The effects of the invasive mussel *Mytilus galloprovincialis* and human exploitation on the indigenous mussel *Perna perna* on the south coast of South Africa

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Abstract

In South Africa, the indigenous mussel *Perna perna* is threatened by both an invasive species and excessive human exploitation.

The Mediterranean mussel *Mytilus galloprovincialis* is an invasive species that has been introduced to many parts of the world. In South Africa, this species arrived in the 1970s and spread rapidly along the west coast where today it is the dominant mussel species. Along the west coast, *M. galloprovincialis* is competitively superior in all aspects to the indigenous mussel species, and, as a result, has displaced some of them.

On the south coast, *M. galloprovincialis* found more oligotrophic waters, higher species richness, and a stronger competitor in the indigenous mussel *P. perna*. The rate of spread of *M. galloprovincialis* along the south coast has decreased over the last 10 years and the present eastern limit of its distribution in South African is East London. On the south coast, *M. galloprovincialis* has not yet completely replaced *P. perna*; instead, the two exhibit spatial segregation, with *P. perna* dominating the low shore, *M. galloprovincialis* the high shore and an overlap zone between the two.

An experiment on competition was carried out at one site on the south coast. The results showed that, on the low shore, *P. perna* is a more dominant competitor for space than *M. galloprovincialis*. Also byssus attachment of the two species differs, *P. perna* being much stronger than *M. galloprovincialis*, which suffers high mortality due to wave action on the low shore, especially in monospecific beds. As a result, mortality of *M. galloprovincialis* through wave action is reduced by the presence of *P.*

perna, which seems to confer protection against dislodgement. However, in the absence of strong wave action, *P. perna* competitively excludes *M. galloprovincialis*.

Human exploitation along 160 km of coast was examined by sampling mussel populations and using aerial surveys to determine where harvesters were distributed. Collectors did not seem to discriminate between species. The study has shown that higher abundances of mussels were found in protected or inaccessible sites, while in unprotected sites mussels were scarce. Coastal nature reserves are being proven to be effective in protecting mussel populations.

Table of contents

List of Figures

List of Tables

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Als meus avis

Josep i Dolors

Chapter One:

General Introduction

Marine mussels play an important role in intertidal communities (Seed 1976, 1996). Mussels are often keystone consumers and bioturbators and their ability to filter selectively and to process large quantities of suspended material can markedly influence the dynamics of coastal and estuarine systems, with consequent implications for local patterns of biodiversity (Seed 1996). As structurally and functionally complex entities, mussel patches provide refuges and suitable habitats for a broad range of associated organisms that include representatives from most of the major invertebrate phyla such as the Polychaeta, Amphipoda and Nemertea (e.g. Tsuchiya 1979, Tsuchiya & Bellan-Santini 1989, Peake & Quinn 1993, Lintas & Seed 1994). In this regard, mussels are well defined as ecosystem engineers (Lodge 1993, Jones *et al.* 1994), because they create complex beds that structure communities, and also because they are also likely to invade and alter communities. Examples are the mussel *Geukensia demissa* (Dillwyn) which facilitates colonization by other species and provides ecosystem stability, or the Zebra mussel (*Dreissena polymorpha*, Pallas), which invades and affects freshwater ecosystems by intense filtering (Rosemond & Anderson 2003).

Environmental conditions have a great impact on mussel biology, including differences in spawning periods, reproduction and growth (see reviews in Seed 1980, Griffiths & Griffiths 1987, Seed & Suchanek 1992). Among environmental conditions, temperature and aerial exposure (as a function of tidal elevation) are key determinants of the population dynamics of mussels (Griffiths & Griffiths 1987). Wave action and wave exposure are also important physical factors influencing the characteristics of mussel populations (McQuaid *et al.* 2000, Steffani & Branch 2003a). Filtration rate (Wildish *et al.* 1992, Wildish & Saulnier 1992, Newell & Wildish 1997, Newell *et al*. 2001), food availability (Griffiths & Griffiths 1987, Hawkins & Bayne 1992) and growth (Fox & Coe 1943, Harger 1970, Wildish & Saulnier 1992, McQuaid & Lindsay 2000) are generally the most important biological factors determined by wave action in mussel beds (Steffani & Branch 2003a).

Temperate mussel species have a single, major, abbreviated, annual reproductive effort (Baird 1966, Dare 1976, Thompson 1979, Dix & Ferguson 1984), restricted to the spring/summer months. This appears to allow synchronization with spring/summer bursts of phytoplankton production that support planktotrophic larval development (Seed 1976). Estimates of the larval life span of mussels range from two to four weeks (Bayne 1965, 1976, de Schweinitz & Lutz 1976), a period in which currents could easily spread the larvae into areas other than that from which they originated (Lasiak 1991).

The Mytilidae family is widely distributed around the world and some 27 species have been documented in southern African waters (Kilburn & Rippey 1982). Three indigenous species: the Brown mussel *Perna perna* (Linnaeus), the Black mussel *Choromytilus meridionalis* (Krauss), the Ribbed mussel *Aulacomya ater* (Molina), and one introduced species, the Mediterranean mussel *Mytilus galloprovincialis* (Lamarck) (Grant *et al.* 1984, Grant & Cherry 1985), attain sufficient size and density to form extensive beds on rocky intertidal and subtidal reefs on the wave beaten shores (van Erkom Schurink & Griffiths 1990).

South Africa has a long, wave-exposed coastline which extends for some 2570 km from the Namibian border (28ºS, 16ºE) in the west to Moçambique (26ºS, 32ºE) in the east (Fig. 1.1). Sea temperatures along the coast are determined largely by two major current systems. To the east the southerly-flowing Agulhas Current transports warm (21-26ºC) water close inshore along the Natal coast, but south of East London (number 9 in Fig. 1.1) this is deflected offshore by the progressively widening continental shelf. The Benguela System of the west coast is characterized by frequent upwelling events resulting in cooler conditions, with minimum temperatures of 9-10ºC being experienced during summer when offshore winds predominate, while maximum of 15-16ºC occur in winter, when sun-warmed surface waters are advected onshore (Branch & Griffiths 1988). Based on these current systems and the marine organisms found along the coast, the southern African coastline can be divided into three major biogeographical provinces: a sub-tropical east coast region extending southwards to about East London; a warm-temperate south coast reaching from there to Cape Agulhas (number 6 in Fig. 1.1) and a cold-temperate west coast region extending northwards into Namibia (Stephenson & Stephenson 1972, Brown & Jarman 1978). Zoogeographically, this coast was divided by Emanuel *et al*. (1992) into five major zoogeographical areas, on the basis of rocky-shore invertebrates. The cool temperate west coast was split into two zoogeographic provinces (the Cool Temperate North-West Coast (Namibia), Cool Temperate South-West Coast (Namaqualand)); the warm-temperate south coast was retained; and, in the Subtropical East Coast province (Kwazulu-Natal), two sub-provinces were separated just north of Durban (Fig. 1.1).

Sea temperature seems to be the main factor determining the geographical distribution of the 4 main species of mussels found in South Africa. *P. perna* is the dominant mussel species in the sub-tropical east and warm-temperate south coast regions and on the west coast of Namibia and Angola, though only isolated individuals occur on the upwelling west coast, south of Namibia, and do not form beds in the area between False Bay (number 4 in Fig. 1.1) and central Namibia (van Erkom Schurink & Griffiths 1990). The other three species, *C. meridionalis*, *A. ater*, and *M. galloprovincialis*, all attain their greatest densities in the cooler, upwelled waters of the west coast, although all three penetrate onto the south coast (van Erkom Schurink & Griffiths 1990, Hockey & van Erkom Schurink 1992, Branch & Steffani 2004).

On the west coast, van Erkom Schurink & Griffiths (1990) described *M. galloprovincialis* as the most abundant mussel species intertidally, occupying a distinct band in the mid intertidal that extends as far as 160 cm above the low water spring tide level (LWS). Its density tends to decline toward LWS and few specimens are found at or below this level where *A. ater* and *C. meridionalis* are more abundant. Of these two species, *C. meridionalis* is faster-growing and larger than *A. ater*, and, before invasion by *M. galloprovincialis*, *C. meridionalis* was regarded as the major intertidal mussel species in this region. Sites in the extreme southwestern Cape, such as False Bay, are the only areas in which sizeable populations of all four mussels coexist. Here both *P. perna* and *M. galloprovincialis* are almost exclusively intertidal, with *M. galloprovincialis* occurring at higher elevations. *C. meridionalis* and *A. ater* become more common at lower levels and predominate sublittorally (Phillips 1995).

Moving from the west coast eastwards, there is a progressive decline in the abundance of all three west coast species and they are supplanted by the warm-water mussel *P. perna*. On the south coast, *C. meridionalis*, *P. perna* and *M. galloprovincialis* coexist on the rocky shores. *P. perna* populations at sites such as Plettenberg Bay (number 7 in Fig. 1.1) in the southern Cape reach their maximum abundance in the lower mid-intertidal, since they are largely excluded from the sublittoral fringe by characteristic dense bands of the limpets, *Patella cochlear*, and the large ascidian *Pyura stolonifera*. On the east coast (Kwazulu-Natal and Transkei, see Fig.1.1), where the cochlear zone is poorly developed or absent, *P. perna* reaches its maximum abundances in areas of heavy wave action from the mid intertidal to LWS and thereafter to depths of at least 5 m (Berry 1978), although it is sometimes replaced in the lowest intertidal levels by dense beds of coralline algae. *P. perna* maintains dominance northwards along the coasts into Moçambique (van Erkom Schurink & Griffiths 1990).

Shell characteristics are usually enough to identify the four main species of mussels of the southern African shores correctly. *P. perna* has a smooth, brown shell, while *M. galloprovincialis* generally has a blue shell that erodes to a white colour and *C. meridionalis* has a typically black shell that erodes to a blue colour. The shell shape of *C. meridionalis* is narrow and high and is quite distinct from those of *P. perna* and *M. galloprovincialis*, which have similarly shaped broad, elongated shells. However, the shell of *P. perna* tends to be more elongated and slender than that of *M. galloprovincialis*, which is squatter with a broad base. Sometimes other characters are required for identification of these two species. For example, on the west coast, *P. perna* is uncommon and tends to occur singly amongst *M. galloprovincialis*, which can also be brown (van Erkom Schurink & Griffiths 1990). Confusion can thus occur, in which case examination of the adductor scars and shape are required. The adductor scars (muscle scars on the interior of the shell and the resilial pitted ridge) of *M. galloprovincialis* are associated with the presence of an anterior and posterior muscle, as well as a resilial pitted ridge. *P. perna* has a divided posterior muscle and a resilial pitted ridge, while *C. meridionalis* has no pitted ridge and an undivided posterior retractor muscle. *A. ater* has a very distinctive ribbed shell which makes this mussel unmistakable from the other three species (van Erkom Schurink & Griffiths 1990, Phillips 1995).

P. perna is widely distributed in the tropical and subtropical regions of the Indian and Atlantic oceans. The endemic range of *P. perna* includes southern India, Sri Lanka, Madagascar, the east coast of Africa from central Moçambique to False Bay, and the African west coast from Luderitz (number 1 in Fig. 1.1) north into the Mediterranean from Gibraltar to the Gulf of Tunis, as well as the Atlantic coasts of Brazil, Uruguay, Venezuela, and the West Indies (Berry 1978).

M. galloprovincialis is a fast-growing species with a high reproductive output and considerable tolerance for desiccation (Hockey & van Erkom Schurink 1992). This animal is indigenous to the Mediterranean region but has established populations on most continents as an invasive species (Grant & Cherry 1985). The presence of this species along the west coast of South Africa was first reported by Grant *et al.* (1984), and it is thought to have been introduced very recently, in the 1970s (Grant & Cherry 1985).

Most invasions by marine organisms since the early 19th Century are attributed to transportation in the ballast waters of shipping vessels (Williamson 1996, Wonham *et al.* 2000). South Africa lies on one of the world's major shipping routes between Europe and the East. A biological invasion occurs when an organism or species naturally encroaches, or is artificially introduced, either deliberately or accidentally, into an area beyond its previous range (Williamson 1996). It is well documented that invasions by non-indigenous species can alter the composition of biotic communities worldwide (Soule 1990, Williamson 1996), and have major effects on the local biota and ecosystems. These influences range from depressing the growth of local populations, causing the displacement or extinction of native species or even to restructuring local ecosystems and the processes that occur within them such as competition, amensalism, predation and vertical and horizontal food-chain processes (Williamson 1996, Simberloff *et al.* 1997). An example of such an invasive species is *M. galloprovincialis*, which has successfully colonised intertidal rocky shores around the world (Williamson 1996, Wonham *et al.* 2000).

On the west coast of South Africa *M. galloprovincialis* has almost completely displaced the dominant indigenous mussel *A. ater* (Ruiz Sebastián *et al.* 2002) and outcompetes other indigenous west coast species, like *C. meridionalis* although this species remains abundant at sites subject to sanding (van Erkom Schurink & Griffiths 1990, Hockey & van Erkom Schurink 1992). At present, *M. galloprovincialis* forms extensive multi-layered beds in the intertidal zone of exposed rocky shores. In this regard, *M. galloprovincialis* has almost certainly increased total mussel biomass, since it occupies both a wider vertical range and attains a higher biomass per m^2 than the species it has displaced (van Erkom Schurink & Griffiths 1990). The main factors contributing to the success of this invasive species are its high productivity, reproductive output, recruitment intensity, growth rate, its considerable tolerance to aerial exposure and its ability to grow in dense beds (van Erkom Schurink & Griffiths 1990, 1991).

The warmer conditions of the south and east coasts of South Africa are very similar to the Mediterranean Sea, where *M. galloprovincialis* originated. This suggests that it has the potential to dominate this region in the future, at the expense of *P. perna* (van Erkom Schurink & Griffiths 1990). As a result, a competitive interaction between *P. perna* and *M. galloprovincialis* on the rocky shores is expected.

P. perna is an exploited species and an important resource for subsistence fishermen on the south and east coasts (Siegfried *et al.* 1985, Hockey & Bosman 1986, Hockey *et al.* 1988, Lasiak 1991, Hockey & van Erkom Schurnik 1992, Lasiak 1993, 1998, Lasiak & Field 1995, Dye *et al.* 1997). For example, *P. perna* forms about 80% of offtake on the Transkei coast (Fielding *et al.* 1994), which means that changes in intertidal community structure are likely to have repercussions for human populations (Griffiths *et al.* 1992). Although there has been considerable research in the Transkei, on the south coast of South Africa, the effect on mussel communities of exploitation by people has not yet been studied.

In some areas, man-mediated introductions of marine species may have altered community functioning as severely as has exploitation elsewhere (Carlton 1989, Griffiths *et al.* 1992). In conclusion, factors such as human harvesting and competition between space-occupying invasive and native species are expected to play important roles in controlling the distribution of *P. perna* (van Erkom Schurink & Griffiths 1990).

The aim of this MSc is to investigate factors that could affect the population structure of *P. perna* on the south coast of South Africa, specifically its interaction with the invasive *M. galloprovincialis* and the effects of human exploitation.

This dissertation comprises three parts. The first part (Chapter 2) is an examination of the spread of *M. galloprovincialis* along the southern and southeastern coasts of South Africa based on data collected between 1994 and 2004. The second part (Chapter 3) investigates the interaction between *P. perna* and *M. galloprovincialis* in the intertidal mussel zone to ascertain whether competitive displacement limits the vertical distribution of either or both species where they co-exist on the south coast of South Africa. The last part (Chapter 4) studies the influence of human harvesting on mussel communities on rocky shores along a 160 Km stretch of coastline, and the consequences for both indigenous and invasive mussels species, in terms of the viability of mussel stocks and the expansion of the invasive species.

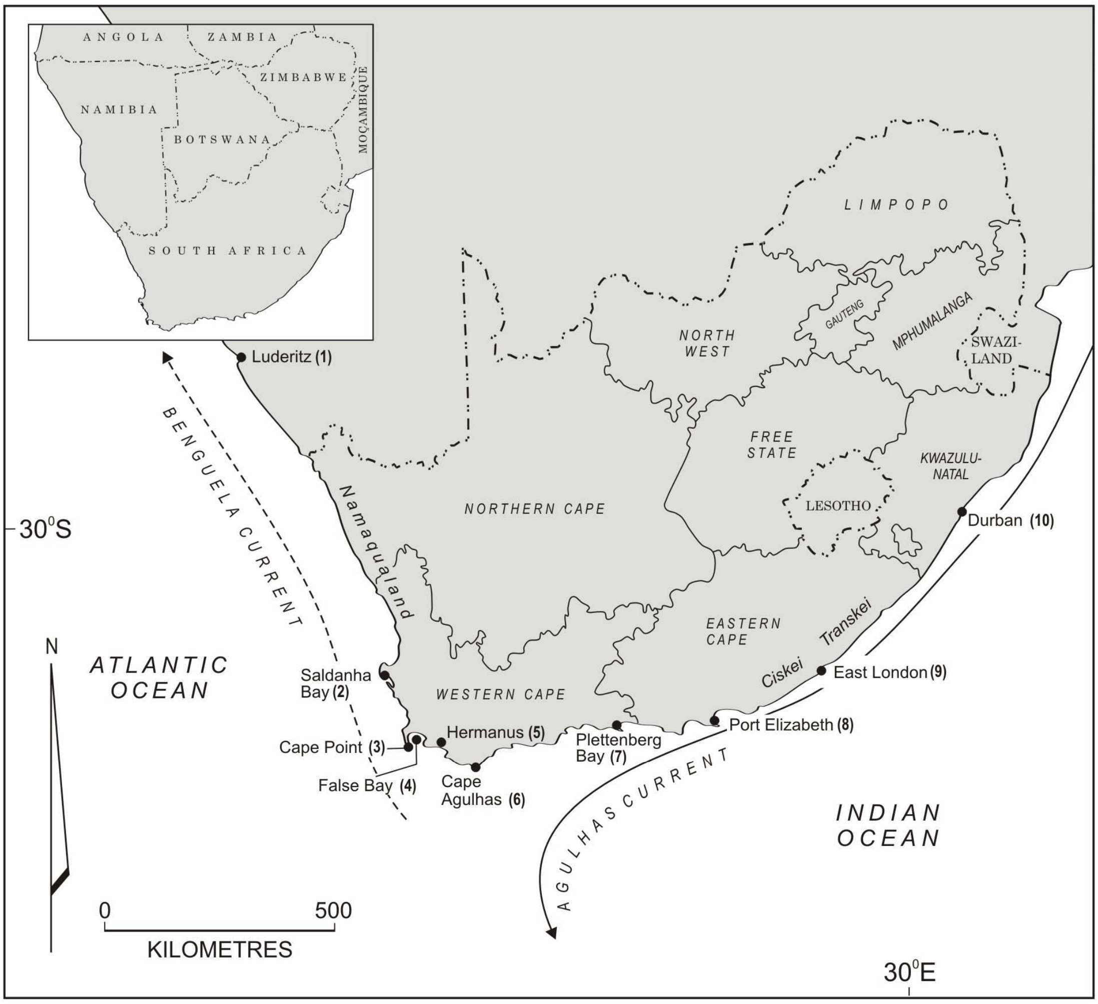


Fig. 1.1. Map of South Africa with the nine Provinces. The main currents and sites (with the corresponding numbers) on the coast are represented. Former Ciskei and Transkei homelands, as well as the Namaqualand region are also represented. The countries that form the southern Africa region are displayed on the map in the upper left hand corner.

Chapter Two:

Current status of *M. galloprovincialis* invasion along the south coast of South Africa

Introduction

When large numbers of alien, or exotic, species are introduced into a new ecosystem, many subsequently become naturalized, i.e. they establish self-sustaining populations in natural habitats. A proportion of these may become invasive, which means that they spread independently to untransformed ecosystems where they may be responsible for causing an imbalance in the community (Griffiths *et al*. 1992).

Lodge (1993) identified the characteristics of species that are predisposed to becoming invasive. The most broadly documented were the capacity to alter physical conditions (‘ecosystem engineers’), to prey on indigenous species, or to compete aggressively for space. However, the best predictor seems to be simply the history of species elsewhere: species are likely to be invasive if they have been shown to be so elsewhere (Branch & Steffani 2004).

Alien species have been identified as one of the major threats to the maintenance of biodiversity and ecosystem functioning in marine systems (Carlton & Geller 1993, Carlton 1996, Crooks & Khim 1999, Mack *et al*. 2000). The scale of the invasive species dispersal is an important factor in determining their invasive success (Carlton 1996).

These species usually arrive at a single locality from where they spread by larval dispersal (Branch & Steffani 2004).

Marine organisms have been accidentally and/or intentionally moved around the world's oceans since people first began navigating the seas (Carlton 1999), and the increase in transoceanic travel of the last century has seen a concurrent rise in the rate of introductions of alien marine species (Carlton & Geller 1993, Carlton 1996, Cohen & Carlton 1998, Mack *et al.* 2000).

Marine introductions may be accidental or intentional, and the five main sources of introduction are via deliberate introductions for food; mariculture or aquaria; in ballast water in ships; attachment to ships' hulls (fouling on ships); and the Lessepsian migration of organisms through canals that now unite seas previously separated by land (Carlton 1999, Branch & Steffani 2004)

The recent increase in prevalence of invasions of the near-shore environment has stimulated much research into the mechanisms of anthropogenic dispersal of marine organisms, and the ecological and economic impacts of such invasions (Crooks & Khim 1999). The majority of this research has, however, focused on Australia, North America and Europe (Orensanz *et al.* 2002), with comparatively little being known about marine invasions in other areas, particularly Africa (Robinson *et al.* in press).

Large numbers of alien species have been introduced into terrestrial and freshwater ecosystems in the southern African subcontinent either accidentally or as biocontrol agents (MacDonald *et al.* 1986). In the marine environment, 22 marine alien species have been recorded in South Africa (De Moor & Bruton 1988, Griffiths *et al.* 1992) but only ten species are known to support well-established populations along the

South African coast. While the majority of these remain restricted to harbours (e.g. *Ciona intestinalis*, *Carcinus maenas*, *Metridium senile*) and sheltered lagoons or estuaries (e.g. *Crassostrea gigas*, *Littorina saxatilis*, *Sagartia ornata*), a single species, the Mediterranean mussel *Mytilus galloprovincialis*, has spread extensively along the South African shores (Robinson *et al.* in press). *M. galloprovincialis* and the green crab *Carcinus maenas* are the only ones considered ‘‘invasive’’ in the sense of Vermeij (1996) in that they have spread and constitute a threat to indigenous species. But the one that is most significantly invasive and the most abundant alien marine species along the South African coast is *M. galloprovincialis* (De Moor & Bruton 1988, Branch & Steffani 2004, Robinson *et al.* in press).

Mussels have frequently featured in lists of alien invasive species (McDonald & Koehn 1988, Hicks & Tunnell 1993, Crooks & Khim 1999). The mode of dispersal of mussels is one of the most important factors that favour them becoming invasive. Their planktotrophic larvae can be transported in ballast water and can also disperse rapidly and widely from any points of introduction (Branch & Steffani 2004). The most notorious mussel invasion worldwide is the Zebra mussel *Dreissena polymorpha*, which has spread from the Black and Caspian Sea basins to most of Europe and eastern North America (Strayer *et al.* 1999). Another example is the Brown mussel *Perna perna*, which has colonised the shores of the Gulf of Mexico (Hicks & Tunnell 1993, Hicks *et al.* 2001), and the European blue mussel *Mytilus edulis* (Linnaeus), which has colonised several sites in the Southern Hemisphere (Carlton 1999).

M. galloprovincialis is widespread in the Mediterranean Sea, along the Atlantic coast of Europe (Gardner 1992) and in northwest Africa, where it may hybridize with *M.*

edulis (Beaumont *et al.* 1989). From its source in the Mediterranean, *M. galloprovincialis* has colonised, as a result of human activity, several outlying areas such as Hong Kong (Lee & Morton 1985), Japan (Wilkins *et al.* 1983), Australasia (McDonald *et al.* 1991), Hawaii (Apte *et al.* 2000), Mexico (Ramirez & Cáceros-Martínez 1999), west and east coast of USA (McDonald & Koehn 1988), and the west coast of Canada (where it hybridises with *Mytilus trossulus* (Gould)) (McDonald & Koehn 1988, Anderson *et al.* 2002), possibly the east coast of Canada (Vario *et al.* 1988), perhaps Britain and Ireland (where it co-occurs and hybridises with *M. edulis*) (Ahmad & Beardsmore 1976) and South Africa (Grant & Cherry 1985, van Erkom Schurink & Griffiths 1990).

Considering that: *M. galloprovincialis* has succeeded in establishing itself widely around the globe; that nearly all introductions are in temperate regions; that all localities invaded by *M. galloprovincialis* are where there are large shipping ports; and, that viable larvae of *M. galloprovincialis*, for example, have been recorded arriving in USA from Japan by way of seawater ballast in ships (Geller *et al.* 1994), it is clear that shipping is the most probable method of introduction of *M. galloprovincialis* to the rocky shores of South Africa (Grant *et al.* 1984, Branch & Steffani 2004).

There is convincing evidence to suggest that *M. galloprovincialis* was introduced accidentally to Saldanha Bay (number 2 in Fig. 1.1) on the west coast of South Africa in about the mid-end of the 1970s (Grant & Cherry 1985, van Erkom Schurink & Griffiths 1990, Hockey & van Erkom Schurink 1992, Phillips 1995, Branch & Steffani 2004). However, genetic confirmation of this species identification was only published in 1984 (Grant *et al.* 1984) and subsequently with a greater sophistication using electrophoresis by Grant & Cherry (1985), by which time the species was already the dominant intertidal mussel along sections of the west coast (Robinson *et al.* in press).

It was forecast that *M. galloprovincialis* would spread rapidly after arrival because it is a broadcast spawner and has a planktotrophic larval stage which allows it to colonise new areas rapidly (Phillips 1995, Branch & Steffani 2004). Settlement of the larvae occurs at staggeringly high densities of up to 2 million individuals.m^{-2} (Harris *et al.* 1998). Indeed, after the introduction of *M. galloprovincialis*, it has spread and expanded its range spectacularly (Branch & Steffani 2004). This mussel spread at expense of *A. ater* on the west coast (Grant & Cherry 1985, van Erkom Schurink & Griffiths 1990, Hockey & van Erkom Schurink 1992).

M. galloprovincialis spread rapidly after being introduced to the west coast and expanded by approximately 900 km in about 10 years, ranging from Luderitz to Hermanus on the south coast by 1988 (numbers 1 and 5 in Fig. 1.1). *M. galloprovincialis*, originating from west coast populations, first appeared on the south coast of the country in 1989 (McQuaid & Phillips 2000) as an isolated population in Port Elizabeth harbour (number 8 in Fig.1.1) in Algoa Bay (Fig. 2.1), where it was deliberately introduced for mariculture purposes (Phillips 1995). The mussel farming in Port Elizabeth used to grow mainly *P. perna*, although some *M. galloprovincialis* were transported from Saldanha and grew well in the warmer water conditions at Port Elizabeth harbour (van Erkom Schurink & Griffiths 1990). Following this introduction in Port Elizabeth, its dispersal was studied by McQuaid & Phillips (2000). They revealed that wind-driven dispersal of mussel larvae (as larvae were dispersed like passive particles matching the speed and direction of surface currents generated by wind) was responsible for its spread. The predominant wind on this stretch of coast is from the southwest, and as a consequence, *M. galloprovincialis* spread primarily to the east. The yearly average increase in distributional range was 42 km to the east compared to 19 km to the west. Three years after the introduction, *M. galloprovincialis* had spread along a total of 223 km of coastline from the initial point of introduction, although numbers further away were very low. About 90% of all *M. galloprovincialis* occurred within 12-20 km of the source (McQuaid & Phillips 2000). The eastward limit of the distribution of *M. galloprovincialis* in the first year after its introduction to Port Elizabeth (1989) lay around 70-97 km from the harbour. By 1990 *M. galloprovincialis* continued its expansion and the eastern limit increased by 56 km, while in 1991 it increased by only 13 km to reach Fish River Mouth (Fig. 2.1), and no further in 1992 (Phillips 1995, Robinson *et al.* in press). Natural spread from *M. galloprovincialis* populations originating from the west coast continued spreading eastwards along the south coast and by 1992 had reached Cape St. Francis (Fig. 2.1). Consequently, by 1992 *M. galloprovincialis* had a more or less continuous distribution from Luderitz on the west coast to the Fish River Mouth on the south coast of South Africa, a distance of some 1859 km of coastline (Phillips 1995).

At present, *M. galloprovincialis* distribution covers most of the west coast of southern Africa, where it is found in extremely high densities (>5000 adults.m^{-2}), is the dominant intertidal mussel species (~96%) in mussel assemblages (Phillips 1995, Robinson *et al.* in press), and constitutes 74% of the mussel biomass on wave-exposed shores (Hockey & van Erkom Schurink 1992, Griffiths *et al.* 1992) over an extensive area stretching between Luderitz and Cape Point (numbers 1 and 3 in Fig. 1.1). On the south coast it has become established occurring in lower density as far east as East London (van

Erkom Schurink & Griffiths 1990, Branch & Steffani 2004) where the indigenous *P. perna* dominates (>90%) the mussel abundance (Phillips 1995).

On the west coast, *M. galloprovincialis* has spread at an average rate of 115 km.y^{-1} in a northerly direction, coincident with the prevailing flow of the Benguela Current (Hockey & van Erkom Schurink 1992). Southerly spread has also taken place, but more slowly at about 25 km.y^{-1}. The rate of spread on the south coast was variable depending on which part of the coast was considered, but a decreasing spread rate to the east appeared to be the pattern, while the spread rate from Port Elizabeth to the east was only 5 km.y^{-1} (Branch & Steffani 2004).

This spread of the invasive species on the south coast has the potential to change communities and displace the indigenous mussels *P. perna* and *C. meridionalis* (Phillips 1995). Previous studies have warned of the possible invasion of the southern and southeastern coast by *M. galloprovincialis* (van Erkom Schurink & Griffiths 1990, Hockey & van Erkom Schurink 1992, Phillips 1995), suggesting that it is probably only a matter of time until *M. galloprovincialis* spreads into the Transkei and further along the east coast of South Africa.

This chapter aimed to determine the current status of the eastern limit of the invasive *M. galloprovincialis* and its evolution in the last 10 years; to estimate the ratio of *M. galloprovincialis*/*P. perna* biomass along the south coast and the biomass of *M. galloprovincialis* supported along South African coast; and, to discuss the ecological and economic impacts of this invasion.

Materials and Methods

Eastern limit of *Mytilus galloprovincialis*

The Department of Zoology and Entomology of Rhodes University had been doing intensive surveys along the south coast of South Africa since 1990. Between 1994 and 2004, six more extensive mussel bed surveys were conducted along the same coast. This chapter reviews these surveys to track changes in the eastern limit of *M. galloprovincialis*.

In 1994 and 1995, T.E. Phillips and L.J. Gurney respectively conducted the first surveys from Betty's Bay to Jeffrey's Bay (numbers 2 and 4 in Fig. 2.1). In 1998 and 2000 the survey was repeated extending the eastern limit to Morgan's Bay (number 20 in Fig. 2.1) (McQuaid unpub. data).

In 2003, surveys were done from Port Elizabeth to Morgan's Bay as a contribution to the project "*Mytilus galloprovincialis* status and spread" (see below for methodology and details). In 2004, a survey from Cannon Rocks to East London (numbers 6 and 17 in Fig. 2.1) was conducted using data extracted from mussel bed photographs (see Chapter 4).

The methodology for the 1994, 1995, 1998 and 2000 surveys was based on mussel bed scrapings of three randomly placed 0.1 x 0.1 m quadrats in each of three mussel zones. These were three vertical zones identified as: low mussel zone defined by the presence of algae, colonial polychaetes and large mussel patches; mid mussel zone where the mussel bed dominates; and high mussel zone characterized by barnacles and scattered mussel patches (barnacle-mussel zone). In addition, total percent cover of mussels, and the relative proportions of each species to total cover were estimated visually from ten randomly placed quadrat of 0.25 x 0.25 m in each of the three zones (Phillips 1995).

For the 2004 survey, 100 digital photographs of 0.5 x 0.5 m quadrats were taken within the mid and low mussels zones of each site. Species were identified from the photographs. Mussels were sparse in the high mussel zone and estimates of % cover for each species were made from visual observations.

***Mytilus galloprovincialis* status and spread**

This chapter formed a contribution to a national-scale study of the current status of *Mytilus galloprovincialis* along the South African coast. The methodology used was designed by T. Robinson and C.L. Griffiths at the Marine Biology Research Institute (Zoology Department, University of Cape Town).

Study sites

The entire coastline was divided into 13 sampling areas of 100 km extending east and north of Cape Point. Here the eastern most areas (numbered A11, A12 and A13), covering the coast from Port Elizabeth to Qora River Mouth (see Fig. 2.1), were sampled between May and June 2003 to identify the eastern limit of *M. galloprovincialis* distribution.

The area A11 ran from Cornville (north of Port Elizabeth) to the Fish River Mouth, A12 from there to East London and A13 from East London to the Qora River

Mouth. Within each area, three rocky-shore sites were randomly selected. The sites were Kenton-on-Sea, Kelly’s Beach and Riet Point in area A11; Old Woman’s River, Christmas Rock and Cove Rock in A12; and Gonubie, Haga-Haga and Morgan’s Bay in A13 (see Fig. 2.1).

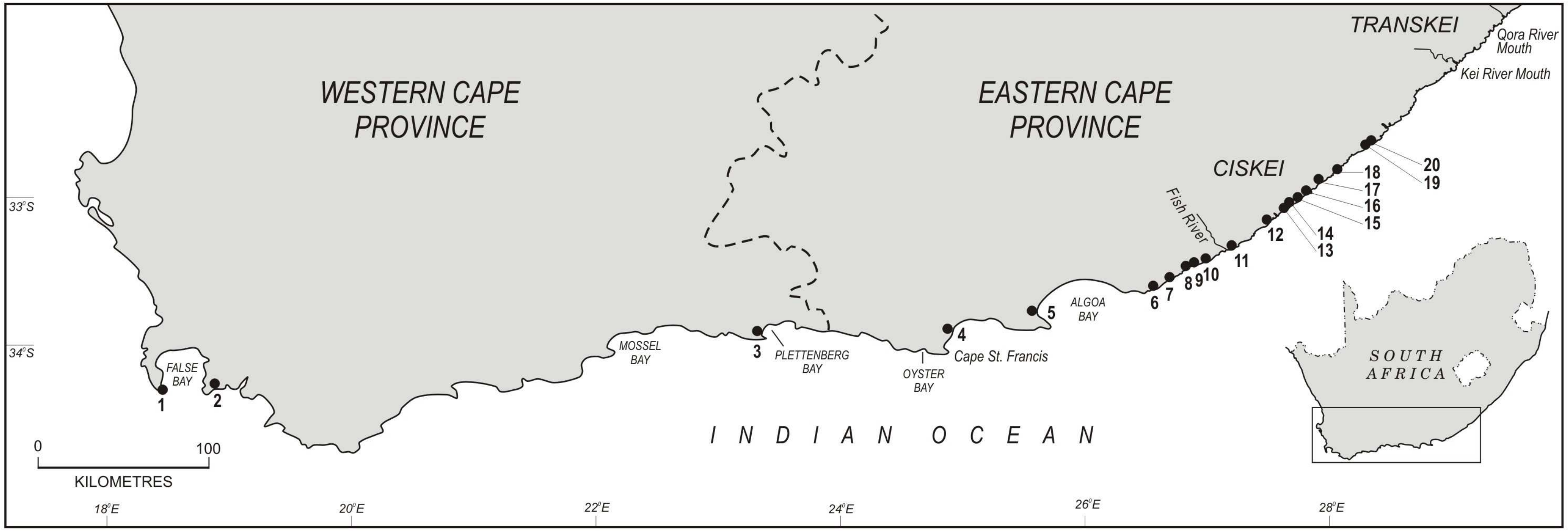


Fig 2.1. Map of the south coast of South Africa, representing relevant bays and rivers, and the study sites: Cape Point (1), Betty's Bay (2), Plettenberg Bay (3), Jeffrey's Bay (4), Port Elizabeth (5), Cannon Rocks (6), Kenton-on-Sea (7), Kelly's Beach (8), Port Alfred (9), Riet Point (10), Old Woman's River (11), Hamburg (12), Kayser's Beach (13), Christmas Rock (14), Kidd's Beach (15), Cove Rock (16), East London (17), Gonubie (18), Haga-Haga (19), Morgan's Bay (20).

Field work

At each site a straight line transect of 100 m parallel to the coast was marked on the intertidal rocks. Within this 100 m, measurements of the actual shoreline length were taken at the mid tidal level (i.e. the mid point between MWLS and MHWS), this was estimated by measuring the length of the intertidal zone, following the same vertical contour, including gullies, bays and around offshore rocks. From this measurement, the shoreline length covered by mussels was estimated.

Within each 100 m stretch, 3 continuous belt transects were established, running from LWS to HWS. Percent mussel cover was estimated along each transect using a 0.5 x 1 m quadrat (long side parallel to the sea) placed at the bottom of the transect, then flipped to the next position up shore, repeated to the top of the transect, forming a 1 m wide belt transect. The quadrat was divided into 10 equal rectangles and % cover were estimated using these rectangles (e.g. if mussels covered all rectangles, then mussel cover was 100%, if only five and a half rectangles were covered, then mussels cover was 55%).

After cover was estimated, two 0.1 x 0.1 m quadrats were scraped from areas with 100% mussel cover in each transect. From the first transect, two quadrats were taken from the high and mid mussel zones; for the second transect, the low and high mussel zones were sampled; and for the last transect, the mid and low mussel zones (i.e. a total of 2 quadrats from each mussel zone in each site).

Laboratory

All individuals of each species were extracted from the destructive samples and weighed together (giving total mussel wet weight). Subsequently all *M. galloprovincialis* individuals >50 mm were separated out and weighed together (giving total *M. galloprovincialis* wet weight).

Finally, 25 randomly selected *M. galloprovincialis* individuals from each transect were measured for maximum shell length (greatest anterior-posterior axis dimension) to the nearest mm using vernier callipers. This information was intended to provide a size-frequency distribution.

Data analysis

The mean percent cover of *M. galloprovincialis* was combined with measures of the mean biomass in 0.1 x 0.1 m quadrats to obtain a measure of biomass.m^{-2} of shore, in each of the mussel zones. The Coastal Sensitivity Atlas of southern Africa (Jackson & Lipschitz 1984) was then used to measure the total length of rocky shore in each 100 km sampling area. The mean biomass.m^{-2} of shore in each mussel zone was multiplied by the area covered by that zone, thus allowing the estimation of total biomass supported in each mussel zone in each sampling area. These area totals were summed, and added to the rest of the survey data, giving an estimate of total *M. galloprovincialis* biomass supported on the west and south coasts respectively (Robinson *et al.* in press).

Results

<u>Eastern limit of *Mytilus galloprovincialis*</u>

The results of the surveys are summarized in Table 2.1. The different mussel zones showed different rates of expansion, with *M. galloprovincialis* spreading most rapidly on the high shore. The shift in the eastern limit of *M. galloprovincialis* and its distance from Cape Point through the period 1994-2004 is represented in Fig. 2.2.

Between 1994 and 1995 the rate of spread was 153 $km.y^{-1}$, for the period 1995 to 1998 the average rate was 97 $km.y^{-1}$, between 1998 and 2000 the average was 18.5 $km.y^{-1}$, and from 2000 to 2004 the mean spread rate was nil. The average rate over the entire 10 years of surveys was 26.85 $km.y^{-1}$, but with a progressive decline from the high rate of spread at the beginning, after which it slowed down until the easternmost limit ceased to move. In the last four years, the easternmost limit remained between Christmas Rock and Kidd’s Beach (numbers 14 and 15 in Fig. 2.1), which are only 10 km apart.

Table 2.1. Change in the eastern limit of the *M. galloprovincialis* distribution in each of the three mussel zones along the south coast of South Africa for the period 1994 - 2004. Numbers in brackets, on the left of the sites names refer to the number corresponding to each site as shown on Fig. 2.1. Values below site names give the distance from each site to Cape Point.

Eastern limit of ***M.galloprovincialis***	**Low mussel zone**	**Mid mussel zone**	**High mussel zone**
1994	(3) Plettenberg Bay (621 km)	(3) Plettenberg Bay (621 km)	(3) Plettenberg Bay (621 km)
1995	(3) Plettenberg Bay (621 km)	(4) Jeffrey's Bay (774 km)	(4) Jeffrey's Bay (774 km)
1998	(9) Port Alfred (1001 km)	(12) Hamburg (1065 km)	(11) Old Woman's River (1023 km)
2000	(11) Old Woman's River (1023 km)	(13) Kayser's Beach (1081 km)	(15) Kidd's Beach (1102 km)
2003	(14) Christmas Rock (1092 km)	(14) Christmas Rock (1092 km)	(14) Christmas Rock (1092 km)
2004	(14) Christmas Rock (1092 km)	(14) Christmas Rock (1092 km)	(15) Kidd's Beach (1102 km)

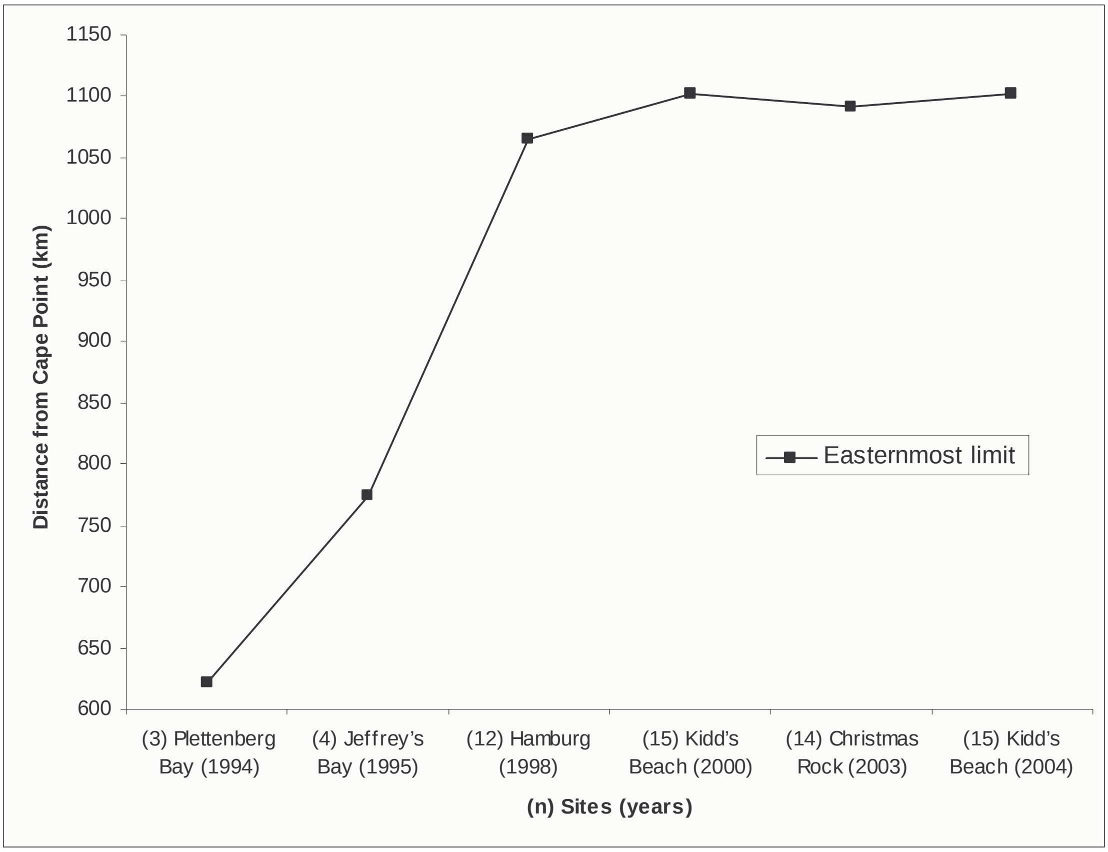


Fig. 2.2. The spread of the easternmost limit regardless of zone of *M. galloprovincialis* distribution in relation to Cape Point in each year sampled. In brackets, on the left, the number corresponding to each site shown in Fig. 2.1, and on the right, the year of sampling.

Mytilus galloprovincialis **status and spread**

Shoreline length was calculated as an indication of how irregular the shoreline was at each site. The mean % of shoreline covered by mussel in each area is given in (Table 2.2). Values for individual sites are given in (Fig. 2.3).

Table 2.2. Mean length (±S.D.) of shoreline sampled (m) and the % of this shoreline length cover by mussels per site for each area.

Area	Mean length of shoreline length sampled per site (m)	% of shoreline length covered by mussels
A11	181.3 (±26.19)	26.94 (±18.99)
A12	205.7 (±32.89)	30.62 (±13.47)
A13	175 (±66.55)	23.92 (±7.35)

Mean biomass of each species was obtained from the scraped samples (Table 2.3) and the mean wet weight biomass ratio (*M. galloprovincialis*/*P. perna*) was calculated. For the first area (A11) the mean biomass ratio was 20:1000, for A12 it was 7:1000, and for A13, the ratio was 0:1000. No individual *M. galloprovincialis* >50 mm were found, and therefore none could be weighed as indicated in the methodology.

Table 2.3. Mean biomass (g) of each mussel species and standard deviation (in brackets) for sites in each area.

	Area					
	A11		A12		A13	
Mean biomass (g)	*M. galloprovincialis*	*P. perna*	*M. galloprovincialis*	*P. perna*	*M. galloprovincialis*	*P. perna*
	39.5 (±25.94)	1953.2 (±164.01)	13.23 (±15.58)	2713.67 (±190.25)	0	2948.1 (±500.33)

Table 2.4. Total number of *M. galloprovincialis* individuals in each mussel zone per area. Data combined from all surveys.

Total number of *M. galloprovincialis*	**Area**		
Mussel zone	A11	A12	A13
High	16	5	0
Mid	12	2	0
Low	16	8	0

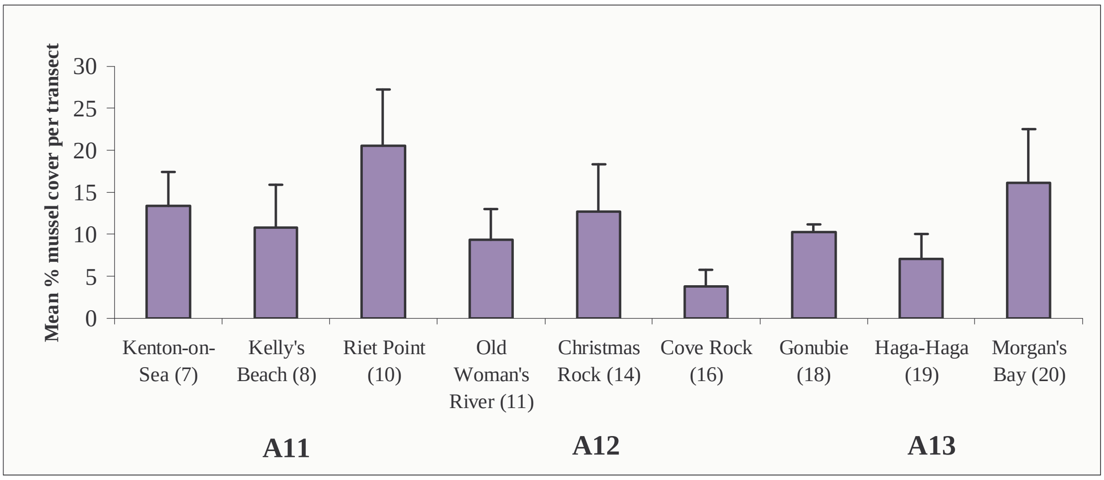


Fig. 2.3. Mean % mussel cover per transect per site (in brackets the number corresponding to each site shown in Fig. 2.1) for each area. Vertical bars denote 95% confidence intervals.

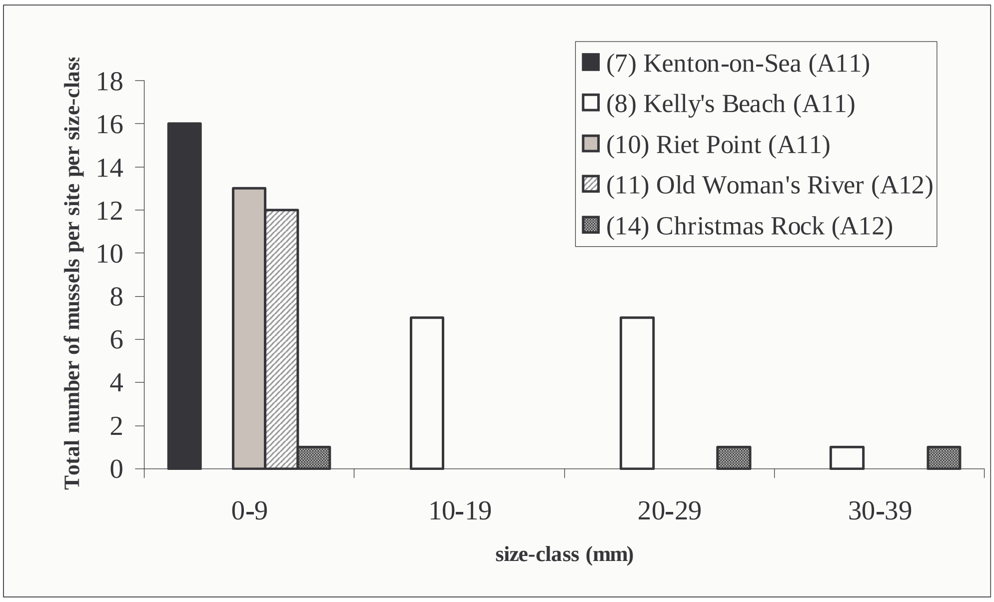


Fig 2.4. Size-frequency distribution of *M. galloprovincialis* at the sites where this species was present. On the legend, the numbers in brackets, on the left of the sites names refer to the number corresponding to each site shown in Fig. 2.1, and on the right, the area in which each site was found. Data combined for all 3 mussel zones.

Sample sizes were too small to allow analyses of size distribution in each zone. Data pooled for all zones and transects are given in Fig. 2.4. Most of the *M. galloprovincialis* individuals were in the 0-9 mm size-class (n = 42), a total of 7 were found in the 10-19 mm, 8 in the 20-29 mm, and only 2 in the 30-39 mm. In A13 no *M. galloprovincialis* were found, and in A12 very few, Kidd's Beach being the limit of distribution. In addition, no clear vertical pattern in the number of individuals was found (Table 2.4).

As a final result, and using all the data obtained from the entire survey along the South African coast, *M. galloprovincialis* was recorded along the entire west coast of South Africa, with populations extending eastwards around Cape Point and intermittently as far as Kidd's Beach, 20 km west of East London. This species presently occupies a total of 2 050 km of the South African coast and supports a total standing stock estimated at 35 403.7 tons (±7 241.4 S.E.), 88% (i.e. 31 054.5 tons ±6 274.1 S.E.) of which occurred on the west coast (Robinson *et al.* in press).

Discussion

This study summarizes most of the information presently available regarding the expansion of *Mytilus galloprovincialis* along the south coast of South Africa. In terms of the *M. galloprovincialis* population in the southern African region, the preliminary conclusion drawn is that *M. galloprovincialis* has become successfully established, which has been verified by the huge amount of *M. galloprovincialis* biomass currently existing along this extensive shoreline.

Most studies on the physiology of *M. galloprovincialis* in South Africa include comparisons with the three main endemic species (*Perna perna*, *Choromytilus meridionalis*, *Aulacomya ater*). These studies comprise measurements of growth rate and tolerance to air exposure (van Erkom Schurink & Griffiths 1993), reproductive output (van Erkom Schurink & Griffiths 1991) and filtration rate (Griffiths *et al.* 1992). Looking at a wide range of environmental conditions, Ehrlich (1989) identified rapid growth of *M. galloprovincialis*. In optimal conditions, van Erkom Schurink & Griffiths (1993) found that *M. galloprovincialis* grew faster than the three native species, and that its growth rate was less diminished by exposure to air. Indeed, *M. galloprovincialis* is more tolerant to desiccation than the three indigenous species tested. Experiments by Hockey & van Erkom Schurink (1992) indicated survival rates for *M. galloprovincialis*, *P. perna*, *C. meridionalis* and *A. ater* as 92%, 78%, 37-46% and 0-10% respectively. Annual reproductive output of *M. galloprovincialis*, expressed as a percentage of its body mass, exceeds 120%, as it reproduces more than once each year; its total annual output is between 20% and 200% greater than that of any of the indigenous species (van Erkom

Schurink & Griffiths 1991). This high reproductive output results in an exceptionally high rate of recruitment (Harris *et al.* 1998). The high tolerance to physiological limiting factors and high reproductive potential are characteristics favouring invasive spread (Branch & Steffani 2004).

Only in terms of tolerance to siltation is *M. galloprovincialis* inferior to one of the local species. Like *A. ater* and *P. perna*, *M. galloprovincialis* is eliminated by sand-burial, whereas *C. meridionalis* survives (Hockey & van Erkom Schurink 1992, Marshall & McQuaid 1993).

Comparisons of the infauna of the four different mussel species showed no important differences. Mussel beds of *M. galloprovincialis* and *A. ater* were found to support similar infaunal communities with species composition and richness, although abundance was twice as much in the former than the latter. This was attributed to the greater depth of *M. galloprovincialis* beds (Griffiths *et al.* 1992).

To escape from parasites in the native region is widely regarded as one of the reasons that aliens can thrive when they occupy new territory. Calvo-Ugarteburu & McQuaid (1998a) explored whether the parasites might explain the ascendancy *M. galloprovincialis* enjoys over indigenous mussels in South Africa. Both native *M. galloprovincialis* populations in Spain and introduced populations from the west and south coasts of South Africa were immune to the trematode parasites that are commonly found in South African indigenous mussels and that reduce both individual growth rates and population reproductive output, by castrating females (Calvo-Ugarteburu & McQuaid 1998a, b). The severe effects and the high prevalence of parasitism of *P. perna*, and the absence of parasites from *M. galloprovincialis* could contribute to its successful invasions on the south coast of South Africa.

Two organisms can damage the shells of *M. galloprovincialis*: the endolithic cyanophyte *Mastigocoleus* sp. and the lichen *Pyrenocolema* sp. (Webb & Korrubel 1994). They are important contributors to the mortality of this mussel, but because the severity of their effects increase with shell size, this only contributes to the mortality of mussels >40 mm shell length. Although they attack the indigenous species *C. meridionalis*, *P. perna* and *A. ater*, it is at a lower frequency and with markedly less severity than for *M. galloprovincialis* (Kaehler & McQuaid 1999, Branch & Steffani 2004). Although these two destructive organisms put *M. galloprovincialis* at a disadvantage relative to the native mussels in South Africa; as these effects are only manifested when the mussels reach a relatively large size, it cannot offset all the other advantages that *M. galloprovincialis* holds over these species.

The fact that its growth, condition, reproductive output and recruitment all peak under wave-exposed conditions gives *M. galloprovincialis* a particular advantage under these conditions and has allowed it to spread along the South African coastline, which is predominantly exposed to direct and strong wave action. Wave action disturbs intertidal communities, generating free space that can be colonised; *M. galloprovincialis* is one of the early colonisers to occupy primary space (Branch & Steffani 2004).

88% of the total *M. galloprovincialis* standing stock was estimated to be on the west coast (Robinson *et al.* in press). Several properties of *M. galloprovincialis* itself, and of the recipient community, conspired to favour the spread and establishment of this alien mussel along the South African coast, especially on the west coast. High productivity, predominantly strong wave action, a sparsity of predators, an absence of parasites, the mussel's fast growth and high reproductive output, are factors that have promoted the success of this invasion on the west coast (Branch & Steffani 2004).

Low species richness is one of the community properties held to increase the chance of aliens becoming invasive (Mack *et al*. 2000). The biodiversity of the west coast of South Africa, where *M. galloprovincialis* registered the fastest spread, is relatively low, and a small number of species dominate the high biomass that exists there (Bustamante & Branch 1996).

M. galloprovincialis beds on the west coast consist of multiple layers and support a higher biomass.m^{-2} than the single layered beds of indigenous mussels. In addition, the vertical range of *M. galloprovincialis* beds is greater than that of the indigenous species and this has lead to a massive increase in mussel biomass along the south African west coast (Griffiths *et al*. 1992), which has inevitably increased the amount of habitat available for infaunal species (Robinson *et al*. in press).

The ecological impacts of the *M. galloprovincialis* invasion have been well studied (Hockey & van Erkom Schurink 1992). Since its introduction to the west coast, *M. galloprovincialis* has proven to be highly invasive, dominant competitor capable of altering community structure and competitively displacing the indigenous west coast mussel *A. ater* and the limpet *Scutellastra granularis* (Linnaeus 1758) (Hockey & van Erkom Schurink 1992) because of its higher physiological performance (Branch & Steffani 2004). Extensive beds of *C. meridionalis* were long regarded as a characteristic feature of west coast rocky shores (van Erkom Schurink & Griffiths 1990), but nowadays *C. meridionalis* remains dominant only in sand-inundated areas (Robinson *et al*. in press).

From the perspective of predators, *M. galloprovincialis* provides an influx of food because it has substantially increased the biomass and vertical extent of mussels on the west coast (van Erkom Schurink & Griffiths 1990). There are three examples of predators that have benefited from the invasion. The first one is people. From an economic perspective, the invasion of *M. galloprovincialis* has had significantly positive impacts because the entire mussel culture industry in South Africa is based on this alien species (Robinson *et al.* in press). The other two predators to benefit are the African black oystercatcher, *Haematopus moquini* (Bonaparte) and the whelk *Nucella cingulata* (Linnaeus). Both benefit from the presence of the mussel but the effects probably arose via different mechanisms - altered and increased food supply in the case of the oystercatcher and provide greater substratum area on the mussels themselves in the case of the whelk *N. cingulata* (Branch & Steffani 2004).

For the oystercatcher, Hockey & van Erkom Schurink (1992) investigated the ways in which this animal has positively been affected by the arrival of *M. galloprovincialis*. During the period when *M. galloprovincialis* first arrived on west-coast shores, oystercatcher middens monitored on two west-coast islands comprised mainly shells of the indigenous mussel *A. ater* and the limpet *S. granularis*. After *M. galloprovincialis* had become established, the composition of middens switched to being dominated by *M. galloprovincialis*, with substantial declines in the contributions by *A. ater* and *S. granularis*. Simultaneously with this change in diet, a dramatic increase in breeding success of this endemic intertidal forager occurred presumably as a result of increased food supply. The proportion of pairs successfully procreating two juveniles rather than one has risen from about 10% to about 28%. In the case of the whelk *N.*

cingulata, considered the most important predator of *M. galloprovincialis* along the west coast, it has increased in overall density on shores invaded by the mussel (Branch & Steffani 2004).

Although predators can normally control prey abundance and distribution (Menge & Sutherland 1987), on the west coast of South Africa, natural predation rates cannot control *M. galloprovincialis* population. Probable reasons for this are: the extremely high rate of recruitment of *M. galloprovincialis* on the west coast of South Africa (Harris *et al.* 1998), and the relative scarcity of predators such as *N. cingulata* and *H. moquini* (Branch & Steffani 2004).

The high rates of recruitment of *M. galloprovincialis* have also allowed it to dominate primary rock surfaces at the expense of various competitively inferior limpet species. The west coast limpet species *S. granularis* and *Scutellastra argenvillei* (Krauss) have been significantly affected by the invasion as *M. galloprovincialis* outcompetes them and dominates the primary substratum (Hockey & van Erkom Shurink 1992, Steffani & Branch 2003b, c, Robinson *et al.* in press). The limpets gain a substitute substratum on the mussels themselves, but only if they are small enough to live and reproduce on the mussels (Branch & Steffani 2004).

In the same way, in many parts of the world that are affected by the invasive freshwater Zebra mussel *Dreissena polymorpha*, while overall species richness is reduced in systems that Zebra mussels have colonized, a few organisms benefit from the shelter and surface area provided by the Zebra mussel shells (Strayer *et al.* 1999).

M. galloprovincialis has also affected some sandy shores, though to a lesser degree. In 1992, *M. galloprovincialis* invaded the centre sand banks of Langebaan

Lagoon, an important marine conservation area along the west coast. Here it significantly altered the natural community composition by inducing a replacement of sandbank communities by those more typical of rocky shores (Robinson & Griffiths 2002).

On the south coast, where the *M. galloprovincialis* standing stock was estimated to be 12% of the total South African stock (Robinson *et al.* in press), the situation is quite different from the west coast. The main characteristic that differentiates *M. galloprovincialis* populations on the two coasts is that, in contrast to the west coast where *M. galloprovincialis* creates multi-layered beds, on the more oligotrophic south coast it forms mono-layered beds (Phillips 1995, Robinson *et al.* in press). This characteristic suggests that conditions on the south coast are less favourable.

Surveys of the eastern limit of *M. galloprovincialis* give an idea of the state of expansion of this species towards the northeast. The rate of spread to the east depended on the intertidal mussel zone considered, being slowest in the low mussel zone. Work by Marshall & McQuaid (1993) on the south coast has shown that *P. perna* and *C. meridionalis* preferentially inhabit different areas of the rocky intertidal zone, i.e. they show habitat segregation which is possibly a result of different competitive hierarchies in different zones. *M. galloprovincialis* was present in the mussel beds dominated by *P. perna*. The present results suggest that the expansion of *M. galloprovincialis* in each mussel zone, and its different competitive hierarchies, was more successful in the high zone than in the other mussel zones, although, in some years, the spread rate in the mid zone was the fastest (Table 2.1).

Fig. 2.2 shows the rate of spread of *M. galloprovincialis* in relation to Cape Point over the period 1994-2004. The easternmost point of *M. galloprovincialis* distribution extended 481 km from Plettenberg Bay in 1994 to Kidd's Beach in 2004. These results showed a decline in the rate of spread from 153 $km.y^{-1}$ between 1994 and 1995 to 0 $km.y^{-1}$ between 2000 and 2004. This suggests that the spread of *M. galloprovincialis* has been delayed by some factor/s (see below) in the last 10 years along this stretch of coast. The same tendency was found by Phillips (1995) in the expansion to the east from the populations of *M. galloprovincialis* introduced to Port Elizabeth. In this case, the rate of spread to the east declined steadily after the first year, giving an average rate of 42 $km.y^{-1}$ (between 1989 and 1992). The distance spread eastwards in 1991 was only 13 km while *M. galloprovincialis* did not spread any further in 1992. The average rate of spread found for the period 1994-2004 was almost 27 $km.y^{-1}$. The easternmost limit over the last 4 years of the survey, stabilized between Christmas Rock and Kidd's Beach sites, which are only separated by 10 km.

The results shown in Table 2.3, Table 2.4 and Fig. 2.4 indicate the same tendency. Numbers of individuals and biomass of *M. galloprovincialis* both decreased to the east. Fig. 2.4 gives the size distribution of *M. galloprovincialis* from destructive samples. Predominantly small individuals (0-9 mm) were found, but always in very small numbers in relation to *P. perna*. This suggests that *M. galloprovincialis* is poorly established in existing *P. perna* beds, presumably because conditions are not adequate to allow growth to large size or the development of mature and viable mussel populations.

Like *M. galloprovincialis*, *P. perna* shows characteristics of invasive species. *P. perna* is a short-lived (±2.5 y) mussel with a rapid growth-rate and a high reproductive output at a relatively young age, high spawning periodicities (Lasiak & Dye 1989) and a short juvenile phase (15 to 20 d) (Hicks *et al.* 2001). Indeed, *P. perna* has itself become invasive, and was first discovered in the Gulf of Mexico in 1990. International shipping, particularly from South America, may have transported *P. perna* to the Gulf of Mexico region (Hicks & Tunnel 1993) where this mussel has become established and is spreading at a rate of 95 km.y^{-1} (Hicks & Tunnell 1993, Hicks *et al*. 2001). The total annual production, growth rate, recruitment and reproductive efforts found in Gulf of Mexico populations fell well within the limits of these parameters recorded for endemic populations of this species throughout its world-wide geographic range. These results proved that this mussel was able to support viable populations in this region and could become invasive in other regions of the globe (Hicks *et al*. 2001).

Hockey & van Erkom Schurink (1992) and van Erkom Schurink & Griffiths (1990) predicted that the process of invasion and dominance exhibited by *M. galloprovincialis* on the west coast would be repeated on south and east coasts of South Africa. This prediction disregards the fact that the south and east coasts have distinctly different physical conditions, characteristics and ecosystems from those of the west coast (Emanuel *et al*. 1992) and are therefore expected to have distinctly different relationships in terms of interspecific interactions, ecosystem processes and ecosystem functioning. Another assumption was that the interaction between *M. galloprovincialis* and *P. perna* was expected to be similar to the interaction between the physiologically less tolerant *A. ater* and *M. galloprovincialis*. *P. perna* has been shown to be physiologically superior to *A. ater* under warm east coast conditions in terms of growth, respiration, filtration and excretion rates (Hockey & van Erkom Schurink 1992), and is therefore expected to provide stronger resistance to invasion pressure from *M. galloprovincialis*, even though

P. perna has been defined as not being a competitive dominant (Lambert & Steinke 1986).

The results suggest that East London, the eastern border of the Warm Temperate South Coast province (defined by Emanuel *et al.* (1992)), is the northeastern limit of *M. galloprovincialis* distribution on the South African coastline. The main evidence for this suggestion is that the easternmost limit did not expand eastwards in the period 2000 to 2004 and that the rate of spread has slowed down in the last 10 years. The fact that East London represents the border between two zoogeographical provinces, where both intertidal communities and physical conditions change, supports this idea.

There are several possible factors that could have delayed the spread of *M. galloprovincialis* along the south coast of South Africa over the last 10 years. The first can be attributed to the physical conditions, i.e. north of East London, subtropical conditions physiologically constrain the expansion of *M. galloprovincialis*. Another factor could be the fact that species-richness along the coast of South Africa increases as one moves from west to east (Emanuel *et al.* 1992, Branch *et al.* 2002b). In this way, along the south coast, while one moves to the east, less possibility exists for alien species to become invasive because of the increase in biodiversity (Mack *et al.* 2000). A third factor that could play a role in stopping *M. galloprovincialis* expansion could be competition for space with other intertidal organisms, particularly *P. perna* (see Chapter 3). An additional possibility is simply time, i.e. the expansion needs more time to develop and maybe in ten years time *M. galloprovincialis* will have expanded beyond East London.

Predators could benefit from the presence of *M. galloprovincialis* on this coast like the ones on the west coast, but only if *M. galloprovincialis* forms multilayered beds, grows and has a turn over rate at the same level as the ones found on the west coast. However, the results suggest that *M. galloprovincialis* biomass does not increase overall mussel biomass on this coast with no subsequent increase of food availability for predators. Oystercatcher populations are also found on the south coast preying on *P. perna* (pers. obs.), but no increment of their breeding is expected as a result of the invasion by *M. galloprovincialis*. As on the west coast, predators should not be considered as agents impeding the spread of *M. galloprovincialis*, because they did not seem to differentiate between different mussel species when feeding (pers. obs.).

Chapter Three:

Spatial competition between the invasive mussel species *Mytilus galloprovincialis* and the indigenous species *Perna perna*

Introduction

A biological invasion is believed to create several interactive processes between the native and the invasive species. For example predation, competition or parasitism, and these interactions determine the viability of both species in the particular situation (Williamson 1996).

The concept of competition was defined by Lincoln *et al.* (1998, p 67) as “the simultaneous demand by two or more organisms or species for an essential common resource that is actually or potentially limiting (exploitation competition) or the detrimental interaction between two or more organisms or species seeking a common resource that is not limiting (interference competition)”. In terms of number of species involved in the competitive interaction, two types of competition have been defined: intraspecific competition (between members of the same species) and interspecific competition (between members of different species) (Branch 1984a). However, two or more species that potentially occupy the same space and have the same food resource do not necessarily always compete, but can coexist (Dumas 1956, Harger 1972a, b), and competitors or potential competitors often coexist without any sign that one species will displace the other (Branch 1984a).

Competitive interactions between species can vary over space and time and the dominance of one species over another is not fixed. Biotic and abiotic factors may change over time (continuously or sporadically), which can further affect interactions between competing species (Branch 1984a). Changes in the competitive interactions can be related to seasonal migration (Race 1982), variable larval supply and recruitment rates (Dayton 1971, Hawkins & Hartnoll 1983, Underwood *et al.* 1983, Menge & Sutherland 1987, Menge *et al.* 1994, Robles 1997, Connolly & Roughgarden 1999), changes in predation intensity (Menge 1976, 1978, Underwood *et al.* 1983), seasonal or annual changes in abiotic factors (Race 1982, Leonard 2000), catastrophic events (Branch *et al.* 1990) or physical disturbance (Dayton 1971, Sousa 1980, 1984, Paine & Levin 1981, Petraitis & Dudgeon 1999).

Two-dimensional space is commonly considered to be a limiting resource on marine rocky shores because without space, post-larvae and juvenile intertidal animals cannot settle and establish themselves. However, this resource is likely to be a limiting factor only on rocky shores where one or more organisms monopolize the space, occupying 100% of the available cover (e.g. Dayton 1971, Sousa 1984, Lively *et al.* 1993, Marshall & McQuaid 1993, McGrorty & Goss-Custard 1995).

Studies on rocky shores have looked at several competitive processes (see review by Branch 1984a). In the case of intraspecific competition, and particularly studies on limpets, it has been shown that high densities of conspecifics result in rising adult mortality and decreasing survival of newly-settled juveniles in the overall population. In another example, Connell (1961a) described the mortality of the barnacle species *Balanus balanoides* (Lamark) occurring as a result of crowding among conspecifics. On the other hand, interspecific competition has been studied in many types of organisms: between mussels and barnacles (Paine 1966); between limpets, barnacles and mussels (Dayton 1971); mussels and limpets (Steffani & Branch 2003b); between two algae species (Lubchenco 1980); mussels and algae (Paine 1971, Lubchenco & Menge 1978, Paine 1979); two mussel species (Harger 1968, 1970, 1972a); and corals and sponges (Hill 1998). In these studies, different experimental techniques have been used. Laudable examples of some of these methods are, for exclusion experiments and observations, Dayton (1971); caging experiments, Lubchenco (1980); transect monitoring, Steffani & Branch (2003b); and for the establishment of enclosure experiments, Lubchenco & Menge (1978).

Some of these studies have observed that the intertidal height where organisms interact and the associated physical and biological characteristics (intertidal zonation) are the major factors affecting the outcome of competitive interactions (Connell 1961a, Lubchenco 1980). For example, Lubchenco (1980) found that the rhodophyte *Chondrus crispus* (Linnaeus) grew faster than the phaeophyte *Fucus vesiculosus* (Linnaeus), but that the removal of *C. crispus* resulted in *F. vesiculosus* growing downshore of its usual zone. The upper limit of *C. crispus* was established by desiccation, while the lower limit was determined by grazers. The lower limit of *F. vesiculosus* was concluded to be determined by competition with *C. crispus*.

Another major determinant of competitive forces is the degree of wave exposure (Steffani & Branch 2003b). Lubchenco & Menge (1978) studied the interaction between

M. edulis and *C. crispus*. They concluded that the space occupied by both species could be dominated by either, depending upon the degree of wave exposure with *C. crispus* predominating in sheltered and *M. edulis* on exposed shores. In another study, Paine (1979) showed that mussels could pre-empt most of the intertidal space excluding macroalgae, but were dislodged by strong wave action. Intermediate levels of disturbance were then necessary to allow algal persistence. In a study by Harger (1970) looking at the interaction between mussel species, it was shown that wave exposure determined competitive processes between mussel species and, as a result, their distributions.

Alongside wave action, predation acts as another disturbance factor. Paine (1971) verified that *Perna canaliculus* (Linnaeus) pre-empted and dominated most of the space reducing species richness when the starfish *Stichaster* spp. was removed. In the presence of the predator, the seaweed *Durvillea antarctica* (Chamisso) and *P. canaliculus* competed for primary space. The same was found between the corals *Dichocoenia stokesii* (Milne-Edwards & Haime) and *Siderastrea sideraea* (Ellis & Solander) in competition for space with sponges *Anthosigmella varians* (Duchassaing & Michelotti) and *Chondrilla nucula* (Schmidt). The removal of sponge predators allowed sponges to outcompete corals. The conclusion was that predators prevented sponges from monopolizing space and allowed the community to increase in diversity (Hill 1998).

Apart from interspecific competition processes, in mussel beds specifically, there exists a high natural mortality rate resulting from intraspecific competition for space (Griffiths & Hockey 1987). As a result, even high predatory pressure does not influence population density, particularly when the mussels are small (Hockey *et al.* 1988). Thus predation is rarely important in controlling mussels on the west coast of South Africa, as settlement overwhelms the effects of predators and leads to intense intraspecific competition for space (Griffiths & Hockey 1987). As mussels grow, space limitations within their beds result in high natural mortality because of competitive interaction between conspecifics, most of this mortality occurring when the mussels are small (Siegfried *et al.* 1985). These juvenile mussels are also fast growing, thus intensifying intraspecific competition for space and resulting in massive losses due to self-thinning (Branch & Steffani 2004). As size increases, growth slows and competition for space diminishes. Griffiths & Hockey (1987) go on to argue that if mussels grow slowly, intraspecific competition diminishes, and the window of vulnerability to predation is prolonged, thus increasing the importance of predation.

Mussels are often very successful competitors for space (Paine 1974, Suchanek 1985, Seed & Suchanek 1992). *M. galloprovincialis* has been described as an invasive species and a competitive dominant on the South African coast, where it is expected to interact with and affect many intertidal species (van Erkom Schurink & Griffiths 1990). Along the South African coast, of the three indigenous mussels, *A. ater* is the most severely affected by the *M. galloprovincialis* invasion, being largely displaced from the west coast (Hockey & van Erkom Shurink 1992). Little effect was registered on the abundance of *C. meridionalis* after the invasion, because *C. meridionalis* lives in silted areas where *M. galloprovincialis* is excluded by sand-burial (Branch & Steffani 2004). On the south coast, the vertical distribution of *M. galloprovincialis* overlaps with that of *P. perna*, which implies some kind of interaction (Phillips 1995). If competitive processes do not take place between *P. perna* and *M. galloprovincialis*, coexistence could be an alternative interaction between these two mussel species on this coast. However, *M.*

galloprovincialis has for the moment had little effect on *P. perna* because the latter occurs predominantly on the south and east coasts, and *M. galloprovincialis* has only been introduced to the south coast in the last fifteen years (McQuaid & Phillips 2000). Interactions between the two are likely to be more balanced than between *M. galloprovincialis* and *A. ater*, but nevertheless should favour *M. galloprovincialis*, not only because of its better performance in terms of growth and reproductive output, but also because *P. perna* has been considered a weaker competitor and slower to recover from disturbance than *M. galloprovincialis* (Lambert & Steinke 1986, Hockey & van Erkom Schurink 1992). On the south coast, experimental removal or exploitation of *P. perna* typically leads to domination of the substratum by coralline algae or barnacles (Hockey & Bosman 1986, Lambert & Steinke 1986). However, with the presence of the invader, empty primary space may become dominated by *M. galloprovincialis*.

Large species of limpets do inhibit recruitment of juvenile mussels, probably by bulldozing them off the rock face. This is, however, not a threat to *M. galloprovincialis* on the west coast because lateral spread of the mussel is not prevented, even by dense groups of large limpets. As a result, *M. galloprovincialis* displaces all limpets from the primary substratum (Branch & Steffani 2004). In particular, *M. galloprovincialis* has invaded much of the low shore, previously the habitat typically dominated by an indigenous limpet *Scutellastra granularis* (Hockey & van Erkom Shurink 1992). *M. galloprovincialis*, by excluding *S. granularis* from open rock, has increased density of this limpet by providing secondary substratum on its mussel bed (Branch & Steffani 2004) and a favorable settlement and recruitment substratum for juveniles (Hockey & van Erkom Shurink 1992). On the other hand, dominance of primary substratum by *M.*

galloprovincialis has resulted in decreased mean sizes of limpets because of the limited size of the host mussels (Griffiths *et al.* 1992).

Another limpet species, *Scutellastra argenvillei*, has also been significantly affected by the *M. galloprovincialis* invasion on the west coast, and it was found that the patterns of relative abundance, biomass and the strength of the interaction could be attributable to competition for primary space between them, this interaction being influenced by the degree of wave force experienced at different sites (Steffani & Branch 2003b). On exposed shores, *M. galloprovincialis* outcompetes *S. argenvillei* and dominates the primary substratum, while on semi-exposed shores the mussel becomes relatively scarce and *S. argenvillei* maintains dominance of open rock space (Steffani & Branch 2003b, c). Additional impacts on *S. argenvillei* include reductions in reproductive output and mean size of individuals that now occur on mussels (Griffiths *et al.* 1992, Branch & Steffani 2004).

On rocky shores of the south coast, particularly in the mid- and high-shore mussel zones, mussels generally tend to grow in clumps rather than in dense beds, leaving large areas of space available for settlement (McQuaid *et al.* 2000, McQuaid & Phillips 2000). In this way, the distribution of *P. perna* is limited to only a few areas where it forms extensive beds like those of *M. galloprovincialis* on the west coast (van Erkom Schurink & Griffiths 1990). This suggests that the interaction between *P. perna* and the invasive *M. galloprovincialis* may involve interspecific competition, determined by the scarcity of available space. In actual fact, the common limiting and limited resource is not essentially the amount of space available, but rather preferred or optimal space - qualitative space rather than quantitative space, assuming both species seek the same space characteristics such as the hydrological conditions, which permit settlement and growth.

Phillips (1995) examined the vertical zonation pattern of mussel beds in the intertidal rocky shores of the south coast and identified three mussel zones. The low mussel zone was defined as the coralline or mixed algal zone, the mid mussel zone as the pure mussel zone and the high mussel zone as the barnacle-mussel zone (see also Chapter 2). Surveys on the south coast showed that rocks below the low mussel zone which were permanently covered or scoured by sand, were dominated by *C. meridionalis*, with a small proportion of *P. perna* present, but no *M. galloprovinciali*s. At the interface of beaches and rocky shores, or on beaches subject to marked seasonal fluctuations in sand level, in the low mussel zone the intertidal rocks were scoured and occasionally buried in sand. These rocks had a mixed mussel fauna consisting of varying proportions of *P. perna* and *C. meridionalis*, and a low percentage of *M. galloprovincialis*. In the mid mussel zone, sand-free rocks were dominated by *P. perna* with a small proportion of *M. galloprovincialis* but no adults of *C. meridionalis*. In the high mussel zone, only *P. perna* and *M. galloprovincialis* were found, with a patchier distribution than in the mid zone.

These observations suggest some pattern of habitat separation between *P. perna* and *M. galloprovincialis*, with higher presence of the Brown mussel in the low and mid mussel zones than the invader, while the latter is more abundant in the high mussel zone. However, there is no knowledge of the interaction between them.

Thus, the aim of this study was to provide a clear understanding of the competitive interactions between these two mussel species in the different mussel zones and to predict if any changes in the mussel community will occur as a result of *M. galloprovincialis* settlement on the south coast of South Africa.

Materials and Methods

Study site

The experiment was set up on the south coast of South Africa, on a rocky sandstone platform at Old Woman's River (33° 30' S, 27° 10' E) (number 11 in Fig. 2.1). This coast has equal semi-diurnal tides, with a maximum tidal range of ~2 m. Most shores are relatively exposed to wave action, but the degree of exposure varies. The site was chosen because the platform was quite flat with a gentle gradient (1/15). The mussel bed was mostly distributed along the southwest side of the platform. The platform showed clear separation of the 3 different intertidal mussel zones as described in Chapter 2. At this location the biomass ratio *Mytilus galloprovincialis*/*Perna perna* was 10:1000 (author's unpub. data).

Experimental design

The experimental treatment was based on the evidence that mussels, when removed from their original mussel bed, can re-attach by creating new byssus threads (King *et al*. 1990, Clarke 1999, Dye & Dyantyi 2002).

The experiment was attempted three times because some problems were encountered with the methodology (see below). The first experiment was implemented during a 6 month period between March 2003 and September 2003 (mostly winter months), the second time the experiment was run for 8 months (from September 2003 to April 2004, spring, summer, and part of autumn) and the last experiment for 9 months (April 2004 until December 2004, autumn, winter, spring and part of summer).

The design of competition experiments is discussed in Underwood (1986) who reviewed many competition experiments. For the first and second attempts a complete experimental design was used (Table 3.1a), where 3 different mussel densities were applied. For the last experiment, because of the problems found in the two previous attempts, a simpler design (Table 3.1b) was used, with two densities of each species. The advantage of the first type of experiment over the second type is that the relationship between competitive effects and starting densities can be unravelled (Underwood 1986). The density values in each plot were based on earlier observations that the most crowded quadrats were filled completely at an early stage of the experiment.

Table 3.1. Designs of experiments used to investigate intra- and interspecific competition between *M. galloprovincialis* (*M.*) and *P. perna* (*P.*). Values in cells are number of mussels per 0.1 x 0.1 m plot. Experimental design used (a) for the first and second experiment and (b) for the last one.

a)

Treatment	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**
M. galloprovincialis (*M.*)	15	30	45	15	15	30	-	-	-
P. perna (*P.*)	-	-	-	15	30	15	15	30	45

	Intraspecific competition	**Interspecific competition**
Comparison	**1** vs **2** vs **3** (*M.* on *M.*)	*M.* in **1** vs **4** vs **5** (*P.* on *M.*)
	7 vs **8** vs **9** (*P.* on *P.*)	*P.* in **4** vs **6** vs **7** (*M.* on *P.*)

b)

Treatment	**1**	**2**	**3**	**4**	**5**
M. galloprovincialis (*M.*)	25	50	25	-	-
P. perna (*P.*)	-	-	25	25	50

	Intraspecific competition	**Interspecific competition**
Comparison	**1** vs **2** (*M.* on *M.*)	*M.* in **1** vs **3** (*P.* on *M.*)
	4 vs **5** (*P.* on *P.*)	*P.* in **3** vs **4** (*M.* on *P.*)

Fieldwork

First and second experiment

Two similar areas of platform ~20 m apart were selected, and the 3 mussel zones were identified in each area. Each of the 9 treatments had 2 replicates in each of the 3 zones in each of the 2 areas, giving a total of 108 plots and 1800 individuals per species.

Quadrats of 0.1 x 0.1 m were placed randomly in the study area and attached with screws. In addition, mussels of between 20 and 30 mm were collected from Plettenberg Bay (See Fig. 2.1), where the densities of both species are very similar. It was necessary to collect mussels of both species from a different site because there were insufficient *Mytilus galloprovincialis* of the required size at the study site. The size of the mussels used was chosen because mussels of this size are in their first year of growth when growth rate is greatest (McQuaid & Lindsay 2000). These mussels were placed in a dry cooler box and transported to the laboratory where they were placed in a biologically filtered tank of circulating seawater (approximately 20°C) for one night. The next day the mussels were transported to the study site and were immediately placed inside the quadrats. The positions of each treatment and its replicates within each zone were randomly assigned to the quadrats. The mussels in the quadrats were covered tightly with shade cloth mesh (2 mm mesh) to enable them to re-attach to the rocks. After 4 weeks, when the mussels were firmly attached, the mesh was removed (Fig. 3.1). This situation was an imitation of the confined area that the mussels would experience in a natural mussel bed. The mortality rate was monitored each month.

The objective was to conclude the experiment when the mussels grew to a stage when the quadrats were completely filled so that the mussels were competing for space.

The growth of the mussels, determined by the limited area of the quadrat, implied intra or interspecific competition for space. Any mussels forced out either laterally or vertically were considered mortalities and, the remaining individuals, the strongest competitors.

However, wave action, especially in the first attempt, removed the mussels from most of the plots. In the first experiment, the remaining mussels after a series of winter storms only partly filled some quadrats in the high zone. The experiment in this last mussel zone was run until March 2004, assuming that lateral migration of mussels would fill the gaps (see Tanaka & Magalhães 2002) caused by the storm, whereafter competition for the space in the quadrats could occur. However, during this period (March 2003 - 2004), the mussels did not grow as rapidly as expected, probably because of the difficult conditions (desiccation) in the high mussel zone and failed to fill the quadrat. As a result, the experiment was abandoned.

The second experiment was started in the summer months because of the high storm-induced mortality observed in the first experiment during winter. The mesh was maintained for 4 months in an attempt to minimize the effect of removal by wave action. The mesh was then removed as it could potentially impede mussel growth. Wave action once again removed mussels from most of the plots and, after two months, the experiment had to be stopped because of the lack of mussels within the quadrats.

The main problem with these two attempts of the experiment was related to the removal of the mesh, which enabled waves to wash away many of the mussels. The lack of replication per treatment was another limitation. Although the experimental design was very complete in terms of treatments, unpredictable high mortality due to wave action did not provide the expected results. The conclusion after the two failed attempts was that, throughout the year, wave action is capable of removing mussels. However, the results obtained from these two experiments were not completely worthless and are shown below.

a)

b)

Fig. 3.1. Photographs of the methodology used in the first and second attempt of the experiment. (a) 2 mm mesh tightly covering the mussels, (b) mesh removed.

Third experiment

The third and last attempt to run the experiment was based on small changes to the methodology. Solving the problem of mesh removal, and the subsequent massive loss of individuals, was the main goal. Greater replication was another important improvement required in the new experimental design. The experiment was set up only in the low mussel zone, where previous experiments revealed that mussel growth was faster, and in a relatively small area. The objective of using only one area in one zone was to reduce the spatial variability affecting the results, ensuring that competition was the main source of variation between replicates of treatments. In order to have more replicates, it was necessary to reduce the number of treatments. The experimental design was based on 5 treatments with 6 replicates each, giving a total of 30 plots, and 600 mussels per species.

The field methodology was the same as that used in the other two attempts, but instead of animals being collected from another shore, they were harvested at the same site and on the same day that they were placed inside the quadrats. The quantity of mussels required for this experiment was lower and the study site provided sufficient individuals of each species to allow this. The mussels collected had an average length of 23.78 ± 2.67 mm for *M. galloprovincialis* and 23.59 ± 2.37 mm for *P. perna*, from a random subsample of n = 100 of the collected individuals from each species.

The mesh was removed after 4 weeks, as in the first attempt, but instead of leaving the quadrats defenceless, cages with mesh protecting the quadrats were placed on top (Fig. 3.2). These cages allowed vertical mussel growth (but not much lateral growth) as the mesh was well attached at the sides but very loose at the center, leaving plenty of space for vertical growth. By the third month, when mussel growth was obvious, the cages were removed and a very loose and wide mesh (4 mm mesh) was placed to provide slight protection to the now securely attached mussels and, at the same time, allow them to grow freely both vertically and laterally. In the last month (November), the mesh was removed, and the experiment was stopped in December (see Fig. 3.2). As in the other experiments, the surviving individuals were counted each month. In this case, it was expected that wave action would not result in the loss of individuals and that plots would only be affected by encroachment and the associated competition for space. In this case, the mussels grew and completely filled the quadrats, competing for space for at least 6 months.

a)

b)

c)

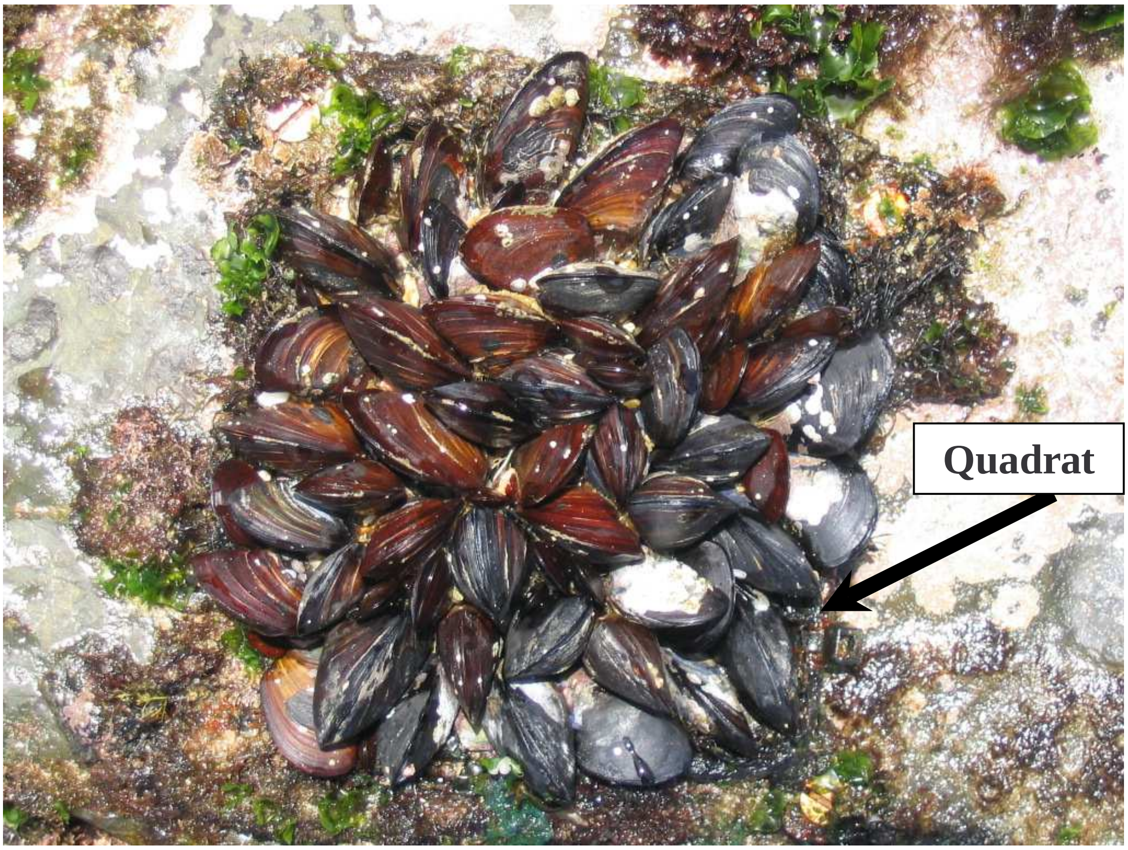


Fig. 3.2. Photographs of the methodology used in the third attempt of the experiment. The first step was the same as Fig. 3.1a. (a) cages with mesh protecting the quadrats, (b) 4 mm mesh loosely covering the mussels, (c) mesh removed.

Laboratory work

At the end of each experiment the remaining mussels were removed from the quadrats, transported to the laboratory, and the number of individuals for each species was counted. The final maximum shell length was measured to the nearest mm with vernier callipers. This value minus the initial length was the estimate of total growth. Because it was not possible to measure the same individuals at the start and at the end of the experiment, the final length was used as a proxy for growth, based on the assumption that all individuals had similar initial length.

In order to obtain an estimate of the condition of the mussels at the end of the experiment, i.e. which species performed better and in which zones, three mussels from each treatment, replicate, species and zone were randomly selected. These mussels were used to calculate the condition index (CI), which relates the flesh mass to the amount of shell. CI methodology was based on Calvo-Ugarteburu & McQuaid (1998b). The soft tissue was carefully removed and then dried in an oven at 60°C for at least 48 hours to measure the dry weight to 0.1 mg. The shell cavity was measured using the water displacement method. CI was the ratio of dry weight to shell cavity volume.

Statistical analysis

All data obtained were tested for normality with the Shapiro-Wilk’s W test and for homogeneity of variance using Levene’s test.

For the mortality results, the data collected during each month were converted to % mortality and then added together to obtain the cumulative % mortality. To determine how mortality varied across each treatment and species through time, the parametric Repeated Measures Analysis of Variance test (RM-ANOVA) was used. 2, 3 and 4-way RM-ANOVA tests were carried out using combinations of the factors area, zone, treatment and species (all fixed factors).

Zar (1984, p 170) argued, “ANOVA has been reported as a very robust test, operating well even with considerable heterogeneity of variances, as long as all n_i are equal or nearly equal” and “the analysis of variance is also robust with respect to the assumption of the underlying population’s normality”. Similarly, Underwood (1981) affirmed than non-normality has little effect on statistical procedures about sampled means of treatments, and that this idea was strengthened for larger samples. Underwood was also aware that analysis of variances is robust to many types and magnitudes of departure from homogeneity of variances. Following these authors, when data from Shapiro-Wilk’s W and Levene’s tests failed to meet the assumptions of the ANOVA, and transformation did not normalize the variables, the parametric ANOVA was still used with the data obtained for all comparisons. However, as there is no non-parametric test equivalent to RM-ANOVA, Kruskal-Wallis ANOVA tests (which compare multiple independent samples) were run as a non-parametric analyses of variance test (Zar 1984) for each month, assuming that the outcome would confirm the RM-ANOVA results.

To compare the samples obtained for the CI and final growth of the mussels, 2- and 3-way Model-I ANOVA and Kruskal-Wallis ANOVA tests were used.

Multiple comparisons of means were carried out using two types of tests dependant on which test was used before. The post hoc Tukey Honest Significance Difference (HSD) test was used after ANOVA or RM-ANOVA tests were performed, and the Multiple Comparisons Kruskal-Wallis test was used in cases of significant differences in the non-parametric tests.

Statistical analyses were done using the software STATISTICA version 6.1 for Windows, StatSoft, Inc. (2003). The significant level for all analyses was $\alpha = 0.05$.

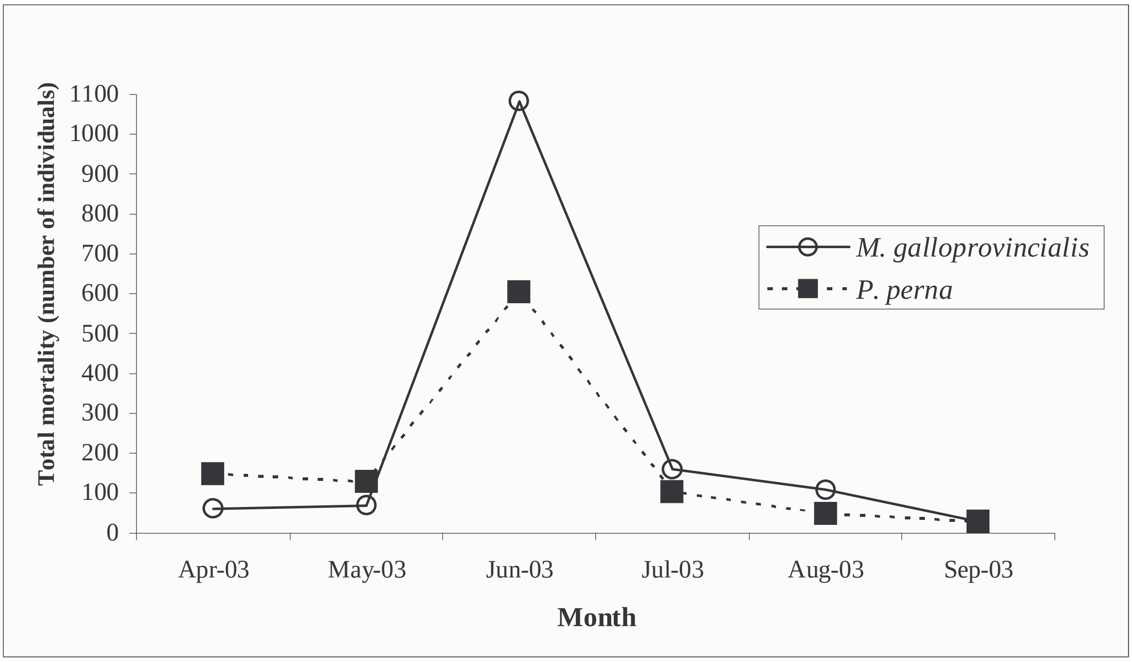
Results

First experiment

Mortality

The first recording of mortality was in April 2003. In early June 2003 a big storm destroyed most of the plots. In the months before and after the storm, total mortality remained low, between 2 and 9% of the total number of individuals per month, with minimal differences evident between species or zones. However, in June, 67.69% and 37.81% of the total number of individuals of *M. galloprovincialis* and *P. perna* respectively were lost (Fig. 3.3a), most of them from the low and mid shore. The results from this storm revealed that different species and zones had different patterns of mortality. On the low shore both mussel species were highly susceptible to displacement by wave action, and mortality decreased upshore, but in all zones mortality of *M. galloprovincialis* was roughly twice that of *P. perna* (Fig. 3.3b).

a)



b)

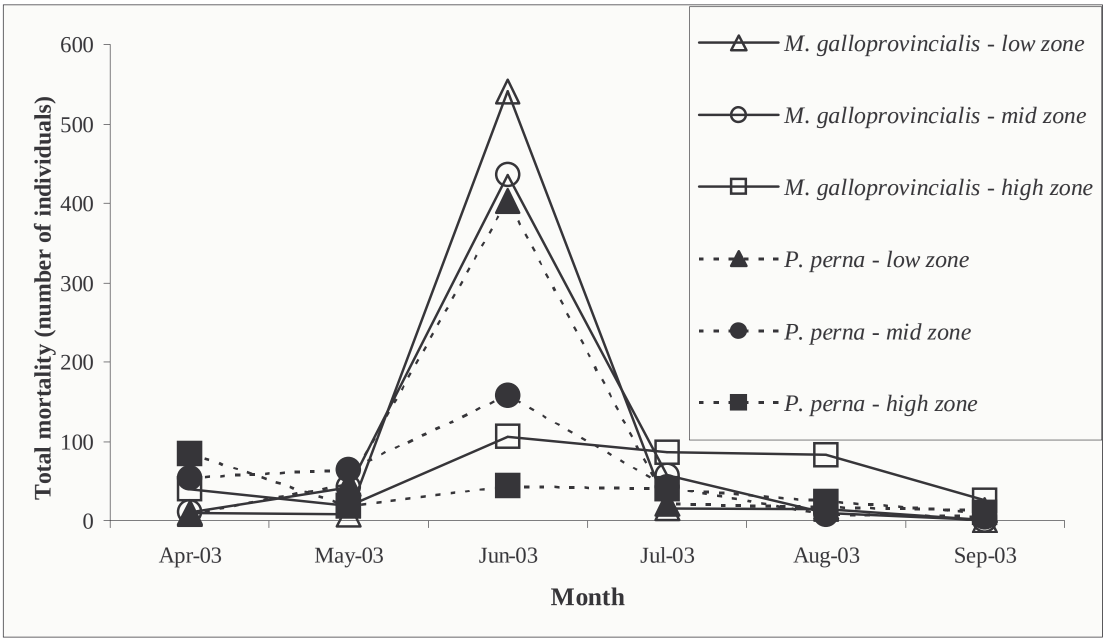


Fig 3.3. First experiment. Monthly total mortality (data pooled from all plots) for (a) all mussel zones pooled for each species; (b) each species in each zone.

Mortality data failed Shapiro-Wilk's W and Levene's tests ($p < 0.05$) in some months and no transformation allowed the data to satisfy the assumptions of parametric tests. The results of the 4-factor RM-ANOVA (factors: area, zone, species and treatment) showed significant ($p < 0.05$) within subjects effects of time and interactions among time and the main factors (Table 3.2). These effects are of limited interest here and attention is focussed on the between subjects effects. There was a weakly significant species x treatment interaction and main factor effects of zone and species. Subsequently, a Tukey test was run on species and treatment interaction. The results of this test indicated that differences existed between treatments 2 and 8, and 3 and 9 (see Table 3.1a), which did not give any indication of intra or interspecific competition. In order to simplify the interpretation, the two factors that were non- or weakly significant (area and treatment) were removed from the analysis. This allowed a 2-factor RM-ANOVA that showed significant between subjects of both zone and species, and, again, there were within subjects effects of time and its interaction with the main factors (Table 3.3).

Tukey post-hoc analysis showed several significant differences, which indicated effect of species (Fig. 3.4a) and the zone effect was due to mortality being lower in the high zone than in other zones for both species (Fig. 3.4b). The interaction between zones and species is shown in Fig. 3.5.

In order to ensure that this approach was valid, six 2-factor RM-ANOVA tests (combining all the possible pairs between the 4 factors, i.e. area, zone, species, treatment) were run to verify that zone and species had statistically significant effects while area and treatment did not. In all cases, the results showed no significant effects for either treatment or area ($p > 0.05$), and significant ($p < 0.05$) effects of species and zones.

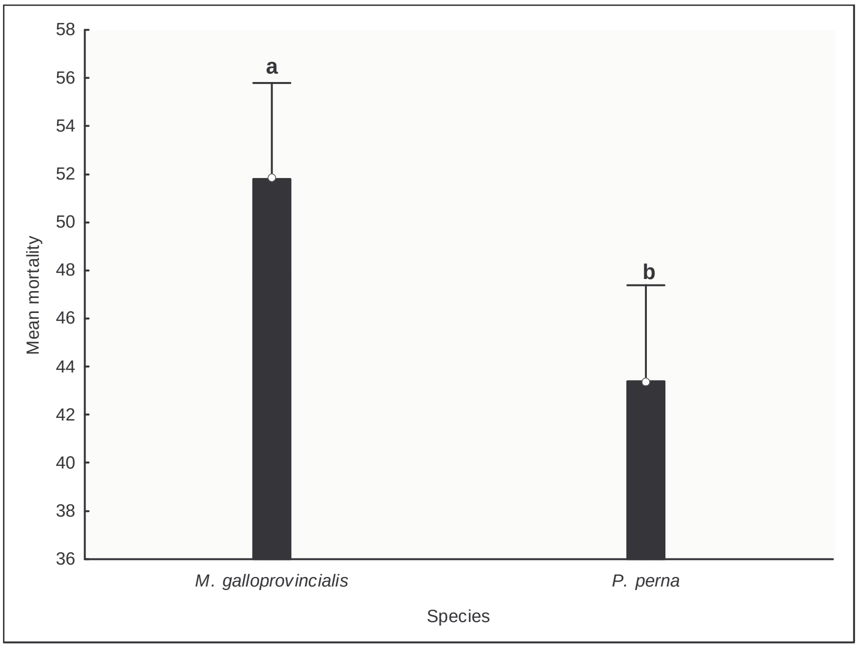
Table 3.2. First experiment. 4-factor Repeated-measures ANOVA testing effects of species, area, zones, treatments, time and their interactions on mortality. MS: mean square, * = $0.01 < p < 0.05$, ** = $0.001 < p < 0.01$, *** = $p < 0.001$, ^{ns} not significant.

Between subjects	**df**	**MS**	**F**
Species	1	15298	9.06**
Area	1	80	0.05^{ns}
Zone	2	72893	43.15***
Treatment	5	1521	0.9^{ns}
Species x area	1	716	0.42^{ns}
Species x zone	2	2202	1.3^{ns}
Area x zone	2	3445	2.04^{ns}
Species x treatment	5	4223	2.5*
Area x treatment	5	1728	1.02^{ns}
Zone x treatment	10	1718	1.02^{ns}
Species x area x zone	2	3622	2.14^{ns}
Species x area x treatment	5	268	0.16^{ns}
Species x zone x treatment	10	996	0.59^{ns}
Area x zone x treatment	10	2032	1.2^{ns}
Species x area x zone x treatment	10	1887	1.12^{ns}
Error	72	1689	
Within subjects			
Time	5	137058	606.15***
Time x species	5	4514	19.96***
Time x area	5	584	2.58*
Time x zone	10	11610	51.34***
Time x treatment	25	386	1.71**
Time x species x area	5	86	0.38^{ns}
Time x species x zone	10	614	2.72**
Time x area x zone	10	374	1.65^{ns}
Time x species x treatment	25	860	3.8***
Time x area x treatment	25	220	0.98^{ns}
Time x zone x treatment	50	161	0.71^{ns}
Time x species x area x zone	10	243	1.07^{ns}
Time x species x area x treatment	25	117	0.52^{ns}
Time x species x zone x treatment	50	206	0.91^{ns}
Time x area x zone x treatment	50	237	1.05^{ns}
Error (Time)	360	226	

Table 3.3. First experiment. 2-factor Repeated-measures ANOVA testing effects of species, zones, time and their interactions on mortality. MS: mean square, * = $0.01 < p < 0.05$, ** = $0.001 < p < 0.01$, *** = $p < 0.001$, ^{ns} not significant.

Between subjects	**df**	**MS**	**F**
Species	1	15298	8.74**
Zone	2	72893	41.63***
Species x zone	2	2202	1.26^{ns}
Error	138	1751	
Within subjects			
Time	5	137058	552.67***
Time x species	5	4514	18.2***
Time x zone	10	11610	46.81***
Time x species x zone	10	614	2.48**
Error (Time)	690	248	

a)



b)

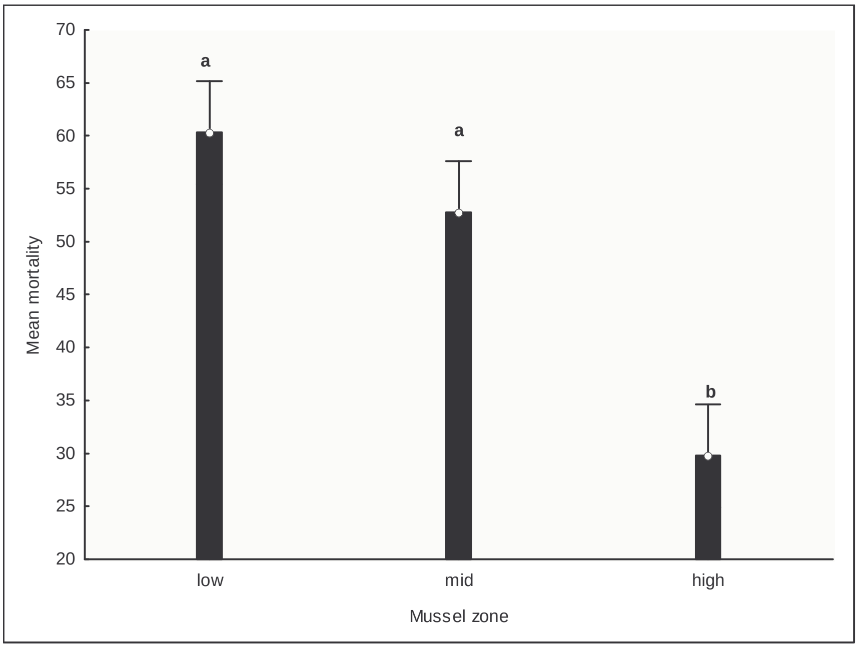


Fig 3.4. First experiment. Mean mortality (a) per species and (b) in each zone. Vertical bars denote 95% confidence intervals. Letters indicate homogenous groups as determined by Tukey tests.

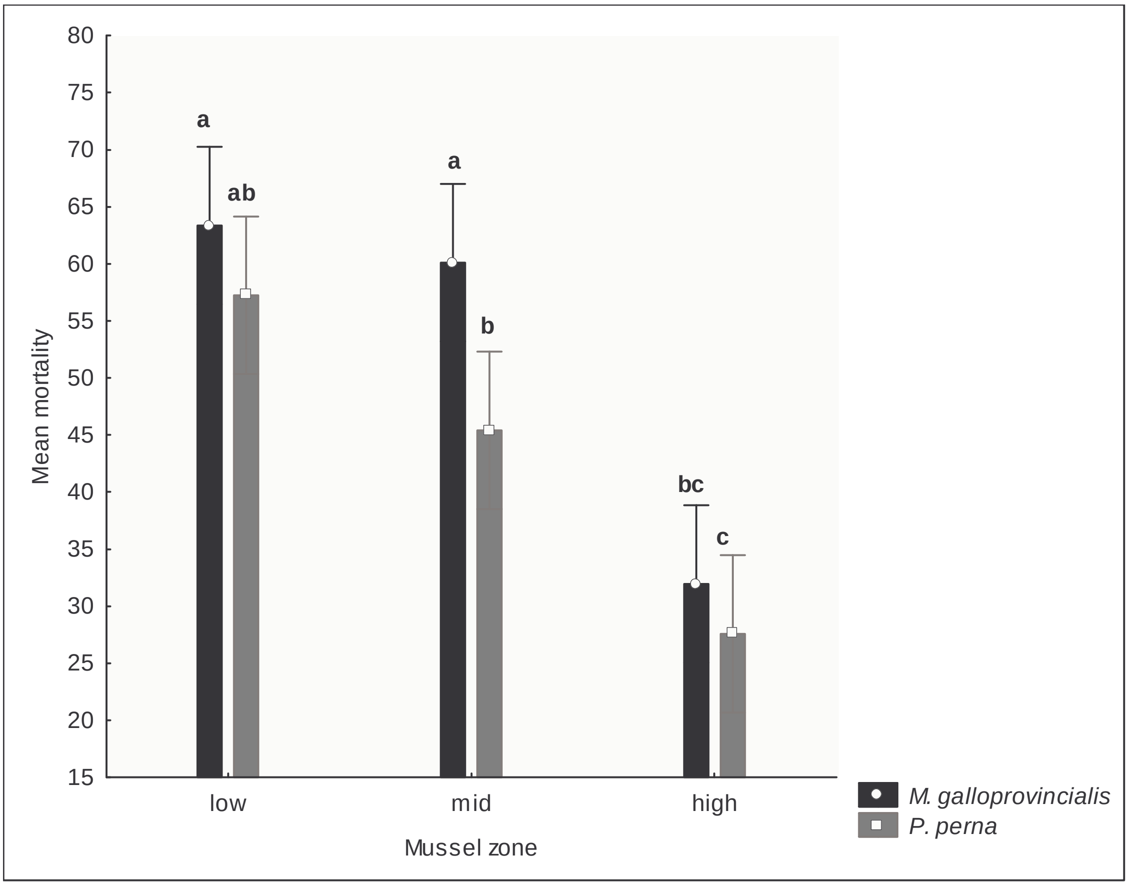


Fig 3.5. First experiment. Mean mortality for each species in each zone. Vertical bars denote 95% confidence intervals. Letters indicate homogenous groups as determined by Tukey tests.

Table 3.4. First experiment. Kruskal-Wallis ANOVA tests for species and zone in each month. * = $0.01 < p < 0.05$, ** = $0.001 < p < 0.01$, *** = $p < 0.001$, ^{ns} not significant.

K-W	April	May	June	July	August	September
Species	*	*	**	*	**	***
Zone	*	*	**	*	***	**

The Kruskal-Wallis ANOVA test results showed significant effects ($p < 0.05$) of species and zone in all months (Table 3.4).

This experiment was continued on the high zones alone where there were sufficient mussels to carry on. The 12-month data obtained were analysed with a 3-factor RM-ANOVA (area, treatment and species) and the results showed non-significant effects ($p > 0.05$) of all factors, even “Time”.

Condition index and growth

At the end of the experiment, the final growth and the CI were calculated from individuals from the high zone. Growth was minimal, the mean maximum length registered was 30.86 mm (±2.82 S.D.) for *P. perna* and 31.28 (±2.61 S.D.) for *M. galloprovincialis*. Growth data showed non-normal distribution (Shapiro-Wilk’s W test, $W = 0.98^{*}$) and no transformation could be applied to normalize the data. The non-parametric Kruskal-Wallis ANOVA test was used and no significant differences were found between species ($H = 2.25^{ns}$) or treatment ($H = 0.89^{ns}$). CI data were log transformed to satisfy the assumptions of the ANOVA test (Shapiro-Wilk’s W test, $W = 0.99^{ns}$, after transformation) and Levene’s test was passed satisfactorily ($F = 0.67^{ns}$). A 2-factor ANOVA (species and treatment) was applied and all effects and interactions were non-significant (species, $F = 1.22^{ns}$; treatment, $F = 1.39^{ns}$; species x treatment, $F = 0.79^{ns}$).

Second experiment

Mortality

The total accumulated mortality recorded (treatments and zones pooled) during the months when the quadrats were covered by mesh (first four months) was 6.67% for *M. galloprovincialis* and 5.89% for *P. perna*. One month after the removal of the mesh, the total accumulated mortality was 52.7% for *M. galloprovincialis* and 49.6% for *P. perna*. At the end of the experiment (one month later) these values had risen to 72.22% and 58.67% respectively.

The data from every month failed the Shapiro-Wilk's W test ($p < 0.05$) and only 2 of the 6 months' data successfully passed Levene's Test ($p > 0.05$). Again, no transformation allowed the data to satisfy the assumptions of parametric tests. Based on the first experiment, the factor "area" was removed from the analysis, with the results then based on 4 replicates. The 3-factor RM-ANOVA is summarized in Table 3.5. All three factors showed significant effects, but only one interaction (species x zone) was significant. The posthoc Tukey analysis statistically confirmed the differences that Fig. 3.6 suggested. The effect of species was only significant ($p < 0.05$) in the low zone, where mean mortality of *M. galloprovincialis* was much higher than that of *P. perna*. Mortality of *M. galloprovincialis* was generally high and not affected by zone, while for *P. perna*, mortality was statistically greater in the high zone than in the mid and low zones, where the mean mortality values were statistically equal (Fig. 3.6). Treatment effect was weak (only treatment 4 differed from treatments 2 and 3 (see Table 3.1a); Tukey Test, $p < 0.05$) (Fig. 3.7). All interactions were significant ($p < 0.05$, Table 3.5), other than those that included treatment, highlighting the irrelevance of this factor.

Table 3.5. Second experiment. 3-factor RM-ANOVA testing effects of species, treatment, mussel zone and their interactions on mortality. MS: mean square, * = $0.01 < p < 0.05$, ** = $0.001 < p < 0.01$, *** = $p < 0.001$, ^{ns} not significant.

Between subjects	**df**	**MS**	**F**
Species	1	11992	8.74**
Treatment	5	4018	2.96*
Zone	2	10747	7.91***
Species x treatment	5	2394	1.76^{ns}
Species x zone	2	6031	4.44*
Treatment x zone	10	807	0.59^{ns}
Species x treatment x zone	10	515	0.38^{ns}
Error	108	1358	
Within subjects			
Time	5	156135	668.59***
Time x species	5	2200	9.42***
Time x treatment	25	330	1.41^{ns}
Time x zone	10	2742	11.74***
Time x species x treatment	25	194	0.83^{ns}
Time x species x zone	10	664	2.84**
Time x treatment x zone	50	200	0.86^{ns}
Time x species x treatment x zone	50	75	0.32^{ns}
Error (Time)	540	234	

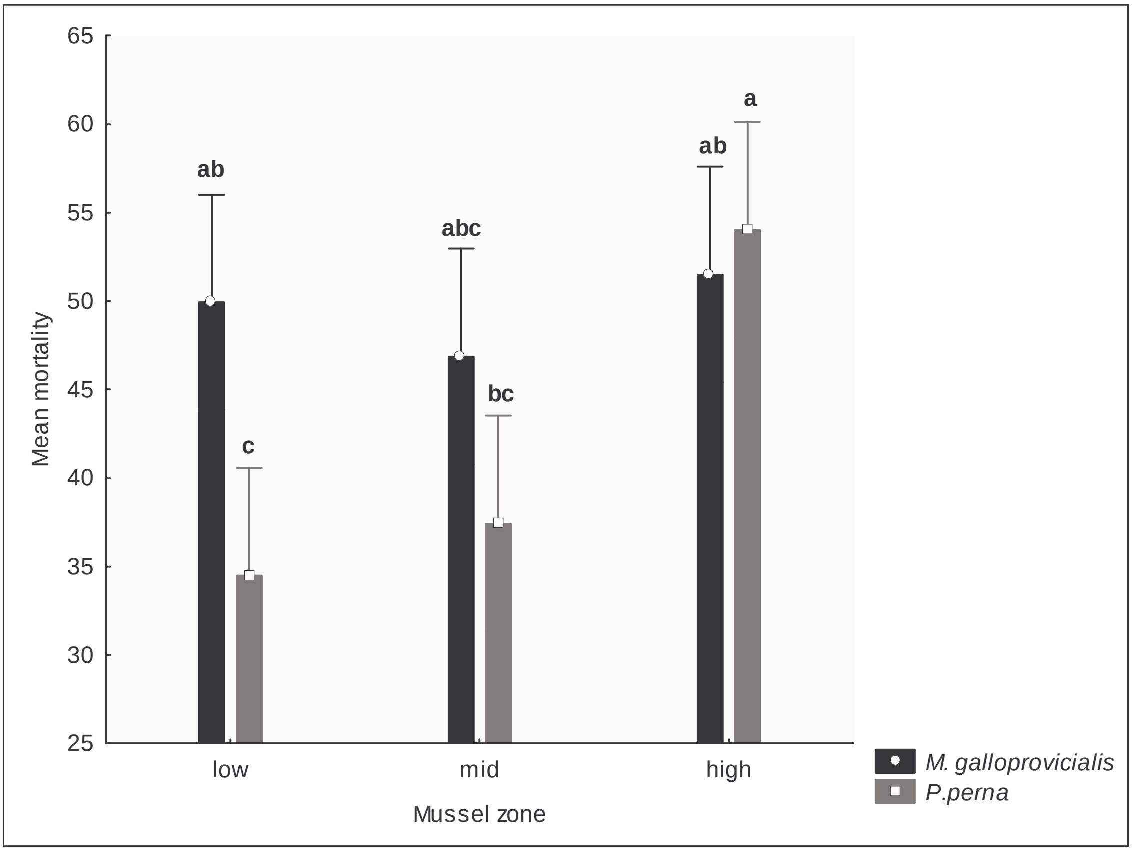


Fig 3.6. Second experiment. Mean mortality (number of individuals) for *M. galloprovincialis* and *P. perna* in each zone (treatments pooled). Vertical bars denote 95% confidence intervals. Letters indicate homogenous groups as determined by Tukey tests.

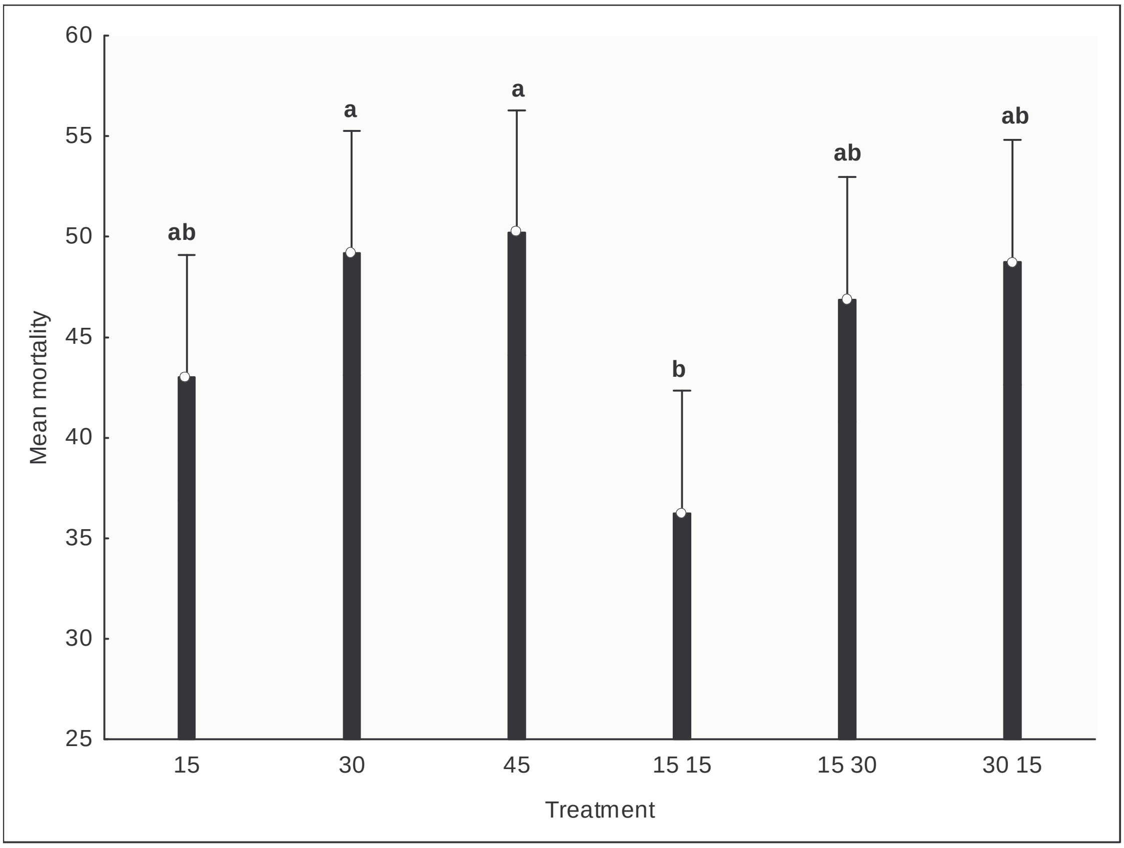


Fig 3.7. Second experiment. Mean mortality (number of individuals) under various treatments (zones and species pooled). Vertical bars denote 95% confidence intervals. Letters indicate homogenous groups as determined by Tukey tests.

The Kruskal-Wallis ANOVA tests showed that in all months there was a significant effect ($p < 0.05$) of species and zone with effects of treatment only in the first months (Table 3.6).

Condition index

Condition index results were log-transformed to satisfy the assumptions of ANOVA (Shapiro-Wilk's W test, $W = 0.90^{ns}$, after transformation). Levene's test showed only weak heterogeneity of variances ($F = 1.83^{*}$). A 3-factor ANOVA (species, zone and treatment) was run (Table 3.7). The results showed a very strong species effect ($p < 0.001$), with *P. perna* showing higher mean values than *M. galloprovincialis*, while the effects of zone and treatment were not significant ($p > 0.05$). For the interaction between species and zones (Fig. 3.8), in all zones the mean CI for *P. perna* was higher than for *M. galloprovincialis*, with the biggest difference between species being found in the low zone. However, differences between species were significant (Tukey test, $p > 0.05$) only on the low and mid shore. The effect of zone was not significant ($p > 0.05$) within species. The interaction between species, treatment and zones confirmed the differences found in the interaction between species and zones while the effect of treatment in this interaction was weak.

Table 3.6. Second experiment. Kruskal-Wallis ANOVA tests on mortality per species and mussel zone. * = 0.01 < p < 0.05, ** = 0.001 < p < 0.01, *** = p < 0.001, ^{ns} not significant.

K-W	October	November	December	January	February	March	April
Species	**	**	*	***	**	*	**
Treatment	ns	ns	ns	*	*	*	*
Zone	**	*	***	**	***	**	**

Table 3.7. Second experiment. 3-factor ANOVA testing effects of species, treatment and zone on CI values. MS: mean square, * = 0.01 < p < 0.05, ** = 0.001 < p < 0.01, *** = p < 0.001, ^{ns} not significant.

Between subjects	df	MS	F
Species	1	0.03	42.57***
Treatment	5	0.01	1.80^{ns}
Zone	2	0.01	1.50^{ns}
Species x treatment	5	0.01	1.03^{ns}
Species x zone	2	0.04	5.03**
Treatment x zone	10	0.01	1.32^{ns}
Species x treatment x zone	10	0.02	2.64**
Error	72	0.01	

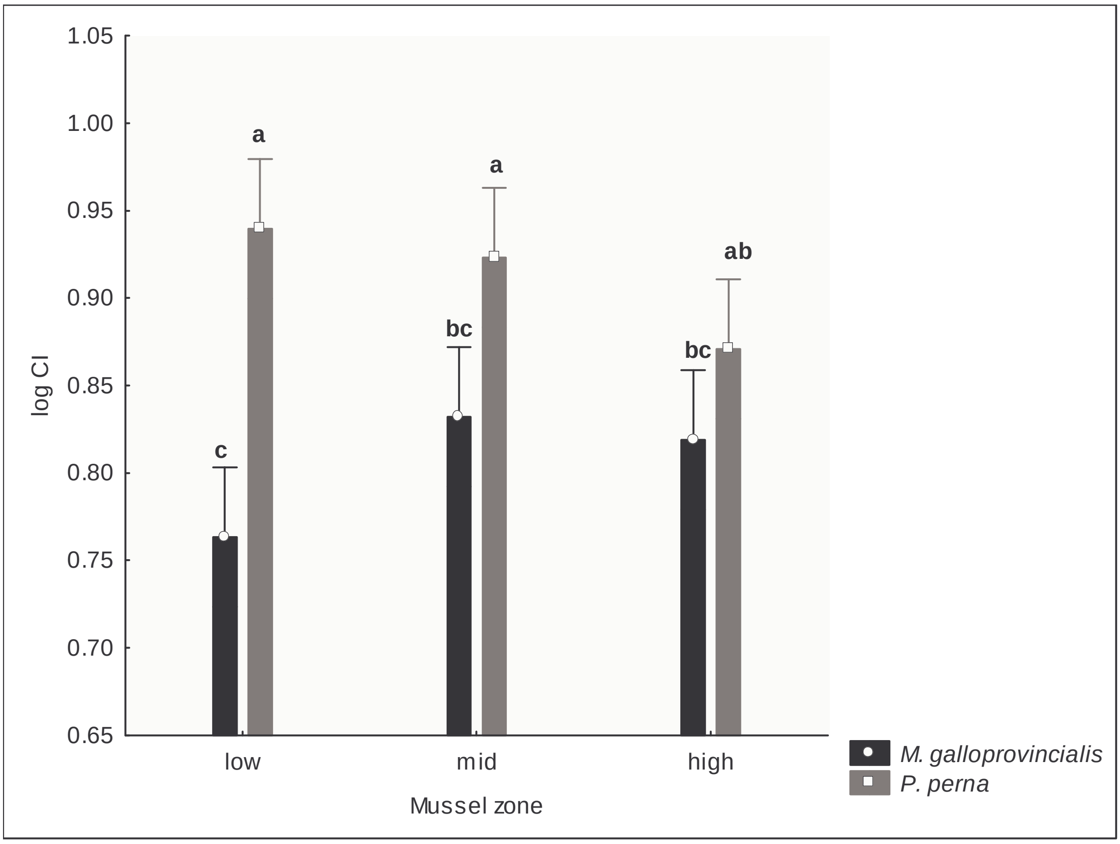


Fig 3.8. Second experiment. Mean log CI values for each species in each zone. Vertical bars denote 95% confidence intervals. Letters indicate homogenous groups as determined by Tukey tests.

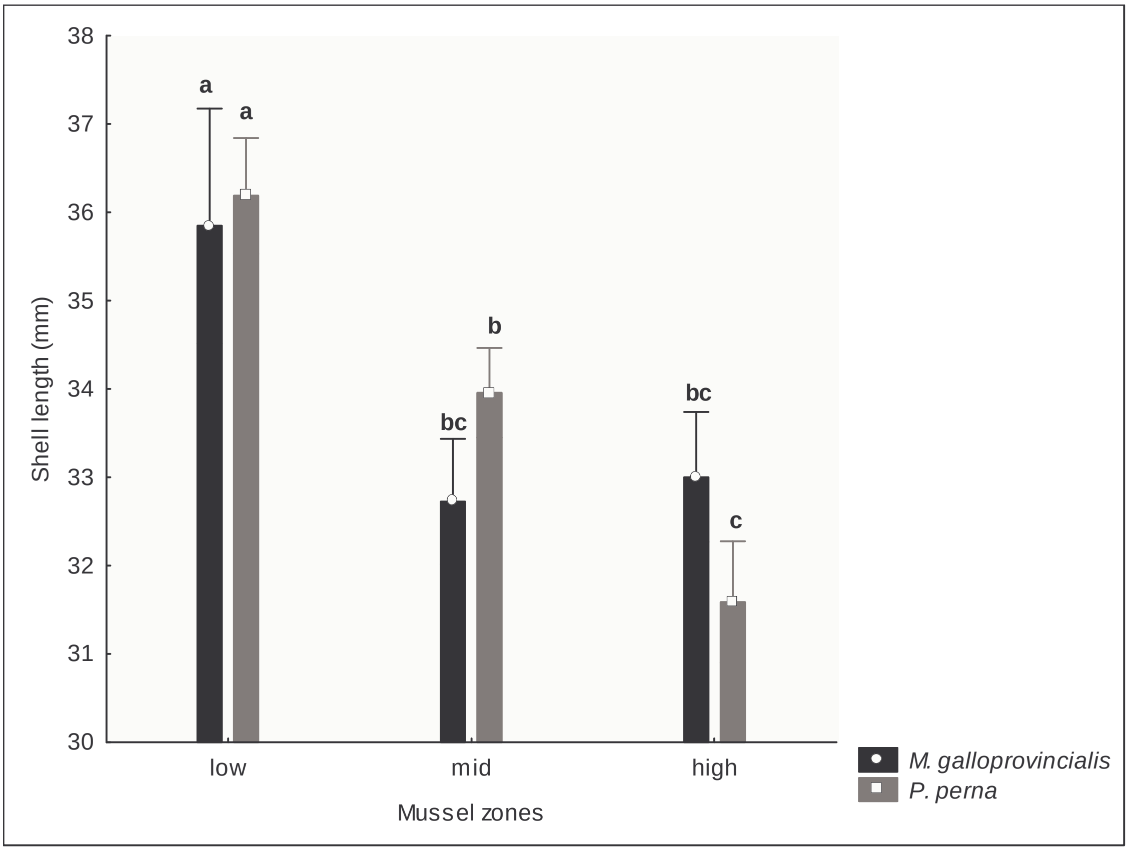


Fig. 3.9. Second experiment. Final shell length (mm) for each species in each zone. Vertical bars denote 95% confidence intervals. Letters indicate homogenous groups as determined by Tukey tests.

Growth

Final length measurements failed the Shapiro-Wilk's W test (W = 0.99*) and no transformation could be applied to normalize the data.

Species, treatment and mussel zone were each tested with the Kruskal-Wallis test (H = 5.46*, H = 0.78^{ns} and H = 88.71*** respectively). The results showed a very strong zone effect, but no effect of treatment while some species effects were found. A 3-factor ANOVA test showed the same results but, additionally, a significant interaction between species and zone (F = 7.62***, Fig. 3.9). The overall data showed that maximum growth for both species occurred on the low zone, minimum growth for *P. perna* on the high zone and for *M. galloprovincialis* on the mid shore. Even though *P. perna* growth was higher than *M. galloprovincialis* on the mid zone, and vice versa on the high zone, the differences were not significant. Multiple Comparisons Kruskal-Wallis tests showed significant differences ($p < 0.05$) between all zones in *P. perna*, while the low zone differed from the mid and high zones in *M. galloprovincialis*. Non-significant differences ($p > 0.05$) were found between species in each zone.

The results of growth on the low zone accord closely with McQuaid & Lindsay (2000). In that study, mussel growth rates were determined from the low zone of sheltered and exposed rocky shores of the south coast. According to their study, Old Woman's River was considered semi-sheltered (author's unpub. data). McQuaid & Lindsay's (2000) growth equation for sheltered shores ($y = -1.4374 \ln(x) + 6.5608$, where x = initial length) indicates growth of 1.93 mm/month, which in the six months that the present study was run, implies total growth of 11.60 mm, resulting in a final length of 36.6 mm. The mean final lengths of *M. galloprovincialis* and *P. perna* on the low shore were found to be 35.85 (±4.19 S.D.) mm and 36.19 (±3.26 S.D.) mm respectively.

Third experiment

Mortality

The total cumulative mortality during the study period until the mesh was removed (8 months) was 7.17% for *P. perna* and 11.84% for *M. galloprovincialis*. One month later, these values had increased to 9.67% for *P. perna* and a remarkable 74.17% for *M. galloprovincialis*. Of total *M. galloprovincialis* mortality, 91.24% were lost from monospecific quadrats. As a result, and to not obscure the results of competitive interaction by the effects of wave action, only data from the first eight months were used in the analysis.

The accumulated % mortality data showed a slightly non-normal distribution (Shapiro-Wilk's W test, W = 0.93*). Levene's Test for Homogeneity of Variances failed for the first 3 months but was successfully passed in the last six months ($p > 0.05$). No transformation could transform the results to satisfy the assumptions of parametric tests.

A 2-factor RM-ANOVA test was run with species and treatments as factors. Both factors and their interaction showed significant effects (RM-ANOVA test, treatment, F = 8.05**; species, F = 17.81***; species x treatment, F = 3.99*; time, F = 18.96***; time x species, F = 3.37**). In general, over time *M. galloprovincialis* had higher mortality than *P. perna*. Treatments with lower densities (25 *P. perna* or 25 *M. galloprovincialis*) had lower mortalities than the rest of the treatments (i.e. treatments with 50 individuals), though this was not the case for *P. perna* in treatment 3 (Fig. 3.10). The post hoc Tukey HSD test on the interaction between species and treatment showed which treatments differed. Significant differences ($p < 0.05$) were found between treatment 3 (for *M. galloprovincialis*) and treatment 4 (see Table 3.1b), between treatments 3 (for *M. galloprovincialis*) and 1, between treatments 2 and 4 and treatments 2 and 3 (for *P. perna*), and between both species in treatment 3. The comparisons in Table 3.1b indicate which differences must be present in order to find evidence of competitive interaction. For intraspecific competition the null hypothesis is tested by comparing treatments 1 vs 2 and 4 vs 5. For interspecific competition the relevant comparisons are treatments 1 vs 3 and 3 vs 4. In this regard, the only relevant significant differences found were the differences in mortality of *M. galloprovincialis* between treatments 1 and 3, which showed a significant effect of *P. perna* on *M. galloprovincialis* mortality (interspecific competition), with a negative effect of *P. perna* on survival of *M. galloprovincialis* (Fig. 3.10).

Kruskal-Wallis ANOVA tests confirmed the results of the RM-ANOVA, showing significant effects of species and zone in all months except for the first (Table 3.8).

Table 3.8. Third experiment. Kruskal-Wallis ANOVA test results for each month.

* = $0.01 < p < 0.05$, ** = $0.001 < p < 0.01$, *** = $p < 0.001$, ^{ns} not significant.

`	May	June	July	August	September	October	November
Species	ns	*	*	***	**	***	**
Zone	**	**	*	*	*	*	*

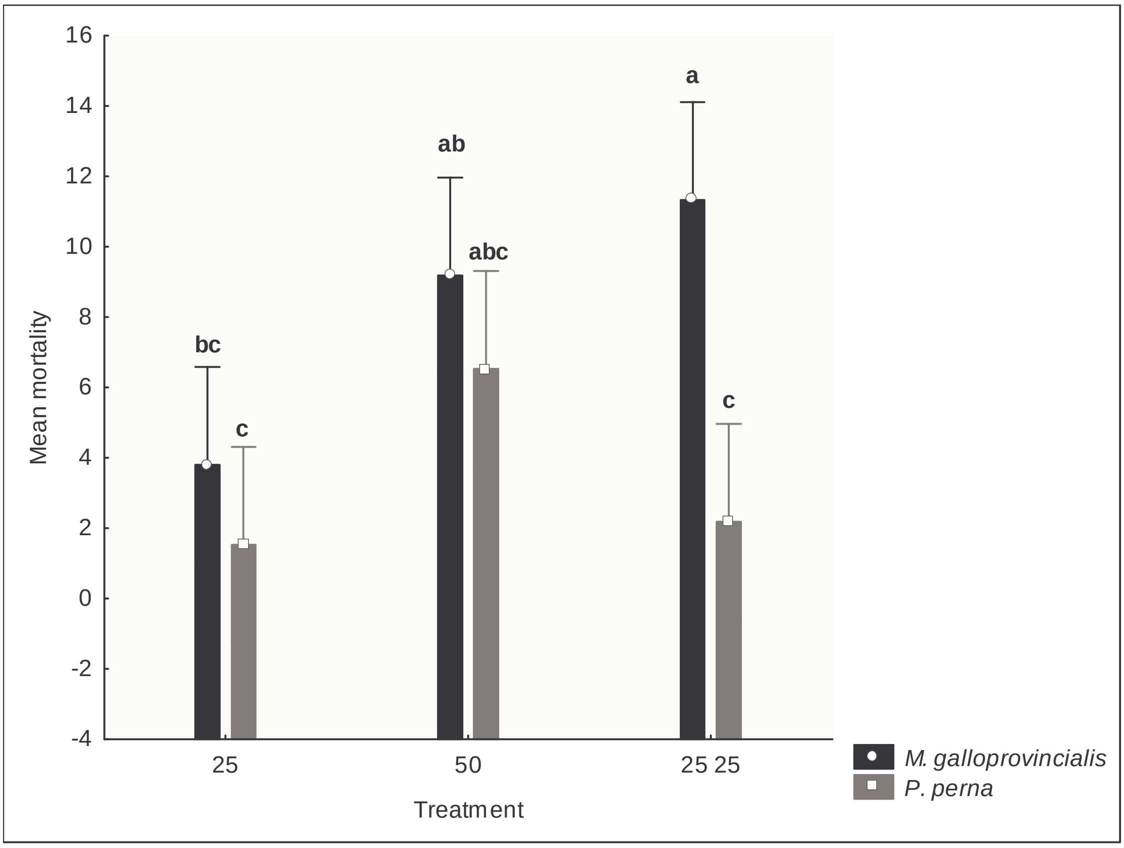


Fig. 3.10. Third experiment. Mean mortality for each species in each treatment. Vertical bars denote 95% confidence intervals. Letters indicate homogenous groups as determined by Tukey tests.

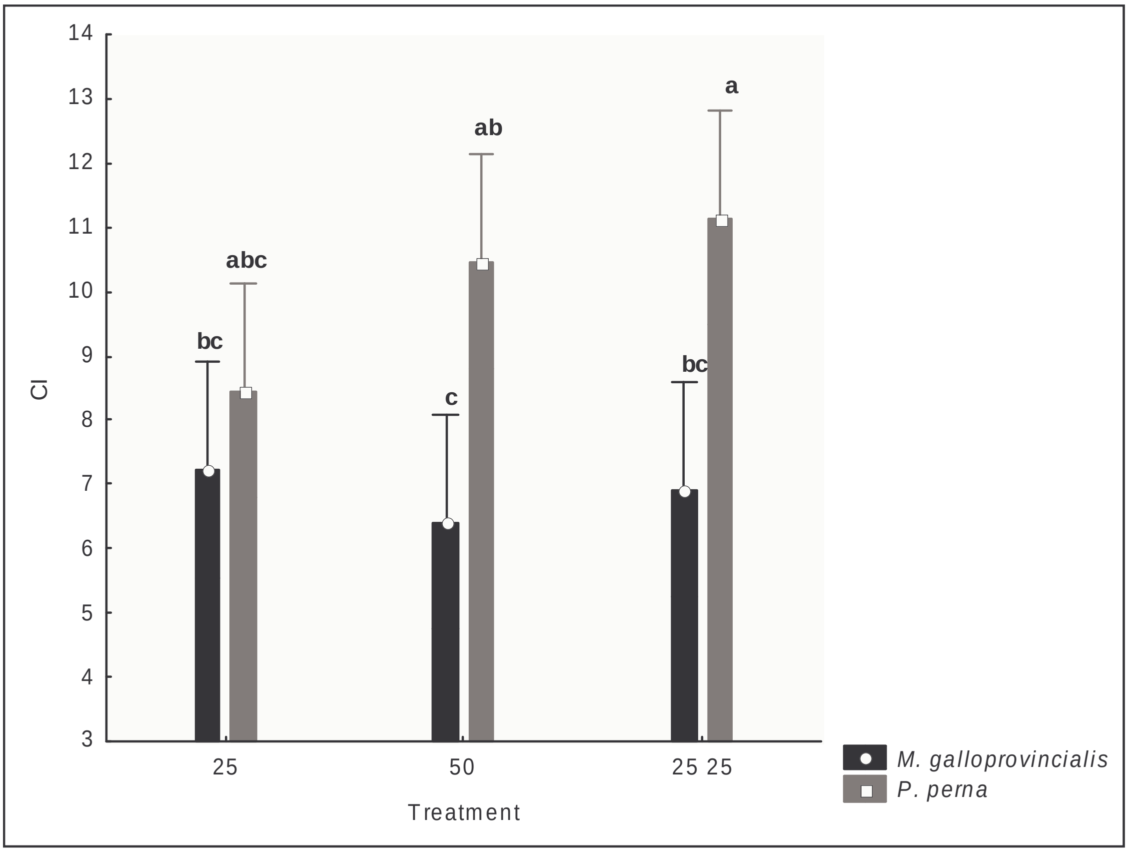


Fig. 3.11. Third experiment. Mean condition index for each species in each treatment. Vertical bars denote 95% confidence intervals. Letters indicate homogenous groups as determined by Tukey tests.

Condition index

Condition index data showed normal distribution (Shapiro-Wilk's W test, W = 0.95^{ns}) and Levene’s test was passed successfully (F = 1.38^{ns}). A 2-factor ANOVA test was used with species and treatment as factors. The results showed a strong species effect (F = 25.6***) while treatment and the interaction were not significant (F = 1.2^{ns}, F = 2.4^{ns}, respectively) (Fig. 3.11).

Growth

Final length data showed normality (Shapiro-Wilk's W test, W = 0.96^{ns}) and Levene’s test was passed successfully (F = 0.62^{ns}). A 2-factor ANOVA test was used with species and treatment as factors. The results showed no significant effects of any factors or the interaction (treatment, F = 0.62^{ns}; species, F = 0.13^{ns}; treatment x species, F = 0.8^{ns}).

In summary, for the third experiment, there was no effect of species on growth, while for mortality and CI, species only differed in treatment 3 (25 *P. perna* and 25 *M. galloprovincialis*). In this treatment, *P. perna* has lower mortality and higher CI than *M. galloprovincialis*.

Discussion

An unexpected result from this study was the influence of wave action on the experiments. Physical disturbance may act in the same way as predation, maintaining non-equilibrium conditions under which competition is reduced and exclusion unlikely (Branch 1984a). Wave action has been described as one of the primary mechanisms creating and/or maintaining open space within established intertidal communities, thereby preventing dominant competitors from monopolizing the primary space on rocky shores and consequently preserving diversity (Paine & Levin 1981, Sousa 1984). However, beds of dominant sessile species can maintain a greater stability on rocky shores through preserving higher turnover rates and lower densities, guaranteeing substrate dominance (Tanaka & Magalhães 2002).

Water movements influence predation rates, food supply, recruitment, growth and condition of mussels and, hence, their capacity to compete with other species (Branch & Steffani 2004). A common form of physical disturbance on exposed rocky shores is the dislodgement of mussels as a result of wave shear. Mussels are prone to removal by waves, leaving bare patches within mussel beds (Dayton 1971, Harger & Landenberger 1971, Paine & Levin 1981, Denny 1987, 1995). Dislodgements are sporadic events, which can occur unpredictably throughout the year, but strong storms during winter render mussels particularly prone to disturbances (Brundrit & Shannon 1989). The hydrodynamic force experienced by mussels in densely packed mussel beds is mainly lift, which acts perpendicular to the substratum (Denny 1987, Bell & Gosline 1997). Mussels in beds are usually positioned with the long axis perpendicular to the substratum, so the area over which this force acts is determined by the width and the height of the mussel (Steffani & Branch 2003a). An increase in shell thickness can protect mussels from the destructive effects of wave action (Raubenheimer & Cook 1990). Steffani & Branch (2003a) found that mussels tended to be both taller and wider at more sheltered sites and lower and narrower at exposed sites, and it was suggested that this tendency could be due to a reduction of the area over which hydrodynamic lift acts as a response to the increased risk of dislodgment (Denny 1987, Bell & Gosline 1997). When mussel density is very high, the byssus matrix can lose contact with the substrate, resulting in a slight elevation of the mussel bed - a hummock (e.g. Seed & Suchanek 1992). These hummocks are relatively easily dislodged by wave action, forming small gaps that can be readily recolonized (Tanaka & Magalhães 2002).

Disturbance can play a key role in retarding the process of competitive elimination (Connell 1978). By removing occupants that can competitively exclude other organisms, the system is maintained in a state of biological undersaturation (Hockey & Bosman 1986). Steffani & Branch (2003b) suggested that, on exposed shores of the west coast of South Africa, mussel beds of the invasive and competitively dominant species *Mytilus galloprovincialis* were periodically disturbed, clearing space and allowing temporary expansion of limpets that are competitively inferior. However, these cleared patches opened by wave action were again recolonized by the invader, while *Scutellastra argenvillei* was outcompeted by lateral encroachment from the primary space. In opposition to this, in sheltered sites, Branch & Steffani (2004) suggested predation as a possible factor that could reduce the presence of *M. galloprovincialis* diminishing maximum sizes, and that this predation will reduce the effects of competition with limpets. In our study, the fact that mortality in controls did not differ between species or zones suggests no preferential effects of predation in either species or any zone.

A storm destroyed most of the first experiment in June 2003. The RM-ANOVA test showed a clear species effect and that in all mussel zones the mortality of *M. galloprovincialis* was nearly double that of *P. perna* (Fig. 3.3b). From the second experiment's mortality data, the first conclusion was that removal of the mesh meant high mortality due, once again, to wave action. In this case, the mortality of both species was similar after the mesh had been removed, however, the final mortality showed a remarkable difference between species, with *P. perna* once again surviving the dislodgment better than *M. galloprovincialis*. Similarly, in the third experiment, during the last month of the experiment, the removal of the mesh produced an increase of 2.5 and 62.33% of the total cumulative mortality of *P. perna* and *M. galloprovincialis* respectively. The results suggest that *M. galloprovincialis* has weaker byssus attachment than *P. perna*.

This accords with Zardi (unpub. data) who concluded that *M. galloprovincialis* has weaker byssus attachment than the Brown mussel because the invader has fewer byssus threads, which were also thinner than those of *P. perna*. Different inferences can be drawn from these results. Both *M. galloprovincialis* and *P. perna* survive well on exposed shores in South Africa (McQuaid & Lindsay 2000, Branch & Steffani 2004), but the former predominantly on the west coast and the latter on the south and east coasts (van Erkom Schurink & Griffiths 1990). Environmental conditions and intertidal communities in these three parts of the South African coastline are very different (Emanuel *et al.* 1992), which could be the general explanation of why byssus tenacity is weaker in the invader. Some of these conditions may affect the attachment of *M. galloprovincialis* and make it more prone to removal by waves (especially in the low mussel zone). One possible cause could be temperature, and the fact that the warmer conditions of the south coast does not provide the same favourable conditions for *M. galloprovincialis* that the west coast cool water does.

Harger (1970) found that *M. edulis* was more sensitive to the effect of waves than *M. californianus* and that the latter held its position more strongly. *M. edulis* was behaviourally better adapted to quiet waters than *M. californianus*. The latter preferred wave exposed coasts rather than sheltered bays. In this case, the most likely reason for this preference was the intolerance of *M. californianus* to low salinity and sedimentation (Harger & Landenberger 1971).

In the third experiment, *M. galloprovincialis* individuals were mostly removed (91.24% of the total *M. galloprovincialis* casualties) from the control quadrats (i.e. those with only *M. galloprovincialis*). In contrast, in the quadrats with both species, *M. galloprovincialis* survived much better than in monospecific plots. These results suggest that the invader shows better survival on this coast when it is found in beds of the indigenous mussel, which provide protection against dislodgement by wave action.

In the intertidal zone, zonation patterns of organisms (i.e. upper and lower limit of each organism's distribution) are limited by biological and physical factors. For the latter, wave action affects the low shore more while desiccation does so more on the high shore (Dayton 1971). The other outcome from the results of the first experiment was the strong zone effect that was found (Table 3.2). Mortality showed a marked decrease from the low zone, through the mid zone to the high zone (Fig. 3.4b), suggesting that mussels on the low shore were more susceptible to storms.

Comparisons of the first and second experiments (Figs. 3.5, 3.6) suggest that *M. galloprovincialis* and *P. perna* survived differentially in each mussel zone. The invader did not show a very clear pattern in its mortality between mussel zones, the only considerable difference was found during the first experiment when the final mortality in the high zone was very low, suggesting higher viability in this zone than in the others. In contrast to this, *P. perna* showed a very clear pattern in both experiments but, curiously, the tendencies were opposite in the two experiments. In the first experiment the effect of the winter storm was clear and diminished from the low (the highest mortality) to the high mussel zone; in the second experiment high zone mortality was the highest while mortality in the other two mussel zones remained at lower levels, suggesting that the high mussel zone was strongly affected by desiccation during the summer months. As a conclusion, the low zone was highly affected by swells, especially in the form of storms, and desiccation did not seem to be a problem through the year. In contrast, in the high zone, desiccation can be a problem during summer months while storms hardly affect this upper mussel zone. The mid zone remained in the middle of both situations in all experiments. The fact that higher mussel zones seemed to benefit *M. galloprovincialis* more than *P. perna* was in accordance with the observation that *M. galloprovincialis* was not found in subtidal areas along the South African coast (Branch & Steffani 2004).

Benthic communities can be strongly influenced by the bottom-up influence of productivity (Menge *et al*. 1999, Menge 2000), which is normally attributed to variation in near-shore phytoplankton concentration (Dahlhoff & Menge 1996). In mussels, Hicks *et al.* (2001) suggested that the productivity of the Texan *P. perna* cohorts might be regulated by physical factors. Within their dense beds, population biomass and productivity may be constrained by available space and degree of tolerated aggregation. Lack of available space may have been the basis of the unsuccessful recruitment at some of their study sites.

The condition index, which relates the flesh weight to the shell volume, is thus an important measure of the physiological status of mussels and the relative allocation of resources to tissue or shell growth (Raubenheimer & Cook 1990, Seed & Suchanek 1992). Several factors, such as predation and competition, play an important role in the condition of intertidal mussels, but it has been shown experimentally that food supply can be, on its own, a sufficient explanation for patterns of filter-feeder biomass (Branch & Steffani 2004). Flesh weight is also influenced by accumulation of gametic tissue, and temporal changes in condition most likely reflect spawning events, rather than seasonal variation in food availability (van Erkom Schurink & Griffiths 1991, Steffani & Branch 2003a). Our experiments were run through spawning periods of *P. perna* (February to September, Lasiak 1986) and the spawning period of *M. galloprovincialis* was assumed to be during the same period in response to changes in the environmental conditions. Another assumption was that both mussel species had the same amount of food supply in each mussel zone.

In our first experiment, the CI results from the high mussel zones did not show any difference between treatments or species. However, in the second experiment, differences in species were found. *P. perna* had higher CI values than *M. galloprovincialis* in the low and mid zones, but they did not significantly differ in the high zone. The third experiment showed that *P. perna* performed better in the low mussel zone and in the overall experimental treatments than *M. galloprovincialis*.

Bivalves from temperate regions commonly grow faster in particular seasons (Griffiths & Griffiths 1987). For the final growth measures it was assumed that both mussel species exhibited the same seasonality in growth during the period that each experiment was run. Environmental conditions have major impacts on growth, reproduction and shell morphology of mussels (Bayne *et al.* 1983, Griffiths & Griffiths 1987, Seed & Suchanek 1992). On the west coast, marked differences in the growth rates, conditions and shell shapes of *M. galloprovincialis* were detected among sites straddling a gradient of wave exposures (Steffani & Branch 2003a). The same was found on the south coast with *P. perna* (McQuaid & Lindsay 2000). *M. galloprovincialis* grew faster and had higher condition values at moderately exposed sites than at sheltered sites. The same was found for the indigenous *A. ater*, *C. meridionalis* and *P. perna*. Faster condition and growth were found in areas of high water circulation than in areas with restricted circulation (van Erkom Schurink & Griffiths 1993). This was most likely related to greater food availability at sites with increased flow (Steffani & Branch 2003a). These observations were very similar to those found among the different mussel zones, where water circulation and available time for feeding in each mussel zone influenced the condition and growth of the mussels. High zones could be comparable to sheltered sites and low zones to exposed sites, while mid zones could be considered equivalent to semi-sheltered sites.

In the first experiment, the growth in the high zone was not significantly different between species or among treatment, while in the second experiment, both zone and species showed significant effects. *P. perna* appeared to grow slightly more in the low and mid zones than *M. galloprovincialis*, while in the high zone *P. perna*'s growth values were lower than those of *M. galloprovincialis*. For *P. perna* a very significant upshore decreasing trend was observed. These results suggest that *P. perna* performs better than *M. galloprovincialis* in the lower mussel zones, while in the high zone both species were in the same condition. *P. perna* results are comparable to the evidence that when mussels are transplanted to ropes in aquaculture, their growth in subtidal areas is far superior to that in the intertidal areas, largely because of the higher period available for feeding (van Erkom Schurink & Griffiths 1990). However, *M. galloprovincialis* did not follow this tendency perfectly. While low zone growth was higher than the other two mussel zones, in the high zone its final mean growth was slightly (but not significantly) higher than in the mid zone. These results, coupled with CI results (almost equal performance of this mussel species in both mid and high zones and less in the low zone), indicated the ability of *M. galloprovincialis* to survive more successfully in higher than in lower mussel zones. Phillips (1995) suggested the existence of habitat segregation in the mussel bed, where *P. perna* lived more abundantly in low and mid zones while *M. galloprovincialis* appeared more on the high mussel zone. These results were in accordance with the findings of Chapter 2.

M. galloprovincialis is an aggressively invasive alien species (Hockey & van Erkom Schurink 1992, Griffiths *et al.* 1992) in South Africa that has established competitive interactions with all intertidal species that geographically overlap with its distribution and occupy similar habitats. Some species have been displaced by *M. galloprovincialis*, as the latter is a superior competitor for intertidal space (Hockey & van

Erkom Schurink 1992). On the west coast, limpet species are faced with local extinction. However, *M. galloprovincialis* flourishes better in exposed localities than in sheltered or semiexposed areas. Limpets such as *Cymbula granatina* (Linnaeus), which favours sheltered coves, is thus not adversely affected by *M. galloprovincialis*, and *Scutellastra argenvillei*, which once dominated the low shore of semi-exposed to exposed shores, can survive on semi-exposed shores even if it faces displacement on exposed shores (Branch & Steffani 2004). Of all indigenous South African mussel species, *A. ater* has the slowest growth, lowest reproductive output and the lowest tolerance to aerial exposure. Its filtration rate is only 28% of that of *M. galloprovincialis* (Griffiths *et al.* 1992). Over the past decade there has been a marked decline in the numbers of *A. ater* in the intertidal zone of semi-exposed and exposed shores of the west coast (Hockey & van Erkom Schurink 1992), and particularly, at monitored sites near Saldanha Bay, where invasion by *M. galloprovincialis* has reduced *A. ater* abundance by 80% (Branch & Steffani 2004).

The mortality results of the second experiment show that treatment 4 for *P. perna* differed from treatments 2 and 3 (see Table 3.1a), which did not give any indication of intra or interspecific competition. In the third experiment evidence of competition for space in the form of interspecific competition was detected. *P. perna* affected *M. galloprovincialis*' viability because mortality of treatment 1 and 3 for *P. perna* and treatment 3 for *M. galloprovincialis* were significantly different. No significant differences between treatment 2 and 3 for *M. galloprovincialis* were found. Statistically higher mortality in treatment 3 than treatment 2 would confirm the existence of interspecific competition, avoiding the influence that density could have on obscuring the results. All in all, the results showed a clear difference between indigenous and invader's treatment 3, which confirmed the occurrence of competition on the low shore.

The fact that byssus attachment of the two species differs, *P. perna* being much stronger than *M. galloprovincialis*, and that the latter appeared to survive better in mixed than in monospecific beds, suggests that *M. galloprovincialis* is enhanced by the presence of *P. perna*. However, the results of the third experiment indicate that at the same time that *P. perna* confers protection against dislodgement by wave action, it competitively excludes *M. galloprovincialis*.

Regarding density, the third experiment showed higher mortality in all control quadrats with 50 individuals than in quadrats with 25 individuals, but the post-hoc Tukey test showed that these differences were not significantly different across each species. This tendency suggests that density effects might possibly be established in a hypothetically longer period study as a result of intraspecific competition.

The results suggest that *P. perna* is a stronger competitor for the space than *M. galloprovincialis* on the low shore. Some studies have described higher performance of pernids than other mytilids. One example is the shell growth rate that in tropical pernids is greater than that found in temperate mytilids (Vakily 1989). Among mytilids, the high growth rates of pernids allow them to sustain higher annual production rates than temperate members of the genus *Mytilus* (Hicks *et al*. 2001). In addition, a high production rate among pernids was detected in the South African *P. perna* population, ranging from 6.45 to 7.61 kg.m^{-2}.y^{-1} (Berry 1978), which is twice that of the highest rate reported for *M. edulis* (Dare 1976). Another favourable property is that pernids either have a greater proportion of shell mass as organic periostracum and matrix or have a proportionately more massive shell relative to tissue biomass than other mytilid species (Hicks *et al*. 2001). This, coupled with our results, suggests that the assumption that *M. galloprovincialis* would inevitably displace *P. perna* from the south coast, as *P. perna* is an inferior competitor, should be reconsidered.

The findings suggest that no further big changes in mussel beds are expected from the *M. galloprovincialis* invasion on the south coast. Its growth, condition, density and number of recruits (author's unpub. data) are all lower than *P. perna*, which indicates that its competitive effects on the indigenous species are less intense than on the west coast (Branch & Steffani 2004), possibly due to less favourable environmental conditions along this coast. A clear example of *M. galloprovincialis* disadvantage on this coast is its weaker byssus tenacity in comparison to *P. perna*. On the west coast, peak biomass, maximum size of *M. galloprovincialis*, the greatest percent cover and depth of mussel beds are all attained at intermediate levels of wave exposure (Branch & Steffani 2004). Our study site, Old Woman's River was defined as semi-sheltered (McQuaid & Lindsay 2000), which, based on west coast studies, would provide ideal conditions for *M. galloprovincialis* to grow and develop. However, the results did not reflect this.

From the mortality results obtained from the third experiment (Fig. 3.10), it was concluded that on the low shore *P. perna* is a better competitor for space than *M. galloprovincialis*. However, this affirmation could be obscured by the zone effect. Fig. 3.8 showed a tendency of better performance of *P. perna* in lower than higher mussel zones, while *M. galloprovincialis* followed the opposite trend. Moreover, the CI values for the low zone were significantly different between the species, with *P. perna* having a much higher mean CI value than *M. galloprovincialis*. However, in each species, mean values did not show significant differences for the different mussel zones. In Fig. 3.11 a clear dominance of *P. perna* mean CI values over *M. galloprovincialis* values was found in quadrats of 50 individuals, which, if these values are compared with CI data from the second experiment, would suggest that this supremacy is not because of competition but rather because of a zone effect, i.e. the experiment was run in a mussel zone where *P. perna* survives better than *M. galloprovincialis*. In this way, it is possible that the competitive effects that *P. perna* inflicts on the invader on the low zone are different in the other two mussel zones.

This suggests that further competition experiments (like the third experiment on the low zone) are required in the other two mussel zones to validate the hypothesis that *P. perna* is a stronger competitor for space than *M. galloprovincialis* is on this stretch of coast.

Chapter Four:

Human exploitation of mussels on the south coast of South Africa

Introduction

Human exploitation of intertidal organisms on rocky shores is an important factor disturbing intertidal communities (Moreno *et al*. 1984, Castilla & Durán 1985, Durán & Castilla 1989, Kingsford *et al*. 1991, Keough *et al*. 1993). In South Africa, exploitation predominantly targets mussels (Siegfried *et al*. 1985, Hockey & Bosman 1986, Lasiak 1991).

In many parts of the world, indigenous cultures have shown exploitation of intertidal organisms at a subsistence levels since prehistoric times (Siegfried *et al*. 1985, Moreno *et al*. 1986, Catterall & Poiner 1987, Underwood 1993). Some of the earliest evidence of subsistence exploitation comes from southern Africa (Avery & Siegfried 1980), where early archaeological evidence for shellfish collecting of marine molluscs indicates that it has been practised on the western, southern and eastern coast of South Africa since the Middle Palaeolithic Era (100 000 years B.P.) (Voigt 1973, Volman 1978, Stringer 2000). The way that humans have exploited intertidal resources has been changing throughout this long period of time and there exists today a clear difference between modern and ancestral ways of pursuing this activity. Prehistoric man may have been migratory or nomadic, and may thus have exploited intertidal animals on an intermittent basis. Modern man, by contrast, is relatively sedentary, and exerts a more continuous pressure on intertidal resources (Hockey 1994).

Modern exploitation of marine resources comprises three types of activity: recreational, commercial and subsistence (Lindberg *et al.* 1998). Recreational activities refer to the harvesting of marine resources that occurs for short periods of time throughout the year and is localized to certain areas. The other two types are more active and persistent activities that can continuously affect ecosystems. Commercial activities are directed at individual, highly profitable species, while subsistence exploitation (generally practised by poor people) targets a wide range of species. As a result, the diversity of species collected by subsistence gatherers is much higher than in commercial exploitation (Siegfried *et al.* 1994).

These three types of exploitation can be found all around the world dependant on many factors such as demography, tradition, economy, etc. For example, Chile and South Africa show many similarities in the ways that people exploit marine resources. In both countries, marine organisms on rocky shores constitute the principal intertidal resource exploited for subsistence, recreation and commerce (Siegfried *et al.* 1994). Australia shows a different pattern in harvesting activity. Recent collection tends to be of a more recreational nature (Catterall & Poiner 1987, Kingsford *et al.* 1991), with intertidal animals and a few algae species being harvested for consumption or use as bait, fertilizer, stock feed or ornamentation (Catterall & Poiner 1987, Underwood 1993). In the same way, Rius & Cabral (2004) suggested that in Portugal, intertidal animals are not collected for subsistence or commerce and that harvesting is not the main professional activity of harvesters.

Most human exploitation on intertidal organisms is concentrated on rocky shores with these organisms predominantly used for food and bait (Hockey *et al.* 1988, Poiner & Catterall 1988, Kingsford *et al.* 1991). On rocky shores, human exploitation and the effects of trampling (particularly during holiday seasons) affect, sometimes dramatically, intertidal communities worldwide (Liddie 1975, Beauchamp & Gowing 1982, Moreno *et al.* 1984, Castilla & Durán 1985, Moreno *et al.* 1986, Durán & Castilla 1989, Kingsford *et al.* 1991, Povey & Keough 1991, Keough *et al.* 1993, Lasiak & Field 1995). Generally, man is a tool-using predator (Hockey & Branch 1984, Durán *et al.* 1987, Hockey 1987) and, as a result, overcomes the spatial refuges of many intertidal animals that are effective against natural predators. This allows man to collect large prey items, which may have achieved a refuge through their size from other predators (Hockey 1994). Prey have no temporal refuge from predation by man, except for short-term refuges afforded by tidal fluctuations, heavy seas associated with the prevailing weather, or seasonal patterns of predation intensity related either to condition of the prey or prey demand (largely in the case of recreational exploitation). Behavioural escape mechanisms are similarly ineffective against man, because of man's high mobility, and morphological or architectural defences of these intertidal animals are overcome through the use of tools. The only anti-predator adaptation that is effective against man is chemical-defence (Hockey 1994).

The predatory impact of man is very different from that of 'natural' predators. Unlike the majority of predators found intertidally, man is mostly a facultative rather than an obligate predator. Man functions both as a predator and as a mega-herbivore in intertidal and shallow subtidal ecosystems. The high mobility and metabolic demands of man make him a potentially important determinant of community structure at lower trophic levels (Hockey 1994). Another characteristic of man as predator is that the principal prey items in subsistence exploitation are large herbivorous and predatory gastropods, bivalves (especially mussels), echinoderms, ascidians, large arthropods, polychaetes and algae (Hockey & Bosman 1986, Bustamante & Castilla 1987, Durán *et al.* 1987). Most invertebrates which are preyed on are occupiers of primary space but some, such as mussels, may provide a substratum for other organisms (Hockey 1994).

Although a wide range of organisms is gathered, human harvesters tend to be selective, both in terms of the species and size of the individual removed (Siegfried *et al.* 1985, Hockey & Bosman 1986). In this regard, shellfish collection by humans affects mostly the largest individuals of particular target species (Moreno *et al.* 1984, Catterall & Poiner 1987, Kingsford *et al.* 1991). As with humans, natural predators are generally size selective in their choice of prey (Hockey 1994). An example of this is predation by the whelk *Thais*, which tends to eliminate the larger individuals and therefore reduce the mean length of prey populations (Connell 1961b). With reference once again to shellfish collection by humans as a form of selective predation, comparisons of the size composition of resident populations with shells in middens (i.e. shells of molluscs that have been consumed) suggests that people preferentially select larger individuals (Siegfried *et al.* 1985, Hockey & Bosman 1986). Direct observation of the bags of collectors shows the same result, with the scarcity of small specimens indicating preferential size selection (Lasiak 1991). Disruption of the space mosaic through selective exploitation may lead to major changes in community structure, which persists in the event of continued exploitation (Moreno *et al.* 1984, 1986, Castilla & Durán 1985, Hockey & Bosman 1986, Oliva & Castilla 1986, Durán & Castilla 1989, Lasiak 1991). Progressive size reduction of prey leads to intensified collecting pressure on the remaining individuals, and this, coupled with the spatial encroachment of inedible species, inevitably leads to the degradation of the intertidal zone communities as a food resource (Hockey & Bosman 1986).

In the case of human predation on molluscs, exploitation is concentrated on large and fecund individuals (major contributors to population spawning events). However, reduction of adult densities through predation may reduce intraspecific competition, resulting in a relatively high density of small animals (most mollusc species become reproductively active at a young age and small size). These densities may be sufficiently high for their collective reproductive output per unit area of shore to approach, or even exceed, that of adults (Griffiths *et al.* 1992, Hockey & van Erkom Schurink 1992). However, in the case of collection of mussels, exploitation seems to not always be selective and does not only affect larger individuals. Lasiak & Dye (1989) in South Africa and Rius & Cabral (2004) in Portugal have described that, for *P. perna* and *M. galloprovincialis* respectively, size selection takes place after the removal of entire clumps of mussels from their point of attachment on the rocks. The numerous small individuals (<30 mm total length), inadvertently collected with clumps of larger mussels, are rejected and discarded on the shore by the collectors because they are of minimal food value. A significant proportion of the population is thus lost because of the mode of collection. The impact of this is increased because of the gregarious tendencies of the mussels (Lasiak 1991) and because settlement preferentially occurs around the periphery of existing clumps (Berry 1978). As a result, in places where human exploitation on mussel beds follows this behaviour, percent mussel cover is the most reliable measure of this activity, while size distribution and other measures can complement the results found.

Although normally patchy in its distribution, human harvesting can have a severe impact, and intensive, localized collection may lead to extensive changes in structure and functioning of the intertidal community (Moreno *et al.* 1984, Castilla & Durán 1985, Siegfried *et al.* 1985, Hockey & Bosman 1986, Moreno *et al.* 1986, Oliva & Castilla 1986, Durán *et al.* 1987, Hockey 1987, Keough *et al.* 1993, Hockey 1994). Exploitation can seriously deplete the stocks of intertidal organisms (Lambert & Steinke 1986). However, there is also evidence that the stability of some rocky-shore communities is high, with rapid recovery when exploitation ceases (Hockey & Bosman 1986, Moreno *et al.* 1986), although this is not always the case (Dye *et al.* 1997).

The consequences of harvesting can be severe, substantially reducing stocks of harvested species, and affecting not only the target species but also other species, which can be indirectly affected (Hockey & Bosman 1986, Oliva & Castilla 1986, Durán & Castilla 1989, Godoy & Moreno 1989, Keough *et al.* 1993, Addessi 1994, Castilla *et al.* 1994). Most studies that have addressed the removal of intertidal shellfish have focused on the direct effects on the target species (Branch 1975, Moreno *et al.* 1984, Hockey & Bosman 1986, Moreno *et al.* 1986, Castilla & Bustamante 1989, Lasiak 1991, Keough *et al.* 1993). Such an effect includes the removal of many large animals which causes a reduction in the abundance, as well as a decrease in the mean size of individuals within the population (Branch 1975, Moreno *et al.* 1984, Castilla & Durán 1985, Hockey & Bosman 1986, Moreno *et al*. 1986, Oliva & Castilla 1986, Castilla & Bustamante 1989, Durán & Castilla 1989, Fairweather 1990, Keough *et al*. 1993), and in the standing stocks (van Erkom Schurink & Griffiths 1990, Addessi 1994, Griffiths & Branch 1997, Foster & Hodgson 2000). This has important repercussions on the future reproductive output of the population, since larger individuals are more fecund than smaller individuals and are the section of the populace with the lowest mortality (Catterall & Poiner 1987, Fairweather 1990, Underwood 1993). This removal of adults could deplete breeding stocks, which, in turn, affects recruitment (Foster & Hodgson 2000).

Indirect effects include the disappearance of the refuge that these large individuals provide against predators, permitting heavy predation pressure on smaller size classes (Hockey & Branch 1984). Species densities within and between communities may also be indirectly affected by shellfish harvesting (Castilla & Duran 1985, Hockey & Bosman 1986, Durán & Castilla 1989, Fairweather 1990). In southern Chile, Moreno *et al.* (1984) studied the impact of human predation on intertidal invertebrates, and demonstrated that reductions in size and density of key grazing gastropods, *Fissurella* spp., led to an increased cover of macroalgae. This is comparable with the situation on islands off the south western Cape in South Africa, where the density of the principal midshore grazing gastropod, *Scutellastra granularis*, is reduced through predation by the African black oystercatcher, *Haematopus moquini*, to the point where the remaining limpet population is no longer able to control algal growth at the sporeling stage, and persistent beds of macroalgae develop. These beds are largely absent on the nearby mainland where the density of oystercatchers, and hence predation pressure on the limpets, is much less

(Hockey & Branch 1984). As a result, algae flourish after the removal of grazers (Branch & Moreno 1994) and prey species that are not harvested may proliferate if predators are diminished (Hockey & Bosman 1986, Castilla 1999). Therefore, in summation, apart from the direct effects of predation, there is always the potential for indirect effects that ripple through the whole community (Castilla *et al.* 1994).

The effects of human exploitation on rocky-shores can be confused with other non-anthropogenic factors affecting the ecosystem. A major point of confusion arises from changes in environmental conditions and in organism productivity (Siegfried *et al.* 1994). Physical factors are also very important bewildering elements. Many of them may influence the density, biomass and population structure of intertidal animals, including the degree of wave exposure (McQuaid & Branch 1984, 1985); substratum type (McQuaid & Branch 1985); and temperature (Branch 1984b, Brink 1987). Biological processes such as predation, competition or recruitment can also complicate the study of the effects of exploitation (Siegfried *et al.* 1994). For example, there is strong evidence to suggest that recruitment processes often control adult populations and are a major determinant of community structure (Eckman 1996, Harris *et al.* 1998).

In areas where collection is prevalent, overall structure and functioning of intertidal communities in exploited areas may change, and there is a tendency for communities to move towards a common state of diversity and abundance (Hockey & Bosman 1986, Fairweather 1990), thus reducing diversity between regions (Sharpe & Keough 1998). Connell (1978) described the intermediate disturbance hypothesis, which avowed that species richness is greater under conditions of intermittent or moderate disturbance (physical or biological) than under heavy disturbance or at the climax equilibrium stage. As a result, an increase in diversity may be noted due to harvesting (Moreno *et al.* 1984, Castilla & Duran 1985, Hockey & Bosman 1986, Branch & Odendaal 2003).

In South Africa, the earliest evidence of marine resource utilization was found in the complex of caves at Klasies River Mouth (40 km west of Cape St. Francis, see Fig. 2.1), where remains of shellfish date between 120 000 and 70 000 years B.P. There is an abundance of open station shell middens of the last 30 000 years along the south coast of South Africa (between Kei River Mouth and Mossel Bay), however the shell middens are concentrated in Cape St. Francis and Oyster Bay areas (Fig. 2.1) (Lubke & Moor 1998). In the Transkei (Fig. 1.1) the exploitation of intertidal shellfish by man for food has been taking place for at least the last 1 300 years (Cronin 1982), and probably for far longer (Volman 1978, Avery & Siegfried 1980). Throughout this period, the most commonly collected species has been the Brown mussel *Perna perna* (Cronin 1982, Siegfried *et al.* 1985, Hockey & Bosman 1986, Hockey *et al.* 1988).

Over the last 10 000 years, significant changes have occurred in the way intertidal organisms have been exploited by man in southern Africa (Siegfried *et al.* 1985). The spatial pattern of subsistence exploitation has changed considerably over time in response to demographic changes in human populations. For example, with European colonization, the hunter-gatherer life-style and extensive subsistence economy on the west coast, based substantially on shellfish, came to an end. The history of the southern and eastern coasts is similar to that of the west coast, although on these coasts the hunter-gatherer lifestyle persisted for slightly longer following colonization (Siegfried *et al.* 1994). Over the past few decades, rapid population growth combined with a concentration of communities along the South African coastline has resulted in increased intensity of shellfish gathering (Siegfried *et al.* 1994, Griffiths & Branch 1997, Foster & Hodgson 2000, Branch & Odendaal 2003). For example, the subsistence and recreational mussel exploitation along parts of the South African coast continue to grow, and exceed levels of sustainable exploitation in some localities (Siegfried *et al.* 1994). Thus, it is likely that many intertidal communities are vastly different from what they were even 50 - 100 years ago (Lindberg *et al.* 1998).

Modern exploitation on the South African coastline is based on the collection of 35 species (Siegfried *et al.* 1994), however, subsistence exploitation is based largely on mussels and limpets, with smaller amounts of winkles, whelks, octopus and the large solitary ascidian *Pyura stolonifera* (Heller) being collected (Branch 1975, Hockey & Bosman 1986, Hockey *et al.* 1988, Lasiak 1993, Dye *et al.* 1997). The exploitation activities along the coast differ markedly regarding types of harvesting methods (Griffiths & Branch 1997). On the west coast, upwelling promotes productivity and most fishing is commercial and concentrates on abundant or lucrative species. On the southeast (Transkei) and east (Kwazulu-Natal) coasts (Fig. 1.1), many resources are less suitable for commercial fishing, but human population densities are much higher and subsistence harvesting is intense (Griffiths & Branch 1997). The south coast is a popular tourist destination, and holidaymakers frequently collect marine organisms for food, particularly during the peak summer season (van Erkom Schurink & Griffiths 1990). Analyses of contemporary shell middens on this coast indicate that *Perna perna* and various limpets (*Patella* spp.) are favoured for harvesting (Voigt 1973, Mills 1985). Other less abundant organisms collected are alikreukels (*Turbo sarmaticus* (Linnaeus)) and periwinkles (*Oxystele* spp.) (Lubke & Moor 1998).

Depletion of mussels along long stretches of coastline reduces structure complexity and can cause serious alteration to the biodiversity of the intertidal communities (Hockey & Bosman 1986). Despite the abundance of mussels along both west and southwest coasts, exploitation is minimal in these regions (van Erkom Schurink & Griffiths 1990). Along the north western Cape coast, a total of less than 100 tons.y^{-1} of mussels is harvested, an insignificant amount compared with the high rates of mortality resulting from intraspecific competition for space and consumption by natural predators (Griffiths & Hockey 1987). A similar situation prevails in the south western Cape region, however, anglers in this area can inflict substantial damage to intertidal mussel beds while collecting mussel worms, *Pseudonereis variegata* (Grube), for bait (Van Herwerden 1989). Here again the total biomass removed is probably less than 100 tons.y^{-1}. The reasons for this are that mussels are not traditional food resources in these areas and, in the case of the west coast, because of the low human population density and the perceived risk of paralytic shellfish poisoning (van Erkom Schurink & Griffiths 1990).

Along the southeast and east coasts the situation is very different. The politically motivated establishment of “Bantu homelands” during the apartheid era, resulted in the black African population becoming concentrated, the main coastal concentration being in the former Ciskei and Transkei, as well as in Kwazulu-Natal (Fig. 1.1). Indigenous coastal peoples of Transkei have supplemented their traditional maize-based diet with marine invertebrates collected from rocky inter- and infratidal areas since prehistoric times (Voigt 1973). In recent years, there has been an increase in intensity of exploitation due to population growth and poverty (Lasiak 1992) in a manner unconstrained by any firmly enforced conservation legislation (Hockey & Bosman 1986, Lasiak 1991). More particularly, an increase in the rate of human population growth (Siegfried *et al.* 1994) and, consequently, the population density of the indigenous coastal people, along with drought and crop failure (Branch 1975), has meant that the intensity of exploitation has been raised to a level at which the species composition and the ecological functioning of intertidal communities are being markedly affected (Siegfried *et al.* 1985, Hockey & Bosman 1986). As a result, shellfish populations are experiencing greater predatory pressure from man than was ever the case previously (Mills 1985). This situation has led to substantial depletions of harvested species in the Transkei, particularly *Perna perna*, *Haliotis spadicea* (Donovan), several species of patellid limpets, *Pyura stolonifera* and *Turbo sarmaticus* (Branch 1975, Siegfried *et al.* 1985, Hockey & Bosman 1986, Hockey *et al.* 1988, Lasiak 1991, 1993, 1998, Lasiak & Field 1995, Dye *et al.* 1997, Griffiths & Branch 1997).

In recent years, political changes in South Africa have seen the abolition of most laws that were in place during apartheid and the removal of constraints limiting the movement and settlement of people. This has produced another demographic relocation, with large numbers of people moving from former homelands to the cities. Some sites could therefore experience very important modifications in human exploitation pressure patterns. Sites previously systematically exploited could now become less exploited, while other shorelines close to the cities, which were previously unexploited (such as the west coast of South Africa), could potentially face huge exploitation pressures (Siegfried *et al.* 1994).

The Brown mussel *Perna perna* is the most important food item collected on the Transkei coast (Mills 1985, Siegfried *et al.* 1985, Hockey & Bosman 1986). In contemporary middens, this mussel accounted for 57% of all shells examined (Hockey & Bosman 1986) and frequently comprises of more than 90% of the total shell mass accumulated monthly (Lasiak 1991). As a result of intense exploitation pressure, extensive intertidal beds are only found within nature reserves and on inaccessible rock faces (Lasiak & Dye 1989, van Erkom Schurink & Griffiths 1990). In 1978, Siegfried *et al.* (1985) found that *P. perna* accounted for 91.7% of all animals transported home by the local people, while the corresponding proportion in 1984 was 57%. This result suggested that the *P. perna* stock was adversely affected, as indicated by the decrease in numbers of this preferred species in the bags of collectors. Another indication of this was the marked decrease in density and modal and mean sizes of the mussels found at persistently exploited sites compared to those that were protected (Lasiak 1991). Comparisons of non-reserve and reserve sites indicated that within the protected sites *P. perna* was considerably larger than those collected at exploited sites (Siegfried *et al.* 1985, Hockey & Bosman 1986, Lasiak & Dye 1989, Lasiak 1991). Therefore, in some sites, *P. perna* appeared to be susceptible to depletion. However, and despite the impoverished state of the exploited population, there was no evidence of recruitment failure (Lasiak 1991), although Harris *el al.* (1998) found that low mesoscale population densities in the Transkei were associated with particularly low rates of recruitment. Siegfried *et al.* (1985) estimated in their study area on the Transkei coast that each collector removed, on average, 6 kg (wet-weight) of mussels (approx. 725 mussels) per collecting trip. If this quantity was extrapolated along the whole Transkei coastline, an estimate of approximately 12 tons of mussels were taken annually per kilometre of shoreline by subsistence collectors (Siegfried *et al.* 1994). Another estimate showed that along 100 km of this coastline, more than 5.5 tons.km^{-1} of shellfish, mainly mussels, are removed annually by subsistence collectors, with maximum removal rates of >14 tons.km^{-1} (Hockey *et al.* 1988).

It has been suggested that shellfish-derived protein is nutritionally important in supplementing the herbivorous diet of the people living along the Transkei coast (Siegfried *et al.* 1985). This is reflected in the reduced incidence of kwashiorkor (a disease resulting from protein deficiency) close to the coast (Siegfried *et al.* 1985, Hockey *et al.* 1988). Most of the collecting is carried out by women and children at low spring tides, and their efforts are concentrated on the infratidal fringe, decreasing up the shore (Hockey & Bosman 1986). This observation is supported by midden analysis; the majority of animals consumed are species abundant low on the shore. Organized intensive collecting is restricted to periods of spring tides; daytime, with mornings preferred for collecting; and takes place during all seasons (Hockey & Bosman 1986).

In most studies of marine resource exploitation, paired comparisons between human non-impacted sites (normally coastal zones that are protected by law enforcement) versus impacted sites have been conducted (Durán *et al.* 1987, Durán & Castilla 1989, Keough *et al.* 1993, Oliva & Castilla 1986, Siegfried *et al.* 1985). South Africa has a long history of establishing Marine Protected Areas (MPAs) and there are currently 57 areas that receive some form of protection. Many of these allow limited fishing, for example, shore angling may be permitted while intertidal communities are fully protected. Thus, about 4.7% of the coastline is fully protected and about 10% receives substantial protection (Attwood *et al.* 1997). The efficacy of these reserves varies, largely dependant on the degree of management in these reserves (Branch & Odendaal 2003).

Various studies have examined the effects that these MPAs have on mussel populations in South Africa (Crawford & Bower 1983, Siegfried *et al.* 1985, Hockey & Bosman 1986, Lasiak & Dye 1989, Lasiak 1991). In the Transkei region, the population size composition of *P. perna* populations at protected and exploited sites in Transkei has been extensively documented (Siegfried *et al.* 1985, Lasiak & Dye 1989). The lack of abundance and truncated size composition of exploited stocks relative to their counterparts in protected areas suggests that they may contribute little to the overall reproductive output of Transkei stocks (Lasiak 1991). Another observation on this coast was the discovery of changes in the communities between exploited and non-exploited sites. The protected site was dominated by *P. perna* and coralline algae, whereas in the unprotected site, corallines and the green alga *Caulerpa* spp. were the dominant species (Hockey & Bosman 1986). On the south coast, marked differences were found between the size-frequency distributions and biomass of *P. perna* inside and outside conservation areas (Crawford & Bower 1983).

The two exploited species studied in this dissertation were *Mytilus galloprovincialis* and *Perna perna*. From previous observations, it was assumed that harvesters would not choose between species when exploiting mussel beds. The selection of these two species was dictated by several factors. Firstly, both are accessible and large species, and therefore extensively harvested (Siegfried *et al.* 1985, Hockey & Bosman 1986). *P. perna* is collected in large quantities along the Natal and Transkei coasts (Hockey *et al.* 1988) and is an important food-item that in 1978 provided approximately

16% of the annual protein requirements of the coastal people in the Transkei (Siegfried *et al.* 1985). Secondly, studies have revealed that *P. perna* is particularly vulnerable to harvesting (Lasiak 1991). Thirdly, both species are gregarious, which makes them more vulnerable to collection by harvesters (Lasiak 1991); and lastly, there is no data available about human exploitation on mussels on the stretch of coast which is the focus of this study.

Information regarding *M. galloprovincialis* stocks along the south coast of South Africa is very scarce (Robinson *et al.* in press). More research has been done on *P. perna* especially on the Transkei coast (Hockey *et al.* 1988, Lasiak 1991) where it has been shown that *P. perna* currently still enjoys healthy subtidal stocks including large adults (Lasiak 1991).

A preliminary study of human exploitation was conducted along the south coast at three sites: Ngqinisa, Hamburg and Port Alfred (Fig. 4.1). In total 436 enquiries about which species people exploit were made to subsistence collectors while they were harvesting marine animals on the beach. In Hamburg, mussels were the second most favourite target species. In all three sites, of all the species exploited, collectors were most concerned about the decline of abalone (*Haliotis* spp), then of alikreukel and finally of mussels. In Port Alfred, owing to its popularity as a tourist destination, 10.34% of mussels collected were for sale to restaurants. Of the animals collected for consumption, mussels accounted for 51.25% in Hamburg and 17.24% in Port Alfred (which shows the importance of subsistence use of the resource, particularly in Hamburg). Mussels were not collected for bait at any of the sites. The average number of mussels collected per person per day in Hamburg was 19.14 and 4.44 in Port Alfred. The average annual take per subsistence collector was 364.23 in Hamburg and 71.17 in Port Alfred (Kaehler unpub. data). These data contrast with the amount of mussels collected in the Transkei, which Siegfried *et al.* (1985) registered as 725 mussels per person per day.

Other studies of exploitation on the south coast have looked at species other than mussels (e.g. Foster & Hodgson 2000, Branch & Odendaal 2003) and no one has focused on mussels as a main target species. In addition, quantitative evaluations of the intensity of exploitation along the south coast are lacking. Moreover, the intensity of predation has been assessed only in small study areas along the Transkei coast where the benefits to the collectors and the rural community have been evaluated (Siegfried *et al.* 1985, Hockey *et al.* 1988).

Most studies of exploitation (e.g. Durán *et al.* 1987, Durán & Castilla 1989, Keough *et al.* 1993, Oliva & Castilla 1986, Siegfried *et al.* 1985) did not attempt to find correlations between man's predatory intensity and his population density, land-use practices or geologic and geographic features. However, Hockey *et al.* (1988) found that the effects of exploitation are confined to the vicinity of resorts or residential areas and, at a local level, the intensity of shellfish collecting in the Transkei was positively correlated with human population density.

van Erkom Schurink & Griffiths (1990) indicated that sustained and intense exploitation pressure occurs around East London (number 13 in Fig. 4.1) because of a recent increase in population density, thereby increasing the number of people who exploit the shore for their domestic needs, however, no quantification of the crop removal rate is yet available. No study has detailed a pre-, during and post-exploitation sequence to determine whether long-term shifts in community structure occur along the coast of South Africa.

The Marine Living Resource Act (Anon. 1998) describes the regulations regarding the exploitation of marine resources on the South African coastline. It stipulates that 30 mussels can be collected per person per day, and that collection must be done by hand or with an implement with a blade or flat edge not exceeding 38 mm wide. As a result, mussel exploitation by coastal people is regulated. However, law-enforcement efforts have been unsuccessful in ensuring that people respect these regulations.

The aims of this study were: (1) to estimate the condition of the mussel community in a wide range of sites along a 160 km stretch of coast; (2) to quantify human exploitation pressure along the same stretch of coast; (3) to relate factors like number of collectors, beach accessibility, distance to the population centers, etc. to the estimated mussel abundance; (4) to create an initial database for future monitoring studies of mussels along the south coast of South Africa; and (5) to discuss the results in terms of conservation and coastal management.

Materials and Methods

Study location

In order to determine whether a relationship exists between the state of intertidal mussel populations and levels of human exploitation on the south coast of South Africa, a stretch of coast of approximately 160 km in length was sampled.

The region of study was between Cannon Rocks (33°45’S, 26°33’E) and East London (32º97’S, 27º87’E) (numbers 1 and 13 in Fig. 4.1) of which approximately 47 km (30%) is rocky shore. This stretch of coast consists primarily of a series of quartzitic sandstone or dune rock (aeolianite) platforms and headlands separated by sandy beaches (Lubke & de Moor 1998).

From a preliminary survey carried out within this region, 13 similar sites, each with a different level of human exploitation, were selected and the mussel community surveyed (Fig 4.1). All sites were exposed to the prevailing westerly swell and the physical conditions at all study sites were similar. As a result, differences in the biota observed between sites were assumed to be due to differences in human exploitation pressures. To determine where the harvesters were distributed, aerial surveys were conducted along this coast.

Four of the thirteen sites were located next to or inside three coastal nature reserves (see Fig. 4.1) that supposedly confer protection to intertidal animals: two of these were Provincial Nature Reserves (East London Coast and Woody Cape Nature

Reserve) and the third was a local Nature Reserve (Joan Muirhead Nature Reserve). The first Provincial reserve comprises 3 544 ha of land west of East London (approx. 25 km of coastline). The Christmas Rock site is located on the western boundary of this reserve and the Kidd’s Beach site is not in the reserve itself, but is surrounded by the Provincial reserve. Woody Cape Nature Reserve is a 24 000 ha reserve southeast of Alexandria (approx. 45 km of coastline), with the Cannon Rocks site adjacent to it. The Joan Muirhead Nature Reserve is located between Bushman’s and Kariega Rivers and comprises 30 ha of land (approx. 2 km of coastline), with the Kenton-on-Sea study site located within the reserve (Lubke & de Moor 1998).

Of the remaining nine sites, three were accessible and situated next to urban areas (East London, Port Alfred, Kayser’s Beach); one was accessible and in the former homeland of the Ciskei (Hamburg); and the rest (Kowie Rocks, Riet Point, Fish River Mouth, Old Woman’s River, Mpekweni) were sites which are difficult to get to, either because access is restricted (e.g. by landowners) or they can only be reached by walking long distances.

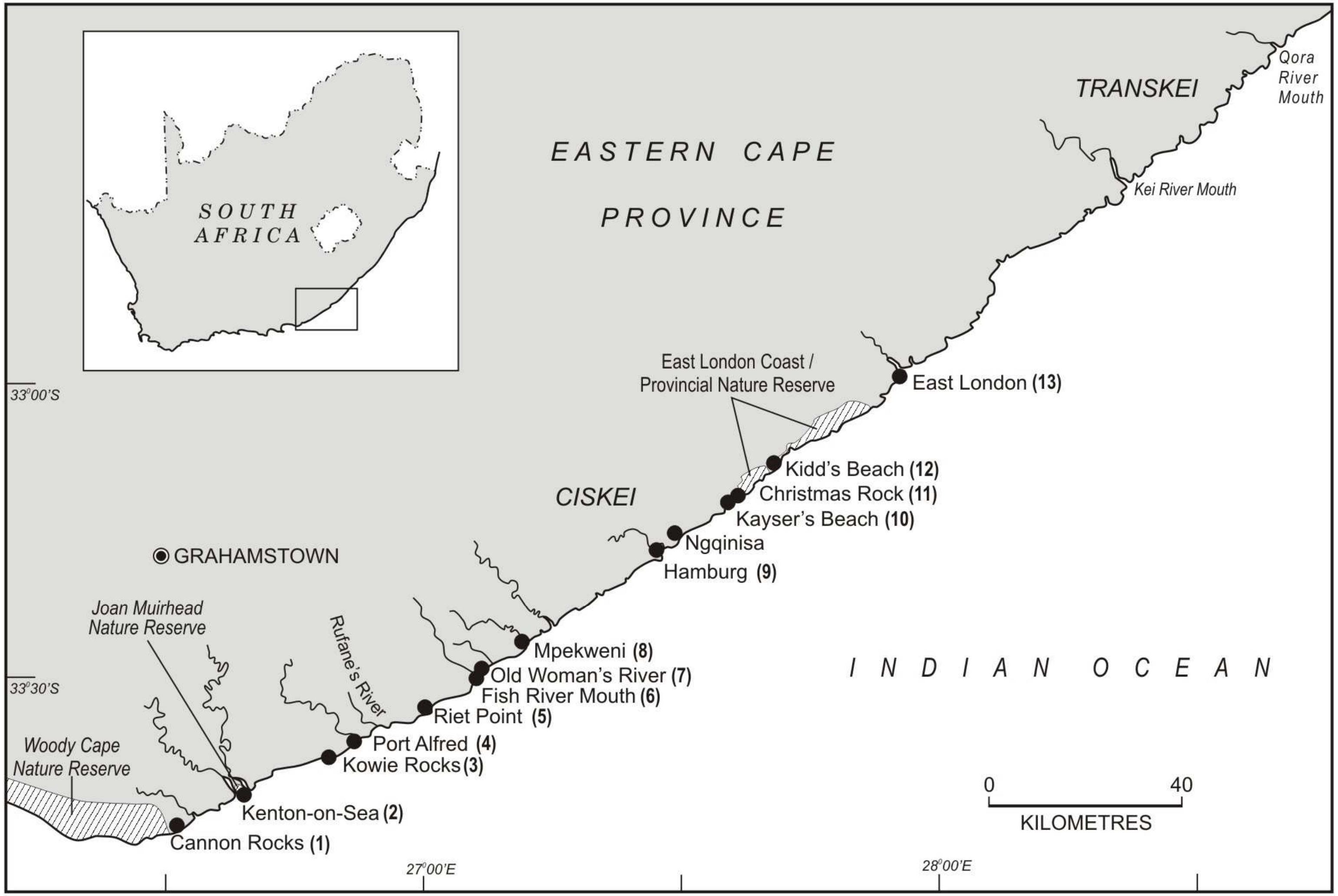


Fig 4.1. Map of the study coastline. The study sites (1 to 13), additional sites, regions, rivers and nature reserves are represented.

Mussel surveys

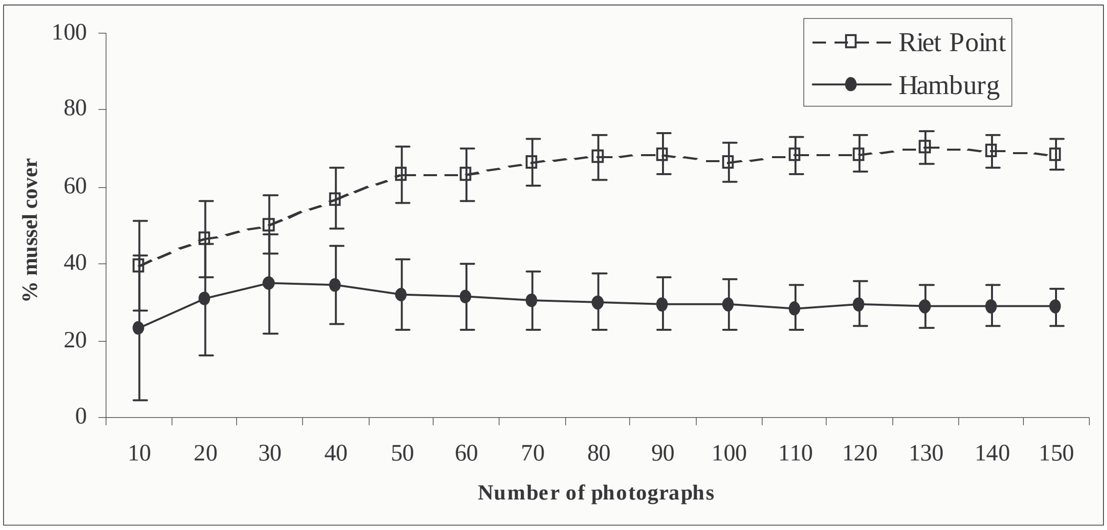
In order to estimate the state of the mussel communities along this stretch of coastline, and to develop an initial database, mussel surveys were conducted during the period June 2003 to April 2004. A single survey was performed in each site except for Hamburg, which was sampled twice, at the beginning and at the end of the study period.

At each site, 100 digital photographs were taken of the intertidal rock surface using 0.5 x 0.5 m quadrats placed randomly along a stretch of up 50 m of shore. The areas sampled were within the limits of mussel bed distribution, either in the mid or low mussel zones (where exploitation pressure is greatest). The camera used was a Canon Power Shot A70 with 3.2 mega-pixels of resolution. The photographs were analysed using the computer program SigmaScan Pro 5 (SPSS Inc) to estimate percent mussel cover as a basic measure, mussel shell width as well as the number of mussel patches.

The number of photographs that were used to analyse each site was determined from a preliminary study. Firstly, 150 photographs were taken in an accessible and thus supposedly exploited site (Hamburg) and a non-accessible and thus non-exploited site (Riet Point) (Fig. 4.1). An empirical approach to determining how large a sample to take was followed as described in Krebs (1989, p 195). The means estimated and their 95% confidence intervals were computed adding the samples (quadrats) in intervals of 10 until the totality of the data was used. As sample size grew, the confidence interval shrank, and the means stabilized. After analysis of around 50 - 60 photographs the graph showed reasonably equalized means and by 70 photographs the confidence interval was judged to be sufficiently small (Fig 4.2a). Examination of two more sites showed that this sample size was appropriate and proved to be applicable to other sites. The first site was away from any population center (Old Woman's River) but relatively accessible, while the other site was close to Port Alfred (Rufane's River) but with difficult access (Fig. 4.1). This time only 100 photographs were taken at each point. At both sites, between 60 and 70 photographs were sufficient to represent the mussel community of the sites (Fig 4.2b). To ensure that all 13 sites had a representative sample size, 100 photographs were taken at all sites.

In addition to % mussel cover, width (to the nearest mm) of the 5 largest mussels in each photograph was measured (i.e. 500 mussels per site). The biggest mussels from each photograph were considered as the first animals that the harvesters would collect (Moreno *et al.* 1984, Tsuchiya & Bellan-Santini 1989). In this way the mean size of the biggest mussels for each site could be determined. Using width as a measure of the size of the mussels proved to be the most reliable measure of size when analysing the photographs. Most studies on the ecology of marine mussels use maximum shell length as a means of measurement (e.g. Berry 1978, Tsuchiya & Bellan-Santini 1989, van Erkom Schurnik & Griffiths 1990, Calvo-Ugarteburu & McQuaid 1998a, b, Guiñez & Castilla 1999, McQuaid & Lindsay 2000, Hicks *et al.* 2001, Rius & Cabral 2004), but in others studies, width has been used successfully (e.g. Seed & Richardson 1999, Steffani & Branch 2003a). Alongside % mussel cover and maximum width, the mean number of mussel patches in each photograph was also determined.

a)



b)

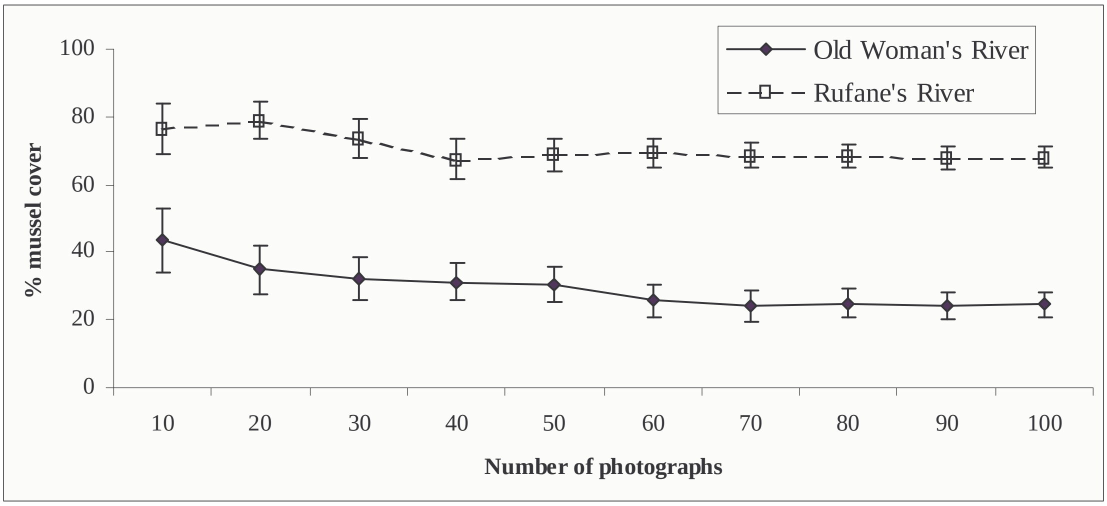


Fig. 4.2. After 10 photographs were counted, the mean % mussel cover and 95% confidence interval were plotted. (a) 150 photographs taken at Riet Point and Hamburg sites; (b) 100 photographs taken at Old Woman’s and Rufane’s Rivers. Vertical bars denote 95% confidence intervals.

Aerial surveys

During spring low tides between February 2002 and September 2004, seven aerial surveys of the study area were conducted (14th February 2002, 28th February 2002, 10th December 2003, 21st February, 22nd April, 6th May and 1st September of 2004). A high-winged PIPER TRIPACER (1957 Model) aeroplane was used, flying between 185 - 215 meters above sea level at 170 - 185 km.h^{-1}. The time taken to fly the 160 km was approximately 1 hour. The survey was conducted twice each day during the outbound and inbound legs of the flight. The first survey was started one hour before low tide while the return journey started at the time of low tide. During each survey, the number of people on shore was counted for 1 km stretches. Each person was classified according to activity which included collecting shellfish (harvesters), angling (fishermen) or ‘other’ (leisure activities such as walking and sunbathing) (following Hockey *et al.* 1988).

Data analysis

Pearson's correlation test was used to examine relationships between the variables: percent mussel cover, maximum width and number of patches.

The data obtained from these three variables from all the sites were tested for normality using the Shapiro-Wilk’s W test, and homogeneity of variances was tested with Levene's test. The three variables were compared between sites by the one-way ANOVA test. If data from the tests failed to meet the assumptions of parametric tests, and transformation did not normalize the variables, the parametric ANOVA was still used to allow all comparison of sites on the assumption that ANOVA is robust (see Chapter 3), given such a large sample size. Nevertheless, the non-parametric Kruskal-Wallis

ANOVA test was used for all the data to check if the results from the ANOVA were the same.

A post hoc Tukey HSD test (when ANOVA test was used) and a Multiple Comparisons Kruskal-Wallis test (in the case of the non-parametric test) were used for multiple comparisons of mean ranks of all groups in order to find homogenous groups among the sites.

A Principal Components Analysis (PCA) was used to relate the three variables and a PCA graph was used to visualize the grouping of sites.

In order to investigate for potential differences between years in Hamburg, the three variables were compared individually using the two dependent-samples Sign test.

For the data obtained from aerial surveys, the Kruskal-Wallis ANOVA test and the Multiple Comparisons Kruskal-Wallis test were used to find out if differences existed between the various types of activities recorded.

All tests were analysed using the STATISTICA computer program (version 6.1) and a critical probability of 5%.

Results

Mussel surveys

Data on % mussel cover, maximum shell width and number of mussel patches from the samplings are summarized in Fig. 4.3. In sites where mussel cover was lower, the maximum shell length was smaller and the mussel population patchier, while in more protected sites the % mussel cover was higher, the largest mussels bigger and the distribution less patchy.

The mean values of the three variables for all sites were scanned for possible correlations. The % mussel cover with mean number of patches were correlated with a linear trendline while % mussel cover and maximum width were correlated using a polynomial trendline (Fig. 4.4). The Pearson Correlation Test confirmed the existence of significant correlations between these variables, negative for % mussel cover and mean number of patches (Pearson correlation = - 0.65***), and positive for % cover and shell width (Pearson correlation = 0.60***).

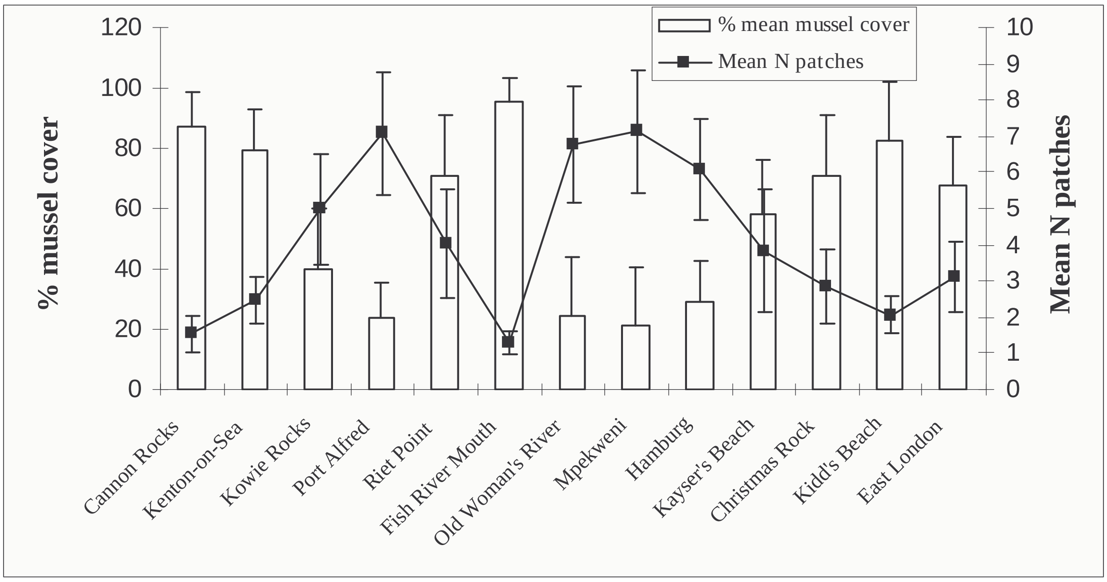
For most sites data obtained from % mussel cover and number of patches failed the normality test (Shapiro-Wilk's W test, $p < 0.05$). Two sites passed the test satisfactorily, though only for % mussel cover. On the other hand, data for shell width showed normal distribution (Shapiro-Wilk's W test, $p > 0.05$) for most of the sites, with only three sites failing the test. However, all data sets failed Levene's test ($p < 0.05$). In the end, no transformation could normalize the distributions.

1-way ANOVA and non-parametric Kruskal-Wallis ANOVA tests both revealed strong site effects for all three variables (ANOVA test: F = 180.26***; F = 146.27***, F

= 40.481***; Kruskal-Wallis test: H = 878.96***, H = 840.95***, H = 539.83***; % mussel cover, maximum width and number of patches respectively).

The results from the post hoc Tukey HSD test were almost equal to the non-parametric test (Multiple Comparisons Kruskal-Wallis test) and provided nearly equal grouping of the sites (see Table 4.1a, b, c). From these results, three groups were commonly discerned from multiple comparisons' test for the three variables (Table 4.1d).

a)



b)

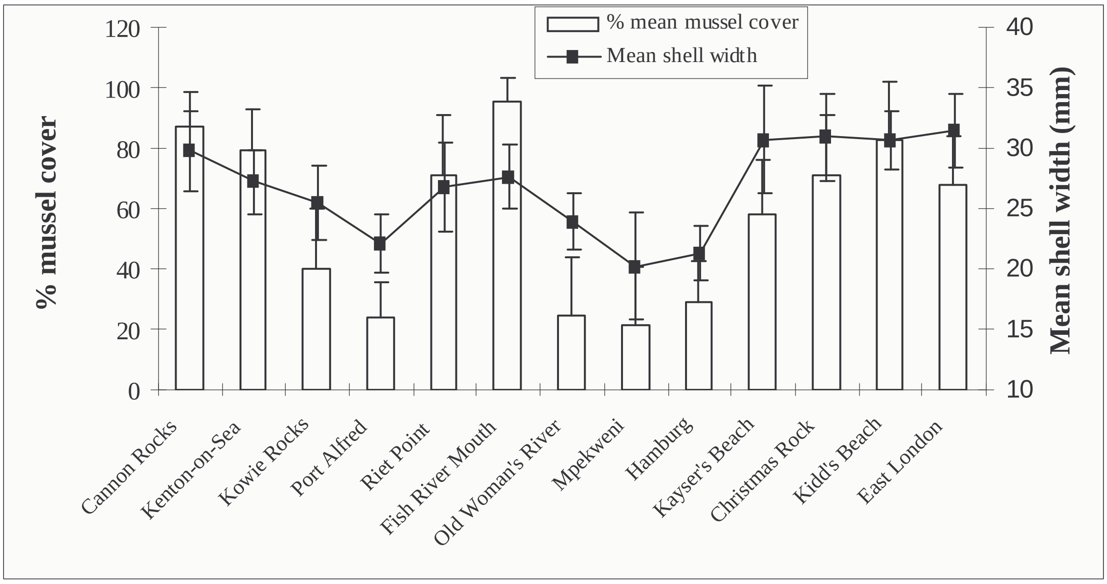
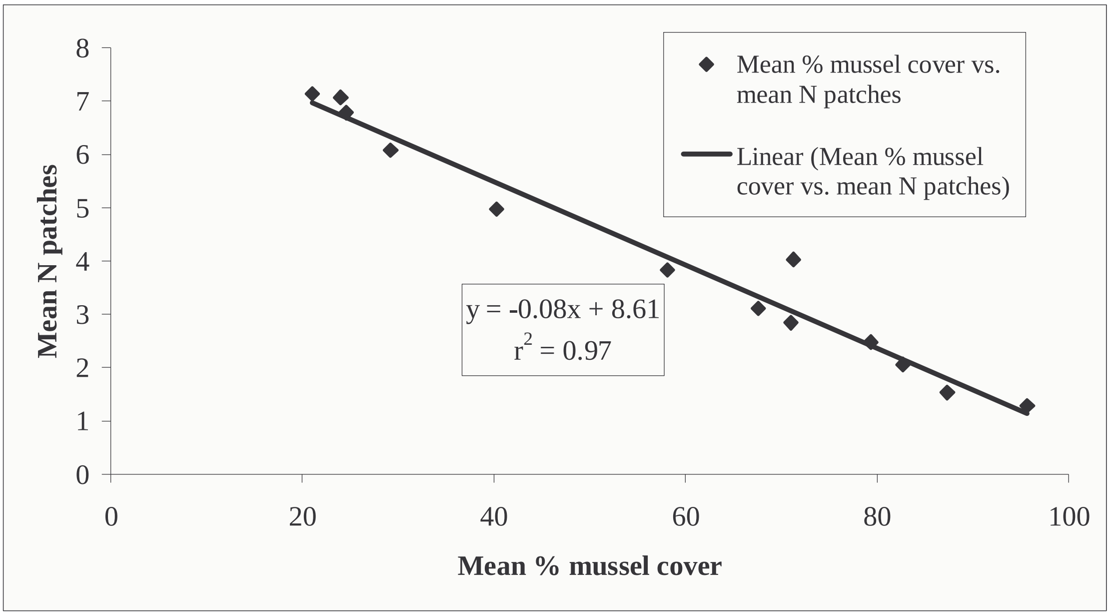


Fig. 4.3. (a) Mean % mussel cover and mean number (N) of patches and (b) mean % mussel cover and mean shell width (mm), per study site. Vertical bars denote 95% confidence intervals. Mean % mussel cover is represented in both graphs in order to facilitate comparison between variables.

a)



b)

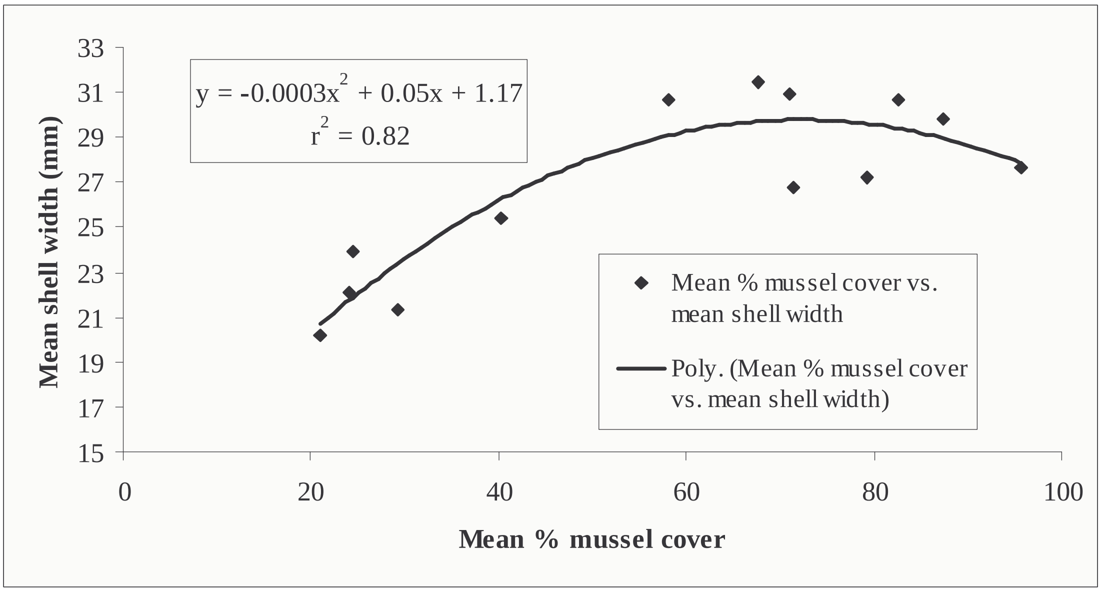


Fig. 4.4. Relationship between (a) mean % mussel cover and mean number (N) of patches and (b) mean % mussel cover and mean shell width.

Table 4.1. Results from the Tukey HSD tests and the Multiple Comparisons Kruskal-Wallis tests to determine where significant differences lay in analyses of % mussel cover (a), maximum shell width (b), number of patches (c) and the final grouping (d). X’s in same column indicate no significant difference between sites.

a)

% mussel cover	***Parametric***			***Non Parametric***		
Site	**Homogenous groups**			**Homogenous groups**		
Cannon Rocks	X			X		
Kenton-on-Sea	X					X
Kowie Rocks		X			X	
Port Alfred		X			X	
Riet Point			X			X
Fish River Mouth	X			X		
Old Woman's River		X			X	
Mpekweni		X			X	
Hamburg 2003		X			X	
Hamburg 2004		X			X	
Kayser's Beach			X			X
Christmas Rocks			X			X
Kidd's Beach			X	X		
East London			X			X

b)

Shell width	***Parametric***			***Non Parametric***		
Site	**Homogenous groups**			**Homogenous groups**		
Cannon Rocks	X			X		
Kenton-on-Sea		X			X	
Kowie Rocks			X			X
Port Alfred			X			X
Riet Point		X			X	
Fish River Mouth		X			X	
Old Woman's River			X			X
Mpekweni			X			X
Hamburg 2003			X			X
Hamburg 2004			X			X
Kayser's Beach	X			X		
Christmas Rocks	X			X		
Kidd's Beach	X			X		
East London	X			X		

c)

Number of patches	***Parametric***		***Non Parametric***		
Site	**Homogenous groups**		**Homogenous groups**		
Cannon Rocks	X		X		
Kenton-on-Sea	X		X		
Kowie Rocks		X			X
Port Alfred		X			X
Riet Point	X			X	
Fish River Mouth	X		X		
Old Woman's River		X			X
Mpekweni		X			X
Hamburg 2003		X			X
Hamburg 2004		X			X
Kayser's Beach	X			X	
Christmas Rocks	X			X	
Kidd's Beach	X		X		
East London	X			X	

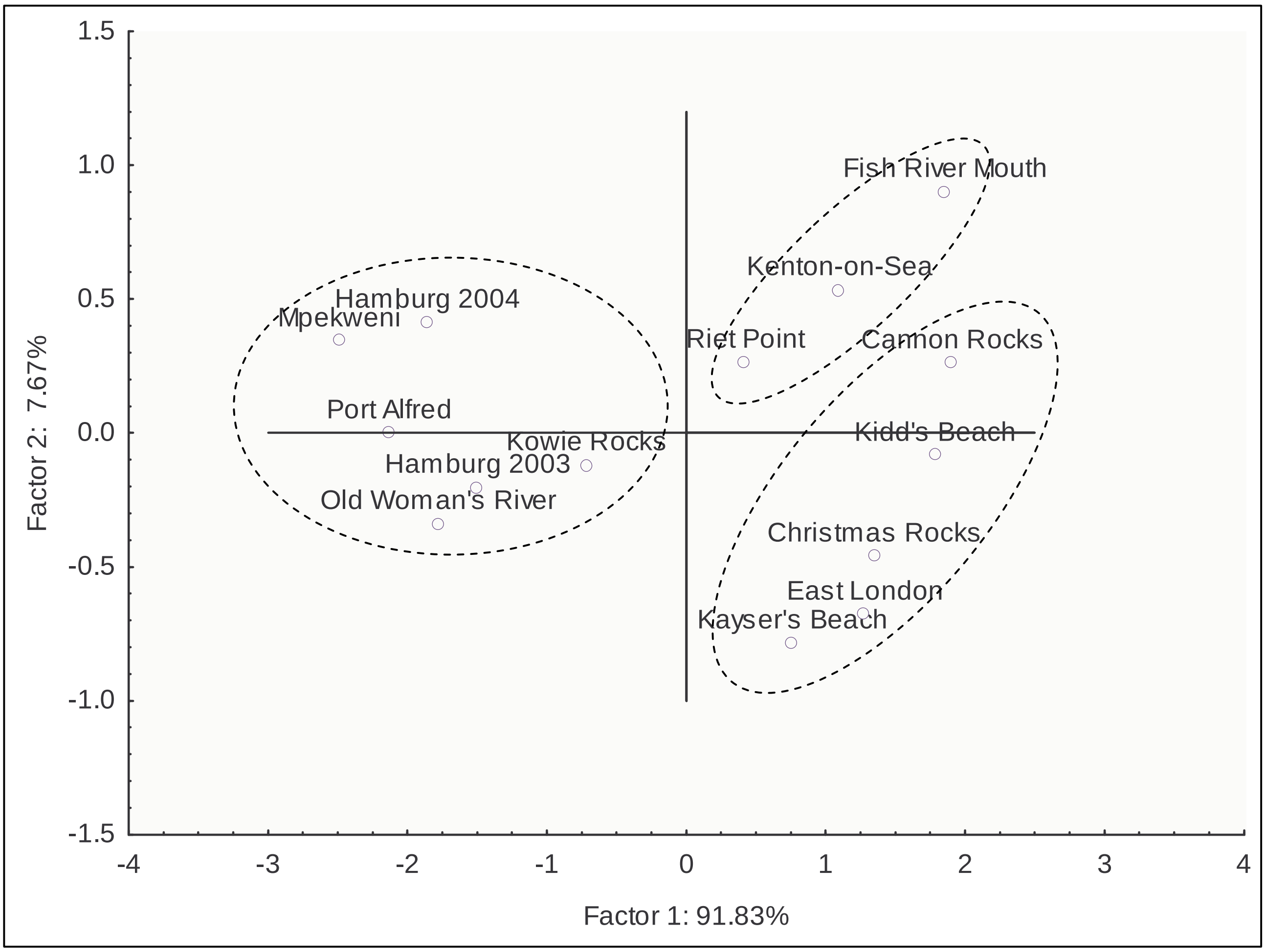
d)

Site	Homogenous groups		
Cannon Rocks	X		
Kenton-on-Sea		X	
Kowie Rocks			X
Port Alfred			X
Riet Point		X	
Fish River Mouth		X	
Old Woman's River			X
Mpekweni			X
Hamburg 2003			X
Hamburg 2004			X
Kayser's Beach	X		
Christmas Rocks	X		
Kidd's Beach	X		
East London	X		

A PCA graph (Fig 4.5a) was used to visualize the final grouping of the sites from the Table 4.1d and to show which variables were most influential at each site (Fig 4.5b). 91.83% of the variability from the three variables was explained by factor 1 (horizontal separation along axis 1), while factor 2 (vertical separation along axis 2) only described 7.62% of the variability. The first factor was directly proportional to the shell width and % cover of mussels and inversely proportional to number of patches. These results were in accordance with the Pearson correlations found above. Factor 2 was affected positively by % mussel cover, and negatively by shell width and number of patches.

Sign tests showed non-significant differences for % mussel cover and number of patches between data collected in Hamburg in 2003 and 2004 ($Z = 1.5^{ns}$, $Z = 0.21^{ns}$ respectively), but significant differences for shell width ($Z = 5.3^{***}$), with a decrease in maximum shell width from 2003 to 2004.

a)


Fish River Mouth
Kenton-on-Sea
Hamburg 2004
Mpekweni
Riet Point
Cannon Rocks
Port Alfred
Kidd's Beach
Kowie Rocks
Hamburg 2003
Old Woman's River
Christmas Rocks
East London
Kayser's Beach
1.5
1.0
0.5
0.0
-0.5
-1.0
-1.5
-4
-3
-2
-1
0
1
2
3
4
Factor 1: 91.83%
Factor 2: 7.67%

b)

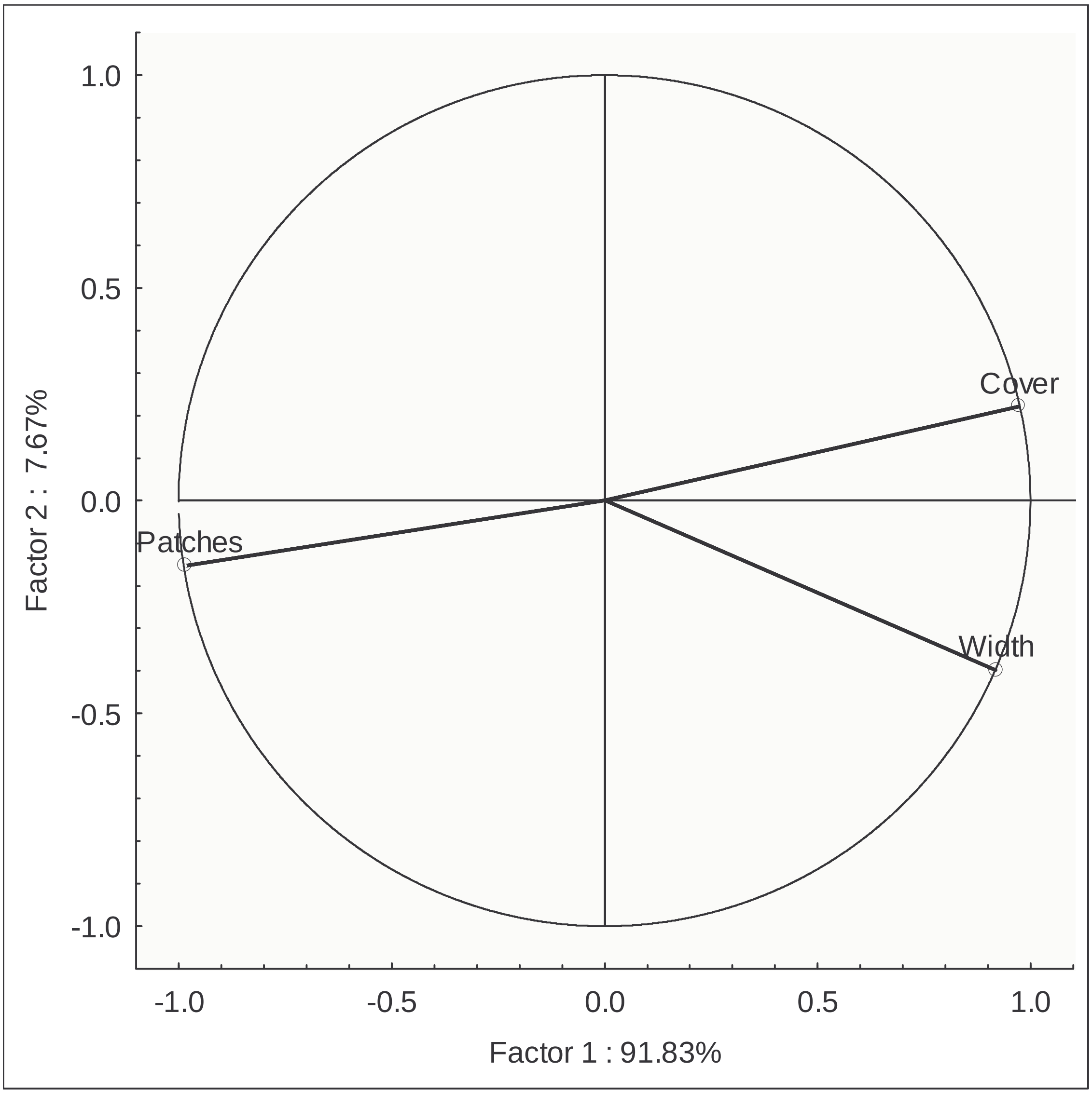


Fig 4.5. PCA graphs representing the study sites (a) and the 3 variables (b). In (a) the results from the final grouping (Table 4.1d) are indicated by dashed lines.

Aerial surveys

The data obtained showed that along the coastline the people who engaged in recreational activities were the most frequent visitors of the shores during low tides, followed by the collectors and finally anglers. A Kruskal-Wallis test on people activities showed significant effects (Shapiro-Wilk's W test, $W = 0.9^*$; Kruskal-Wallis test, $H = 7.72^*$) and Multiple Comparisons Kruskal-Wallis test showed that the number of anglers and those engaging in recreational activities differed significantly ($p < 0.05$), while collectors did not significantly differ from any of the other groups ($p > 0.05$).

From all the surveys, a mean density of 0.86 collectors.km^{-1} was found along this coastline. The distribution of the harvesters along the coast is represented in Fig. 4.6, with counts of people within a 3 km and a 5 km radius from the study sites. Central sites showed low densities of collectors, while at eastern, and especially western sites, the densities were higher.

The % mussel cover, maximum shell width and number of mussel patches (dependent variables) were plotted against number of collectors within 3 km and 5 km radii (independent variables). Poor correlations were found in all 6 combinations (correlations coefficients between 0.19 and - 0.25). The trendline that gave the best fit in all combinations was the exponential, and, for all three variables, 3 km showed a closer relationship than 5 km. In this way, for % mussel cover and collectors within 3 km, the equation was $y = 0.4088e^{0.0108x}$, $r^2 = 0.10$; for shell width and collectors within 3 km, it was $y = 0.041e^{1.0925x}$, $r^2 = 0.22$; and for number of patches and collectors within 3 km, $y = 1.5677e^{-0.1756x}$, $r^2 = 0.16$. The Pearson Correlation Test confirmed that no correlations among all 6 combinations were significant ($p > 0.05$).

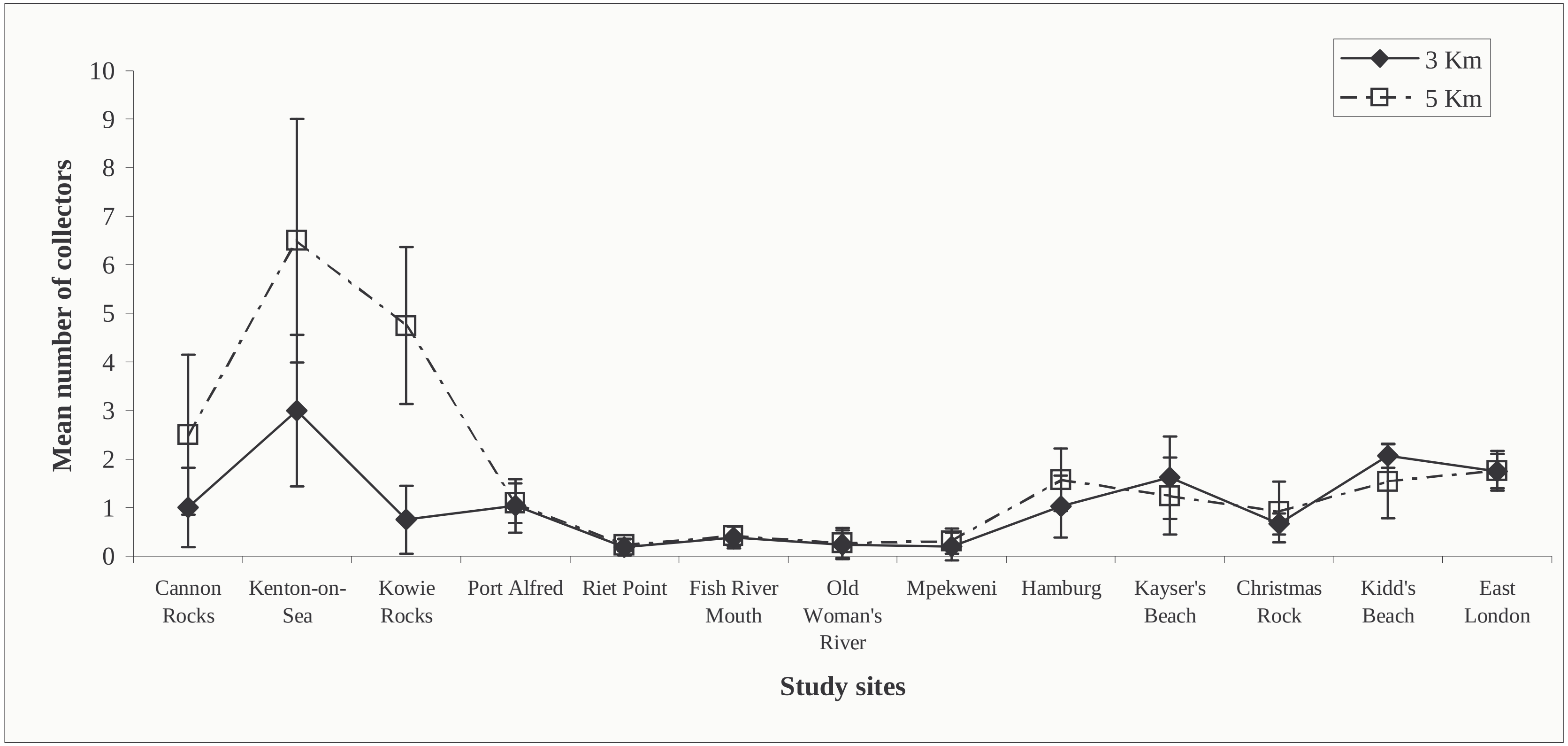


Fig. 4.6. Mean number of collectors within a 3 km and a 5 km radius from each study site. Data pooled from all surveys. Vertical bars denote 95% confidence intervals.

Discussion

This work is the first approach to the study of human exploitation of mussels on the south coast of South Africa. As a general conclusion, this study found that protected and inaccessible sites showed healthy mussel populations, while at accessible and unprotected sites, less cover and abundance of big mussels were encountered. However, no correlations were found between the presence of collectors and the status of the mussel populations.

Over-exploitation of many stocks of mollusc fisheries has resulted in their collapse or severe decline (Breen & Adkins 1980, Sluczanowski 1984, Breen 1986, Bustamante & Castilla 1987). The reason for this centres around recent changes, both quantitative and qualitative, in the patterns of exploitation. These changes have come about as a result of, among other factors, the rapid growth of human populations (particularly in coastal areas), the replacement of subsistence by commercial exploitation, as well as technological advances both in methods of collection, processing, storage and transportation (Eekhout *et al*. 1992). There are some instances where recent and intensive exploitation has brought exploited populations down to very low levels (e.g. *Choromytilus chorus* in Chile; Winter *et al*. 1984), or to local extinction (e.g. *Patella candei* in the Canary Islands; Hockey 1987). In the latter example, intensive exploitation of the intertidal organism is considered to be a factor contributing to the global extinction of the endemic Canarian black oystercatcher *Haematopus meadewaldoi* (Hockey 1987), although, there is no evidence that subsistence collection alone has led to the global extinction of any algal or invertebrate species (Siegfried *et al*. 1994).

Marine mussels have high natural mortality rates resulting from intraspecific competition for space (Griffiths & Hockey 1987), and populations can withstand high predatory pressure because of this, particularly when the mussels are small (Hockey *et al*. 1988). Human exploitation on mussels can be severe and in harvested areas, densities and the maximum and mean sizes of mussels can potentially be depressed (Siegfried *et al*. 1985, Hockey & Bosman 1986). The susceptibility of mussels to stock depletion is related to the sessile habit and gregarious tendencies of mussels, and thus collectors can easily engage in large-scale removal of clumps of individuals (Lasiak & Dye 1989, Rius & Cabral 2004). On the Transkei coast, the decreasing number of *Perna perna* in recent shellfish collections and its increasing scarcity on the shore (i.e. decrease in density and average size) indicate a situation of overexploitation (Siegfried *et al*. 1985, Hockey & Bosman 1986, Hockey *et al*. 1988). Subsequently, the reduced availability of mussels for collection has led to increased exploitation-pressure on other intertidal species such as limpets (Siegfried *et al*. 1985).

Along the south coast, the present results suggest that at some sites, mussel communities are affected by harvesting. A significant decrease in percent mussel cover and mean sizes of the mussels, in some sites, could indicate stock depletion. In relation to size, the size at sexual maturity for mussels depends on its relationship with the size preferences of the shellfish gatherers. If the size at sexual maturity is less than the collected size, the exploited population normally includes some reproducing individuals. If, however, the size at maturity is greater than the collected size there is a serious risk that removal of large numbers of reproductively active individuals will drastically reduce the recruitment of the population (Lasiak 1991). At the study sites, measurements of maximum shell width reflected reduced mean size of the biggest mussels in unprotected sites in relation to inaccessible or protected sites, which suggests the effects of harvesting activity. The size of *P. perna* at maturity is 25 - 30 mm total length (Lasiak 1991). From one of the present study sites, a sample (n = 100) of *P. perna* was collected and measurements of the shell (width and maximum length) were undertaken. Linear regression between width (as y) and maximum length (as x) was obtained: $y = 0.45x + 4.13$ ($r^2 = 0.58$, F = 21.65***) (author's unpub. data). According to this equation, 25 - 30 mm of maximum length would equate to 15.35 - 17.6 mm width respectively. All sites showed larger mean shell width than 20.24 mm (this value was from Mpekweni, the site where the largest mussels were smaller) that, according to the previous equation, correspond to a maximum length of 35.89 mm. Therefore, the biggest mussels at all study sites were larger than the size at sexual maturity. This suggests that even though some populations were severely harvested, human harvesting pressure is not yet strong enough to produce a complete reproductive failure of these mussel populations.

Pearson correlation analysis between the variables % mussel cover, maximum shell width and number of patches, resulted in % mussel cover being positively related to the size of the mussels and negatively related to number of patches. These results show that at sites where mussel community distribution was patchier, less mussel cover and a decrease in mussel size mussels were encountered, presumably because of the effect of human exploitation. Because of the big sample size and the highly significant Pearson correlations found among these three variables, the use of all three variables in future studies along this stretch of coast is not imperative. For example, to evaluate the state of the mussel beds it may be sufficient to measure only % mussel cover and apply the equations provided above to estimate maximum shell width and number of patches.

All three variables showed significant differences among the various sites. Multiple comparisons analysis tests provided homogenous groups that were classified in three categories. In Fig. 4.5a, eight sites (Cannon Rocks, Kenton-on-Sea, Riet Point, Fish River Mouth, Kayser's Beach, Christmas Beach, Kidd's Beach and East London) showed positive values of factor 1 in the PCA analysis, i.e. they were the most unexploited sites where mean shell width and % mussel cover were the highest and mean number of patches the lowest (see Fig. 4.5b), and these sites were divided into two groups (Tukey test). These two groups differed presumably because the group including Riet Point, Fish River Mouth and Kenton-on-Sea showed comparatively higher % mussel cover and a decrease in mussel size than the other group.

Non-exploited sections of the coast act as important "buffer zones" or "source areas" from which species can recolonise providing recruitment to adjacent shorelines where collection takes place (Siegfried *et al.* 1994). However, absence of adults and recruits has been registered despite an existing source of larvae next to exploited sites (Harris *et al.* 1998). Along the studied coastline, extensive sections of shoreline are inaccessible to man due to their geomorphology, the fact that they support very low human population densities, or are proclaimed nature reserves. Such macro-spatial refuges are most likely critical in promoting recovery of exploited populations, in preventing species extinctions and long-term or irreversible disequilibria (Hockey 1994). Eight of the thirteen sites sampled had a mean % mussel cover higher than 50%, and mean shell width larger than 26 mm (i.e. mean maximum length of 48.6 mm - from previous equation): four were next to or within a nature reserve (see Fig. 4.1), two more (Riet Point, Fish River Mouth) were not easily accessible sites, and another two (Kayser's Beach and East London) were situated next to urban centers. These last two sites were accessible and non-protected areas, but they were close to predominately Caucasian middle class settlements, which apparently confer protection against illegal harvesting of intertidal animals. Interviews with local Caucasian people revealed that they do not allow any subsistence collectors (mostly African people) to undertake any illegal activity on the shore next to their settlements (author's unpub. data).

Worldwide, wherever poor communities are situated next to protected areas, there exists tensions between the demands for access and use of resources versus the needs of conservation and management. In South Africa some MPAs are under threat, especially in the Transkei region. Political transformation in the country has lead to expectations that land previously set aside for conservation may be re-allocated, and several legal land-claims have been made in order to achieve this (Branch & Odendaal 2003). Along the studied stretch of coast, the findings suggest that the presence of existing nature reserves effectively confers protection on the mussel population, including sites that fall on the boundaries of the reserves.

On the other hand, five sites (Kowie Rocks, Port Alfred, Old Woman's River, Mpekweni and Hamburg) were located in the negative values region of factor 1 in Fig. 4.5a, i.e. the most exploited sites where mean shell width and % mussel cover were the lowest and mean number of patches the highest. The results from these sites were more difficult to interpret, as they were very different, in terms of demography, accessibility, geographical location, etc. Hamburg is an accessible site in the Ciskei region (one of the former homelands), where, as on the Transkei coast, subsistence exploitation affects mussel stocks enormously (Siegfried *et al.* 1985, Hockey & Bosman 1986). Port Alfred is an urban centre and a very important tourist destination, which suggests that seasonal recreational exploitation would drastically affect mussel populations, while through the year subsistence collectors coming from the areas where the African population and poverty are concentrated, would harvest in the same areas. Kowie Rocks is a site with difficult access but it is close to Port Alfred (ca. 5 km), which could explain the moderately affected mussel population found there. However, inside this group of exploited sites, Kowie Rocks showed the highest values of % mussel cover and maximum shell width, while the mean number of patches was the lowest (Fig. 4.3). The Old Woman's River and Mpekweni sites are away from urban areas, but in both sites a hotel is close to the zone were the sampling was conducted. Access is normally restricted to guests and staff of the hotel, and recreational exploitation by these people could therefore be the reason for the decreased abundance and size of the mussels found in these sites. Another hypothesis could be that other factors, such as physical disturbance or lack of recruitment, are affecting the mussel community at these sites.

The aerial survey results showed that this coastline is not as highly exploited as, for example, the Transkei coast. During the surveys, a mean of 1.18 people.day^{-1}.km^{-1} were recorded and, in comparison, on the Transkei coast Hockey *et al.* (1988) counted 2.74 people.day^{-1}.km^{-1}. Popular sites where people could always be found harvesting were possible to identify, but never at the same density as in the Transkei, where Mills (1985) found that the density of collectors in one location had increased from 5 to 20 people.day^{-1}.km^{-1} in the last 30 years. Mills (1985) also recorded that during one day in the middle of a drought 316 women were collecting intertidal organisms at one site.

In our aerial surveys, no counts of sex, age or race of the collectors could be accurately conducted, however, most of them appeared to be African men followed by Caucasian males. In the Transkei, Hockey *et al.* (1988) registered that 91% of the collectors were Africans and the remainder were Caucasian, while contrarly, in terms of sex, women dominated the collecting activities (80.9% of all collectors). On the other hand, almost all recreational people and fishermen were Caucasian.

Comparisons between Fig. 4.3 and Fig. 4.6 show that the number of harvesters registered from the aerial surveys did not correlate with apparent damage to mussel populations on this stretch of coast. It was expected that the number of collectors would correlate negatively with maximum shell width and % mussel cover, and positively with number of patches, but there was no significant correlation between numbers of collectors and the variables. Paradoxically, in sites next to or in nature reserves, the mean number of collectors was generally greater than in non-protected areas (Fig. 4.6). A possible reason for this would be that people observed from the plane were collectors of other organisms (for example, abalone or alikreukel) and not of mussels. Another interpretation is that the collectors registered were not in fact collectors but were rather recreational people observing the rocky shores (particularly suggestible at the western sites). Another reason explaining the results from the aerial surveys could be that mussel harvesters, after removing most of the big mussels from the exploited sites, are moving to other zones where mussels are abundant. This hypothesis is, however, improbable as subsistence collectors can not generally travel long distances to favoured sites. On the Transkei coast, collectors walk an average of 1.5 km between home and the intertidal zone to exploit mussels and other organisms during low spring tides. Other collectors living as far as 10 km inland, visit the shore on foot, but these people restrict their visits to the coast to one or at most two days per month, when low spring tides coincide with favourable weather (Mills 1985, Hockey *et al.* 1988). As a result, subsistence collectors are not expected to travel distances further than 10 km, which means that collectors from one of our study sites would most likely not travel to another of the study sites to collect mussels. In summary, these unexpected results strongly suggest the necessity of more aerial surveys and enquiries on the beach in order to understand the distribution of collectors along this coast.

Hamburg was the only site monitored over time. From 2003 to 2004, a statistically significant decrease in the mean shell width of mussels was found. These results suggest active size-selection of the mussels harvested from one year to the next. The fact that no significant differences were found between years of % mussel cover and number of patches, suggests that the method used to exploit mussels was selective removal and not the method observed by Lasiak & Dye (1989) and Rius & Cabral (2004), where large clumps of mussels were removed and the few large animals subsequently selected.

The results suggest that the mussel populations on this stretch of the south coast are affected by human exploitation but are not under imminent threat of stock-depletion. The non-continuous harvesting pressure distribution along the coastline theoretically allows larvae from less exploited sites to supply the highly exploited sites with new recruits (Siegfried *et al.* 1994), even though this is not always the case (Harris *et al.*

1998). Mussels are not the main target of the collectors and are not economically very valuable (Kaehler unpub. data). The importance of mussels as a food resource for subsistence collectors appears to be of only moderate importance at a few sites along the coast, particularly in the Ciskei. A second and separate conclusion is that the presence of the invasive Mediterranean mussel *M. galloprovincialis* does not seem to affect the harvest activity, as harvesters collect both species indiscriminately (author's unpub. data).

On the South African coast the intensity of exploitation varies. The most intense exploitation and higher population density are found on the east and southeast coasts where the smallest stocks have traditionally existed. On the other hand, the extensive resources along the unpopulated west coast remain virtually pristine (van Erkom Schurink & Griffiths 1990). Along the south coast, under a properly managed regional management policy, this resource could probably support a crop of larger magnitudes than that taken at present.

Subsistence exploitation is extremely difficult to control with legislation, partly because it involves a large number of people, all operating at a local level (Siegfried *et al.* 1994). Appropriate legislation could be introduced to limit gathering practices through a conservative size-selective harvesting quota approach (see Eekhout *et al.* 1992) and to ensure that the method used to remove organisms must be by hand or by means of a narrow iron bar (Lasiak 1991). A successful co-management system has been established in Kwazulu-Natal, where mussel-gatherers use screwdrivers instead of broad-bladed pangas to remove mussels, thereby reducing the harvesting of juvenile mussels and other species (Harris *et al.* 2003). Research is required into methods of improving coastal management in the study area, so that the level of exploitation of shellfish can be made sustainable. The maintenance of current, and the establishment of new, protected areas, which may act as reproductive refuges, 'buffer' zones, and nurseries for exploited invertebrate species (Hockey *et al.* 1988), should be the first management priority before a definitive management plan is prepared. A comprehensive management plan must be developed when more information regarding the mussel populations and other organisms along this stretch of coast is available.

In the exploited areas, aside from quotas and sizes limits, the use of closed areas and closed seasons, provides another way to manage exploitation. This could be done on a rotational basis. *P. perna* is a short-lived mussel with high growth and turnover rates, and relatively early sexual maturity (Berry 1978). As such, it is one of the easiest intertidal food-resources to manage effectively, and one option would include administering stocks on a rotational-cropping basis in order to spread the exploitation efforts along the coast. This will leave time for the settling cohorts to spawn and should be implemented with the protection of nursery areas for about 14 months (Siegfried *et al.* 1985). However, rational management of living resources requires a holistic approach (Hockey & Bosman 1986, Eekhout *et al.* 1992). The multi-faceted approach must combine measurement of population parameters in undisturbed and experimentally harvested populations, assessment of the effects of exploitation on the intertidal community as a whole, as well as the development of quantitative population and economic models. This provides the basis for the rational management of living (particularly intertidal) resources (Eekhout *et al.* 1992).

On the Ciskei coast (as in the Transkei), management plans must be considered in order to allow the sustained exploitation of intertidal food resources for subsistence, the maintenance of high diversity through disturbance is unwanted due to the resulting dominance of inedible species and small individuals under these conditions. Active management of the intertidal zone in this area should be implemented, as the value of the resources to the inhabitants is considerable. The effectiveness of this management will depend on the involvement of local methods, traditions, and knowledge, of the people associated with the resource use, rather than studying the resource alone. In this subsistence collector community, the efficacy of the implementation of a policy will depend on the cooperation of the local people, rather than direct law-enforcement. This cooperation will only be achieved through education of the local community. Successful management implementation in this matter has been the establishment of a local management committee at Arniston (southwest coast), which has re-invested parts of the profits from fishing quotas back into community bursaries to uplift the education standards of local youth (Branch *et al.* 2002b).

The Marine Living Resource Act (Anon. 1998) established the legislation for the protection of the marine ecosystem and the sustainable use of living marine resources. Previous studies of subsistence fisheries were undertaken in order to gain an understanding of how many subsistence fishermen there were, where they operate, what resources they exploit, and what the uses of the resources were, in order to develop the Act (Branch *et al.* 2002a, b, Clark *et al.* 2002, Cockcroft *et al.* 2002, Harris *et al.* 2002a, b, Hauck *et al.* 2002). This legislation recognizes and protects the rights of subsistence gatherers who rely on marine resources to sustain their livelihoods, and determines which resources are most appropriate for their use. On the south coast (in the former Transkei and Ciskei) intertidal rocky shore invertebrates are intensively harvested or over-harvested by subsistence collectors (Hockey & Bosman 1986, Hockey *et al.* 1988). However, the application of this Act in recent years, indicated that changes in management strategy can yield more efficient and more sustainable fishing practices, with benefits for subsistence fishermen and improvements in the state of the resources (Branch *et al.* 2002b).

The existing data presents evidence of the substantial impact of the collectors on mussel communities along the south coast, and provide an initial database for further monitoring studies, from which a management plan for this specific area can be proposed.

Long-term biological studies linked with socio-economic studies of the region are necessary to assemble a holistic approach to management of intertidal resources along the south coast of South Africa.

Chapter 5:

Final Conclusion

Records regarding the introduction and spread of *Mytilus galloprovincialis* in several temperate parts of the world are relatively recent (from the 1970s), and are presumably as a result of increases in speed and size of ships that facilitate the viable transport of alien species. In this respect, the arrival and rapid spread of *M. galloprovincialis* in South Africa, could be easily predicted, as the South African coast is one of the major shipping routes worldwide. The only surprising feature of the arrival of *M. galloprovincialis* on the South African shores was that it first arrived at the relatively small port of Saldanha Bay and not at a larger and much more utilized harbour such as Cape Town (Branch & Steffani 2004).

On the west coast, *M. galloprovincialis* is competitively superior in all aspects to the indigenous mussel species (van Erkom Schurink & Griffiths 1990, Hockey & van Erkom Schurink 1992) and to prevent being controlled by predation, high recruitment rates overwhelmed the effects of predators (Branch & Steffani 2004). Another effect of the invasion was the impact on the limpet community, particularly on the species *Scutellastra granularis* and *S. argenvillei*. The different characteristics of the two limpet species results in completely different dynamics in their interactions with *M. galloprovincialis*. This is in accordance with the idea that invasions are informative about the structure of communities and the strength of interactions that occur between the species that form that community (Williamson 1996). As a result, the effects of alien invaders are as much due to the properties of the recipient community as they are due to the nature of the invaders themselves (Branch & Steffani 2004).

The capacity to predict and detect the consequences of an invasive species in one particular environment will always be limited by the occurrence of unexpected outcomes of introductions. For example, Branch & Steffani (2004) described one unpredictable effect of the *M. galloprovincialis* invasion: the mass mortalities of the swimming crab *Ovalipes trimaculatus* (De Haan), as a result of large numbers of *M. galloprovincialis* recruits settling on the eyestalks and mouthparts of the crab, as they constitute the only hard substratum on which the mussel larvae can settle on sandy shores. These unpredictable consequences of the invasion strengthen the scepticism of Mack *et al.* (2000) regarding the value of predictions based on qualities of the invaders, and their view that prevention is better than cure and must be the prime means of avoiding future unwanted introductions of invasive species (Branch & Steffani 2004).

Once a species has become established and spreads from its point of introduction, eradication is almost impossible (Mack *et al.* 2000). Primary means of prevention are actions directed at fouling organisms on ships, ballast-water procedures, as well as rigorous controls imposed on the mariculture and aquarium trades (Minchin 1996). Another consideration that must be taken into account is that all species with long-lived planktonic larvae are likely to be invasive and with the potential to spread rapidly. Avoiding their introduction must therefore be a priority (Branch & Steffani 2004).

Biological invasions are not always detrimental, depending on the context and point of view that people have regarding the problem. From an ecological perspective, invasions can have broadly positive and negative ecological consequences in the community. The arrival of *M. galloprovincialis* in South Africa is, for example, unfavourable because it displaces some local species, but, on the other hand, it has positive effects in terms of conservation because it supplements the food supply of a rare and endangered species, the oystercatcher *Haematopus moquini* (Hockey & van Erkom Schurink 1992).

Economically, and from the human perspective, introductions can be highly beneficial or detrimental. The entire South African mussel industry is based on *M. galloprovincialis* (Robinson *et al.* in press). Ironically, the properties that make *M. galloprovincialis* attractive for mariculture (fast growth, tolerance of stress, immunity to parasites and disease, high survivorship) are the same as the ones that make it likely to become invasive (Branch & Steffani 2004). Mussel culture is not a traditional activity in southern Africa, but on the west coast, such operations have shown an exponential growth over the past few years (van Erkom Schurink & Griffiths 1990). The presence of this species in massive concentrations on the shore will benefit this industry, as settlement of its larvae on culture ropes will be facilitated. As a result, the introduction of a species for mariculture may make economic sense until inadvertent introductions of associated diseases or pest species appear, or until the environmental costs are incorporated (Mack *et al.* 2000). For example, in the case of the Zebra mussel *Dreissena polymorpha* invasion in North America, the economic implications have been greater than any other mussel invasion worldwide (Strayer *et al.* 1999).

As a result, there is a need for clear national and international policies that take into account both human needs for food and industry, as well as conservation goals (Branch & Steffani 2004).

On the south coast, *M. galloprovincialis* found more oligotrophic waters, higher species richness (Emanuel *et al.* 1992), and a stronger competitor in the indigenous mussel species (*Perna perna*) than on the west coast.

The rate of spread of the *M. galloprovincialis* invasion along the south coast has decreased in the last 10 years and the present easternmost limit of its distribution on South African shores is East London. This city represents the boundary of two zoogeographical zones, which could be the reason as to why no *M. galloprovincialis* were found further east. Other possible reasons could be the higher species richness of the South African coastline when moving further east (Emanuel *et al.* 1992, Branch *et al.* 2002b), competition for space with *P. perna* or, simply, the need for more time to spread to the east. As a result, no effect of the invasion is expected further east than East London, and on the south coast, no big community changes are expected as a result of the invasion, as the density of this invasive species on this coast is not comparable to the west coast, where it drastically changed the intertidal communities.

In summation, on the south coast, *M. galloprovincialis* has not yet completely replaced *P. perna*, instead, the two exhibit spatial segregation with *P. perna* dominating the low shore, *M. galloprovincialis* the high shore and an overlap zone between the two (author's unpub. data; Robinson *et al.* in press).

From the results on the rate of spread, *M. galloprovincialis* showed faster spread on the high shore than on the low shore suggesting better performance in higher intertidal zones, which strengthens the idea of spatial segregation. The same was found in the competition experiment where the survival of *P. perna* appeared to be better on the low shore than on the high shore with the opposite pattern for *M. galloprovincialis*.

P. perna shows characteristics of invasive species, and, as a result, is an invasive species in America and is spreading in regions along the prevailing environmental conditions of the Gulf of Mexico (Hicks *et al.* 2001). On the South African coast, *P. perna* is a stronger competitor than was thought in the past, and on the south coast and in the presence of *M. galloprovincialis*, the present study showed that it is a more dominant competitor for the space on the low shore than the alien species. Another observation from this study was that the byssus attachment of the two species differs, *P. perna* being much stronger than *M. galloprovincialis*. As a result, the survival of the invasive species on the south coast seems to be limited by the presence of *P. perna* beds, which confer protection against dislodgement by wave action. However, in the absence of strong wave action, *P. perna* competitively excludes *M. galloprovincialis*.

Further study would be necessary to confirm these results and to corroborate that the situation found on one particular shore could be extrapolated to the whole South African shore. Firstly, an experiment in the three different mussel zones on different parts along the south coast should be conducted. Another necessary study would be to determine whether the interactive processes change as one approaches the west coast, where the invader was initially introduced. A further test would be to run the same experiment in other parts of the world where these two species interact, for example in Morocco or in Namibia, to determine whether the same pattern is encountered.

P. perna forms an important part of the diet of the people of Transkei, and has been overexploited in unprotected areas (Siegfried *et al.* 1985, Lasiak & Dye 1989, van Erkom Schurink & Griffiths 1990, Hockey & van Erkom Schurink 1992). It has been predicted that *M. galloprovincialis* will spread into the Transkei in the next few years, settling in these exploited areas, proving advantageous for people that rely on mussels as a food resource. From the present results, it is highly unlikely that this will ever happen, however, further studies will be necessary to continue monitoring the spread of this invasive species and assess possible consequences of this alien invasion in the future.

Competitive interactions that involve more than two species may introduce an additional outcome, namely indirect effects. If, for example, a predator feeds on two species, which are competitors, its direct effects on them must be negative. Indirectly it may however, have a positive effect on one of these species, by suppressing the numbers of its competitor (Castilla *et al.* 1994). In our study, human exploitation seemed not to discriminate between species, and in some sites it can be a very important factor in altering mussel communities. As a result, human exploitation appeared not to be to the benefit or detriment of *M. galloprovincialis*.

The study has shown that higher abundances of mussels were found in protected or inaccessible sites, while in unprotected sites mussels were scarce. Another question raised was whether the observed imbalances could lead to broader community changes in the long term, particularly in areas where collection occurs regularly (Sharpe & Keough 1998). This indirect effect and others, including changes to the size, or structure of the community can lead to changes in resource availability and imbalances in competitive interactions. Other species may also become more abundant because of increased food availability or reduced competition for space or other resources (Moreno *et al.* 1984, Godoy & Moreno 1989). These indirect effects can often be more important than the direct effects, since they reflect changes to the whole community. The indirect effects of collection are likely to be amplified in communities where the targeted species are very abundant and interact competitively with many other species (Sharpe & Keough 1998). Further studies looking at indirect effects will be necessary to assess the effects that the invasive species and human exploitation can have on the intertidal community along the south coast.

From the study of human exploitation the presence of collectors on the studied stretch of coast appeared to be lower (i.e. less exploitation) than on other parts of the South African coast (namely the Transkei). However, linked with the evidence that nature reserves along this coast effectively protect the mussel community, it is highly recommended that current nature reserves are preserved and protected, and that new protected coastal regions are implemented.

Aquaculture is being seen as a solution in reducing the exploitation of wild stocks. However, mariculture output is directed to the luxury market and is unlikely to play any role in reducing the pressure on wild stocks by subsistence harvesters, which, with the currently increasing human population pressure, remains a serious management problem (van Erkom Schurink & Griffiths 1990).

There are few cases of management in which the extraction of wild benthic resources is done through the implementation of rotational fishery schemes and/or the use of no-take areas as a source for ‘overspilling’ of adults or seeding grounds (Castilla 1999). In South Africa, where there is an integrative coastal management plan, the rigor of implementation is poor. Several improvements in terms of efficiency of environmental policies, legislation and fiscalization need to be developed in the near future. More control of coastal activities will help to improve the viability of all stocks of intertidal resources.

Long-term studies are necessary to determine the real magnitude and effects of both invasive species and human exploitation and would be extremely useful in outlining management guidelines.

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