The effects of mussel bed structure on the associated infauna in South Africa and the interaction between mussels and epibiotic barnacles

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Abstract

Mussels are important ecological engineers on intertidal rocks where they create habitat that contributes substantially to overall biodiversity. They provide secondary substratum for other free-living, infaunal or epifaunal organisms, and increase the surface area for settlement by densely packing together into complex multilayered beds. The introduction of the alien invasive mussel *Mytilus galloprovincialis* has extended the upper limit of mussels on the south coast of South Africa, potentially increasing habitat for associated fauna. The aim of this study was to describe the structure of mussel beds, the general biodiversity associated with multi- and monolayered mussel beds of indigenous *Perna perna* and alien *M. galloprovincialis*, and to determine the relationship between mussels and epibiotic barnacles. This was done to determine the community structure of associated macrofauna and the role of mussels as biological facilitators. Samples were collected in Plettenberg Bay, South Africa, where *M. galloprovincialis* dominates the high mussel zone and *P. perna* the low zone. Three 15 X 15 cm quadrats were scraped off the rock in the high and low zones, and in the mid zone where the two mussel species co-exist. The samples were collected on 3 occasions. In the laboratory mussel-size was measured and sediment trapped within the samples was separated through 75 µm, 1 mm and 5 mm mesh. The macrofauna was sorted from the 1 mm and 5 mm sieves and identified to species level where possible. The epibiotic relationship between mussels and barnacles was assessed by measuring the prevalence and intensity of barnacle infestation and the condition index of infested mussels. Multivariate analysis was used on the mean abundance data of the species for each treatment (Hierarchical clustering, multi-dimensional scaling, analysis of similarity and similarity of percentages) and ANOVA was used for most of the statistical analyses. Overall, the results showed that tidal height influences the species composition and abundance of associated fauna. While mussel bed layering influenced the accumulation of sediments; it had no significant effect on the associated fauna. Time of collection also had a strong effect. While there was an overlap of species among samples from January, May and March, the principal species contributing to similarity among the March samples were not found in the other two months. The outcomes of this study showed that low shore mussel beds not only supported a higher abundance and diversity of species, but were also the most structurally complex. Although the condition index of mussels did not correlate to the percentage cover of barnacle epibionts, it was also evident that low shore mussels had the highest prevalence. The levels of barnacle infestation (intensity) for each mussel species were highest where it was common and lowest where it was least abundant. This is viewed as a natural artefact of the distribution patterns of *P. perna* and *M. galloprovincialis* across the shore. Mussels are more efficient as facilitators on the low mussel zone than the high mussel zone possibly because they provide habitats that are more effective in protecting the associated macrofauna from the effects of competition and predation, than they are at eliminating the effects of physical stress on the high shore. Although mussels create less stressful habitats and protect organisms from the physical stress of the high shore, there are clear limitations in their ability to provide ideal habitats. The biological associations in an ecosystem can be made weak or strong depending on the external abiotic factors and the adaptability of the affected organisms.

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"For we are God's workmanship, created in Christ Jesus to do good works, which God prepared in advance for us to do." (Ephesians 2:10)

Amen

Declaration

This thesis is a presentation of the author's original research work. Wherever contributions of others are involved, every effort is made to indicate this clearly, with due reference to the literature, and acknowledgement of collaborative research and discussions. The work described in this thesis was carried out in the Department of Zoology and Entomology at Rhodes University under the supervision of Prof. C.D. McQuaid and Dr. F. Porri. These studies have not been submitted in any form to another university.

Dedication

I would like to dedicate this to my beloved Grandmother, Nomsa Beauty Mnyele, who is the light of my life, and my dearest uncle, Ntsikelelo Nomgca, who is my guardian angel…may your soul rest in God’s hands…Zwane, Malinge, Zikode, Zazabezulu, Mbambo, Ntsele. Mlambo ongawelwayo! Owelwa ziinkonjane ezibhabha emafini!!

Chapter 1

General Introduction

In marine ecosystems, the physical and biological processes affecting rocky shores communities and structuring their species distribution have been broadly investigated (Bertness *et al.* 1999; Raffaelli & Hawkins 1999). The effects of physical and physiological stress are observed more rapidly on rocky shores than in other ecosystems, at species, population and even at an ecosystem level. Rocky shores are the ideal environment to study the effects of direct positive associations by habitat-structuring organisms (Bertness *et al.* 1999). This is because rocky shores support many species and offer a steep gradient of abiotic conditions over short distances (Raffaelli & Hawkins 1999). The number of species declines from low to high shore (Hammond 2001) because almost all are originally marine species (Lewis 1964).

Along the vertical gradient of the shore, organisms experience different limiting factors (Bertness & Leonard 1997). The environmental factors that structure intertidal mussel beds include aerial exposure or “wave exposure”, heat stress, dehydration and biological processes such as predation and competition (Levine 1976; Hammond 2001). The species composition of rocky shores differs vertically because different heights on the shore experience different periods of aerial exposure and immersion times. Organisms that settle on the high shore have shorter immersion periods than those on the low shore (Hammond 2001), and their distribution is sporadic. However, high shore organisms are generally more tolerant to heat stress and desiccation and low shore organisms endure wave action and a host of other biological factors (Bertness & Leonard 1997).

The community structure and population abundances on rocky shores are influenced by various factors (Westerbom & Jattu 2006). This is often the reason why the shore is divided into distinct levels, as commonly observed on most rocky coasts (Stephenson & Stephenson 1949). The manner in which the species are distributed vertically is termed zonation (Grutter & Irving 2000). A typical rocky shore in South

Africa is divided into three zones, namely the "*Littorina*", "*Balanoid*" and "*Sublittoral*" zones (Stephenson & Stephenson 1949). However, they may not always be conspicuous or obvious to the eye (Stephenson & Stephenson 1949). Rocky shores are not exactly the same worldwide because of differences in coastal features and the intensity of the environmental and biological factors experienced on different coasts as well as biogeographic effects (Stephenson & Stephenson 1949). However, the common trend on all rocky shores is that organisms occur according to their tolerance to the factors that they are exposed to intertidally (Mouristen & Poulin 2002) and because of modifying factors, the distribution of species within zones can be very patchy (Raffaelli & Hawkins 1999).

Zonation is not only noticeable or applicable to marine environments, but can also be observed in terrestrial habitats (Raffaelli & Hawkins 1999). In terrestrial environments, a gradient can be seen on the side of a mountain because altitude also represents a gradient of environmental conditions, and again organisms are distributed along this gradient according to their ability to endure the environmental stress (Raffaelli & Hawkins 1999). Intertidal ecosystems make it easier to observe the factors affecting the community structure at small scales (Bertness & Leonard 1997). This is because intertidal ecosystems are easily manipulated and they respond readily to physical stress and the alleviation of this stress (Bertness & Leonard 1997).

Assemblages are also structured by both positive and negative biological interactions (Bertness & Callaway 1993; Jones *et al.* 1994; Brooker & Callaghan 1998). One of the most prominent negative interactions in marine ecosystems such as in corals, rocky shores and in plant communities is competition (Brooker & Callaghan 1998; Underwood 2007). Because most organisms intertidally are sessile, space is often a limiting resource, and thus competition is usually driven by the increasing demand for settlement space, especially when the number of species increases (Underwood 2007). Predation also has effects on community structure (Dunson & Travis 1991). However, under adverse conditions, predation becomes less important and competition becomes the fundamental factor that structures species communities (Raffaelli & Hawkins 1999). As living conditions become even more stressful, communities are structured primarily by physical factors (Raffaelli & Hawkins 1999). Nevertheless, the general prediction that low shore organisms are controlled by biological factors, and high shore organisms by physical factors, is not entirely true. A good example of this is shown by Zardi and co-authors (2006b; 2007; 2008) when they observed that wave action influences the structure of mussel communities on the low shore on the south coast of South Africa. The force of the waves dislodges alien mussel *Mytilus galloprovincialis* on the low shore while indigenous *Perna perna* can withstand these conditions (Zardi *et al.* 2006b).

There is a growing body of literature investigating ecosystems where organisms co-exist and share or compete for the available resources (Underwood 2007). Competition is determined and affected by the surrounding physical and biological conditions of the environment (Birch 1957). It is governed by the abundance or scarcity of resources that are needed by organisms of the same or different species (Birch 1957). This negative association usually achieves one of two things. It is either a survival strategy or an attempt to attain dominance over other organisms (Birch 1957). However, when the availability of resources is high, competition is reduced (Underwood 2007).

At some stage organisms depend on other organisms for the provision of essential primary resources such as shelter, relief from physical stress and predators, and food (Grutter & Irving 2000). Organisms engage in three kinds of symbiotic associations, where one benefits and the other is harmed (“parasitism”), where both organisms benefit (“mutualism”), or where one organism benefits while the other is unharmed (“commensalism”) (Grutter & Irving 2000).

Bertness & Leonard (1997, p. 1976) defined positive interactions as “any direct or indirect interactions among two or more organisms that positively affects the growth or reproduction of one or more organisms without negatively affecting the other(s)”. In ecological systems, there are many positive associations (Holmgren *et al.* 1997; Grutter & Irving 2000) which can enhance biodiversity. For instance, in a mutualistic relationship between coral and algae, the algae facilitate the increase of coral reef and this expands settlement space for organisms associated with corals (Grutter & Irving 2000; Crooks 2002). Another example is that of sea grass and the clam *Mercenaria mercenaria* in North Carolina. Irlandi and Peterson (1991) observed that the clam has better growth rates when living in the sea grass, perhaps because this is a high energy habitat. In terrestrial habitats, for instance, trees provide habitat for many organisms (e.g. birds, bees, lichens and epiphytes) and the understory of trees provide living space for a variety of insect species (Hacker & Gaines 1997; Hutcheson & Jones 1999).

Positive interactions or facilitation can sometimes have negative effects on ecological communities (Jones *et al.* 1997; Grutter & Irving 2000). This happens because positive interactions are governed by physical factors and the life stage of the affected organisms (Grutter & Irving 2000). There are organisms that by simply growing and changing in their physical structure facilitate the existence of other organisms (Jones *et al.* 1997; Grutter & Irving 2000). These organisms provide suitable habitat so that other organisms can take refuge and expand (Grutter & Irving 2000). Examples of such organisms include mussels, corals, algae, trees and other plant species (Jones *et al.* 1997; Grutter & Irving 2000). These habitat-forming species are usually ubiquitous and they create habitats that not only increase species abundance but also provide habitat for unique species that would not have existed otherwise (Suchanek 1985; Tsuchiya & Nishihira 1985; Grutter & Irving 2000). They modify their environment and create complex multidimensional habitats that cater for a diversity of species (Grutter & Irving 2000; McKindsey & Bourget 2001). The distribution of species is also affected by this association (Bertness & Callaway 1994; Brooker & Callaghan 1998). Until recently the positive impact of structure-forming organisms did not receive the attention it deserved (Bertness *et al.* 1999).

Positive interactions have not yet been incorporated into most models of the ecological processes affecting communities and are under appreciated in ecology (Bertness & Shamway 1993; Bertness & Callaway 1994; Bruno & Bertness 2001; Bruno *et al.* 2003). Although there are many examples of positive interactions occurring in nature, it is still quite an unpopular concept amongst most ecologists (Bertness & Callaway 1994; Bruno *et al.* 2003). However, although no one has quantified the proportion that positive interactions contribute in changing communities their importance has been realised (Bertness & Leonard 1997).

Positive interactions can be direct or indirect and these associations have been observed in stressful environments (Bertness & Callaway 1993; Holmgren *et al.* 1997; Brooker & Callaghan 1998; Bertness *et al.* 1999; Menge 2000). Even in stressful desert environments, positive interactions are prominent in vascular plants (Bertness & Leonard 1997). During succession, the initial space occupiers often facilitate additional less stressful habitat for other organisms (Bertness & Callaway 1994). Bertness and Leonard (1997) stated that positive interactions are important to intertidal communities because of the stressful physical conditions regularly experienced on the rocky shores. Rocky shores are not as stable as most people think (Lewis 1964). However, unlike plant communities the change in community structure can be observed at smaller scales intertidally (Bertness & Leonard 1997). Facilitation can be regarded as an important succession process (Begon *et al.* 2006) where the establishment of the primary settler can encourage the settlement of many more organisms (Menge & Branch 2001). One such example of facilitation is ecosystem engineering. Jones and co-authors (1994, p. 374; 1997, p. 1947) eloquently defined ecosystem engineers as “organisms that directly or indirectly control the availability of resources to other organisms by causing physical state changes in biotic or abiotic materials”. Coastal communities depend on the presence of habitat-forming organisms, or foundation species, to provide suitable living spaces that are less stressful or shielded from the adverse factors experienced intertidally (Bertness & Callaway 1993; Bruno & Bertness 2001; Norkko *et al.* 2006). These organisms affect other organisms just by being present in that habitat (Menge & Branch 2001).

Mussels occur extensively on rocky shores worldwide (Suchanek 1985) and they have been proven a reliable biogenic habitat for a number of species. South Africa has four mussel species occurring intertidally - namely, *Aulacomya ater* (Molina), *Choromytilus meridionalis* (Krauss) and *Perna perna* (Linne), and the exotic *Mytilus galloprovincialis* (Lamarck) (van Erkom Schurink & Griffiths 1990). Their distribution is determined by the Benguela (cold) and Agulhas (warm) currents that brush along the South African coast (see Figure 1.1) (van Erkom Schurink & Griffiths 1990; Ndzipa 2002). These mussel species can coexist (Hammond 2001) and form single layered beds, individual mussels attaching directly onto the rock; or with time, they can form multilayered beds, settling one on top of each other (Hammond 2001; Brinkman *et al*. 2002).

The focal mussel species for this thesis were *P. perna* and *M. galloprovincialis*. *M. galloprovincialis* is a dominant and competitive invasive on the west and southwest coasts (Hammond 2001). Vertical zonation of these two mussel species on the south coast of South Africa reflects their tolerance of physical stress. *Perna* usually inhabits the low shore up to the mid zone (Lasiak & Dye 1989) and *Mytilus* occupies the high mussel zone (van Erkom Schurink & Griffiths 1990; Bownes & McQuaid 2006).

The main aims of this MSc were to investigate the structure of intertidal mussel beds and determine whether mussel bed architecture affects the richness, diversity or abundance of associated macrofauna. The intertidal mussel zone was divided into three zones that were distinctly demarcated by the occurrence of the indigenous *Perna perna* on the low mussel zone and *Mytilus galloprovincialis* on the high mussel zone. The third mussel zone was the transitional zone where *M. galloprovincialis* and *P. perna* overlap and cohabit. Furthermore, this study looked at the epibiotic association between mussels and the barnacles that settle on their shells, to determine the type of symbiotic interaction occurring between the two organisms.

This thesis contains three main data chapters. The first of these (Chapter 2) describes the physical structure of mono- and multilayered mussel beds of *M. galloprovincialis* and *P. perna* from the high to low mussel zone. The sediment content (organic and inorganic) and bed volume of the mussel bed was calculated to see how this affects the species diversity and richness of the associated macrofauna. Chapter 3 details the biodiversity of the macro-organisms associated with the mussels *M. galloprovincialis* and *P. perna* and the effects of mussel bed structure on this diversity. The third data chapter (Chapter 4) investigates the epifaunal association between barnacles and mussels to identify whether this is a negative epibiotic association by calculating the condition index of mussels from the high to the low shore with and without epibionts. This study was conducted in Plettenberg Bay, South Africa. A single site was chosen for sample collection because of the main hypothesis testing the effect of zonation and mussel bed layer on associated macrofauna. The selected site contained both mono- and multilayered *M. galloprovincialis* and *P. perna* beds.

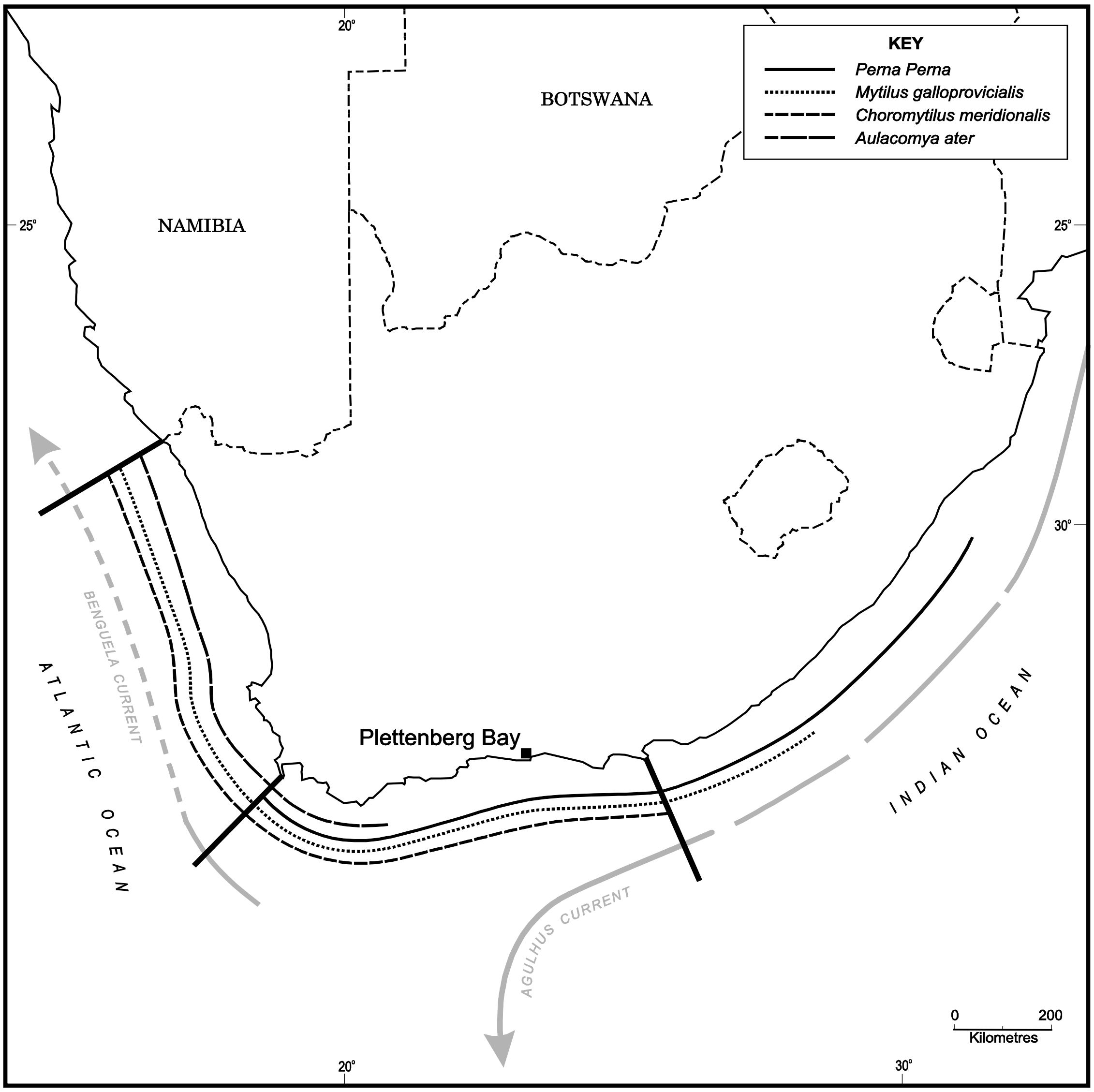

Figure 1.1 Map of South Africa (adapted from van Erkom Schurink & Griffiths 1990 and Viladomiu 2004). The study site, Plettenberg Bay, is located at the south-east end of the Western Cape Province. The black, bold lines radiating seawards corresponds to the approximate climatic sub-regions of the South African coast (i.e. the Temperate, Warm temperate and Subtropical regions from Atlantic to the Indian Ocean).

Chapter 2

Small scale mussel bed structure: sediment characteristics and bed architecture.

Introduction

There are many factors that influence the structure of intertidal communities worldwide (McQuaid & Branch 1984, 1985; Lasiak 1991; Bustamante *et al* 1997; Westerbom & Jattu 2006; Porri *et al* 2007) on the high and low shore, ranging from physical processes to biological interactions (Dayton 1975; Menge 1979; Bustamante & Eekhout 1997; Hammond 2001). Community structure is the result of a combination of processes and interactions that modify a given set of populations (Menge 1979). This includes elements such as species distributions, abundances, sizes, diversity and trophic relationships (Menge 1979).

Habitat complexity is important for structuring species communities (Ricciardi *et al* 1997). Ecosystems with a complex structure often provide habitats that encourage the success of some species that are able to establish and make use of the space provided (Werner & Hall 1977; Crowder & Cooper 1982; Gutierrez *et al* 2003). Ecosystems are created by unique combinations of biological interactions, physical factors and structure that change at different spatio-temporal scales. The community structure and distribution of species is also defined by, amongst other things, the architecture of the environment and the availability of habitable space. No habitat can exist without space and structure. The physical structure of an ecosystem contributes positively to the abundance and richness of associated species (Cocito 2004) in coastal and terrestrial ecosystems (Kelaher 2003).

There are organisms that function in providing suitable habitats for other species. “Bioconstructors” create habitats by modifying the existing structure of the environment for various organisms to settle (Cocito 2004). Structure-forming organisms add to the naturally existing space, by providing unique conditions for different organisms to take refuge. There are biological and physical factors that influence the structure provided by these habitat-forming organisms (Kelaher 2003).

Some primary settlers unintentionally provide habitat for the next settlers and facilitate their survival by providing suitable environments that are less stressful (Qvarfordt 2006), have enough food resources and reduced predation (e.g. mussel beds in Gosselin & Chia 1995). There are certain species that make a unique contribution to the systems they live in, by changing the functioning and the structure of its community (Jones *et al* 1994). A number of organisms serve as "foundation species" and modify their environments, creating defined habitats just by being present (Dayton 1975; Jones *et al* 1994; Bruno *et al* 2003). For example, *Atrina zelandica* is a sessile structure-forming bivalve on the east coast of North Island in New Zealand that provides habitat for different species (Norkko *et al* 2006). Keystone species also play an influential role in structuring some species communities (Aubry & Raley 2002). This is because, at even small densities, they alter the functioning of an ecosystem, however, not all organisms that alter species communities are keystone species (Aubry & Raley 2002). As compared to foundation species, keystone facilitators actively change their environment and create unique habitats that cater for different species (Menge & Branch 2001). An example of a keystone species that alters systems is the beaver that physically reconstructs a dam changing the hydrological and eventually the biological features of the ecosystem (Jones *et al* 1995).

Ecological engineers are identified as organisms that change their environment directly and indirectly, but the importance of their impact on communities is not always obvious and is very difficult to measure. Beavers, for instance, are also ecological engineers because they make a noticeable change in their environment and community (Jones *et al* 1994). Another good example of an ecological engineer is the burrowing crab *Chasmagnathus granulatus* in the Argentinean salt marshes (Daleo *et al* 2007). Their burrowing activity increases soil drainage and traps oxygen, encouraging mycorrhizal growth on the roots of cordgrass *Spartina desiflora* (Daleo *et al* 2007). Corals are also ecological engineers because they provide favourable habitats with ameliorated conditions for associated organisms, and regulate nutrient flow (Crooks 2002). Ecological engineers modify their habitat, by creating liveable conditions in stressful environments to allow a range of organisms to take refuge there (Suchanek 1978; Norkko *et al* 2006). Hastings and co-authors (2007) looked at the effects of ecological engineers through space and time to determine their long-term function in a community. They discovered that the effectiveness of ecological engineers depends on how strongly they affect their communities and the number that is required to make a significant effect (Hastings *et al* 2007). Byers and co-authors (2006) suggested that ecological engineers can help restore or rehabilitate human degraded environments to an acceptable state. The ability of ecological engineers to alter the physical environment into different abiotic states, leading to a biotic change is the quality that is useful in restoring communities (Byers *et al* 2006). However, the community will not be restored to its original state, but into a near-natural and functional state (Byers *et al* 2006). This depends on the ability of the engineering organism to change the abiotic structure of an environment and the nature and severity of the damage to the environment.

Positive and negative biological interactions occur side by side in nature (Callaway & Walker 1997; Holmgren *et al* 1997; Schmitt & Holbrook 2003). The efficiency of facilitation is greatly affected by the surrounding physical and biological factors that differ through space and time (Norkko *et al* 2006). The importance of facilitation in plant communities, for instance, can be identified by examining the density, structure, life stage, trophic interactions and physical factors (Callaway & Walker 1997) changing through space and time. A classic example of a positive interaction in marine ecosystems is the mutualistic relationship between the anemone fish and the sea anemone (Schmitt & Holbrook 2003). The anemone fish takes refuge in the poisonous stinging tentacles of the sea anemone that ward off most predatory fish (Schmitt & Holbrook 2003). Positive interactions play an influential role in species communities and they affect trophic interactions and other ecological processes, extending the tolerance of certain organisms to harsh environmental factors (Bruno *et al* 2003). The potential impact of these interactions on communities is such that many ecological theories that have been previously studied will be affected and need to be re-assessed in the light of these processes (Bruno *et al* 2003). For instance, if habitat forming organisms create less stressful living spaces for other species to inhabit, it means that the "fundamental niche" of some organisms is extended (e.g. intertidal seaweeds in Bruno *et al* 2003 and algae in Chapman *et al* 2005; mussels in Tokeshi 1995; Tsuchiya 2002). The significance of a structure-forming organism is determined by its functional role or purpose in a given environment and how the productivity of the affected population responds (Dayton 1975). To determine the importance of an organism in structuring its community and maintaining that structure, "quantitative" (e.g. abundance and diversity) and "qualitative" (e.g. the functional and biological role) aspects have to be assessed (Dayton 1975; Kelaher 2003).

Organisms that create living space for other organisms often also affect the community structure and distribution of these organisms (Norkko *et al* 2006). In intertidal systems, mussels support a higher diversity of species than the surrounding rock substratum (Commito 1987; Commito & Boncavage 1989; Dittman 1990). Mussels are identified as important for structuring coasts worldwide (Suchanek 1985; Harris *et al* 1998). Examples include many mytilids such as *Brachidontes rodriguezii* in Argentina (Hanekom 2007), *Perna perna*, *Choromytilus meridionalis* and *Aulacomya ater* in South Africa (van Erkom Schurink & Griffiths 1990), *Mytilus californianus* and *Mytilus edulis* in the northern hemisphere (Paine 1974; Suchanek 1978). They encourage secondary settlers by providing refuge for them (Lasiak & Dye 1989) and their shells provide living space for a number of "hard bottom" organisms (Dittman 1990), and generally support a variety of species (Hockey & van Erkom Schurink 1992). The functional role of mussels as ecological engineers has been acknowledged on intertidal rocky shores and mudflats, and in other habitat types (Tsuchiya & Nishihira 1986; Lintas & Seed 1994; Crooks & Khim 1999; Cocito 2004) like freshwater communities (e.g. the zebra mussel *Dreissena polymorpha* in Ricciardi *et al* 1997). The habitat created by mussels is very rich because it supports trophic groups such epibiotic, free-living and infaunal associations (Dittman 1990). The efficiency of mussels in providing suitable microhabitats is affected by the organic and inorganic materials that accumulate in the formation of mussel beds (Cocito 2004) and the physical factors, such as humidity, experienced intertidally (Crook 2002). Mussels are filter-feeders that sieve energy rich material and planktonic organisms from the incoming water (Dittman 1990; Stoeck & Albers 2000). Sedimentation in mussel beds can affect the species composition and richness of associated organisms (Hammond 2001; Tsuchiya 2002; Prado & Castilla 2006).

Mussel beds provide habitat for many organisms that in turn service mussel beds by decomposing organic material collecting within the bed, for example, microbial activity in *Mytilus edulis* beds (Stoeck & Albers 2000). Mussel beds are energy rich habitats and the network of byssal threads that attach the mussels to the rock or any substrata encourages the trapping of loose shell fragments, sand and organic material (Dittman 1990; Lintas & Seed 1996; Brinkman *et al* 2002; Cocito 2004). Mussel beds from the low shore trap a lot more sediment than mussels on the high shore (Lwasaki 1995). However, the sediment trapped in mussel beds is usually lacking in oxygen (Dittman 1990). The packing density of the sediment determines that amount of available interstitial spaces for free-living organisms to inhabit.

Most scientists anticipate a negative association between indigenous and exotic organisms (Crooks 2002), which is mostly the case. They usually compete for space and resources and can indirectly increase predation (Crooks 2002). Some invasive organisms, however, are also beneficial to humans (Crooks 2002). The establishment and persistence of an alien invasive species is maintained by the availability of settling space, a reliable source of food and other resources (Heiman *et al* 2008).

Studying exotic ecological engineers is complicated and needs more attention (Crooks 2002). Invasive species sometimes have ecosystem level effects (Crooks 2002) and modify the structure of some ecosystems (Simberloff 1991; Crooks & Khim 1999). Alien organisms can create physical structures that serve as habitat for other indigenous organisms (Ricciardi *et al* 1997; Crooks 2002). Alien ecosystems engineers have similar engineering abilities to indigenous ecosystem engineers (Crooks 2002). However, the resultant environment is usually disturbed and more prone to biological invasions (Heiman *et al* 2008). The organisms colonising habitats engineered by invasives, are merely taking advantage of the available settlement space regardless of whether the providers of this habitat are indigenous, alien invasive species or artificial (Crowder & Cooper 1982; Crooks 2002). The inclusion of artificial reconstructions of the habitat formed by some organisms in experiments demonstrated the importance of structural complexity in increasing biodiversity (e.g. Crooks & Khim 1999; Chapman *et al* 2005).

Alien invasive organisms that modify an environment and create habitable spaces may facilitate an increase in the existing population of aliens by encouraging more to settle (Heiman *et al* 2008). The response of indigenous species to the newly modified environment formed after a biological invasion is important (Crooks 2002). For instance, a study by Hutcheson and Jones (1999) in terrestrial habitats showed that the understory of exotic trees provides living space for a variety of insect species. However, the older, more complex pine stands harboured less unique species than younger less complex stands, although they still had a higher diversity of species (Hutcheson & Jones 1999).

M. galloprovincialis is an aggressive alien invasive on several coasts around the world (Zardi *et al* 2006). In South Africa, the effects of the invasion by *Mytilus galloprovincialis* on the species diversity of the associated macrofauna were not quantified (Hockey & van Erkom Schurink 1992), until Hammond (2001). Overall, the introduction of *M. galloprovincialis* in South Africa has had a negative effect on indigenous organisms although some native species have benefited from the invasion of this alien mussel species (Hockey & van Erkom Schurink 1992). For instance, *M. galloprovincialis* has out-competed some indigenous species on the west coast, but increases the food resource for oystercatchers and potentially for subsistence harvesters on the west and south coasts of South Africa respectively (Hockey & van Erkom Schurink 1992), *M. galloprovincialis* also provides additional habitats for other organisms, and it extends the upper shore limit of species associated with mussel beds (Hammond 2001).

The purpose of this study was to describe the physical make-up of *Perna perna* and *Mytilus galloprovincialis* beds in Plettenberg Bay, South Africa. The structural characteristics of the mussel beds in each zone were described by the layering of the mussel bed, bed volume, and the amount of sediment trapped in the bed. This was done to observe the relationship between the mussel species, and the structure of the mussel bed, and whether this affected the community structure of coexisting macrofauna. The main hypotheses of this study were, firstly, that multilayer mussel beds had the highest bed volume and trapped more organic and inorganic sediment than monolayered beds. Furthermore, I predicted that mussel beds on the low shore contained more sediment (organic and inorganic) than those on the high shore.

Materials and Methods

Sample site

Data collection for this study was conducted in Plettenberg Bay (34°05´S, 23°19´E), on the south coast of South Africa. This coast is characterised by the warm Aguhlas Current that flows south-westerly (Bownes 2005) and the granite rocks are generally vertically inclined (Bownes 2005; McQuaid & Bownes 2009). All samples were collected during spring low tides from rocks that were horizontal and moderately wave exposed.

The intertidal mussel zone on this coast has three distinct zones that support different organisms, reflecting their tolerance of physical stress (Bownes & McQuaid 2006). The two mussel species studied coexist and are partially segregated, with *P. perna* dominating the low mussel zone and *M. galloprovincialis* taking advantage of the high shore, extending the upper shore limits of intertidal mussels (Bownes & McQuaid 2006). *P. perna* and *M. galloprovincialis* overlap and coexist in the mid mussel zone (Bownes & McQuaid 2006). The sampling site was at Keurbooms Strand, where the densities of *Mytilus galloprovincialis* and *Perna perna* were more or less equal (von der Meden *et al* 2008). The two mussel species can normally be identified using their external features, such as shell colour and shape. *Perna perna* generally has a brown, slightly narrow and stubby shell and the blue mussel, *Mytilus galloprovincialis*, is usually wider and flatter. However, the outer appearance (i.e. colour, etc.) of a mussel can be deceptive because the shell can either erode or lose colour because of wave action, or the individuals may be too small to tell apart. In this study, all the mussels were identified using the internal scarring caused by the adductor muscles (Figure 2.1) because this method of identification is reliable.

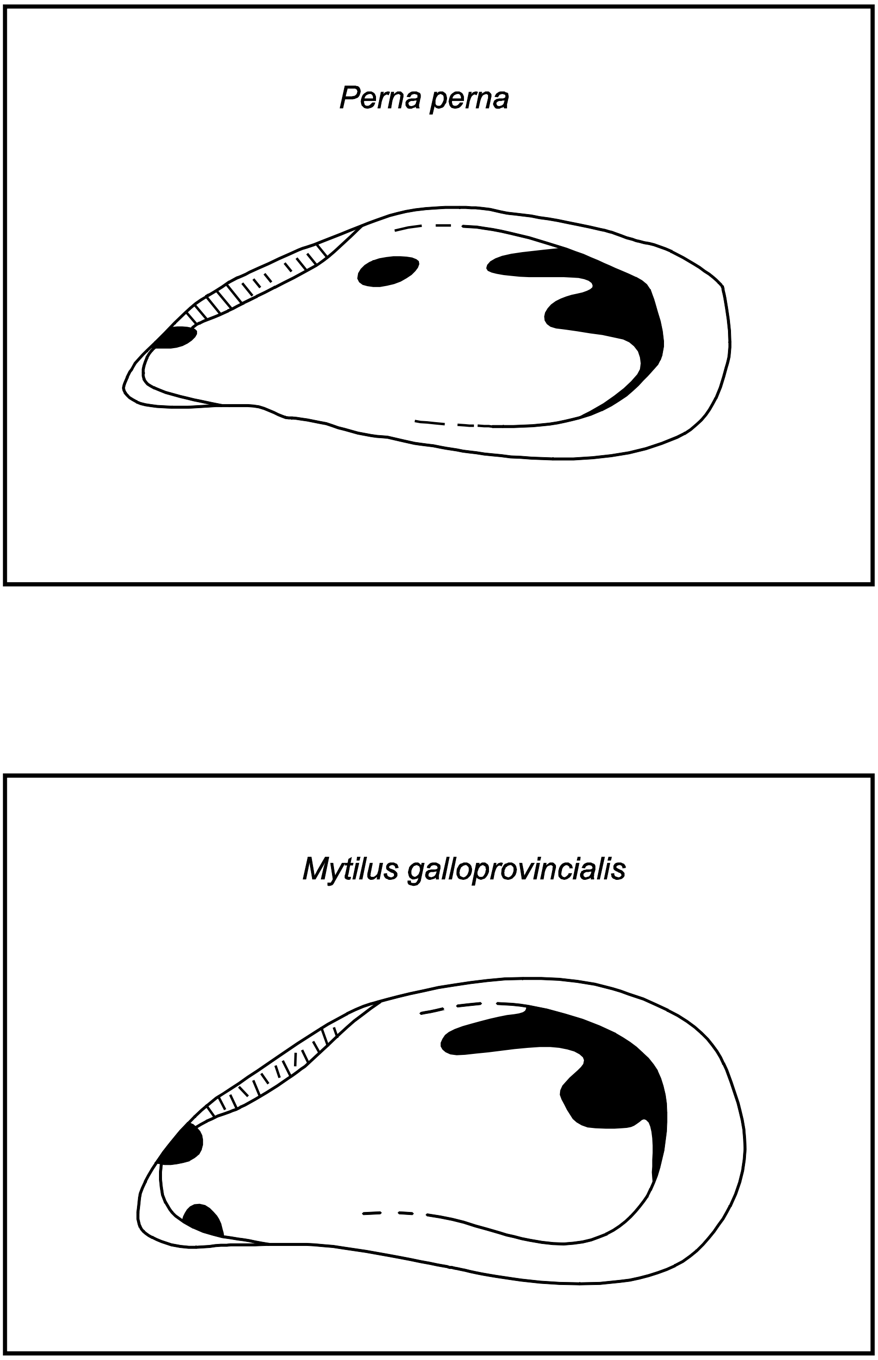

Figure 2.1 Muscle scars (shaded in black) on the inner shell of *Perna perna* and *Mytilus galloprovincialis* (source: van Erkom Schurink & Griffiths 1990).

Sample collection

Three replicate 15 X 15 cm quadrat samples from areas of 100% mussel cover were scraped off the rocks using a paint scraper, in each of the high, mid and low mussel zones in both multi and monolayered mussel beds. The samples were bagged, labelled and frozen until they were sorted in the laboratory. Sampling was done in January (summer) and May (winter) 2004, and in March (autumn) 2007 for seasonal and inter-annual comparisons. One site was chosen to test the hypothesis of the effect of zonation and mussel bed layer on associated sediment content (inorganic and organic). All statistical analyses were performed using the program STATISTICA version 7.1 software (StatSoft 2006). The homogeneity and normality of the data were tested using the Cochran's and Kolmogorov-Smirnoff tests, respectively.

Sample processing:

Organic and inorganic content of sediments

In order to measure the organic and inorganic content, each sample was washed under running water through 5 mm, 1 mm and 75µm mesh to separate coarse, medium and fine sediment fractions. Coarse sediment consisted of mussel shells, other Molluscan and gastropod shells, byssal threads and other organic material that was retainable in a 5mm mesh. Medium sediment was mostly crashed shells and smaller gastropod shells and fine sediment consisted mainly of marine sediment and sand. The macrofaunal organisms were removed from the samples before drying. The mussels were measured to the nearest 0.05 cm using vernier callipers to determine the size range in each sample. Aluminium foil containers were weighed beforehand to the nearest 0.0001g, and the sediment was transferred into the containers and placed in an oven where it was dried at 60°C for 24 hours to determine the dry sediment weight. After drying, the aluminium containers with the sediment were weighed and burnt in a furnace at 500-600°C for 24 hours to determine organic content (dry sediment weight - the burnt weight) and the inorganic content. The weight of the aluminium foil container was deducted from the total weight to calculate the weight of the inorganic (abiotic) and organic (biotic) content in the sediment.

A 4-way analysis of variance (ANOVA) was employed to test for the inter-annual effects (fixed, 2 levels: January 2004 and March 2007), zone (fixed, 3 levels: high, mid and low), sediment texture (fixed, 3 levels: coarse, medium and fine) and mussel bed layering (fixed, 2 levels: mono- and multilayer) on the sediment organic content. Similarly, a 3-way ANOVA was performed to test for the effects of seasonality (fixed, 3 levels: January 2004, May 2004 and March 2007), zone and sediment texture on the mean organic content of sediment in monolayered beds only. The multilayer samples of May 2004 were spoilt and so only samples from monolayered mussel beds could be analysed in this study, from the respective collection dates. However, the effects of monolayer beds were still worth being investigated because of the regular occurrence of this type of beds along this coast (McQuaid, pers com), therefore justifying the separate analyses. For both analyses, the data were log transformed and they satisfied the ANOVA assumptions for homogeneity and normality, tested using Cochran’s and Kolmogornov-Smirnoff tests respectively (Zar 1996; Underwood 1997). The significant groups were further examined using the student Newman-Keuls post hoc test (Zar 1996).

For the mean inorganic content, the same variables were used for the 3- and 4-way ANOVA tests as for the mean organic content. Tests for normality and homogeneity were significant even after the data were log transformed. To analyse the data using a method or statistical package that does not take these assumptions into consideration or violating the assumptions out of negligence would distort the interpretation of the results (Underwood 1997). However, because the total sample size (*n*) of this study was large (81 and 108 samples respectively), the ANOVA assumptions of homogeneity were neglected because ANOVA is considered to be robust. Untransformed data were used for the two above mentioned analyses to avoid type 1 errors (Underwood 1997).

Bed volume

Mussel bed volume was calculated for January 2004. The mussels' soft tissue was removed and the shells were refilled with oil based clay (plastocine), then the two valves of each mussel were joined to simulate the original shape of a living mussel. Volume was calculated using the water displacement technique (Tsuchiya & Nishihira 1985; Calvo-Ugarteburu 1996a, b). The mussels from each sample (quadrat) were all placed into a 2 litre cylinder that had a known volume (800 ml) of water. A reading was taken below the meniscus and the displaced water difference was taken as the approximate volume of the sample. A 2-way ANOVA was performed to investigate the effects of the independent variables zone (fixed, 3 levels: high, mid and low) and layer (fixed, 2 levels: mono- and multilayer mussels beds) on mussel bed volume.

The individual mussel sizes were used to calculate average mussel size for each of the samples that were used for bed volume. A 2-way ANOVA was performed to investigate the effects of zone (fixed, 3 levels: high, mid and low) and layer (fixed, 2 levels: mono- and multilayer mussels beds) on average mussel size. Both data sets satisfied the assumptions for parametric analysis.

Results

Organic content

The results of the 4-way ANOVA showed that mussel bed layer had a significant effect on organic content (Table 2.1). Multilayer mussel beds contained a significantly higher mean organic content than monolayer beds ($p<0.00001$; Figure 2.2). Furthermore, there were three significant interactions between month and zone ($p < 0.05$; Figure 2.3), month and sediment texture ($p < 0.01$; Figure 2.4) and zone and sediment texture ($p < 0.05$; Figure 2.5).

Table 2.1 Four-way ANOVA for the organic content of mussel beds in January 2004 and March 2007. The asterisks indicate significant p-values.

	Df	SS	MS	F	p
Month	1	4.971	4.971	20.293	0.00003*
Layer	1	8.100	8.100	33.065	<0.0001*
Zone	2	2.809	1.404	5.732	0.01*
Sediment texture	2	69.052	34.526	140.935	<0.0001*
Month X Layer	1	0.844	0.844	3.445	0.068
Month X Zone	2	1.807	0.903	3.688	0.03*
Layer X Zone	2	0.318	0.159	0.649	0.526
Month X Sediment texture	2	3.621	1.810	7.390	0.001*
Layer X Sediment texture	2	0.274	0.137	0.558	0.575
Zone X Sediment texture	4	3.240	0.810	3.307	0.02*
Month X Layer X Zone	2	0.302	0.151	0.615	0.543
Month X Layer X Sediment texture	2	0.512	0.256	1.044	0.357
Month X Zone X Sediment texture	4	0.114	0.029	0.117	0.976
Layer X Zone X Sediment texture	4	0.959	0.240	0.979	0.425
Month X Layer X Zone X Sediment texture	4	0.560	0.140	0.571	0.684
Error	72	17.638	0.245		
Cochran's *C* test		0.73			

Df = degrees of freedom; SS = sum of squares; MS = mean squares; F = f-ratio; p = significance level.

The Student Newman-Keuls post hoc test revealed two significant groups for the month and zone interaction (Figure 2.3). January 2004 samples generally had a higher mean organic content than March 2007 samples. However, the mean organic content for January 2004 was significantly higher than in March 2007 in the mid and low mussel zones. Moreover, the high, mid and low mussel zones of March 2007 and the high mussel zone of January 2004 were in the same group according to the Student Newman-Keuls post-hoc test (Figure 2.3). For the month and sediment texture interaction, the mean organic content of January 2004 and March 2007 were highest for coarse sediment. The mean organic content of medium and fine sediment was higher in January 2004 than in March 2007 (Figure 2.4). The coarse sediment of the high, mid and low mussel zones contained the highest mean organic content. On the low mussel zone, the fine sediment contained the second highest mean organic content. Post-hoc tests showed three significant groups. The mean organic content of fine and medium sediment on the high and mid mussel zones and the mean organic content of medium sediment on the low mussel zone were similar (Figure 2.5).

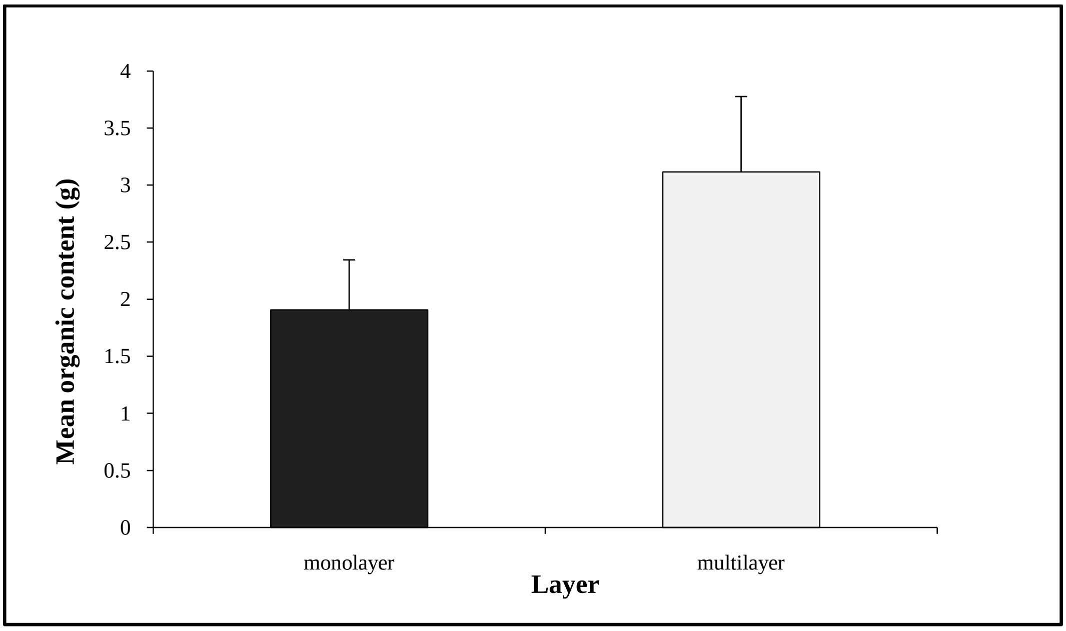

Figure 2.2 Effect of layer. Four-way ANOVA of mean organic content of mono- and multilayer mussel beds ($p < 0.0001$). The error bars indicate the standard errors.

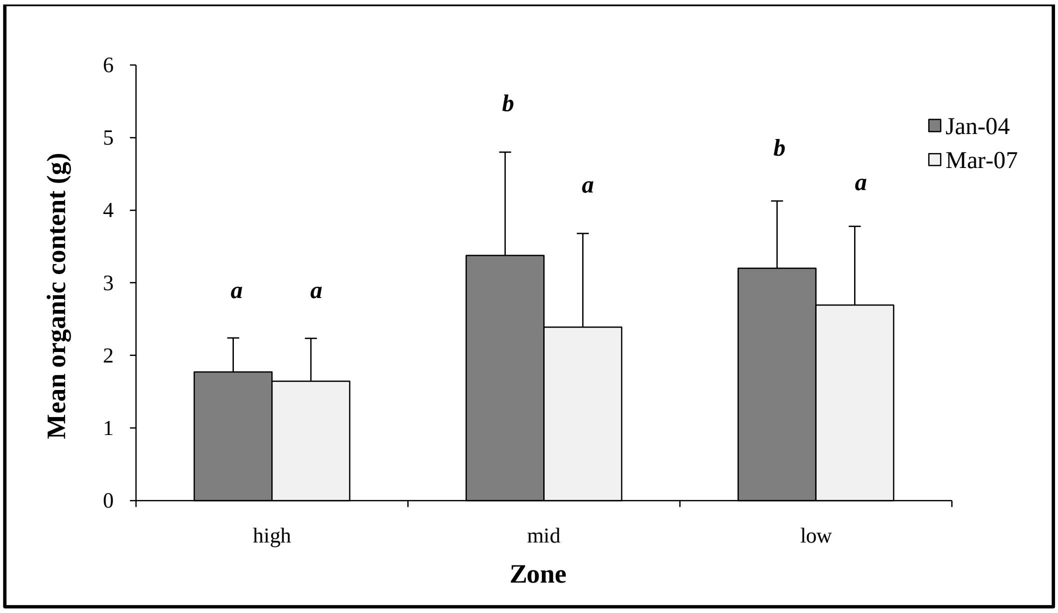

Figure 2.3 Interaction between month and zone. Four-way ANOVA of mean organic content of high, mid and low mussel zones in January 2004 and March 2007 ($p < 0.05$). The error bars indicate the standard errors and the letters represent homogenous groups from the results of the Student Newman-Keuls post-hoc test.

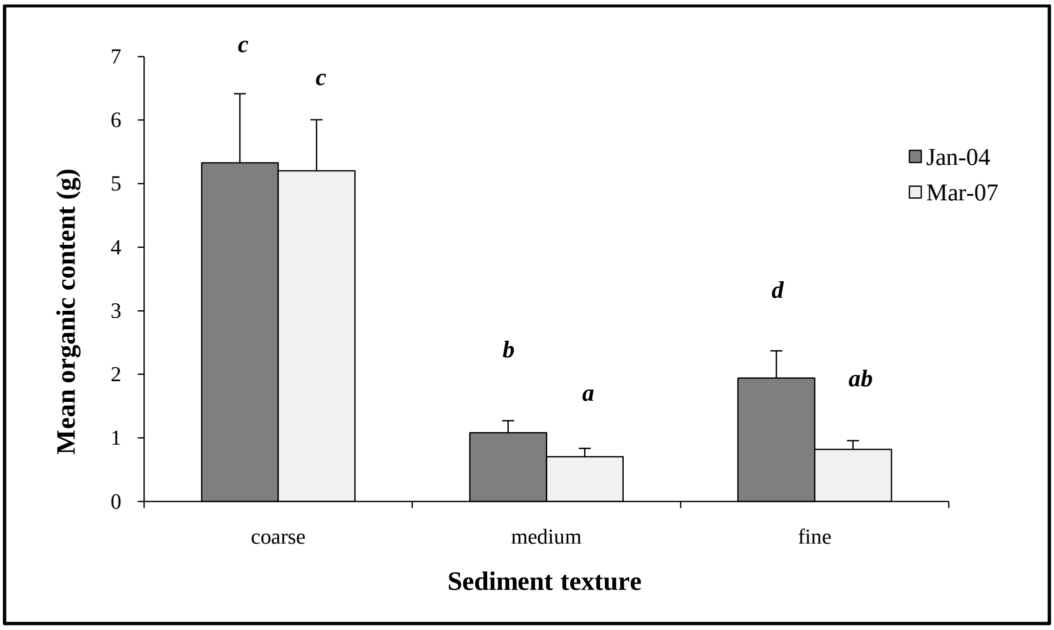

Figure 2.4 Interaction between month and sediment texture. Four-way ANOVA of mean organic content of the coarse, medium and fine sediment in January 2004 and March 2007 ($p < 0.001$). The error bars indicate the standard errors and the letters represent homogenous groups from the results of the Student Newman-Keuls post-hoc test.

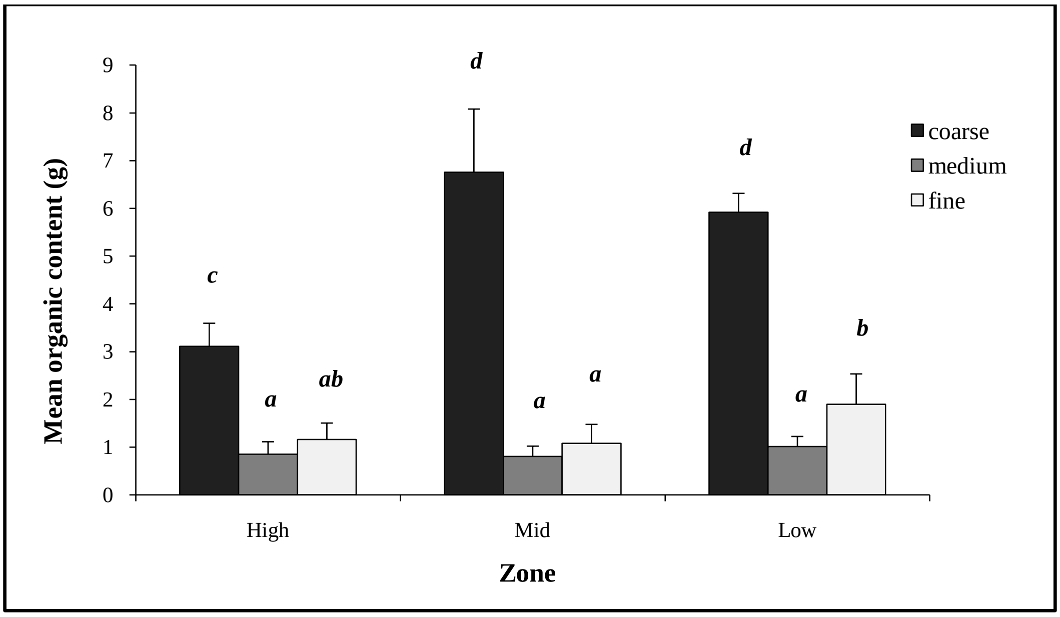

Figure 2.5 Interaction between zone and sediment texture. Four-way ANOVA of mean organic content of the coarse, medium and fine sediment in high, mid and low mussel zones ($p < 0.02$). The error bars indicate the standard errors and the letters represent homogenous groups from the results of the Student Newman-Keuls post-hoc test.

The 3-way ANOVA results for mean organic content in January and May 2004 and March 2007 in monolayer mussel beds were only significant for zone ($p < 0.01$; Figure 2.6), texture ($p<0.0001$) and for the interaction between month and sediment texture ($p < 0.001$; Figure 2.7, Table 2.2). The low mussel zone had the highest mean organic content. The Student Newman-Keuls post-hoc test showed that mean organic content in the low zone was significantly higher than in the high and mid mussel zones (Figure 2.6). For the month-sediment texture interaction, the mean organic content of coarse sediment was highest for January 2004 and March 2007. According to the post-hoc test there were only two groups that contributed to the significant difference – coarse sediment in January 2004 and March 2007 in one group (***c***) and medium sediment for May 2004 and March 2007 in the other (***a*)** (Figure 2.7). Overall, these results imply that within monolayer beds, low mussel zones generally harboured the most organic content and coarse sediment was a higher contributor of organic material than medium and fine sediment.

Table 2.2 Three-way ANOVA for the organic content monolayer beds in January, May 2004 and March 2007. The asterisks indicate significant p-values.

	Df	SS	MS	F	p
Month	2	0.862	0.431	1.423	0.250
Zone	2	3.335	1.668	5.505	0.01*
Sediment texture	2	48.087	24.043	79.370	<0.0001*
Month X Zone	4	2.120	0.530	1.750	0.153
Month X Sediment texture	4	6.572	1.643	5.423	0.001*
Zone X Sediment texture	4	1.021	0.260	0.843	0.504
Month X Zone X Sediment texture	8	3.117	0.370	1.270	0.270
Error	54	16.360	0.303		
Cochran's *C* test		0.476			

Df = degrees of freedom; SS = sum of squares; MS = mean squares; F = f-ratio; p = significance level.

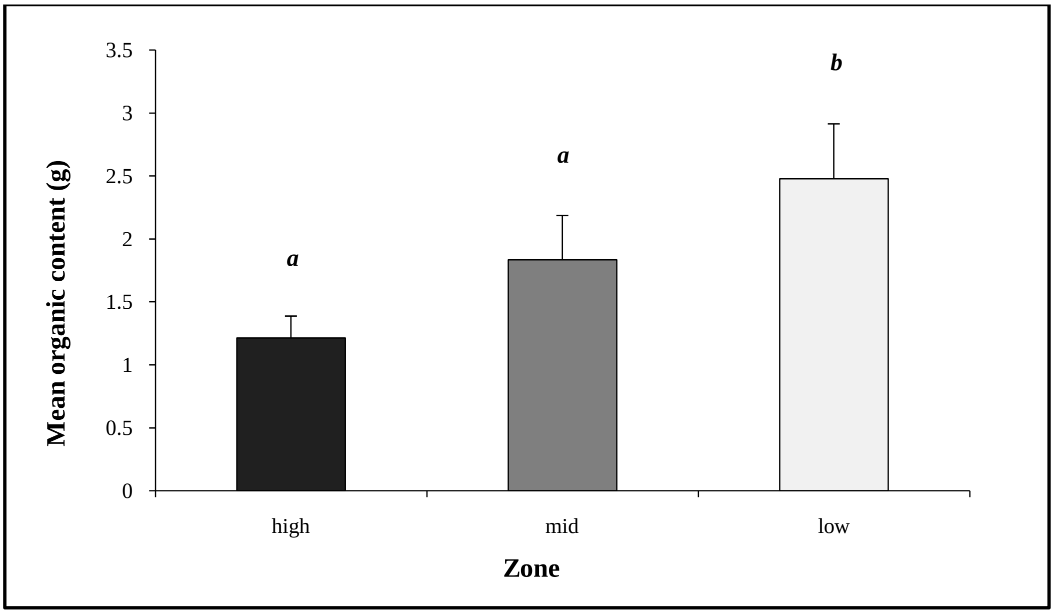

Figure 2.6 Effect of zone. Three-way ANOVA of mean organic content of the high, mid and low zones for monolayer mussel ($p < 0.01$). The error bars indicate the standard errors and the letters represent homogenous groups from the results of the Student Newman-Keuls post-hoc test.

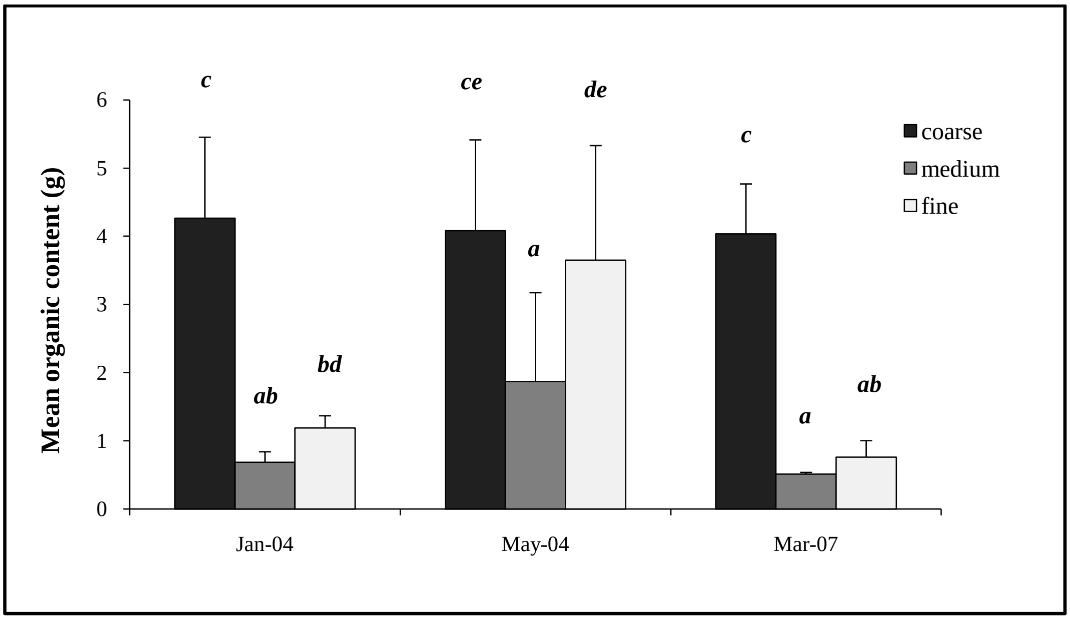

Figure 2.7 Interaction between month and sediment texture. Three-way ANOVA of mean organic content in coarse, medium and fine sediment for January and May 2004, and March 2007 ($p < 0.001$). The error bars indicate the standard errors and the letters represent homogenous groups from the results of the Student Newman-Keuls post-hoc test.

Inorganic content

The data did not satisfy the ANOVA assumptions of homogeneity even after log transformation. Larger experiments, with *n* that is greater or equal to 6 and more than 5 treatments (total N of at least 30) may be allowed to avoid the requirement for heterogeneity of the data (Underwood1997). For this study, the above mentioned requirements were not fully met. However, the total N (27 and 36 for the 3 and 4-way ANOVAs, respectively) was relatively large. ANOVA is considered robust to heterogeneous variances (Zar 1996). However, the results were interpreted cautiously and conservatively. The alpha value was set to be significant at $p < 0.01$ and anything above this was ruled as non-significant to avoid a type 1 error. The untransformed data were used for these analyses.

The results of the 4-way ANOVA for mean inorganic content were significant for mussel bed layer ($p < 0.01$), zone ($p < 0.0001$) and sediment texture ($p < 0.00001$) with no significant interactions (Table 2.3). Multilayer beds had significantly higher mean inorganic content than monolayer beds (Figure 2.8). The mean inorganic content of the low mussel zone was significantly higher than the high and mid mussel zones. According to the Student Newman-Keuls post-hoc test, the mid and high mussel zones were no different from each other (Figure 2.9). Fine sediment contained a significantly higher mean inorganic content than the other two textures, and medium sediment contained the least (Figure 2.10).

Table 2.3 Four-way ANOVA for the inorganic content of mussel beds in January 2004 and March 2007. The asterisks indicate significant p-values.

	Df	SS	MS	F	p
Month	1	28426.1	28426.1	6.955	0.0102
Layer	1	49651.3	49651.3	12.15	0.001*
Zone	2	114120.4	57060.2	13.961	0.00001*
Sediment texture	2	123790.5	61895.3	15.144	0.000003*
Month X Layer	1	8908.4	8908.4	2.18	0.144
Month X Zone	2	3818.4	1909.2	0.47	0.629
Layer X Zone	2	19307.5	9653.8	2.362	0.102
Month X Sediment texture	2	33992.6	16996.3	4.159	0.02
Layer X Sediment texture	2	20115.1	10057.5	2.461	0.093
Zone X Sediment texture	4	55394.5	13848.6	3.39	0.014
Month X Layer X Zone	2	7402.7	3701.4	0.906	0.409
Month X Layer X Sediment texture	2	33015.7	16507.9	4.04	0.022
Month X Zone X Sediment texture	4	2430.5	607.6	0.149	0.963
Layer X Zone X Sediment texture	4	11663.8	2916.0	0.713	0.585
Month X Layer X Zone X Sediment texture	4	15256.1	3814.0	0.933	0.45
Error	72	294274.8	4087.1		
Cochran's *C* test		0.000			

Df = degrees of freedom; SS = sum of squares; MS = mean squares; F = f-ratio; p = significance level.

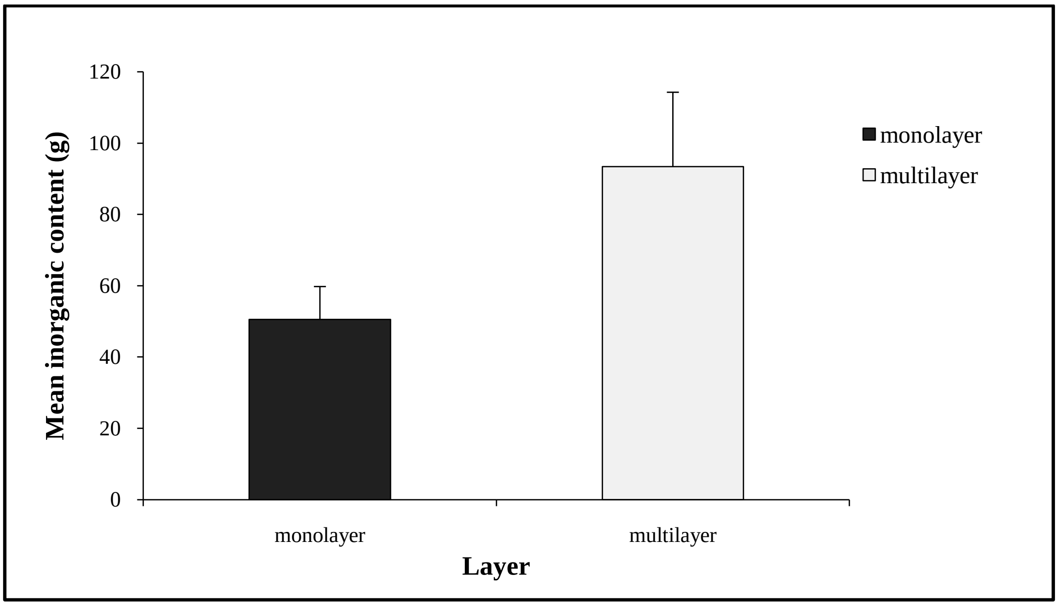

Figure 2.8 Effect of layer. Four-way ANOVA of mean inorganic content of mono- and multilayer mussel bed ($p < 0.01$). The error bars indicate the standard errors.

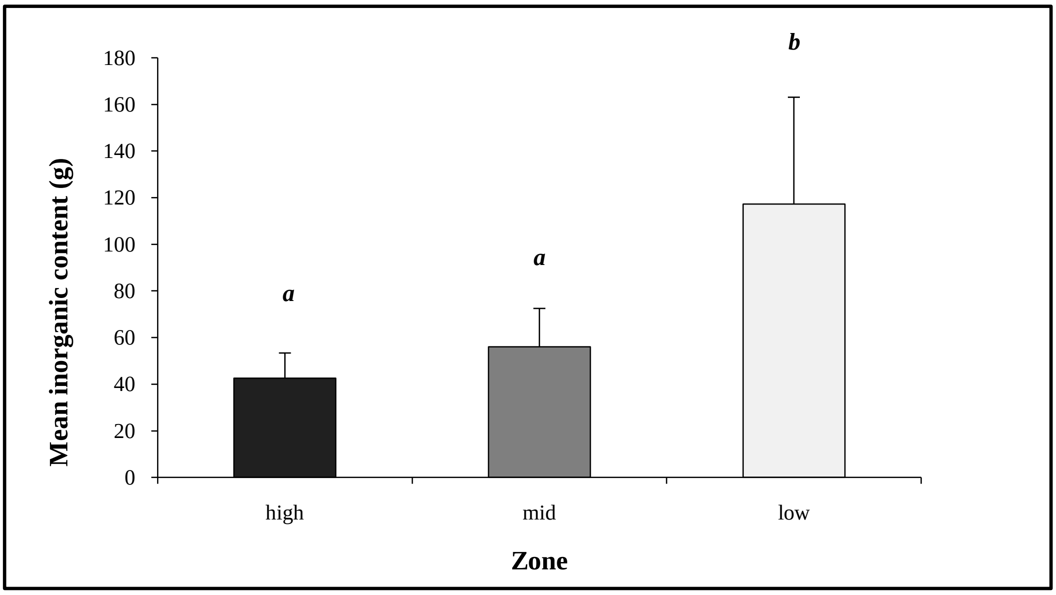

Figure 2.9 Effect of zone. Four-way ANOVA of mean inorganic content of high, mid and low mussel zones ($p < 0.0001$). The error bars indicate the standard errors and the letters represent homogenous groups from the results of the Student Newman-Keuls post-hoc test.

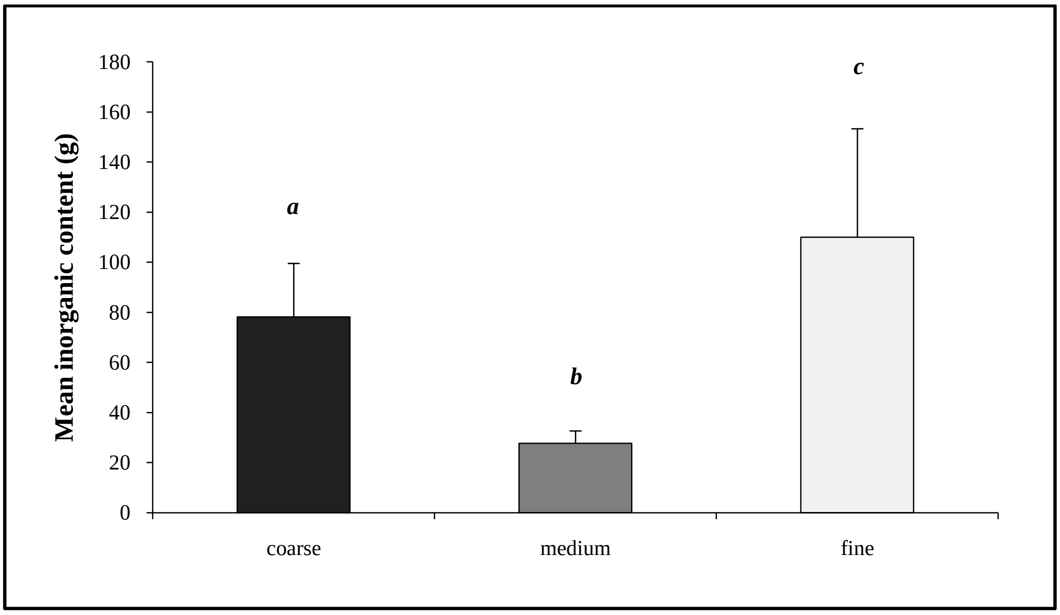

Figure 2.10 Effect of sediment texture. Four-way ANOVA of mean inorganic content of coarse, medium and fine sediment from mussel beds ($p < 0.0001$). The error bars indicate the standard errors and the letters represent homogenous groups from the results of the Student Newman-Keuls post-hoc test.

For the 3-way ANOVA of monolayered beds only, there weren't any significant interactions. However, mussel zone and sediment texture had significant effects on mean inorganic content ($p < 0.01$ and $p < 0.0001$ respectively; Table 2.4). The Student Newman-Keuls post-hoc test showed that inorganic sediment from the mid and low mussels zones were significantly higher than that of the high mussel zone (Figure 2.11). Furthermore, fine sediment had the highest inorganic content and medium sediment contained the least inorganic material (Figure 2.12).

Table 2.4 Three-way ANOVA for the inorganic content monolayer beds in January, May 2004 and March 2007. The asterisks indicate significant p-values.

	Df	SS	MS	F	p
Month	2	23477.4	11738.7	4.784	0.012
Zone	2	30555.0	15277.5	6.23	0.004*
Sediment texture	2	91213.7	45606.8	18.59	0.000001*
Month X Zone	4	23375.2	5843.8	2.382	0.063
Month X Sediment texture	4	25464.2	6366.0	2.595	0.05
Zone X Sediment texture	4	15002.1	3750.5	1.529	0.207
Month X Zone X Sediment texture	8	32414.3	4051.8	1.651	0.132
Error	54	132497.6	2453.7		
Cochran's *C* test		0.000			

Df = degrees of freedom; SS = sum of squares; MS = mean squares; F = f-ratio; p = significance level.

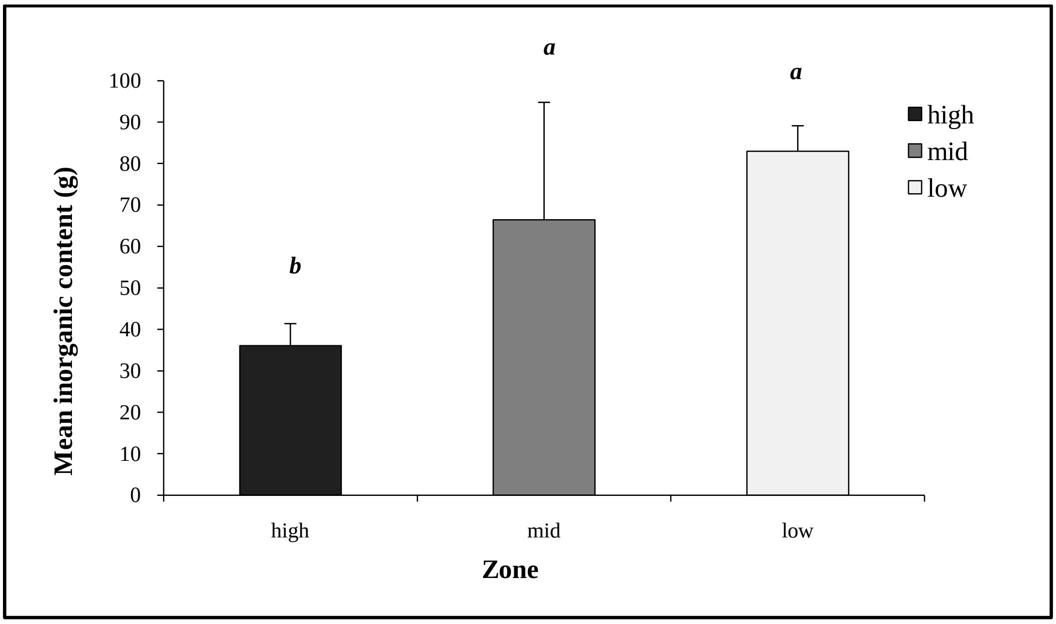

Figure 2.11 Effect of zone. Three-way ANOVA of mean inorganic content of the high, mid and low zones for monolayer mussel beds ($p < 0.01$). The error bars indicate the standard errors and the letters represent homogenous groups from the results of the student Newman-Keuls post-hoc test.

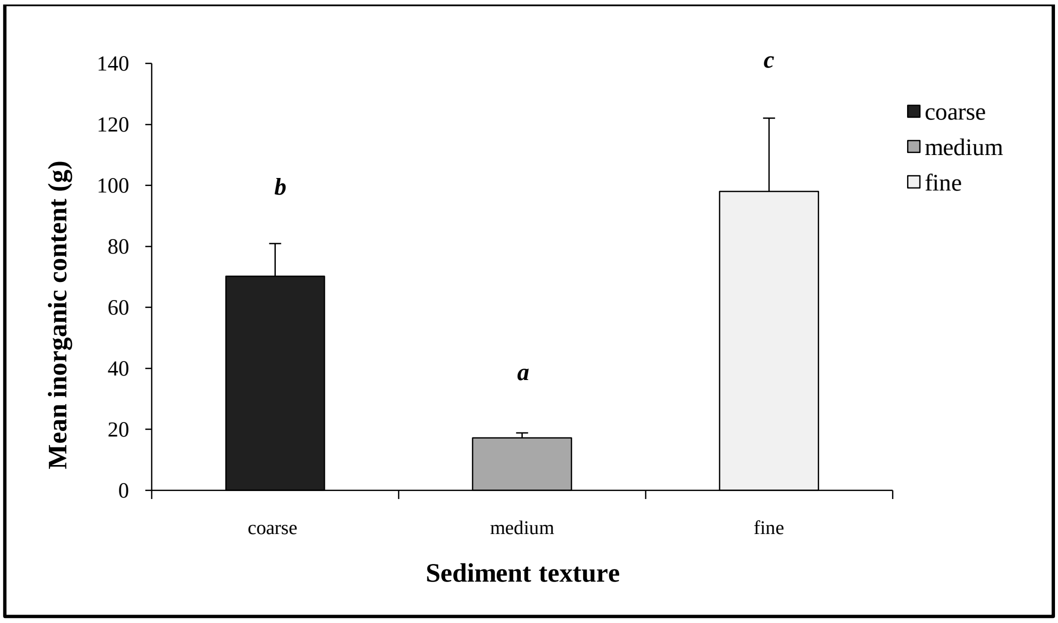

Figure 2.12 Effect of sediment texture. Three-way ANOVA of mean inorganic content of the coarse, medium and fine sediment in monolayer mussel beds ($p < 0.00001$). The error bars indicate the standard errors and the letters represent homogenous groups from the results of the student Newman-Keuls post-hoc test.

Bed volume

The results of the 2-way ANOVA for bed volume were significant for both layer ($p < 0.001$) and zone ($p < 0.008$), with no significant interaction (Table 2.5). Mussels occurring on the mid and low mussel zones had a higher bed volume than high shore mussels regardless of mussel bed layering (Figure 2.14). Moreover, the post-hoc tests revealed that multilayer mussel beds contained a significantly higher volume of mussels than monolayer mussel beds regardless of the mussel zone that they occupy (Figure 2.13).

Table 2.5 Two-way ANOVA for mussel bed volume in January 2004 samples. The asterisks indicate significant p-values.

	Df	SS	MS	F	p
Layer	1	49592	49592	18.12	0.001*
Zone	2	40078	20039	7.32	0.01*
Layer X Zone	2	13590	6795	2.5	0.13
Error	12	32849	2737		
Cochran's *C* test		0.44			

Df = degrees of freedom; SS = sum of squares; MS = mean squares; F = f-ratio; p = significance level.

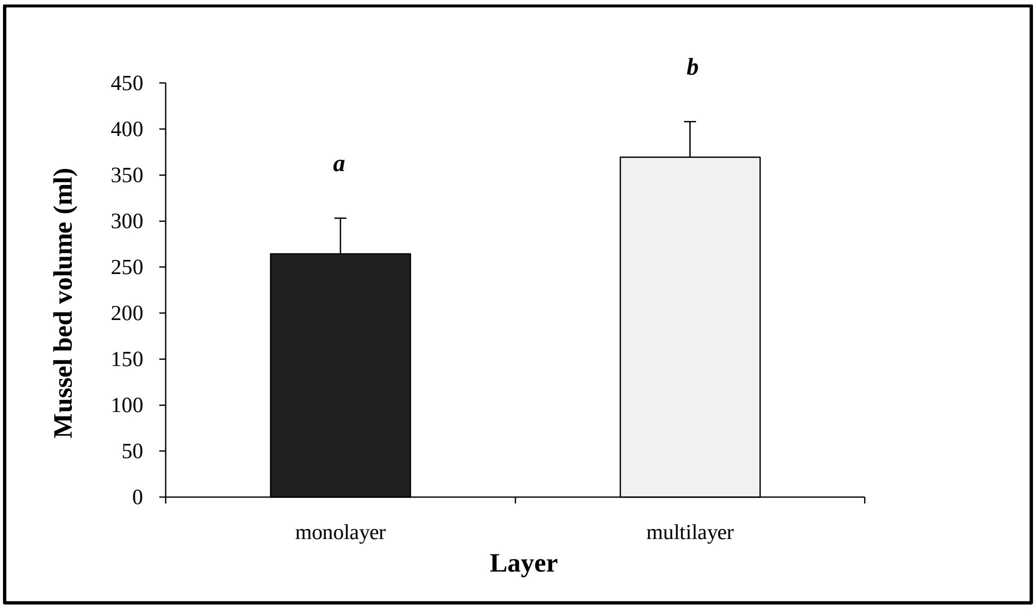

Figure 2.13 Bed volume of mono- and multilayer mussel beds ($p < 0.01$). The error bars indicate the standard errors and the letters represent homogenous groups from the results of the Student Newman-Keuls post-hoc test.

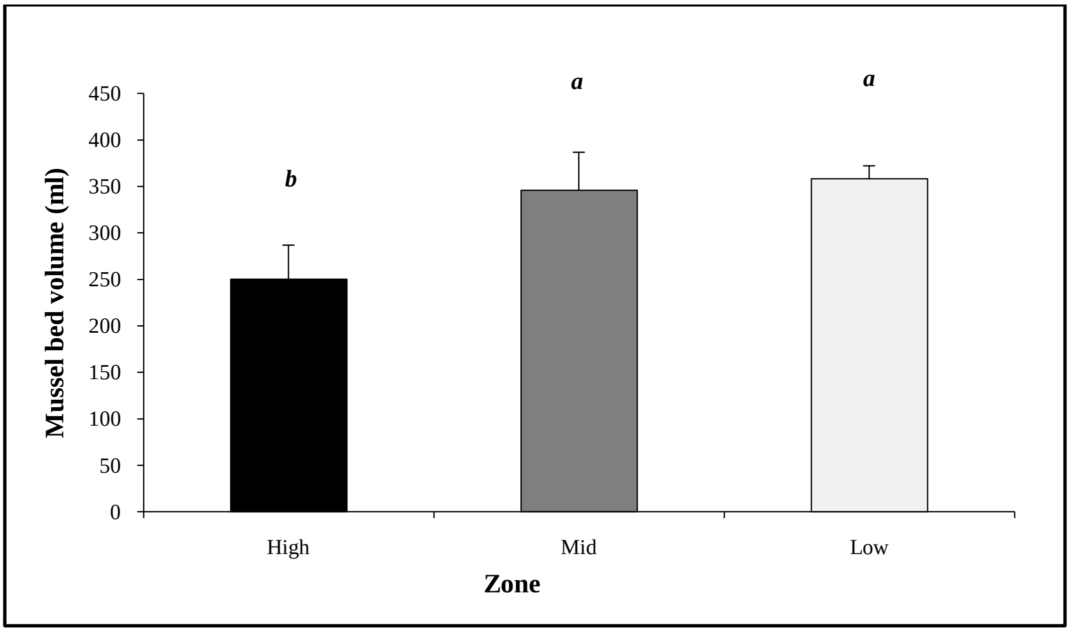

Figure 2.14 Bed volume of high, mid and low mussel zones ($p < 0.05$). The error bars indicate the standard errors and the letters represent homogenous groups from the results of the Student Newman-Keuls post-hoc test.

The results of the 2-way ANOVA of average mussel size showed a significant interaction between mussel zone and mussel bed layer (p = 0.03; Table 2.6). However, the size distribution of mussels was strongly influenced by zonation (zone: p < 0.00001; Table 2.6). The average mussel size of mussels from the low zone was greater than that of mussels from high and low zones, irrespective of bed layering (Figure 2.15).

Table 2.6 Two-way ANOVA for average mussel size in January 2004 samples. The asterisks indicate significant p-values.

	Df	SS	MS	F	p
Layer	1	0.0185	0.0185	0.410	0.534
Zone	2	14.7079	7.3539	163.041	<0.00001*
Layer X Zone	2	0.4095	0.2047	4.539	0.034*
Error	12	0.5413	0.0451		
Cochran's *C* test		0.4			

Df = degrees of freedom; SS = sum of squares; MS = mean squares; F = f-ratio; p = significance level.

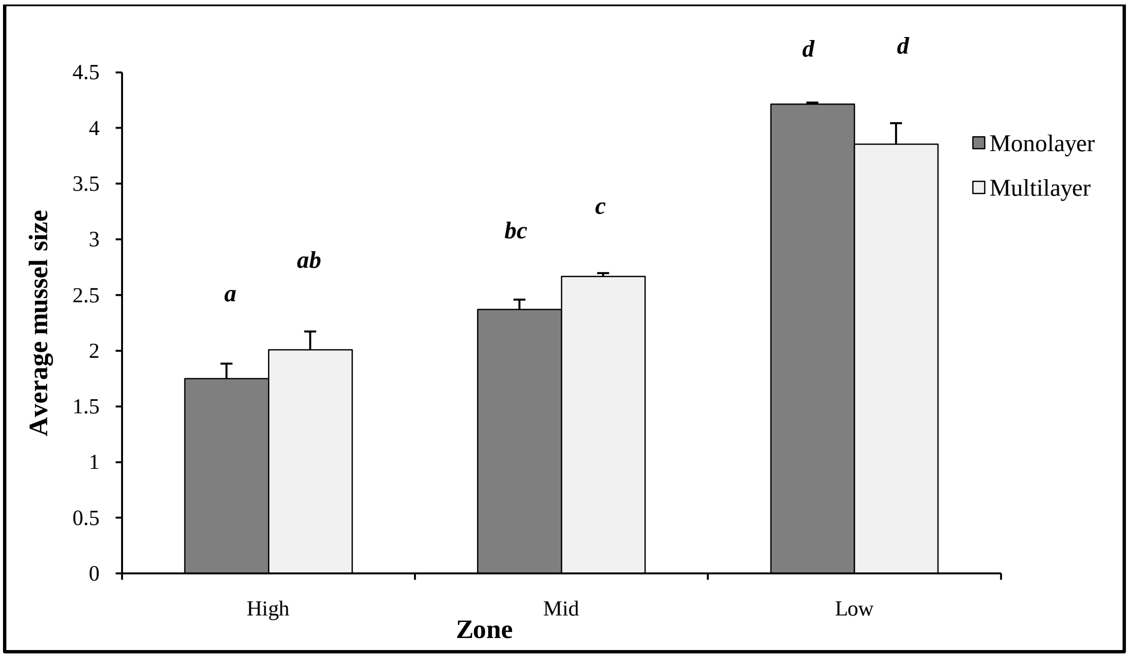

Figure 2.15 Interaction between layer and zone. Two-way ANOVA of average size of mussels in mono- and multilayer beds, on the high, mid and low mussel zones, in January 2004 ($p < 0.03$). The error bars indicate the standard errors and the letters represent the results of the Student Newman-Keuls post-hoc test.

Discussion

Organisms that provide additional living space with ameliorated stress may be beneficial for the conservation of biodiversity (Norkko *et al* 2006). However, the interaction between habitat-forming organisms and the inhabiting species is not always positive (Kelaher 2003). Habitat complexity may have a positive effect on the diversity and abundance of species associated with mussels and algae (McKindsey & Bourget 2001; Kelaher 2003), but species richness decreases as habitat complexity increases as shown in algal mats (Kelaher 2003). Mussels generally occupy and often dominate much of the primary space on rocky shores (Paine & Levin 1981; Lwasaki 1995). Because mussels are ubiquitous and form complex mats on rocky shores, sediment is easily trapped in the interstitial spaces of mussel beds (Tsuchiya 2002; Gutierrez *et al* 2003). The physical structure of mussel beds differs from species to species and so the associated macrofauna may also differ (Lwasaki 1995; Hammond 2001).

In this context, the overall results of this study were predictable and in agreement with the original hypotheses even if there was some degree of variability between the two data sets. The inorganic content was highest for low shore, multilayer mussel beds, irrespective of mussel species. In addition, the low and mid zone mussel beds accumulated the most organic content regardless of the sampling times. This can be a result of exposure to waves that carry sediment onto the low shore (Zardi *et al* 2006a) and the longer emersion periods. Rocky shore communities respond readily to the effects of the incoming and outgoing waves (Stephenson & Stephenson 1949). Multilayer mussel beds contained the most biotic content regardless of zone, probably because they are structurally more complex and older than monolayer mussel beds (Hammond 2001). Moreover, it was generally coarse sediment that contributed the most to the organic value of the mussel beds and inorganic content was found to be highest for fine sediment because this was mostly sand.

Although the volumes of the mussel beds were not drastically different from each other in the present study, multilayer mussel beds had a significantly higher bed volume, especially on the low and mid mussel zones (Figure 2.13 and 2.14).

However, these results should be taken cautiously because different size structures in the samples may have affected the volume measurements. Biologically, this can be attributed to the higher emersion periods experienced on the low and mid shores (Zardi *et al* 2006a), which means that the mussels have a longer feeding time and are generally also bigger (Figure 2.15). Because the waves suspend organic materials and food particles, (Menge 1978, Paine & Levin 1981; Sousa 1985; Bustamante & Branch 1996) mussels that are exposed to waves grow faster than those that are sheltered (McQuaid & Lindsay 2000), unless exposure becomes extreme (Steffani & Branch 2003).

The factors that influence the physical structure of an engineered habitat become more challenging to assess because of the biological processes that also influence the associated organisms in biogenic habitats (Kelaher 2003). Similar to mussel beds (Tsuchiya 2002), the organisms associated with coralline turfs are mainly influenced by the physical structure of the habitat (Kelaher 2003). Kelaher (2003) found that biological processes are far less important than the physical characteristics in structuring communities in coralline turfs. The physical structure of the fronds controls the biological processes (Kelaher 2003), and these differ across the vertical gradient of intertidal rocky shores (Dayton 1971; Paine 1974). Intertidally, low shore communities are mostly influenced by biological factors and the high shore communities are regulated mostly by physical factors because the high shore has more stressful environmental conditions (Lewis 1964; Menge 1979; Bustamante & Eekhout 1997; Raffaelli & Hawkins 1999).

Intertidal zones vary from coast to coast because of the difference in biogeography, topography and other physical differences (Dayton 1975). The rocky shores of Plettenberg Bay constitute a simple intertidal community. Mussels are the most conspicuous feature on most intertidal rocky shore. The compactness of mussel beds can increase or decrease the abundance and diversity of species. Because mussel beds are so complex in their structure, they present an opportunity for habitat heterogeneity to be further explored and quantified (Tsuchiya 2002). Although the details of the communities associated with mussel beds will be further explored in the next chapter, the relationship between communities and sediment are discussed below.

Mussel beds suspend different amounts of sediment because of their tidal positioning and they can support different species (Lwasaki 1995). The byssal threads pack the live mussels tightly with shell remains of other Mollusca and other organic material, and the sediment is suspended in between the interstitial spaces of a mussel bed. Large amounts of sediment encourage the persistence of polychaetes and other infauna (Dittman 1990; Tsuchiya 2002). An increase in the abundance and diversity of species has an optimal sediment concentration in *Atrina* habitats, after which a negative correlation exists (Norkko *et al* 2006). However, Prado and Castilla (2006) saw an increase in species richness with increased sand in *Perumytilus purpuratus* habitats. Tsuchiya and Nishihira (1986) spoke of mussel beds as “islands” that are constantly changing because of the biotic and abiotic components that they are made of. Sedimentation may encourage the existence of certain species, but it excludes some as well (Ragnarsson & Raffaelli 1999). Ragnarsson and Raffaelli (1999) proved, through rigorous experimentation, that control patches with no mussels trapped a less sediment and organic matter than transplanted mussel patches, and that the trapped sediments were anoxic. However, the oxygen concentration of the sediment was not measured in this study.

The relationship between habitat structural complexity and species richness is not always positive, and this can possibly be observed in several associations with habitat-forming organisms (Kelaher 2003). For instance, in other biogenic habitats, such as coralline algal, there is a negative relationship between habitat complexity and the diversity of associated species (Kelaher 2003). This is mostly owing to sedimentation and the density of foliage that reduces the spaces that associated organisms can occupy (Kelaher 2003). Therefore, increasing habitat or structural complexity may decrease the diversity of associated organisms (Kelaher 2003).

The results of this study indicate that the low and mid mussel zone probably support the highest number of species because mussel beds from these zones are more structurally complex. Although high sediment content in mussel beds may lead to unfavourable anoxic conditions, mussel patches with sediment still have higher species richness then those without sediment (Norling & Kautsky 2008). Species richness is not only increased by the habitat structure provided by mussels, but also their functional characteristics of clearing the water by filter-feeding and providing food for associated organisms (Norling & Kautsky 2008).

Chapter 3

Biodiversity of fauna associated with mussel beds in relation to bed structure

Introduction

South Africa's coastline constitutes only 0.5% (2881 km) of the world's coasts, but has a surprisingly high number of endemics and is one of the most diverse coasts in the world (Gibbons *et al* 1999). Its biodiversity needs to be conserved because the loss of species through extinction means that valuable genetic and medicinal information, food resources and other materials that are vital to the existence of mankind, e.g. aesthetics, heritage etc. will be lost (Loreau *et al* 2001). In addition, the loss of biodiversity in an ecosystem will make it more vulnerable to biological invasions and less resilient to disturbance than species rich ecosystems (Chapin III *et al* 2000; Loreau *et al* 2001). It is for these reasons that matters concerning biological diversity have received so much attention in different ecotypes.

The importance of biodiversity is increasingly recognised and the factors that influence it are frequently investigated (Schmitt & Holbrook 2003) because of its close association with ecosystem processes and functioning (Loreau *et al* 2001). Some scientists were oblivious to the impacts of the loss of biodiversity and rapid changes in dominance patterns among ecological assemblages (Loreau *et al* 2001). As a result, research around the effects of biodiversity loss and variability has increased over the years (e.g. McGrady-Steed *et al* 1997; Coleman & Williams 2002; Solan *et al* 2004; Hanekom 2008). For instance in marine ecosystems, researchers have started questioning how ecological processes would be affected if biodiversity would be depleted (Solan *et al* 2004).

It is a challenge for most scientists to describe and understand the intricacy of the physical and biological structure of an ecosystem and its resident species (Steneck & Watling 1982). There are a number of physical and biological factors that affect the community structure of an ecosystem (Wilson & Lundberg 2004). An ecosystem that supports a diversity of organisms is generally functions differently and is more stable than one that has few species (Chapin III *et al* 2000; Tilman 2000; Loreau *et al* 2001). Moreover, a greater variety of interactions are possible with high species diversity (Johnson *et al* 1996). The functioning of ecosystems depends on the different species (composition, richness and abundance) it supports, and the ways in which organisms interact with one another through space and time (Chapin III *et al* 2000). The world's ecosystems and ecological communities are constantly changing because of various anthropogenic and biological activities (Loreau *et al* 2001), like the over-exploitation of natural resources by humans (Lasiak 1991; Lasiak & Field 1995; Lasiak 1999) and invasion by alien species such as *Mytilus galloprovincialis* in South Africa (Grant & Cherry 1985; van Erkom Schurink & Griffiths 1990).

The distribution and abundance of organisms are influenced by both positive and negative associations among each other (Jones *et al* 1994; Stachowicz 2001; Wright & Jones 2006). A lot of attention has been focused on negative interactions such as competition, and predation (Menge 1976), while there are positive interactions that are as influential in structuring communities (Stachowicz 2001). A positive interaction occurs when an organism facilitates and improves the existence of another organism by modifying its surroundings (Stachowicz 2001), making the environment more habitable (Pettersson 2006). For instance, mussel beds and algae accommodate a variety of invertebrates (e.g. gastropods and polychaetes) in their interstitial spaces (Hacker & Gaines 1997; Chapman *et al* 2005).

One phenomenon that involves positive interactions is ecological engineering (Stachowicz 2001; Jones *et al* 1994, 1997; Hastings *et al* 2007). Jones *et al*. (1994, p. 374) defined ecological engineers as "organisms that directly or indirectly modulate the availability of resources (other than themselves) to other species, by causing physical state changes in biotic and abiotic materials". Coleman and Williams (2002) defined ecological engineers as a kind of keystone species. This probably depends on how trivial or big a change the engineering organism makes in an ecosystem, because keystone species make a substantial difference to their communities (Mills *et al* 1993). Ecological engineers such as mussels (Thiel & Ullrich 2002) occupy an ecosystem for long periods of time, change it and create conditions that facilitate the existence of other species (Borthagaray & Carranza 2007). However, at small scales, the presence of ecological engineers may exclude some species that were once present

(Jones *et al* 1997; Wright *et al* 2002) because they destroy or alter the habitat (Commito *et al* 2005; Badano *et al* 2006).

The role of bioengineers in modifying and managing their environment is probably as important as any of the other biological (e.g. competition, predation) and physical (e.g. wave action) processes (Jones *et al* 1994; Wright & Jones 2006). It is important to identify native and alien ecological engineers (Wright & Jones 2006) because of the physical and, inevitably, biological changes that can be induced by alien species such as alien *Musculista senhousia* (Crooks & Khim 1999) and *Mytilus galloprovincialis*, (Robinson *et al* 2007). Understanding how ecological engineers affect their ecosystems and investigating the species they affect directly and indirectly (either positively or negatively) could assist in the preservation and management of biodiversity (Jones *et al* 1997). Ecological engineers and biogenic habitats may be a strategic starting point for conservation (Coleman & Williams 2002; Borthagaray & Carranza 2007) because of the diverse communities they can support.

Mussels are important intertidal ecological engineers (Ndzipa 2002; Thiel & Ullrich 2002; Commito *et al* 2005). They add substratum and complexity, which contribute substantially to species diversity in marine ecosystems (Hammond & Griffiths 2004). Mussels create structurally complex (Cocito 2004; Prado & Castilla 2006) microhabitats for marine invertebrates and increase surface area for settlement by densely packing together into complex multilayer beds (Crooks & Khim 1999; Brinkman *et al* 2002; Ndzipa 2002; Beadman *et al* 2004). Mussel beds provide secondary substratum for other free-living, infaunal or epifaunal organisms (Lohse 1993; Ragnarsson & Raffaelli 1999; Tsuchiya 2002). In addition, they retain the receding sea water and organic materials (Commito & Boncavage 1989), thus increasing moisture content (Kelaher *et al* 2001) and food availability for resident organisms (Gutiérrez *et al* 2003). This means that mussel beds control nutrient flow to associated organisms (Hastings *et al* 2007). Mussels also provide some organisms with protection from predators (Commito & Boncavage 1989; Lohse 1993), and reduce physical stress (Bruno & Bertness 2001; Gutiérrez *et al* 2003). The communities supported by mussel beds are also influenced by physical disturbances, (Chintiroglou *et al* 2004; Lohse 1993), physical factors such as rock type, wave action, aerial exposure, vertical zonation or tidal height, and biological interactions including competition and predation (Bustamante *et al* 1997; Hammond 2001; Schiel 2004). Rocky shore communities are also influenced by mussel bed age (Commito & Rusignuolo 2000), sediment accumulation (Crooks & Khim 1999), and mussel size and mussel species (Lwasaki 1995; Tsuchiya 2002).

The introduction of the alien invasive *M. galloprovincialis* has extended the upper shore limit of mussels on the south coast of South Africa, potentially increasing habitat for associated fauna (Hammond & Griffiths 2006). It has also substantially increased mussel biomass on the west coast, making it the highest amount throughout the whole coast (van Erkom Schurink & Griffiths 1990; Hammond 2001). *M. galloprovincialis* has managed to spread because of its enhanced fecundity, endurance to stressful environmental extremes that normally limit the distribution of native species (van Erkom Schurink & Griffiths 1990), resistance to trematode parasites (Calvo-Ugarteburu & McQuaid 1998a, b), sand resistance (Zardi *et al* 2006) and the absence of predators (Branch & Steffani 2004). It has out-competed most of the indigenous species intertidally (van Erkom Schurink & Griffiths 1990). *M. galloprovincialis* has almost naturalised following its introduction in the late 1970s, probably because South Africa has warm temperate climatic conditions similar to its native environment (Viladomiu 2004).

P. perna, on the other hand, is most dominant on the south-eastern coast. However, over the years, it has been over-exploited by locals on the Transkei and Natal coasts for sustenance and commercial gain (Lasiak & Dye 1989). Many of these shores are denuded of mussels (Lasiak & Dye 1989). When the dominant species is cleared from the rock, competition for space among sessile or sedentary species increases (Bolton & Anderson 1997). Some organisms, such as oligochaetes (Commito & Boncavage 1989) decrease in abundance when mussels are removed from the rock. Lasiak and Dye (1989) reported that the overexploitation of mussels on intertidal rocks leads to a change in the community structure - more especially since different organisms, like algae and limpets, soon take over most of the rock (Lasiak & Field 1995). This is because *P. perna* is slow to replenish and so other fast growing species (usually macroalgae) take over, changing the whole community (Lasiak & Dye 1989; Lasiak & Field 1995).

The introduction of *M. galloprovincialis* and its establishment has caused a growing concern with its impacts on the biodiversity of coastal communities. The purpose of this study was to investigate the species abundance and composition of macrofauna associated with mussel beds of *M. galloprovincialis* and *P. perna*, in multi- and monolayer beds by looking at two hypotheses. To look at the effects of mussels as ecological engineers, I investigated the biodiversity associated with mussels in relation to the structure of the mussel beds. The first aim looked at whether structurally complex multilayer mussel beds support a greater variety of invertebrate species at higher abundances than monolayer beds. Secondly, I predicted that there would be differences in species composition and abundance decreases from the low, mid and high mussel zone.

Materials and methods

Study site

Samples were collected from the intertidal rocky shores in Plettenberg Bay (34°05´S, 23°19´E), in the Western Cape province of South Africa. The sample collection was performed in Keurbooms Strand, where *M. galloprovincialis* and *P. perna* are more or less equally represented (Viladomiu 2004, von der Meden *et al* 2008). The samples were collected during spring low tides in January and May 2004, and March 2007.

Sample collection and processing

Samples were scraped from the substratum with a paint-scraper, from multi- and monolayer mussel beds using a 15 X 15 cm quadrat. Three replicates of each layer type were collected from the high, mid and low mussel zones. *Perna perna* is most dominant on the low shore and it is restricted by the ascidian *Pyura stolonifera* and the limpet *Patella cochlear* from expanding further down shore (Viladomiu 2004). *Mytilus galloprovincialis* inhabits the higher part of the mussel zone that is characterised by the barnacles *Octomeris angulosa* and *Tetraclita serrata*, where *P. perna* is absent. The mid mussel zone is where the two mussel species co-occur; hence this zone was sometimes called the mixed zone. The samples were bagged, labelled and taken to the laboratory where they were frozen until they were processed.

The samples were washed under running water through a series of mesh (5 mm, 1 mm and 75 µm) and the macrofauna (invertebrates greater or equal to 1mm) associated with mussels were removed from the 1 mm and 5 mm mesh. They were then preserved in 70% ethanol, identified to species level where possible and counted.

Statistical analysis

The infaunal abundance data were analysed using PRIMER v6 (multivariate statistical software) (Clarke & Gorley 2006). The data were log(x+1) transformed to enhance the representation of rarer species by decreasing the importance of the most abundant species. A standard Bray-Curtis similarity matrix was used to run the CLUSTER (hierarchical clustering) analysis, a SIMPROF analysis to test for structure in the raw data, a non-metric MDS (multi-dimensional scaling). For each treatment, the mean abundance value was used for the analysis for the MDS. This was calculated by averaging the replicates to minimize the effect of an outlier identified by the SIMPROF. Two 2-way crossed ANOSIM (analysis of similarity) test was employed with only the month and zone factors. The effect of layer is not presented in the results as it proved to be non-significant in a-priori ANOSIM test. The CLUSTER analysis and the MDS helped in identifying the samples that were more similar to each other in species composition and abundance. A dendrogram and a two-dimensional (and 3D) scatter-plot are the diagrammatic representations given by the above-mentioned analyses, respectively. The results of the analysis are interpreted as a parametric analysis of variance, testing the significance of the treatments set by hypotheses and not the groups defined by the cluster analysis (Clarke & Gorley 2006). The resulting R statistic value represents the degree of difference among the groups, and the p value considers the sample size (numbers of replicates) of each treatment or observation (Clarke & Gorley 2006).

A two-way SIMPER (similarity of percentages) calculation was performed on the transformed abundance means, for month and zone. The purpose of this analysis was to highlight the species that contribute most to the differences or similarities between samples by assigning a cumulative percentage using abundance values. A separate SIMPER analysis was performed for the factor layer. The sub-routine DIVERSE was used to calculate the following diversity indices: log based Shannon (H' = -Sum (Pi*Log (Pi))) species diversity, Margalef (d = (S-1)/Log (N)) species richness, Pielou’s (J'= H'/Log (S)) evenness index. These analyses were based on the total number of individuals per sample and the total number of species. Thereafter, 3-way and 2-way analyses of variance (ANOVAs) were run for each index to test for significant differences among the different treatments. A full analysis was done for January 2004 and March 2007 to test for the fixed factors month (fixed, 2 levels: January 2004 and March 2007), zone (levels: high, mid and low) and mussel bed layering (2 levels: mono- and multilayer). Because there were no multilayer data for May 2004, a second analysis included the monolayer bed data only for all three months, to test for the effects of month (fixed, 3 levels: January 2004, May 2004 and March 2007) and zone (fixed, 3 levels: high, mid and low). For the Margalef index (species richness), the data were log transformed to satisfy the assumptions of homogeneity and tested using Cochran's test. The species diversity and evenness indices satisfied the ANOVA assumptions of homogeneity after log transformation.

Results

A total of 52 macrofaunal invertebrate species (Table 3.1) predominantly arthropods, gastropods and molluscs were found associated with mussel beds over the duration of this study. The mean abundance of species from each sample differed among months and with the zonation of the mussel species.

Using a cut-off level of 34% similarity as computed by the SIMPROF test, the dendogram from the cluster analysis (Figure 3.1) showed six distinct groups, with one outlier (January Monolayer High zone 1). Although the smaller groups did not seem to follow a specific pattern, the bigger groups divided the samples in accordance to zonation: Group A contains mostly high shore samples and groups B and C include samples from the mid and low shore (Figure 3.2). .

The MDS plot (Figure 3.2) shows how the average samples were distributed two-dimensionally. If the sample points were close to each other, this meant that the samples had similar communities in abundance and/or composition. The stress factor value on the MDS plot indicates how much the points on the diagram had been stressed to make them viewable in 2-dimensions. If the value is close to 1, the representation of the sample points is deceptive. However, the stress factor value of 0.1 in the MDS plot (Figure 3.2) means that the relationship among the samples is well-represented (Clarke & Gorley 2006).

Table 3.1 Mean species abundances of fauna associated with mussel bed assemblages for mono- and multilayer beds in January, May 2004 and March 2007 (See Appendix I for key to abbreviations).

Species	JanMonLw	JanMonHi	JanMonMd	JanMulLw	JanMulHi	JanMulMd	MayMonLw	MayMonHi	MayMonMd	MayMulLw	MayMulMd	MarMonLw	MarMonHi	MarMonMd	MarMulLw	MarMulHi	MarMulMd
Annelida																	
Polychaeta																	
Eunicidae (family)	0	0	0	0	0	0.67	0	0	0	0	0	0	0	0	0	0	0
Lumbrinereis tetrauna	0	0	0	1	0	0.33	0.33	0	1	0.33	0	0	0	0	0	0	0
Pseudonereis variegata	0.33	1.33	1.67	4	0.33	2.67	1.33	1	1.33	1.67	6.67	1.67	0	2.67	8.67	1.67	3.33
Arthropoda																	
Insecta																	
Hexapoda																	
Anurida maritima	0	0	0	0	0.67	0	0	0	0	0	0	0	0	0	0	0	0
Diptera																	
Chironomidae (family)	0	0	0	0.33	0	0	0	0	0	0	0	0	0	0	0	0	0
Crustacea																	
Amphipoda																	
Atylus swammerdamei	0	0	0	0	0	0	0	0	0	0.33	0	0	0	0	0	0	0
Guerra rhomba	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	4.33	0.33
Hyale sp.	0	0	0	0.33	2.33	0.33	0	5	7.67	0	0	0.33	1.67	13	0	0	1.33
Hyale grandicornis	0	0	0	0	0	0	0	0	0.33	0	0	0.33	1.33	32.67	2	0	8
Maera bruzeli	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0.33
Isopoda																	
Cirolana vesticaude	0.33	0.33	1	0.33	5.67	0	0.33	0.33	1.33	0	0	0.67	0	0.33	0.33	0	1.33
Dynamenella huttoni	0.67	0	0	0.67	0	1	1.33	0	0	0	0	2.33	0	0	8	0	0
Dynamenella ovalis	0	0	0	0	0	0	0	0	0	0	0	0.33	0	0	0	0	0
Dynamenella scabricula	0	0	0	0	0	0	0.33	0	0	0	0	0	0	0	0	0	0
Exosphaeroma porrectum	0.33	0	0.33	0	0	1	0	0	0.33	0	0	0.33	0	0	0	0	0
Sphaeramene polytylops	0	0	0	0	0	0	0	0	0	0	0	15	0	0	24.67	0	0

Species	JanMonLw	JanMonHi	JanMonMd	JanMulLw	JanMulHi	JanMulMd	MayMonLw	MayMonHi	MayMonMd	MayMulLw	MayMulMd	MarMonLw	MarMonHi	MarMonMd	MarMulLw	MarMulHi	MarMulMd
Cirripedia																	
Balanus sp.	0	0	0	0	0	0	0	0	0	0	0.33	0	0	0	0	0	0
Balanus trigonus	0	0	0	0	0.33	0	0	0	0	0	0	0	0	0	0	0	0
Chthamalus dentatus	1.67	0.33	12	3	6.33	5.67	0	33.33	3	1.33	4	24	8	0	2	3.67	4.33
Octomeris angulosa	0.67	0	3.33	0	2	0	0	4.67	0	0	0	0	70.67	60.67	35.33	20	1.67
Tetraclita serrata	0	0.33	0	0	0	0	0	0	0	0	0	0.67	0	0.33	0	0.33	0
Chelicerata																	
Arachnida																	
Desis formidabilis	0	0	0	0	0.67	0	0.67	0.33	0	0	0	0	0	0	0.33	0.33	0
Pycnogonida																	
Tanystylum breviceps	0.33	0	0	0	0	0.33	0	0	0	0	0	0.33	0	0	1.33	0	0
Cnidaria																	
Anthozoa																	
Bunodactis reynaudi	2	0	2.33	1.67	0	0	1	0	1.33	0	0.33	2.33	0	0	0	0	0
Echinodernata																	
Asteroidea																	
Patiriella exigua	0.67	0	0.33	0	0	0	1	0	0	0	0	4.33	0	0	1	0	0.33
Echinoidea																	
Parechinus angulosus	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0.67	0	0
Holothuroidea																	
Cucumaria sylcion	0	0	0	0	0	0	0	0	0	0	0	0.67	0	0	0	0	0
Mollusca																	
Polyplacophora																	
Acanthochitona garnoti	0	0	0	0	0	0	0	0	0	0	0	0	0.33	0.33	0	0.33	0.33
Gastropoda																	
Burnupena cincta	0	0	0	0	0	0	0	0	0	0	0	1.33	0	0	0	0	0
Burnupena lagenaria	6	0	7	9.67	0	7.33	11.33	0.33	12.33	7	2	10.33	0	0	7.33	0	0
Clionella rosaria	0	0	0	0.33	0	0	0	0	0	0	0	0	0	0	0	0	0

Species	JanMonLw	JanMonHi	JanMonMd	JanMulLw	JanMulHi	JanMulMd	MayMonLw	MayMonHi	MayMonMd	MayMulLw	MayMulMd	MarMonLw	MarMonHi	MarMonMd	MarMulLw	MarMulHi	MarMulMd
Fissurella mutabilis	0	0	0	0	0	0	0	0	0	0	0	2	0	0	2.33	0	0
Fissurella natalensis	0	0	0	0	0	0	0	0	0	0.33	0	0	0	0	0	0	0
Helcion dunkeri	0	0	0	0	0	0	0	0	0.33	0	0	0.33	0	0	0	0	0
Helcion pruinosus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.33	0	0
Nodilittorina africana	0	0	0	0.33	0	0	0	0	0	0	0	0	0	0	0	0	0
Nucella dubia	1	0.33	2.33	0	0	0	0	1.33	0	0	0	0.33	0.33	1.33	4.33	2.67	1
Nucella squamosa	1	1.67	2	1.67	0.33	1	0	1	0	1.67	1	0	0	1.67	1.33	0.33	0.33
Oxystele impervia	0	0	0	0	0	0	0	0	0.33	0	0	0	0	0	0	0	0
Oxystele sinesis	0	0	0	0	0	0	0	0	0	0	0	0	0	0.33	0	0	0
Oxystele tabularis	0	0	0	1.33	0	0	0	0	0.67	0	0	0	0	0	0	0	0
Oxystele tigrina	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Oxystele variegata	0	0	0	0	0	0	0	0	0	0	0	0.33	0	0	0	0	0
Protomella capensis	0	0	0	0	0	0	0	0	0	0.33	0	0	0	0	0	0	0
Scutellastra longicosta	0	0	0	0	0	0	0	0	0	0	0	0.33	0	0	0	0	0
Scutellastra granularis	2.33	0	0.67	1.67	0.67	0	1.33	0.67	1.33	0.33	2.33	6.33	2.67	1.67	6.67	3	7.67
Siphonaria capensis	0	0	0	0	0	0	0	0	0	0	0	0	0	0.33	0.33	0	0
Tricolia neritina	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.33	0	0
Vermetus corallinaceae	0	0	0.33	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Bivalvia																	
Lasaea adansoni turtoni	0	0	0	0.33	87.33	0.33	0	6	0	0	0	0	17.67	25	1.33	47	5.33
Other	0	0	0	0	0.33	0	0	0	0	0	0	0	0	0	0	0	0
No. of individuals	17.33	4.33	33.33	26.67	107	20.67	19	54	31.33	13.33	16.67	75.67	103.67	140.33	109	83.67	35.67
No. of species	12	6	12	14	12	11	10	11	13	9	7	23	9	13	21	11	14
d	5.381	4.581	4.333	5.618	4.244	4.538	4.378	3.945	4.849	4.337	3.036	7.093	3.049	4.07	6.138	3.698	4.906
Shannon Index (H')	2.377	1.626	2.274	2.466	2.055	2.136	2.06	2.084	2.307	1.916	1.759	2.793	1.878	2.161	2.752	2.069	2.395
J'	0.9267	0.9077	0.915	0.9106	0.827	0.8909	0.8947	0.8689	0.8996	0.8718	0.9039	0.8908	0.8548	0.8424	0.9039	0.8629	0.9076

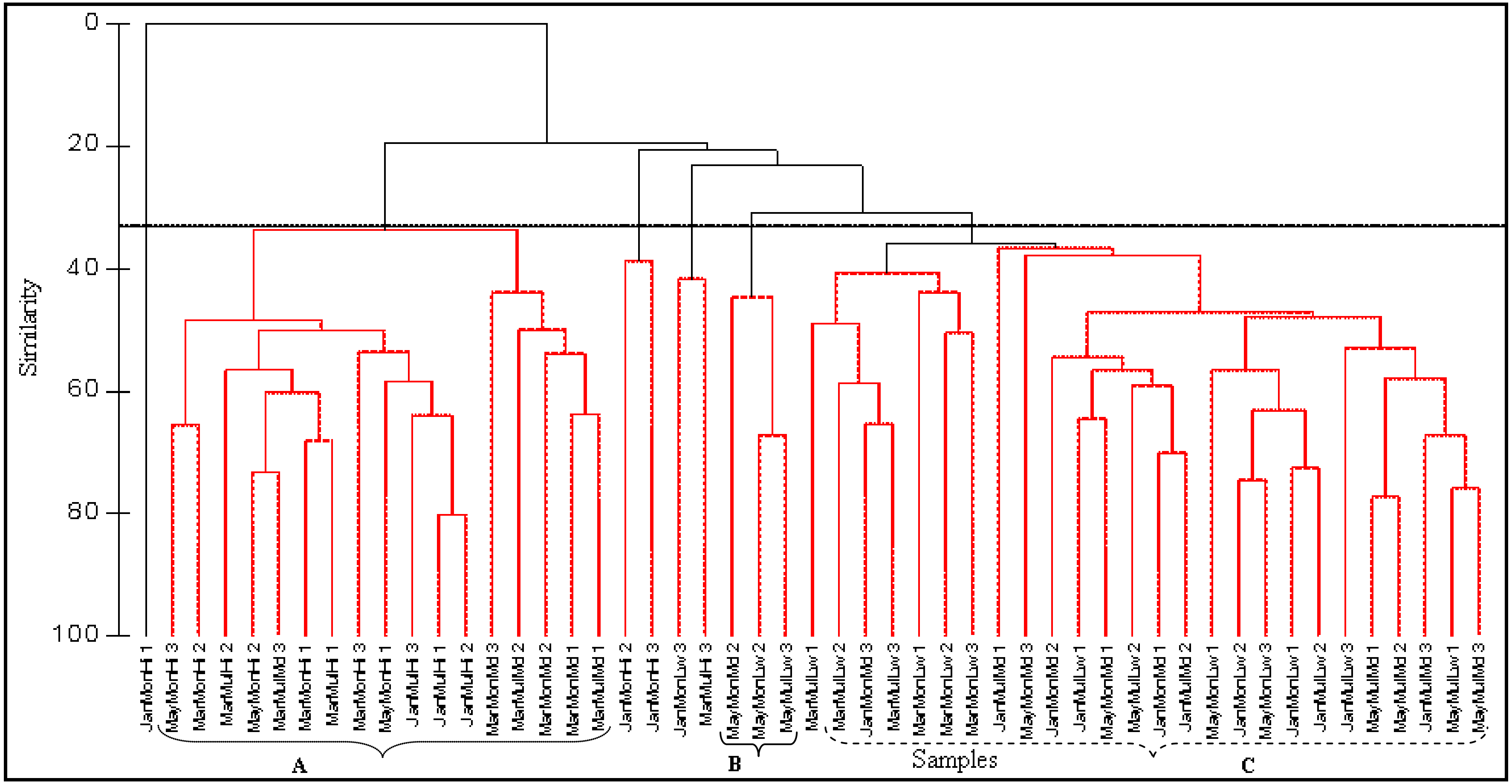

Figure 3.1 Hierarchical cluster analysis (log-transformed data) of macrofauna associated with mussel beds (see Appendix I for key to labels). At 34% similarity, the dendogram forms five groups excluding the outlier. Group A contains mostly high shore samples and groups B and C include samples from the mid and low shore, respectively.

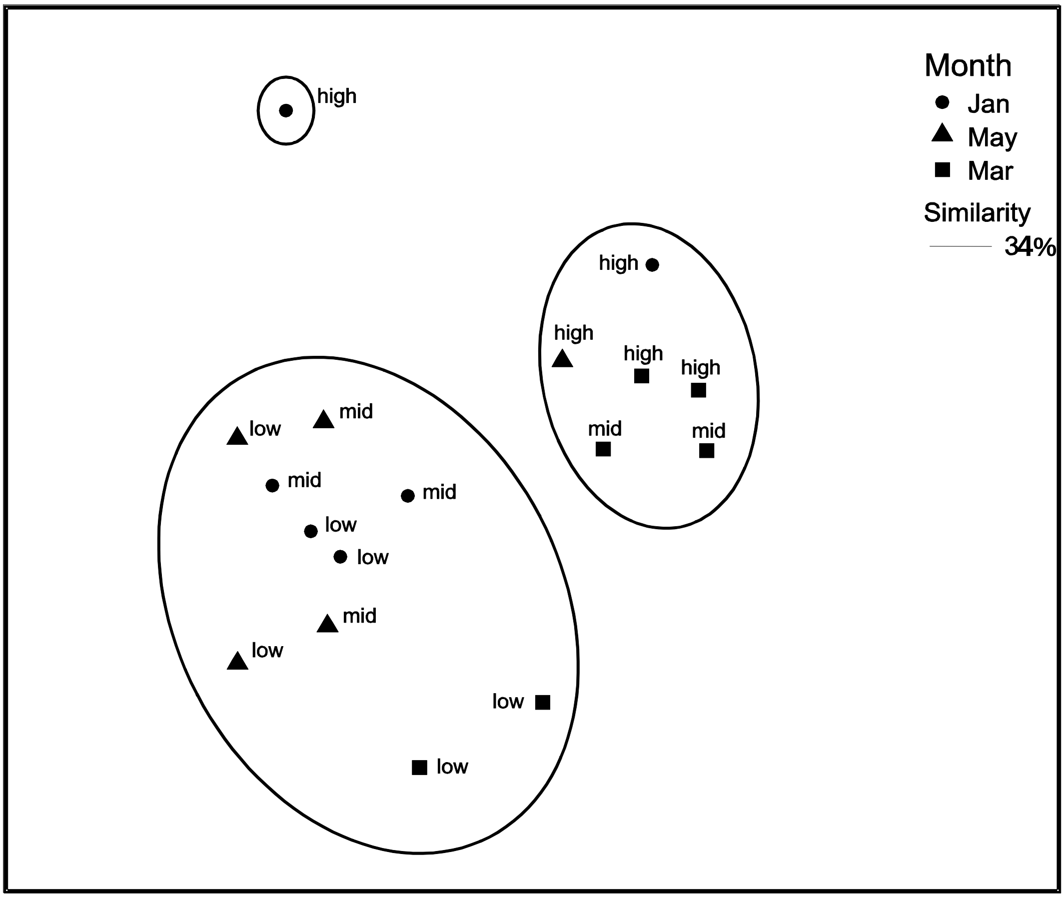

Figure 3.2 Two-dimensional MDS diagram grouping samples according to zonation (high, mid and low zones) for three months (0.1 stress factor).

The global test results of the crossed ANOSIM between the factors month ($p<0.025$; R= 0.53) and zone ($p<0.03$; R= 0.25) were significant. However, for zone, the pairwise tests could not detect or distinguish where the significant differences were (Table 3.2a) because the zones were not significantly different from each other. This is probably because of the common species that occurred in the mid zone and in either the high or the low zones as well (Figure 3.2). Another possible explanation for the non-significant effect of the pairwise test for the zone treatment could be a methodological one due to the low number of replication ($n = 3$) that may lead to low statistical power.

In the case of month, March 2007 was significantly different from both January ($p = 0.04$; $R = 0.75$) and May 2004 ($p = 0.04$; $R = 1$) (Table 3.2b). The crossed ANOSIM between month and layer was non-significant.

Table 3.2 Pairwise tests for differences between zone (a) and month (b) groups across all zones.

a)

Groups	R statistic	Significance level (p)	Possible permutations	Actual permutations	Number >= observed
Low, high	0.605	0.11	27	27	3
Low, mid	0.167	0.3	27	27	8
High, mid	0.309	0.11	27	27	3

b)

Groups	R statistic	Significance level (p)	Possible permutations	Actual permutations	Number >= observed
Jan, May	-0.309	0.85	27	27	23
Jan, Mar	0.75	0.04	27	27	1
May, Mar	1	0.04	27	27	1

The similarity of percentages was calculated to identify the species that contributed most to the dissimilarities for factors month and zone. The species listed in Tables 3.3 and 3.4 are those contributing substantially to the differences among the months and zones respectively. A percentile value was used to report the average dissimilarity in the species composition and abundance between months (Table 3.3) and zones (Table 3.4). The higher the value, the less similar the groups were. January and May 2004 were more similar to one another than March 2007 was with either month (Table 3.3).

Table 3.3 Average dissimilarity percentages between month groups and the percentage contributions of key species to the total dissimilarity of communities in each month. The cut off for low contributions is between 90-91%.

Month	Jan-04 / May-04	Jan-04/Mar-07	May-04/Mar-07
Average dissimilarity %	46.69	62.62	61.23
Species	**Percentage contribution to community abundance (%)**		
Acanthochiton garnoti		1.28	1.08
Burnupena lagenaria	5.34	4.5	5.32
Bunodactis reynaudi	6.01	1.99	2.68
Chthamalus dentatus	12.22	7.1	7.73
Cirolana vesticaude	3.8	3.31	2.03
Desis formidabilis	1.77		
Dynamenella huttoni	3.7	2.51	2.64
Eunicidae (family)	1.19		
Exosphaeroma porrectum	2.39	1.21	
Fissurella mutabilis		1.76	2.41
Guerea rhomba		2.34	1.39
Hyale grandicornis	7.77	4.64	5.25
Hyale hiripalma		7.61	8.69
Lasaea adansoni turtoni	6.08	11.45	8.89
Lumbrinereis tetrauna	3.06		1.41
Maera bruzeli		1.2	
Nucella dubia	5.63	3.94	4.53
Nucella squamosa	5.15	3.03	2.89
Octomeris angulosa	7.11	14.62	11.99
Oxystele tabularis	2.87		
Parechinus angulosus			1.28
Patiriella exigua	2.24	1.74	2.24
Pseudonereis variegata	6.44	3.22	3.53
Scutellastra granularis	6.85	6.98	5.82
Sphaeramene polytylops		4.6	6.3
Tanystylum breviceps	1.43		1.16
Tetraclita serrata		1.03	1.07

Table 3.4 Average dissimilarity percentages between zone groups and the percentage contributions of key species to the total dissimilarity of communities in each zone. The cut off for low contributions is between 90-91%.

Zone	low/high	mid/low	high/mid
Average dissimilarity %	70.32	50.84	55.30
Species	**Percentage contribution to community abundance (%)**		
Burnupena lagenaria	13.31	7.58	11.18
Bunodactis reynaudi	4.85	4.67	3.12
Chthamalus dentatus	8.89	10.1	11.32
Cirolana vesticaude	2.73	3.06	5.33
Desis formidabilis	1.19	1.2	1.57
Dynamenella huttoni	4.75	5.37	1.6
Eunicidae (family)		0.85	
Exosphaeroma porrectum		1.83	2.35
Fissurella mutabilis	1.7	1.86	
Guerea rhomba	1.22		1.94
Helcion dunkeri		0.74	
Hyale grandicornis	4.87	6.68	6.84
Hyale hiripalma		3.97	5.79
Lasaea adansoni turtoni	12.67	3.86	12.61
Lumbrinereis tetrauna	1.46	2.39	
Nucella dubia	3.41	2.9	4.91
Nucella squamosa	2.28	3.39	3.07
Octomeris angulosa	7.37	5.48	9.77
Oxystele tabularis	1.27	2.1	
Parechinus angulosus	0.98		
Patiriella exigua	3.18	3.85	
Pseudonereis variegata	4.08	5.8	5.61
Scutellastra granularis	4.42	5.58	3.31
Sphaeramene polytylops	4.44	4.85	
Tanystylum breviceps	1.33	1.34	
Tetraclita serrata	0.99		

The high and low mussel zones were very dissimilar in their species composition and abundance, but the mid zone was predictably similar to the other zones (Table 3.4). The whelk *Burnupena lagenaria*, the bivalve *Lasaea adansoni turtoni* and the barnacle *Chthamalus dentatus* contributed the most to the percentage dissimilarities between the high/low, mid/low and high/mid zones respectively (Table 3.4).

The 3-way ANOVA for species evenness (J') and richness (d) for the factors layer and zone between January 2004 and March 2007 showed all factors and interactions to be non-significant. However, species diversity (H') differed significantly across zones (p= 0.00007) regardless of layer or month (Table 3.5).

Table 3.5 Three-way ANOVA for Shannon diversity index (H') between January 2004 and March 2007. The asterisks indicate significant p-values.

	Df	SS	MS	F	p
Month	1	0.127	0.127	0.783	0.385
Layer	1	0.010	0.010	0.062	0.805
Zone	2	4.746	2.373	14.678	< 0.001*
Month X Layer	1	0.001	0.001	0.007	0.935
Month X Zone	2	0.211	0.105	0.652	0.530
Layer X Zone	2	0.004	0.002	0.014	0.987
Month X Layer X Zone	2	0.337	0.168	1.041	0.369
Error	24	3.880	0.162		
Cochran's *C* test		0.790			

Df = degrees of freedom; SS = sum of squares; MS = mean squares; F = f-ratio; p = significance level.

The zones were all significantly different from each other (see Student Newman-Keuls post-hoc groups in Figure 3.3) and species diversity increased from the high to the low mussel zone.

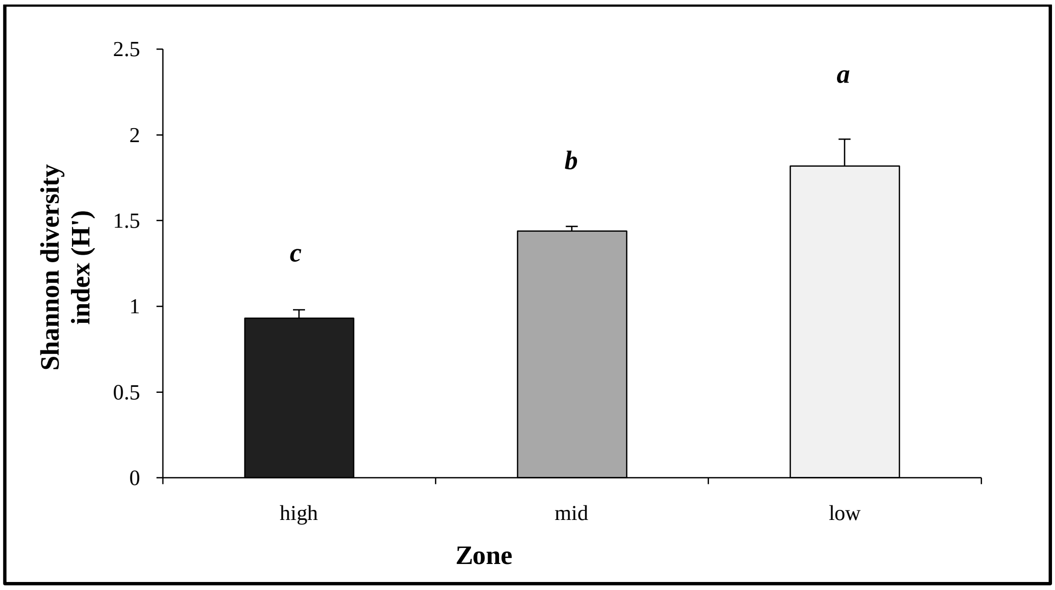

Figure 3.3 Shannon diversity index (H') results for the effect of zone in the 3-way ANOVA for January 2004 and March 2007. Labels ***a***, ***b*** and ***c*** define homogenous groups identified using the student Newman-Keuls post-hoc test. The error bars indicate the standard error.

The 2-way ANOVAs between the monolayer samples of January and May 2004, and March 2007 were non-significant for all three indices. However, the results of the Shannon diversity index showed a similar pattern to the 3-way ANOVA between January 2004 and March 2007 samples. Although the results were non-significant, the ranking of the species diversity index also decreased from the low to the high zone (Figure 3.4).

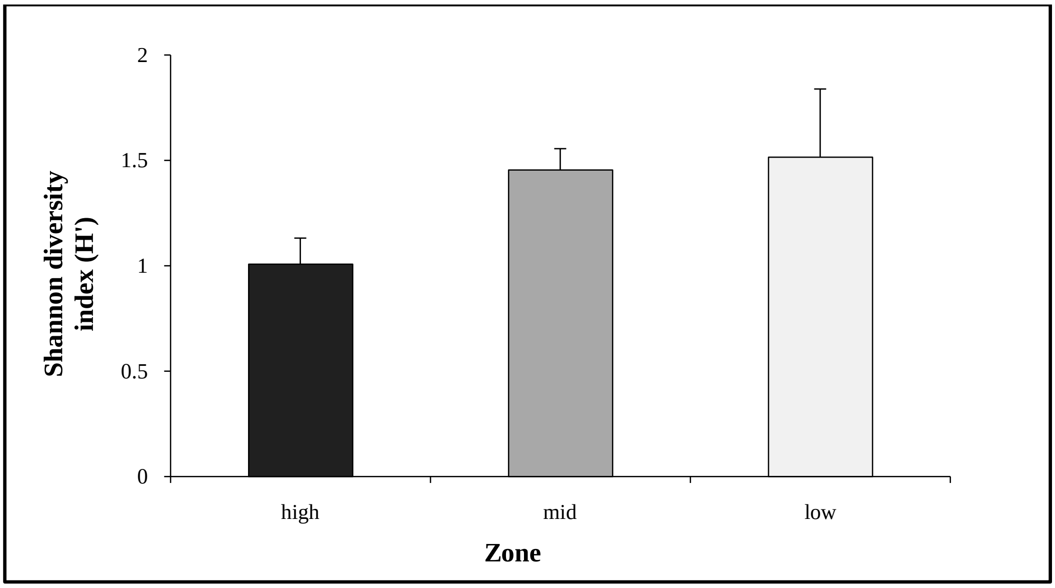

Figure 3.4 Shannon diversity index results for the 2-way ANOVA for monolayer samples of January and May 2004, and March 2007 showing the effcet of Zone. The error bars indicate the standard error.

Discussion

Mussel beds are generally very productive habitats that support high levels of biodiversity (Tsuchiya 2002). From this study, a total of 52 species were collected, most of which belonging to the phyla Arthropoda and Mollusca. This study tested how the community structure of the macro-invertebrates associated with mussel beds are affected by mussel bed layering, mussel zonation and time, at small scales.

The species that occur intertidally differ throughout the South African coast, even at small scales (Hammond 2001). Apart from the difference in biogeographic regions, two significant events that have changed the communities on South African shores are the over-harvesting of mussels on the east (Lasiak & Dye 1989) and invasion by *Mytilus galloprovincialis* on the west and south-east coasts (Hammond 2001; Robinson *et al* 2005; Hanekom 2007; Robinson *et al* 2007). The introduction of *M. galloprovincialis* to South Africa has affected the indigenous mussels dramatically (van Erkom & Schurink 1990; Hammond 2001), and the population structure of mussels has changed (Grant & Cherry 1985; Viladomiu 2005). *M. galloprovincialis* has out-competed some mussel species (e.g. *Aulacomya ater* in Hockey & van Erkom Schurink 1990 and *Choromytilus meridionalis* in Brown & Jarman 1978; Robinson *et al* 2007) intertidally because of its high endurance of aerial exposure, high fecundity (van Erkom & Schurink 1990), resistance to predators and some trematode parasites (Calvo-Ugarteburu 1996).

Although larval settlement for *Mytilus* and *Perna* is similar and highest on the low shore (Porri *et al* 2007), *M. galloprovincialis* also settles on the high shore (van Erkom & Schurink 1990). Consequently, the introduction of *Mytilus* has extended the upper shore limit and the biomass of mussels on these rocky shores (Robinson *et al* 2007), increasing settlement space for associated organisms (Hammond 2001).

While *Mytilus* can survive on the high shore (Hammond 2001), the harshness of physical factors there may limit some species normally associated with mussels. At the same time, like *Musculista senhousia* in California, (Crooks & Khim 1999), *Mytilus* creates more habitable space for a number of organisms which previously could not exist. This is because of the ameliorated stress and increased water retention and suspension of food material for the infauna (Hammond 2001; Robinson *et al* 2007). Both biological and physical factors affect the community structure of the marine organisms associated with mussel beds (Crooks & Khim 1999; Hammond 2001). Species abundance and composition differs from coast to coast because it is governed by a combination of environmental factors and biological interactions (Chintiroglou *et al* 2004).

For this study, different species were found abundantly at different tidal levels, but few were exclusive to a specific zone. *Burnupena lagenaria* and the limpet *Scutellastra granularis* were most abundant on the low shore, the barnacle *Chthamalus dentatus* and the polychaete *Pseudonereis variegata* on the mid shore, and the barnacle *Octomeris angulosa* and the bivalve *Lasaea adansoni turtoni* on the high shore. However, there were a few species that were found exclusively in specific zones and months (Table 3.3, 3.4 and 3.5). March 2007 samples had a wider representation of species contributing to the community abundance than January and May 2004. The sea anemone *B. reynaudi* and the whelk Nucella *squamosa* characterized the community differences between January 2004 and March 2007 (Table 3.4).

From the present study, the distribution, composition and abundance of the fauna associated with mussels were strongly influenced by zonation even though degrees of variability were observed. This could partially be due to the fact that samples were collected haphazardly within zones with chances that some collections from the mid zone were collected near its upper and lower edges. The low and high zones were not exclusively different from each other because some species were found in both zones, but at different densities (Hammond 2001). The transitional (mid) zone contained the same species occurring in the high and low zones (Table 3.5). This was unexpected because biogenic habitats are considered to be buffers of physical disturbance, and their presence should limit the usual patterns of physical stress associated with tidal height. In Hammond (2001), tidal height only affected species composition and not the abundance of the infauna. If the structure of mussel bed cover for each mussel species is different, similarly the structure of the infaunal community may differ (Hammond 2001; Viladomiu 2005). In addition to the distinct vertical zonation of the two study mussels (Bownes & McQuaid 2006), there are three other possible reasons for differences in community structure associated with the beds of different mussel species. The differences in shell morphology, mussel size or sediment accumulation (of byssal threads, fragments of mussel shells, and sand) could affect the associated invertebrate community (Hammond 2001). Since sediment accumulation differed from low to the high shore (see Chapter 2 for details), this study seem to be in partial agreement with Hammond's study.

The findings of Lawrie and McQuaid (2001) that multilayer beds had the highest recruitment of mussel larvae because of the complex mussel bed structure were contrary to the data on numbers of species from the samples collected during the present study. Mussel bed layering had no effect on the community structure of the associated macrofauna. Beadman *et al* (2004) reported that abundance of the infauna has a negative correlation with mussel density. Thus, smaller patches of mussels cater for a larger number of organisms. Multilayer beds are more complex in structure and are expected to provide habitats for a wider diversity of species (Hammond 2001). However, in the present study there was no effect of layer. The packing density of sediment and biodeposition in the multilayer beds may reduce the interstitial spaces between the mussels, and create an oxygen deficient environment that may be less conducive for organisms to persist in greater abundances (Tsuchiya & Nishihira 1985; Hammond 2001).

Because the intertidal zone experiences harsh physical stresses (e.g. aerial exposure, desiccation, etc.), species richness was expected to decrease gradually when moving up shore (Saier 2002). The results of the present study agreed with this and the species diversity index (H') decreased from the low to high shore. However, very few species were found to be different and restricted to either the high or low shore. The gradual change in the abundance patterns of some species with tidal height could presumably be because of the changing environment and tolerance for physical stress (Hammond 2001) or mussel species. Moreover, the high dissimilarity between the high and low shore groups indicated that the species that contributed most to the mean abundances differed. The whelk *Burnupena lagenaria*, the limpet *Scutellastra granularis* and the polychaete *Pseudonereis variegata* were the main contributors to community abundance on the low mussel zone. On the high mussel zone, the bivalve

Lasaea adansoni turtoni, and barnacles *Chthamalus dentatus* and *Octomeris angulosa* were most abundant. Hammond (2001) also found that *P. variegata* was most abundant on the low shore, but only for one of the three sampling sites on which the amphipod *Paramoera capensis* dominated. Contrary to my findings, Hammond (2001) found that *Pseudonereis variegata* was most abundant on the high shore as well. The mid zone included a variety of species that occurred in both the high and low zones, possibly because this is a transitional zone with moderate stress levels that can be endured by a wider selection of species.

Mussels occupy most of the low rocky shore in Plettenberg Bay. However, their densities differ from site to site (Bownes & McQuaid 2006), especially at small scales (e.g. *Perna perna* in Erlandsson *et al* 2005). At the study site, *Mytilus galloprovincialis* on the high shore had a lower mussel cover than on the lower zones (pers. obs.; von der Meden *et al* 2008) probably because of increased wave exposure and subsequent dislodgement due to their weak attachment strength (Zardi *et al* 2006a; Hanekom 2007). The changing density of mussels may negatively affect the abundance of associated species and the types of species that occupy mussel beds (Beadman *et al* 2004). Wright and Jones (2006) claimed that the consequences of the removal of a foundation species have not been explored. However, a few other researchers (Lasiak & Dye 1989; Lasiak & Field 1995; Hammond 2001) have documented potential and existing threats to the loss of mussels, as foundation species. The biomass and abundance of associated fauna decreases when mussels are removed intertidally (Hammond 2001).

Lohse (1993) compared the species occurring in mussel beds and on the rock and found them to be similar, proving that these substrata are not so different. However, Thiel and Ullrich (2002) claimed that associated organisms were more abundant within mussel beds than surrounding substrata or habitats. The comparison of biodiversity between the adjacent rock substratum and in the mussel beds was not considered in this study. The presence of mussels on rocky shores does not necessarily mean that species biomass is increased (Thiel & Ullrich 2002), but mussel beds do facilitate the existence of some species (Hammond & Griffiths 2004) while excluding others (Ragnarsson & Raffaelli 1999). The introduction of *Mytilus* has not only extended the occurrence of mussel beds vertically, but it has subsequently increased the benign, habitable spaces for other organisms to survive on the high shore (Robinson *et al* 2007). Mussels on hard substrata cater for a distinct group of organisms that need to take refuge from wave action and predators on rocky shores (Thiel & Ullrich 2002). The uniformity of species richness in this study was probably because the samples were collected from the same site (Bustamante *et al* 1997). The apparent trend observable from the results of the present study is that the effectiveness of mussels in providing this shelter changes from the low to the high shore, regardless of the structural and temporal component. This suggests that zonation may govern biodiversity patterns at the scales that were examined in this study, overcoming parameters like structural and temporal variability. Although the choice of one site was appropriate for the hypothesis test in this study, the results cannot be extrapolated as general patterns of this coast. In conclusion, therefore a study over a larger area (e.g. Hammond 2001) and the addition of more sites is necessary to detect the general long-term structural effects of mussel beds on biodiversity.

Appendix 1

Key to labels in Table 3.1 and Figure 3.2

Label	Layer	Month	Zone
JanMonLw	Mono	Jan	Low
JanMonHi	Mono	Jan	high
JanMonMd	Mono	Jan	mid
JanMulLw	Multi	Jan	low
JanMulHi	Multi	Jan	high
JanMulMd	Multi	Jan	mid
MayMonLw	Mono	May	low
MayMonHi	Mono	May	high
MayMonMd	Mono	May	mid
MayMulLw	Multi	May	low
MayMulMd	Multi	May	mid
MarMonLw	Mono	Mar	low
MarMonHi	Mono	Mar	high
MarMonMd	Mono	Mar	mid
MarMulLw	Multi	Mar	low
MarMulHi	Multi	Mar	high
MarMulMd	Multi	Mar	mid

Chapter 4

The effect of barnacles on invasive (*Mytilus galloprovincialis*) and indigenous (*Perna perna*) mussels on the south-east coast of South Africa

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Introduction

Mussels make an important contribution to biodiversity on rocky shores (Tsuchiya 2002; Hammond 2001; Gilek *et al* 2001). They increase the surface area for the settlement of marine invertebrates (Hammonds & Griffiths 2006; Bustamante *et al* 1997; Lohse 1993). The introduction of *Mytilus galloprovincialis* on the South African coast may help in increasing infaunal and epifaunal biodiversity and abundance (Hammond 2004; Robinson *et al* 2005). This is because it has increased volume of mussels per unit area and mussel cover on these rocky shores (van Erkom Schurink & Griffiths 1990; Branch & Steffani 2004). Although alien invasive species are said to have negative influences on ecosystems and indigenous species (Hoddle 2004; Robinson *et al* 2005), they also increase the settlement range and biomass of mussels by settling higher up the shore than *Perna* can go (van Erkom Schurink & Griffiths 1999; Bownes & McQuaid 2006). In a study conducted by Wernberg *et al* (2004), sampling at different times of the year increased the variation in the biomass of fauna found within indigenous and invasive macroalgae. Although the two macroalgal species provided different habitat types, the species found occupying these microhabitats were almost identical (Wernberg *et al* 2004). This may imply that biological invasions do not necessarily have the expected negative effect on ecosystems (Branch & Steffani 2004; Wernberg *et al* 2004). For example, in this case an invasive species increased the habitat range for many more epifaunal marine invertebrates to be supported (Wernberg *et al* 2004). The marine invertebrates found living in and amongst mussels can be categorised into three groups, namely "free-living" invertebrates that live in the spaces among the mussels and organisms found in the sediments among the mussels (e.g. polychaetes) and epibiotic organisms living on the mussels that could be sessile (e.g. bryozoans and barnacles) or errant (e.g. limpets) (Tsuchiya 2002). The epibiotic species could be sessile (like bryozoans and barnacles) or errant (meaning free living, like limpets).

Epibiosis refers to an ecological relationship in which an organism (the epibiont) lives on or attaches itself onto the outer body surface of another (the "basibiont") (Wahl *et al* 1997). Epibiosis can be considered as one of the many positive interactions observed in ecological systems (Stachowicz 2001). Laudien & Wahl (2004) describe this interaction as one of the closest symbiotic associations in subtidal ecosystems. Epibionts may alter or have an effect on a number of biological interactions between the living and non-living aspects of their environment and their host. The exterior appearance and texture of the host organism is modified, making it either harder for predators to recognize or more palatable to starfish or easier to handle for others (e.g. shore crabs) (Laudien & Wahl 2004). However, Brande (1982) found that the presence of barnacles on bivalve shells does not encourage predation. Epibionts influence not only predator-prey interactions, but can also decrease the mobility, the reproductive output and the survival of the host organism. For example, Buschbaum and Reise (1999) observed that when the barnacle *Balanus crenatus* settled intensely on the outer shell of *Littorina littorea*, the periwinkles were disadvantaged because they struggled to move and their fitness was reduced. Although there are an array of other factors that could be contributing to this, the reduced motility and decreasing reproductive rates may build up and become fatal (Buschbaum & Reise 1999). This interaction could eventually result in the local alteration of the structure of marine communities (Buschbaum & Reise 1999). Laudien & Wahl (2004) warned of the potential critical destruction of mussels as a result of the symbiotic association with barnacles.

Here, I investigated the epibiotic relationship between barnacles and mussels. In marine ecosystems, of the various biological interactions that affect the community structure and species composition, mutualisms are known to contribute to the coexistence of potentially competing species (Laihonen & Fürmen 1986; Schmitt & Holbrook 2003). The epibiotic association between barnacles and mussels could be commensal (Laihonen & Fürmen 1986), because barnacles benefit from the settlement space (Buschbaum & Reise 1999) and increased food availability due to the currents generated by mussels (Laihonen & Fürmen 1986). Mussels and barnacles are both filter-feeders and they feed from the same water that washes over the rocky shores (Laihonen & Fürmen 1986). Thus, there is also the possibility of competition for food between the two organisms in such an association (Laihonen & Fürmen 1986).

Intertidally, the persistence and distribution of barnacles depend on a number of biological interactions, for example, predator-prey interactions (Brande 1982; Buschbaum & Reise 1999; Buschbaum 2000; Buschbaum 2002), their general tolerance of the physical factors encountered on the rocky shore (Pineda & Caswell 1997; Buschbaum 2002; Delafontaine & Flemming 1989) and salinity ranges (Chan *et al* 2001). Their distribution and population structure also depends on the amount of suitable space that is available for settlement (Pineda & Caswell 1997).

Many scientists have shown that barnacle larvae exhibit active behaviour during settlement for example in Grosberg (1982) and Hills *et al* (1998). They do this by being selective of where they settle, preferring habitats that are favourable and avoiding those that are not (Delafontaine & Flemming 1989; Hills *et al* 1998). However, it has also been suggested that barnacle larvae settle on the first hard substratum that they come into contact with (Walter 1992).

The main focus of this study was to examine the close epibiotic association between mussels (basibionts) and barnacles (epibionts), and provide a broader understanding of whether or not barnacles are a threat to the health status of mussels. The relationship between mussels and barnacles was investigated on the south coast of South Africa by measuring the health status of barnacle-infested (hereafter infested) and non-infested mussels for two mussel species, namely *Mytilus galloprovincialis* and *Perna perna*. The main barnacle species occurring on the south coast of South Africa, and the focal epibionts for this study, are *Chthamalus dentatus*, *Tetraclita serata* and *Octomeris angulosa* (Delafontaine & Flemming 1989). The aim was to detect whether the condition index of either mussel species decreases with increasing barnacle infestation. This was done by examining the prevalence and the intensity of infestation at different tidal levels (high, mid and low mussel zones) on single-layered mussel patches. Subsequently, positive and negative interactions between epibionts and basibionts were examined by measuring the condition index of mussels in symbiosis and those without epibionts. The aim was to understand the epibiotic association between mussels and barnacles better and if possible to define it as a commensal, a mutualistic or a parasitic relationship.

Materials and Methods

Data collection for the research study was conducted in Keurbooms, Plettenberg Bay, South Africa, where there was a relatively equal representation of both mussel species *P. perna* and *M. galloprovincialis* (von der Meden *et al* 2008). The area of the shore occupied by mussels is divided into the high, mid- and low zones, with *Mytilus galloprovincialis* colonising the high zone and *Perna perna* inhabiting the low zone. The mid zone was the region between the high and low zone where the two species overlap and coexist forming a mixed zone (Bownes & McQuaid 2006). For the description of the study site, please refer to the materials and methods of Chapter 2.

The statistical analyses were performed using the STATISTICA package version 7.1 (StatSoft 2006). For the epifaunal study, data collection was divided as follows:

Condition index versus percentage cover of epibionts

The purpose of this analysis was to determine whether the health status of infested mussels was different from that of mussels that were not infested. This sample collection was conducted in monolayered mussel beds in the mid mussel zone in order to control for a number of factors, both physical and biological, experienced on opposite extremes of the shore; such as, differences in wave exposure and emersion periods, desiccation stress, predation and competition and shore topography. It was essential that samples were collected at the same tidal level to ensure that the two mussel species that naturally co-occur on this zone are exposed to the same food and environmental conditions.

A total of 216 individuals of infested and non-infested *P. perna* and *M. galloprovincialis* within the size range 2.15-8 cm were haphazardly collected from the mid zone. The samples were kept frozen until they were processed. For this study, an infested mussel was identified as one on which one or more barnacles had settled. Different levels of infestation were represented to broaden the spectrum of percentage cover of barnacles across the size range of mussels sampled.

Mussel length and the number of individuals per species were also controlled to allow a balanced comparison of condition index (CI) of infested and non-infested individuals within both species. The condition index was calculated using the equation below (Davenport and Chen 1987):

$$CI = \frac{\text{Dry soft tissue weight}}{\text{Dry shell weight}} \times 100$$

The maximum posterior-anterior length of the mussel shell was measured to the nearest 0.05 mm using a pair of vernier callipers, to ensure that they were within the preferred size range. The infested individuals were opened with a scalpel and the exterior of both valves was photographed and labeled according to the treatment they belonged to. This was done in order to calculate the area of the mussel shell and the area that the barnacle(s) covered on the two valves, so as to calculate percentage cover of epibionts. The areas were estimated using Image Tool software (UTHSCSA, version 3.00). Subsequently, the soft tissue of each mussel was scraped out, placed on aluminium foil pieces that were previously weighed and oven-dried to constant weight at 60°C for about 24 hours, along with the shells. The dried mussel soft tissue and shell were then weighed after the barnacles were removed from the shells in order to calculate the condition index for each mussel.

Statistical analysis

A partial correlation analysis was computed in order to establish whether there was any significant relationship between the condition index of the mussels and the percentage cover of barnacle epibionts. In addition, a 2-way ANCOVA was performed, with the CI as the dependent variable, mussel shell length (size) as the co-variate, and “infestation” (2 levels: infested or non- infested) and species (2 levels: *Mytilus* and *Perna*) as the independent variables (fixed factors). A post-hoc test (Student Newman-Keuls) was done in order to identify homogenous groups for significant results. Cochran’s test was used *a-priori* to the 2-way ANCOVA to test for the homogeneity of variances in the data set. Normality was tested using the

Kolmogornov-Smirnoff test. The percentage cover of epibionts was arc sine transformed to normalise the data and make homogenize variances.

Prevalence and intensity of barnacle infestation

To examine differences in the prevalence and intensity of barnacle infestations between the two mussel species, ten samples from the monolayer *Perna* (low zone), *Mytilus* (high zone) and mixed (mid zone) beds were collected using a 15 X 15 cm quadrat, bagged and frozen until further processing. Although there is a clear dominance of different mussel species in these zones, it was possible to find enough individuals of each species in each zone to be able to conduct this analysis.

The samples were washed under running water to remove any sediment and to separate the mussels, making sure that any epibiotic barnacles did not detach from the mussel shells. The maximum anterior-posterior length was measured to the nearest 0.05mm using vernier callipers. Only mussels greater than or equal to 1mm were considered for further processing and analysis. The percentage cover of epibiotic barnacles on each mussel individual and the mussels' CI were calculated using the dry soft tissue and dry shell weight (Davenport & Chen 1987). The number of infested individuals for each species and the intensity of the infestation in each zone were calculated and the results were related to the condition index (CI) of infested and non-infested mussels.

Statistical analysis

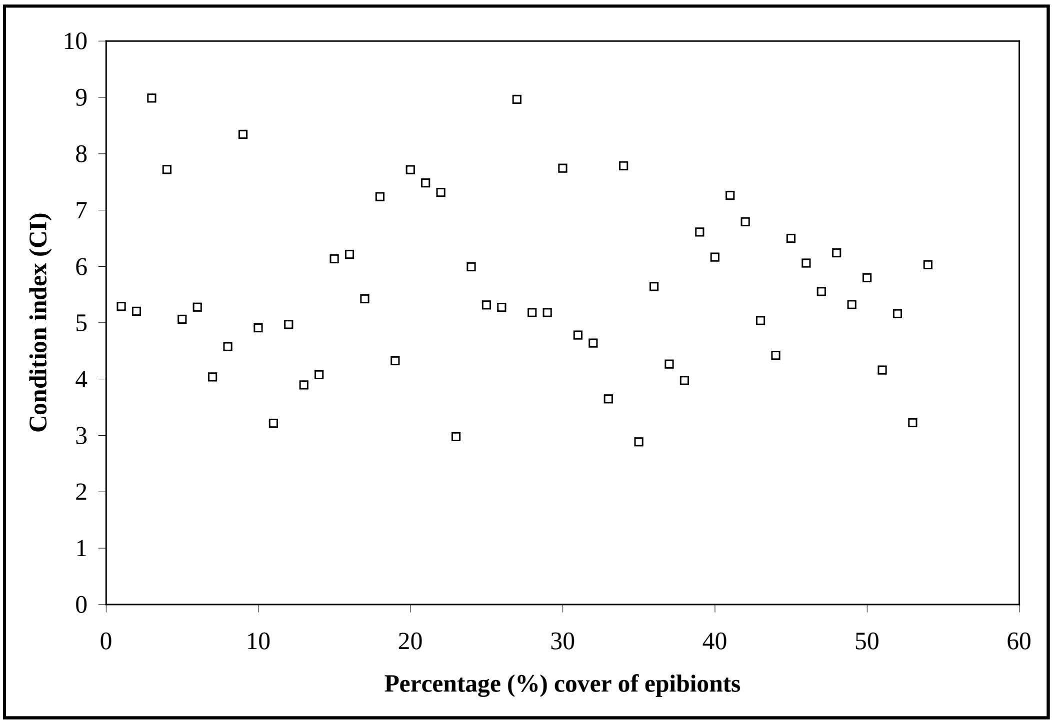
To test for the effect of the fixed factors zone (3 levels: high, mid and low) and species (2 levels; *Mytilus* and *Perna*) on the prevalence and the intensity of barnacle infestations, two 2-way ANOVAs were computed after the data had been arc sine transformed to homogenise the percentage values (percentage cover of epibionts). Homogeneity and normality were tested using the Cochran's and the Kolmogornov-Smirnoff tests, respectively.

The test for the assumptions of homogeneity of variances for both prevalence and intensity came out highly significant. However, Underwood (1997) has indicated that experiments of this nature - that have more than 5 treatments and where *n* was at least more than 6 - are robust to heteroscedasticity, as long as the data set is balanced. In such circumstances, the analysis of variance can still be used and the results are interpretable.

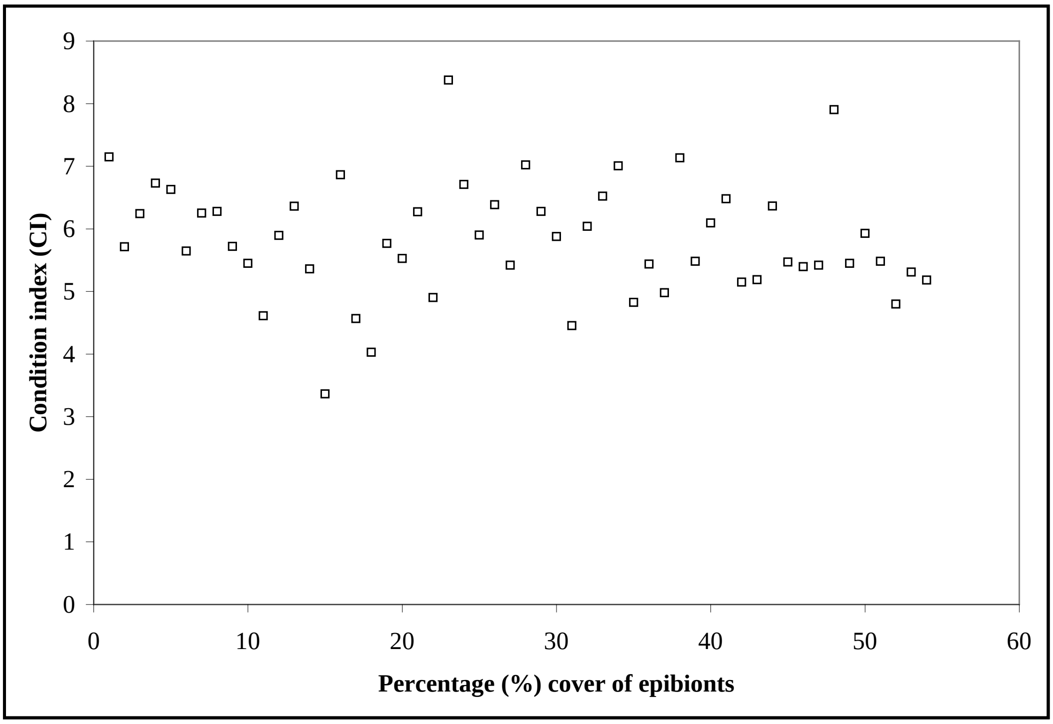
Results

Effects on CI

Chthamalus dentatus was by far the most common barnacle in this study, forming approximately 65 percent of all epibiotic barnacles, followed by *Octomeris angulosa* (~30 %) and *Tetraclita squamosa* (~5 %). Correlation coefficients (r) between mussel CI and barnacle cover on the shell -0.254 and -0.1001 were very low for *Mytilus* (Figure 4.1a) and *Perna* (Figure 4.1b). These values were non-significant, supporting the null hypothesis (Ho), at 95% confidence, that there is no significant correlation between the CI and the percentage cover of epibionts. This means that the CI of mussels is not correlated to the percentage cover of barnacles over this size range of mussels.



a) *Mytilus galloprovincialis*



b) *Perna perna*

Figure 4.1 Correlation of *Mytilus galloprovincialis* (a) and *Perna perna* (b) condition indexes with percentage cover of epibionts (barnacles). The sample size was 54 for both mussel species.

Although Figure 4.2 shows a general decline in the condition index of infested mussels compared to those that were not infested, the results of the 2-way ANCOVA were marginally non-significant for infestation (p = 0.053; Table 4.1). The data suggest that infestation has an effect on *M. galloprovincialis*, but not *P. perna*, though the interaction too was non-significant (p = 0.093).

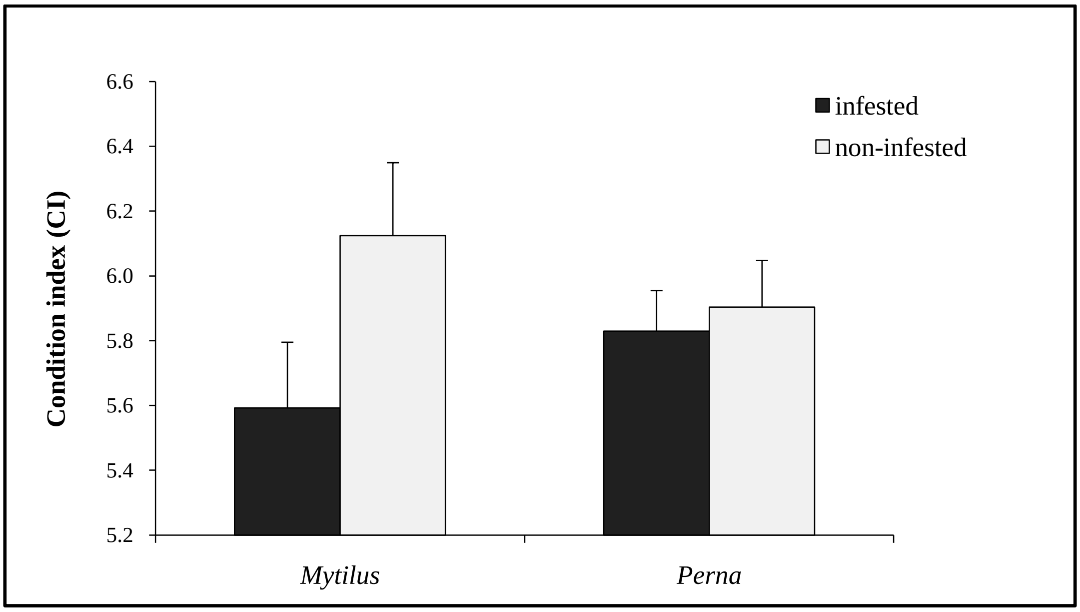


Figure 4.2 Condition indices of infested and non-infested *Mytilus galloprovincialis* and *Perna perna*. Error bars indicate the standard error.

Table 4.1 Two-way ANCOVA to test the effect of barnacle infestation on the CI of *Mytilus galloprovincialis* and *Perna perna*.

	Df	SS	MS	F	P
Size (cm)	1	1.330	1.330	0.746	0.388
Species	1	0.375	0.375	0.210	0.647
Infestation	1	6.736	6.736	3.776	0.053
Species X Infestation	1	5.067	5.067	2.840	0.093
Error	21	376.410	1.784		
Cochran's *C* test		0.476			

Df = degrees of freedom; SS = sum of squares; MS = mean squares; F = f-ratio; p = significance level.

Prevalence of Epibiosis

The prevalence of infestation (proportion of mussel individuals infested) showed a noticeable gradient, increasing in frequency from the high *Mytilus*-dominated zone to the low *Perna*-dominated zone (Figure 4.3), for both mussel species. This pattern was confirmed by the results of the 2-way ANOVA which showed a significant zone effect (p < 0.00001; Table 4.2). The post-hoc test (Student Newman-Keuls) indicates that the proportion of infested mussels (prevalence) was significantly different for each zone (*a*, *b* and *c* in Figure 4.3). There was no significant effect of species, but there was a marginally non-significant (p = 0.055) interaction between species and zone (Table 4.2) as the trend was identical for the two mussel species, but stronger for *P. perna*.

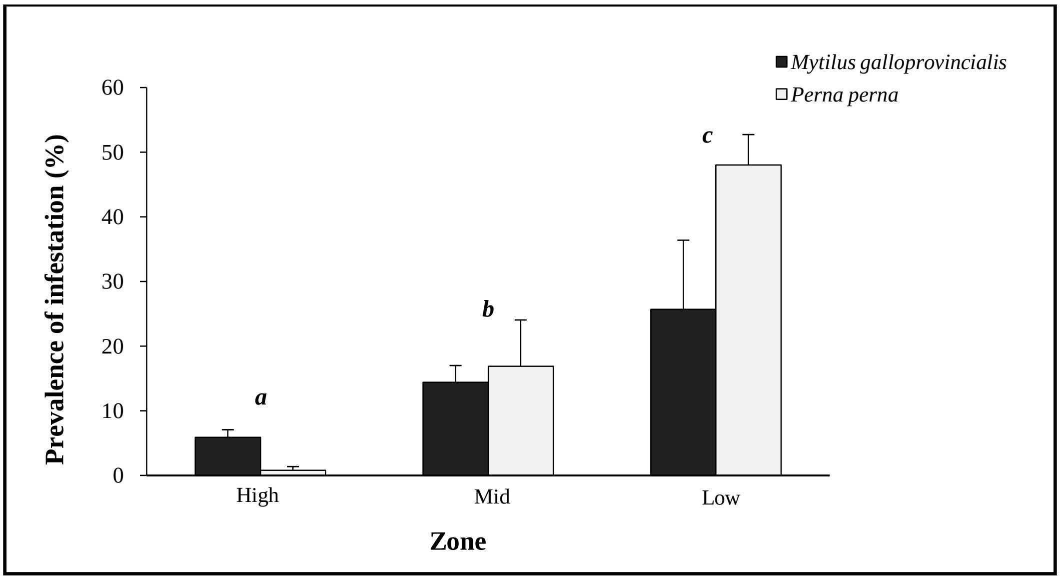


Figure 4.3 Two-way ANOVA on the prevalence of barnacle infestation for *M. galloprovincialis* and *P. perna* in high, mid and low zones. The error bars indicate the standard error.

Table 4.2 Two-way ANOVA of arc sine transformed prevalence. The asterisks indicate significant p-values.

	Df	SS	MS	F	p
Species	1	647.56	647.56	1.9840	0.165
Zone	1	11474.13	5737.07	17.578	<0.0001*
Species X Zone	1	2001.35	1000.67	3.066	0.055
Error	21	17624.59	326.38		
Cochran's *C* test		0.6			

Df = degrees of freedom; SS = sum of squares; MS = mean squares; F = f-ratio; p = significance level.

Intensity of epibiosis

For the intensity of infestation (mean number of barnacles per infested mussel) there was a strong significant interaction between zone and species (Table 4.3; p < 0.0001). The Student Newman-Keuls post-hoc test for this interaction displayed two significant groups (labelled "*a*" and "*b*" in Figure 4.4). The intensity of epibiosis was highest on both *M. galloprovincialis* and *P. Perna* in the mid mussel zone, and on either species respectively in the high or low mussel zone. In the high mussel zone, *P. perna* had a lower intensity of epibiosis by barnacles as did *M. galloprovincialis* in the low mussel zone (Figure 4.4). Thus levels of infestation were uniformly high where each species was common and lowest where each mussel species was rare or least abundant.

Table 4.3 Two-way ANOVA of arc sine transformed intensity. The asterisks indicate significant p-values.

	df	SS	MS	F	p
Zone	2	185.22	92.610	10.821	<0.0001*
Species	1	33.139	33.139	3.872	0.054
Zone X Species	2	282.531	141.266	16.506	<0.0001*
Error	54	462.156	8.558		
Cochran's *C* test		0.367			

Df = degrees of freedom; SS = sum of squares; MS = mean squares; F = f-ratio; p = significance level.

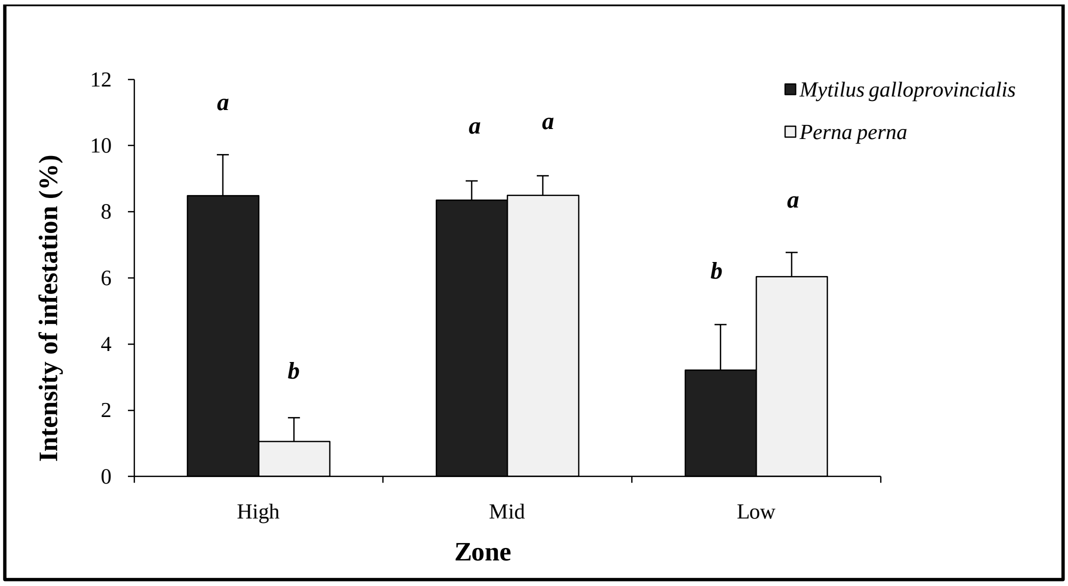


Figure 4.4 Intensity of barnacle infestations for *M. galloprovincialis* and *P. perna*, on the high, mid and low zones.

Discussion

Buschbaum and Reise (1999) found that the barnacle *Balanus crenatus* had deleterious effects on its host, *Littorina littorea*, reducing its fitness by affecting mobility, and reproductive effort. However, in this study, the presence of barnacle epibionts on mussels did not significantly affect the health status of the host regardless of species, even though trends in the data suggest that infested individuals generally have a lower condition index than those that are not infested.

Barnacle settlement is influenced by various biological and physical factors (Chan *et al* 2001) on the shore and in the water. These in turn affect their distribution and population structure (Buschbaum 2002; Chan *et al* 2001; Buschbaum 2000). Grosberg (1982) postulated that larvae from different species may either settle non-randomly on the shore or be attracted to familiar traces from habitats that favoured their success.

The frequency of species of barnacle epibionts reported during this study ranked, from the greatest to the least, *Chthamalus dentatus*, *Octomeris angulosa* and *Tetraclita serata*. Although these barnacle species co-occur on the intertidal rocks, certain species may be found dominating a specific part of the shore (Delafontaine & Flemming 1989). They can coexist without competing, because of their preferences for unique combinations of physical and environmental conditions (Delafontaine & Flemming 1989).

The overall distribution of barnacle infestation across the three zones in this study, as expressed by prevalence and intensity, can be discussed from a physical and a biological point of view. The prevalence of infestation revealed a noticeable gradient with increasing numbers of infested mussel individuals from the high *Mytilus* zone, to the low *Perna* zone, which had the highest count of infested mussels. This may be due to the differences in submergence time of the respective zones. There is extensive published literature on the factors that influence barnacle settlement and distribution on rocky shores (Walters 1992; Pineda & Caswell 1997; Hills *et al* 1998; Navarrete & Wieters 2000; Chan *et al* 2001; Kent *et al* 2003). Wave patterns are partially responsible for determining the spatial dispersion of larvae on the rocks (Delafontaine & Flemming 1989). The physical characteristics of the intertidal rocks, together with the effects of wave force and the difference submergence times, have an important effect on the manner in which the barnacle species orientate and arrange themselves in the microhabitats provided (Delafontaine & Flemming 1989).

Pineda and Caswell (1997) found that the movement of the waves (and tides) in and out of the shore affected barnacle settlement. At the same site where this study was conducted, mussel preferential settlement on the low shore was attributed to tidal height (Porri *et al.* 2007). The low shore has a relatively longer submersion time than the zones higher up shore (Pineda & Caswell 1997). Logically, this means that barnacle larvae have more time to settle onto the shells of mussels on the low shore. Conversely, the high and the mid zone are more exposed to air, and settlement time is limited to the consecutive arrival and departure of the waves (sea water), that transport cyprid larvae onto the rocky shores.

A second explanation for the patterns of prevalence observed is related to mussel coverage on the shore. The high zone on the study site has relatively poor mussel coverage and ranged from 0 to 40% cover (von der Meden *et al* 2008), with rock substratum still available as an alternative for barnacles to settle on. On the other hand, the mid and low shores were predominantly covered with mussels, with close to 100% cover, and no other alternative substratum was available for barnacle settlement. This could mean that barnacles actively prefer to settle onto the rock with the mussels as a second option, but have little option where mussel cover is nearly 100%. On the contrary, the settlement of barnacle larvae could also be random. Barnacles opportunistically inhabit all the available hard substrata (Brande 1982) in favourable environments. Barnacles on mussel shells opportunistically make use of the best available substrata by settling close to the siphonal edges, where feeding or respiratory currents are generated (Brande 1982; per obs.).

The intensity of barnacle infestation displayed surprisingly different results from prevalence. Generally, the mussel species that suffered the most in terms of intensity was *Mytilus*, even though the results were narrowly non-significant. The mid zone showed the highest intensity for both *Perna* and *Mytilus*. At the opposing ends of the shore (high and low), the highest infestations were endured by the most abundant mussel species occupying that particular tidal level. In the mid zone, where the two mussel species overlap and coexist, each species sustained high infestation levels, conversely each species had its lowest infestation where it was rare. This is difficult to interpret. The results for intensity of infestation in this study could be viewed as a natural artefact of the distribution patterns of the two mussel species across the shore, but then we would expect to see the same pattern in prevalence, which was not the case.

For barnacles, the presence of adult conspecifics encourages settlement (Pineda & Caswell 1997; Jeffery 2002) because of the need for barnacle larvae to settle gregariously (Pineda & Caswell 1997; Kent *et al* 2003). For instance, barnacles have been shown to use the presence of adult conspecifics (Jeffery 2002; Grosberg 1982; Kent *et al* 2003; Pineda & Caswell 1997) as part of an array of cues that are used to detect favourable environments on which to settle. For barnacles, settling in groups is necessary because they exhibit internal fertilization (Jeffery 2002; Kent *et al* 2003). Moreover, group-living is beneficial to barnacles because the harshness of the physical factors experienced intertidally, is reduced (Stachowicz 2001). Since barnacles become sessile almost as soon as they are settled, and depend on the close proximity (a penis length away) of sexually mature conspecifics for reproduction, they are a model example of how organisms generally evaluate the possibilities prior to settlement to settle in a more favourable situation regardless of intraspecific competition for space (Kent *et al* 2003; Buschbaum 2000).

Because of the limitations of immobility after settlement, it is necessary that barnacles respond to the appropriate cues and tend towards a suitable environment (Hills *et al* 1998). The fact that in this study most barnacles on mussel shells were found to have settled in groups may explain why there was increased settlement on the mid zone indicating an “intensification effect” (Pineda & Caswell 1997). Space has to be made available for hard bottom (sessile) organisms to settle (Pineda & Caswell 1997) and the manner in which larvae encounter the settlement habitat and the intensity of recruitment per unit area differ for each barnacle species (Navarrete & Wieters 2000). The gregariousness of barnacles could effectively explain the patterns observed in this study, because it appears that the distribution or barnacle settlement across the rocks may be congruent with the small-scale availability for settlement of suitable (and possibly unsuitable) substrata (Pineda & Caswell 1997). However, the results also showed that submergence time had a great influence in the prevalence of infected mussels. Walter (1992) also confirmed that of the different treatments set to simulate the different conditions on the shore, the ones that had the highest occurrence of barnacle larvae had the highest food availability because of increased flow rates and submersion period. This may explain the trend of barnacle infestation observed on mussels across shore in the results of the current study.

The barnacles' prevalence and intensity showed different patterns, with prevalence increasing down shore and intensity being lowest where each mussel was rarest. Overall, the barnacle epibionts had no significant effect on CI of mussels, but the ANCOVA was extremely close to significant. The data suggest that CI is lower with infestation, but that the effects are not correlated to the intensity of infestation.

A useful recommendation for future studies is, perhaps, to measure the mussels' more integrated physiological components (such as growth) along with the condition index to make more dependable conclusions. This could be helpful in giving better insight as to how barnacles, as epibionts, affect mussels throughout their adult life.

Chapter 5

General Discussion

The creation of unique habitats by ecosystem engineers is important because it affects the distribution and the diversity of the associated species (Norkko *et al* 2006). The qualities that make a facilitator successful in providing liveable conditions for other organisms have not been explored in detail (Bruno & Kennedy 2000) and understanding these positive interactions is important for conservation planning because natural habitats are disappearing at an alarming rate (Norkko *et al* 2006).

Mussels have been broadly described, in most parts of the world, as facilitators and providers of habitat for organisms that seek refuge from harsh environmental factors (Suchanek 1985; Prado & Castilla 2006; Seed 1996). The functions of mussels in their communities are four-fold: 1) mussels dominate space on rocky shores and alter the physical state and the appearances of the rock, creating structurally complex beds that directly interfere with trophic interactions; 2) mussel beds create habitable spaces that have reduced physical stress, and therefore, increase species abundance and diversity; 3) they involuntarily trap organic material and food that sustains these associated organisms and their shells increase the potential surface settlement area for encrusting and epibiotic organism; 4) mussels filter food from the water column and serve to link the pelagic and benthic ecosystems (Seed 1976; Suchanek 1985; Tsuchiya & Nishihira 1986; Jacobi 1987; Seed & Suchanek 1992; Lohse 1993; Lintas & Seed 1994; Crooks & Khim 1999; Ragnarsson & Raffaelli 1999; Stachowicz 2001; Bruno *et al* 2003; Gutiérrez *et al* 2003; Schiel 2004; Borthagaray & Carranza 2007). The presence of intertidal mussels provides the opportunity for different communities to survive on the rocky shores because of the favourable and tolerable conditions that mussel beds provide, and the various habitat options they offer. Although habitat complexity often translates to a species rich assemblage, the relationship between habitat structure and species diversity is not always positive because species diversity eventually declines with increasing habitat complexity (Kelaher 2003).

This research was conducted to establish if mussel bed architecture affects the species richness and abundance of the associated macro-invertebrates, and to determine the nature of mussels' epibiotic relationship with barnacles. These results were further used to investigate if the presence of an alien invasive mussel, *Mytilus galloprovincialis,* affects the local assemblages and the abundance and diversity of the associated organisms.

The results of this study suggest that mussel beds that contained high amounts of sediment supported a higher number of species, as shown in other studies (e.g. Tsuchiya & Nishihira 1986; Lintas & Seed 1994; Hammond 2001). However, the species diversity was not significantly affected by mussel bed layering or bed volume (mussel bed architecture). The abundance of species was significantly different between the high and low mussel zone and species diversity was highest on the low mussel zone. The same species were found distributed throughout the mussel zone (high, mid and low zone), but at different abundances and very few species occurred exclusively on the high or low mussel zone. The macrofauna associated with mussels was mostly influenced by zonation because species diversity increased from the high to the low mussel zone.

The distribution of barnacle epibionts on the rocky shore suggests that in the mussel zone, the barnacles take advantage of any available hard substrata. However, barnacle infestations on mussel shells were more prevalent in the low mussel zone. Mussels have a positive influence on their community, even though the association with barnacles may compromise their health status. Dittman and Robles (1991) have proven this association to be negative because the mussels' reproductive rates are decreased as a result of this association. In this study, the epibiotic barnacles did not have a significant effect on the condition index (CI) of the host mussels, but the result of the analysis was only marginally non-significant and the general trend suggests that the CI of infested mussels was lower than for infested mussels, particularly in the case of *M. galloprovincialis* (Fig. 4.2 in Chapter 4). Laudien and Wahl (2004) observed a mutualistic relationship between mussels and barnacles because the epibiotic barnacle *Balanus improvisus* protects the blue mussel from predation by the starfish *Asterias rubens*. Alternatively, Laihonen and Fürmen (1986) found that the association between epibiotic barnacles and mussels was commensal. The barnacles benefit from the settlement space on the shell of mussels and increased food availability due to the currents generated by mussels, and the mussels are unharmed (Laihonen & Fürmen 1986).

The introduction of alien invasive species, intentionally and non-intentionally, has been a great concern for many years (Mooney & Drake 1989; Crooks 2002). When the exotic species colonises the host environment, the ecosystem will drastically change because of the ecological associations that are established between the alien species and the existing indigenous species (e.g. in competition, predation, facilitation, etc) (Wallentinus & Nyberg 2007). The exotic species are able to take advantage of the newly found environment partly because they have no natural enemies there and their fecundity is usually high to ensure their survival and development in the host environment. Alien species compete with native species for resources, occupy unused open spaces or habitats and sometimes displace organisms from their habitats (Wallentinus & Nyberg 2007). Habitat modifying exotic species can also create habitats that are providing shelter from harsh environmental factors (Wallentinus & Nyberg 2007). The complex structure provided by the alien habitat modifier will increase species diversity because of the unique habitats that are created (Wernberg *et al* 2004; Wallentinus & Nyberg 2007).

The existence of *Mytilus* on the rocky shores has certainly increased the mussel biomass on South African coasts (van Erkom Schurink & Griffiths 1990) and expanded the realised niche of most associated organisms by providing suitable living conditions upshore (e.g. Bruno *et al* 2003). The bare rock that previously existed on what is now the high mussel zone has been modified into spatially heterogeneous and structurally complex living spaces (e.g. Wallentinus & Nyberg 2007). The suspension of sediments will have been increased by the presence of mussels and this can encourage the existence of some species and exclude some infauna (Ragnarsson & Raffaelli 1999). The existence of mussels intertidally introduces a physical and biological aspect that creates conditions that are favourable to organisms that need refuge from harsh environmental conditions and predators (Crooks & Khim 1999; Gosselin & Chia 1995).

The efficiency of habitat modifiers in providing less stressful living spaces for other organisms changes along environmental gradients such as the rocky intertidal shores (Kelaher 2003; Mullan & Bertness 2006). Furthermore, the quality of carpet-like biogenic habitats created by habitat-forming organisms is influenced by structural complexity, the functioning of the species in its community (Davenport *et al* 1999; Kelaher 2003) and other contributing environmental factors. Evidently, in this study the effectiveness of mussels in providing these habitats was enhanced on the low and mid shore, and because of the underlying physical effects experienced along the vertical gradient of the rocky shores there are clear limitations in the ability of mussels to provide ideal habitats for intertidal macro-organisms. The significance of an ecosystem engineer changes along these stress gradients according to the "ecosystem functions of interest" (Mullan & Bertness 2006, p. 211) because the needs of the associated organisms also change along this gradient. A facilitator that is able to cater to the needs of the associated organisms in different environmental circumstances is surely a good investment for conservation because it supports a diversity of species (Mullan & Bertness 2006). A good example of such is the role of mussels on the intertidal rocky shores as observed in this study and many others. Mussel beds protect the associated organisms on the low shore from biological factors such as predation and competition, and they create less stressful habitats for high shore organisms that did not previously exist (Mullan & Bertness 2006). The biological associations in an ecosystem can be weak or strong depending on the external abiotic factors and the adaptability of organisms (Hartvigsen *et al* 1998).

When an alien and indigenous ecosystem engineer operate in the same ecosystem, it is important to investigate how the native engineer responds because of the possible cascading effects on the community (Bruno & Bertness 2001; Gribben *et al* 2009). Studying the role of ecosystem engineers in their communities may assist in developing a model that may allow us to restore damaged ecosystems (Mullan & Bertness 2006) and promote the conservation of biodiversity. Although many have acknowledged the presence of positive associations in nature, not many studies have looked at how positive interactions affect species diversity (Hacker & Gaines 1997).

For future studies, it would be interesting to see how other parameters like the density of mussels affect species abundance and diversity, considering sediment content, mussel size and the relative sizes of the interstitial spaces in the mussel beds.

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