Identification and evaluation of key factors for rehabilitation of shores denuded of mussels (*Perna perna*) along the Transkei Coast, South Africa

Thesis submitted in fulfilment of the requirements for the degree of

MASTERS OF SCIENCE

at

RHODES UNIVERSITY

by

LUKHOLO MACALA

January 2013

Abstract

Mussels play an important supplementary role in the diet of local communities on the Transkei coast in the Eastern Cape province of South Africa. The exploitation of mussels date back to about 1350 years ago, but in the last 3 decades, exploitation of the brown mussel *Perna perna* has become unsustainable with mussels collected as small as 30-40mm when they are only just sexually mature. Dye and Dyantyi (2002) developed a technique to rehabilitate areas denuded of adult mussels. The government sponsored Mussel Rehabilitation Project (MRP) to use this technique but only some sites have been successfully rehabilitated, reaching c. 80 % cover within a year whilst others only reach about 5%. At an unexploited site (Riet River), I tested the effects of mussel size and wave strength on the effectiveness of the rehabilitation technique, hypothesizing that different size classes may respond differently due to differences in their energy allocation (growth vs reproduction), while wave action determines food supply. Small (1-2cm) and large mussels (3-4cm) were deployed for rehabilitation at 2 exposed and 2 sheltered sites, separated by 100s m.

A similar study was repeated in Coffee Bay where shores are exploited. Six sites were selected, 3 sites that had been successfully rehabilitated and 3 that were unsuccessful according to the MRP. Again, two size classes were used but these differed from the first experiment. Mussels of 3-4cm size were now rated as small and 5-6cm as large. Two methods were used to re-attach mussels, the original and the same method with the addition of mesh bags during mussel deployment. Treatments were examined on three occasions at approximately one month intervals.

At Riet River, the sites chosen did not show differences in wave strength (measured using dynamometers) or water flux (measured using erosion of cement balls) so that water motion was excluded from the analyses. Small mussels grew faster and had weaker attachment than large mussels. There was no difference in condition index between small and large mussels, or in the numbers of recruits settling among the byssus threads of deployed mussels of the two size classes.

In Coffee Bay, there was no relationship between rehabilitation success and maximum wave force, and no difference in bulk water flux among sites. Small mussels deployed using mesh bags survived better than non-meshed or large mussels of either treatment. There was no difference in condition index (CI) between mesh and no-mesh, or between small and large mussels. As in the case of Riet River, small mussels grew faster than large mussels, but large mussels attached stronger than small mussels, with no effect of mesh. Although the factors that improve reseeding of mussels can be identified (use of mesh, use of small mussels, choice of sites with high recruitment rates), successful long-term rehabilitation requires appropriate subsequent management of re-seeded sites.

TABLE OF CONTENTS

Acknowledgments

I would like to thank my supervisor Professor Christopher McQuaid for his guidance and patience throughout my research, especially on the language. He respected my ideas and gave me a chance to prove them thus empowered and drove my ambition. Most importantly, I thank him for inviting me to join his laboratory. I regard that as undeserved kindness and a grateful opportunity. I also thank Dr. Victoria Cole for her advice in this study. The team; Vuyolwethu Kofi, Mpumelelo and Sonwabo Memani I appreciated your dedication, and hard working. Simone Baldanzi, Dr. Francesca Porri, Adam Ludford, Pamela Cramb and Linda Johnson thank you for helping with the set up of the experiment. I also appreciate Dr. Porri's ideas and making herself available when I needed. Thanks to Dr. Charles Von Der Meden for advice on dynanometers. Thanks you to everyone in Professor McQuaid's laboratory. I appreciate help from Mussel Rehabilitation Project (MRP). The social support from my parents, Titi family (my family away from my family), my fiancée Ziyanda Samela and friends kept me going in Grahamstown during the period of this study. I would like to thank SIDA, NRF and Department of Agriculture and Fisheries for financial support. Thanks to the Almighty God, Jehovah for giving me an opportunity to study the complexity of his creation, that brought me closer to him even more.

Chapter 1

General Introduction

The distribution, diversity and abundance of marine ecosystems differ from region to another depending partly on geographical conditions. Variation in ecosystems is controlled by chemical, biological and physical factors such as coastal topography, size of the continental shelf, upwelling (Ganachaud *et al*. 2010) and water motion (Steffani & Branch 2003a, b, c), which influence recruitment, growth and survival of organisms (Griffiths 1980; Palumbi 1984; Dahlhoff & Menge 1996; McQuaid & Lindsay 2000; Steffani & Branch 2003a; Alfaro 2006; Westerbom & Jattu 2006). In the southern part of the African continent, oceanographic conditions vary resulting into different bioregions with different species distribution, although some species are ubiquitous (Hockey *et al.* 1988). Apart from natural patchiness, anthropogenic activities also affect the spatial distributions of marine organisms.

1.1. Influence of anthropogenic activities on the distribution of marine resources

Marine ecosystems have important social, economic and political roles in many countries (Marinesque *et al*. 2012) and have played a significant role from the existence of mankind (Hilborn *et al.* 2003). Marine animals had been used for human consumption from big animals such as whales (Bowett & Hay 2009) to small animals such as shellfish (Underwood 1993; Branch & Monero 1994; Siegfried *et al.* 1994; Dye *et al*. 1997; Dye & Dyantyi 2002 & Ruis & Cabral 2004) and more recently, global marine ecosystems have been described as is in decline (Russ & Zeller 2003). The catch per unit effort of fish is in decline, showing a decrease of stocks in the sea due to unsustainable utilization (Hardin 1976). At the end of 20th century there was a global increase in exploitation of marine resources (Watson & Pauly 2001; Pauly *et al.* 2002), resulting in a decline of fish stocks. Commercial, recreational and artisanal fishing contributed to the decline, with commercial fishing regarded as the major contributor (Hilborn *et al.* 2003). The 2009 FAO report estimated that ~57.4% of the world fish stock is exploited, 29.9% over-exploited and 12.7% are depleted. The use of modern technology with the capability of catching fish in deeper areas including nursery grounds led to the decline of marine stocks (Hilborn *et al.* 2003). Attempts to manage this problem through Marine Protected Areas are weaker in the developing countries (Marinesque *et al*. 2012) and this may be associated with the dependence of poor rural households on natural resources in developing nations (Narain *et al.* 2008).

Cooke and Cowx (2006) assumed that issues that lead to the decline of fish stocks in commercial fisheries can be applied to recreational fisheries. The implication that recreational fishing can lead to a decline of fish stock has not received wide attention (Cooke & Cowx 2006). Recent studies have emphasized the need to consider recreational fisheries as another contributor to the decline of marine fisheries (Cooke & Cowx 2004; Cooke & Cowx 2006; Post *et al.* 2002). Studies report that recreational fishing is high in developed countries (Cooke & Cowx 2006) mainly due to increases in human population size (Yapp 1986). Recreational fishing has been reported to show marked effects in developed worlds such as Europe, Australia and North America (Cooke & Cowx 2006). According to the US Department of Commerce (2002), reported in Cooke & Cowx (2006), only 12% of the entire population have never participated in recreational fishing, yet in Australia alone >70 million finfish were caught recreationally in

2002 (Cooke & Cowx 2006), and over 47 billion fish are estimated to be caught globally each year for recreational purposes (Cooke & Cowx 2004).

There is another fisheries sector which is often not considered, subsistence fisheries, and a clear distinction has not been made between subsistence and recreational fisheries. Subsistence fishing can be intense in developing countries (Cooke & Cowx 2004). Data for recreational fisheries is difficult to quantify (Post *et al.* 2002), but data for subsistence fisheries are even more scarce (Cooke & Cowx 2004). According to Cowx (2002), the primary objective of recreational fishing is pleasure or leisure, while the primary reason for subsistence fishing is to make a meal for the day (Cooke & Cowx 2004). The subsistence sector directly benefits local communities by providing food and alleviates poverty (FAO 2005). Subsistence fishers tend to consider needs for food over environmental protection and as result bag limits are not an effective form of management. That might be due to the open approach in recreational and subsistence fishing as McConnell and Sutinen (1979) concluded that recreational fisheries under open access result into overfishing. Looking at the decline of mussel stocks in the Transkei region of South Africa, it is clear that subsistence fishing, like commercial and recreational fishing, contributes to the decline of marine stocks, although each is most pronounced in different regions and at different spatial scales. As a result of deteriorating marine ecosystems, a call for the restoration of world fisheries by 2015 was proposed (World Summit on Sustainable Development Plan of Implementation, 2002. Johannesburg, South Africa). Although attempts have been made since then, they fall below expectations and may take as much as four decades to achieve their targets (Marinesque *et al*. 2012).

1.2. Intertidal harvesting

Humans are a major predator of rocky shore organisms all around the world (Underwood & Kennelly 1990; Underwood 1993; Branch & Monero 1994; Dye & Dyantyi 2002; Ruis & Cabral 2004). Their rate of exploitation changes over time due to changes in human population growth and economic status. Exploitation of rocky shore organisms is not a new phenomenon, but it has increased in recent years due to increases in human populations (Keough *et. al.* 1993). Consequently, the exploitation of rocky shore organisms seems to be a worldwide problem (Addessi 1994; Hardin 1976; Branch & Monero 1994). In New South Wales (Australia) as in Transkei (South Africa), non-consumable species are also killed in the pursuit of species for bait and the search for consumable species (Underwood 1993). Rocky shore exploitation is most intense in areas where human populations are high. That has been observed in Australia, the exploitation of marine resources is intense in New South Wales where there is highest population of people along the Australian coast line (Yapp 1986). In Transkei, there is a high population of natives along the coast line (for reasons that are explained later), which has led to overexploitation of resources. In artisanal utilization, various animal species may be exploited (Farrago *et al*. 1993) but the target species is determined by the history and economy of the region (Farrago *et al*. 1993). There are several species that have been harvested from rocky shores for generations by Transkei coastal communities, such as limpets, crayfish, abalone, octopus and the brown mussel *Perna perna* (Dye *et al*. 1997). For example, crayfish are harvested for economic reasons, mainly by men and boys, to sell to tourists. Recently there has been intrusion of men in mussel collection but again, mainly to sell mussels to tourists (Figure 1.1a). Along the South African coast, mussels are the most targeted intertidal resource (Siegfried *et al.* 1994). The brown mussel, *P. pern*a (Linnaeus), is a dominant species in the subtropical and warm temperate regions of South Africa (van Erkom Schurink & Griffiths 1993), including Transkei (Griffiths 1980). It is the major constituent of harvesting on rocky shores. It is mainly harvested by women and young girls Figure 1.1b. In different parts of the world mussels may be exploited for different reasons, but human consumption is always a common factor (Underwood 1993; Branch & Monero 1994; Dye & Dyantyi 2002; Ruis & Cabral 2004). Mussels are exploited for consumption in countries such as Australia (Underwood 1993), Portugal (Ruis & Cabral 2004) and in the southern part of California (Addessi 1994). In Portugal, mussels are also exploited as bait organisms (Ruis & Cabral 2004). Intertidal organisms are vulnerable to predators due to their limited mobility (Branch & Monero 1994), but in the case of humans, the use of sophisticated tools and technology allows them to change the entire ecology of a rocky shore within a short period of time. Although humans are regarded as major disturbers or modifiers of the natural environment, they are often excluded from ecological questions (Castilla 1999).

Figure 1.1.a. Two gentlemen who harvest mussels to sell to tourists in Coffee Bay

Figure 1.1.b. Women harvest mussels in Coffee Bay

Other organisms are also known to modify natural mussel beds. For example rock lobsters (Griffiths & Seider 1980), sea stars (Sommer *et al*. 1999) and sea birds (Kamermans *et al*. 2009) all feed on mussels. Sea stars are known as one of the main predators on mussels (Sommer *et al*. 1999). In the study by Sommer *et al*. (1999) it was found that > 95% of stomach content in sea star was mussel derived diet. Although natural predation on mussels by sea stars may lead to local extinction (Saier 2001), their effects are not as fast as those of humans. Starfish and rock lobsters are size selective, preferring smaller mussels as they struggle to dislodge big mussels (Griffiths & Seiderer 1980, Sommer *et al*. 1999). In populations of rock lobster there are few individuals that can feed on large mussels (Griffiths & Seiderer 1980). Predation is believed to have less effect on mussel populations in South Africa than competition for space (Griffiths and Hockey 1987). Intraspecific competition is generally especially important, although more recently competition with the alien mussel *Mytilus galloprovincialis* has completely re-shaped mussel populations on the west coast (Robinson *et al.* 2005).

1.3. Human exploitation of the brown mussel *Perna perna (Linnaeus)* in South Africa

In South Africa, the harvesting of intertidal resources is focused in KwaZulu Natal and the Eastern Cape province, particularly the Transkei region in the Eastern Cape (Hockey *et al.* 1988), between Kei River mouth and Port St Johns (Figure 1.2) (Hockey & Bosman 1986). Such exploitation dates back to about 1350 years ago (Cronin 1982). In this region, harvesting is traditionally for subsistence purposes (Siegfried *et al.* 1994) and is done by females, while men catch pelagic species or species with commercial value. Mussels had been harvested to supplement a diet predominated by starch/maize (Lasiak 1991). Along the Transkei coast mussels are often over-exploited for food consumption (Siegfried *et al.* 1994), as in Chile (Branch & Monero 1994).

Mussels are a significant proportion of the annual protein intake of indigenous local people (Siegfried *et al.* 1985). Hockey *et al.* (1988) found that shellfish constitute about 8% of annual protein intake of local people along the Eastern Cape coast, especially between Port St Johns and Kei River Mouth. The 8% of annual protein intake from shellfish might subsequently have increased while the 48% from agricultural products might have decreased due to poor agricultural practises. The importance of marine resources as a source of protein is highlighted by low cases of kwashiorkor along the Transkei coast (Branch & Monero 1994). In the Transkei region there is a higher level of poverty than in any other coastal provinces of South Africa (Sowman 2006). Yoko-Ono Maya (2007) reported that in Coffee Bay particularly, children harvest mussels as a source of meat as in some households meat is only available on pay days, i.e. once a month. Mussels therefore have important nutritional value to indigenous communities along the east and south coasts (Lasiak & Dye 1989). The brown mussel is the most targeted and preferred prey item for subsistence fisheries from rocky shores in the region (Dye 1992; Hockey & Bosman 1986; Lasiak & Field 1995). The limited commercial exploitation is caused by the scarcity of large populations of mussels along the coast. In Coffee Bay, mussels gain commercial value by being sold to tourists. That leads to the intrusion of men into mussel harvesting. Men swim beyond easily accessible areas by tying ropes to the shore to get to inaccessible rocks where there are big mussels. Mussels in inaccessible areas can be double the size of those in accessible areas (Ruis & Cabral 2004). In areas where mussel harvesting is prohibited, as in rehabilitated shores in Coffee Bay and in Dwesa Nature Reserve, mussels form extensive beds (pers. obs.) confirming the profound effects of human exploitation (Underwood 1993).

There are several factors that determine the timing of exploitation of intertidal resources. In southern California for example, exploitation is intense in winter and spring because in summer low tides occur at night (Addessi 1994). In South Africa exploitation occurs in late spring, summer and in autumn, since there are rough seas in winter, and is most intense in summer. In New South Wales and Portugal, as in Transkei, there is high exploitation of intertidal organisms in summer, when the weather is good and the sea is calm, providing suitable low tides and exploitation is exacerbated by school holidays (Kingsford *et al.* 1991).

According to Botsford *et al*. (1997) due to human settlement patterns and population growth along the coast, rocky shores experience habitat degradation, overexploitation of organisms and food-web modifications. Increases in coastal human populations mean higher exploitation rates that result in declines in species diversity and richness in many parts of the world (Adessi 1994). Botsford *et al*. (1997) reveals that in order to understand rocky shore ecology there is a need to promote links between ecological studies and social sciences. Underwood (1993) emphasized the importance of understanding all aspects of exploitation for better management of resources when he said "Without detailed knowledge of the patterns of exploitation, the reasons for and the possible effectiveness of management, the usefulness of any procedure of management cannot be predicted" (page 42). To understand the exploitation of mussels in Transkei, it is necessary to understand the history of human settlement and livelihoods in the Eastern Cape Province.

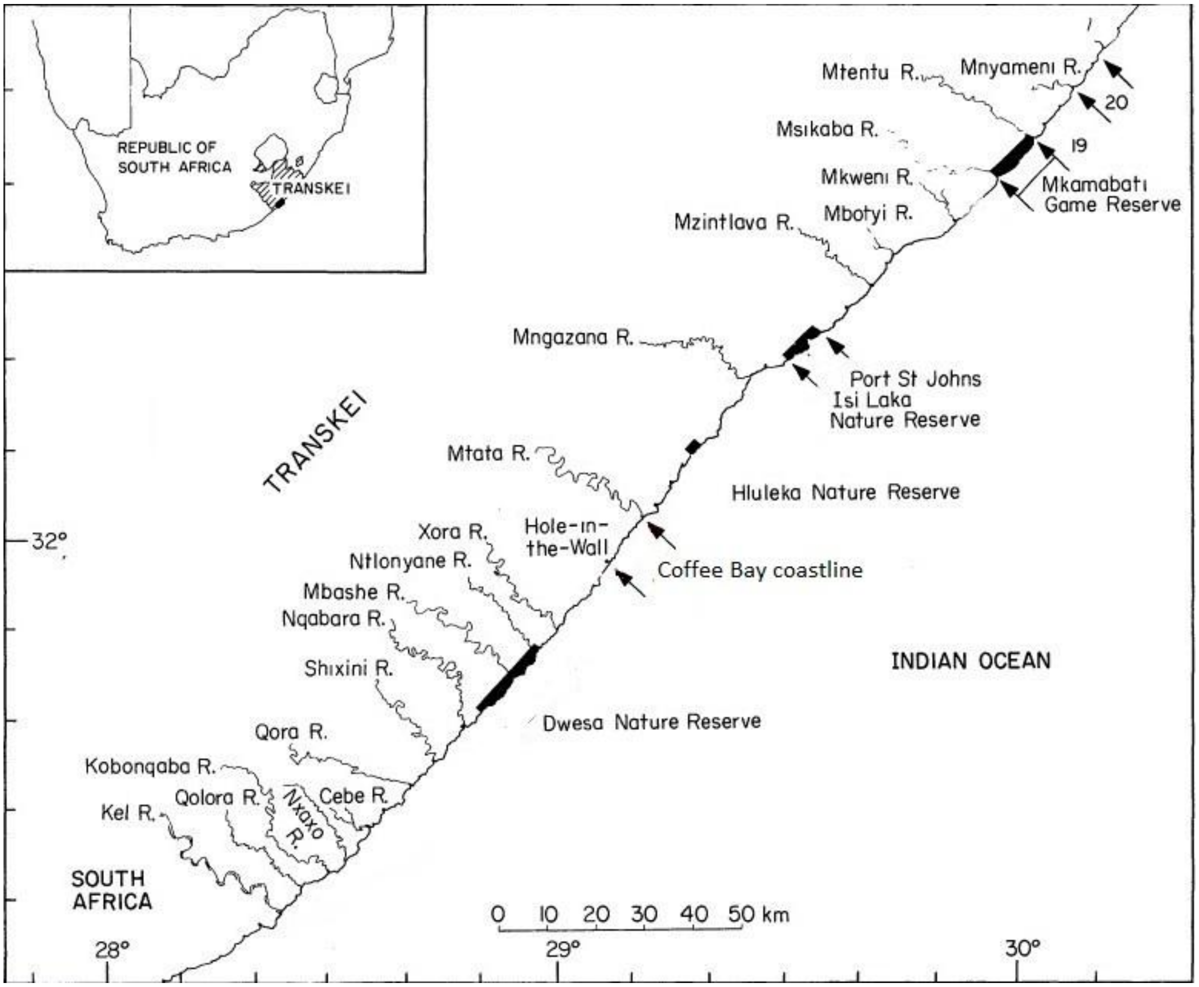

Figure 1.2. Map of South Africa showing Transkei region, black lines indicate nature reserves and arrows indicate Coffee Bay coastline (Map taken from Hockey *at al*. 1988).

1.4. The Eastern Cape province of South Africa and the Transkei region: Why so much pressure on natural resources?

The Transkei coast covers about 250 km between the Kei River mouth (south) and the Mtamvuna River mouth (north) (Figure 1.3). The area is known for its exquisite natural beauty and direct link between people and natural resources. Colonisation by settlers during the 1800s and the role of the apartheid government during the 1900s in what is now the Eastern Cape Province might have had an effect on the exploitation of marine resources by changing human populations along the Transkei coast line. According to Siegfried *et al.* (1994), the establishment of homelands in the 1960s, which located native South Africans along the coast of Transkei and KwaZulu Natal, had severe effects on shellfish due to increased human population growth. In South Africa, as in other parts of the world, numbers of rocky shore visitors decrease with increasing in distance from public access (Addessi 1994). This is associated with the energy and time required to get to the sea. Along the Transkei coast there are rural people who have direct access to the coast and use intertidal resources for subsistence, except in areas where there are marine reserves as within the Dwesa/ Cwebe Nature Reserve. As a result it is common to find that densities of intertidal organisms are higher where accessibility is limited (Addessi 1994).

The major occupation in the area started about 1850s and after 1878 at the end of Frontier wars when native South Africans were moved from the former Cape Province to Transkei by European settlers (Fay 2009). That concentrated native South Africans into Transkei. That is supported by low exploitation of mussels and other intertidal resources in the Western Cape Province of South Africa, where human populations are lower (Branch & Monero 1994). The major exception is the abalone *Haliotis midae* (Branch & Monero 1994), which is also exploited commercially. During the 1990s the exploitation of abalone became totally commercialised (Hauck & Sweijd 1999).

Native South Africans were dependent on farming and natural resources. The increase in dependence on natural resources might have begun in the 1940s when the state subsidised and supported the farming descendants of settlers, thus reducing the maize market production of native South Africans (Bundy 1979). The dependence on agriculture was then replaced by migrant labouring, which took men to cities like Cape Town and Johannesburg in search of work (Fay 2009) leading to a reduction in agricultural production. Agricultural practises continued at a lower rate and agricultural production became a way to supplement labour income other than *vice versa* (Fay 2009). Poor agricultural practise, lack of labour for subsistence agricultural practise, lack of technology, including fencing, and lack of irrigation and damage of produce by livestock and wild animals led to a severe reduction in agricultural production (Andrew 1992; Timmermans 2004). In 2005 for example, pigs were slaughtered by the Department of Agriculture due to an air bone disease, swine fever, pandemic in other parts of the Transkei coast. In the last decade there has been a remarkable decline in agricultural practise that might have increased the dependence on coastal resources. The increase of school attendance among youth and migrant labourers has led to lack of labourers for subsistence agricultural practise and now agricultural fields are abandoned (Fay 2009).

The shrinking of the world economy and high inflation rates led to lack of jobs and fluctuating mineral prices left the immigrant labourers in danger of retrenchment (Timmermans 2004). There have been high levels of unemployment in South Africa which has increased dependence on natural resources as a cheap food source and has led to unsustainable utilisation of intertidal resources, thus putting pressure on marine resources and exacerbating nutritional problems in the region. In this region, pension funds are a major source of income (Timmermans 2004). Low income rural people eat a small amount of protein compared to the middle and upper classes, and marine derived protein is their main source of animal protein along the coast line (Kent 1997).

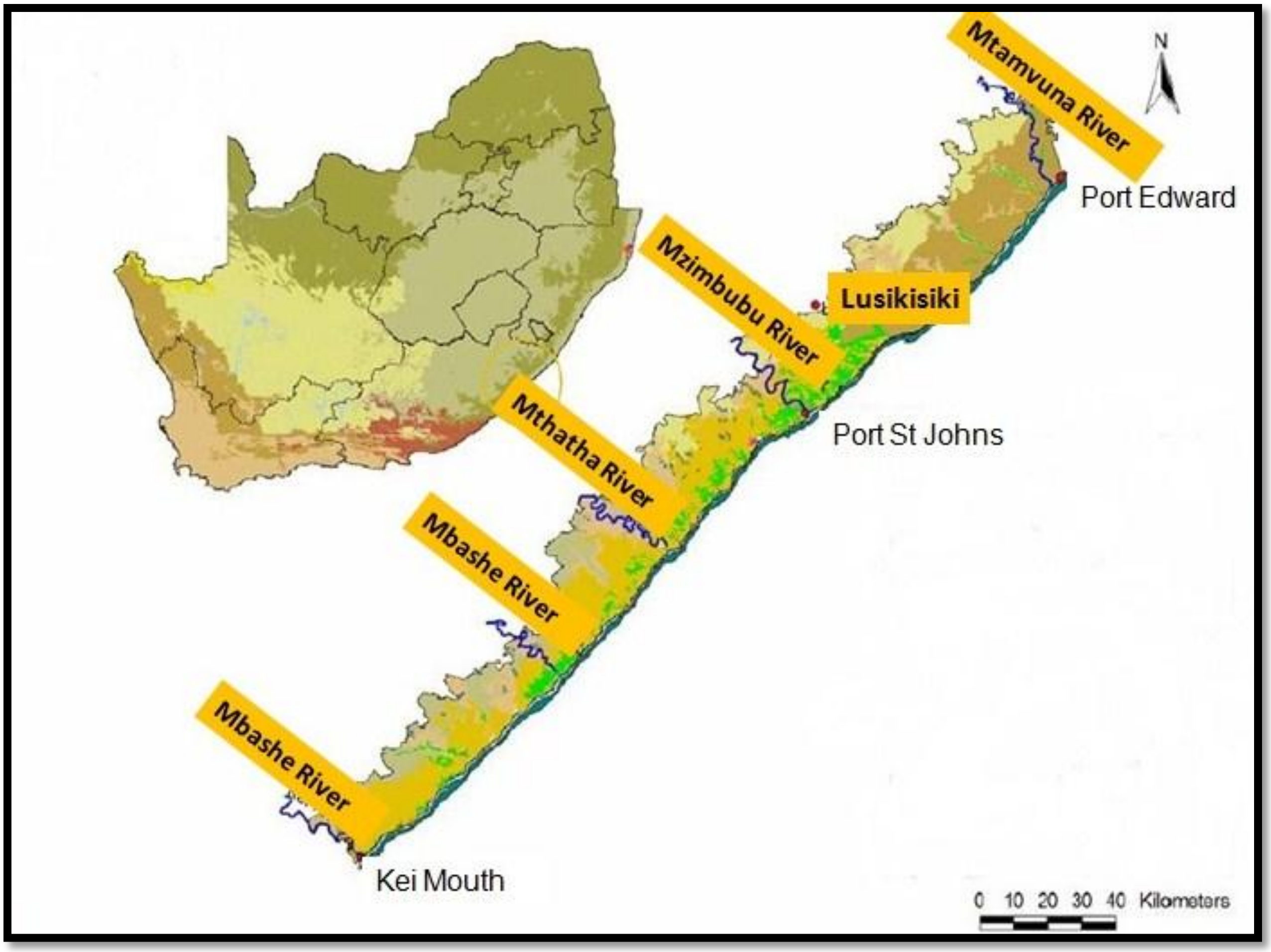

Figure 1.3. Map of South Africa showing Transkei coast covers about 250 km between the Kei River mouth and the Mtamvuna River mouth (Map taken from Reyers & Ginsburg 2005).

1.5. Control measures

Although there are control measures regulating the collection of marine organisms, they are not effective for subsistence fisheries in the region (Siegfried *et al.* 1994; van Erkom Schurink & Griffiths 1993). The problem with the management of fisheries is that only species with direct economic benefit are given priority, species harvested and directly consumed for subsistence are given a lower value (Sowman 2006).

For example, although the collection of mussels is currently standardised in South Africa, along the Transkei coast local people continue to harvest illegally by not considering bag limits. According to the Marine Recreational Activity Information Brochure (2009/2010), an individual with a permit is allowed to harvest only 30 mussels per day. That is not the case in Coffee Bay where people remove the entire population without selecting by size (pers. obs.). Although there is a standard number of mussels to be collected, there is no size limit for collection of *P. perna* in South Africa (Dye *et al*. 1994). Along the Transkei coast, harvesters collect mussels as small as 30-40 mm (Lasiak & Dye 1989) when they are just sexually mature. Since the rocky shore is such a dynamic environment, harvesters do not have enough foraging time to select large individuals and the situation is exacerbated by depletion of mussels in easily accessible parts of the shore. The removal of entire mussel clumps without considering animal sizes creates gaps within mussel beds, leading to loss of the breeding population, food for species dependent on mussels, including humans, and loss of habitat for species associated with mussels (Underwood 1993). With over exploitation, individuals that are capable of producing sufficient offspring are removed, thus making natural recovery impossible (Underwood 1993). Also the use of blades 10cm wide or larger to harvest mussels in Transkei leads to the opening of patches within mussel beds (pers. obs.). As in New South Wales, there is a bag limit for every species of mollusc in Transkei/ South Africa (Marine Recreational Activity Information Brochure 2009/2010; Underwood 1993). Surprisingly in both countries harvesters for whom the bag limit is meant do not know about the bag limit (Yapp 1986). For example, although the majority of people along the Transkei Coast cannot read English, the Marine Recreational Activity Information Brochure is only written in English, which makes it inaccessible to the majority of people in the region. Therefore the management of natural resources through bag limits is ineffective and will remain ineffective unless there is a proper introduction of environmental education (Underwood 1993). Too, bag limits are not a guarantee of successful management of organisms due to the fact that they are not based on ecological assessments or the current state of the species in question and how much exploitation can be sustained by a specific shore (Underwood 1993). That shows the current management of mollusc is inappropriate. As a result, the current status of natural mussel beds is one of overexploitation (Lasiak & Bernard 1995; Dye *et al.* 1997) and *P. perna* is vulnerable to depletion in accessible areas which are denuded, leaving bare rocks (Dye 1992). Currently along the Transkei coast, natural mussel beds are restricted to protected and inaccessible areas. Bag limits need to be revised, adjusted and to be site or region specific depending on the population of organisms (Underwood 1993; McQuaid &Payne 1998). Artisanal fishing is indeed the most complicated fishing to monitor, manage and is expensive to assess (Matić-Skoko *et al.* 2010). Standardization of quotas for mussels throughout the country is not effective for sustainable exploitation. It is not based on a scientific basis, nor does it take into account social value. Spatial abundance and exploitation of species depend on the local history, economy and social life in the area, and species biology in response to environmental factors (Farrago *et al.* 1993). Although there has been a decline of brown mussels along the Transkei coast no measures have been taken to recover the situation. In order to reduce mussel exploitation in Transkei a new approach that strengthens interdisciplinary research of ecology, sociology and economics is required. Unsustainable exploitation not only leads to environmental problems but also to social problems.

1.6. Current study

In Coffee Bay, exploitation is exacerbated in summer by the fact that there is an increase in numbers of tourists and at the same time monitors or control officers, who are scarce year round, are on holiday, promoting overexploitation. Humans affect rocky shore communities in several ways by disturbing or modifying them (Castilla 1999). Human influence on rocky shore communities is predominantly perceived as negative (Castilla 1999) but this is not always the case. In order to establish the original state of mussel beds, human intervention is required (Erlandsson *et. al.* 2011). For example, human effects through experimental and research interference can bring positive results. In addition, humans can be regarded as key stone predators (Castilla 1999) which can destroy rocky shore communities, but also have the capacity to save them. To rehabilitate overexploited population to their original state is challenging and it may seem impossible (Branch & Monero 1994).

Dye and Dyantyi (2002) developed a technique to attach mussels on denuded areas, in order to accelerate recovery. The Mussel Rehabilitation Project (MRP) uses the technique to rehabilitate shores denuded of mussels in Coffee Bay. Results from the MRP show that some sites have been successfully rehabilitated, reaching c. 80 % cover within a year whilst others only reach about 5%. Although in South Africa an individual with a permit is legally allowed to collect only 30 mussels per day, from rehabilitated sites local communities have exceptional permits to harvest and fill 10 litre containers. The successful rehabilitation sites are easily accessible and the harvest is monitored.

It seems that there are factors preventing recovery of mussel beds to their original condition (Erlandsson *et. al.* 2011). For example denuded areas are replaced by coralline algae (Dye *et al.* 1997), which is the major opportunist occupying space after the removal of mussel beds (Lambert and Steinke 1986; Keough *et al.* 1993) and also covers unsuccessful rehabilitation sites. According to Sousa (1979), during early succession once an area has been cleared there tends to be an increase in the diversity of newly recruits but eventually one species dominates and monopolises the entire area. Lambert and Steinke (1986) found that disturbance of natural mussel beds by algae impedes other species associated with mussel beds. Along the Transkei rocky shores coralline algae are the monopolising species. Coralline algae prevent recruitment of mussels and attachment of settlers to the hard substratum, making them vulnerable to dislodgment and reducing natural recovery (Dye 1992; Dye & Dyantyi 2002; Erlandsson *et al.*, 2005). That is proved by the disappearance of large recruits from algae coupled with the lack of evidence of secondary settlement from macroalgae onto mussel beds, suggesting elevated mortality of recruits from algae that is expected to approach 100% (Erlandsson *et al.* 2011).

There are factors known to affect natural mussel beds by affecting settlement, growth and mortality (Steffani & Branch 2003a, b, c; Alfaro 2006, Porri *et al.* 2006). Therefore the present study aims to investigate both physical and biological factors which are known to affect natural mussel beds such as availability of settlers and recruits, water motion, wave exposure on re-attached mussels. Physical factors, particularly wave force, might explain differences between successful and unsuccessful rehabilitation sites in Coffee Bay as it is known to affect the distribution and abundance of mussel populations (Denny 1987; McQuaid & Lindsay 2000; Carrington 2002; Steffani & Branch 2003a, b, c; O’Donnell & Denny 2008).

Chapter 2

Does energy allocation to maintenance and growth affect mussel (*Perna perna*) attachment strength and survival on denuded shores?

2.1. Introduction

Wave force/action

Numerous studies shown that wave force affects the distribution (Palumbi 1984; Dahlhoff & Menge 1996; Steffani & Branch 2003a; Alfaro 2006; Westerbom & Jattu 2006), growth (McQuaid & Lindsay 2000), attachment strength (Hunt & Scheibling 2001), condition index (Moeser & Carrington 2006), recruitment (Lasiak & Barnard 1995), density and size (Westerbom & Jattu 2006) of mussels. Alvarado and Castilla (1996) found that the population structure of mussels differs with the degree of wave action. Generally, biomass is positively correlated to wave exposure (Bustamente *et al*. 1997). At exposed sites there tend to be large mussels and high growth rates (van Erkom Schurink and Griffiths 1993; McQuaid & Lindasay 2000) as food is brought by high water motion to sessile organisms (Dahlhoff & Menge 1996). Wave action keeps food particles suspended freely in the water column (Bayne 1993). That has been supported by Ackerman and Nishizaki (2004) who found in a laboratory study that an increase in water flow led to an increase in clearance of seston from the water column, reflecting increased feeding rates.

For mussels, the drawbacks of sites exposed to strong wave action are high mortality due to wave action (McQuaid & Lindsay 2000; Steffani & Branch 2003b) and high energy expenditure due to the high demand for maintenance (Steffani & Branch 2003b), and some studies have shown reduced growth due to increased water velocity (Ackerman & Nishizaki 2004). High wave force is one of the factors known to cause mortality of mussels by dislodging them from the substratum (Hunt & Scheibling 2001; Steffani & Branch 2003a; Prowse & Pile 2005). In wave exposed areas, mussels use about 8% and 44% of energy consumed for the maintenance of byssus threads and the shell respectively (Hawkins & Bayne 1985). The chances of dislodgement are determined by attachment strength, which is determined by the number of byssus threads used for attachment (Bell & Gosline 1997) and their tensile strength. Attachment strength increases with increased wave exposure (Witman & Suchanek 1984; Hunt & Scheibling 2001). Mussels attach to the substratum by means of a byssus which is made up of three parts: root, stem and byssal threads. The root connects the byssal threads to the retractor muscles, the stem supports the byssal threads and the byssal threads attach the mussel to the substratum by means of an adhesive plaque (Carrington 2002). Although byssal threads attach mussels firmly to the rocks, they are flexible to avoid breakage. The byssal thread is composed of elastic protein and fibrous protein, and it attaches to the substratum by an adhesive protein (Deming 1999). In order for mussels to be kept firmly attached onto the rock, old and decaying byssus threads need to be replaced by new ones. It is not known exactly how long a thread remains attached on the rock but is assumed to be 3-4 weeks (Carrington unpublished data cited in Caro *et al.* 2008). On rocky shores, water applies three types of forces onto mussels: lift, drag and acceleration reaction (Denny 1987; Blanchette 1997). It is suggested that lift forces are responsible for dislodgement of mussels, and Carrington (2002) suggests that mussels are dislodged from the substratum when the force (lift) applied by a given wave is greater than mussel attachment strength but, although this provides a mechanical explanation for the dislodgment of mussels, there is no reason to regard it as the only cause of patch formation in mussel beds (Denny 1987). Wave velocity generated by breaking waves on exposed shores can be as high as 10m.s^{-1} but storms can produce velocities as high as 25m.s^{-1} (Denny *et. al.* 2003).

In 2009, the Mussel Rehabilitation Project (MRP) determined that strong winter storms dislodged re-attached mussels, leading to reduction of mussel cover of 90% to 60% (MRP unpublished data). Therefore, although there are better feeding opportunities at wave exposed sites, there are also the challenges of high energy expenditure and dislodgment. Steffani and Branch (2003a, b & c) showed that severe wave forces suppress growth. According to net production models, assimilated energy is immediately available for maintenance, then for growth and any remaining energy is reserved (Ren & Ross 2005). Therefore, if more energy is used for maintenance there would be little or no energy available for growth.

In contrast to exposed sites, sheltered sites have lower food supply but mussels need to use less energy for maintenance (Steffani & Branch 2003b), therefore available energy may be used for other biological activities rather than maintenance (Steffani & Branch 2003a, b & c). In a laboratory experiment, Ackerman and Nishizaki (2004) discovered that growth decreases when water velocity becomes too high. Steffani & Branch (2003a, b & c) and Westerbom & Jattu (2006) reported that mussels living at intermediate levels of wave exposure grow faster than mussels living under high exposure or low exposure. At intermediate levels, the risks of dislodgment and mortality are reduced. It is clear that, although water flux is required for high growth of mussels, this effect depends on the degree of wave exposure or wave force (Denny 1987; McQuaid & Lindsay 2000). Not only does growth cease at extreme wave force, Carrington *et al.* (2008) showed that byssal thread production may be hindered above a certain level of water velocity.

Higher water motion may lead to high turbidity and bring sand particles. It might also affect mussels differently. Kaehler (1999) associated high water motion with increased shell erosion or abrasion and removal of the periostracum layer that can initiate infestation by cyanobacterial endoliths. Both wave force and water motion or flux affect growth of mussels and are assumed to affect the onshore arrival of mussel larvae from the water column. Porri *et al.* (2006) suggested that larval delivery to the shore is strongly affected by local hydrodynamic conditions.

Recruitment and settlement

According to Petraitis (1995) there are three general processes which maintain mussel beds: the recruitment of larvae, mortality and growth. Mussels have planktonic larvae (Sprung 1984), potentially leading to high dispersal. When they leave the plankton and join the benthos, they are called settlers. It is important to know the difference between recruits and settlers. Recruits are the number of individuals surviving for a certain period after settlement (Pineda *et al*., 2006). According to Connell (1985) settlement is the stage when intertidal organisms attain permanent residence on the substratum. In the case of sessile species, this occurs when an organism has attached itself to the substratum after the planktonic stage. Thus settlement is the process by which planktonic larvae of benthic organisms establish permanent contact with the substratum (Jenkins *et al.* 2000) and once marine larvae have passed the settlement stage they can be interpreted as having recruited (Keough & Downes 1982). Recruits are individuals that have attached themselves permanently onto substratum (Connell 1985). It is known that *P. perna* requires adult mussels for successful recruitment (Lasiak & Barnard 1995). At local scales, dispersal processes affect the distribution of recruits and may also affect the distribution and density of adult mussels at scales of a few meters (Harris *et al.* 1998). It is possible to find high variability in recruitment at a scale of meters, indicating that larval supply may be patchy even within an individual site (Harris *et al.* 1998; Porri *et al.* 2008).

There are three possible factors that may limit settlement: limited numbers of settlers, unsuitable substratum and sweeping away of larvae by water movement (Yildiz *et al.* 2010). Philips (2002) assumed that larvae with low energy reserves at metamorphosis may have poor growth even as juveniles after metamorphosis. Post settlement mortality following delayed metamorphosis can be attributed to energy depletion, i.e. settlers of poor quality show poor post-settlement performance. According to Moran and Emlet (2001), larval condition depends on a site's environmental conditions. Availability of food is one of the important factors that plays a role during larval stages and may determine the survival of recruits (Philips 2002). Good larval condition may help recruits to withstand harsh conditions on the substratum after metamorphosis (Philips 2002).

Recruitment of benthic organisms in the near shore region varies in space and time (Connell 1985). There are three factors that may cause differences in abundances of settlers between sites. These are: differences in numbers of settlers arriving at a site, the circulation of the water at a site and the nature of the substratum. These factors are both physical and biological, for example the difference in number of recruits arriving at a site may be caused by reduced numbers of larvae produced by adults (in the case of populations showing self-recruitment), mortality or failure of currents to transport settlers to a site. Conditions within a site may be unfavourable for recruits to settle on the substratum. Alvardo and Castila (1996) suggested that the complexity of mussel beds, together with reduced water flow leads to high retention of recruits. The nature of the substratum may be unfavourable due to the absence of physical or biological cues required by larvae, or the presence of predators killing larvae shortly after settlement. Successful recruitment seems to require pre-established mussel patch or beds (Lasiak & Bernard 1995). That might be due to the fact that, beyond a certain size, recruits may be dislodged very easily from filamentous algae (Dye & Dyantyi 2002). Lasiak and Bernard (1995) further suggest that the availability of small mussels (less than 500µm) during unexpected recruitment periods shows that larvae may suppress growth during unfavourable conditions. If that is so, it would mean larvae maintain a certain size until they find and settle on a suitable substratum (Bayne 1965). Lasiak and Dye (1989) suggested that there are several reasonable explanations for differences in the recovery of overexploited mussel beds among sites, for example settlement may vary among sites. Along the Transkei coast, spawning occurs from February to September, and mussels attain 30-40mm length in their first year of growth (Lasiak & Dye 1989). That is different from the KwaZulu Natal (KZN) coast where mussels attain a length of ~50mm in the same period (Berry 1978).

Condition Index

As condition index (CI) relates the amount of shell to the quantity of living tissue (Davenport & Chen 1987), it can be assumed that CI will be higher in successful rehabilitation sites. It is important to determine whether the allocation of resources is to the tissue or shell (Raubenheimer & Cook 1990). In a study of *Mytilus galloprovincialis* by Steffani and Branch (2003b), it was found that growth was better at sites with intermediate wave exposure. Therefore, it is assumed that CI will be better in sites where growth and rehabilitation are better.

Tenacity

Tenacity or attachment strength seems to be an adaptive response for mussels (Caro *et. al.* 2008). The ability of mussels to resist waves is crucial since they will be dislodged if the applied force is greater than their attachment strength. In wave exposed sites, mussels use more energy for the production of byssus threads, therefore it is assumed that at exposed sites tenacity would be higher than at sheltered sites since increase in tenacity is due to increased byssus thread production (Cheung *et. al.* 2006).

Growth

Growth depends on the amount of energy remaining after metabolic maintenance (Ren & Ross 2005). Food ingested by animals is used as a source of energy. Since blood has a low capacity for energy storage, but high transportation rates, it effectively transports energy to the somatic and reproductive tissues. Energy requirements are different between young and adult mussels, young mussels need energy for growth and maintenance whilst adult mussels need energy for growth, maintenance and reproduction. *Perna perna* of ≥ 25 mm are sexually mature (Ruis *et al.* 2006). Although small mussels do not use energy for reproduction, they do invest energy in the development and maturation of the reproductive organs (Ren & Ross 2005). Energy allocated for reproduction is stored in a buffer zone before it is converted into eggs or sperm and released during spawning. Maintenance competes with growth and is more important than growth (Ren & Ross 2005), so that maintenance precedes growth, which is retarded if all available energy is expended on maintenance Kooijman (2000). Energy spent on attaining maturity by juveniles is spent on reproduction by adults. Maintenance processes encompass maintenance of concentration gradients across membranes, the turnover of structural body proteins, a certain level of muscle tension and movement, and the production of hairs, feathers, scales or leaves in the case of plants Kooijman (2000). This means that large mussels require some energy for maintenance (including the production of byssal threads for stronger attachment due to an increased surface area and associated drag) and for reproduction, which reduces the energy available for allocation to growth. Besides the energy required for reproduction by large mussels, there can be a direct relationship between maintenance costs and structural volume, so that larger or adult mussels are assumed to use proportionally more energy on maintenance than small mussels (Kooijman 2000). Carrington (2002) found that from the beginning of gamete development, byssal thread development halts and tenacity decreases so that after the release of gametes there is more energy available for production of byssal threads, resulting in higher tenacity. Therefore byssal thread development and attachment strength interact in terms of energy allocation (Carrington 2002; Zardi *et al.* 2007).

Size of mussels influences the surface complexity of mussel beds (Erlandsson & McQuaid 2004). A bed of small mussels is more complex than a bed of large mussels due to high density of the matrix because of reduced surface area per individual mussel (Alvarado & Castilla 1996). Due to high growth rates, intraspecific competition can be problematic for small mussels due to space limitation (Griffiths & Hockey 1987; McQuaid & Lindsay 2000; Branch & Steffani 2004). As a result of complexity and high growth rates, a large proportion of mussels will be dislodged from the substratum, largely through competition for space (Griffiths & Hockey 1987). In dense mussel clumps, individuals are attached to the substratum by their byssus threads and the byssus threads of others (Bertness & Grosholz 1985; Carrington 2002). That provides additional advantages of attachment over solitary mussels (Bertness & Grosholz 1985). Mussels are affected by the density of individuals in the patch; solitary mussels experience stronger hydrodynamic force, have higher tenacity and have a higher probability of dislodgment than mussels within a bed (Bell & Gosline 1997; Nicastro *et al.* 2010). As a result, dislodged mussels leave adjacent mussels vulnerable to dislodgement (Witman & Suchanek1984). Tightly packed mussel beds provide better physical support to resist hydrodynamic forces (Denny 1987). In addition, Alvarado and Castilla (1996) suggested that the complexity of mussel bed increases retention of recruits.

Seed and Richardson (1990) bring out another important aspect of growth. They suggest that the use of one parameter to measure growth is not enough because, while mussel do not show increases in length (or height), another parameter might determine growth. It is possible to find an increase in shell length while the soft tissue in fact decreases (Seed & Richardson 1990). In this study I have used biomass as a second parameter to measure growth.

Given the interacting effects of size, tenacity, growth and condition, the aim of this study is to determine which size class of mussels, small and immature (1-2cm) or large and sexually mature (3-4cm), is most suitable for optimal rehabilitation of shores. This was assessed in terms of mussel survival, growth and increase in biomass.

2.2. Materials and Methods

The study was carried near Riet River (Figure 2.1), at four sites (**Site 1** S 33° 33’ 39”, E 27° 01’ 17”, **Site 2** S 33° 33’ 47”, E 27° 01’ 17”, **Site 3** S 33° 33’ 47”, E 27° 01’ 27”, and **Site 4** S 33° 33’ 55”, E 27° 02’ 15”) on rocky platforms at Three Sisters near port Alfred on the south coast of South Africa. The area has equal semi-diurnal tides with a maximum tidal range of ~2 m (McQuaid & Lindsay 2000). Two sites were described *a priori* as exposed sites and other two as sheltered, with exposure types arranged interspersed. Estimates of exposure were based on the topography of the coast, exposed sites were located at open shores while sheltered sites were located in small bays. Sites were about 100-150 meters apart. Two size classes of mussels (1-2cm and 3-4 cm) were collected from mussel beds using small chisels to avoid destroying the whole mussel bed and removing non-required individuals. Thirty-six patches of mussel were attached in haphazard positions on each of the four sites, with 18 patches of small mussels (1-2cm) and 18 patches of large mussels (3-4cm) per site. Each patch comprised 40 mussels kept in a plastic bag of ~1x1cm mesh size and allowed to attach to the rocks by covering them for a month with a half section of PVC drainage pipe. This piping has an extremely coarse mesh of about 1x5cm mesh size. To re-attach mussels onto shores, holes were drilled into the rocks located in the zone normally occupied by mussels and the pipes fixed onto the shore using coach screws with nylon plugs. Care was taken to ensure that mussels were held firmly under the pipes but still could open their valves. Pipes were removed after a month, but mussels were still kept in the mesh bags, which were secured using eye bolts. The mesh protected mussels, allowing them to re-attach if they were detached or dislodged during pipe removal. The use of mesh bags was necessary as during preliminary experiments all mussels were washed away overnight immediately after removal of the pipes. That made me to try a new method, with mesh (compare

Dye and Dyantyi 2002). Four patches of each size class of mussel were removed from each site on each of three occasions to measure attachment strength, growth, condition index, and survival. The first patches were collected one month after the removal of the PVC drainage pipe (occasion 1). The second after three months (occasion 2) and the last patches after 5 months (occasion 3). The data were analyzed using GMAV 5 software (1997). Data for each occasion were analysed separately because I measured wave force, water flux, growth, CI, survival, attachment strength, recruitment into mussel clumps and biomass repeatedly over each month and occasion therefore months and occasions are non-independent factors.

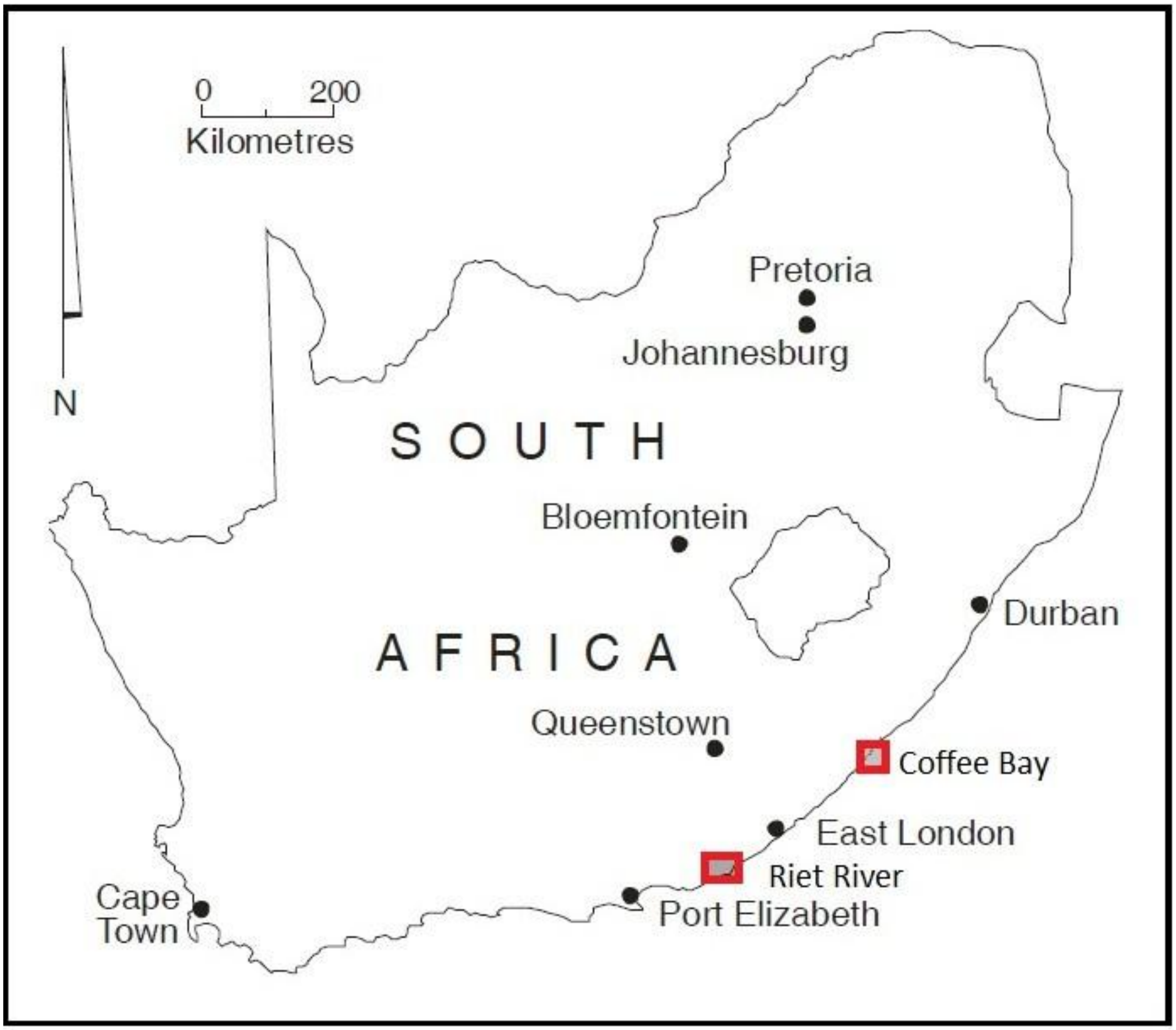

Figure 2.1. Map of South Africa showing study areas along the coast of South Africa

2.2.1. Wave force

Wave force was measured once a month at each site following the method described by Bell & Denny (1994), using a force recorder/dynamometer (Fig. 2.2a). The recorder consists of a spring secured in a Chlorinated Poly Vinyl Chloride (CPVC) pipe which is closed at both ends by means of plugs. A stainless steel spring is held firmly at one end of the CPVC pipe using nylon bolts, while a fishing line is tied to the free end of the spring. The fishing line is passed through a small rubber indicator and through the upper plug at the other end of the CPVC pipe. A practise golf ball is tied outside the CPVC pipe to the free end of the fishing line. To measure the length travelled by the rubber indicator, and also to reset the indicator, a slot is cut into the CPVC. Oncoming waves push the practise golf ball leading to extension of the spring. The force was recorded by measuring the length travelled by the rubber indicator along the fishing line during the extension of the spring. The rubber indicator only moves when the applied force is greater that the force applied previously (Figure 2.2) so that the device measures maximum wave force during deployment. Before deployment, each dynamometer was calibrated by hanging 5 weights from it to determine what force was needed to move the rubber slide a given distance inside the PVC pipe.

To measure wave force, six dynamometers were deployed for 24 hours at each site once a month for a period of six months from October 2010 to March 2011. January and March were removed from the analysis because many dynamometers were washed away by waves. This allowed me to measure the wave force experienced by reattached mussels *in situ* (O' Donnell & Denny 2008). To determine the effect of site and exposure on wave force, 2-way ANOVA was performed using site (random factor, orthogonal, 4 levels) and exposure (fixed factor, 2 levels: sheltered and exposed) on wave force. Site was nested in exposure.

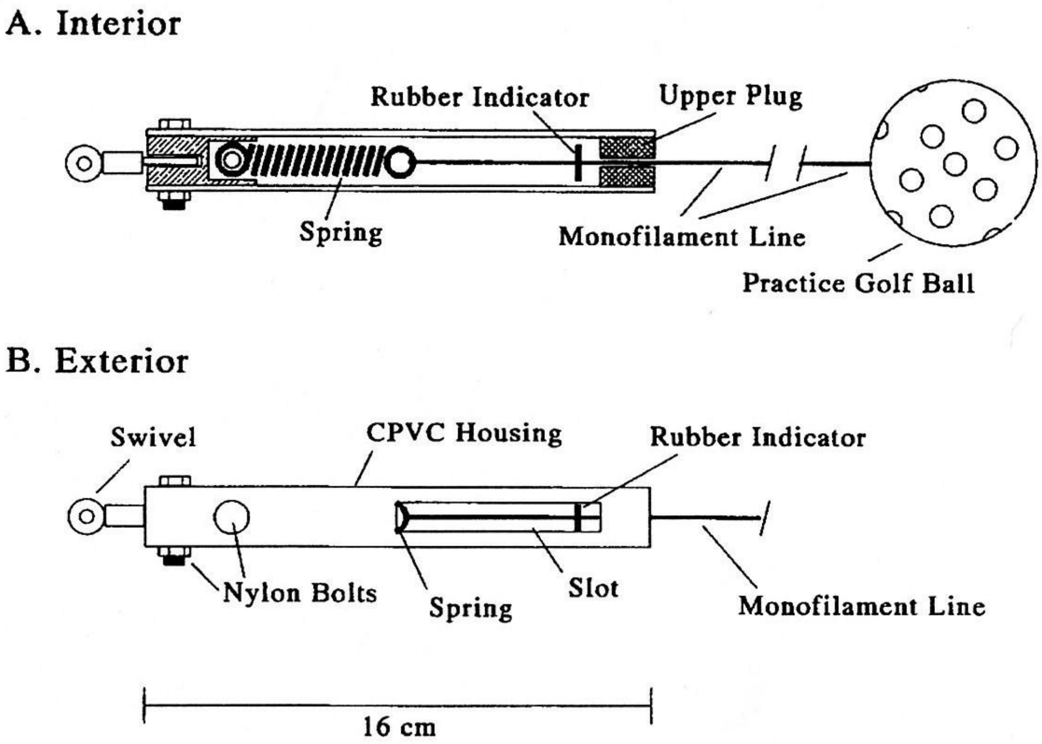

Figure 2. 2. Design of wave recorder or dynamometer (from Bell & Denny 1994)

2. 2. 2. Water flux/ flow or circulation

To measure bulk water flow or flux, six cement balls made from fast anchoring cement, Rockset Cement Polycell Products, were used (Kaehler 1999). Rockset seemed to be less diffusional than other materials used to measure water motion (Bell & Denny 1994). Balls were made by opening 1cm diameter holes in ping-pong balls and filling the balls with liquid cement using a syringe. The head of a screw was inserted through the hole into the wet cement. When the cement balls were dry, the plastic ping-pong balls were removed and the balls were dried at 60 °C for 24 hours until reaching constant weight. Six cement balls were attached using the screws at each of the four sites once a month for 24 hours during spring tides, for six months from October 2010-

March 2011. After removal, the balls were dried and re-weighed. The relative water flow was determined by measuring percentage mass loss (Kaehler 1999). The data for January and February 2011 were removed from the analysis because many balls were lost. One factor ANOVA was used to determine the effect of site on water flux/ water motion. Each month (October 2010, November 2010, December 2010 and March 2011) was analyzed separately to determine if there was consistency in water flux among the sites.

2. 2.3. Attachment strength

Four patches of small and four of large mussels were removed from each site on each of the three occasions. Tenacity or attachment strength was measured for 5 mussels from each of the removed patches (5mussels × 4 patches = n 20 per size class per site). Tenacity was measured using a fish hook attached to a spring balance using 15cm of 25kg fishing line. A small hole (1.5-2mm) was drilled through the posterior lip of each mussel shell. The fish hook was inserted through the hole and the mussel was pulled off the rock (Figure 2.3). The force used to dislodge each mussel was recorded as tenacity (Caro *et al.* 2008). Force was calculated from the reading (in kilograms) from the spring balance (F=ma). The data were analyzed using two-way ANOVA to determine the effects of site and mussel size on attachment strength on each of three occasions. Occasions were analyzed separately. In the experimental design, site had 4 levels, was orthogonal, random, and size had 2 levels, was fixed and orthogonal. Number of replicates was 20.

Figure 2.3. Measurement of tenacity/ attachment strength of mussel using a spring balance.

2.2.4. Growth

To measure growth, mussels in each patch were dried with a cloth allow them to be tagged at the growing edge using Tipex. When Tipex tags were dry, they were coated with super glue. This method did not work as in some mussels the tags were washed away. As an alternative, growth checks were used as markers for the time of translocation to the experimental plots (Figure 2.4). Growth history of mussels is frequently recorded on the shell in the form of growth-increments (Seed 1969). Growth-increments are thought to be due to seasonal rhythms or disturbance (Seed 1969). Although growth after deployment can be detected from growth-increments, they do not show how long growth was delayed after deployment or disturbance.

Removing mussels from the substratum, transporting, tagging, and covering them with pipes is likely to lead to stress, which may affect growth (Seed and Richardson 1990) resulting in distinct growth checks. Growth rings or increments of importance are distinctive (Figure 2.4). Vernier Callipers were used to determine growth from growth checks. Growth-increments were defined as the difference between length at collection and length at deployment (Millstein & O'Clair 2001), which was taken to be indicated by the growth check. Growth per day was determined by dividing the total growth by the number of days mussels were attached on the rocky shore. Each of the three occasions was analyzed separately.

Two factor ANOVA was performed to determine the effect of site and size on growth. The first factor, site had four levels, was orthogonal and random, the second factor, size had two levels, was orthogonal and fixed. Forty mussels were measured from each size class from each site on each occasion.

Figure 2.4. Growth from the distinctive growth check to the new growing edge of the shell.

2. 2.5. Condition Index

The method used of Davenport & Chen (1987) was used to determine CI. Ten mussels from each removed clump were placed in boiling water to remove the flesh from the shell. The flesh was dried in an oven at 60° C for 48 hours until reaching a constant weight, and then shell and flesh were weighed separately using a balance (Steffani & Branch 2003b). CI was calculated as:

$$CI = \frac{\text{dry flesh weight (g)}}{\text{shell weight (g)}} \times 100$$

The data were analyzed using 2-way ANOVA to determine the effect of site and size on CI. In the analysis there were 2 factors, site had two levels, orthogonal and random, and size had two levels, orthogonal and fixed. Number of replicates was 40. Each occasion was analyzed separately.

2. 2. 6. Survival

Each attached mussel patch contained 40 mussels at the time of deployment. Survival rate was determined by counting the number of surviving mussels from each of four removed patches, on each occasion.

Two-way ANOVA was used to determine the effects of site and size on survival. In the experimental design site had four levels, was orthogonal and random, and size had two levels (small and large mussels) was orthogonal and fixed. There were four replicates, being the number of patches removed for each size class, from each site on each occasion.

2.2.7. Recruitment into mussel clump

Two types of recruitment were analysed in this study. To avoid confusion they are named recruits 1 and recruits 2. Recruits 2 were collected from scouring pads and will be dealt later. Recruits 1 were collected from mussel patches after removal. Mussel patches were removed on three consecutive occasions, collected into ziploc bags, taken to the lab, and examined under a dissecting microscope to determine number of recruits found. Recruits 1 were ≤5mm and were usually found attached to the byssus of re-attached mussels. To ensure that there were no recruits 1 at the start of the experiment, the byssus threads of re-attached mussels were thoroughly cleaned before deployment. To determine which size class of mussels attracted more recruits (recruits 1) the data were analyzed by 2-way ANOVA. As above, with sample size being the number of clumps per site, per size class and per occasion, i.e. 4. Each occasion was analyzed separately. Three-way ANOVA was also performed to determine the effects of site, occasion and size on recruitment. In this analysis occasion was included as a factor to determine if there was accumulation of recruits into mussel clumps over time.

2.2.8. Settlement and recruitment

Settlement was measured once a month at each site during spring low tides from October 2010-March 2011 using scouring pads. Six eye bolts were fixed at each site among the experimental patches and plastic scouring pads were deployed using four cable ties were inserted through the centre of each pad and an eye bolt. Scouring pads were deployed for two weeks of each month. After removal, scouring pads were kept in 70% alcohol. To determine the number of settlers, scouring pads were soaked for 5 minutes in 9ml of bleach solution. After 5 minutes, the contents of the solution were sieved through a 75 µm mesh and the bottle was rinsed over the sieve with running water. Scouring pads were unrolled and washed in a bucket and the bucket contents were sieved through the 75µm mesh and the bucket was rinsed with running tap water. Rinsing was repeated until the scouring pad was clean, with no debris, to ensure that no settlers remained in the sieve or pad. The contents were gently transferred into a bottle to which 15-20 ml of 99 % ethanol were added. To count the number of settlers, the extracted samples from each scouring pads were examined at 32X under a dissecting microscope. In the current study settlers were differentiated from recruits (recruits 2) on the basis of size. Mussels of ≥ 400µm are described as recruits, while mussels < 400µm are described as settlers following Bownes *et al.* (2008).

Data were analyzed using 2-way ANOVA. In the experimental design, occasion had 6 levels, was orthogonal and random, and site had 4 levels, was orthogonal and random. Number of replicates was 3.

2.2.9. Biomass

Increments in biomass were calculated from the length (growth) measurements using the regression equation ($y=0,00260219x^{1,3402}$) derived by McQuaid *et. al*. (1985). The initial length was used to determine biomass at deployment and final length was used to determine biomass during mussel removal on the three occasions.

2.3. Results

2.3.1. Effect of site and exposure on wave force

The dynamometer results showed no consistent difference in wave force between sites that had been described *a priori* as exposed or sheltered sites. As a consequence, the effect of exposure is not considered in this chapter. One would expect exposed sites to have higher wave forces than sheltered sites. Although site 1 and 3 appeared exposed, and sites 2 and 4 appeared sheltered, the fact that sites were close to each other (100-150 meters apart) may explain the lack of difference in maximum wave force (Figure 2.5).

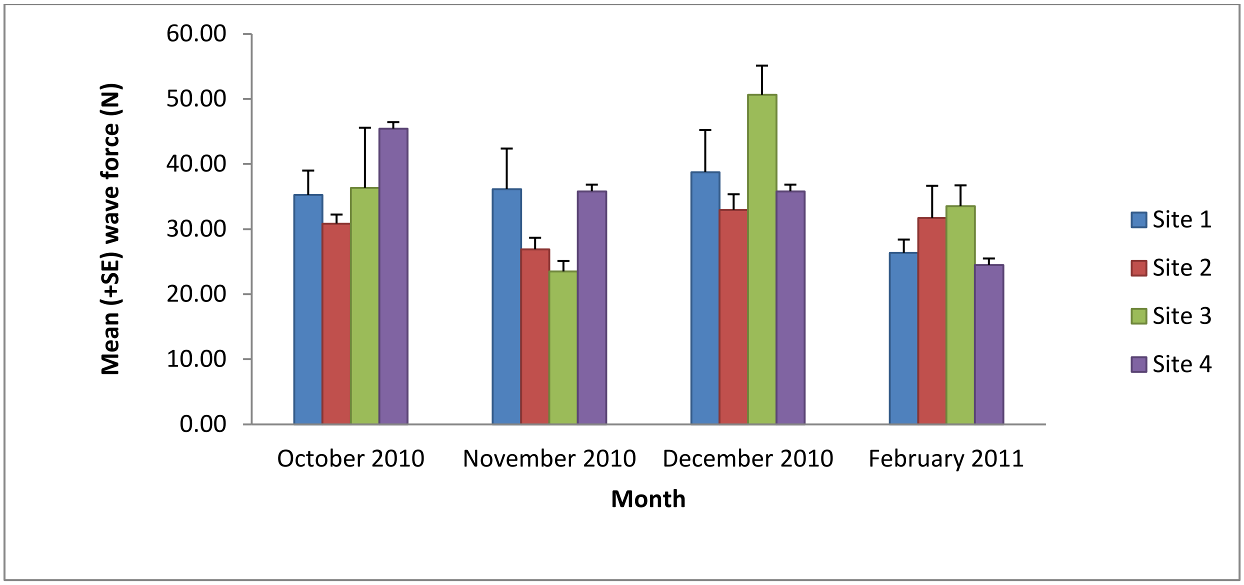

Figure 2.5. Wave force (mean +SE) on supposedly exposed (1 and 3) and sheltered sites (2 and 4).

2.3.2. Water flux/ flow or circulation

As in the case of wave force, the results showed no consistent difference in water flux between presumed exposed and sheltered sites (Figure 2.6). As a result the effect of water flux was not considered. Exposed sites were expected to have higher water flux than sheltered sites.

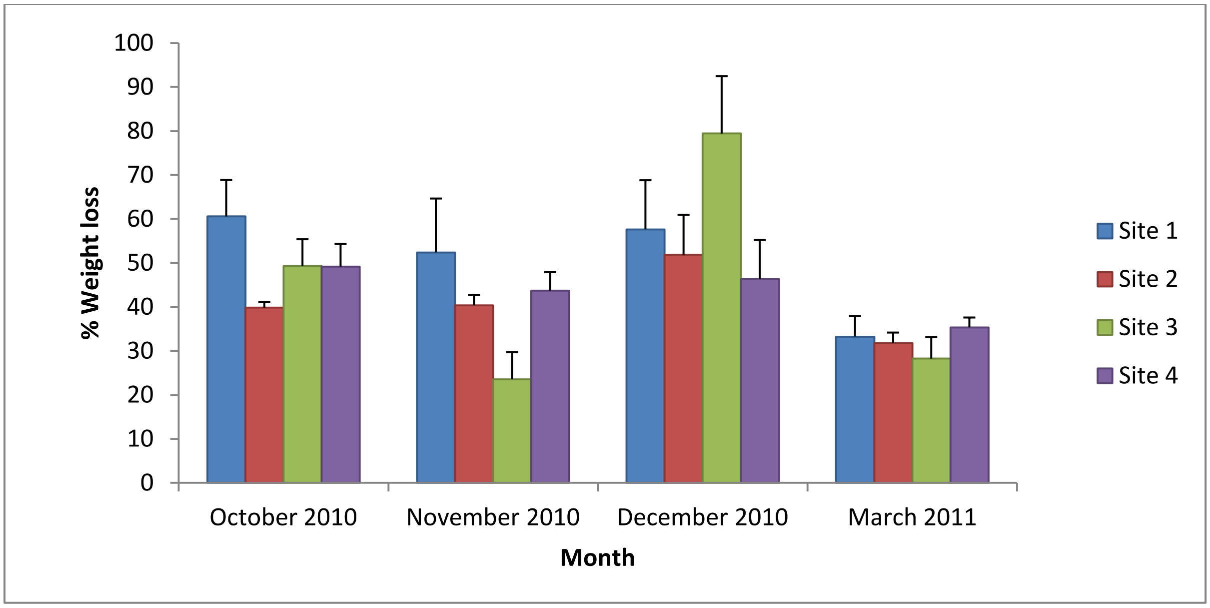

Figure 2.6. Water flux represented by % water loss (mean +S.E) among sites in different months. Sites categorised *a priori* as in Fig. 2.5

2.3.3. Attachment strength

Occasion 1

On occasion 1, 2-way ANOVA showed that both site and size had effects on attachment strength, with a significant interaction between the two (Table 2.1). Post hoc tests showed large mussels attached more strongly than small mussels at all sites. The effects of site were different between size classes (Figure 2.7).

Source	SS	DF	MS	F	P
Site	1206.2624	3	402.0875	7.24	0.0001*
Size	11102.2240	1	11102.2240	61.35	0.0043*
Site*Size	542.9141	3	180.9714	3.26	0.0232*
RES	8436.7298	152	55.5048		
TOT	21288.1304	159			

Table 2.1. Results of 2 factor (Size and Site) ANOVA of attachment strength for occasion 1

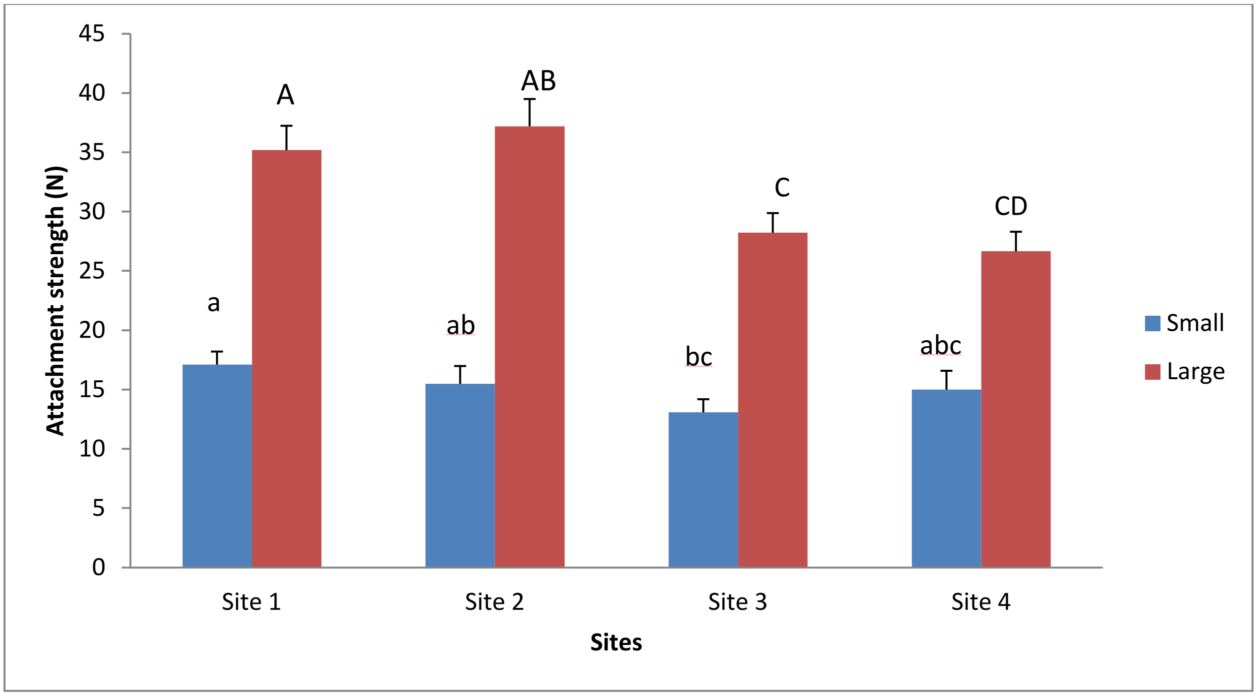

Figure 2.7. Attachment strength (mean force +S. E.) among sites and between size classes on occasion 1. Letters indicate homogenous groups for small and large mussel (upper and lower case letters respectively). Large mussels showed significantly higher values at all sites.

<u>Occasion 2</u>

Again on occasion 2 there were significant effects of size and site, but no interaction between them (Table 2.2). Post hoc tests showed that large mussels had higher attachment strengths (mean 33.16N) than small mussels (mean 18.62N). There were also differences among sites (Figure 2.8) for both size classes.

Source	SS	DF	MS	F	P
Site	1343.4222	3	447.8074	5.42	0.0014*
Size	8454.4867	1	8454.4867	100.83	0.0021*
Site*Size	251.5465	3	83.8488	1.02	0.3875
RES	12547.3811	152	82.5486		
TOT	22596.8365	159			

Table 2.2. Results of 2 factor (Size and Site) ANOVA of attachment strength for occasion 2

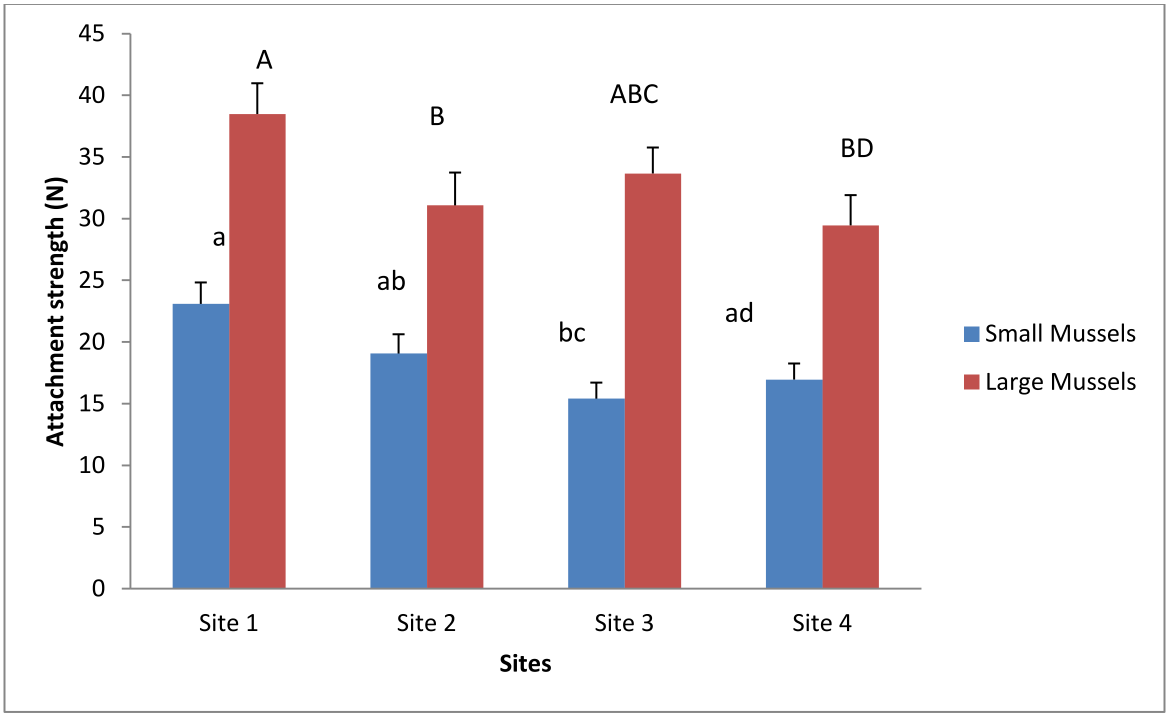

Figure 2.8. Attachment strength (mean force +S. E.) among sites and between size classes on occasion 2. Letters indicate homogenous groups for small and large mussel (upper and lower case letters respectively).

Occasion 3

On occasion 3 there were significant effects of site and size, but the interaction was marginally non-significant (Table 2.3). SNK tests showed that large mussels had stronger mean attachment strength (mean 37.33N) than small mussels (mean 24.65N). There were no differences in attachment strength among large mussels at different sites. As on occasion 2, site 1 had the strongest attachment, though the difference from Site 4 was not significant.). When the effect of site was compared from all occasions, site 1 always had stronger attachment strength than all other sites, although the effect of site differed from one occasion to another (Figure 2.9). Also, when the occasions are compared, it was clear that attachment strength was directly proportional to time.

Source	SS	DF	MS	F	P
Site	1617.8598	3	539.29	4.79	0.0032*
Size	6430.0281	1	6430.03	22.12	0.0182*
Site*Size	872.0132	3	290.67	2.58	0.0556
RES	17116.2968	152	112.67		
TOT	26036.1979	159			

Table 2. 3. Two way ANOVA table shows the effect of site and size on attachment strength on occasions 3.

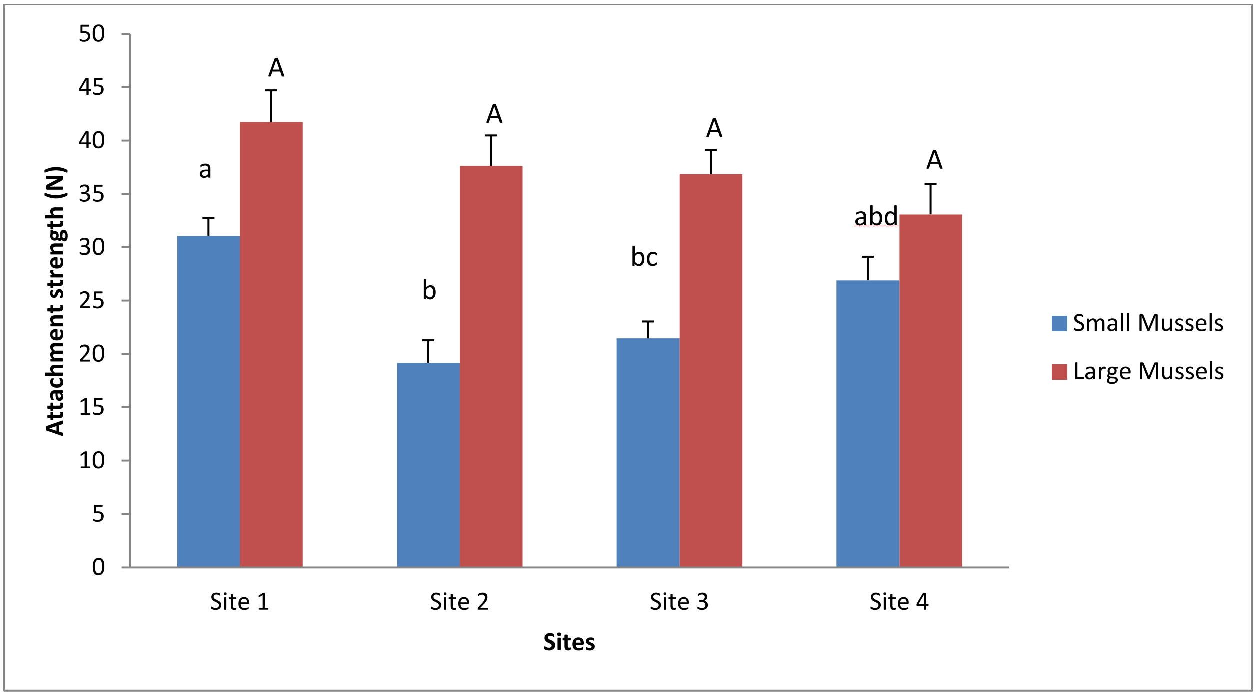

Figure 2.9. Attachment strength (mean force +S. E.) among sites and between size classes on occasion 3. Large mussels showed no significant differences among sites. Letters indicate homogenous groups for small and large mussel (upper and lower case letters respectively).

2.3.4. Growth

Occasion 1

Both factors had significant effects (ANOVA, Site, $F_{3, 312}$=11.46, p<0.001 and Size, $F_{1, 312}$=25, 40, p<0.05) with significant interaction between them ($F_{3, 312}$=7.65, p< 0.001). Small mussels grew faster than big mussels at an average of 0.0306mm and 0.0075mm per day respectively (Figure 2.10).

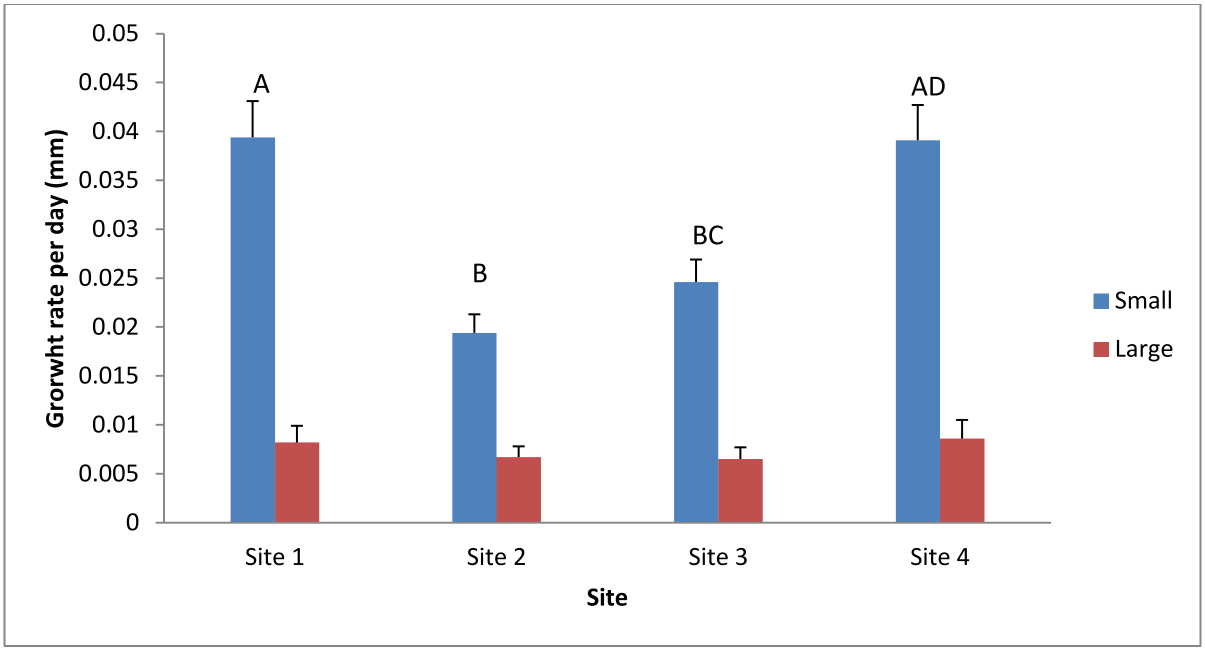

Figure 2.10. Difference in growth rate (mean +S. E.) between small and large mussels on occasion 1. Large mussels showed no significant differences among sites. Letters indicate homogenous groups for large mussel.

Occasion 2

Small mussels grew faster than large mussels (ANOVA, $F_{1,\,312}$=620.27, $p< 0.001$) and Site 3 had the lowest growth rate (ANOVA, $F_{3,\,312}$=9.36, $p<0.001$) with no significant interaction between the two factors (Figure 2.11).

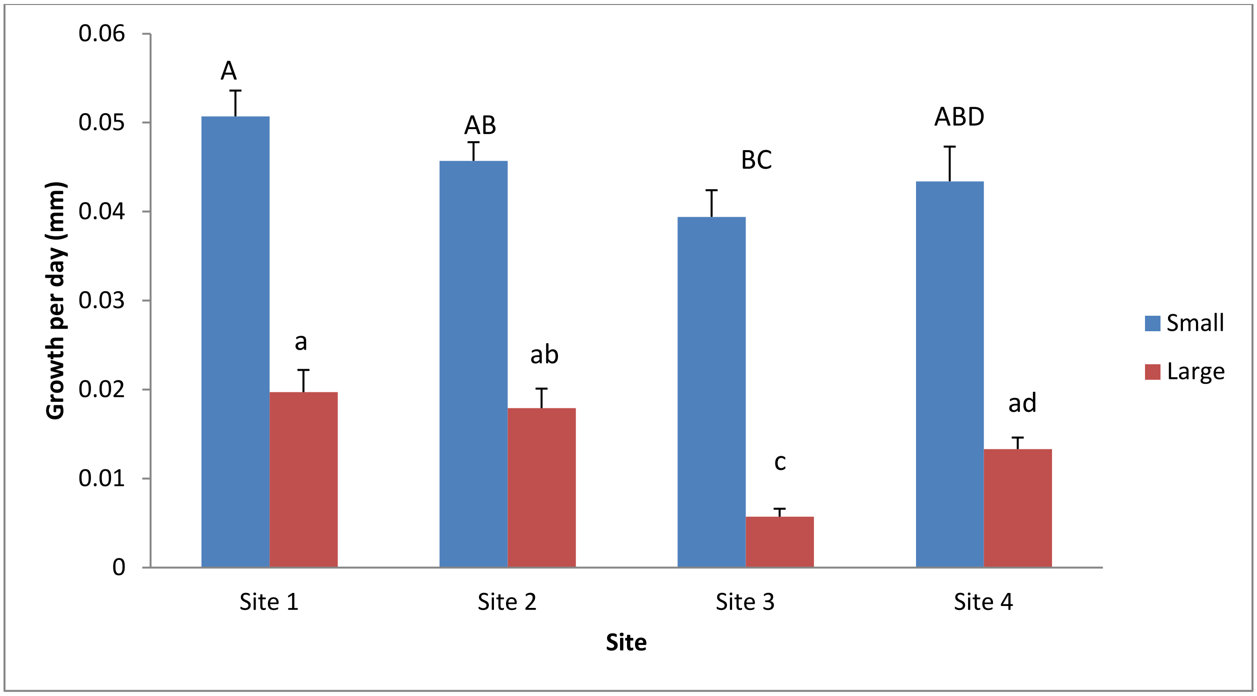

Figure 2.11. Difference in growth rate (mean S. E.) between small and large mussels on occasion 2. Letters indicate homogenous groups for small and large mussel (upper and lower case letters respectively).

Occasion 3

On occasion 3 there were effects of site and size with a significant interaction (Table 2.4). SNK tests showed that for small mussels each site was different from one another. Small mussels grew faster than large mussels in all cases but the effect was stronger at some sites than others, resulting in the significant interaction (Figure 2.12).

Source	SS	DF	MS	F	P
Site	0.0084	3	0.0028	19.09	< 0.0001*
Size	0.0424	1	0.0424	93.08	0.0024*
Site*Size	0.0014	3	0.0005	3.10	0.0271*
RES	0.0459	312	0.0001		
TOT	0.0982	319			

Table 2.4. Two-way ANOVA to determine the effect of site and size on growth on occasion 3

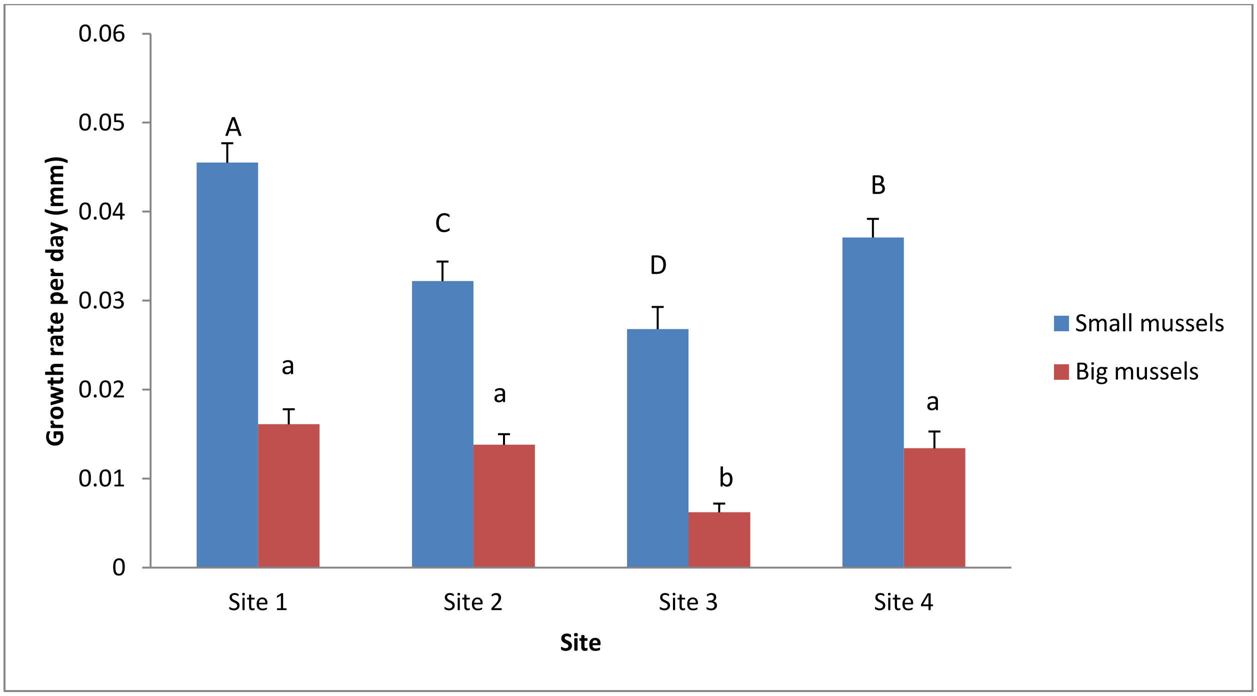

Figure 2.12. Difference in growth rate (mean S. E.) between small and large mussels on occasion 3. Letters indicate homogenous groups for large and small mussel (upper and lower case letters respectively).

2.3.5. Condition Index

Occasion 1

On occasion 1, there were significant effects of site and of size on CI with no interaction (Table 2.5). Site 4 had higher CI than other three sites (Figure 2.13). Small mussels had higher CI values (mean 6.9330) than large mussels (mean 6.1619).

Source	SS	DF	MS	F	P
Site	99.2503	3	33.0834	11.96	0.0001*
Size	47.5763	1	47.5763	10.98	0.0453*
Site*Size	12.9955	3	4.3318	1.57	0.1976
RES	863.0386	312	2.7661		
TOT	1022.8608	319			

Table 2.5. Two-way ANOVA to determine effect of site and size on CI

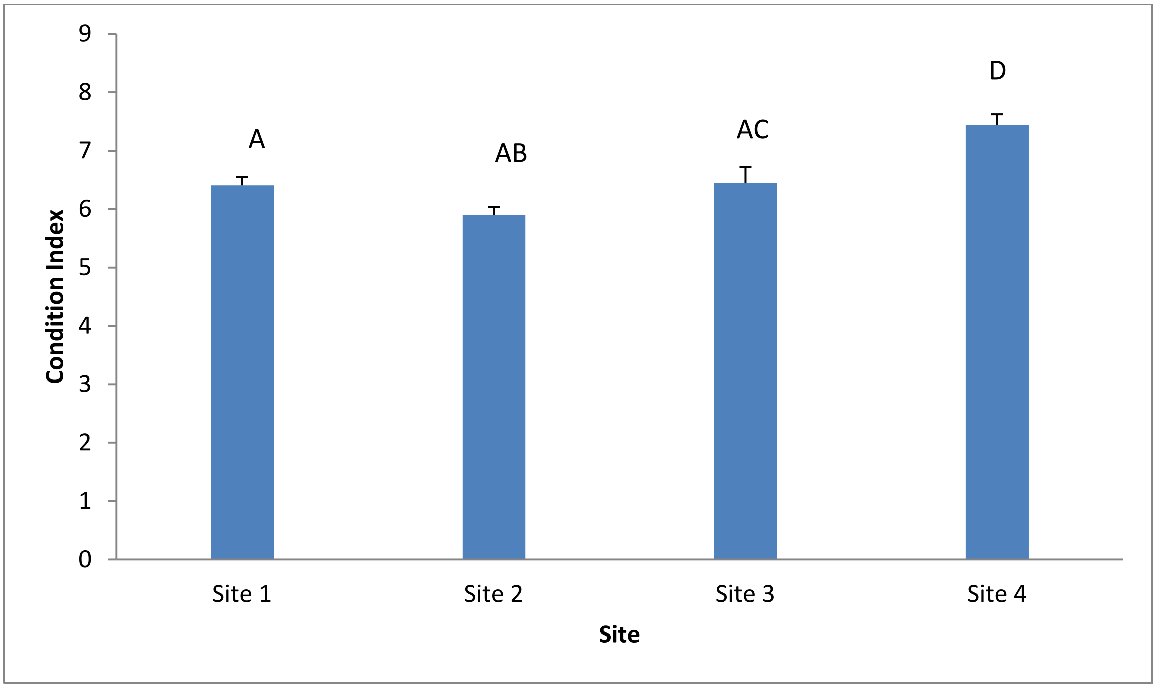

Figure 2.13. Mean values (S. E.) of CI on Occasion 1. Letters indicates homogenous group

Occasion 2

Size had no effect on CI on occasion 2. There was an effect of site and there was a significant interaction between site and size (Table 2.6). Large mussels had significantly better CI only at site 4, while small mussels had significantly better condition at site 3 (Figure 2.14).

Source	SS	DF	MS	F	P
Site	127.9264	3	42.6421	23.77	< 0.0001*
Size	0.3956	1	0.3956	0.04	0.8597
Site *Size	32.0361	3	10.6787	5.95	0.0006*
RES	559.7888	312	1.7942		
TOT	720.1469	319			

Table 2.6. Two- way ANOVA to determine effect of site and size on CI on occasion 2

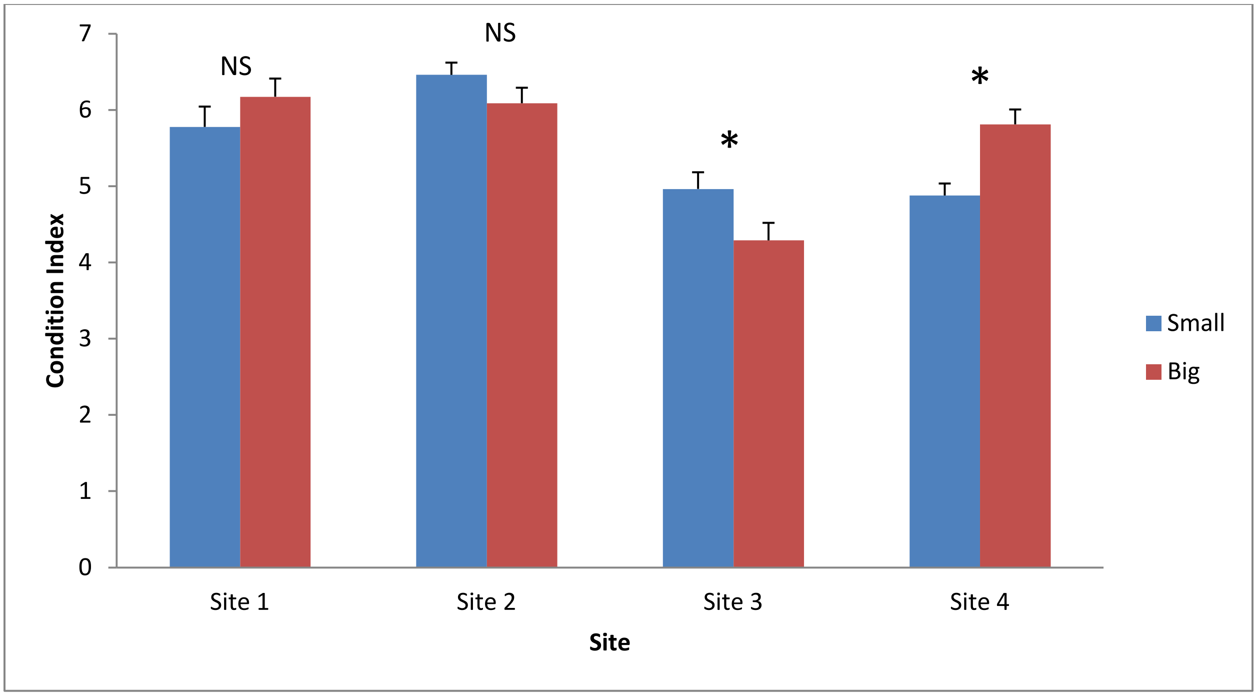

Figure 2.14. Mean values (S.E.) of CI on occasion 2. Asterisk indicates significant difference (p<0.05) and N.S. no significant different in comparison if size classes with sites.

Occasion 3

There was an effect of site and a significant interaction between site and size on occasion 3 (Table 2.7). SNK showed that small mussels had better CI at sites 1, 2 and 3 (Figure 2.15).

Source	SS	DF	MS	F	P
Site	22.5822	3	7.5274	9.68	0.0001*
Size	54.2894	1	54.2894	8.22	0.0642
Site*Size	19.8117	3	6.6039	8.49	0.0001*
RES	242.5584	312	0.7774		
TOT	339.2416	319			

Table 2.7. Two-way ANOVA to determine effect of site and size on CI on occasion 3

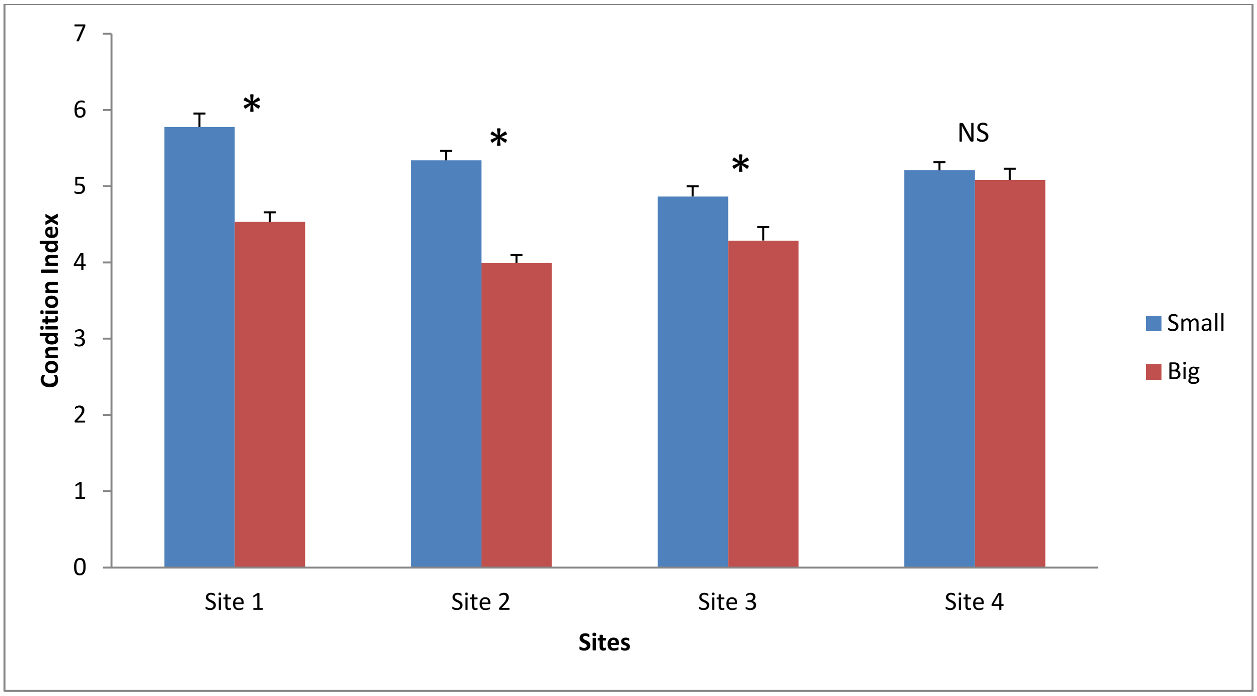

Figure 2.15. Mean values (S.E.) of CI on occasion 3. Asterisk indicates significant difference (p<0.05) and N.S. no significant different in comparison if size classes with sites.

Overall these results show that small mussels generally had better CI values than large mussels.

2.3.6. Survival

On occasion 1, both small and large mussel had exactly equal mean numbers of survivors among sites. The mean survival was 30.43 for both small and large mussels. On occasion 2 there were no significant differences in mean numbers of survivors between small and large mussels among sites (Figure 2.16).

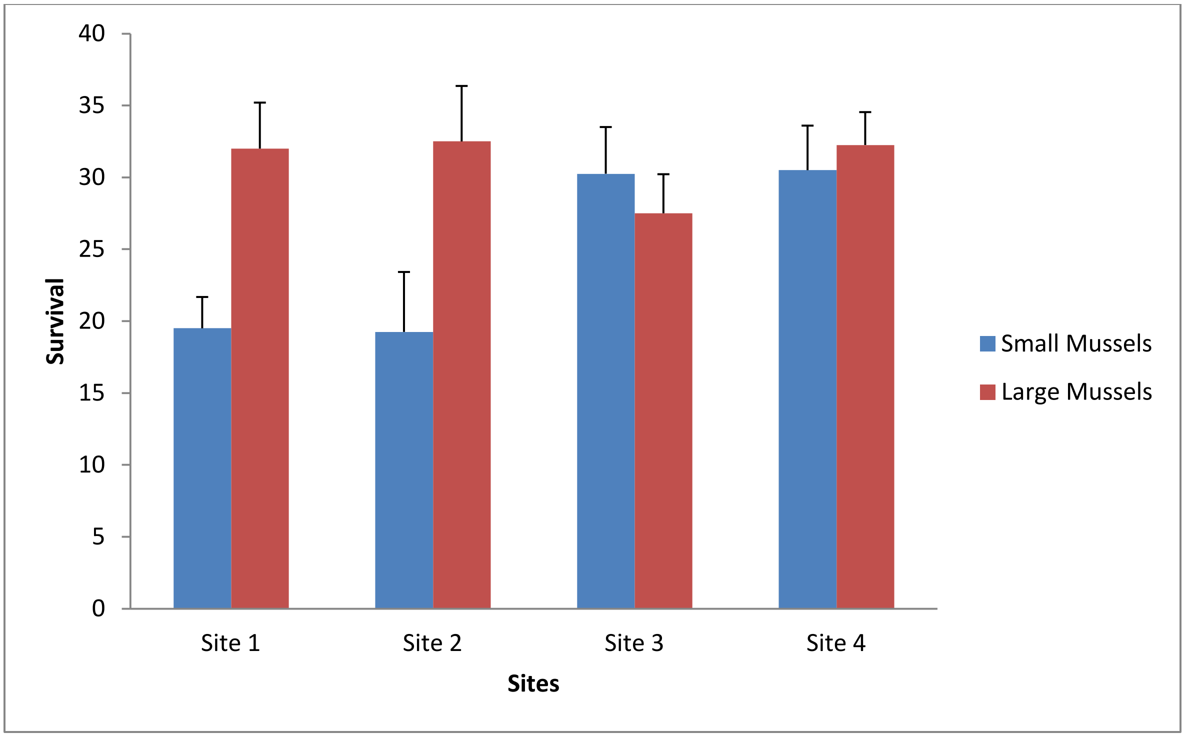

Figure 2.16. Differences in mean survival (S. E.) among sites between small and large mussels from 40 attached mussels on occasion 2.

Occasion 3

On occasion 3 there was no effect of site or size and there was no interaction between site and size (Table 2.8). Although small mussels had higher average numbers of survivors, the difference from large mussels was not significant.

Source	SS	DF	MS	F	P
Site	223.0000	3	74.3333	1.21	0.3288
Size	28.1250	1	28.1250	0.31	0.6160
Site*Size	271.3750	3	90.4583	1.47	0.2483
RES	1479.0000	24	61.6250		
TOT	2001.5000	31			

Table 2.8. Two-way ANOVA for the effect of site and size on survival, on occasion 3.

2.3.7. Recruits 1 (recruits into byssus threads of mussels)

On no occasion were there significant differences in numbers of recruits between small and large mussels. There were differences among sites on occasion 2 (Table 2.9). On occasion 3 SNK tests showed that site 1 was different from site 4 (Figure 2.17).

Source	SS	DF	MS	F	P
Site	62.7500	3	20.9167	4.92	0.0084*
Size	4.5000	1	4.5000	1.26	0.3441
Site*Size	10.7500	3	3.5833	0.84	0.4837
RES	102.0000	24	4.2500		
Total	180.0000	31			

Table 2.9. Two 2-way ANOVA table for effect of site and size on recruitment into mussel patches on occasion 3.

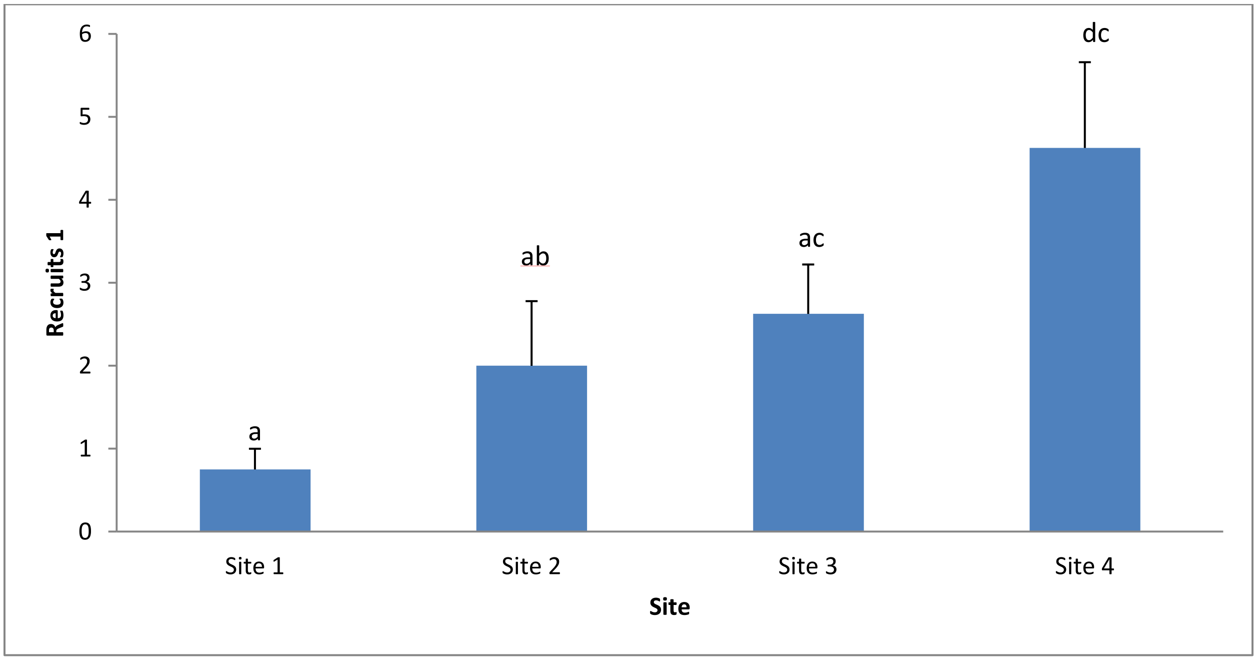

Figure 2.17. Numbers of recruits 1 among sites on occasion 3

2.3.7. Settler results

Three-way ANOVA revealed a significant effect of occasion. There was no effect of site. There was a significant interaction between occasion and site (Table 2.10). Numbers of settlers were markedly higher on Occasion 2 than on any other occasion (Figure 2.18). On occasion 2, there were significant differences in numbers of settlers among site, except between Site 2 and Site 4.

Source	SS	DF	MS	F	P
Occasion	363.5694	5	72.7139	10.43	0.0002*
Site	23.4861	3	7.8287	1.12	0.3712
Occasion *Site	104.5972	15	6.9731	2.24	0.0176*
RES	149.3333	48	3.1111		
TOT	640.9861	71			

Table 2.10. Two-way ANOVA for effect of occasion and site on number of settlers.

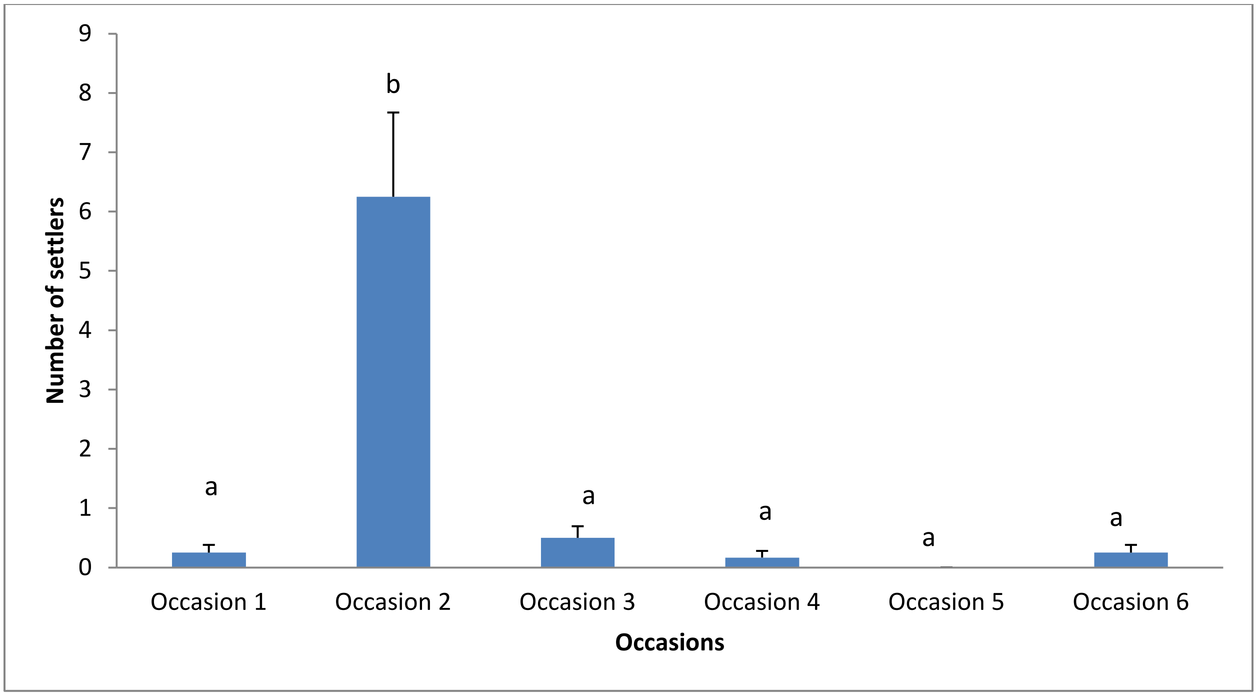

Figure 2.18. Difference in number of settlers (mean +S. E.) among different occasions.

2.3.8. Recruit 2 (results from scouring pads)

There were differences in numbers of recruits among occasions and sites, with no interaction between the two factors (Table 2.11). SNK tests showed that the differences were on occasion 2 (Figure 2.19). Post-hoc tests showed that the numbers of recruits differed significantly among sites but there was no consistent ranking of sites among occasions.

Source	SS	DF	MS	F	P
Occasion	179.9028	5	35.9806	23.20	< 0.0001*
Site	15.4861	3	5.1620	3.33	0.0483*
Occasion * Site	23.2639	15	1.5509	0.37	0.9817
RES	203.3333	48	4.2361		
TOT	421.9861	71			

Table 2.11. Two-way ANOVA for effect of occasion and site on number of recruits.

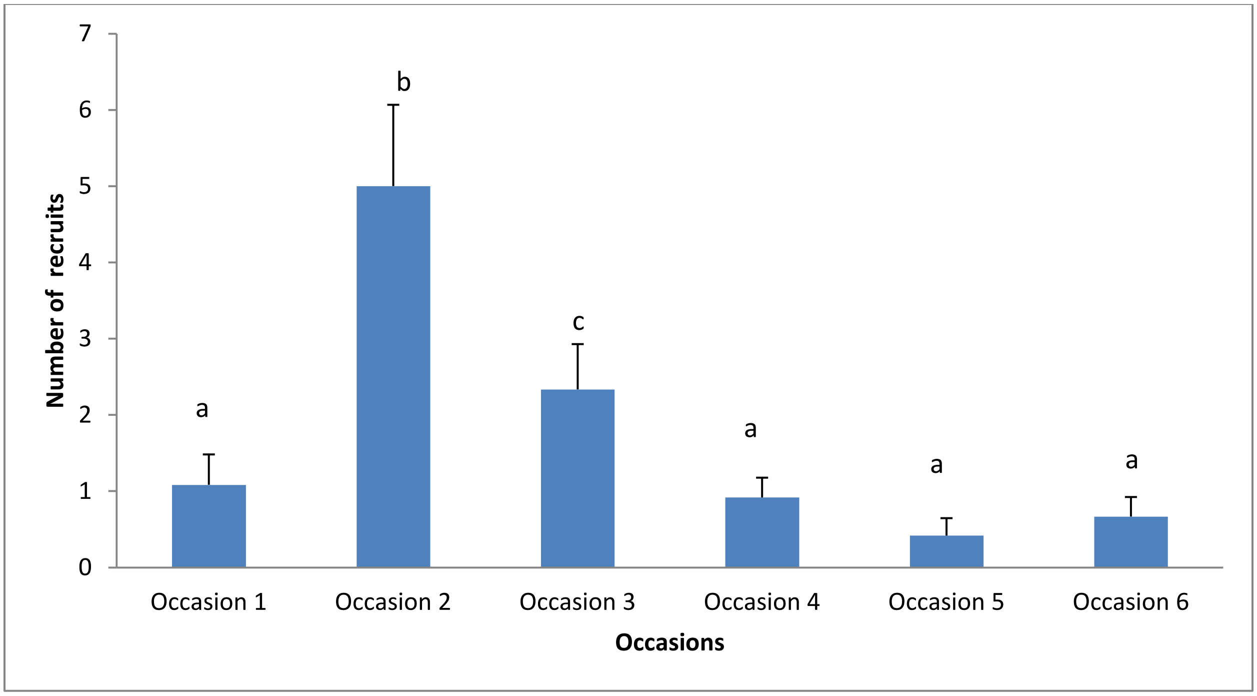

Figure 2.19. Graph showing difference in number of recruits (mean +S. E.) among different occasions.

2.3.9. Biomass

In all cases biomass increased among occasions and biomass increases were greater for small than large mussels. Large mussels had higher biomass than small mussels, at the time of deployment and also during removal of mussel patches. The change in biomass, however, was higher for small than large mussels due to their faster growth rates.

Occasion 1

There were differences in changes to biomass among sites, and between size classes with a significant interaction between site and size (Table 2.12). Post-hoc tests showed that change in biomass was greater for small mussels than large mussel. The differences in biomass between small and large mussels were not consistent among sites. For example, there were no differences in biomass for large mussels among sites, whilst for small mussels biomass varied among sites (Figure 2.21).

Source	SS	DF	MS	F	P
Site	0.0052	3	0.0017	15.33	< 0.0001*
Size	0.0200	1	0.0200	19.04	0.0222*
Site*Size	0.0032	3	0.0011	9.34	< 0.0001*
RES	0.0351	312	0.0001		
TOT	0.0635	319			

Table 2.12. ANOVA of change in biomass between size classes, and among sites.

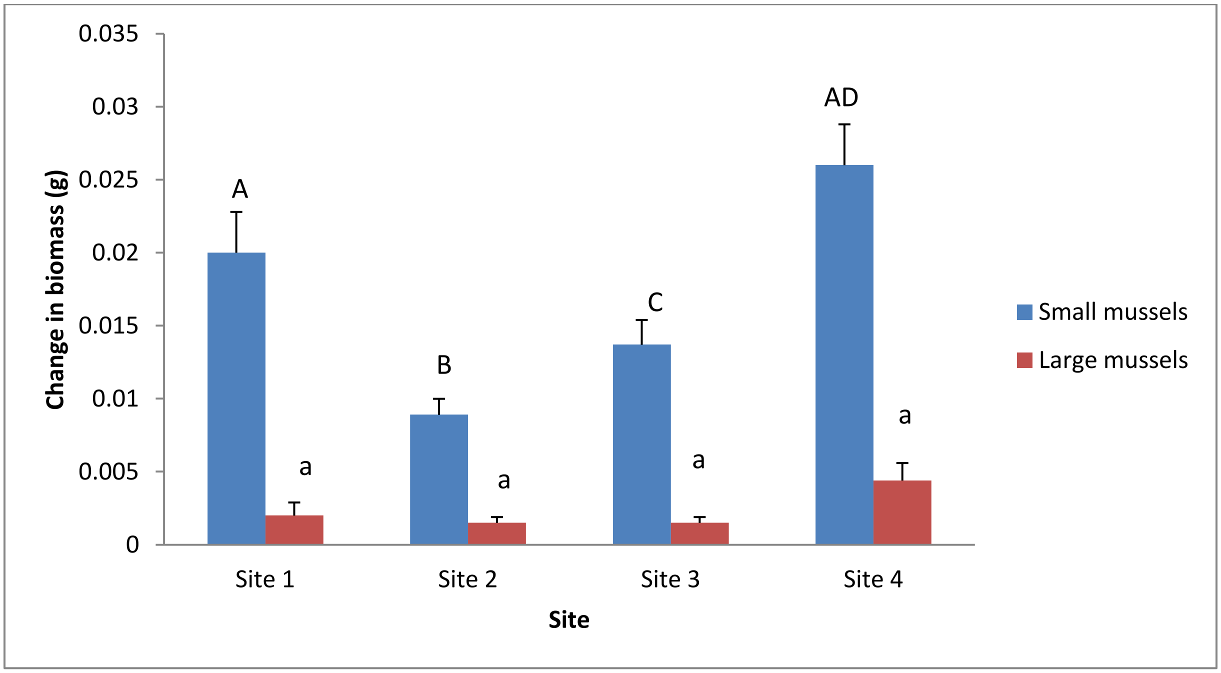

Figure 2.21. Differences in change in biomass (mean +S. E.) between size classes, and among sites on occasion 1. Letters indicate homogenous groups for small and large mussel (upper and lower case letters respectively).

Occasion 2

Both site and size both affected the change in biomass, with no interaction (Table 2.13). Post-hoc tests showed change in biomass was greater for small mussels than large mussels (Figure 2.22).

Source	SS	DF	MS	F	P
Site	0.0193	3	0.0064	6.27	0.0004*
Size	0.2494	1	0.2494	473.15	0.0002*
Site*Size	0.0016	3	0.0005	0.51	0.6731
RES	0.3200	312	0.0010		
TOT	0.5903	319			

Table 2.13. Two-way ANOVA table shows change in biomass (mean +S. E.) between size classes, and among site.

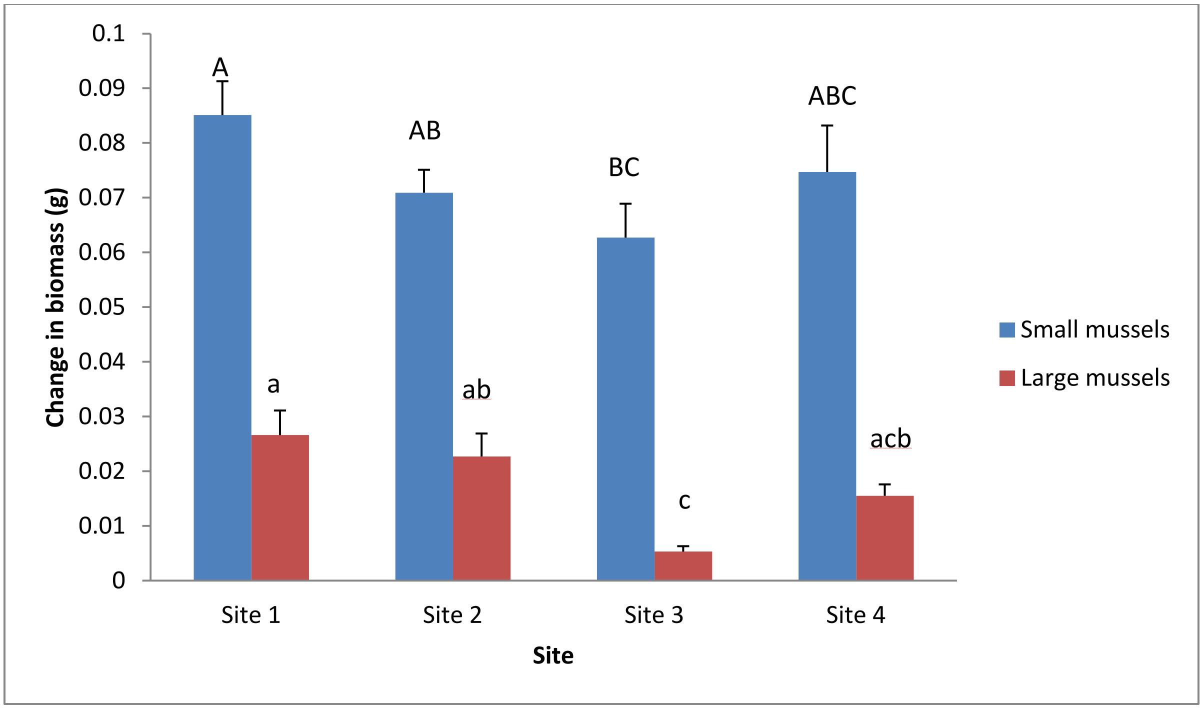

Figure 2.22. Differences in change in biomass (mean +S. E.) between size classes at each site on occasion 2. Letters indicate homogenous groups for small and large mussel (upper and lower case letters respectively).

Occasion 3

Both factors and their interaction had significant effects (Table 2.14). Post-hoc tests showed that change in biomass for small mussels was greater than on large mussels (Figure 2.23).

Source	SS	D	F	MS	P
Site	0.0711	3	0.0237	15.65	< 0.0001*
Size	0.3656	1	0.3656	59.50	0.0045*
Site*Size	0.0184	3	0.0061	4.06	0.0075*
RES	0.4728	312	0.0015		
TOT	0.9280	319			

Table 2.14 Two-way ANOVA table shows change in biomass between size classes, and among site.

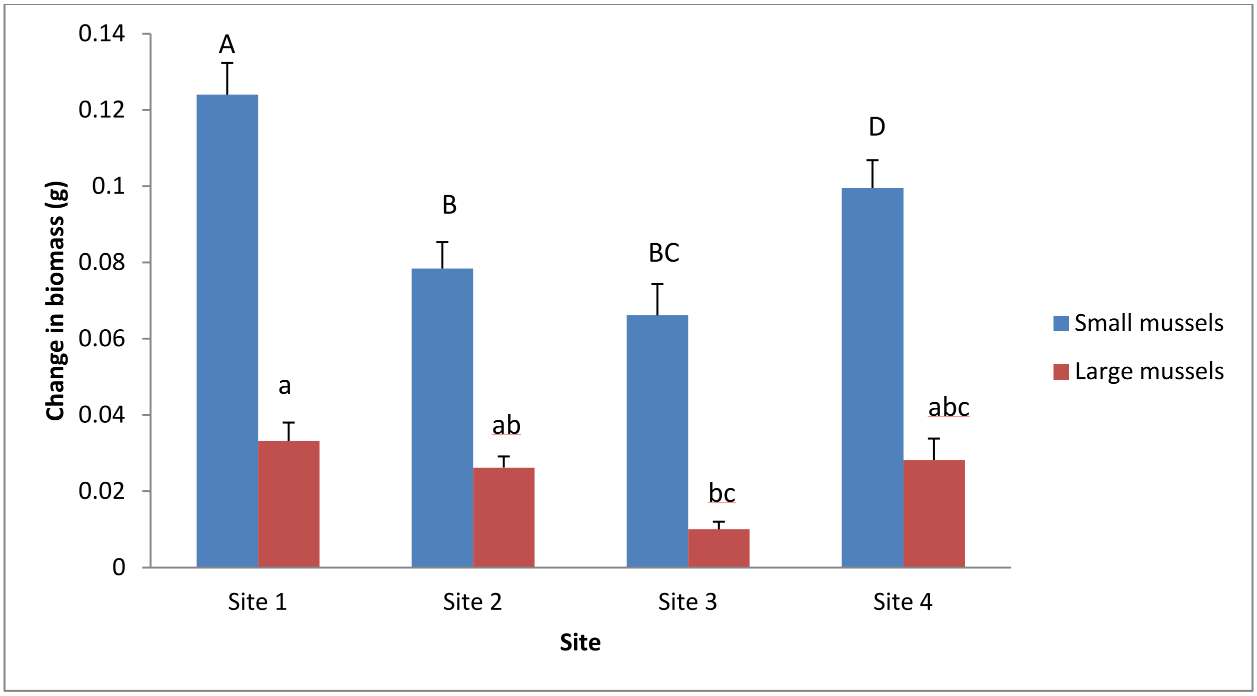

Figure 2.23. Change in biomass (mean +S. E.) between size classes, and among sites on occasion 3. Letters indicate homogenous groups for small and large mussel (upper and lower case letters respectively).

2.4. Discussion

The results from measurements of wave force and water flux taken during different months did not show a consistent pattern among sites, so that I cannot categorise sites according to their degree of wave exposure. Looking at the topography of the coast, two sites are located in bays and two on open shores. It was assumed that sites on the open shore would experience higher wave force throughout the sampling period, but this was not the case. In this study it was possible to find sites on bays with higher wave force than on open shores. This might be due to two reasons: (1) all selected sites are within the same vicinity separated by only 100-150 m, and

(2) dynamometers were not deployed in fixed spots throughout the period of the study so that the results provided a random sample of maximum wave forces experienced in each site as a whole. Due to inconsistency in the results, the effects of wave force and exposure are no longer considered.

The ability of mussels to re-attach determines the number of surviving mussels after deployment. Tenacity or attachment strength seems to be an adaptive response for mussels (Caro *et. al.* 2008), allowing them to resist dislodgment. As large mussels have bigger surface areas than small mussels, they experience more drag. In order to resist the drag, lift and acceleration reaction which remove mussels from the rock surface (Denny 1987; Blanchette 1997), strong attachment is required. Stronger tenacity is energy consuming. According to Kooijman (2000) maintenance has a higher priority than growth. Production of byssus threads falls under maintenance, therefore large mussels might allocate more energy to production of byssus threads than growth. In the current study it can be concluded that large mussels used more energy for attachment than growth, resulting in reduced growth and low CI but high tenacity. Consequently small mussels had higher CI values than big mussels, that means small mussels are in better condition than big mussels. One factor which might contribute to low growth rates by affecting energy demands is reproduction (Carrington *et al.* 2002). Three centimetre mussels are sexually mature (Ruis *et al.* 2006). That might also contribute to reduced growth as reproduction is an energetically expensive process. Although small mussels had weaker attachment strength than big mussels, they had higher growth rates. Most of their energy is spent on growth rather than reproduction, while in large mussels more than 90% of energy can be allocated to reproduction (Seed and Suchanek 1992).The higher change in biomass of small mussels was due to high growth rates.

That suggests that the reduced growth in big mussels might be due to higher energy demands for maintenance and reproduction.

In this study it was found that the numbers of recruits into mussel patches increased with time, and were equal between patches of small and large mussels. One would expect large mussels to attract more recruits than small mussels since they have more and longer byssus threads. After fertilization, pelagic larvae swim in the water column and once they are old enough and find a suitable substratum they settle (Eyster & Pechenik 1987). Mussel larvae are known to recruit into pre-existing mussels beds (Lasiak & Barnard 1995), especially among the byssal threads, as found in this study. Recruited larvae determine the distribution, density and abundance of mussel beds (Underwood & Fairweather 1989; Underwood & Keough 2001). In this case, recruited larvae can contribute to the success of rehabilitation. In the current study it was found that numbers of mussel larvae recruiting *onto mussel clumps* increased with time at an equal rate for patches of small and large mussels.

It was important to determine the availability of settlers and recruits (recruits 2) from the water column using scouring pads as this helps to link recruits onto mussel beds (recruits 1) and availability of larvae in the water column. It is assumed that the number of recruits onto mussel beds depends on the availability of settlers. Lasiak and Bernard (1995) found that smaller larvae of less than 350µm were found on filamentous algae whilst bigger ones greater than 750 µm in length were found recruited into mussel beds, while mussels do not settle permanently on unsuitable substratum (Eyster & Pechenik 1987). Eyster and Pechenik (1987) in their laboratory study found that larvae of *Mytilus* settle on adult threads, which suggests that some larvae may be recruited directly onto adults even in the field. Of course, the larvae recruited into a population help to determine the distribution and abundance of benthic populations (Underwood & Fairweather 1989; Underwood & Keough 2001). It is possible that in both successful and unsuccessful rehabilitation sites there might be mussel larvae which die due to post settlement factors like competition, predation, and the physiological stresses of desiccation, salinity and sediment which have been suggested as explaining differences in post larval survival at wave exposed and sheltered sites (Seed and Suchanek 1992). There are several important stages in the development of mussel larvae: dispersal of larvae in the planktonic form, primary settlement, pelagic migration, secondary settlement and recruitment into mussel beds (Bayne 1964; Eyster & Pechenik 1987; Phillips 2002; Yildiz *et al.* 2010). Bayne (1964) found that small mussel larvae settle on filamentous algae while larger recruits detach and re-settle (1.0-1.5mm) on mussel beds and hence are regarded as secondary settlers. From algae to mussels beds larvae migrate through wave action and currents searching for a suitable substratum (Bayne 1964). Testing of suitable habitat and settlement involves attachment and metamorphosis (Bayne 1964). Some studies refute this hypothesis of primary and secondary hypothesis (McGrath & Gosling 1988; Lasiak and Barnard 1995). Lasiak and Barnard (1995) found that larvae <500 μm were present on both filamentous algae and within mussel populations. The question is: What happens to the larvae on filamentous algae or other unsuitable habitats? Larvae of benthic marine invertebrates can delay metamorphosis if conditions are unsuitable (Bayne 1965; Eyster & Pechenik 1987). If conditions remain unsuitable or settlement stimuli are not triggered larvae may then die (Bayne 1965). The main factor that influences the delay of metamorphosis in under natural conditions is lack of suitable substratum (Bayne 1965). Marshall and Keough (2003) hypothesised that the delayed larvae become desperate to settle and become less discriminating about substratum quality as their energetic reserves run low. They found that larvae settled sooner when offered preferred substratum. Eyster and Pechenik (1987), in laboratory studies, found that even water agitation has an effect on the settlement of larvae and that when water agitation was reduced mussels remained unattached. Insufficient energy during metamorphosis may determine the chances of survival and growth rates in the juvenile stage (Philips 2002). Therefore the success of rehabilitation might depend on two things: successful attachment of adults, and supply of successful settlers onto attached mussels patches.

Was small the best size class for rehabilitation? No, according to the MRP (Marine Rehabilitation Project) the success of rehabilitation was based on numbers of survivors and on increases in percentage cover. Increase in percentage cover depends on a combination of growth and numbers of recruits into mussels beds (recruits 1). For the MRP, success means increase in number individual mussels, which depends on survival and number of recruits. Therefore for the MRP, recruitment is more important than growth. In this study there were no differences in number of recruits into small and large mussel patches. Although in this study I measured some factors such as biomass, attachment strength, growth and condition index, for the MRP success is not based on those factors. In my study these factors were important as they are related to energy allocation and provide insight into how and why final numbers vary among sites.

Chapter 3

Effects of mesh and mussel (*Perna perna*) size on rehabilitation success in Coffee Bay

3.1. Introduction

This study was done in Coffee Bay in the former Transkei region along the Wild Coast of South Africa. The area is different from Riet River (Kaehler 1999) as it has long stretches of rocky shores and intermittent sandy beaches (Lasiak & Dye 1989). *Perna perna* is the dominant mussel species in both the Transkei and Riet River areas (Lasiak & Dye 1989; Kaehler 1999), but due to high exploitation pressure along the Transkei coastline and high dependence on subsistence, it faces local extinction in some places. Between Nqabara estuary and the Mbhashe-Cwebe Nature Reserve (Figure 3.1), rocky shores are covered by algae, even in areas which used to be covered by mussel beds. Mussels are not the only rocky intertidal species that face local extinction, the abalone is also over-exploited along the West Coast of South Africa (Hauck & Sweijd 1999; Troell *et al.* 2006). A major problem with the exploitation of abalone was the lack of bag limits *prior* to 1970. The mass quota system was introduced in 1983 (Hauck & Sweijd 1999). The introduction of bag limits for mussels is ineffective in Transkei as local communities do not comply, only 30 mussels should be harvested by a permit holder per day but in the region harvesters collect as many mussels as are available. The lack of a Marine Recreational Activity Information Brochure in South African native languages makes bag limits ineffective or misunderstood in Transkei. Currently where natural mussel beds have been over-exploited, they are replaced by coralline algae. Effective methods to rehabilitate denuded shores are required.

There are methods which are used to grow mussels, in aquaculture using the longline culture method (de Sa *et al.* 2007; Narváez *et al.* 2009; Ren & Ross 2005; van Erkom Schurink & Griffiths 1993), and in several studies cages have been used to attach mussels onto the natural rocky shores for research purposes (Dickie *et al.* 1984; Okamura 1986; Miller & Etter 2008) while to rehabilitate denuded shores, PVC drainage pipes have been used (Dye & Dyantyi 2002).

The longline culture method was developed in the Marlborough Sounds of New Zealand in the early 1970s after adaptation from the Japanese oyster longline culturing method (Ren & Ross 2005). Unlike the method used by the Mussel Rehabilitation Project (MRP) to rehabilitate denuded shores which reattach mussels onto natural rock substratum, in the longline method mussels are grown on ropes which are suspended in the water column. This method is used for commercial production of *P. perna* in Venezuela (Narváez *et al.* 2009), Brazil (de Sa *et al*. 2007), *Mytilus* species in Spain (Pérez-Camacho 1995; van Erkom Schurink & Griffiths 1993), and has been used in South Africa to growth *M. galloprovincialis* (van Erkom Schurink & Griffiths 1993). In 1990 only two areas in South Africa were used to farm mussels for commercial production, these were in Saldana Bay and in Algoa Bay (van Erkom Schurink and Griffiths 1990). Longline methods have been a successful method to grow mussels, for aquaculture, but aquaculture is not the best solution to reduce pressure on marine resources because farmed animals depend on kelp for feeding. Increases in kelp harvesting for aquaculture may have negative impacts on kelp and the kelp associated ecosystem.

The method developed by Dye and Dyantyi (2002) is the only method which has been used for natural restoration of mussels. Due to overexploitation of *P. perna* along the Transkei coast line, the Mussel Rehabilitation Project, a project formed by Coffee Bay local communities together with Walter Sisulu University, selected sites that were once covered by mussel beds for mussel restoration or shore rehabilitation. At all the selected sites rehabilitation was attempted, but three were successfully rehabilitated and three were unsuccessful (pers. Obs.) and remained colonised by opportunistic coralline algae. The PVC drainage pipe method needs to be modified to improve survival or attachment of reattached mussels. From the MRP it was noted that during removal of PVC drainage pipes some mussel remained unattached. Hence two different methods, meshed and unmeshed, were used in this study to attach mussels of each size class at each site. The first method (unmeshed) was the one used in Coffee Bay by the MRP as developed by Dye and Dyantyi (2002). The second method (meshed) was different from the method used by MRP in two ways: mussels were kept in a mesh before being covered with drainage pipes (as in chapter 2), and after removal of pipes the mesh was firmly tied onto bolts either side so that unattached mussels had the opportunity to attach themselves on the substratum without being washed away by waves. In this study I assumed that keeping mussels in a mesh before covering them with PVC drainage pipes will improve mussel attachment, survival and rehabilitation of denuded shores.

The previous study (chapter 2) aimed to determine which size class between sexually mature (3-4cm) and sexually immature (1-2cm) mussels is most suitable for optimal rehabilitation of shores. The aim of this chapter is twofold: to determine the most suitable size, between 3-4cm and 5-6cm (both sexually mature), for optimal rehabilitation of shores, and to determine the optimum method for rehabilitation, comparing treatments involving mesh or no mesh.

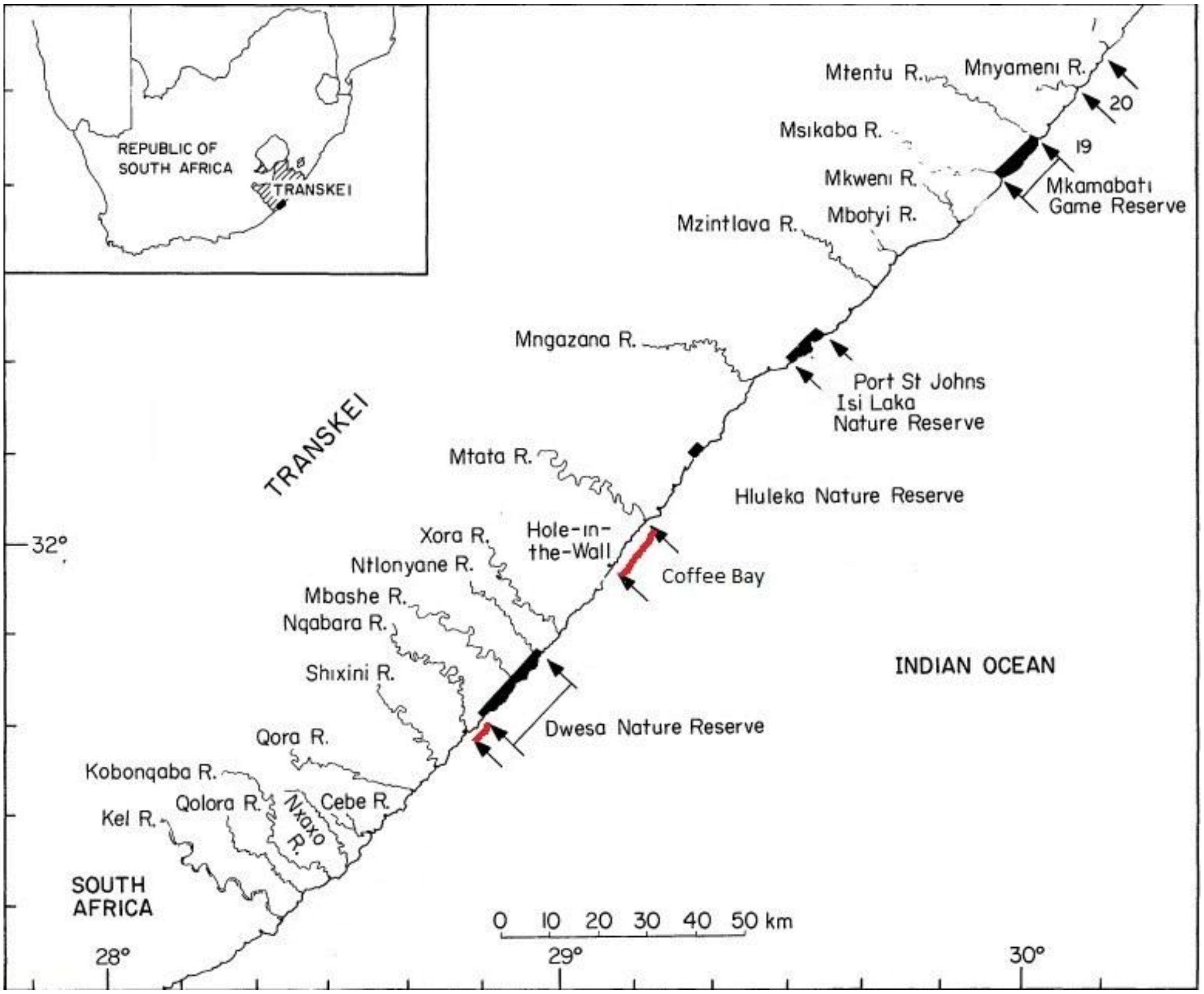

Figure 3.1. Map of South Africa showing Transkei, and an area between Nqabarha estuary and Dwesa-Cwebe Nature Reserve where rocky shores are covered by algae while the area used to be covered by mussel beds.

3.2. Materials and Methods

Six sites were selected along the coast around Coffee Bay (Figure 3.1.), in the Transkei region. The sites were all sites where rehabilitation had been attempted and were arranged so that successful and unsuccessful sites were interspersed as follows: Mthini (unsuccessful-S 31° 57’ 20.6” E 029° 11’ 01.6”), Rhini (successful-S 31° 57’ 45” E 29° 10’ 24”), Lwandlana (unsuccessful- S 31° 58’ 39” E 29° 09’ 43”), Ocean (successful- S 31° 58’ 45” E 29° 09’ 20”), Nqutheni (successful- S 29° 8’ 51” E 32° 0’ 12”) and Hlungulwana (unsuccessful-S 32° 00’ 53’’ E 29° 07’ 48”). Sites were approximately ~2.5km apart. Fifteen patches of small mussels with mesh, fifteen patches of small unmeshed, fifteen patches of large mussels with mesh and fifteen patches of large unmeshed mussels were deployed at each of the six sites. After a month PVC pipes were removed. Three patches of mussels from each size class/method combination were removed from each site on each of three consecutive occasions. The first patches were collected one month after the removal of the PVC drainage pipe (occasion 1). The second after three months (occasion 2) and the last patches after 5 months (occasion 3). The methods used to determine wave force, water motion, survival, attachment strength, CI and growth are described in chapter 2. The data were analyzed using GMAV 5 software (1997).

3.2.1. Wave force and Water flux/ flow or circulation

Wave force and water flux were measured once a month from November 2011-March 2012 at the six sites in Coffee Bay. One-way ANOVA was used to determine the effect of site on wave force and water motion.

3.2.2. Survival

On deployment, each mussel patch comprised 30 mussels. To determine which size class and method yield optimum production, number of surviving mussels was recorded from each removed patch, on each occasion. Three-way ANOVA was used to determine the effect site, size and method on survival of mussels. In the experimental design there were six sites, (random factor), two size classes (fixed and orthogonal), and two methods (fixed and orthogonal). Each occasion was analyzed separately because I measured survival repeatedly over each occasion so that occasions were non-independent.

3.2.3. Attachment strength, Growth and Condition Index

Attachment strength, growth and CI were measured for five mussels from each of the removed patches on each occasion. Due to loss of treatments, different combinations of sites were used for the analyses on different occasions (Table 3.1).

Occasion	Mthini (unsuccessful)	Rhini (successful)	Lwandlana (unsuccessful)	Ocean (successful)	Nqutheni (successful)	Hlungulwana (unsuccessful)
1 November	3SM, 2SU, 3LM, 3LU	3SM, 3SU, 3LM, 3LU	3SM, 0SU, 0LM, 0LU	3SM,0SU, 3LM, 0LU	3SM, 3SU, 3LM, 3LU	2SM, 0SU, 0LM, 0LU
2 January	3SM, 0SU, 3LM, 0LU	3SM, 3SU, 3LM, 2LU	3SM, 0SU, 0LM, 0LU	3SM, 0SU, 2LM, 0LU	3SM, 3SU, 3LM, 1LU	0SM, 0SU, 0LM, 0LU
3 March	3SM, 0SU, 0LM, 0LU	3SM, 0SU, 3LM, 0LU	0SM, 0SU, 0LM, 0LU	3SM, 0SU, 0LM, 0LU	3SM, 3SU, 3LM, 0LU	0SM, 0SU, 0LM, 0LU

Table 3.1. Number of patches removed at each site on each occasion. SM-small meshed, SU-Small unmeshed, LM-large meshed and LU-large

Occasion 1

3.2.3. i. Effect of site, size and method on CI at Mthini, Rhini and Hlungulwana

Three-way ANOVA was used to determine the effects of site, size and method on attachment strength, CI and growth. Only three sites (Mthini, Rhini and Nqutheni – a mixture of successful and unsuccessful sites) were used in the analysis on occasion 1 since at the other three sites (Lwandlana, Ocean and Hlungulwana) all unmeshed mussels were washed away. Site had three levels, and was random, size had two levels, was orthogonal and fixed, and method had two levels, was orthogonal and fixed. There were 10 mussels for each combination.

3.2.3. ii. Effect of site, size, method, and patch on (a) CI, (b) growth and (c) attachment strength between two sites, Rhini and Nqutheni

The effects of site, size, method and patch were tested on (a) CI, (b) growth and (c) attachment strength between Rhini and Nqutheni using four-way ANOVA. In the experimental design site had two levels (Rhini and Nqutheni), and was random, size had two levels, was orthogonal and fixed, method had two levels, was orthogonal and fixed, and patch had three levels, was nested in site and random. There were five replicates.

3.2.3. iii. Effect of site and patch on (a) CI, (b) growth and (c) attachment strength on small meshed mussels among five sites

The effect of site and patch on (a) CI, (b) growth and (c) attachment strength on small meshed mussels were tested at five sites (Hlungulwana was omitted), using two-way ANOVA. In the experimental design site had five levels, and was random, and patch had three levels, random and nested in site. There were five replicates.

Occasion 2

3.2.4. Effect of site and size on (a) CI, (b) growth and (c) attachment strength between small meshed and large meshed mussels among four sites

Two-way ANOVA was used to determine the effect of site and size on (a) CI, (b) growth and (c) attachment strength between small meshed and large meshed mussels among four sites (Mthini, Rhini, Ocean and Nquthemi). Unmeshed mussels were washed away at Lwandlana, and Hlungulwana, therefore I could not test the effect of method. In the design there were four random sites, and two size classes with fifteen replicates.

Occasion 3

3.2.5. Effect of site and patch on (a) Condition Index, (b) Growth and (c) attachment strength among four sites

The effect of site and patch on CI, growth and attachment of small mussels at Mthini, Rhini, Ocean and Nqutheni was determined using two-way ANOVA. There were four random sites, patch had three levels, was random and nested in site with five replicates.

3.2.6. Recruits 1 (recruits into byssus threads of adults)

Recruits 1 were measured as in chapter 2 (counting number of recruits under a dissecting microscope). Three-way ANOVA was used to determine the effect of site, size and method was performed for three sites Mthini, Rhini and Nqutheni on occasion 1. Other sites where excluded from the analysis since unmeshed mussels were washed away from other sites. In the experimental design there were three factors: site, had three levels and was random, size had two levels, orthogonal and fixed, and method had two levels, orthogonal and fixed. There were three observed mussel patches per treatment.

3.2.7. Settlers and recruits 2 (from scouring pads)

Scouring pads were deployed at six sites in Coffee Bay to determine if there were differences in the numbers of settlers and recruits between successfully rehabilitated sites and unsuccessful sites. Scouring pads were processed as in chapter 2. Two-way ANOVAs were used to determine the effects of site and occasion on settlers, and the effect of site and occasion on recruits 2 separately. In the experimental design the six sites were random, with five orthogonal, random occasions, Three scouring pads were processed for each site for each occasion.

3.3. Results

3.3.1. Wave force

One-way ANOVA showed that there were effects of site on wave force (Table 3.2) with Mthini significantly lower wave forces than other sites. There was no consistent relationship between wave force and rehabilitation success. Therefore there was no clear effect of wave force on rehabilitation success (Figure 3.2).

Source	SS	DF	MS	F	P
Site	935.7555	5	187.1511	4.04	0.0084*
RES	1111.4867	24	46.3119		
TOT	2047.2422	29			

Table 3.2. One-way ANOVA table to determine the effect of site on wave force.

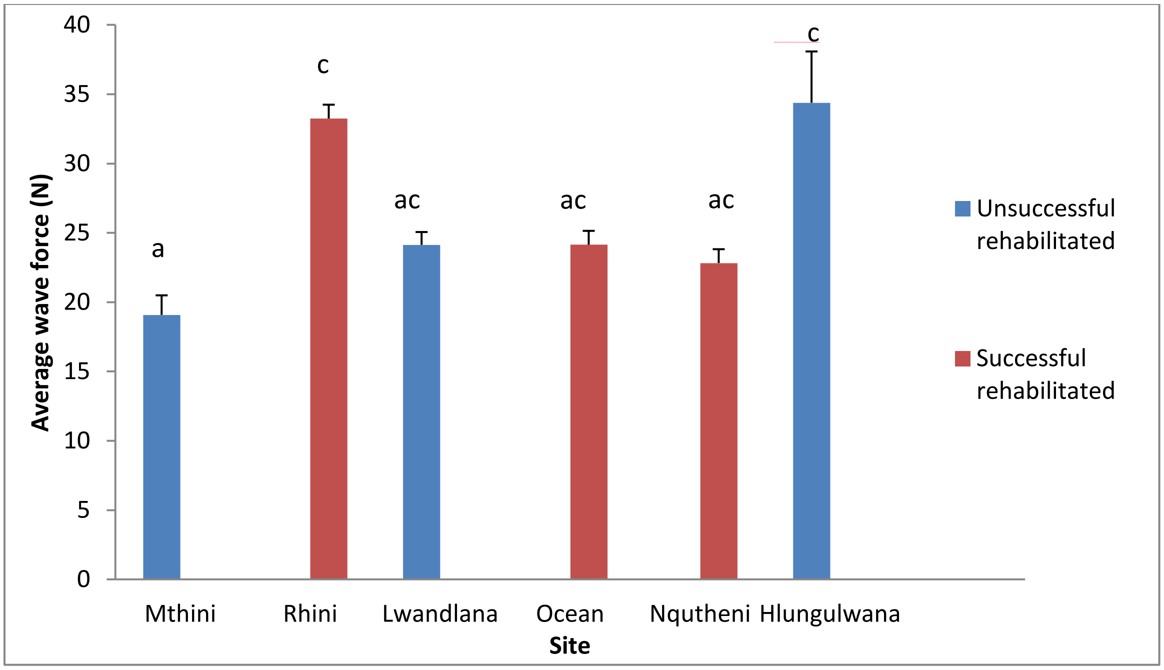

Figure 3.2. Differences in wave force (mean +S.E.) between successfully and unsuccessful rehabilitated sites. Letters indicate homogeneous groups.

3.3.2. Water flux

There was no effect of site on water circulation or flux (Table 3.3).

Source	SS	DF	MS	F	P
Site	512.05	5	102.41	1.79	0.15
RES	1370.65	24	57.11		
TOTAL	1882.70	29			

Table 3. 3. ANOVA table shows that there was no effect of site on water flux

3.3.3. Survival

3.3.3. a. Occasion 1

For occasion 1, three-way ANOVA showed that site, method and size had effects on survival of mussels. There were significant interactions between site and method, and between size and method (Table 3.4). SNK tests showed that there were no differences in survival between large meshed and large unmeshed. In general meshed mussels survived better than unmeshed mussels, with no unmeshed animals surviving at three sites, but the difference was not significant at all the remaining sites (Figure 3.3). Small mussels survived better than large, but size interacted with method. Mesh improved survival of both size classes, but not significantly so for large mussels (Figure 3.4).

Source	SS	DF	MS	F	P
Site	3525.33	5	705.07	24.21	< 0.0001*
Size	382.72	1	382.72	7.07	0.0449*
Method	1901.39	1	1901.39	12.06	0.0178*
Site*Size	270.61	5	54.12	1.86	0.1194
Site*Method	788.28	5	157.66	5.41	0.0005*
Size*Method	696.89	1	696.89	16.85	0.0093*
Site*Size*Method	206.78	5	41.36	1.42	0.2341
RES	1398.00	48	29.15		
TOT	9170.00	71			

Table 3. 4. ANOVA table shows effect of site, size and method on survival on occasion 1.

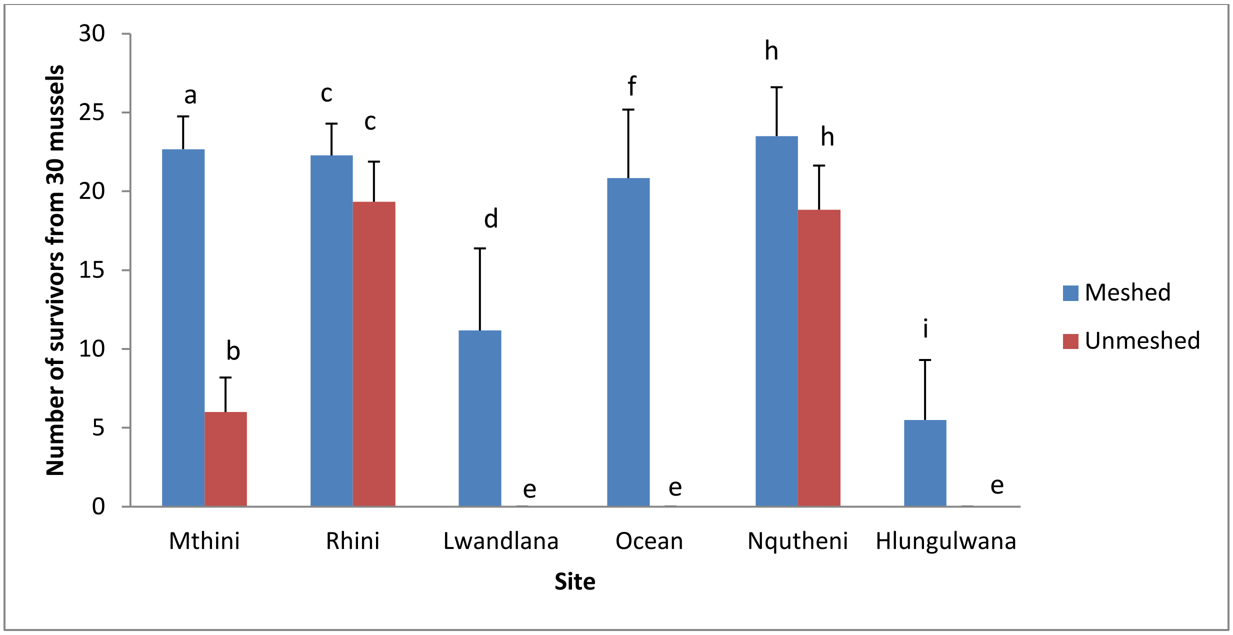

Figure 3.3. Shows that for both size classes, meshed mussels survived better than unmeshed mussels (mean +S.E.). Letters indicate homogeneous groups among sites.

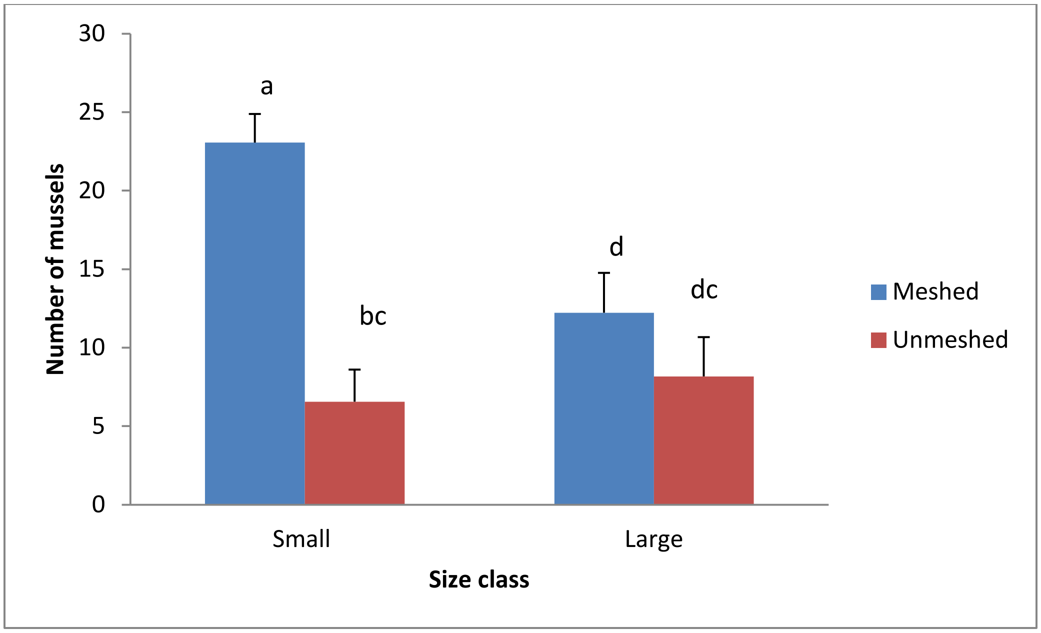

Figure 3.4. Difference in number of survivors (mean +S.E.) between size classes and methods. Letters indicate homogeneous groups between methods and size classes.

3.3.3. b. Occasion 2

Results showed that there were effects of site, small mussels survived better than large mussels and meshed survived better than unmeshed mussels. However, there was a 3-way interaction among site, size and method (Table 3.5). SNK tests showed that small meshed mussels survived better than other treatments (large meshed, small unmeshed and large unmeshed respectively). There were no differences in survival of small meshed mussels among Mthini, Nqutheni, Ocean and Nqutheni, while the difference between Nqutheni and Lwandlana ws significant. At Hlungulwana all mussels were dislodged just after removal of pipes so small meshed could not be sampled on occasion 2 (Figure 3.5). For small unmeshed, there was no difference in survival among Mthini, Lwandlana, Ocean and Hlungulwana, where all small umeshed mussels were washed away. Only Rhini and Nqutheni had surviving large meshed mussels with Nqutheni having higher numbers of survivors than Rhini ($p<0.05$). There was no difference in the number of surviving large unmeshed mussels among the sites. In general, the results showed that meshed mussels survived better than unmeshed mussels (Figure 3.6).

Source	SS	DF	MS	F	P
Site	2966.24	5	593.25	28.82	< 0.0001*
Size	741.13	1	741.13	11.70	0.0188*
Method	2485.13	1	2485.13	17.29	0.0088*
Site*Size	316.79	5	63.36	3.08	0.0173*
Site*Methods	718.79	5	143.76	6.98	0.0001*
Size*Methods	30.68	1	30.69	0.24	0.6439
Site*Size*Methods	635.24	5	127.05	6.17	0.0002*
RES	988.00	48	20.58		
TOT	8881.99	71			

Table 3.5. ANOVA table shows effect of site, size and method on survival of re-attached mussels on occasion 2

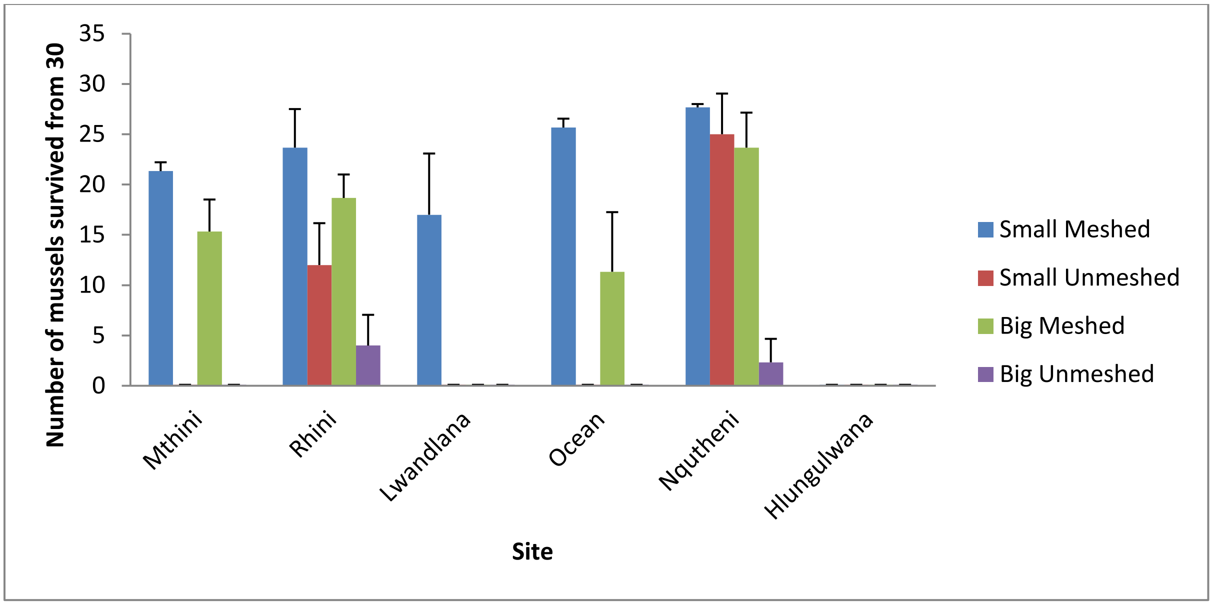

Figure 3.5. Survival of mussels (mean +S.E) at occasion 2 at different site and on different method

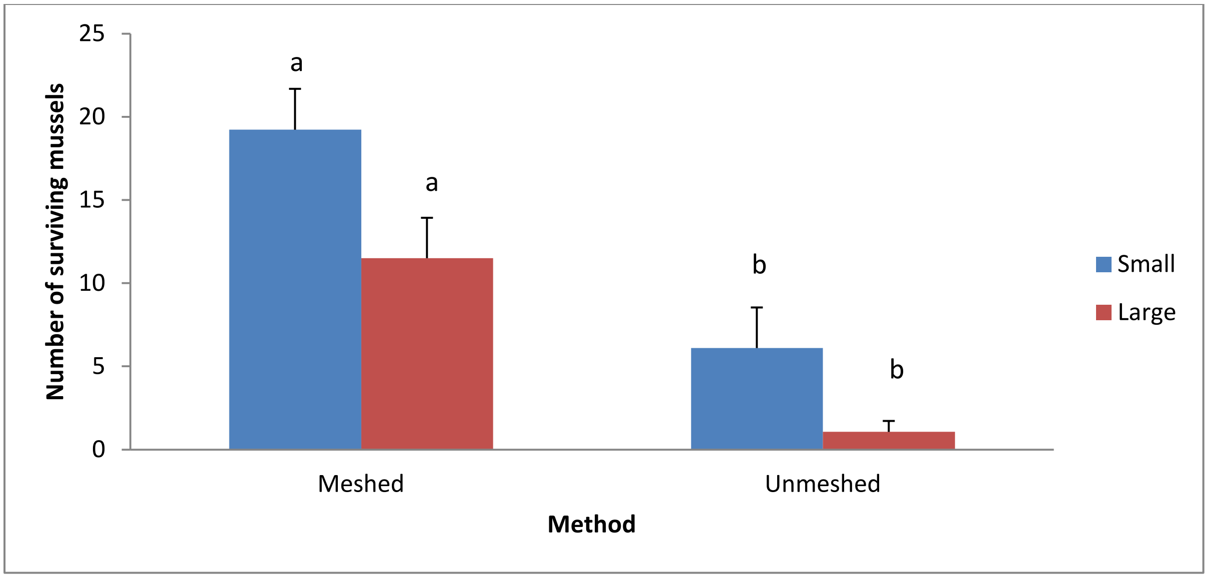

Figure 3.6. Number of survivors (mean + S.E.) between size classes and methods. Letters indicate homogeneous groups between methods and size classes.

3.3.3. c. Occasion 3

On occasion 3, Hlungulwana was excluded from the analysis. Site, size and method all had significant effects on survival of re-attached mussels, with a significant 3-way interaction (Table 3.6). SNK tests showed that for small meshed mussels Mthini was significantly different from Rhini and Nqutheni, while there was no difference no among Rhini, Ocean and Nqutheni. For small unmeshed, there were no surviving mussels at any site, whether sites previously successful or unsuccessful at rehabilitation. For large meshed mussels there were no differences between Rhini and Nqutheni, with no surviving mussels at Mthini, Lwandlana and Ocean. In general, small mussels survived better than large mussels and meshed survived better than unmeshed mussels (Figure 3.7).

Source	SS	DF	MSF	P	F versus
Site	898.67	4	224.67	23.36	< 0.0001*
Size	558.15	1	558.15	10.84	0.0301*
Method	2220.42	1	2220.42	9.88	0.0347*
Site*Size	205.93	4	51.48	5.35	0.0015*
Site*Method	898.67	4	224.67	23.36	< 0.0001*
Size*Method	558.15	1	558.15	10.84	0.0301*
Site*Size*Method	205.93	4	51.48	5.35	0.0015*
RES	384.67	40	9.62		
TOT	5930.58	59			

Table 3.6. ANOVA table shows results for occasion 3 to test the effect site, size and method on survival.

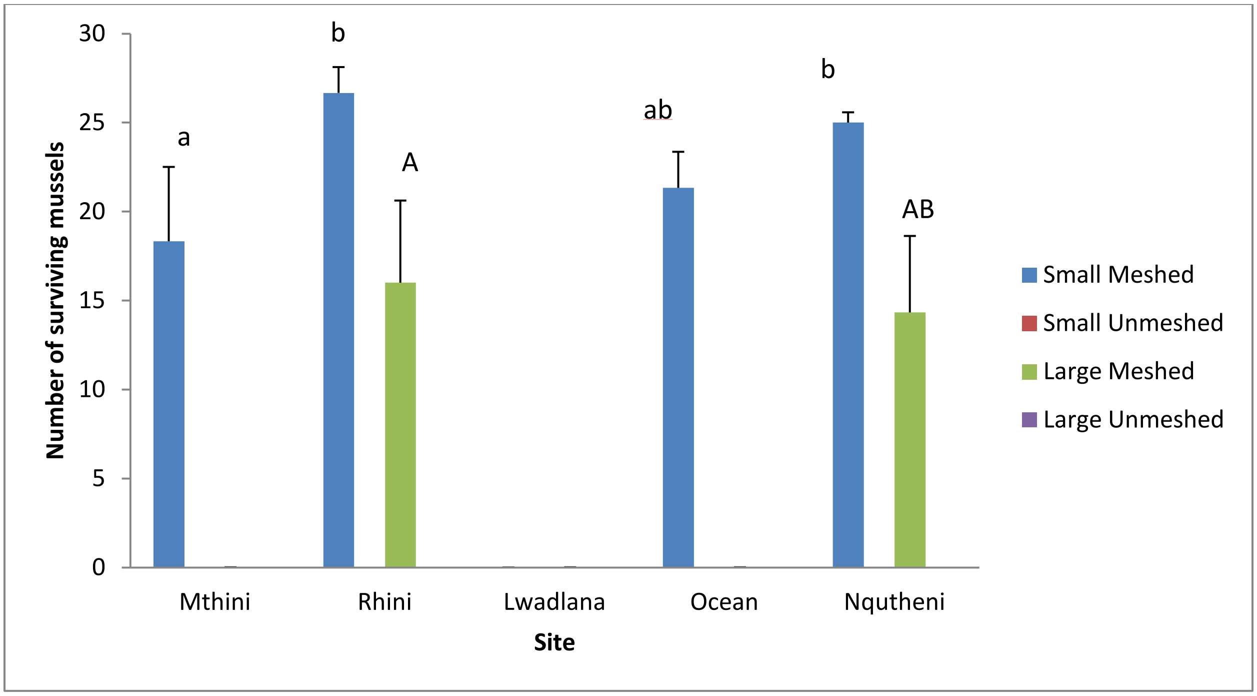

Figure 3.7. Number of survivors (mean + S.E.) between size classes and method on occasion 3. Letters indicate homogenous groups for small meshed and large meshed mussel (lower and upper case letters respectively).

3.3.4. a. Effect of site, size and method on CI among Mthini, Rhini and Nqutheni

Occasion 1

There were no differences in CI among sites, between small and large mussels or between mesh and unmeshed mussels and no interactions among factors (Table 3.7).

Source	SS	DF	MS	F	P
Site	1352.03	2	676.02	0.93	0.3975
Size	685.49	1	685.49	1.20	0.3877
Method	655.19	1	655.19	0.76	0.4757
Site*Size	1143.03	2	571.51	0.79	0.4580
Site*Method	1728.05	2	864.02	1.19	0.3084
Size*Method	740.37	1	740.37	1.08	0.4085
Site*Size*Method	1375.42	2	687.71	0.95	0.3913
RES	78467.54	108	726.55		
TOT	86147.12	119			

Table 3.7. Three-way ANOVA table for the effect of site, size and method on CI among Mthini, Rhini and Nqutheni.

3.3.4. b. Effect of site, size and method on growth among Mthini, Rhini and Nqutheni

Site had significant effects on growth, with no differences in growth between small and large mussels on occasion 1. There was an interaction between site and size (Table 3.8). For small mussels, SNK tests showed that there was no significant difference between Mthini and Rhini, while at Nqutheni small mussels grew faster than at Mthini and Rhini ($p < 0.01$). There were differences in growth between small and large at Mthini ($p<0.01$), Rhini ($p<0.05$) and Nqutheni

($p < 0.05$), but the effect was strongest at Nqutheni, resulting in the interaction between size and site (Figure 3.8).

Source	SS	DF	MS	F	P
Site	0.0066	2	0.0033	5.63	0.0047*
Size	0.0270	1	0.0270	8.99	0.0955
Method	0.0000	1	0.0000	0.02	0.8925
Site*Size	0.0060	2	0.0030	5.12	0.0075*
Site*Method	0.0026	2	0.0013	2.19	0.1172
Size*Method	0.0000	1	0.0000	0.02	0.8939
Site*Size*Method	0.0012	2	0.0006	1.00	0.3717
RES	0.0633	108	0.0006		
TOT	0.1067	119			

Table 3.8. Three-way ANOVA table for the effect of site, size and method on growth among Mthini, Rhini and Nqutheni.

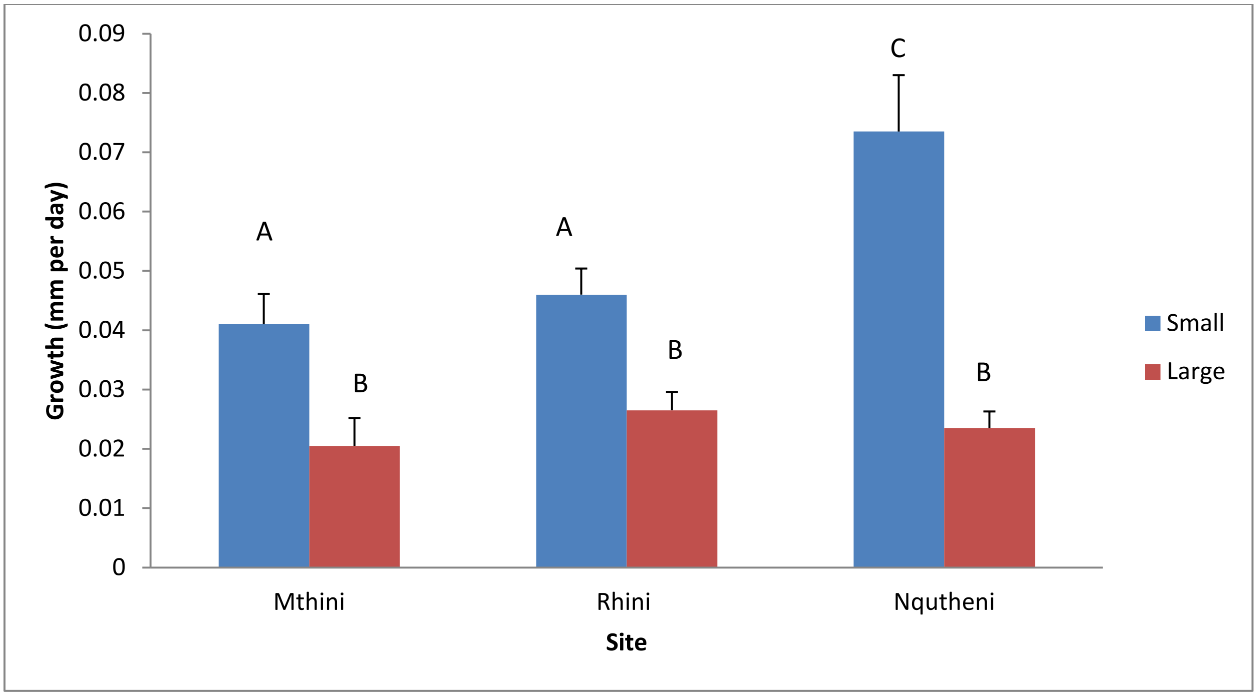

Figure 3.8. Differences in growth (mean +S.E.) between size classes in each site. Letters indicate homogeneous groups between size classes.

3.3.4.c. Effect of site, size and method on attachment strength among Mthini, Rhini and Nqutheni

There were significant effects of site and size on attachment strength, with no effect of method (Table 3.9). SNK tests showed that Rhini and Nqutheni had stronger attachment strength than Mthini, and large mussels had stronger attachment strength (mean 58.16N) than small mussels (mean 42.71N).

Source	SS	DF	MS	F	P
Site	2869.74	2	1434.87	5.39	0.0059*
Size	7147.18	1	7147.18	333.72	0.0030*
Method	95.09	1	95.09	0.14	0.7427
Site*Size	42.83	2	21.42	0.08	0.9228
Site*Method	1341.74	2	670.87	2.52	0.0853
Size*Method	66.28	1	66.28	0.16	0.7272
Site*Size*Method	824.09	2	412.04	1.55	0.2175
RES	28764.08	108	266.33		
TOT	41151.02	119			

Table 3.9. Three-way ANOVA table for the effect of site, size and method on attachment strength among Mthini, Rhini and Nqutheni.

3.3.5. Effect of site, size, method, and patch on (a) CI, (b) growth and (c) attachment strength between two sites, Rhini and Nqutheni

3.3.5. a. Effect of site, size, method, and patch on CI between Rhini and Nqutheni

There was a significant interaction among size, method and patch (Table 3.10). SNK tests showed that Nqutheni had better CI than Rhini, that unmeshed mussels had better CI than meshed mussels and that there was an effect of patch only on large meshed mussels at Nqutheni (Table 3.11).

Source	SS	DF	MS	F	P
Site	29.76	1	29.76	93.88	0.0006*
Size	1.85	1	1.84	0.28	0.6898
Method	11.95	1	11.95	1197.46	0.0184*
Patch (Site)	1.27	4	0.32	0.37	0.8294
Site*Size	6.56	1	6.58	2.86	0.1662
Site*Method	0.01	1	0.01	0.01	0.9279
Size*Method	0.19	1	0.19	0.22	0.7181
Size*Patch (Site)	9.20	4	2.30	2.69	0.0358*
Method*Patch (Site)	4.31	4	1.08	1.26	0.2921
Site*Size*Method	0.85	1	0.85	0.40	0.5632
Size*Method*Patch (Site)	8.58	4	2.15	2.50	0.0472*
RES	82.23	96	0.86		
TOT	156.77	119			

Table 3.10. Four-way ANOVA table for the effect of site, size, method and patch on CI between Rhini and Nqutheni.

Site	Small meshed			Small unmeshed			Large meshed			Large unmeshed		
	P 1	P 2	P 3	P 1	P 2	P 3	P1	P 2	P 3	P 1	P 2	P 3
Nqutheni	a	a	a	b	b	b	c	c	c	d	d	d
Rhini	e	e	e	f	f	f	g	h	g	i	i	i

Table 3.11. Difference in CI among patches at each site. Letters indicate homogenous groups, P stands for patch.

3.3.5.b. Effect of site, size, method, and patch on growth at Rhini and Nqutheni

There was a 3-way interaction among size, method and patch (Table 3.12). SNK tests showed that the effect of patch was found only at Rhini on small meshed mussels (Table 3.13).

Source	SS	DF	MS	F	P
Site	0.0046	1	0.0046	2.54	0.1860
Size	0.0301	1	0.0301	6.96	0.2306
Method	0.0000	1	0.0000	0.02	0.9137
Patch (Site)	0.0072	4	0.0018	3.93	0.0053*
Site*Size	0.0043	1	0.0043	4.16	0.1111
Site*Method	0.0016	1	0.0016	1.11	0.3509
Size*Method	0.0002	1	0.0002	7.11	0.2284
Size*Patch (Site)	0.0042	4	0.0010	2.28	0.0665
Method*Patch (Site)	0.0058	4	0.0014	3.18	0.0170*
Site*Size*Method	0.0000	1	0.0000	0.01	0.9096
Size*Method*Patch (Site)	0.0082	4	0.0021	4.50	0.0022*
RES	0.0438	96	0.0005		
TOT	0.1100	119			

Table 3.12. Four-way ANOVA table for the effect of site, size, method and patch on growth between Rhini and Nqutheni.

Site	Small meshed			Small unmeshed			Large meshed			Large unmeshed		
	P 1	P 2	P 3	P 1	P 2	P 3	P 1	P 2	P 3	P 1	P 2	P 3
Nqutheni	a	a	a	b	b	b	c	c	c	d	d	d
Rhini	e	e	e	f	g	f	h	h	h	i	i	i

Table 3.13. Difference in patches at each site among patches of the same size and method (P stands for patch).

3.3.5.c. Effect of site, size, method, and patch on attachment strength between Rhini and Nqutheni

There were no significant effects or interactions among factors (Table 3.14).

Source	SS	DF	MS	F	P
Site	2282.20	1	2282.20	0.86	0.4053
Size	15021.46	1	15021.46	4.13	0.2911
Method	5045.59	1	5045.59	8.40	0.2115
Patch (Site)	10568.11	4	2642.03	0.99	0.4179
Site*Size	3635.72	1	3635.72	1.36	0.3085
Site*Method	600.86	1	600.86	0.21	0.6740
Size*Method	2421.01	1	2421.01	8.74	0.2076
Size*Patch (Site)	10701.10	4	2675.27	1.00	0.4113
Method*Patch (Site)	11711.63	4	2927.91	1.10	0.3635
Site*Size*Method	276.88	1	276.88	0.11	0.7524
Size*Method*Patch (Site)	9698.18	4	2424.55	0.91	0.4633
RES	256692.26	96	2673.88		
TOT	328655.00	119			

Table 3.14. Four-way ANOVA table for the effect of site, size, method and patch on attachment strength between Rhini and Nqutheni.

Occasion 2

3.3.6. Effect of site and size on (a) CI, (b) growth and (c) attachment strength for small meshed and large meshed mussels among four sites

3.3.6. (a). Condition Index

There were differences in CI between sites and a significant interaction between site and size (Table 3.15). Post-hoc tests showed that Rhini had significantly lower CI than other sites (Figure 3.9). Small meshed mussels had significantly higher CI values than large meshed mussels at Mthini and Ocean (Figure 3.10).

Source	SS	DF	MS	F	P
Site	93.8797	3	31.2932	19.36	< 0.0001*
Size	13.1622	1	13.1622	2.22	0.2328
Site*Size	17.7659	3	5.9220	3.66	0.0145*
RES	180.9888	112	1.6160		
TOT	305.7968	119			

Table 3.15. Two-way ANOVA table for the effect of site and size on CI between small and large meshed mussels among sites

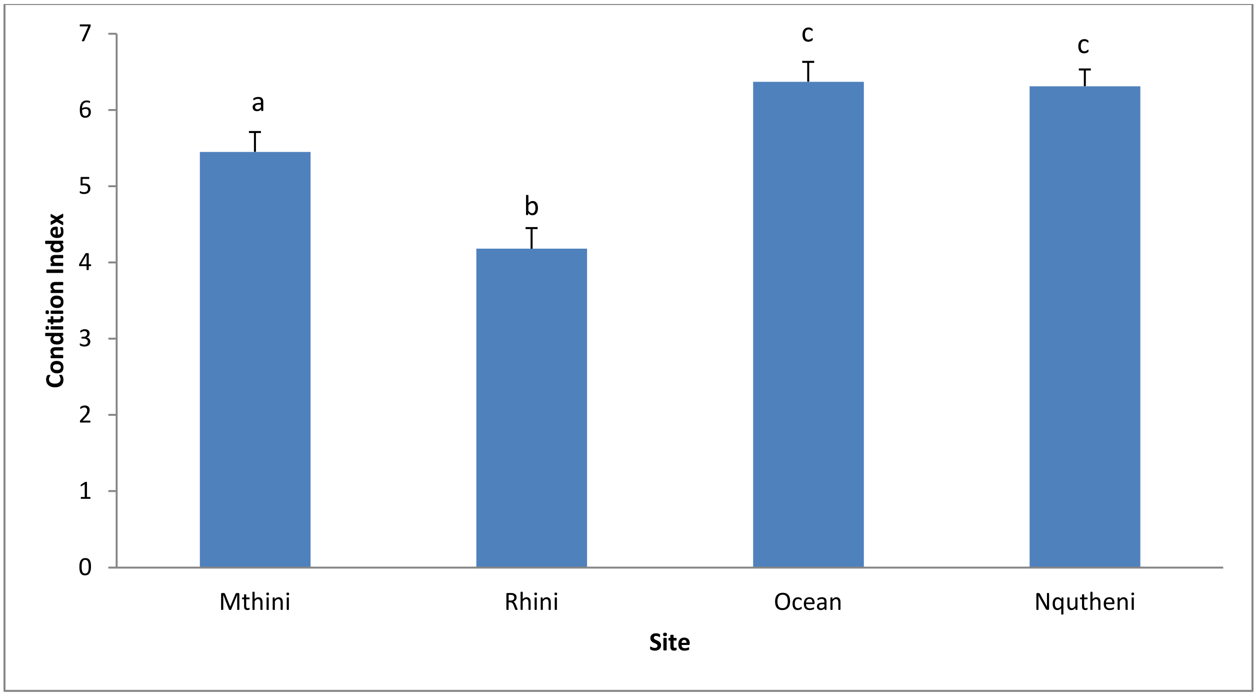

Figure 3.9. Differences in CI (mean +S.E.) between small and large meshed mussels among sites. Letters indicate homogeneous groups among sites

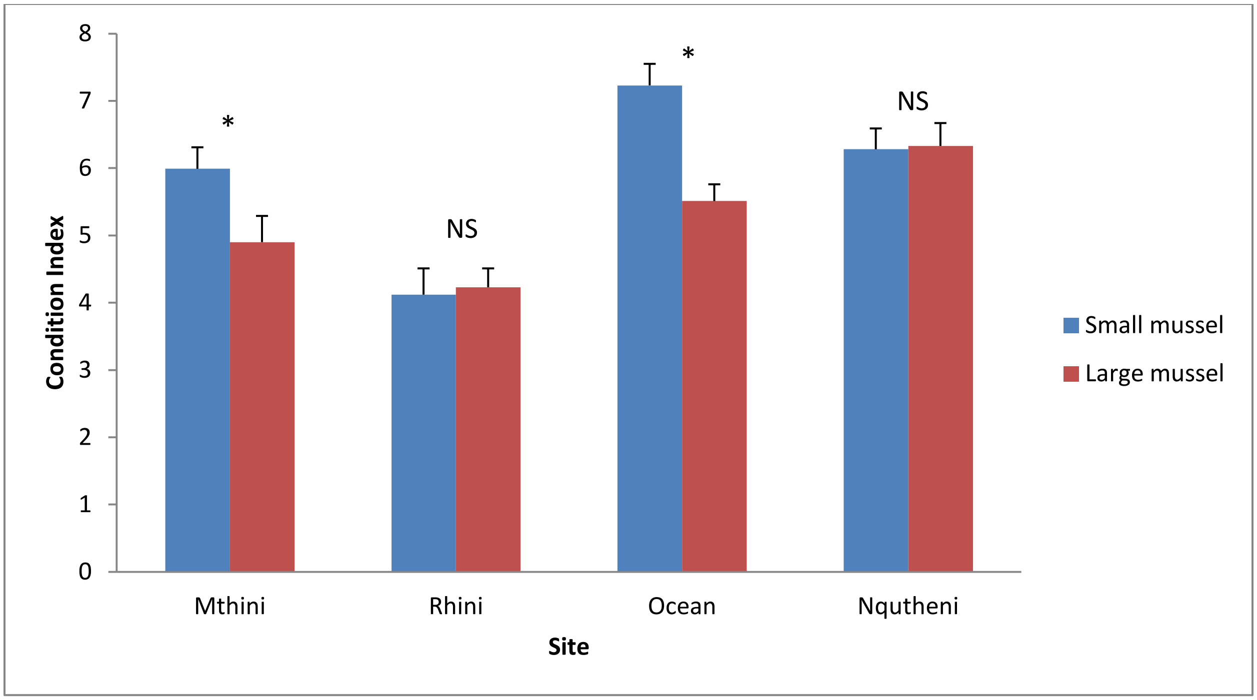

Figure 3.10. Post-hoc results for CI (mean +S.E.) between small and large meshed mussels. Asterisks indicate significant difference and N.S. indicates no significant difference in comparisons of size classes within a site.

3.3.6. (b). Growth

There was a significant interaction between site and size (Table 3.16). As for CI, Rhini showed the lowest values (Figure 3.11). Small meshed mussels grew faster than large meshed mussels at all sites ($p < 0.01$ at Mthini, Rhini, Ocean and $p < 0.05$ at Nqutheni), the significant interaction reflecting the fact that the strength of the effect of size differed among sites. The highest growth was at Ocean for small mussels and at Nqutheni for large mussels (Figure 3.12).

Source	SS	DF	MS	F	P
Site	0.0146	3	0.0049	8.75	< 0.0001*
Size	0.0431	1	0.0431	25.32	0.0151*
Site*Size	0.0051	3	0.0017	3.07	0.0308 *
RES	0.0621	112	0.0006		
TOT	0.1249	119			

Table 3.16. Two-way ANOVA table for the effect of site and size on growth between small and large meshed mussels among four sites

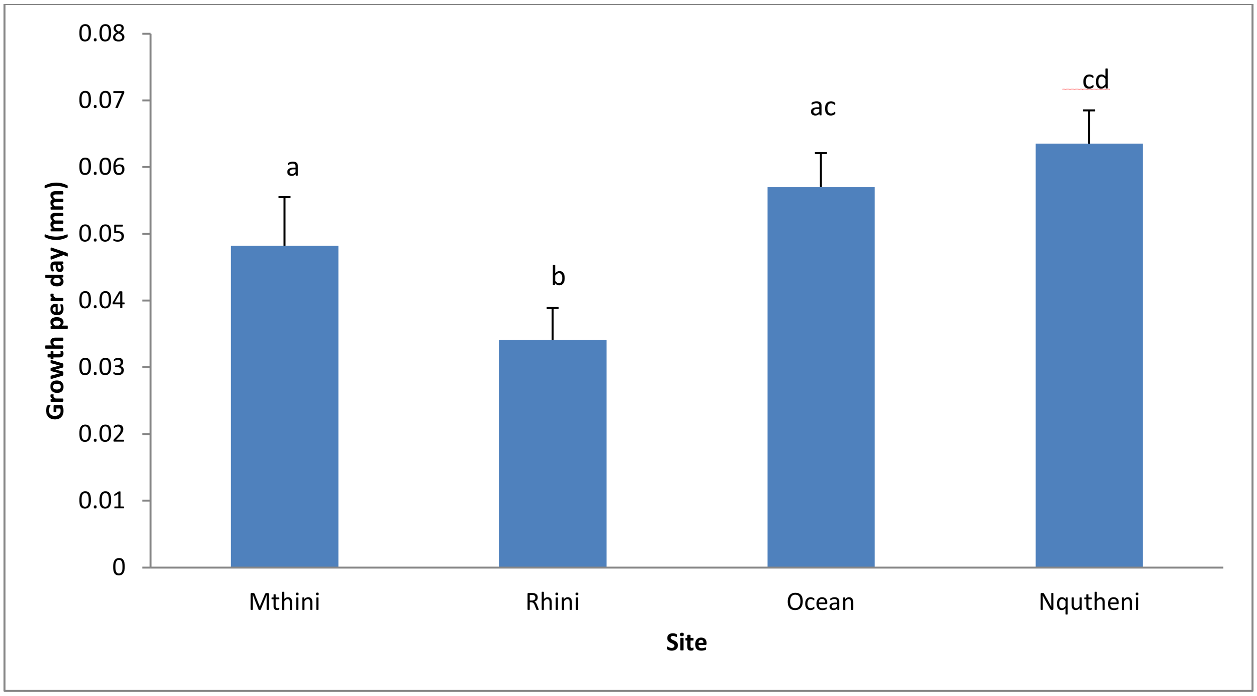

Figure 3.11. Differences in growth (mean +S.E.) among sites. Letters indicate homogeneous groups among sites.

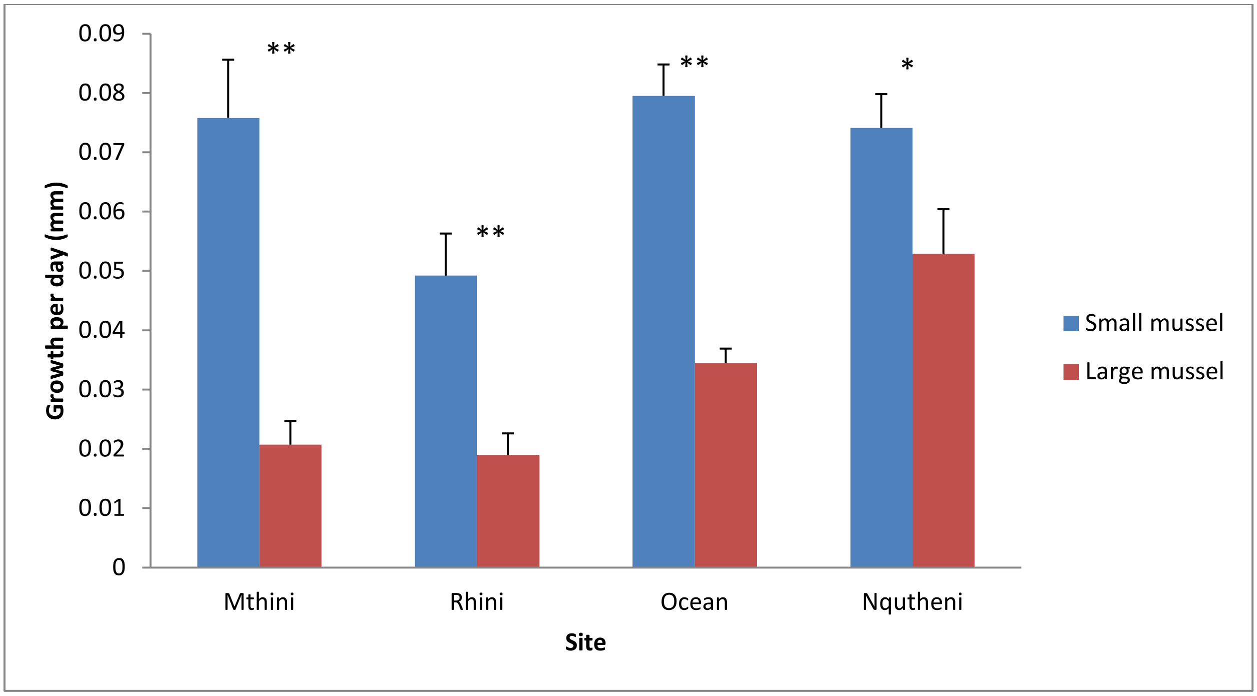

Figure 3.12. Differences in growth (mean +S.E.) between size classes at each site. One asterisk (*) indicates significant difference at $p < 0.05$, and two asterisks (**) at $p < 0.01$.

3.3.6. (c). Attachment strength

There were effects of both size (large mussels were more strongly attached) and site, but no interaction between the two (Table 3.17, Figures 3.13, 3.14).

Source	SS	DF	MS	F	P
Site	3857.89	3	1285.96	4.68	0.0041*
Size	8540.27	1	8540.27	13.37	0.0353*
Site*Size	1915.83	3	638.61	2.32	0.0787
RES	30766.61	112	274.70		
TOT	45080.59	119			

Table 3.17. Two-way ANOVA table for the effect of site and size on attachment strength between small and large meshed mussels among four sites

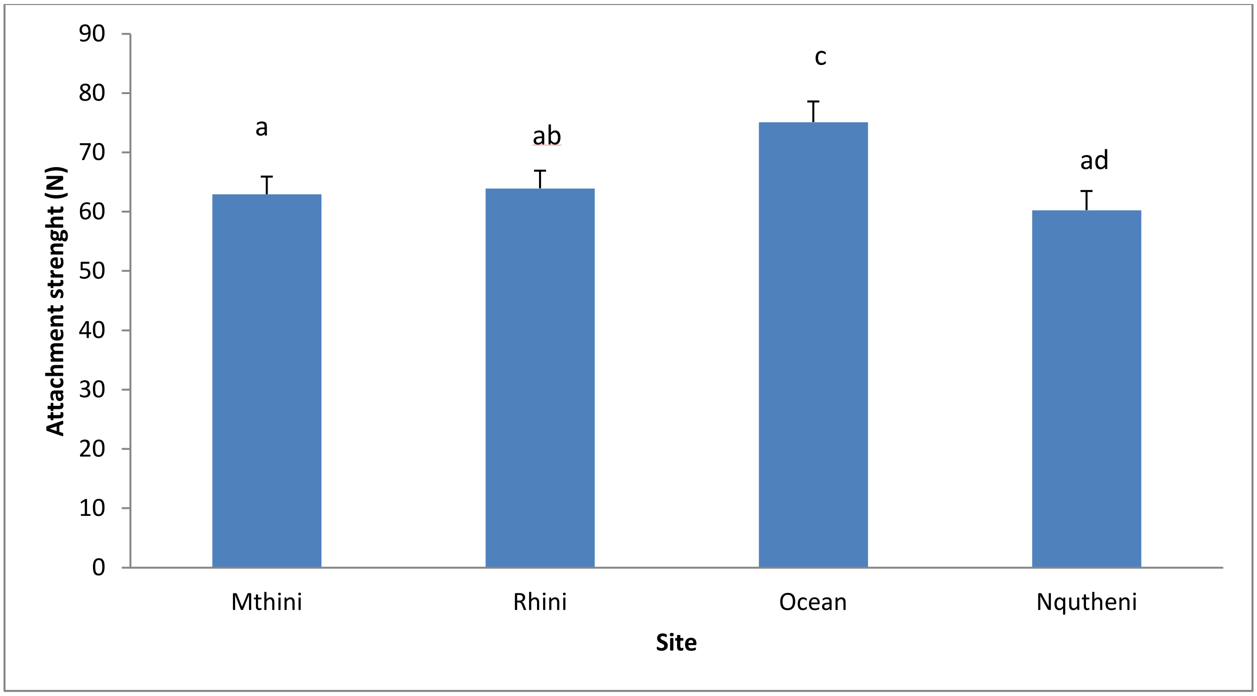

Figure 3.13. Difference in attachment strength (mean +S.E.) among sites

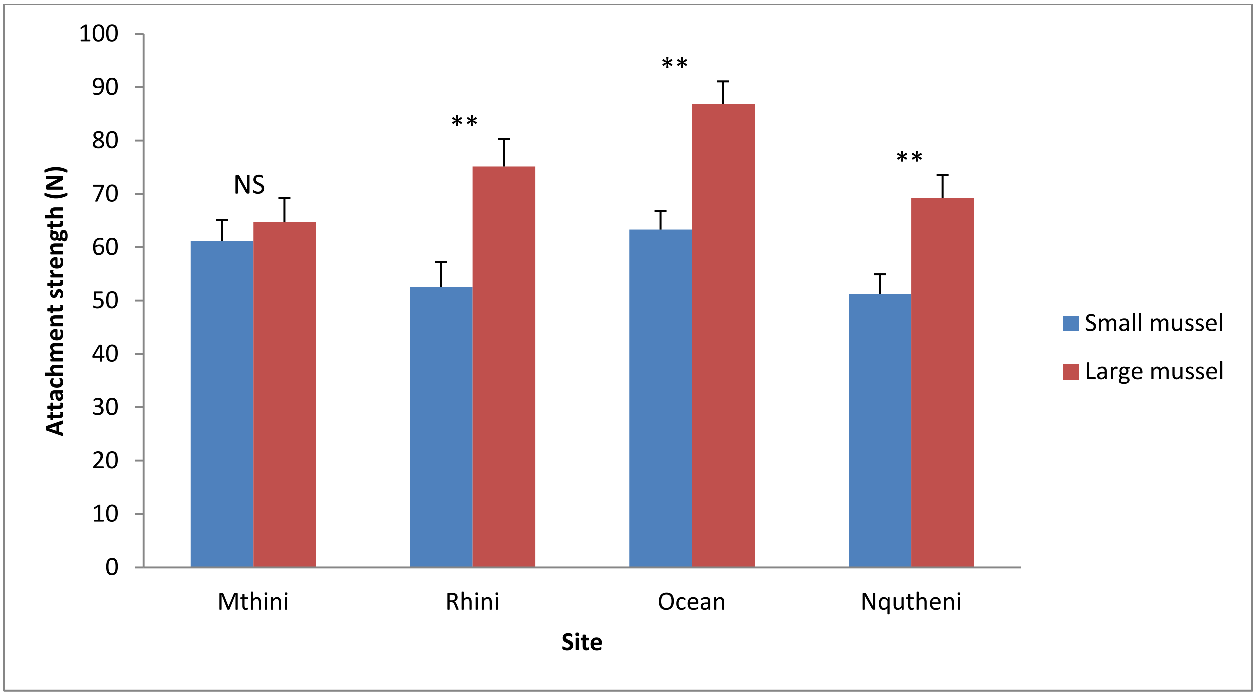

Figure 3.14. Post-hoc results showing differences in attachment strength (mean +S.E.) between small and large meshed mussels at the $p < 0.01$ level of significance. N.S. indicates no significant difference in the comparison of size classes within a site.

3.3.7. Occasion 3

3.3.7. Effect of site and patch on (a) Condition Index, (b) Growth and (c) attachment strength among four sites

3.3.7.a. Condition Index

There were differences in CI among sites, with highest CI at Nqutheni, but not among patches within sites (Table 3.18, Figure 3.15).

Source	SS	DF	MS	F	P
Site	146.6064	3	48.8688	17.15	0.0008*
Patch (Site)	22.8015	8	2.8502	1.68	0.1275
RES	81.3792	48	1.6954		
TOT	250.7871	59			

Table 3.18. Two-way ANOVA table showing the effect of site and patch on CI of small meshed mussels among site and between patches

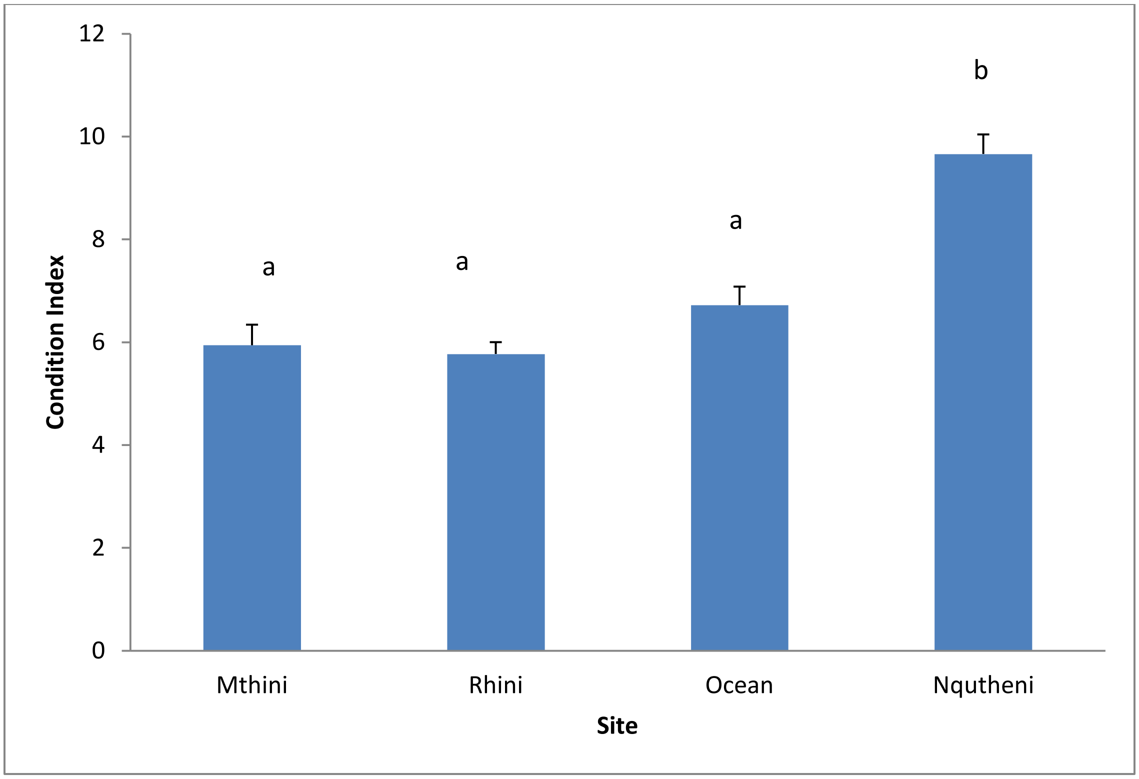

Figure 3.15. Differences in CI (mean +S.E.) of small meshed mussels among sites on occasion 3

3.3.7. b. Growth

There were differences in growth among sites (fastest growth at Nqutheni) and patches (Table 3.19, Figure 3.16).

Source	SS	DF	MS	F	P
Site	0.0359	3	0.0120	8.21	0.0080*
Patch (Site)	0.0117	8	0.0015	3.36	0.0039*
RES	0.0208	48	0.0004		
TOT	0.0684	59			

Table 3.19. Two-way ANOVA for the effects of site and patch on growth

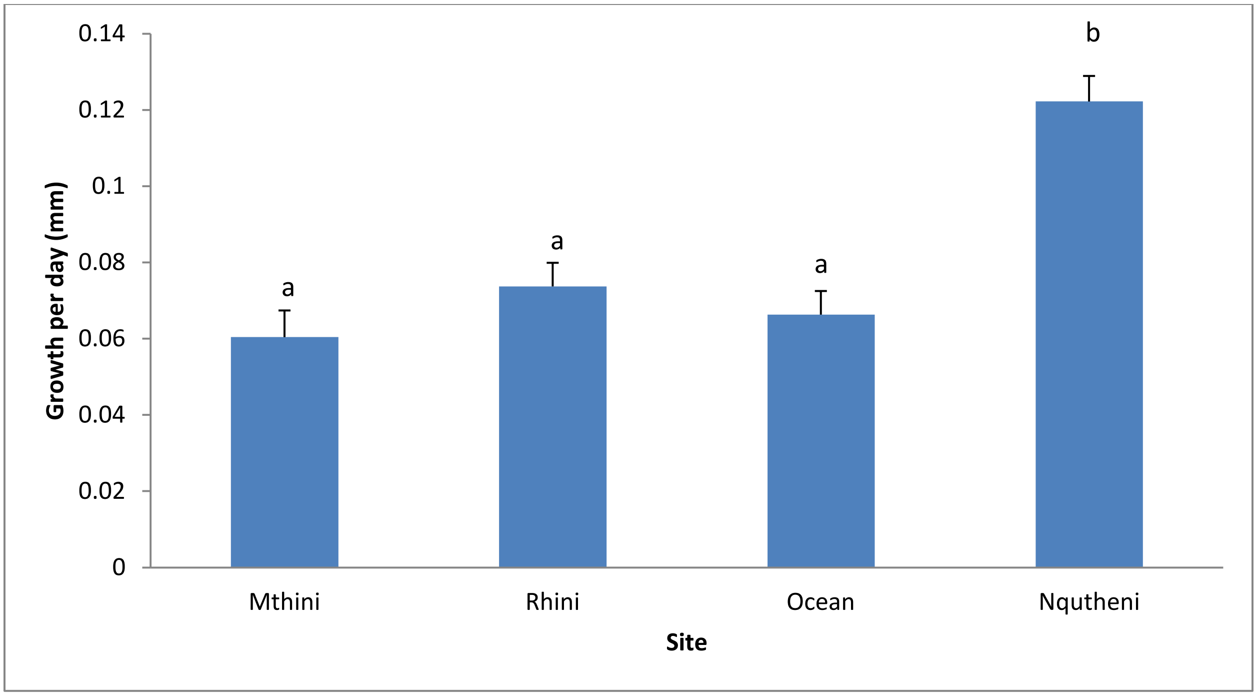

Figure 3.16. Growth (mean +S.E.) of small meshed mussels among sites in occasion 3. Letters indicate homogenous groups.

3.3.7. c. Attachment strength

There were no effects of site on attachment strength, while patch had a significant effect (Table 3.20). At Rhini patch 3 was significantly different from patch 1.

Source	SS	DF	MS	F	P
Site	553.7666	3	184.5889	0.17	0.9149
Patch (Site)	8778.5682	8	1097.3210	2.42	0.0278*
RES	21777.6462	48	453.7010		
TOT	31109.9811	59			

Table 3.20. Two-way ANOVA table for effect of site and patch on attachment strength

3.3.8. Recruits 1 (recruits into byssus threads of adults)

There were differences among sites, and an interaction among site, size and method (Table 3.21). For small meshed mussels Nqutheni (known by local people as the best site for rehabilitation) had higher numbers of recruits 1 than Mthini and Rhini ($p < 0.01$). For small, unmeshed mussels there were no significant differences between sites. For large meshed mussel there were no differences between sites while for large unmeshed mussels, Nqutheni had higher numbers than Mthini and Rhini ($p < 0.01$).

Source	SS	DF	MS	F	P
Site	169.56	2	84.77	20.90	< 0.0001*
Size	2.78	1	2.78	3.57	0.1994
Method	1.78	1	1.78	0.24	0.6734
Site*Size	1.56	2	0.78	0.19	0.8267
Site*Method	14.89	2	7.44	1.84	0.1812
Size*Method	81.00	1	81.00	2.08	0.2863
Site*Size*Method	78.00	2	39.00	9.62	0.0009*
RES	97.33	24	4.06		
TOT	446.89	35			

Table 3.21. Three-way ANOVA table to determine the effect of site, size and method on recruits

3.3.9. Settlers onto scouring pads

There were no differences in numbers of settlers between successful and unsuccessful rehabilitation sites, though Hlungulwana had the lowest numbers of settlers. There were differences in numbers of settlers among occasions (Table 3.22). Numbers of recruits generally increased after occasion 2 (January), with highest numbers on occasions 3 (February) and 5 (April) (Figure 3.17).

Source	SS	DF	MS	F	P
Site	511.39	5	102.28	1.20	0.3463
Occasion	2647.33	4	661.83	7.74	0.0006*
Site*Occasion	1709.33	20	85.47	1.11	0.3672
RES	4633.33	60	77.22		
TOT	9501.39	89			

Table 3.22. Two-way AOVA table for the effect of site and occasion on settlers

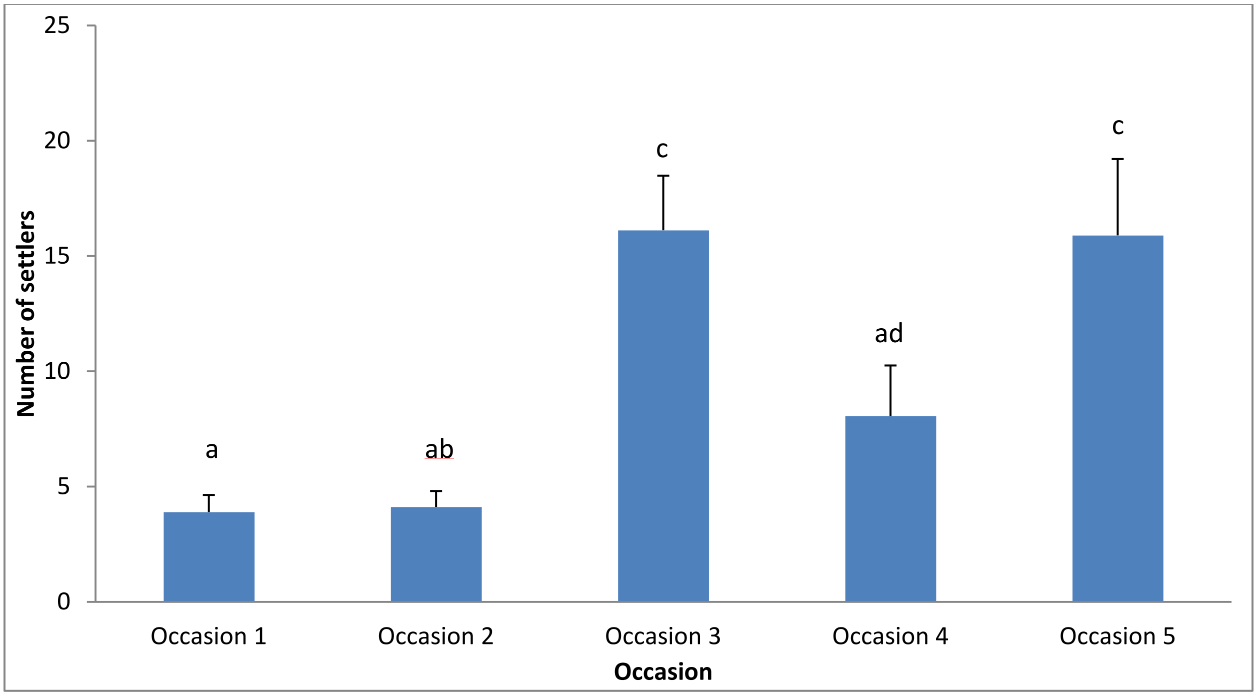

Figure 3.17. Number of settlers (mean +S.E.) among occasions letters indicate homogenous groups.

3.3.10. Recruits 2 (onto artificial substrata)

Again there were no differences in numbers of recruits 2 between successful and unsuccessful rehabilitation sites, but an effect of occasion, with numbers increasing as the study progressed to a maximum on occasion 5 (Table 3.23, Figure 3.18).

Source	SS	DF	MS	F	P
Site	627.12	5	125.42	1.23	0.3319
Occasion	2893.71	4	723.43	7.09	0.0010*
Site*Occasion	2039.49	20	101.97	1.49	0.1187
RES	4103.33	60	68.39		
TOT	9663.6556	89			

Table 3.23. Two-way ANOVA for site and occasion on recruits 2

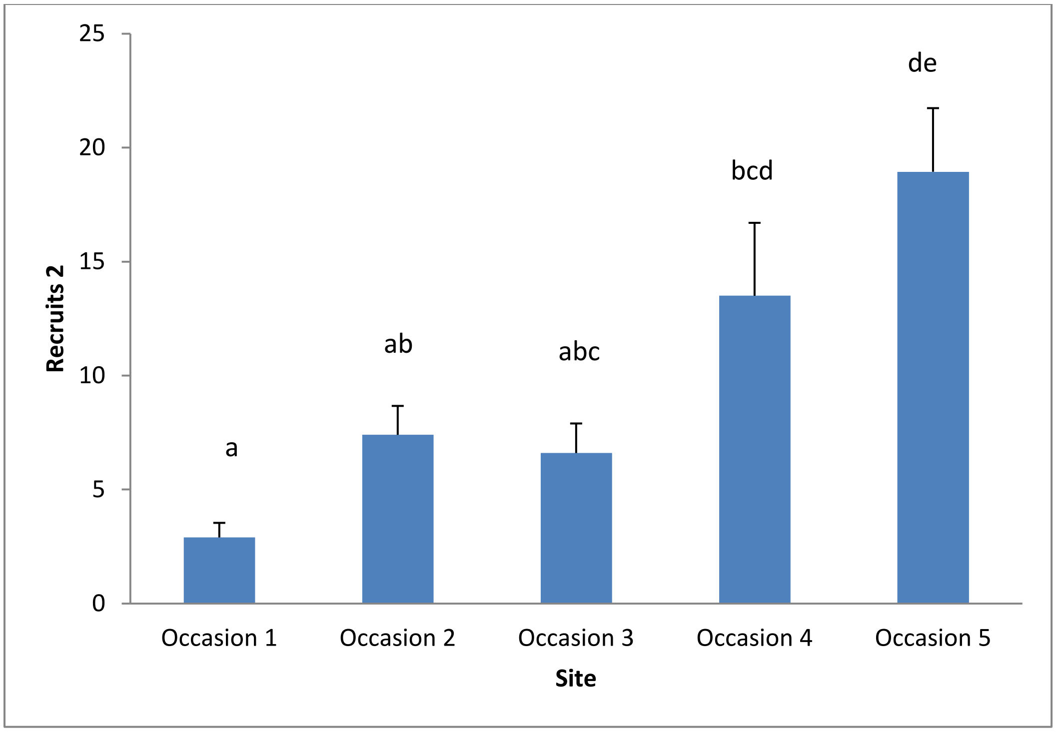

Figure 3.18. Numbers of recruits 2 (mean +S.E.) among occasions (December, January, February, March, April). Letters indicate homogenous groups.

3.4. Discussion

There was no relationship between wave force or water flux and rehabilitation success and, while there were differences in wave force among sites, that was not the case for water flux, Success of rehabilitation was rather correlated with the number of surviving mussels and recruited mussels. Therefore it was important to monitor the survival of reattached mussels, and the difference in survival between the two size classes (3-4cm and 5-6cm). On occasion 1 it was found that there were no differences in survival between small and large mussels attached using the Dye and Dyantyi (2002) method, or method 1. The use of mesh (method 2) improved survival of mussels, small meshed mussels survived better than large meshed, and both large and small meshed survived better than unmeshed mussels. Even at one site where rehabilitation has never been successful, Mthini, the mesh improved the survival of mussels. The aim of this study was to determine the most suitable size for rehabilitation, and to determine the optimum method, comparing the mesh and no-mesh approaches and I conclude that small (3-4cm) meshed mussels performed best. It was determined that there were no differences in survival between small and large unmeshed mussels, using method 1. As in the Riet River study (Chap. 2) that compared 1-2cm and 3-4cm mussels, there were differences in growth between 3-4cm and 5-6cm on occasion 1 and 2. On occasion 2 small mussels (3-4cm) grew faster than large mussels (5-6cm). On occasion 3, growth between size classes could only be compared between Rhini and Nqutheni, as they were the only sites where large (meshed) mussels could be found. Although small mussels grew faster than large mussels, the difference was not significant. The fact that large meshed mussels could only be found at Rhini and Nqutheni on occasion 3 supports the conclusion that the use of mesh (method 2) together with 3-4cm mussel size can optimize production of rehabilitated shores.

As expected, small mussels grew faster than large mussels in this study while both size classes (3-4 and 5-6cm) need energy for reproduction. That might be associated to the size of reattached mussels between the two studies. In the Coffee Bay study large mussels (5-6cm) might exert more resistance to wave force due to their greater surface area, which is likely to affect energy allocation. In the Riet River study, small mussels (1-2cm) were sexually immature and large mussels (3-4cm) were sexually mature according to Ruis *et al*. (2006). Both mature and immature mussels will experience physiological stress after removal, transportation, tagging, and deployment, which may affect growth (Seed and Richardson 1990). That has been proved by reduced growth which was more pronounced at the shell edge by growth mark or growth lines which were fused on occasion 1. Unlike immature mussels, sexually mature mussels need energy not only for maintenance and growth, but also for reproduction (Seed and Suchanek 1992). Drag also increases with size leading to additional stress on larger mussels.

It was sometimes possible to find differences in growth among patches of the same sized mussels at the same site. This was presumably associated with patch position within a site. Any natural landscape has features of spatial heterogeneity that influence ecological processes and patch dynamics, among other processes (Levin 1992). The influence depends on the nature and scale of heterogeneity (Miller and Etter 2008). Therefore mussel patches within a site can experience different degrees of wave exposure due to spatial heterogeneity and unevenness, and that might affect their growth. In fact experimental manipulation in the field of water flow at cm scales has been shown to affect the growth rates of mussels (McQuaid & Mostert 2010). The absence of a patch effect on most occasions reflects the fact that sites selected for possible rehabilitation are generally fairly flat, homogenous platforms.

Although there were no differences in growth between size classes on occasion 1, there were differences in attachment strength. On both occasions 1 and 2, large mussels showed greater attachment strength than small mussels. On occasion 3 there were not enough data to test this effect as large mussels were washed away from several sites. When the difference was tested between the remaining two sites (Rhini and Nqutheni), it was found that large mussels attached more strongly but that the difference was not significant. The site with strongest attachment strength differed among occasions: Nqutheni on occasion 1 and Ocean on occasion 2 with no differences between sites on occasion 3 when small mussels were compared among Mthini, Rhini, Ocean and Nqutheni. Thus, there was no clear relationship between attachment strength and rehabilitation success.

In contrast to growth, there were no differences in CI among sites on occasion 1. The differences in CI on occasion 2 depended on the site. According to the MRP, Nqutheni is known as the best site for rehabilitation followed by Rhini. On occasion 2, Nqutheni and Rhini had better CI than Mthini and Lwandlana (the worst sites for rehabilitation), and on occasion 3, Nqutheni had better CI than the other sites, so that the suitability of a site for rehabilitation seems to be strongly reflected in the CI of deployed mussels. It was also noted that whenever there were differences in CI between size classes, large mussels had better CI than small mussels. Those results were different for 1-2cm and 3-4cm at Riet River where small mussel undoubtedly had better CI.

This study revealed that there were higher numbers of recruits 1 (recruits into adult byssus) at Nqutheni than any other sites. This was expected as Nqutheni is the best site for rehabilitation (according to the MRP). At Nqutheni mussels were depleted by poachers in 2010, but in 2011 Nqutheni underwent rapid natural recovery. In March 2011 at Nqutheni, the entire area was covered by ~2-3cm mussels (pers. obs.). This study showed that at both successfully and unsuccessfully rehabilitated shores there were equal numbers of settlers, even at Hlungulwana, the worst site for rehabilitation. At Hlungulwana mussels were washed away just after removal of pipes, this happened to both the MRP and in this study. Out of 60 experimentally attached mussel patches, only two small meshed patches remained attached a month after removal of pipes at Hlungulwana. The number of settlers varied with occasion. Very interestingly, settlers and recruits did not consistently show the same patterns. This might provide one of the explanations about differences in rehabilitation success. Nqutheni had highest numbers of recruits onto artificial substrata and the highest numbers of mussels recruited into byssus threads of adults. The fact that there were no differences in number of settlers, recruits 2 (large settlers) and recruits 1 (into mussel beds) between successfully and unsuccessful rehabilitated sites suggests that adult mussels are required for successful rehabilitation of denuded shores. As mussel denuded shores are covered by coralline algae (Dye *et al.* 1997), mussel larvae must initially settle onto algae. Settlers and recruits might migrate (Bayne 1964; Eyster & Pechnik 1987) or die if there is no suitable substratum (Bayne 1965), in this case adult mussels (Lasiak & Barnard 1995; Erlandsson *et al.* 2011). As mesh improved attachment of small mussels almost at all sites, both successful and unsuccessful, it proves to be the best method to attach adult mussels on denuded shores, providing suitable substratum for settlers and recruits. In this study it was difficult to agree that Mthini was a bad site for rehabilitation (as found by the MRP) as there were no differences in survival of small meshed between Mthini and Ocean up to occasion 3. Also on occasion 2 there were no differences in survival of large meshed mussels among Mthini, Rhini and Nqutheni. Therefore it was not surprising to find similar attachment strength between Mthini and successful rehabilitated sites. From this study it seemed that rehabilitation is impossible at some sites, as at Hlungulwana, although the exact cause is not yet known. It can be concluded that mesh can be used to improve rehabilitation of denuded shores, and although large mussels can be attached better with a mesh, the use of small mussels can optimise rehabilitation.

Chapter 4

General discussion

Prior to the Marine Living Resource Act of 1998, fisheries management in South Africa did not address subsistence harvesting of shellfish and law enforcement was limited. For government to meet international standards there have been suggestions for the promotion of partnerships between authorities and local communities to promote sustainable harvesting practices (Dye and Dyantyi 2002), as in the case of the MRP in Coffee Bay.

In 2002 the MRP developed a method to reseed mussels and suggested that the reseeding of mussels as a community activity can create employment and attract both local and national visitors. It was suggested that through mussel reseeding a method of rehabilitation could be developed and research studies could be carried out. The method developed by Dye and Dyantyi (2002) has been used in Coffee Bay to rehabilitate overexploited shores. This has been successfully at some sites whilst not at others. The use of a mesh in chapter 3 showed that the reseeding at unsuccessful sites can be improved. The question is, what is the status of successfully rehabilitated sites now, and how would be it be if there were no monitors?

In 2009 there were 5 successfully rehabilitated sites (Rhini, Ocean, Macosana, Nqutheni and Siqikini) with mussel beds composed of ~6cm long mussels (pers. obs.). In 2011, at the beginning of the study in chapter 3 there were only two sites (Rhini and Siqikini) with large mussel beds and opened for mussels harvest, at the third site Nqutheni re-attached mussels were depleted by poachers but the site was exhibiting natural recovery with mussels ~3cm long. It is not known how Nqutheni is capable of fast natural recovery, but this is presumably linked to the large numbers of mussel recruits there (Chap. 3). Along the Transkei coast in general, including Coffee Bay, law enforcement is weak. Without monitors to watch the sites during spring tides there would be no mussels at rehabilitated sites in Coffee Bay. Macosana for example is only ~150 meters from the main road and houses. During 2011 all mussels that had been there in 2009 were poached at night (pers. obs.). Currently mussel populations at Macosana are in the same condition as those at unsuccessfully rehabilitated sites. In 2011 at Ocean, there were few mussel patches due to poaching, while in 2009 the site was covered by mussel beds. In 2011, Siqikini had large mussels, ~5-6cm in length. Thus there are still mussels at effectively monitored sites.

At each successfully rehabilitated site there should be monitors to watch and control the harvest, while during chapter 3 study I hired people to watch the unsuccessfully rehabilitated sites for the duration of the study. The MRP was funded by the Department of Environmental Affairs and Tourism (DEAT) to pay mussel monitors. In 2009 the contract between MRP and DEAT expired and as result some MRP staff, including some monitors, stopped working for MRP. Therefore sites that had been successfully rehabilitated were not properly monitored. That led to the degradation of mussel beds between 2009 and 2011 at some of the sites that had been successfully rehabilitated (Macosana, Ocean and Nqutheni), while others that were still monitored remained in good condition (Rhini and Siqikini). This information is important because it shows that even if the two methods can be used successful to rehabilitate denuded shores, without proper management of mussels, law enforcement and compliance, the restoration of mussel beds in Transkei and their sustainable use can never be achieved. As mussels play an important role, nutritionally (Branch & Monero 1994) and economically, in Transkei special attention to the management of mussels is required.

The abundance of *P. perna* varies from region to region around the coast of the country (van Erkom Schurink & Griffiths 1990). Therefore the standardized bag limits defined by the Department of Environmental Affairs (DEA) may be inappropriate in areas where the carrying capacity and recruitment rates are too low to sustain the standard bag limits. Also the number of people dependant on these natural resources varies from region to region so that regional differences in levels of exploitation should be incorporated into management plans (McQuaid and Payne 1998). Results from the MRP showed that management of mussels *P.perna* should be site specific, depending on the abundance and biomass of mussels and the density of human populations in the region of concern. Dye and Dyantyi (2002) suggested that access may be controlled by introducing rotational cropping of mussels or protected sites which could act as exporters of recruits. Under the current management system that would be difficult and expensive, since stock assessment would need to be monitored regularly. The number of collected mussels should be linked to the percentage cover in the area. Too, without reducing or shifting the need and focus on mussels along the Transkei coast there will be pressure on *P. perna* and marine natural resources. In order to manage *P. perna* species along the Transkei coast, management decisions should be based on social aspects rather than technical or generalized national standards. The only management technique which can be used to manage mussels in the region is Community Based Natural Resource Management (CBNRM).

Muehling-Hofmann (2007) suggested that the devolution of resource management via a system of community-based marine resource management (CBMRM) may have much to contribute to small scale fisheries management worldwide. CBNRM focuses more on resource use and the human community than the resources. It is about the management of human activities in relation to resources (Jentoft 1998). In order for CBNRM to be effective, the root causes of exploitation need to be determined as was discussed in chapter 1.

A holistic approach, involvement of different stake holders such as the Department of Agriculture, social development organizations, universities and NGO's is required (Muehling-Hofmann 2007) along the Transkei coast. For example universities and NGO's can help in environmental education, while the agricultural sector can play an important role in reducing the focus on mussels by training local people and establishing community gardens as alternative sources of food. Local communities need to be taught how mussels produce and settle. For example an old female of ~60 years of age at Kentani once reported that mussel beds should be cleared yearly to avoid layering of previous year allowing space for the new generation. She argued that layering of new and old mussels causes all mussels to be vulnerable to dislodgment and the quality of flesh reduces. This shows that mussel harvesters need to be taught about mussel, their reproduction, growth and development. Her argument might be partially correct as Griffiths and Hockey (1987) recorded that recruitment and high growth rates dislodge large individuals from the substratum, largely through competition for space. In dense mussel clumps, individuals are attached to the substratum by their byssus threads and byssus threads of others (Bertness & Grosholz 1985; Carrington 2002). That provides additional advantages of attachment over solitary mussels (Bertness & Grosholz 1985). Mussels are affected by the density of individuals in the patch; solitary mussels experience more hydrodynamic force, have higher tenacity and have a higher probability of dislodgment than mussels within a bed (Bell & Gosline 1997; Nicastro *et al.* 2010). As a result, dislodged mussels leave adjacent mussels vulnerable to dislodgement (Witman & Suchanek 1984). At the same time, tightly packed mussel beds provide better physical support to resist hydrodynamic forces (Denny 1987). In addition, Alvarado and Castilla (1996) suggested that the complexity of mussel beds increases retention of recruits. That was confirmed by Dye and Dyantyi (2002). It is known that adult mussels are needed for successful recruitment (Lasiak & Barnard 1995) and indeed, in this study recruits were found attached to the byssus threads of adult mussels.

From the Mussel Rehabilitation Project it has been shown that management of subsistence fisheries should focus on sustainability rather than on strategies to reduce fishing effort, restricting access and reducing the limit. In Coffee Bay the MRP together with Walter Sisulu University attempted an approach close to CBNRM, but mussel monitors and community garden workers were paid about $92.34 (R800) per month. That is where the MPR approach differed from CBNRM where local communities take responsibility of their own natural resources. As a result of paying monitors, when the MRP ran out of funds, rehabilitated sites and community gardens were abandoned. The Coffee Bay community and MRP workers viewed the project as job opportunities rather than as a management tool for community's own needs and natural resources. In order for CBNRM to be successful, communities need to be empowered to take responsibility of their resources for their own benefit. According to Muehlig-Hofmann (2007) traditional authority and community leadership are key factors in CBNRM. The question is: Was or is traditional authority a key factor in MRP in Coffee Bay? The answer is NO. Walter Sisulu

University (WSU) was the authority or key factor in the MRP. That led the MRP and Coffee Bay community to rely on WSU.

From this study it can be concluded that including mesh improves the chances of rehabilitation, but it is not the only factor which affects rehabilitation. In chapter 3, the better success of small (3-4cm) meshed mussels compared to large meshed animals (5-6cm) was probably associated with differences between size classes in their energy allocation. Although the effect of wave force was not clear among sites, its effects differed between size classes. On top of energy used for reproduction by large mussels, increased surface area in large mussels leads to higher resistance to wave force which also requires more energy. As result wave force might affect different size classes differently at one site. Wave force is associated with energy expenditure, therefore all the energy associated processes such as growth, condition index, attachment strength might be affected differently. This shows that there are several factors affecting mussel re-attachment, the use of the mesh provides mussels with second chance to re-attach thus creating suitable habitat for settlers and recruits.

It is not exactly known why some sites are better than the others but it seems that, if small (3-4cm) mussels can be attached, successful rehabilitation can be achieved. That is supported by the findings in Chapter 3 that showed that there were no differences in numbers of settlers between successfully and unsuccessful rehabilitated sites, but that there were differences in the numbers of survival of re-attached mussels. At successfully rehabilitated sites, mussels attached better than at unsuccessfully rehabilitated sites, but mesh improved attachment at both site types. Also juvenile mussels improved rehabilitation, there were larger number of re-attached small mussels than larger mussels, although larger mussels had stronger attachment. Although it is possible to identify the factors that improve reseeding of mussels (use of mesh, use of small mussels, choice of sites with high recruitment rates), successful long-term rehabilitation requires appropriate management.

References:

ACKERMAN, J.D. & NISHIZAKI, M.T. 2004. The effect of velocity on the suspension feeding and growth of the marine mussels *Mytilus trossulus* and *M. californianus*: implications for niche separation. *Journal of Marine Systems.* **49:**195–207.

ADDESSI, L. 1994. Human disturbance and long-term changes on a rocky intertidal community. *Ecological Applications*. **4:** 786-797.

ALFARO, A. C. 2006. Byssal attachment of juvenile mussels, *Perna canaliculus*, affected by water motion and air bubbles. *Aquaculture*. **255:** 357-361.

ALVARADO, J.L. & CASTILLA, J.C.1996. Tridimensional matrices of mussels *Perumytilus purpuratus* on intertidal platforms with varying wave forces in central Chile. *Marine Ecology Progress Series.* **133:**135–141. ANDREW, M. 1992. A geographical study of agricultural change since the 1930s in Shixini location, Gatyana District, Transkei. M.A. Thesis, Rhodes University.

ANDREW, M. 1992. A geographical study of agricultural change since the 1930s in Shixini location, Gatyana District, Transkei. M.A. Thesis, Rhodes University.

BAYNE, B. L. 1964. Primary and Secondary settlement in *Mytilus edulis.* L. (Mollusca). *Journal of Animal Ecology*. **33:** 513-524.

BAYNE, B. L., 1965. Growth and the delay of metamorphosis of the larvae of Myrilus *edulis* L. *Ophelia.* **2**: l-47.

BAYNE, B. L. 1993. Feeding physiology of bivalves: time-dependence and compensation for changes in food availability. In:. *Bivalve filter feeders in estuarine and coastal ecosystem processes*, (ed) DAME, R. F. NATO ASI Series. G 33: 1-24. Springer-Verlag, German.

BELL, E. C., GOSLINE, J. M. 1997. Strategies for life in flow: tenacity, morphometry, and probability of dislodgment of two *Mytilus* species. *Marine Ecology Progress Series.* **159:**197–208.

BELL, E. C. &. DENNY, M. W. 1994. Quantifying ‘‘wave exposure’’: a simple device for recording maximum velocity and results of its use at several field sites. *Journal of Experimental Marine Biology and Ecology*. **181:** 9–29.

BERTNESS, M. D. & GROSHOLZ, E. 1985. Population dynamics of the ribbed mussel, Geukensia demissa: The costs and benefits of an aggregated distribution. *Oecologia*. **67.** 192-204.

BERRY, P. F. 1978. Reproduction, growth and production in the mussel *Perna perna* (Linnaeus) on the east coast of South Africa. *Oceanographic Research Institute*. **48:** 1-28.

BLANCHETE, C. A. 1997. Size and Survival of Intertidal Plants in Response to Wave Action: A Case Study with Fucus Gardneri. *Ecology*. **78:** 1563-1578.

BOSTFORD, L. W., CASTILLA, J. C. & PETERSON, H.C. 1997. The management of fisheries and marine ecosystems. *Science.* **277**:509-514.

BOWETT, J. & HAY, P. 2009. Whaling and its controversies: Examining the attitudes of Japan's youth. *Marine Policy*. **33**: 775-783.

BOWNES, S., BARKER, N. P. & McQUAID, C.D. 2008. Morphological identification of primary settlers and post-larvae of three mussel species from the coast of South Africa. *African Journal of Marine Science.* **30:** 233–240.

BRANCH, G. M. & MONERO, C.A. 1994. Intertidal and Subtidal Grazers. In : Rocky shores: Exploitation in Chile and South Africa. *Ecological studies*. **103:** 75-100.

BRANCH, G. M. & STEFFANI, C. N. 2004. Can we predict the effects of alien species? A case-history of the invasion of South Africa by *Mytilus galloprovincialis* (Lamarck). *Journal of Experimental Marine Biology & Ecology*. **300:**189–215.

BUNDY, C. 1979. The rise and fall of the South African peasantry. Cape Town: David Philip. London, pp 132.

BUSTAMENTE, R.H., BRANCH, G.M. & EEKHOUT, S. 1997. The influence of physical factors on the distribution and zonation pattern of South African rocky-shore communities. *South African Journal of Marine Science*. **18**: 119-136.

CARO, A.U., ESCOBAR, J., BOZINOVIC, F., NAVARRETE, S.A. & CASTILLA, J.C. 2008. Phenotypic variability in byssus thread production of intertidal mussels induced by predators with different feeding strategies. *Marine Ecology Progress Series*. **372:** 127–134.

CARRINGTON, E. 2002. Seasonal variation in the attachment strength of blue mussels: Causes and consequences. *Limnology and Oceanography*. **47:**1723-1733.

CARRINGTON, E., MOESER, G. M., THOMPSON. S. B, COUTTS, L. C. & CRAIG, C. A. 2008. Mussel attachment on rocky shores: the effect of flow on byssus production. *Integrative and Comparative Biology*. **48:** 801–807.

CASTILLA, J. C. 1999. Coastal marine communities: Trends and perspectives from human-exclusion experiments. *Trends in Ecology & Evolution*. **14:** 280-283.

CHEUNG, S.G, LUK, K.C, SHIN, P.K.S. 2006. Predator-labeling effect on byssus production in marine mussels *Perna viridis* (L.) and *Brachidontes variabilis* (Krauss). *Journal of Chemical Ecology*. **32:**1501–1512.

COOKE, S.J. & COWX, I.G., 2004. The role of recreational fishing in global fish crises. *Bioscienc*e. **54:** 857–859.

COOKE, S. J. & COWX, I. G. 2006. Contrasting recreational and commercial fishing: Searching for common issues to promote unified conservation of fisheries resources and aquatic environments. *Biological Conserva*tion. **128:** 93-108.

CONNELL, J. H. 1985. The consequences of variation in initial settlement vs post-settlement mortality in rocky intertidal communities. *Journal of Experimental Biology and Ecology*. **93:**11–45.

COWX. 2002. Recreational fisheries. In: Handbook of Fish Biology and Fisheries., P.B.J. Hart & J.D. Reynolds, pp.367-390. Blackwell Science, United Kingdom.

CRONIN, M. 1982. Radiocarbon dates for the early Iron Age in Transkei. *South African Journal of Science*. **78:** 38-29.

DAHLHOFF, E. P. & MENGE, B. A. 1996. Influence of phytoplankton concentration and wave exposure on the ecophysiology of *Mytilus californianus. Marine Ecology Progress Series*. **144:** 97-107.

DAVENPORT, J. & CHEN, X. 1987. A comparison of methods for the assessment of condition in the mussel (*Mytilus edullis* L.). *Journal of Molluscan Study*. **53:** 293-297.

DEMING, T. J. 1999. Mussel byssus and biomolecular materials. *Current Opinion in Chemical Biology*. **3:** 100-105.

DENNY, M. W. 1987. Lift as a mechanism of patch initiation in mussel beds. *Journal of Experimental Marine Biology and Ecology*. **113:** 231–245.

DENNY, M. W., MILLER, I. L. P, STOKES, M. D., HUNT, L. J. H. & HELMUTH, B. S. T. 2003. Extreme water velocities: Topographical amplification of wave-induced flow in the surf zone of rocky shores. *Limnology Oceanography*. **48:** 1-8.

de SÁ, S. F., NALESSO, R.C. & PARESQUE, K. 2007. Fouling organisms on *Perna perna* mussels: is it worth removing them*? Brazilian Journal of Oceanography*. **55:** 155-161.

DICKIE, L. M., BOUDREAU, P. R. & FREEMAN, K. R. 1984. Influences of Stock and Site on Growth and Mortality in the Blue Mussel (*Mytilus edulis*). *Canadian Journal of Fisheries and Aquatic Science.* **41:** 134-140.

DYE, A.H. 1992. Experimental studies of succession and stability in rocky intertidal communities subject to artisanal shellfish gathering. *Netherlands Journal of Sea Research.* **30:** 209-217.

DYE, A. H., LASIAK, T. A. & GABULA, S.1997. Recovery and recruitment of the brown mussel, Perna perna (L.), in Transkei: implications for management. *South African Journal of Zoology.* **32:** 118-123.

DYE, A. H., SCHLEYER, M. H., LAMBERT, G, & LASIAK, T. A. 1994. Intertidal and subtidal filter-feeders in Southern Africa. In: Ecological studies—rocky shores: exploitation in Chile and South Africa. **103:** 57–73.

DYE, A. H., LASIAK, T. A. & GABULA, S.1997. Recovery and recruitment of the brown mussel, Perna perna (L.), in Transkei: implications for management. *South African Journal of Zoology.* **32:** 118-123.

DYE, A. H. & DYANTYI, N. 2002. Reseeding of Mussels on denuded rocky shores:

Preliminary studies with the Brown Mussel, *Perna perna. South African Journal of Marine Science*. **24**: 65-70.

ERLANDSSON, J. & McQUAID. C.D. 2004. Spatial structure of recruitment in the mussel *Perna perna* at local scales: effects of adults, algae and recruit size. *Marine Ecology Progress Series*. **267**: 173–185.

ERLANDSSON, J., MCQUAID, C. D. & KOSTYLEV, V. E. 2005. Contrasting spatial heterogeneity of sessile organisms within mussel (*Perna perna* L.) beds in relation to topographic variability. *Journal of Experimental Marine Biology and Ecology*. **314:** 79-97.

ERLANDSSON, J., MCQUAID, C.D. & STANCZAK, S. 2011. Recruit/algal interaction prevents recovery of overexploited mussel beds: Indirect evidence that post-settlement mortality structures mussel populations. *Estuarine, Coastal and Shelf Science.* **92**:132-139.

EYSTER, L. S. & PECHENIK, J. A. 1987. Attachment of *Mytilus edulis* L. larvae on algal and byssal filaments is enhanced by water agitation. *Journal of Experimental Marine Biology and Ecology*. **114:** 99-110.

FAO, 2005. Increasing the contribution of small-scale fisheries to poverty alleviation and food security. FAO Technical Guidelines for Responsible Fisheries. No. 10. Rome, FAO, pp11.

FAO, 2012. The state of world fisheries and aquaculture. Rome, FAO, pp 11.

FARRUGIO, H., OLIVER, P. & BIAGI, F., 1993. An overview of the history, knowledge, recent and future research trends in Mediterranean fisheries. *Scientia Marina.* **57:** 105–119.

FAY, D. 2009. Land Tenure, Land Use, and Land Reform at Dwesa–Cwebe, South Africa: Local Transformations and the Limits of the State. *World Development*. **37**: 1424–1433.

GANACHAUD, A., VEGA, A., RODIER, M., DUPOUY, C., MAES, C., MARCHESIELLO, P. ELDIN, G., RIDGWAY, K., LE BORGNE, R. 2010. Observed impact of upwelling events on water properties and biological activity off the southwest coast of New Caledonia. *Marine Pollution Bulletin.* **61**: 449-464.

GRIFFITHS, R. J. 1980. Filtration, Respiration and Assimilation in the Black Mussel *Choromytilus meridionalis. Marine Ecology Progress Series*. **3:** 63-70.

GRIFFITHS, C. L. & SEIDERER, J. L. 1980. Rock-lobsters and mussels-limitations and preferences in a predator-prey interaction. *Journal of Experimental Marine Biology and Ecology*. **44:** 95-109.

GRIFFlTHS C. L. & HOCKEY, P. A. R.1987. A model describing the interactive roles of predation, competition and tidal elevation in structuring mussel populations. In: *The Benguela and Comparable Ecosystems. South African Journal of Marine Science.* **5:** 547-556.

GROTIUS, H. 1901. The general rights of things. In : The right of war and peace. 2nd edition. pp. 85-102. M. Walter publisher, New York & London.

HARDIN, G. 1976. Fishing the commons. *Natural History*. **857**: 9-15.

HARRIS, J. M., BRANCH, G. M. , ELLIOTT, B. L., CURRIE, B., DYE, A., MCQUAID, C. D., TOMALIN, B. J. & VELASQUEZ, C. 1998. Spatial and temporal variability in recruitment of intertidal mussels around the coast of southern Africa. *South African Journal of Zoology*. **33:**1–11.

HAUCK, M. & SWEIJD, N. A. 1999. A case study of abalone poaching in South Africa and its impact on fisheries management. *Journal of Marine Science.* **56:** 1024–1032.

HAWKINS, A. J. S. & B. L. BAYNE, B. L. 1985. Seasonal variation in the relative utilization of carbon and nitrogen by the mussel *Mytilus edulis:*budgets, conversion efficiencies and maintenance requirements. *Marine Ecology Progress Series*. **25:** 181-188.

HILBORN, R., BRANCH, T.A., ERNST, W., MAGNUSSON, A., MINTE-VERA, C.A., SCHEUERELL, M.D., VALERO, J.L. 2003. State of the world's fisheries. *Annual Review of Environment and Resources*. **28**: 359–399.

HOCKEY, P. A. R., BOSMAN, A. L. 1986. Man as an intertidal predator in Transkei: disturbance, community convergence and management of a natural food resource. Oikos. **46**: 3-14.

HOCKEY, P. A. R., BOSMAN, A. L. & SIEGFRIED, W. R. 1988. Patterns and correlates of shellfish exploitation by coastal people in the Transkei: An enigma of protein production. *Journal of Applied Ecology*. **25:** 353-363.

HUNT, H. L. & SCHEIBLING. R.E. 2001. Predicting wave dislodgment of mussels: variation in attachment strength with body size, habitat, and season. *Marine Ecology Progress Series*. **213:** 157–164.

JENKINS, S. R., A°BERG, P., CERVIN, G., COLEMAN, R. A., DELANY, J., DELLA SANTINA, P., HAWKINS, S. J., LACROIX , A., MYERS, A. A., LINDEGARTH, M., POWER , A.M., ROBERTS, M. F., & HARTNOLL, R.G. 2000. Spatial and temporal variation in settlement and recruitment of the intertidal barnacle *Semibalanus balanoides*

(L.) (Crustacea: Cirripedia) over a European scale. *Journal of Experimental Marine Biology and Ecology*. **243:** 209–225.

JENTOFT, S. 1998. Commons in a cold climate, coastal fisheries and reindeer pastoralism in north Norway: The Co-Management Approach. Man and the Biosphere Series. Paris, France: UNESCO.

KAMERMANS, P., BLANKENDAAL, M. & PERDON, J. 2009. Predation of shore crabs (*Carcinus maenas* (L.) and starfish (*Asterias rubens* L.) on blue mussel (*Mytilus edulis* L.) seed from wild sources and spat collectors. *Aquaculture*. **290:** 256-262.

KAEHLER, S. 1999. Incidence and distribution of phototrophic shell-degrading endoliths of the brown mussel *Perna perna*. *Marine Biology*. **135:** 505-514.

KENT, G. 1997. Fisheries, food security, and the poor. *Food Policy*. **22:** 303-404.

KEOUGH, M. J. & DOWNES, B. J. 1982. Recruitment of Marine Invertebrates: the Role of Active Larval Choices and Early Mortality. *Oecologia*. **54:** 348-352.

KEOUGH, M. J., QUINN, G.P. & KING, A. 1993. Correlations between human collecting and intertidal mollusc populations. *Conservation Biology*. **7:** 378-390.

KINGSFORD, M. J., UNDERWOOD, A. J. & KENNELLY, S. J. 1991. Humans as predators on rocky reefs in New South Wales, Australia. *Marine Ecology Progress Series*. **72**:1-14.

KOOIJMAN, S. A. L. M. 2000. Dynamic Energy and Mass Budgets in Biological Systems. 2nd edition. Press Syndicate of the University of Cambridge. Cambridge.

LASIAK, T. & DYE, A. 1989. The Ecology of the Brown Mussel *Perna perna* in Transkei, Southern Africa: Implications for Management of a Food Resource. *Biological Conservation*. **47:** 245-257.

LASIAK, T. 1991. Is there evidence of over-exploitation of mussel stocks on the Transkei coast? *South African Journal of Marine Science.* **10**: 299-302.

LASIAK, A. & BARNARD, T. C. E. 1995. Recruitment of the brown mussel *Perna perna* onto natural substrata: a refutation of the primary/ secondary settlement hypothesis. *Marine Ecology Progress Series.* **120:** 147-153.

LASIAK, T. & DYE, A. 1989. The Ecology of the Brown Mussel Perna perna in Transkei, Southern Africa: Implications for Management of a Food Resource. *Biological Conservation.* **47:** 245-257.

LASIAK, T.A. & FIELD, J.G. 1995. Community-level attributes of exploited and non-exploited rocky infratidal macrofaunal assemblages in Transkei. *Journal of Experimental Marine Biology and Ecology*. **185:** 33-53.

LAMBERT, G. & STEINKE, T.D., 1986. Effects of destroying juxtaposed mussel-dominated and coralline algal communities at Umdoni Park, Natal Coast, South Africa. *South African Journal of Marine Science.* **4**: 203-217.

LEVIN, S. A. 1992. The problem of pattern and scale in ecology. *Ecology*. **73:**1943–1967.

Marine Recreational Activity Information Brochure 2009/2010. Department of Environmental Affairs, South Africa.

MARINESQUE, S., KAPLAN, D. M. & RODWELL, D. L. 2012. Global implementation of marine protected areas: Is the developing world being left behind? *Marine Policy*. **36:** 727-737.

MARSHALL, D. M. & KEOUGH, M. J. 2003. Variation in the dispersal potential of non-feeding invertebrate larvae: the desperate larva hypothesis and larval size. *Marine Ecology Progress Series*. **255:** 145-153.

MATIĆ-SKOKO, S., STAGLIČIĆ, N. PALLAORO, A., KRALJEVIĆ, M. DULČIĆ, J. TUTMAN, P. DRAGIČEVIĆ,B. 2010. The effectiveness of conventional management in the Mediterranean type artisanal fisheries. *Estuarine, Coastal and Shelf Science.* **91**: 314-324.

McCONNELL, K. E. & SUTINEN, J. G. 1979. Bioeconomic models of marine recreational fishing. *Journal of Environmental Economics and Manegement.* **6:** 127-139.

McGRATH, D. & GOSLING, E. M. 1988. Evidence for the direct settlement of *Mytilus edulis* larvae on adult mussel beds. *Marine Ecology Progress Series*. **47:** 103-106.

McQUAID, C. D., BRANCH, G. D. & CROWE, A. A. 1985. Biotic and abiotic influences on rocky intertidal biomas and richness in the south Benguela region. *South African Journal of Zoology*. **20**: 115-122.

McQUAID, C.D. & LINDSAY, T. L. 2000. Effect of wave exposure on growth and mortality rates of the mussel *Perna perna*: bottom-up regulation of intertidal populations. *Marine Ecology Progress Series*. **206**: 147–154.

McQUAID, C.D. & PAYNE, A. I. L. 1998. Regionalism in marine biology: the convergence of ecology, economics and politics in South Africa. *South African Journal of Science*. 94: 433-436.

MILLER, R. L. & ETTER, R. J. 2008. Shading facilitates sessile invertebrate dominance in the rocky subtidal Gulf of Maine. *Ecology*. **89:** 452–462.

MILLSTEIN, J. & O'CLAIR, C. E. 2001. Comparison of age-length and growth-increment general growth models of the Schnute type in the Pacific Blue Mussel, *Mytilus trossulus* Gould. *Journal of Experimental Marine Biology and Ecology*. **262:** 155–176

MOESER, G. M. & CARRINGTON, E. 2006.Seasonal variation in mussel byssal thread mechanics. *Journal of Experimental Biology*. **209:** 1996-2003.

MORAN, A.L. & EMLET, R.B. 2001. Offspring size and performance in variable environments: field studies on a marine snail. *Ecology*. **82:** 1597–1612.

MUEHLIG-HOFMANN, A. 2007. Traditional authority and community leadership: Key factors in community-based marine resource management and conservation. *SPC Traditional Marine Resource Management and Knowledge Information Bulletin.* **21**:33-44.

NARVÁEZ, M., FREITES, L., MENDOZA, J. & GUEVARA. M. 2009. Influence of spat origin and environmental parameters on biochemical composition and biometry of the brown mussel *Perna perna* (Linneus 1758), under culture conditions. *Revista de Biología Marina y Oceanografía*. **44**: 343-355.

NARAIN, U., GUPTA, S. & van 't VELD, K. 2008. Poverty and resource dependence in rural India. *Ecological Economics*. **66**: 161-176.

NICASTRO, K. R., ZARDI, G. I. & McQUAID, C. D. 2010. Differential reproductive investment, attachment strength and mortality of invasive and indigenous mussels across heterogeneous environments. *Biological Invasions*. **12:** 2165–2177.

O'DONNELL, M. J. & DENNY, M.W. 2008. Hydrodynamic forces and surface topography: Centimeter-scale spatial variation in wave forces. *Limnology and Oceanography*. **53**: 579–588.

OKAMURA, B. 1986. Group living and the effects of spatial position in aggregations of *Mytilus edulis*. *Oecologia*. **69:** 341-347.

PALUMBI, S. R. 1984. Measuring intertidal wave forces. *Journal of Experimental Marine Biology and Ecology***. 81**:171-179.

PAULY, D., CHRISTENSEN, V., GUÉNETTE, S., PITCHER, T. J., SUMALIA, U.R., WALTERS, R. W., & ZELLER, D. 2002. Towards sustainability in world fisheries. *Nature*. **418**: 689-695.

PÉREZ-CAMACHO A, LABARTA, U. & BEIRAS. R. 1995. Growth of mussels (*Mytilus edulis galloprovincialis*) on cultivation rafts: influence of seed source, cultivation site and phytoplankton availability. *Aquaculture*. **38:** 349-362.

PETRAITIS, P. S. 1995. The Role of Growth in Maintaining Spatial Dominance by Mussels (*Mytilus Edulis*) . *Ecology*. **76:** 1337-1346.

PHILLIPS, N. E. 2002. Effects of nutrition-mediated larval condition on juvenile performance in a marine mussel. *Ecology*. **83**: 2562-2574.

PINEDA, J., STARCZAK, V., STUECKLE, T.A. 2006. Timing of successful settlement: demonstration of a recruitment window in the barnacle *Semibalanus balanoides*. *Marine Ecology Progress Series*. **320**: 233–237.

PORRI, F., McQUAID. C.D. & RADLOFF. S. 2006. Temporal scales of variation in settlement and recruitment of the mussel Perna perna (Linnaeus, 1758). *Journal of Experimental Marine Biology and Ecology*. **332**:178– 187.

PORRI, F., McQUAID, C.D. & LAWRIE, S. M. & ANTROBUS, S. J. 2008. Fine-scale spatial and temporal variation in settlement of the intertidal mussel *Perna perna* indicates differential hydrodynamic delivery of larvae to the shore. *Journal of Experimental Marine Biology and Ecology*. **367:** 213-218.

POST, J.R., SULLIVAN, M., COX, S., LESTER, N.P.,WALTERS, C.J., PARKINSON, E.A., PAUL, A.J., JACKSON, L. & SHUTER, B.J. 2002. Canada's recreational fishery: The invisible collapse? *Fisheries*. **27:** 6–17.

PROWSE, T. A. A. & A. J. PILE. 2005. Phenotypic homogeneity of two intertidal snails across a wave exposure gradient in South Australia. *Marine Biology Research*. **1**: 176-185.

RAUBENHEIMER, D. & COOK, P. 1990. Effects of exposure to wave action on allocation of resources to shell and meat growth by the subtidal mussel, *Mytilus galloprovincialis*: *Journal Shellfish Research.* **9**:87–93.

REN, J.S. & ROSS, A.H. 2005. Environmental influence on mussel growth: A dynamic energy budget model and its application to the greenshell mussel *Perna canaliculus. Ecological Modelling.***189**: 347–362.

REYERS, B. & GINSBURG, E. A. 2005. Wild Coast Conservation and Sustainable Development Project: Conservation Assessment of the Wild Coast. CSIR Report No. ENV-S-C-2005-022.

RIUS, M., KAEHLER, S. & McQUAID. C. D. 2006. The relationship between human exploitation pressure and condition of mussel populations along the south coast of South Africa. *South African Journal of Science*. **102:** 130-136.

RUIS, M. & CABRAL, N. 2004. Human harvesting of *Mytilus galloprovincialis* Lamark, 1819, on the central coast of Portugal. *Scientia Marina*. **68**: 545-551.

RUSS, G.R. & ZELLER, D.C. 2003. From Mare Liberum to Mare Reservarum. *Marine policy*. **27**: 75-78.

ROBINSON, T.B., GRIFFITHS, C.L., McQUAID, C.D. & RIUS, M. 2005. Marine alien species of South Africa – status and impacts. *African Journal of Marine Science.* **27:** 297-306.

SAIER, B. 2001. Direct and indirect effects of seastars Asterias rubens on mussel beds (Mytilus edulis) in the Wadden Sea. *Journal of Sea Research*. 46: 29-42.

SEED, R. 1969. The ecology of *Mytilus edulis* L. (Lamellibranchiata) on Exposed Rocky Shores. II. Growth and Mortality. *Oecologia.* **3:** 317-350.

SEED, R., RICHARDSON, C.A., 1990. *Mytilus* growth and its environmental responsiveness. In: Neurobiology of *Mytilus edulis,* G.B. Stefano, pp. 1–37. Manchester University Press, Manchester.

SEED, R. & SUCHANEK, T.H. 1992. Population and community ecology of *Mytilus*. In: *The mussel Mytilus: ecology, physiology, genetics and culture*. *Developments in Aquaculture and Fisheries Science*, GOSLING, E. Elsevier, 87-170.

SEIGFRIED, W.R., HOCKEY, P.A. & CROWE, A. A. 1985. Exploitation and conservation of brown mussel stocks by coastal people of Transkei. *Environmental Conservation.* **12:** 303-307.

SIEGFRIED, W. R., HOCKEY, P. A. R. & BRANCH, G.M. 1994. The Exploitation of intertidal and subtidal biotic resources of Rrocky shores in Chile and South Africa. In: Rocky Shores Exploitation in Chile and South Africa. *Ecogical Studies:* **103***:*1-15.

SPRUNG, M. 1984. Physiological energetic of mussel larvae (*Mytilus edulis*). I. Shell growth and biomas. *Marine Ecology Progress Series.* **17**: 283-293.

STEFFANI, C. N. & BRANCH, M. G. 2003a. Spatial comparisons of populations of an indigenous limpet *Scutellastra argenvillei* and alien mussel *Mytilus galloprovincialis* along a gradient of wave energy. *African Journal of Marine Science.* **25**: 195-212.

STEFFANI, C. N. & BRANCH, G. M. 2003b. Growth rate, condition, and shell shape of *Mytilus galloprovincialis*: responses to wave exposure. *Marine Ecology Progress Series* **246**: 197-209.

STEFFANI, C. N. & BRANCH, M. G. 2003c. Temporal changes in an interaction between an indigenous limpet *Scutellastra argenvillei* and an alien mussel *Mytilus galloprovincialis*: effects of wave exposure. *African Journal of Marine Science* **25**: 213-229.

SOMMER, U., MEUSEL, B. & STIELAU, C. 1999. An experimental analysis of the importance of body-size in the seastar-mussel predator-prey relationship. **20:** 81-86.

SOWMAN, M. 2006. Subsistence and small scale fisheries in South Africa: A ten-year. *Marine Policy*. **30:** 60-73.

SOUSA, W.P. 1979. Experimental Investigations of Disturbance and Ecological Succession in a Rocky Intertidal Algal Community. *Ecological Monographs.* **49:** 227-254.

TIMMERMANS, H. 2004. Rural livelihoods at Dwesa/Cwebe: Poverty, development and natural resource use on the wild coast, South Africa. M.Sc. Thesis, Grahamstown: Rhodes University.

TROELL, M., ROBERTSON-ANDERSSON, D., ANDERSON. R. J., BOLTON, J.J., MANEVELDT, G., HALLING.C. & PROBYN. T. 2006. Abalone farming in South Africa: An overview with perspectives on kelp resources, abalone feed, potential for on-farm seaweed production and socio-economic importance. *Aquaculture.* **257:** 266–281.

UNDERWOOD, A. J. & FAIRWEATHER, P. G. 1989. Supply side ecology and benthic marine assemblages. *Trends in Ecology and Evolution.* **4**:16–21.

UNDERWOOD, A. J. & KENNELLY, S. J. 1990. Pilot Studies for Designs of Surveys of Human Disturbance of Intertidal Habitats in New South Wales. *Australian Journal of Marine and Freshwater Research* 41: 165-173.

UNDERWOOD, A.J. 1993. Exploitation of species on the rocky coast of New South Wales (Australia) and options for its management. *Ocean & Coastal Management.* **20:** 41-62.

UNDERWOOD A. J. & KEOUGH, M. J. 2001. Supply-side ecology—the nature and consequences of variations in recruitment of intertidal organisms. In: Bertness MD, Gaines SD, Hay ME (eds) Marine community ecology. Sinauer Associates, Sunderland, MA, p 183–200.

van ERKOM SCHURINK, C. & GRIFFITHS, C. L. 1990. Marine mussels of southern Africa - their distribution patterns, standing stocks, exploitation and culture. *Journal of Shellfish Research.* **9:** 75-85.

van ERKOM SCHURINK, C. & GRIFFITHS, C. L. 1993. Factors affecting relative rates of growth in four South African mussel species. *Aquaculture.* **109**: 257–273.

WATSON, R. PAULY, D. 2001. Systematic distortions in world fisheries catch trends. *Nature*. 414: 534-536.

WESTERBOM, M. & JATTU, S. 2006. Effects of wave exposure on the sublittoral distribution of blue mussels *Mytilus edulis* in a heterogeneous archipelago. *Marine Ecology Progress Series*. **306:** 191–200.

WITMAN, J. D, SUCHANEK, T. H. 1984. Mussels in flow: drag and dislodgement by epizoans. *Marine Ecology Progress Series.* **16:** 259–268.

World Summit on Sustainable Development Plan of Implementation. 2002. Johannesburg, South Africa.

YAPP, G. A. 1986. Aspects of population, recreation, and management of the Australian coastal zone. *Coastal Zone Management Journal*. **14:** 46-66.

YILDIZ, H., L, LOK, A., ACARLI, S., SERDAR, S. & KOSE, A. 2010. A Preliminary Survey on Settlement and Recruitment Patterns of Mediterranean Mussel (*Mytilus galloprovincialis*) in Dardanelles, Turkey. *The Journal of the Faculty of Veterinary Medicine. University of Kafkas.* **16:** S319-S321.

YOKO-ONO MAYA, U. 2007. Children's contribution to brown mussel *Perna perna* harvesting in Coffee Bay. Honours thesis, Walter Sisulu University, Mthatha, South Africa.

ZARDI, G. I, McQUAID, C. D. & NICASTRO, K. R, 2007. Balancing survival and reproduction: seasonality of wave action, attachment strength and reproductive output in indigenous *Perna perna* and invasive *Mytilus galloprovincialis* mussels. Marine Ecology Progress Series. **334:** 155–163.