stages of kelp development are susceptible to different mechanisms of mortality. For instance, adult kelps are more vulnerable to wave action causing mechanical dislodgement, than developing stages (Vadas et al. 1992), while grazing is the main cause of mortality for recruits but not adults (Vadas et al. 1992). Mortality of kelp individuals from thermal stress has been documented and studied in the literature (Wernberg et al. 2010, Smale and Wernberg 2013). Recently, this is mostly in the form of short-term heat wave events; however, changes over time can affect kelp survival and distribution. Bordjies Reef gets warm during the summer months but this is not above the thermal limit of *E. maxima* of 22.5°C, as identified by (Bolton & Levitt 1985). Those periods of warming coincided with deterioration of adult kelps, particularly the fronds (pers. obs.). Bordjies Reef experienced multiple heat wave events during the study, which may be pushing adult kelp past their thermal tolerance. Sampling at sites either occurred after or during heat wave events (Figure 3.3). Furthermore, the heat wave events may be influencing zoospore release. Kelp, such as *E. maxima*, releases spores throughout the year with a seasonal peak between spring and summer. However, a study by Bolton (1985) investigating the light and temperature requirements for growth and reproduction in gametophytes of *E. maxima*, showed a possible ecological adaption. The average number of eggs per female was greater in sub-optimal conditions (<22.5°C), which the authors concluded to be an ecological adaption to increase the probability of survival for populations on their range edges. The physiological cost of ameliorating thermal stress has also been documented (Wernberg et al. 2010). The heat waves may be causing thermal stress to the plants, which then releases spores as a succession tactic. If this was the case, a similar situation should have been at Betty's Bay.

However, this was not the case. Possible reasons are not temperature related, and will be discussed later. Oudekraal has an ideal temperature regime for *E. maxima* growth and development (Bolton & Levitt 1985), and a suitable nutrient environment is inferred due to Oudekraal's location in an upwelling cell (Field et al. 1980). It is therefore then surprising that recruitment is not higher at this site. The lack of correlation between kelp recruits and kelp adults suggests that many recruits do not reach the adult phase. Oudekraal also experienced a heat wave event during data collection for this chapter, and if thermal stress is altering zoospore release in *E. maxima*, high recruitment can be expected. However, there is significantly lower recruit abundance at Oudekraal compared to Bordjies Reef. Oudekraal is dominated by foliose Rhodophyta species, such as *P. cornea* and *P. carnosa*, which may be dominating the benthic environment. The dense foliose cover and limited space may reduce the amount of kelp gametophytes able to attach and settle (Vadas et al. 1992). Therefore, other factors may be important in determining the kelp population structure at Oudekraal, such as availability of space.

Bordjies Reef is host to a suite of benthic grazers such as the sea urchin *P. angulosus*, the abalone *H. midae*, and the turbinid snails *Turbo sarmaticus*, and *T. cidaris*. However, the significantly positive correlation between kelp recruit abundance and adult kelp abundance at Bordjies Reef, suggests that kelp recruits at that site are likely to reach the adult phase. Also, past research shows that the sea urchin *P. angulosus* can feed on kelp recruits, but that they tend to prefer drift kelp. Work by Rothman et al. (2006) showed that once kelp recruits at Bordjies Reef have attained a length between 11 cm and 25 cm, they have approximately a 70% chance of reaching the canopy. The thinning mechanism may therefore not be acting on kelp recruits, but rather on established kelp adults. Grazing may be indirectly facilitating recruitment at Bordjies Reef by reducing competition for space between other macroalgae types and space for kelp gametophyte settlement. Research conducted at the same location (Bordjies Reef) found light not to be the main driving mechanism of kelp recruitment. Rothman et al. (2006) investigated the effects of harvesting on *E. maxima* population structure, growth rate and recruitment. The authors found light not to be an important factor, and suggested other drivers such as reduction in competition for space to be a possible factor that future studies should investigate. This, in combination with the negative correlation between percentage cover of foliose algae and sea urchin abundance at Bordjies Reef, supports the claim that sea urchins may be playing an indirect facilitative role in recruitment at this particular site. If grazing is a mechanism influencing kelp populations, then a different situation should be evident at Oudekraal, where there were little to no sea urchins recorded. This is the case, as there is a larger variation in stipe lengths at Oudekraal than Bordjies Reef, which suggests a larger variation in cohorts. However, there are other factors such as light and space availability, sedimentation and depth, which may also be driving the kelp populations at the various sites. This is true for Betty's Bay plots, which were inundated with sediment. The siltation at Betty's Bay is unfortunate, as Betty's Bay provided a study site of similar temperature to Bordjies Reef, but differed in abundance of grazers, due to the invasion of rock lobsters. The study at Betty's Bay would have provided more insight into the effects of grazers, but the siltation seems to be the main limiting mechanism for kelp recruitment in this example.

Betty's Bay had no recruits and was characterised by established sporophytes that had reached the surface, with no sub-canopy. All the sampled kelps were of similar length, with

little variation compared to the kelps at Oudekraal and Bordjies Reef. This is most likely due to the lack of recruitment at Betty's Bay, given that zero recruits were recorded. A lack of recruitment would prevent variation in cohorts, which leads to established sporophytes dominating, which the sedimentation may be facilitating. Schiel, Wood, Dunmore, et al. (2006) concluded that sedimentation is a potential driver of settlement and survival of marine algae, as unstable sediments do not allow for successful settlement and development of kelp spores (Schiel et al. 2006). Sedimentation/silt may also 'choke' any settled juveniles by reducing irradiance (Vadas et al. 1992, Schiel et al. 2006). This may also explain the low percentage of foliose cover recorded at Betty's Bay (see Chapter 2). However, outside the plots, a mixture of foliose turf algae and juvenile kelp were observed (pers. obs.). Therefore, the siltation may be a localised impact that is only affecting areas closer to the shore. Also, the silt cover is dense and in some places forms dense mats (pers. obs.), which could not have resulted from a single short event; rather, it seems as if it has accumulated over time. The adult sporophytes present may have been able to avoid the effects of sedimentation. However, siltation may be reducing turn-over of individuals, which leads to a particular cohort dominating. This may also be the reason why there is little variation in stipe lengths at Betty's Bay.

Other factors such as light, space and wave action are also important, but may play less of a significant role in structuring kelp population compared to temperature and grazing. Light is important in the growth and survival of kelp gametophytes and sporophytes (Novaczek 1984, Reed and Foster 1984, Bolton and Levitt 1985, Deysher and Dean 1986a, Altamirano and Murakami 2004, Tait 2014, Bennett et al. 2015), and the kelp population structure may be influencing this. The variation in canopy types at Oudekraal could be reducing bottom irradiance significantly, which may be allowing species better adapted for low light conditions to outcompete other species. A study by Toohey et al. (2004) investigated the effects of light and thallus scour from *E. radiata* canopies on associated algal assemblage. Their results showed that light and not thallus scour significantly affected algal community composition. The authors also concluded that in low light conditions foliose algae tended to dominate the benthic environment. This may be a reason why foliose algae dominates the benthic environment at Oudekraal (see Chapter 2). Space and substrata are also important factors. Sedimentation and silt have been shown to be important in determining the settlement of kelp gametophytes. The dense foliose cover at Oudekraal, may be reducing the amount of space available for kelp gametophytes to settle. Wave action from storms, causing mechanical dislodgment of individuals, may also be a factor. Dislodged adult kelp also provide an important input into the overall detrital food chain in the form of drift kelp, which supports various benthic organisms including sea urchins. Bordjies Reef may be more exposed to storm disturbance than the other sites, which may be thinning the adult population, as well as sustaining the high sea urchin abundance through providing sufficient quantities of drift kelp. However, this is only an inference, as temperature was the only abiotic variable measured in this study.

3.5 Conclusion

The dependence of kelp on cool-temperate water for survival, as well as the fact that temperature has been shown to have negative effects on kelp physiology, means that cooling or warming of oceans around the South African coastline could have negative impacts for kelp populations in terms of their distribution and population structure (Bolton and Levitt

1985, Vadas et al. 1992, Wernberg et al. 2011, Bearham et al. 2013, Smit et al. 2013). Temperature may be structuring the kelp populations at the various sites through thermal stress, which thins the population, at various stages of development, which also leads to variation in cohorts. Grazing may also be thinning the populations through feeding on juvenile stages, which ultimately leads to a variation in cohorts.

It is difficult to determine the direct effects of temperature and grazing, as they may be acting in combination with one another, as well as with other abiotic (light, wave motion, and siltation) and biotic factors (competition). Furthermore, mechanisms structuring kelp communities may differ between sites and it is important that future studies encompass a 'multi-stressor' approach to aid in teasing out direct *vs.* combined effects. Based on the literature and the findings in this study, the null hypothesis that kelp population structure will not differ between the three contrasting sites is rejected.



**Chapter 4 – Recovery of kelp population and associated benthos after
a pulse disturbance event**



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4.1. Introduction

Most of the past research in South Africa on kelp forests has focused on kelp population dynamics in relation to different harvesting techniques, effects of temperature on physiology, growth, function and distribution, and benthic community structures (see Chapter 1). In South Africa, no work has investigated how recovery of these ecosystems may be affected by differing site characteristics. This chapter therefore aims to shed light on *Ecklonia maxima* and benthic composition recovery under different temperature regimes in South Africa.

4.1.1 Temperature

Climate change will have a wide range of spatially and temporally variable effects for ecosystems around the world, which will be driven by changes in regional and global climate patterns, with predicted impacts such as a change in SST and changes in storm frequency and magnitude (Walther et al. 2002; Doney et al. 2012; Vergés et al. 2014; Blamey et al. 2015b; Smit et al. 2016; Vergés et al. 2016). SST and storm disturbance are important drivers of kelp ecosystems (Bolton & Stegenga 2002; Byrnes et al. 2011; Smale & Wernberg 2013; Krumhansl et al. 2016). Changes in SST and storm disturbance may have implications for kelp forest functioning and species composition (see Chapter 1 for detailed literature review). Temperature effects on ecosystems are not limited to long-term consequences, but the impacts may also manifest themselves from short-term events such as heat waves. Populations that are already on the fringe of their distribution range may be most at risk to these types of events.

4.1.2 Storm disturbance

Storms can play an important role in structuring kelp communities through alterations in top-down processes and in abundance of organisms because of mechanical dislodgement. In this way storms help maintain the complexity of kelp forest food webs. However, if storm frequency and magnitude increases past the tolerable threshold of kelp ecosystems, this may result in kelp populations being unable to recover, which may also have broad-scale implications for other coastal food webs (Byrnes et al. 2011).

If storm frequency and magnitude increase in future climate scenarios, as some authors suggest (Doney et al. 2012), then an increase in disturbance to kelp forest ecosystems can be expected. As with temperature, if storm frequency and magnitude increases past the tolerable threshold of kelp, it may inhibit recovery of these ecosystems.

4.1.3 The South African context

Kelp is abundant along the South African west and south-west coasts. Most of the research has focused on the economically important kelp *E. maxima*, which is a canopy-forming species as well an important ecosystem engineer. *Ecklonia maxima* provides a 3-dimensional habitat to various fauna and flora and is also highly productive (Dayton 1985), with *E. maxima* producing approximately 3.07×10^{10} spores per individual sporophyte in a single reproduction event (Joska and Bolton 1987).

In South Africa, the most recent work regarding temperature and kelp is by Bolton et al. (2012). This work attributed the expansion of kelp along the south coast to be largely

temperature related. Other work by Leliaert et al. (2000) investigated subtidal understory seaweed communities around the Cape Peninsula, and found significant differences in composition and biomass between Atlantic and False Bay sites. These differences were similarly concluded to be largely temperature related. Important past research by Bolton & Levitt (1985) showed that *E. maxima* has an optimal temperature conditions of ~22.5°C making it a warm temperature organism, as these temperatures are much higher than the environment occupied by northern hemisphere Laminariales. No research currently exists that investigates the effects of different temperature regimes on kelp forest recovery.

Currently, there is no research investigating simulated storm disturbance in South Africa. Instead, because of the economic importance of *E. maxima*, research has focused mainly on the effects of harvesting on kelp populations and its recovery after harvesting. However, the effects of harvesting may be regarded as similar to those of storm disturbance and therefore the literature is relevant. For instance, a study by Rothman et al. (2006) investigated the effects of three different harvesting techniques on *E. maxima* population structure, growth rate, and recruitment. The different harvesting techniques essentially altered the light environment, through changes in canopy cover. The authors found no differences between the treatments and concluded that factors other than light may play role in kelp recruitment, particularly at Bordjies Reef, False Bay. Levitt et al. (2002) investigated the effects of harvesting on re-growth and the understory benthic community at Danger Point, South Africa. The results showed a recovery time of 2 years in terms of associated benthos, biomass and density of kelp. Another example is the study by Anderson et al. (2006), which investigated the effects of kelp harvesting on three obligate, red algal epiphytes. The results of field manipulation experiments showed that epiphyte communities only fully recovered ~4.5 years later. Climate change research in South Africa has mainly focused on upwelling regimes in the northern and southern Benguela on the west coast. The change in upwelling dynamics may influence kelp forest functioning, but this is beyond the scope of this study. However, the relevant literature pertinent to South Africa is discussed briefly here. There is variability in upwelling along the west coast and between the northern and southern Benguela, but there seems to be no consensus on general climate change patterns for southern Africa (García-Reyes et al. 2015). Other recent work by Wang et al. (2015) show strong and consistent changes in the timing, intensity and spatial heterogeneity of coastal upwelling in response to future warming for the majority of the Eastern Boundary Upwelling Systems (EBUSs). Work by Rouault et al. (2010) showed that the South African coastline is exhibiting a cooling trend, which may be as a result of increased upwelling frequency. Blamey & Branch (2012) and Blamey et al. (2015) have shown an increase in both mean upwelling and upwelling variability during the mid-1990s, likely a result of increased summer wind speed due to a shift in the South Atlantic High Pressure system (Jarre et al. 2015). Following that García-Reyes et al. (2015) showed that future climate scenarios may favour upwelling, although deeper thermoclines, as a consequence of greater thermal stratification in the water column, may hinder upwelling in the EBUS. Although future climate scenarios for South Africa are difficult to project, changes are still expected. These changes could have important implications for ecosystems, particularly habitat-forming organisms such as kelp.

4.1.4 Aims and objectives

4.1.4.1 Aim

The overarching aim of this chapter was to measure the recovery of *E. maxima* and its associated benthos between two contrasting sites, in terms of thermal regime and grazer presence/absence, following a pulsed disturbance event. I will then seek to establish whether or not the outcome is congruent with studies that have linked similar responses to temperature as the main driver.

4.1.4.2 Objectives

1. To apply a simulated pulse disturbance event to kelp beds at two contrasting sites.
2. To make repeated measurements of the recovery of *E. maxima* populations and its associated benthos over 13 months, and to examine the outcome relative to measurements taken in un-cleared (control) plots.

4.1.4.3 Null hypotheses

1. H₀: Kelp population recovery will not differ between sites.
2. H₀: Benthic community recovery will not differ between sites.
3. H₀: Sites will not fully recover over the 13-month period.

4.2 Methods

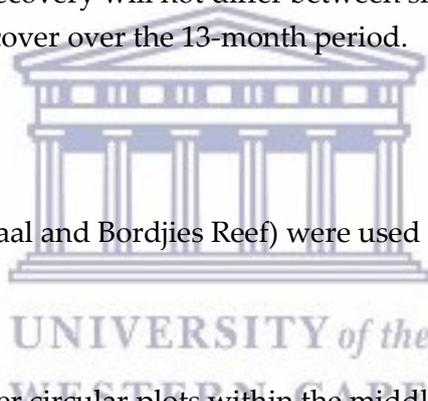
4.2.1 Study sites

The same study sites (Oudekraal and Bordjies Reef) were used as reported in Chapter 2 (section 2.2.1, page 20).

4.2.2 Data collection

At each site, four 16 m diameter circular plots within the middle of the kelps beds were selected. Each plot was approximately 200m² in area. Two of these plots acted as controls and the remaining two acted as experimental plots (removal plots).

Each plot was permanently marked with a 0.5 m railway bar placed in the center of the plot and a GPS position recorded. Sampling of the plots involved SCUBA divers attaching a transect line to the center of the plot and swimming out 8 m along predetermined compass bearings. Rock lobster and abalone were counted within 1m either side of the transect and on the return swim towards the center of the plot, two 1 × 1m and two 0.5 × 0.5m quadrats were sampled at 1 m and 4 m along the transect. In the 1 × 1m quadrats the number of adult and, recruit kelp individuals were recorded. A kelp <50 cm was considered a juvenile. In the 0.5 × 0.5 m quadrats percentage cover of sand, rock, foliose algae, encrusting coralline algae, sponge, mussel and silt were estimated and recorded. Larger invertebrates such as sea urchins, abalone and rock lobster were counted and recorded. All species in the 0.5 × 0.5 m quadrats were identified as far as possible *in situ*. This step was repeated four times on different compass bearings, giving: (1) a total of eight 0.25 m² (0.5 × 0.5 m) quadrats; (2) a total of eight 1m² (1 × 1 m) quadrats sampled per plot; and (3) a total of four 8 m transects for the rock lobster and abalone counts. This sample regime was repeated at 3-months, 6-months and 13-months.



4.2.3 Data analyses

All data analyses were done using the R software (R Core Team, 2016) and the vegan package (Oksanen et al. 2016), and ggplot2 (Wickham 2009). To reveal patterns in overall recovery at each site, non-metric multidimensional scaling (nMDS) was performed on all community data. Kelp abundance data were first 4th root transformed for comparison with percentage cover and benthic invertebrate species for the nMDS.

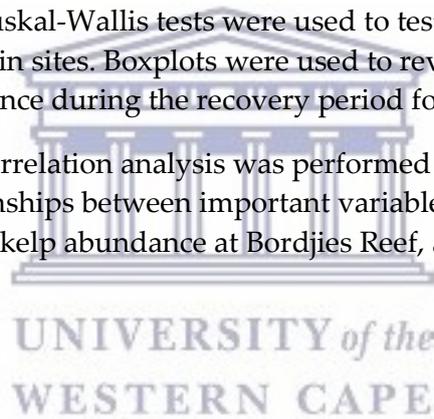
To investigate benthic recovery an ANOSIM was performed between %-cover data for control and removal plots for both sites to reveal any similarities. A SIMPER analysis was performed on %-cover data to help identify which cover types were most responsible for differences between sites and plots, and recovery period. The recovery period was categorised into 'control', 'before', '3-months', '6-months', and '13-months.' Boxplots were used to compare summary statistics of cover categories and abundance data visually across phases and sites, for both macrobenthic and kelp population data. Boxplots were also used to show any relevant changes in %-cover classes. For these analyses, all cover type data were pooled per site, recovery period, and cover type. A Kruskal-Wallis test was used to test for significant differences in %-cover within sites during the recovery period. This was to allow for identification of important patterns that could then be tested with correlations. To assess kelp population recovery, Kruskal-Wallis tests were used to test for significant differences over the recovery period within sites. Boxplots were used to reveal any differences in kelp recruit and adult kelp abundance during the recovery period for each site.

Pearson's product-moment correlation analysis was performed for sea urchin and kelp data to investigate possible relationships between important variables. Correlations were only performed for sea urchin and kelp abundance at Bordjies Reef, as high sea urchin abundance is characteristic of this site.

4.3 Results

4.3.1 Benthic community

The nMDS biplot showed very little variability during the recovery process at Bordjies Reef (Figure 4.1a). The pattern was not clear, but there was a slight grouping with some overlap between phases. If sites had recovered one should see a close clustering of A (before) and D (13-months), followed by C (6-months) and B (3-months). The 'before' phase and the samples taken 13-month after clearance tended to group closer to one another, suggesting that Bordjies Reef recovered to a state close to its original pre-removal state.



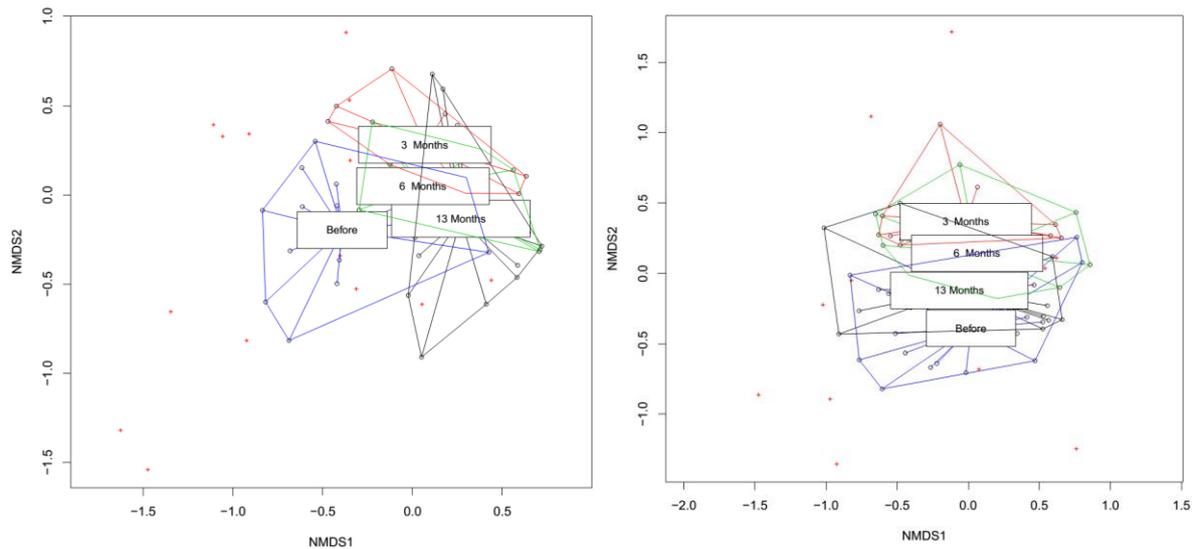


Figure 4.1a-b: Multidimensional scaling of macrobenthic and kelp population data for Bordjies Reef (left, Figure 4.1a) and Oudekraal (right, Figure 4.1.b) recovery phases. Phase are colour coded, “blue” = ‘before’, “red” = 3-months, “green” = 6-months, “black” = 13-months.

An ANOSIM comparing %-cover between the ‘before’ phase plots and control plots showed no significant differences for Bordjies Reef ($r = 0.05$, $p = 0.25$) or Oudekraal ($r = 0.05$, $p = 0.14$). There was a higher amount of variability at Oudekraal compared to Bordjies Reef (Figure 4.1b). This may be due to variability between plots within the Oudekraal site, which was most likely due to the high mussel cover at only one of the plots. If sites had recovered one should see a close clustering of A and D, followed by C and B. In the Bordjies Reef nMDS, clustering of before and 13-month phases were seen, which indicates that the overall community had recovered to a similar state as before. The Oudekraal cluster was more variable; however, there was a similar pattern of recovery compared to Bordjies Reef.

Differences and variation in mean %-cover types during the recovery process can be seen in Figure 4.2. The Kruskal-Wallis test showed a significant difference in sand cover over the recovery period at Bordjies Reef ($\chi^2 = 11.534$, d.f. = 4, $p < 0.05$). The SIMPER analysis showed that at Bordjies Reef there was a significant difference in mean %-cover of sand between the 6-months and 13-months ($p < 0.05$) phase, which contributed 4% to the dissimilarity. A difference in mean %-cover of sponge between ‘before’ and 13-months ($p < 0.001$), was also found, however, a Kruskal-Wallis test did not show any significant changes. The SIMPER also revealed %-cover of encrusting coralline and foliose algae to contribute most to the dissimilarity (12% and 10%, respectively) between the ‘before’ and 13-months phases. However, a Kruskal-Wallis test showed no significant differences in encrusting coralline and foliose over the recovery period.

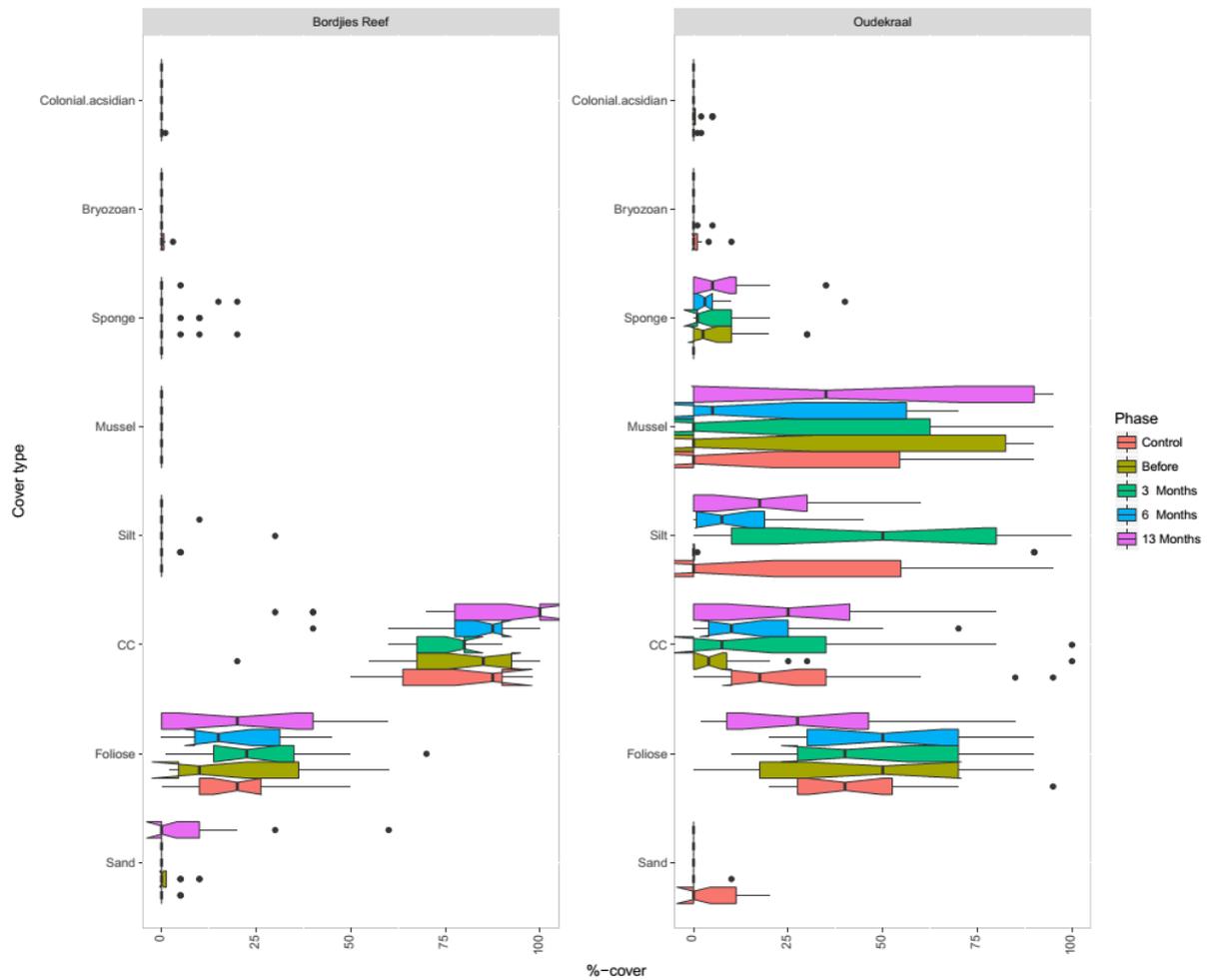


Figure 4.2: Boxplot of %-cover types for both sites during the recovery process, for each site. If 'notches' do not overlap, the medians are considered to be statistically different. The lower and upper 'hinges' correspond to the first and third quartiles. Box widths are proportional to the square-roots of the number of observations in the groups. The dots indicate outliers.

At Oudekraal a SIMPER analysis showed a significant difference in sand ($p < 0.05$) between the 6-month and 13-month phases. The SIMPER also revealed mussel, foliose and encrusting coralline algae as the cover types contributing most to dissimilarities between the before and 13-months phases. Mussel contributed most to the dissimilarity (19%), followed by foliose algae (14%) and encrusting coralline (12%). However, a Kruskal-Wallis test showed no significant differences in mussel, foliose algae and encrusting coralline cover over the recovery period. Significant differences in percentage cover of sand ($\chi^2 = 21.366$, d.f. = 4, $p < 0.001$) and silt ($\chi^2 = 13.518$, d.f. = 4, $p < 0.05$) were found over the recovery period. From Figure 4.2 the significant differences can be seen between the control and recovery plot for sand, with the control plot having a significantly higher median. In terms of silt, significant differences can be seen between 'before' and 3-month phases (Figure 4.2).

Figure 4.3 shows all counts of abalone and rock lobster for each phase at each site. The abundance of *Jasus lalandii* was not significantly higher at Oudekraal than at Bordjes Reef and the abalone *Haliotis midae* is more prevalent at Bordjes Reef than at Oudekraal, in this study. However, a Kruskal – Wallis test showed no significant difference in abalone and rock lobster counts between phases for each site and between sites for each phase. No

abalone or rock lobsters were recorded for the 3-month and 6-month phases at both sites. No clear patterns in recovery were present and the sparse data set limits possible analyses.

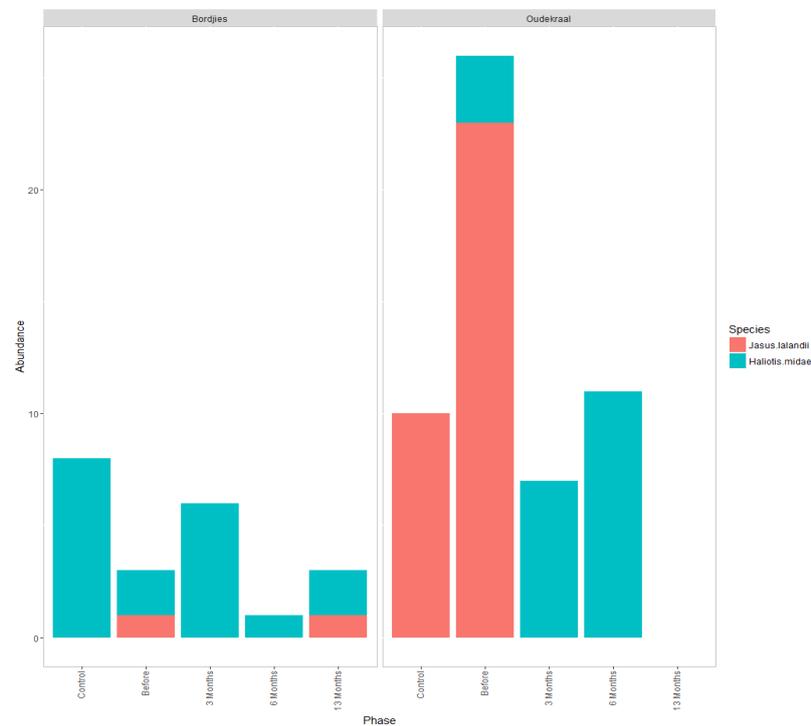
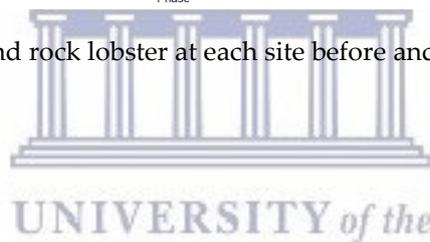


Figure 4.3: Number of abalone and rock lobster at each site before and 3, 6 and 13 months after kelp removal.



4.3.2 Kelp population

Figure 4.4a-b shows adult and recruit kelp abundance during the recovery phase. The before plots were very similar between sites. As expected there was no adult kelp at the 3-month phase at both sites, for this reason the 3-month phase for adult abundance was excluded from the analyses. There were also few adult kelp at the 6-month phase for both sites, however at 13-month Oudekraal had a similar number of adults compared to the before phase. There was no significant difference in adult kelp abundance over the recovery period for both Bordjies Reef and Oudekraal (Figure 4.4a-b). In terms of recruit abundance, there were no significant differences during the recovery phase for both sites (Figure 4.4a-b). No significant differences in sea urchin abundance were found in relation to kelp recovery over the recovery period.

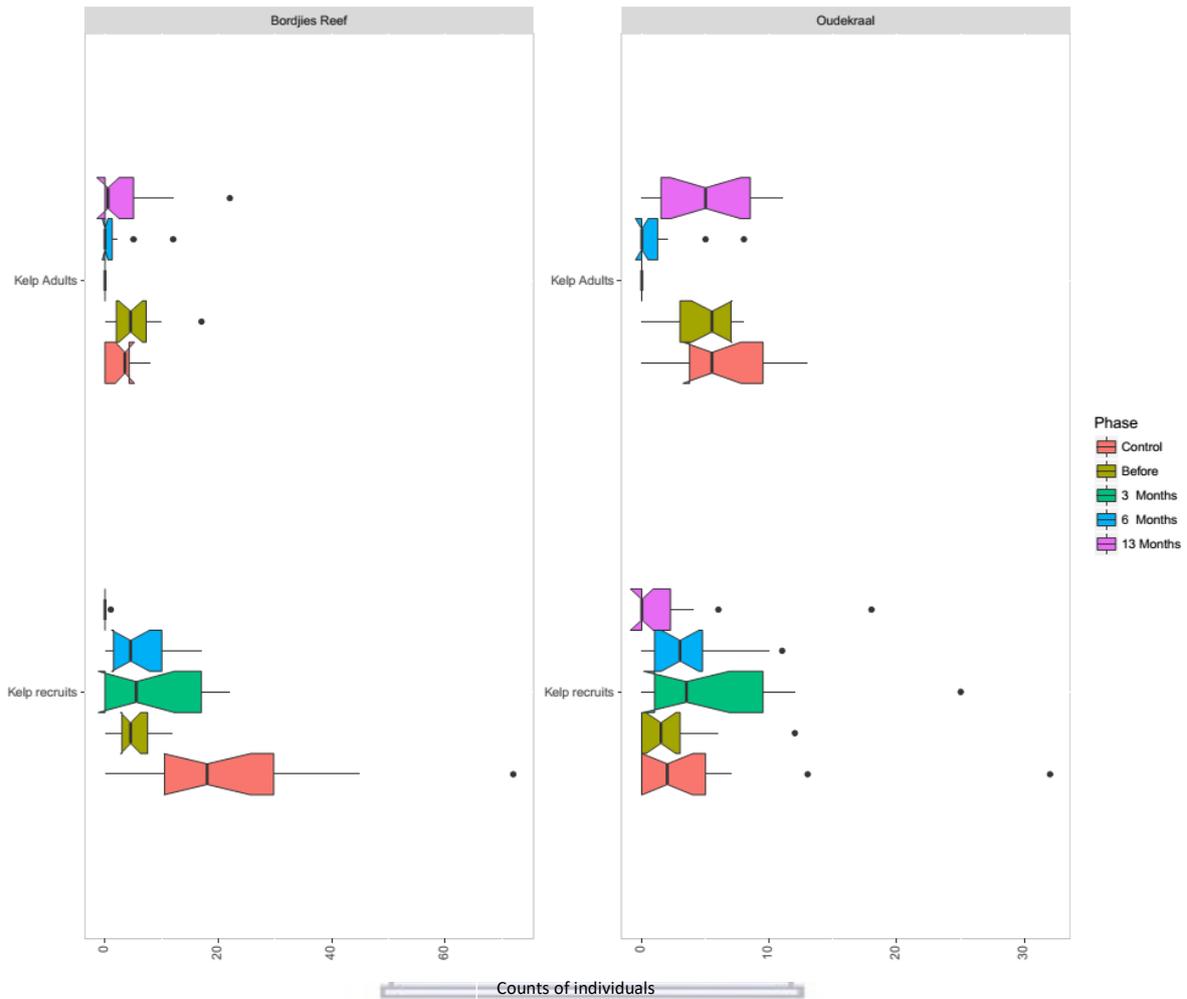


Figure 4.4a-b: Adult and recruit kelp recovery at each site for each phase. Bordjies Reef is the left-hand plot (Figure 4.4a), and Oudekraal is the right-hand plot (Figure 4.4b). If “notches” do not overlap, the medians are considered to be different. The lower and upper “hinges” correspond to the first and third quartiles. Box widths proportional to the square-roots of the number of observations in the groups.

4.4 Discussion

Increases in ocean SST and storm disturbance could have negative impacts on coastal ecosystems, particularly kelp ecosystems. Changes in ocean temperatures have been linked to macroalgae extirpation, range shifts and regime-shifts (Harris et al. 1984, Ebeling et al. 1985, Cury and Shannon 2004, Soule et al. 2005, Blamey and Branch 2012, Kortsch et al. 2012, Wernberg et al. 2016). Kelp ecosystems also support an array of fauna and flora, and changes in kelp forests structuring could ultimately affect the associated benthos. Furthermore, increases in storm disturbance frequency and changing ocean temperatures has been shown to decrease the resilience of kelp to disturbance (Wernberg et al. 2010, 2013), and if this continues, could cause loss of kelp ecosystems from coastal environments. The effect of storm disturbance, and the ability of kelp and its associated benthos to recovery are important aspects that have lacked attention in the South African context.

4.4.1 Benthic community

The slight variations in percentage cover of mussels is likely due to variability among quadrats within the sites. The second removal plot at Oudekraal has a high %-cover of mussels, while the other plot has very little to none recorded. This may be the reason why a clear separation between plots is seen at Oudekraal per the nMDS. The closer clustering of replicates within the 'non-mussel' plot suggests a quicker recovery and a more uniform distribution of cover types and kelp individuals. Mean %-cover of foliose algae increases during the recovery process, with a large increase between the 6-month and 13-month recovery stages. This may be due to slight canopy recovery, which resulted in reduction of light penetration into the water column. A study by Toohey et al. (2004) showed that foliose algae tend to dominate in low light environments. This may allow species that are tolerant of low light conditions to outcompete other species. Kelp canopies have been shown to reduce bottom irradiance by as much as 95% (Arkema et al. 2009). Also, Rhodophyta (which was the dominant phylum at Oudekraal) can outgrow other algae types due to rapid cell division (Vadas et al. 1992; Goff and Coleman 1986), and therefore may be able to outcompete other benthic algae species for light (Dayton 1985, Dayton et al. 1992). This may also be the reason why Rhodophyta dominate the benthic environment at Oudekraal (see Chapter 2).

Encrusting coralline and foliose algal cover was the most influential cover types at Bordjies Reef during the recovery process. Encrusting corallines did not show any significant patterns. Other species of macroalgae may settle and grow on encrusting corallines and therefore the overall coverage may not be affected. The variation of %-cover of foliose algae was most likely due to the increase in available space due to the removal of kelp. The decrease at the 6-month phase may be because of competitive interactions as space becomes more limited over the recovery process, or because of grazing pressure by sea urchins. Preferential feeding of *Parechinus angulosus* has been investigated by Anderson and Velimirov (1982). The authors showed that palatability of algae is based on H₂SO₄ content, and that species with a lower H₂SO₄ content would be preferred. For instance, *Pachymenia cornea* (Kützting) Chiang, *Gigartina bracteata* (Gmelin) Setchell & Gardner, *Carradoria virgate* (C. Agardh) Kylin, *Suhria vittata* (Linnaeus) Endlicher, and *Gelidium* sp. are preferred species, while *Hymenena venosa* (Linnaeus) C. Krauss, *Botryocarpa prolifera* Greville, *E. maxima*, *Axillariella constricta* (Kützting) Gruber, *Desmarestia firma* (C. Agardh) Skottsberg, and *Neuroglossum binderianum* Kützting, will still be eaten in small amounts, but are not preferred. This may also be the reason why these species are absent/present at Bordjies Reef, as they are palatable to *P. angulosus*. This preferential feeding may also be reducing the competition for space between benthic species and kelp. For instance, a study by Levenbach (2009) showed that under high grazer intensity the competition for space between macroalgae is reduced, while under low grazer intensity competition for space increases. The significant, albeit weak, inverse relationship between %-cover of foliose algae and sea urchin abundance also suggests a possible relationship between grazer abundance and facilitation in reducing the competition for space. The nMDS plot for Bordjies Reef shows very little variability between recovery plots, suggesting that the recovery plots are similarly structured. Bordjies Reef also shows a pattern of recovery, with little variability in %-cover types.

4.4.2 Kelp population recovery

The patterns of juvenile abundance recovery can be seen at Bordjies Reef and Oudekraal. The recovery of recruit abundance at both sites may be due to seasonality of zoospore release in *E. maxima*. A study by Joska & Bolton (1987) demonstrated that zoospore release was low in winter (April to August) and increases in spring and summer (September to January), with a peak at the end of the year (December). Therefore, both sites had undergone a natural peak in zoospore release, which may have aided the recovery process. Also, the sites were not sampled in the same month, with the experiment beginning in May at Oudekraal and July at Bordjies Reef. Therefore, the kelp population at Bordjies Reef was further along in seasonal trend of zoospore release, which may account for the higher recruit abundance compared to Oudekraal. The initial increase at the 3-month phase may also be due to an increase in space available for settlement, as well as light. The role light plays in structuring kelp-associated benthos has been well documented (Duggins et al. 1990, Melville and Connell 2001, Clark et al. 2004, Toohey et al. 2004, Wernberg et al. 2005, Arkema et al. 2009). This is also true for Bordjies Reef, which shows a similar pattern with an average juvenile kelp abundance similar to that at Oudekraal. However, light may play less of a role at Bordjies Reef in juvenile kelp recruitment. Rothman et al. (2006) conducted canopy manipulation experiments regarding different harvesting techniques. Their results showed no difference in net abundance of kelp recruits between treatments despite the increased light environment. The authors concluded that factors other than light may be driving recruitment patterns at Bordjies Reef. The decrease of juvenile abundance at 6-month at both sites is most likely due to juveniles from the previous phase reaching an adult phase (>50 cm); however, this was not tracked.

Interestingly, the abundance of adult kelp is similar between sites despite Bordjies Reef having a higher juvenile abundance at the 3-month phase. This may be due to differences in grazer abundance, as the 6-month phase is also marked by the presence of sea urchins. In South Africa, sea urchins rarely feed on adult kelp as their small size and wave action in the water column makes it difficult for them to attach and graze (Fricke 1979, Anderson et al. 1997). However, they may graze on juvenile kelp (Fricke 1979). Therefore, they may have grazed some of the juvenile kelp from the 3-month phase, which may explain the lack of difference of adult kelp abundance at the 6-month phase between sites, despite more recruits measured at Bordjies Reef for the previous phase. The main food source for sea urchins is drift kelp, and therefore grazing on kelp recruits may only occur under food limited conditions. Under such conditions, sea urchins may begin to 'actively feed' and in severe cases this may lead to elimination of kelp from an area. For instance, a study by (Ebeling et al. 1985) investigated the effects of storm disturbances on community structure in a southern California kelp forest. The loss of kelps after winter storms resulted in loss of 'drift' kelp, which is the primary food source for sea urchins *Strongylocentrotus franciscanus* Agassiz, and *Strongylocentrotus purpuratus* Stimpson, causing them to seek an alternative food source (Ebeling et al. 1985). The loss of the giant kelp caused a trophic cascade and shifted the system from a kelp-dominated system to an urchin barren. The impacts on the detritus-based food web, which is an integral part in these ecosystems for kelp, fish and sea urchin populations, were severe (Ebeling et al. 1985). However, a subsequent storm removed grazing sea urchins from the newly formed barren, allowing the giant kelp and understory kelp to regrow, and this in turn allowed drift kelp to accumulate on the bottom again,

reversing the effects of severe kelp loss (Ebeling et al. 1985). Therefore, the sea urchin population at Bordjies Reef may have to actively feed on kelp recruits due to unknown mechanism which may be limiting their food source.

At 13-months, Oudekraal returned to an average adult abundance similar to that during the 'before' phase, whereas at Bordjies Reef this did not happen. This once again may be due to grazing by sea urchins, as very little or no juveniles were recorded at the 13-month phase, as well as an increase in the average number of sea urchins. There were no correlations between kelp stages (recruit/adult) and urchin abundance, suggesting that grazing may not be a major role player in structuring kelp populations at Bordjies Reef. Sea urchins primarily feed on drift kelp and therefore their grazing may not have a profound effect on kelp populations. Competition for space at Bordjies Reef may only play a minor role in structuring the benthic community at, as constant grazing may be freeing up space for settlement of various fauna and flora.

4.4.3 Conclusion

Overall, both sites showed no differences in kelp population and benthic structure between the start and the end of the experiment. This suggests a full recovery in terms of kelp abundance, and associated cover types, and community structure. The findings in this study are similar to a study by Levitt et al. (2002) which showed that biomass and density of kelp biomass had recovered to a similar state to control plots two years after harvesting whole kelp individuals. Also, the associated benthic communities showed no significant differences before and after the experiment. Levitt et al. (2002) covered a larger area (two 100 x 20m) compared to the current study, which may account for the longer recovery time of 2 years compared to 13 months. Furthermore, the study by Levitt et al. (2002) removed kelp individuals in lanes rather than circular plots (two 200m² plots). The results from this study show no notable differences in recovery, suggesting that kelp populations and their associated benthos are similar in their ability to recover from a pulse disturbance event. There may be differences in rate of recovery however this was beyond the scope of the current study. Future studies should measure kelp individuals during each monitoring interval and attain biomass estimates, which allow the investigation into possible differences in rate of recovery.

Chapter 5 – Synthesis



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Temperature and its effect on marine organisms and their distributions have been well documented. Temperature ultimately determines species ranges, which are expected to change under future climate scenarios due to an expected increase in SST. Marine organisms are expected to shift their distributions pole-wards, which would increase species interactions that in turn may lead to local extinctions due to species outcompeting one another for resources. For instance, a study by Vergés et al. (2016) showed using long-term empirical evidence, that loss of kelp communities in Australia was as a result of long-term temperature changes. Also, these temperature changes resulted in range extensions of herbivorous tropical fish, which overgrazed existing kelp communities, causing them to disappear. Effects of temperature on marine organisms may also occur through short-term events, or heat waves. Heat waves are significant, short-term increases in SST that may persist for days or weeks (Smit et al. 2013).

Temperature has also been shown to decrease resilience to disturbance, through altering physiological processes within an organism. This is particularly important for organisms on the edge of their distributions. For instance, a study by Wernberg et al. (2010) showed that although macroalgae may be able to survive in non-ideal temperature conditions, this is done at a physiological cost. Kelps have to spend more energy on adjusting physiological processes, such as growth, to acclimation. This in turn, makes kelps less resilient to disturbance, such as storms, and under extreme scenarios these ecosystems may not be able to recover at all. Storms increase wave exposure and wave energy exerted on kelp communities.

Storm disturbance in kelp communities manifests itself through mechanical dislodgment of individuals, creating drift kelp. Drift kelp is an important input into the detrital food web for coastal communities. Therefore, this is a natural process. However, the effects of storm disturbance may be enhanced through increases in storm frequency and magnitude. Enhanced effects may reduce kelp populations to the extent where the detrital food web is impacted negatively, which in turn may cause a regime shift through alteration in grazing of mesograzers, such as sea urchins. Temperature and storm disturbance are important drivers of kelp ecosystems, and given the importance of kelp at an ecosystem engineer, it is imperative that these aspects are better understood to help better the possible effects of future climate scenarios on these ecosystems.

In Chapter 2, the research characterised the associated benthic fauna and flora of three study sites which contrasted in temperature regimes and predator abundance. These sites were Oudekraal (Benguela Marine Province), Bordjies Reef (Benguela-Agulhas Transition) and Betty's Bay (Benguela-Agulhas Transition). Oudekraal and Bordjies Reef have opposite temperature regimes, while Betty's Bay has a similar temperature range compared to Bordjies Reef, but is characterised by high predator abundance of *Jasus lalandii* Edwards. Results showed clear distinction of species composition between sites, however, no significant differences in diversity was found between them. The nMDS analysis showed that sites were structured differently from one another in terms of both flora and fauna. Further analysis showed that these differences were in terms of grazer abundance (*Parechinus angulosus* Leske) and macroalgae types. Bordjies Reef had a mixture of Chlorophyta, Rhodophyta, and Ochrophyta, while Oudekraal was dominated by Rhodophyta. There was also significantly lower foliose cover at Bordjies Reef compared to Oudekraal, which was attributed to differences in grazing pressure between sites. Betty's

Bay had a low biomass of algae, and diversity of fauna and flora, which is a result of observed localised sedimentation at the site. I conclude that other abiotic and biotic factors may be acting synergistically with temperature to determine species composition, such as space, and grazing intensity. Other factors such as wave motion and light, could only be inferred, however it is important that future studies take a combination of these factors into account. This will allow teasing apart of direct and indirect effects.

In Chapter 3, I investigated if kelp population structure differed between sites, and if this may be due to differing temperature regimes or grazing pressure. The results showed no significant difference in adult abundance between sites; however, significant differences between recruit abundance were found between Bordjies Reef and Oudekraal. No recruits were recorded at Betty's Bay, which was attributed to the high percentage cover of silt at the study site. Correlations performed showed a significant, positive correlation between kelp recruits and kelp adults for Bordjies Reef, but not for Oudekraal, which suggests a higher succession of kelp individuals at Bordjies Reef. The major findings were that (1) there was a significant difference in recruit abundance between sites, with more recruits seen at Bordjies Reef, but (2) that the clear differences in juvenile kelp abundance did not result in differences in the adult kelp abundance between sites. This evidence suggests a possible thinning mechanism on the adult kelp population at Bordjies Reef. The mechanisms may be attributed to thermal extremes experienced at each site prior to sampling. Thermal stress may manifest itself in terms of heat wave events, which have been shown to be detrimental to kelp survival. The presence of grazers may also be contributing to the thinning of the kelp population through feed on early life stages of kelp. Wave motion may be another factor, thinning the adult population, however this was not measured and could only be inferred, through observations. Future studies should investigate the direct effects of wave motion on kelp population structure, as this will help elucidate further the roles that different abiotic and biotic factors.

In Chapter 4, I investigated the effects of a pulse disturbance event on kelp ecosystem recovery, between two contrasting study sites. The nMDS analyses showed patterns of recovery at both sites. The associated benthic cover was largely unaffected at both sites, by the end of the removal experiment, with small amounts of variation detected over the recovery period. The kelp population in terms of adult and recruit abundance had also recovered to a similar state, at the end of the experiment. This study revealed that temperature as well as an array of other factors (grazer abundance, wave action, light, and space) could be responsible for shaping kelp forest structure and associated benthos. The direct effects of temperature alone are unclear, and it may be acting in combination with other abiotic or biotic variables which may be site specific. For instance, in the case of Bordjies Reef, temperature may be acting in combination with grazing to structure the kelp and associated benthos, while at Oudekraal the lack of grazers and high foliose cover makes space a more limiting factor compared to Bordjies Reef. Therefore, future studies should incorporate a multi-factorial approach in order to tease out the direct and indirect effects of important abiotic and biotic variables. In addition, future studies investigating recovery of kelp forests, should be run over a longer time period, as this would allow seasonality to be taken into account. Lastly, this chapter lacked replication, and future studies should include at least two study sites on each of the coast respectively. The lack of replication in this

chapter did not allow for thorough investigation into direct and indirect effects of abiotic and biotic variables.

To conclude the work covered in this thesis shows that there are clear differences in kelp population structure and the associated benthos between sites. Although the sites in this study have different temperature regimes, it is difficult to state whether these differences are directly attributed to temperature alone. The results from the current study are similar to a study by Leliaert et al. (2000) investigate the subtidal understory algal community structure in kelp beds around the Cape Peninsula (Western Cape, South Africa). The results showed significant differences in benthic community structures between sites which differed in thermal regime. The authors concluded that the differences in benthic community structure could largely be attributed to temperature, as well as other factors such as wave exposure, grazing and sand cover to a lesser degree. Therefore, other factors which may be site specific such as grazing pressure, wave exposure and siltation may be acting synergistically with one another and/or temperature to structure *E. maxima* kelp forests, and its associated benthos along the South African coastline. Furthermore, this study also agrees with findings from a study by Rothman et al. (2006) that factors other than light may be driving kelp recruitment, such as grazing. The sites also show no difference in terms of recovery, further indicating that temperature may not be the only environmental driver. A study by Levitt et al. (2002) investigating the effects of kelp harvesting on its re-growth and the understory benthic community at Danger Point, South Africa, had similar findings. Levitt et al. (2002) showed that the kelp biomass and density had recovered by the end of the 2 year harvesting experiment, and no significant changes in associated benthic community structure over the recovery period.

In the current study, grazing pressure reveals itself as a possible role player, which may be acting in combination with temperature to structure kelp forests. Therefore, temperature may determine the regions where species may reside, however, these differences may be compounded by other factors (grazer abundance, light, and wave motion) to structure kelp forests. Furthermore, the results from this study show that the site specific characteristics do not alter the ability of kelps to recover from a pulse disturbance event.

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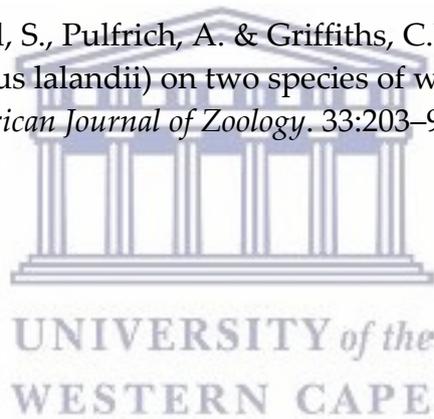
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Appendix: List of figures

Figure 2.1: Map of South African coastline, and study sites.....	28
Figure 2.2: Monthly temperature data showing the yearly trend at each site for 2015. The black line represents the mean. The lower and upper ‘hinges’ correspond to the first and third quartiles, and the ‘whiskers’ are the 5th and 95th percentiles	29
Figure 2.3: nMDS plot of all samples across the three sites, based on standardized fourth-root transformed biomass data for species. Black circles represent site scores, and red ‘+’ signs represent species scores.....	31
Figure 2.4: Hierarchical clustering of the quadrats across all sites for both flora and fauna (top), flora only (middle) and fauna only (bottom) using Ward’s agglomeration method. B: Bordjies Reef; O: Oudekraal; Y: Betty’s Bay.....	32
Figure 2.5: Shannon-Wiener index of diversity averaged over all replicates within each site. Error bars represent the 95% confidence interval. The symbols indicate significance; if bars share the same letter they are significantly different.....	33
Figure 2.6: Presence/Absence scatter graph for quadrats across all sites for both fauna and flora. B: Bordjies Reef; O: Oudekraal; Y: Betty’s Bay.....	34
Figure 2.7: Boxplots comparing percentage cover types across sites. If ‘notches’ do not overlap, the medians are considered to be significantly different. The lower and upper “hinges” correspond to the first and third quartiles. Box widths are proportional to the square-roots of the number of observations in the groups.....	35
Figure 2.8: Boxplot showing abundance (averaged over all 16 m ²) of abalone <i>Haliotis midae</i> and rock lobster <i>Jasus lalandii</i> between sites. Each point represents a total measure of <i>H. midae</i> and <i>J. lalandii</i> respectively. The lower and upper ‘hinges’ correspond to the first and third quartiles. Box widths proportional to the square-roots of the number of observations in the groups.....	36
Figure 2.9: Heatmaps for correlations for each site. In the top-left is Oudekraal, top-right is Bordjies Reef, and bottom is Betty’s Bay. Values within block represent the <i>r</i> – value. Red represents a ‘+’ correlation coefficient and blue a ‘-’ correlation coefficient.....	37
Figure 3.1: Box plot with data points comparison of the median recruit (left plot) and adult (right plot) kelp abundance within 1 m ² quadrats across sites. Each point represents the count of recruits or adults recorded per quadrat and horizontal black lines represent the median. The lower and upper ‘hinges’ correspond to the first and third quartiles, and the ‘whiskers’ are the 5th and 95th percentiles. Box widths are proportional to the square-roots of the number of observations in the groups.....	46
Figure 3.2: Box plot comparison of stipe lengths across sites. Each point represents a length of an individual kelp, which is colour coded by canopy-type. The label ‘None’ indicates a quadrat where no kelp was recorded. The lower and upper ‘hinges’ correspond to the first and third quartiles. Box widths proportional to the square-roots of the number of observations in the groups.....	47
Figure 3.3: Temperature regimes for each site, showing extremes and their duration. The measured temperature series is indicated by solid black line, the seasonal climatology is represented by the grey line, the thermal threshold is indicated by the green line and heat extremes are indicated in pink.....	49
Figure 4.1a-b: Multidimensional scaling of macrobenthic and kelp population data for Bordjies Reef (left, Figure 4.1a) and Oudekraal (right, Figure 4.1.b) recovery phases. Phase are colour coded, “blue” = ‘before’, “red” = 3-months, “green” = 6-months, “black” = 13-months.....	58

Figure 4.2: Boxplot of %-cover types for both sites during the recovery process, for each site. If 'notches' do not overlap, the medians are considered to be statistically different. The lower and upper 'hinges' correspond to the first and third quartiles. Box widths are proportional to the square-roots of the number of observations in the groups. The dots indicate outliers.....59

Figure 4.3: Number of abalone and rock lobster at each site before and 3, 6 and 13 months after kelp removal.....60

Figure 4.4a-b: Adult and recruit kelp recovery at each site for each phase. Bordjies Reef is the left-hand plot (Figure 4.4a), and Oudekraal is the right-hand plot (Figure 4.4b) If "notches" do not overlap, the medians are considered to be different. The lower and upper "hinges" correspond to the first and third quartiles. Box widths proportional to the square-roots of the number of observations in the groups.....61

List of abbreviations

ANOSIM	Analysis of similarity
ANOVA	Analysis of variance
EBUS	Eastern Boundary Upwelling Systems
NRF	National Research Foundation
SIMPER	Similarity percentage
SST	Sea surface temperatures

