POPULATION STRUCTURE AND RECRUITMENT PATTERNS OF THE INDIGENOUS MUSSEL *Perna perna* AND THE ALIEN MUSSEL *Mytilus galloprovincialis* ON THE CENTRAL COAST OF NAMIBIA

THESIS

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ABSTRACT

Invasive species disrupt ecosystems and may consume resources and eventually replace indigenous species. This has been well documented for the Mediterranean mussel *Mytilus galloprovincialis* throughout the world. This study assessed the spatial and temporal variation of population structure, recruitment patterns, condition index and abundance of the indigenous mussel *Perna perna* and alien mussel *M. galloprovincialis* at three different sites on the central Namibian coast.

Sampling took place during spring tide, once every season along Dolphin Beach, Long Beach, and Shipwreck, near Swakopmund during 2014. At regular intervals of 2 m one 10 x 10 cm quadrat was placed along a line transect from the spring low water level to the spring high water level. Everything was removed within the quadrat and stored at -20 °C. Thereafter, samples were sorted with two sets of sieves with mesh 2 mm and 0.5 mm into different size classes. Mussels were identified to species level.

Significantly higher recruitment for *P. perna* during January and September 2014 was observed ($p = 0.006$). *M. galloprovincialis* displayed no significant seasonal difference ($p = 0.102$). *P. perna* recruits and adults dominated the low shore zone, while the juveniles dominated the mid shore zone. *M. galloprovincialis* recruits, juveniles and adults dominated the mid shore zone.

The condition index of adults was significantly higher for *P. perna* in the low shore zone and for *M. galloprovincialis* in the mid- and high shore zones. No significant difference in the condition index of juveniles between the zones existed for both species. No significant seasonal difference was found in the condition index of juveniles and adults for *M. galloprovincialis*. There was also no significant seasonal difference in the condition index of juveniles for *P. perna*, however the condition index of adults was significantly higher for *P. perna* during September compared to the other months. The abundance of recruits of *M. galloprovincialis* observed during this study might be a sign of possible invasion which needs to be monitored.

Key words: Recruitment, Invasive, Condition Index, *Perna perna, Mytilus galloprovincialis*

TABLE OF CONTENTS

ABBREVIATIONS

LB	Long Beach
DB	Dolphin Beach
SW	Shipwreck
CI	Condition Index

LIST OF FIGURES

LIST OF APPENDICES

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DECLARATIONS

I, Cathleen Deelie, declare hereby that this study is a true reflection of my own research, and that this work or part thereof has not been submitted for a degree in any other institution of higher education.

I, Cathleen Deelie, grant The University of Namibia the right to reproduce this thesis in whole or in part, in any manner or format, which The University of Namibia may deem fit, for any person or institution requiring it for study and research; providing that The University of Namibia shall waive this right if the whole thesis has been or is being published in a manner satisfactory to the University.

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Chapter 1

Introduction

1.1 General Background

Intertidal rocky shores are of the most easily accessible marine habitats and constitute a transition zone between land and sea (Branch & Branch, 1998). They are also among the most physically harsh environments on earth. Organisms that live in the intertidal zone frequently deal with changing environmental conditions and, therefore, have to be hardy and diverse. Intertidal animals experience extreme physiological stress during the low tide period and those species inhabiting the higher intertidal zone are often more tolerant of thermal and desiccation stress than those found in other zones (Little, Williams & Trowbridge, 2010). The intertidal rocky shore is considered the most productive with a greater diversity of life than any other ecosystem around the world (Denny & Wethey, 2001).

The intertidal zone is the part of the continental shelf in the ocean that is exposed twice a day and covered by seawater twice a day. The part close to the sea where water retracts the furthest during spring tide is referred to as the spring low tide mark, while the part where water moves the farthest up to the land is referred to as the spring high tide mark. The intertidal zone is thus the area between the low and high water marks or levels. The intertidal zone is shallow and consists of soft (sand or mud) and/or hard substrate (rocks). Tides are produced by the gravitational pull on the earth by the sun and the moon. The water level of shores changes constantly, and the height to which the tide rises and falls varies daily (Knox, 2001).The tides control the shore environment by affecting the periods of submersion and emersion (Branch & Branch, 1998). The Namibian intertidal sites consist mainly of either rocks, sand or both with differences in topography and wave action (Nashima, 2013). It falls within the Namaqua and Namib biogeographic provinces (Sakko, 1998).

1.2 Zonation Patterns

The organisms inhabiting the intertidal zones of rocky shores are often distributed in vertical bands over the entire spring tidal range called zones (Benson, 2002).This vertical banding of organisms is caused by the different physical environmental conditions due to the difference in exposure times during low tides. The lower limits of a species vertical distribution range may be set by biotic factors such as competition or predation and its higher limits different physical environmental conditions (Levinton, 2001).

The zonation patterns of rocky shores are not exactly the same everywhere, because of differences in coastal features. This study followed the zonation pattern as described by Little et al. (2010) where three distinct zones are recognised as high-, mid- and low shore zones. The low shore zone is referred to as the Infratidal zone, the mid shore zone is called the Balanoid zone and the high shore zone is referred to as the Littorina zone. The low shore zone is mostly submerged and is only exposed during extreme low tides. This area has more marine vegetation, like red algae and brown seaweeds, than other zones and organisms in this zone are generally not well adapted to long periods of exposure and temperature extremes. The mid shore zone is regularly both exposed and covered by the tide and can support more life than the high shore zone due to the length of time that it is submerged in water. This zone is usually broader and dominated by barnacles and mussels. The mid shore zone also has a higher density of marine vegetation, specifically seaweeds like green, brown and red algae. Organisms in this area include anemones, barnacles, crabs, green algae, mussels, snails and sponges.

The distribution and vertical zonation of intertidal communities are affected by steep gradients in temperature, desiccation and oxygen availability. These factors are typical of an intertidal habitat, especially for sessile and inactive organisms that are not capable of moving to escape environmental stresses imposed.

1.3 Recruitment Patterns

Many intertidal organisms have in their life cycle a stage that involves dispersal in water, allowing the wide distribution of species (Bayne, 2009). The distribution of mussels is no exception to this, according to Branch and Branch (1998), dispersal of the larval stage away from an area already occupied by adults prevents overcrowding.

Recruitment can be defined as the process of successful settlement of larvae when they attach to a substrate (Gosling, 2003). Measurement of recruitment patterns of mussels is, therefore, an important part in studies of its population dynamics. Broitman and Kinlan (2006) recognised temporal and spatial variation in the rates of larval recruitment as a strong ecological driver of populations and communities.

The population dynamics of marine species is strongly influenced by interactions with their physical environment. These interactions are particularly complex in benthic animal species inhabiting hard substrates (Porri, McQuaid & Radloff, 2006). The nature of the substrate can affect the density of recruits on a shore which in turn may affect the population structure of the adult community (Bownes, 2005). Variations in settlement and recruitment may be important factors in determining the patterns of distribution and abundance of adult populations. According to Porri et al. (2006), there is a difference in recruitment rates between the low and high shores in terms of the distribution of a species. Species ability to cope with high temperatures and aerial exposure will set the upper limit for recruitment while competition with other species will set the lower limits (Rius, 2005). Intertidal mussel distribution may be very patchy and it has been suggested that the sizes of such patches on hard substrates are maintained by recruitment, mortality and growth (Erlandsson & McQuaid, 2004). Larval patchiness and dispersal are affected by the seasonality of reproduction, water temperature, as well as temporal variations in larval availability (Porri et al., 2006). Seasonal recruitment is, therefore, important in determining the pattern of succession and population growth. The patterns of distribution and abundance of organisms vary both spatially and temporally in response to a variety of physical and biological factors (Menge & Sutherland, 1987).

1.4 Distribution Patterns of *Mytilus galloprovincialis* and *Perna perna*

The Mediterranean mussel *Mytilus galloprovincialis* is one of the most widespread, alien, invasive species and is now globally distributed throughout the temperate zones of the northern and southern hemispheres (Bownes & McQuaid, 2006). It was first discovered in Saldanha Bay in South Africa in 1979 (Branch & Steffani, 2004). It appeared only on the south coast of South Africa in 1988 (McQuaid & Phillips, 2000). It has subsequently spread along the entire west coast of the country, extending into Namibia, and has more recently spread for 800 – 900 km along the south coast as far as East London (Robinson, Griffiths, McQuaid & Rius, 2005). It is now the dominant mussel form Cape Peninsula to Lüderitz in Namibia (Branch & Steffani, 2004). The alien *M. galloprovincialis* and the indigenous mussel, *Perna perna* show partial habitat segregation on the south coast of South Africa, while the lower and upper areas of the mussel zone are dominated by *P. perna* and *M. galloprovincialis* respectively, with overlap in the middle zone (Hockey & Van Erkom Schurink, 1992; Nicastro, Zardi & McQuaid, 2009).

The Brown mussel, *P. perna,* is a dominant species on the sub-tropical east, warm-temperate south coasts and northwards from Namibia (Hammond & Griffiths, 2006). The cold waters of the Benguela upwelling system explain the absence of *P. perna* between the Cape Peninsula and Lüderitz (Zardi, McQuaid, Teske & Barker, 2007). *P. perna* appears again in small numbers at Lüderitz in Namibia and becomes more abundant at Walvis Bay. Since *P. perna* and *M. galloprovincialis* are similar in their tolerance to desiccation and siltation, and both grow rapidly, any interaction between them within the intertidal zone is likely to be more evenly balanced (Hockey & Erkom Schurink, 1992).

Invasive species can disrupt intertidal ecosystems by occupying space previously occupied by various organisms (Branch & Stefani, 2004). Thus far the presence of *M. galloprovincialis* does not appear to have had any effects on the intertidal ecosystem on the Namibian coast according to Sakko (1998), however the lack of impact studies and the rapid spread of *M. galloprovincialis* observed along the South African coastline (Robinson, Branch, Griffiths, Govender & Hockey, 2007) makes it essential to study the population growth of *M. galloprovincialis* on the Namibian coast.

1.5 Statement of the Problem

M. galloprovincialis may have the potential to outcompete and displace native mussels and become the dominant mussel species in certain localities (Robinson et al., 2007). This is because *M. galloprovincialis* may grow faster than native mussels, is more tolerant to air exposure and has a reproductive output of between 20 % and 200 % greater than that of indigenous species (Van Erkom, Schurink & Griffiths, 1992). *M. galloprovincialis* displays great tolerance to environmental variability, a characteristic which makes it an aggressive invasive species on South African shores (Robinson et al., 2005). Its rapid growth rate at different water temperatures and its resistance to desiccation is regarded as significant (Levinton, 2001). The Sub-Sahara Annual Report in 1998 reported that by the early 1990s the species was well established in southern

Namibia as far as the Kunene River mouth. Only isolated individuals of *M. galloprovincialis* were found in the early 1990's (Sakko, 1998).

In 1995 large numbers settled in the Swakopmund area amongst the indigenous species. The rapid growth rate and high fecundity of the alien species are matched by those of the indigenous species, and it remains to be seen which species will become dominant (Sakko, 1998). Thus far the no impact study has been done of *M. galloprovincialis* along the Namibian coast, so it does not appear to have any effect on the ecosystem (Sakko, 1998). Trophic relationships seem to remain unaltered and biodiversity on a regional scale is unaffected, although the intertidal distributions of indigenous species have been locally altered (Sakko, 1998). There is a need to assess the current status of the alien mussel species in relation to indigenous species on both the southern and central coasts of Namibia. This study is the first phase in addressing this need by focusing on the population dynamics of *M. galloprovincialis,* as well as on the indigenous *P. perna* on the central coast of Namibia.

1.6 Research Questions

This study aims to answer the following research questions:

(i) When does recruitment of *Mytilus galloprovincialis* and *Perna perna* occur on the central Namibian coast?

(ii) In which part of the intertidal zone does recruitment of *M. galloprovincialis* and *P. perna* occur?

(iii) Is the abundance of the three size classes (Recruits, Juveniles and Adults) of *M. galloprovincialis* and *P. perna* significantly different throughout the intertidal zone?

(iv) Does the condition index of juveniles and adults vary between tidal zones and seasons for *M. galloprovincialis* and *P. perna*?

1.7 Research Hypotheses

(i) Recruitment of *Mytilus galloprovincialis* and *Perna perna* is not seasonal on the west coast (Reaugh-Flower et al., 2011). Thus, recruitment occurs throughout the year.

(ii) There exists no significant difference in recruitment of *M. galloprovincialis* between the different zones on the west coast (Robinson et al. 2007), while recruitment of *P. perna* occurs in the low shore zone (Bownes & McQuaid, 2006).

(iii) The abundance of recruits and juveniles is higher in the mid- and high shore zones, while adults dominate the low shore zone, for both mussel species (McQuaid, Lindsay & Lindsay, 2000)

(iv) Condition indices of juveniles and adults exhibit spatial and temporal variation for both mussel species (Rius & McQuaid, 2006).

1.8 Significance of the Study

The introduction of *M. galloprovincialis* into southern African waters, its distribution and impacts (ecological and socio-economic) have been well studied in South Africa (Harris et al., 1998; Hammond & Griffiths, 2006; & Pfaff et al., 2011).

Recent studies conducted on both mussels along the south and west coast of South Africa, indicated a concern that the indigenous mussel, *Perna perna,* might be replaced by the alien mussel *Mytilus galloprovincialis*, when one takes into account its rapid spread around the world (Bownes & McQuaid, 2006; Robinson et al., 2007; Zardi et al., 2007).

To date little is known about the recruitment patterns of these mussels along the Namibian coast. This study is essential to assess the current situation along the Namibian coast, as well as improve the understanding of those factors that affect settlement, recruitment, growth and reproduction of these mussels at different spatial scales on the Namibian coast. It can serve as a baseline for future, continuous monitoring and evaluation of the distribution range and impact of *M. galloprovincialis* on the environment.

Chapter 2

Literature Review

2.1 Introduction

Several studies were conducted on the population structure, growth and recruitment patterns of *Mytilus galloprovincialis* and *Perna perna* (Hockey & Erkom Schurink, 1992; Bownes & McQuaid, 2006; Hammond & Griffiths, 2006; Robinson et al., 2007). The majority of these studies focused on South Africa as *M. galloprovincialis* invaded the harbour at Saldana Bay in the early seventies (Branch & Steffani, 2004; McQuaid & Phillips, 2007). Studies that that were conducted on the Namibian coast include Sakko, (1998); Harris et al. (1998); Hammond & Griffiths, 2006; Reaugh-Flower et al. (2010, 2011). Reaugh-Flower et al. (2010 & 2011) focused on spatial patterns of mussel recruitment and the use of artificial substrates to study recruitment patterns, while Sakko (1998) reported on the status of intertidal marine invertebrates and Harris et al. (1998) studied temporal and spatial recruitment patterns of intertidal mussels. Findings from these studies will be elaborated on within this section.

There are limited historical data available for the central coast in Namibia. Therefore, studies conducted in South Africa were used as the main literature sources. As these studies included several sites on the central and southern coast of Namibia, the information will be relevant for the current study.

This section will mainly focus on literature regarding the growth and recruitment patterns of *P. perna* and *M. galloprovincialis* and environmental tolerant ranges of these species.

2.2 Growth and Recruitment of *Mytilus galloprovincialis* and *Perna perna*

Growth rate of *Mytilus galloprovincialis* is fast, since it can grow up to 70 mm within twelve months under favourable environmental conditions (Picker & Griffiths, 2011). In South Africa growth of *M. galloprovincialis* and *Perna perna* is faster in areas of higher water circulation (Van Erkom Schurink & Griffiths, 1993). Studies from Van Erkom Schurink & Griffiths (1993) showed *M. galloprovincialis* grows faster than *P. perna*. Similar results were found by Steffani & Branch (2003a) and they explained the faster growth rate of *M. galloprovincialis* by better food supply. Comparing growth rates at the different tidal heights showed a consistent decrease of growth rate and mussel size structure towards the high shore zone (Van Erkom Schurink & Griffiths, 1993; McQuaid et al., 2000).

Growth rates of mussels directly affect their condition index (Steffani & Branch, 2003a). The condition index relates the flesh weight of mussels to their shell mass and reflects the physiological status of mussels and the partitioning of resources for growth between tissue and shell (Steffani & Branch, 2003a). Rius and McQuaid (2006) found that the condition index of *P. perna* and *M. galloprovincialis* displayed spatial variation. Condition index for *P. perna* was higher in the low- and mid- zones compared to the condition index of *M. galloprovincialis*. Studies conducted by Steffani & Branch

(2003a) on the growth rate and condition of *Mytilus galloprovincialis* found that greater wave action led to a higher water influx and therefore greater food availability, which resulted in higher growth rates and condition indices.

Recruitment in general is the arrival of new individuals on the shore. It has been defined as the process of successful colonisation after a specified amount of time during which some post-settlement larval mortality would have occurred (Bayne, 2009); thus, it is the rate at which juveniles join the population. On the west coast of South Africa a study conducted by Pfaff et al. (2011) indicated that recruitment of mussel larvae is influenced by upwelling, wave exposure and prevailing near shore ocean currents. These factors were positively related to the settlement of mussel larvae on rocky shores along the west coast of South Africa. Robinson et al. (2007) reported extremely high recruitment of up to 8.7 million recruits per m^2 along the west coast for *M. galloprovincialis*. A study conducted by Reaugh-Flower et al. (2011) predicted that recruitment of *P. perna* and *M. galloprovincialis* along the Namibian coast did not show any obvious seasonality in recruitment patterns. Greater recruitment was established for *P. perna* on the Namibian coast, while *M. galloprovincialis* displayed greater recruitment patterns at the Cape Peninsula (Reaugh-Flower et al., 2011).

Spawning of *P. perna* and *M. galloprovincialis* does not occur at the same time, with spawning of *M. galloprovincialis* peaking in October and April, while that for *P. perna* peaking in winter and spring (McQuaid & Phillips, 2007). Primary settlement of *P. perna* usually occurs during April and between September and November (McQuaid & Phillips, 2007). This is also true of *M. galloprovincialis*, which on the west coast, settles in the summer months and particularly in April. In many cases spawning displays a single event for *P. perna* and two spawning events for *M. galloprovincialis* (Nicastro et al., 2009).

In contrast to shores with 100% recruitment, mussel biomass appears to be restricted by recruit supply and constraints of food, especially on sheltered shores. On exposed shores density is regulated through intra-specific competition for space primarily on smaller, spatial scales (McQuaid & Lindsay, 2000).

The fact that mussel beds of *M. galloprovincialis* consist of several layers and support a higher density in mono-layered beds of *P. perna*, has led to a massive increase in the mussel density of *M. galloprovincialis* along the South African west coast (Robertson et al., 2005). Another concern is the fact that *M. galloprovincialis* is not infected with trematode parasites that are common in indigenous mussels, such as *P. perna*. This reduces both individual growth rates and population reproductive output (Robertson et al., 2005).

Field experiments conducted by Erlandsson, Pal and McQuaid (2006) suggested that *P. perna* has higher attachment strength than *M. galloprovincialis*, because it produces more and thicker byssus threads under more exposed conditions (McQuaid & Lindsay, 2007). This ability gives *P. perna* a higher resistance against wave action and, therefore, recruitment rates of *P. perna* are higher throughout the year in the lower zone, but in the upper mussel zone, it suffers greater post-settlement mortality of recent recruits than *M. galloprovincialis* (Erlandsson et al., 2006).

2.3 Environmental Tolerance Ranges

Mytilus galloprovincialis has become an aggressive invasive species on South African shores due to its greater tolerance to environmental variability compared to indigenous mussel species (Van Erkom Schurink & Griffiths, 1992). At different water temperatures it shows rapid growth and displays significant resistance to desiccation (Van Erkom Schurink & Griffiths, 1993; Nicastro, et al., 2009). Anestis, Lazou, Portner and Michealidis (2007) have shown significant mortality rates of *M. galloprovincialis* at temperatures greater than 24 °C with the upper limit (i.e. 100% mortality) occurring within 20 days of exposure to water at 30°C. It is not clear what the minimum temperature tolerance limit of this species is, yet it is known to exist in beds on the west coast of South Africa where temperatures can drop to a minimum of approximately 7°C during peaks of upwelling seasons (Van Erkom, Schurink & Griffiths, 1992). Temperature has been widely acknowledged as an important factor in controlling growth of this species. Bayne (2009) reported that growth for *M. galloprovincialis* even occurred between 3 and 25°C. The largest growth rates were found at water temperatures between 10°C and 20°C. There seems to be a strong relationship between temperature and the growth of larvae between 17 to 20°C, but not between 20 and 24°C (Anestis et al., 2007).

A study conducted by Nicastro et al., (2009) concluded that in the lower mussel zone, where hydrodynamic stress is higher, *Perna perna* initially facilitated the survival of *M. galloprovincialis* by providing protection against waves, but later it excluded the invasive species through interference competition for space. In addition, recruitment failure due to low settlement and high mortality contributed to the exclusion of *P. perna* from the high shore, while the exclusion of *M. galloprovincialis* from the low mussel zone was likely to be by post-recruitment mortality according to McQuaid and Lindsay (2000).

Studies conducted by Steffani & Branch (2003b) showed that *M. galloprovincialis* is a very good competitor for primary rock space on the low shore zone with increasing wave action. *M. galloprovincialis* had the highest cover at exposed sites compared to sheltered sites most likely due favourable environmental conditions. The different behaviour of these two mussel species towards wave action and tenacity is well known and outlined in previous studies conducted on the south coast of South Africa. The attachment strength of the species varied spatially and temporally (Nicastro et al. 2009). *P. perna* has significantly higher attachment strength than *M. galloprovincialis* at the expense of a lower reproductive output (McQuaid & Lindsay, 2007). The attachment opportunities may be fewer at exposed sites compared to those at sheltered shores (Steffani & Branch, 2003b).

The ability of *M. galloprovincialis* to keep its valves closed during exposure to terrestrial conditions is a valuable adaptation to survive without oxygen and therefore, minimising water loss (Nicastro, Zardi & McQuaid, 2010). This ability to open and close its shells (gaping) will affect the tolerance of mussels to desiccation and thus also their position on the shore in terms of vertical zonation. Tolerance to air exposure and desiccation in *M. galloprovincialis* is reported to be double that of any other indigenous species in South Africa (Branch & Steffani, 2004). Studies conducted by Van Erkom

Schurink & Griffiths (1993) on the effects of tidal exposure on the growth of mussels, indicated that *M. galloprovincialis* and *P. perna* were the two mussel species that best tolerated aerial exposure and maintaining growth in the intertidal area. Branch & Steffani (2004) reported that *M. galloprovincialis* had a 92% survival during aerial exposure in the high shore zone compared to 78% for *P. perna*.

Many of the existing literature on population growth and recruitment patterns of mussels on the Namibian coast were conducted as part of broader studies that covered large geographical areas including both the Namibian and South African coastlines (Harris et al., 1998; Reaugh-Flower et al., 2010, 2011). However, very few studies concentrated on the Namibian coast only (Sakko, 1998) investigating small localised patterns of recruitment and population structure of the two mussel species. This study can provide a baseline for monitoring and future research on small scale patterns of intertidal mussels on the coastline of Namibia.

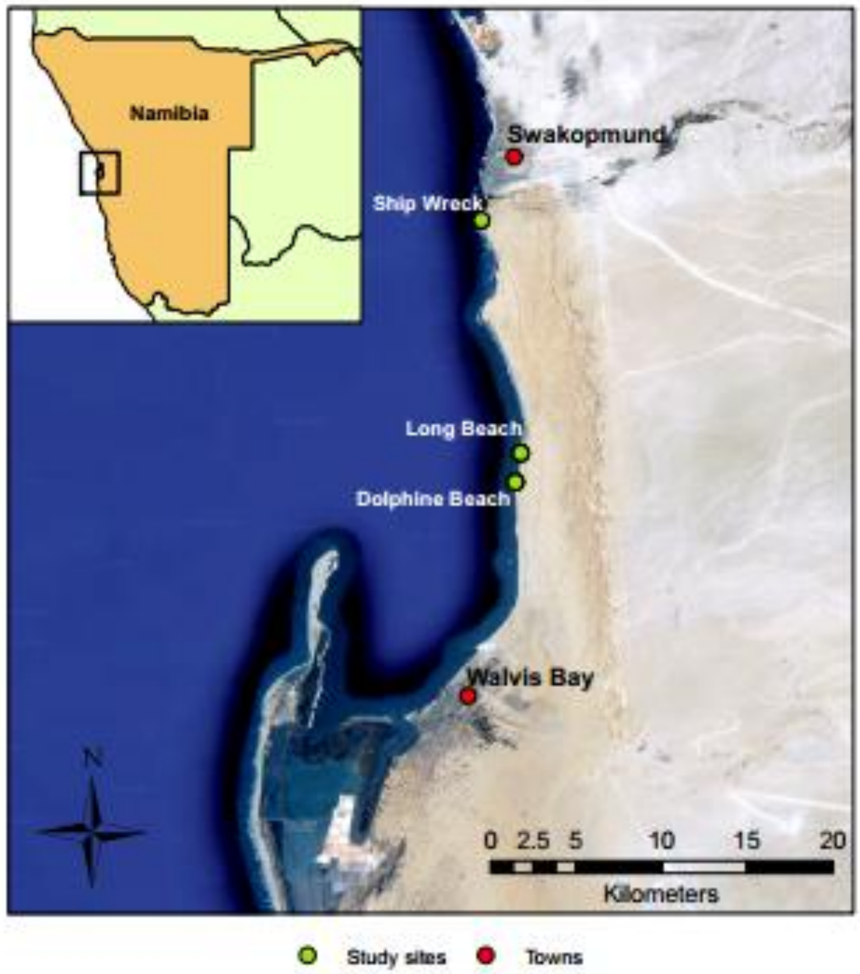
Chapter 3

Materials and Methods

3.1 Study Sites

This study was conducted along the central coast of Namibia, and included three sites, namely Long Beach (22° 94´ 80´´ S, 014° 51´ 38´´ E) and Dolphin Beach (22° 50´ 7´´ S, 014° 32´ 25´´ E) near Walvis Bay, as well as the rocky shore just outside Swakopmund, referred to hereafter as "Shipwreck" (22° 42'021''S 014° 31'234''E) (Figure 1). The two sites near Walvis Bay are just 2 km apart, while the site near Swakopmund is 12 km from the other two sampling sites (Figure 1).

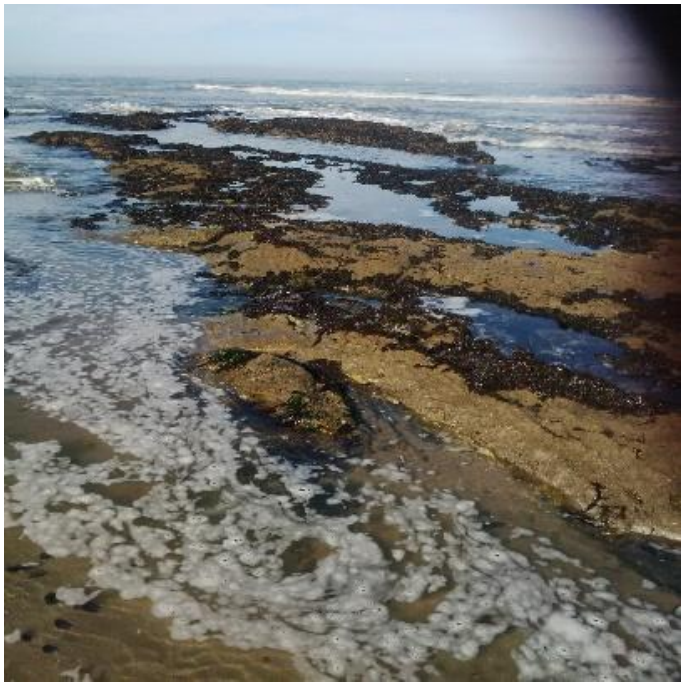
The Long Beach site (Figure 2a) consists mainly of sedimentary rock material dominated with ripples and small canyons and has a shallow slope (Nashima, 2013). Dolphin beach is a relatively wide rocky shore with several rock pools (Figure 2b). The Shipwreck area consists of patchy rocky outcrops which block tide waves; therefore, most rocks were exposed during low tide (Figure 2c). At Long Beach the area tends to be formed by a uniform rock layer along the coast. Almost 50% of its rocks are submerged even during low tides.



Sources: Atlas of Namibia Google Earth (2014). Cartography: Cathleen Deelie.
Projections: WGS 84

Figure 1: Map of Sampling Sites at Central Coast of Namibia.

(a)



(b)

(c)

Figure 2: Study Sites (a) Long Beach, (b) Dolphin Beach and (c) Shipwreck.

3.2 Sampling Methods

Sampling was done in January (summer), May (autumn), July (winter) and September (spring) during spring tide, since the low tide is then exceptionally low.

At each site one line transect was laid from the spring low tide mark to the spring high tide mark (Figure 3). The exact length of transects varied, depending on the magnitude of the spring tide. The total length of the intertidal zone of Long Beach was approximately 29 m, Dolphin Beach 54 m and Shipwreck 109 m.

Figure 3: Line Transect at Long Beach.

At regular intervals of 2 m 10 x 10 cm quadrats in the lower zone were placed along the line transect (Figure 4) to allow capturing of approximately three quadrats in the low shore zone. Thereafter, the intervals were extended to every 5 m so that at least three quadrats could be sampled in the mid shore zone and three in the high shore zone.

Figure 4: Quadrant along transect on Long Beach

The depth of the mussel-bed was measured within each quadrat by placing a ruler vertically across the removed section and measuring its height above the rock surface (Figure 5).

Figure 5: Measuring of the mussel bed depth at Long Beach

At each quadrat along the transect all the organisms were removed, using a trowel. The samples were placed in a marked zipper seal plastic bag (Figure 6). The plastic bag was labelled according to the date, site as well as the distance from the low tide mark. After sampling, the samples were immediately frozen at -20°C until analysis in the laboratory.

Figure 6: Marked zipper sealed bag indicating Site and Distance

3.3 Sorting, Measuring and Identification

In the laboratory each marked zipper bag was sorted by using two sieves with a mesh size of 2 mm and 0.5 mm. All the mussels were removed and identified, using several guides (Bownes et al., 2008, Branch et al., 2010). The two mussel species were identified by using their external features, such as shell colour and shape. *Perna perna* generally has a brown, slightly narrow and stubby shell and the blue mussel, *Mytilus galloprovincialis* is usually wider and flatter. In cases where the shell colour was eroded, the mussels were identified by using the internal scarring (Lourenço, Nicastro, Serrao, Zardi & Gerardo, 2012) caused by the adductor muscles (Figure 7).

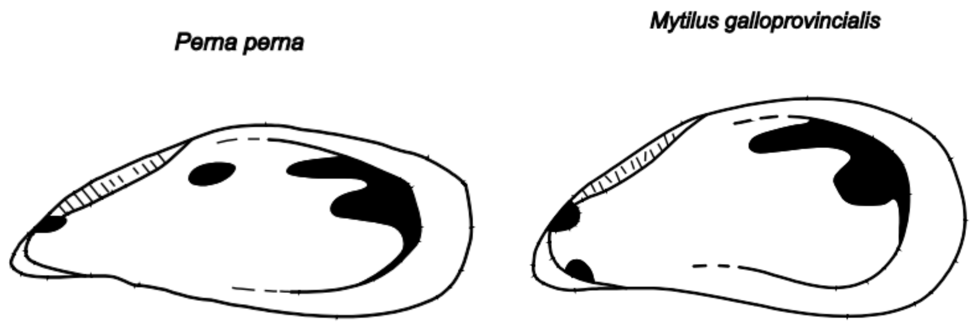


Figure 7: Muscle Scars on the Inside of the Shells shaded in black (Jordaan, 2010).

The mussels were classified into recruits, juveniles and adults depending on their size. The length classes for *P. perna* were as follow: organisms smaller than 6 mm represented recruits, 7 – 16 mm represented juveniles and those larger than 17 mm represented adults (Hammond & Griffiths, 2006). The length classes for *M. galloprovincialis* were as follows: organisms smaller than 5 mm represented recruits, 6 – 15 mm represented juveniles and those larger than 16 mm represented adults (Anestis et al., 2007).

Adults and juveniles were collected from the larger sieve with a pair of forceps. They were then identified and measured with bio-digital callipers from the front part of the shell to the end of the shell to the nearest 0.01 mm (Figure 8).

Figure 8: Shell Length Measurement of *Perna perna* with Digital Callipers

The recruits were washed from the 0.15 mm sieve into a Petri dish. The dish was examined under a dissecting microscope and the recruits were identified and counted.

Morphological features were used to distinguish between the recruits as discussed by Bownes, Barker and McQuaid (2008). *P. perna* recruits displayed a typical zig-zag pattern or triangular shaped marks (Figure 9), while the shells of *M. galloprovincialis* recruits ranged from bluish/brown to black/blue in colour (Figure 10).

Figure 9: Shell Markings and Colour of *P*. *perna* recruits (Bownes et al., 2008)

Figure 10: Shell Markings and Colour of *M*. *galloprovincialis* recruits (Bownes et al., 2008)

3.4 Condition Index

All the adult mussels were used to calculate the biomass condition index. Only 50% of the juveniles were used, if there were more than 100. The biomass condition factor was not determined for recruits. The shell of each mussel was separated from the soft tissue and both the wet shell mass and wet soft tissue mass were obtained. All weight measurements were made with a digital balance up to two decimal places. The gonads were observed for all the adult mussels and were classified as either male or female. The male gonads of both mussels are white or off white, while female gonads are orange or bright orange (Branch & Branch, 1998). The soft tissue and the wet shells were dried separately at 104°C for 24 hours, after which they were cooled down and weighed. The condition index (CI) was calculated by using the formula $CI = \frac{dry\ flesh\ mass}{dry\ shell\ mass} \times 100$ (Branch & Steffani, 2003).

3.5 Data Analysis

The Shapiro - Wilks test was used to determine whether the data were normally distributed. As data were not normally distributed ($p > 0.05$), the data was log transformed. The General Linear Model (GLM) with multivariate comparisons was used to simultaneously consider the effect of shore zone, season and species on recruits, juveniles, adults and condition index. Additionally post hoc analysis (Bonferroni) was performed to clarify significant differences at a probability level of 0.05. In all cases the computer package IBM SPSS statistics 22 was used to perform all the statistical analysis.

Chapter 4

Results

4.1 Seasonal Recruitment Patterns for *Perna perna*

Multivariate analysis performed using the General Linear Model (GLM) showed that there was a significant effect of season on the recruitment pattern of *Perna perna* (Wilks'Lambda (λ) = 0.032, F (15, 22.49) = 3.735, p = 0.002). The Bonferroni test indicated that recruitment was significantly higher in January compared to September (p = 0.006. Recruitment was significantly higher in September compared to July. (p = 0.007).

The results indicated that recruitment of *P. perna* occurred throughout the different seasons and was the highest at Dolphin Beach and lowest at Shipwreck (Figure 11). The highest recruitment for *P. perna* was recorded during January and September at Dolphin Beach and Long Beach.

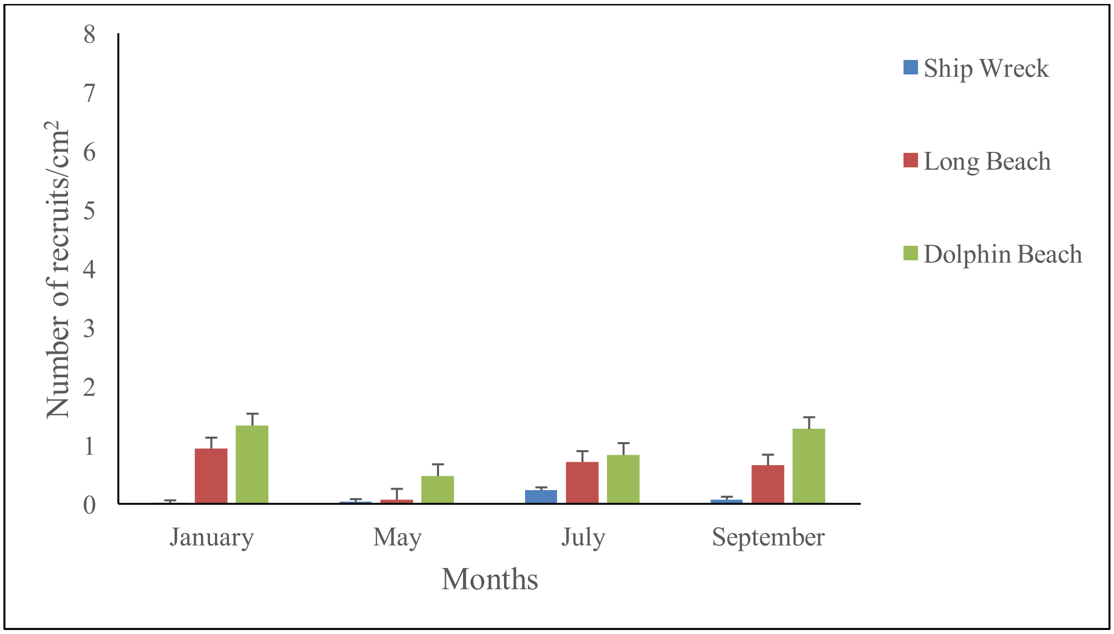


Figure 11: Mean number of recruits (+SE) of *Perna perna* during the different months at the different sampling sites (Ship Wreck – blue; Long Beach - red; Dolphin Beach – green).

4.2 Seasonal Recruitment Patterns of *Mytilus galloprovincialis*

Multivariate tests using the GLM procedure showed no significant effect of season on the recruitment pattern of *Mytilus galloprovincialis* ($\lambda = 0.114$, $F (15, 22.49) = 1.795$, $p = 0.102$).

The highest number of recruits (5-6 recruits/cm^2) was recorded during May and July at Dolphin Beach (Figure 12). Recruitment of *M. galloprovincialis* was low (< 1 recruit/cm^2) at Shipwreck throughout the seasons (Figure 12).

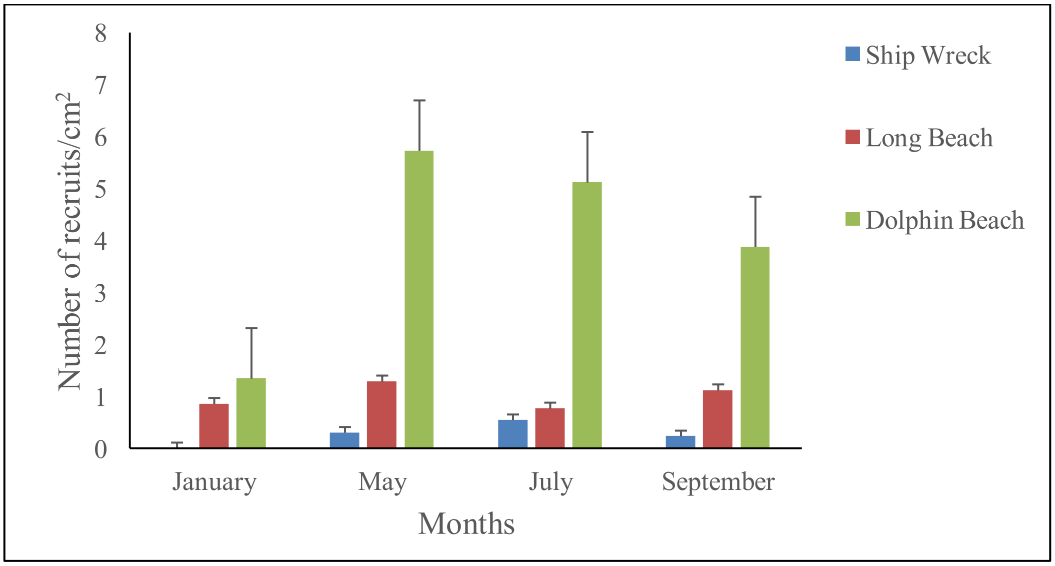


Figure 12: Mean number of recruits (+SE) of *M. galloprovincialis* during the different months at the different sampling sites (Ship Wreck – blue; Long Beach - red; Dolphin Beach – green).

4.3 Spatial Recruitment Patterns of *Perna perna* and *Mytilus galloprovincialis*

The spatial recruitment pattern for *P. perna* showed a significant difference between the different zones (λ =0.028, F (10.16) = 8.040, $p < 0.0001$). Multiple post doc comparisons with Bonferroni indicated a significant difference in recruitment for *Perna perna* between the low- and high shore zone ($p = 0.001$) as well as a significant difference in the recruitment pattern between mid- and low shore zones ($p = 0.003$).

The recruitment of *P. perna* occurred mainly on the low – and mid-shore zone (Figure 13 a-d). The highest number of recruits were recorded at Dolphin Beach on the low shore zone during January as well as in September (Figures 13 a and d). At Long Beach the greatest recruitment for *P. perna* was on the low shore zone in July, while at Dolphin beach the highest recruitment occurred on the mid shore zone (Figure 13b).

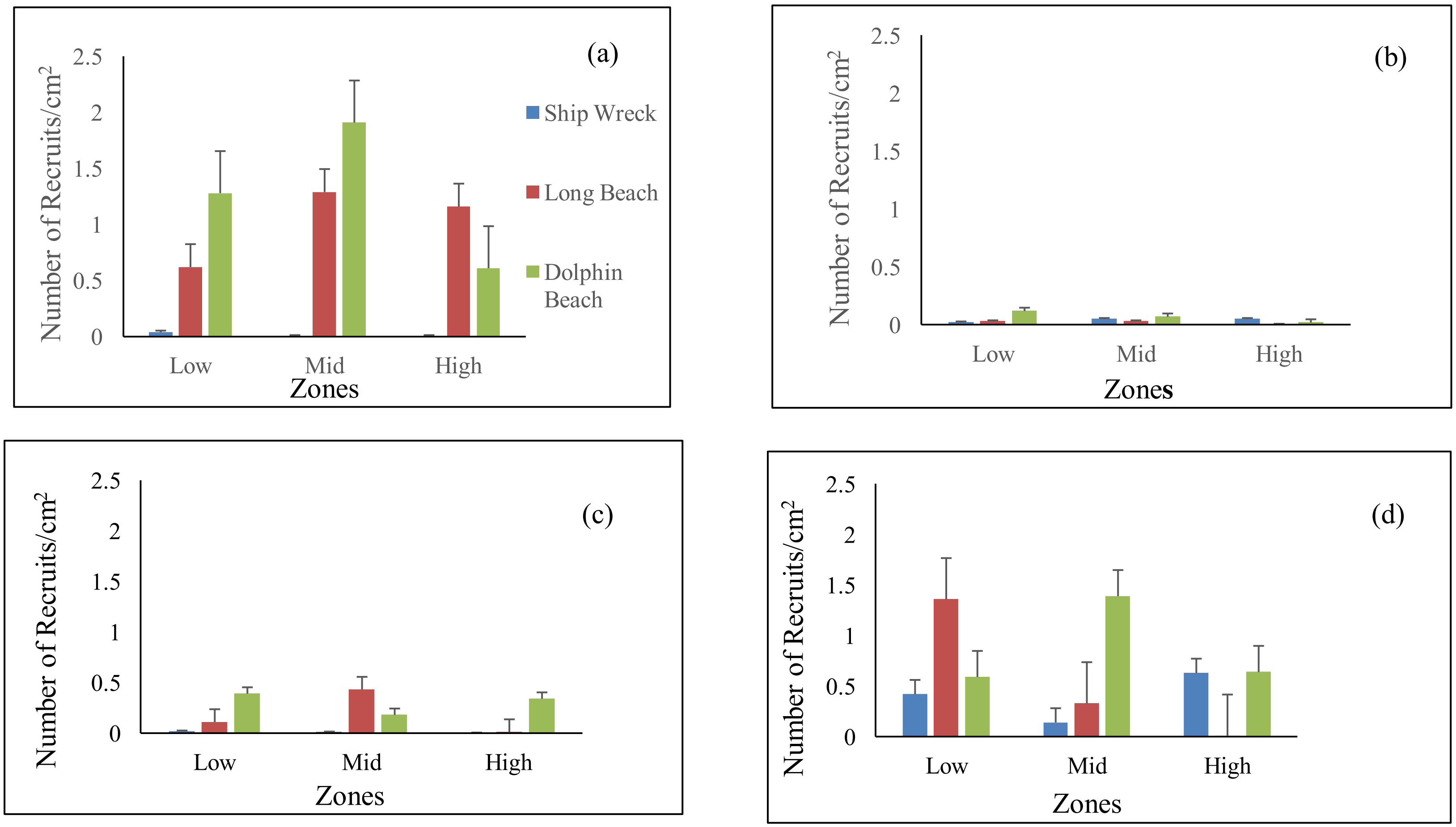


Figure 13: Mean number of recruits (+SE) of *Perna perna* in the different intertidal zones during (a) January (b) May (c) July and (d) September 2014. (Ship Wreck – blue; Long Beach - red; Dolphin Beach – green)

The spatial recruitment pattern for *Mytilus galloprovincialis* showed a significant difference between the zones ($\lambda = 0.133$, $F(10, 16) = 2.780$, $p = 0.033$). Multiple post doc comparisons with Bonferroni showed a significant difference for *M. galloprovincialis* between the low-and mid-shore zone ($p < 0001$) as well as a significant difference in the recruitment pattern between high- and low shore zones ($p = 0.044$). Recruitment of *M. galloprovincialis* was highest on the mid shore zone at Dolphin Beach (Figures 14 b and c). At Shipwreck and Long Beach recruitment was low throughout the intertidal zones (Figures 14 a-d).

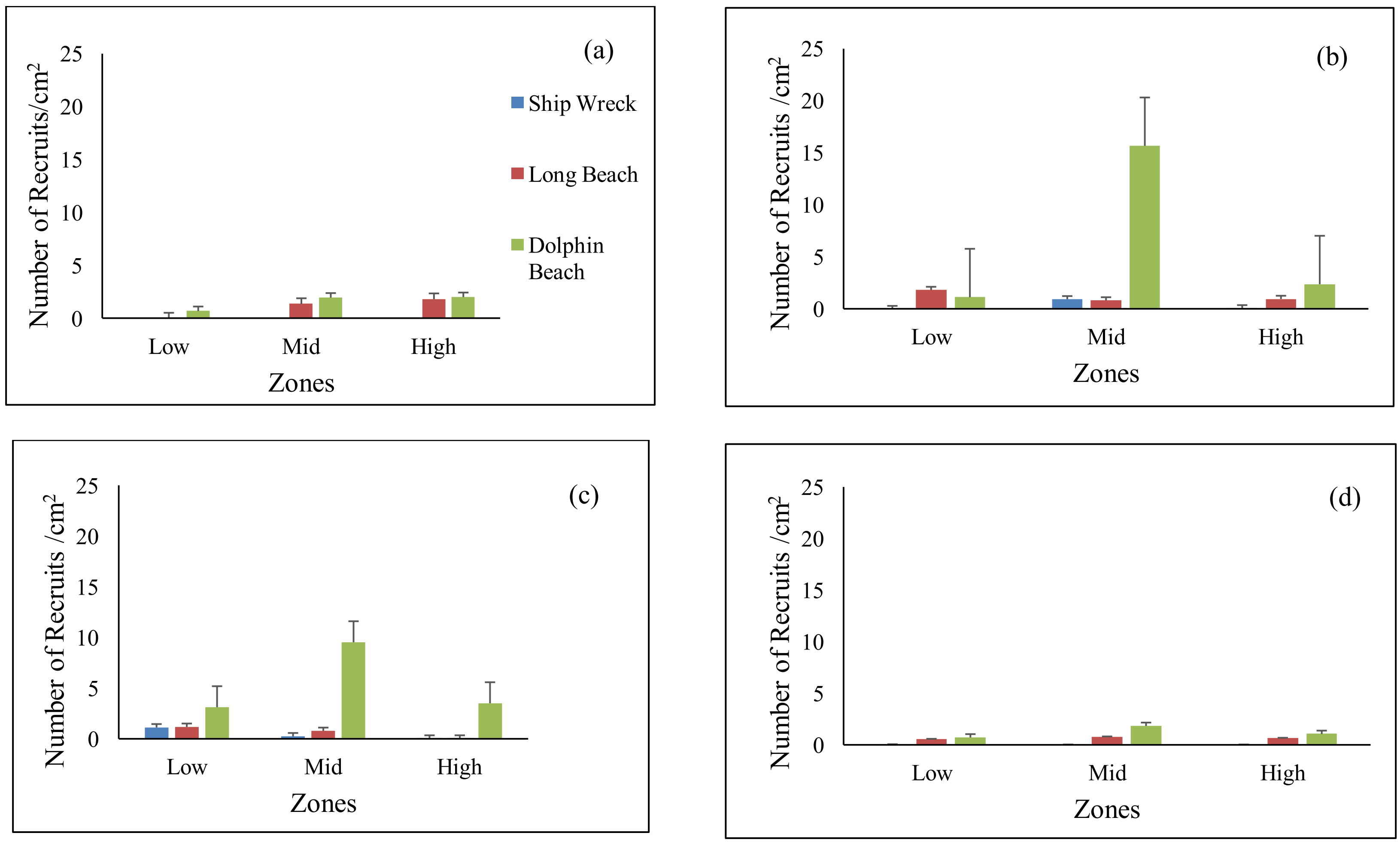


Figure 14: Mean number of recruits (+SE) of *M. galloprovincialis* in the different intertidal zones during (a) January (b) May (c) July and (d) September 2014. (Ship Wreck – blue; Long Beach - red; Dolphin Beach – green)

4.4 Population structure and Abundance of *Perna perna* and *Mytilus galloprovincialis*

Post hoc test comparisons regarding population structure and shore zones indicated no significant difference for *Perna perna* recruits between low- and high shore zones (Bonferroni $p = 0.593$) as well as between mid- and high shore zones ($p = 0.462$). Juvenile abundance of *P. perna* was not significantly different between low- and high shore zones ($p = 0.749$) at all sampling sites.

Perna perna adult abundance was significantly higher in the low shore zone compared to the mid- and high shore zones ($p < 0.0001$), while they were more abundant in the mid shore zone compared to the high shore zones ($p < 0.0001$) at all sites.

P. perna adult and juvenile mussels were more abundant at Dolphin Beach than at Long Beach (Figures 15 a and b). At Shipwreck no juveniles were recorded throughout the zones (Figure 15 c).

Recruits of *Mytilus galloprovincialis* showed no significant difference in abundance between low- and mid-shore zones ($p = 0.332$) and between mid- and high shore zones ($p = 0.418$). The abundance of juveniles was significantly different between low- and mid-shore zones ($p = 0.025$). No significant differences was found between low- and high shore zones ($p = 0.198$) as well as between low- and high shore zones ($p = 0.840$).

Adult *Mytilus galloprovincialis* reflected a significant difference in abundance between the low- and high shore zone ($p = 0.001$) and a significant difference between low – and mid-shore zones ($p = 0.001$).

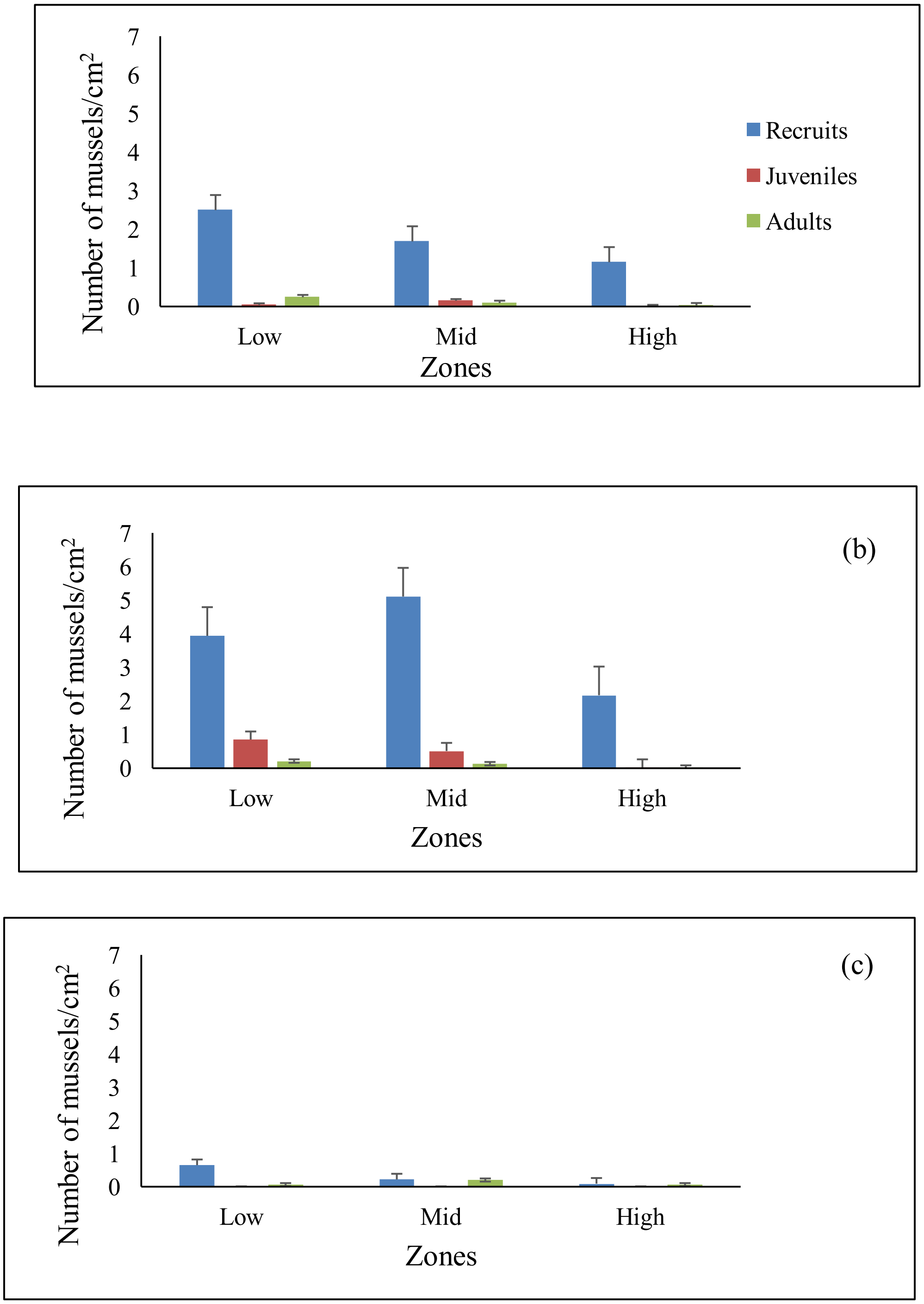


Figure 15: Mean number of mussels (+SE) P. *perna* (a) Long Beach; (b) Dolphin Beach and (c) Shipwreck (Recruits – blue; Juveniles – red; Adults – green)

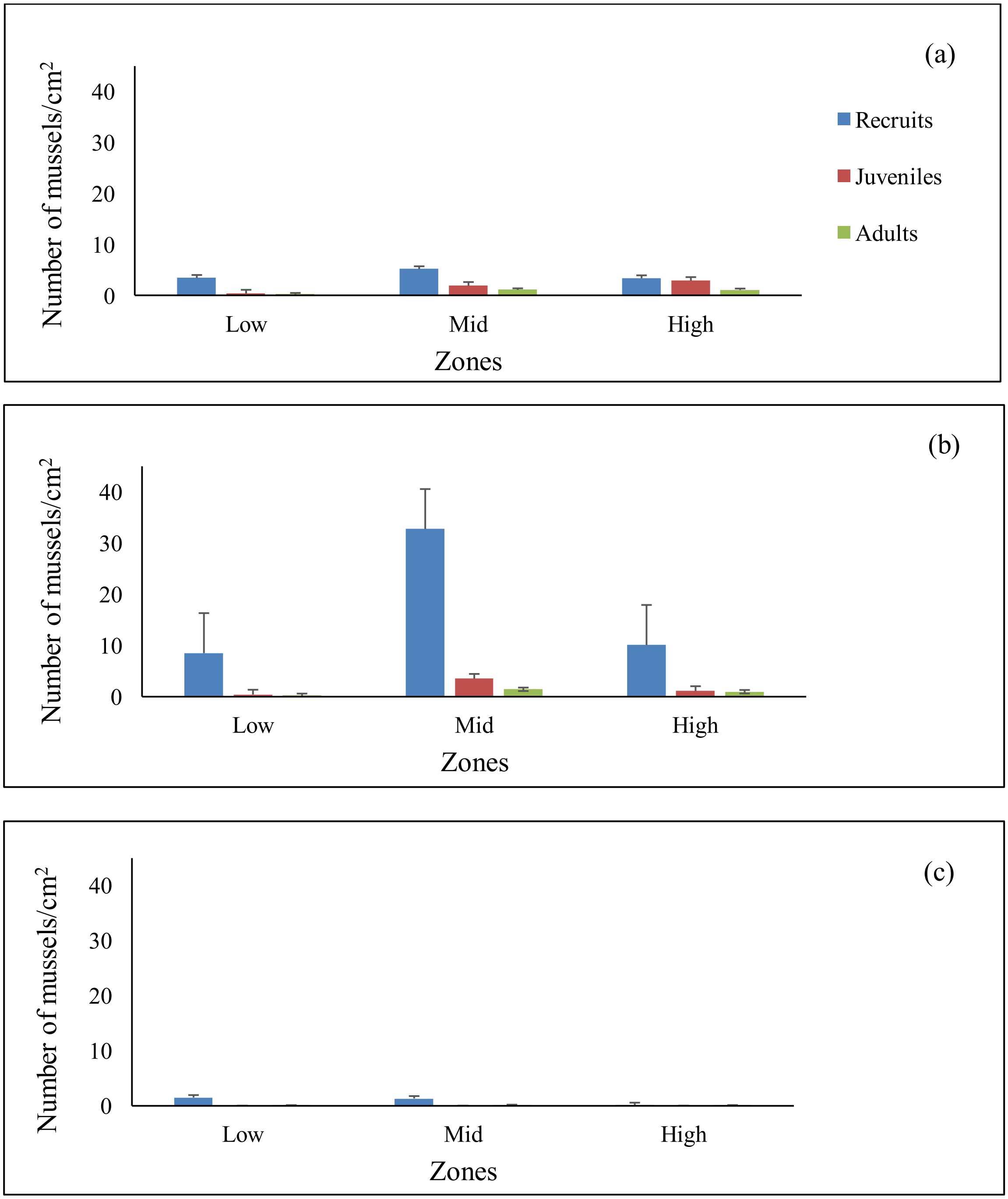


Figure 16: Mean number of mussels (+SE) *M. galloprovincialis* (a) Long Beach; (b) Dolphin Beach and (c) Shipwreck (Recruits – blue; Juveniles – red; Adults – green)

No significant difference was found between mid- and high shore zones ($p = 0.058$). Juveniles of *M. galloprovincialis* were more abundant at Dolphin Beach on the mid shore zone (Figure 16b). Long Beach recorded more juvenile and adult mussels throughout the zones (Figure 16c). At Shipwreck no juveniles of *M. galloprovincialis* were recorded (Figure 16c).

4.5 Condition Indices of *Perna perna* and *Mytilus galloprovincialis* adults

Multiple post hoc tests regarding the effect of season and location within the intertidal zone on the condition index (CI) of adults and juveniles were performed. This was tested only for Dolphin Beach and Long Beach, since Shipwreck had no juveniles. The Bonferroni test indicated a significant effect of season on the CI of adult *Perna perna* between January (summer) and September (spring) ($p < 0.0001$), between May (autumn) and September (spring) ($p = 0.005$) as well as between July (winter) and September (spring) ($p = 0.001$). *Mytilus galloprovincialis* CI showed no significant seasonal differences ($p = 1$).

The Bonferroni test also indicated a significant difference in CI for adult *P. perna* between low- and high shore zones ($p = 0.010$) as well between mid- and high shore zone ($p = 0.026$). The CI of *P. perna* was highest during September in all the zones at Long Beach. The lowest CI was recorded during January in the low shore zone (Figure 17a) at Long Beach. During May the highest CI was measured for *P. perna* at Dolphin Beach (Figure 18a).

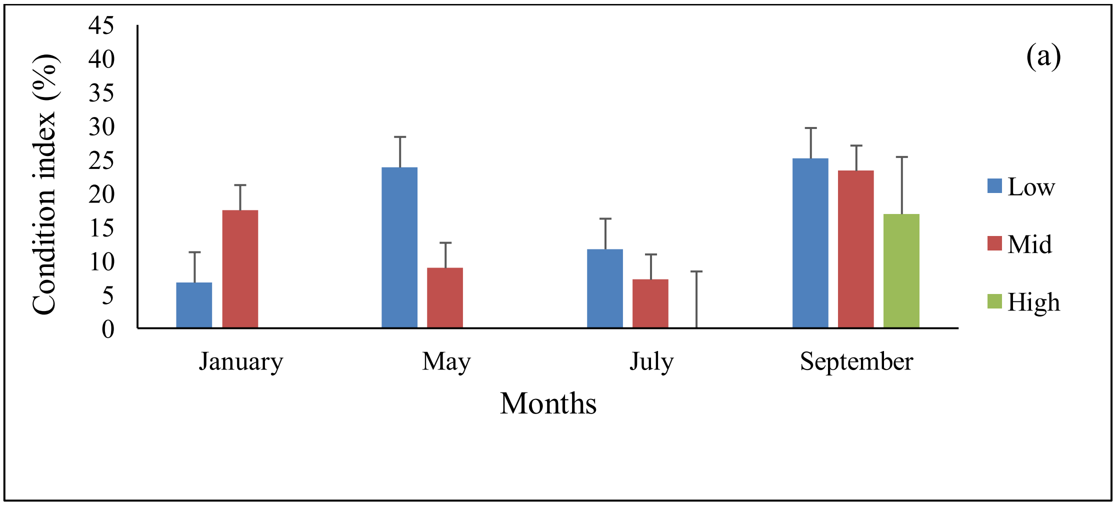
The CI for adult *M. galloprovincialis* indicated no significant difference between the shore zones ($p = 0.255$) throughout the year at all the sampling sites. At Long Beach and

Dolphin Beach adult mussels of *M. galloprovincialis* displayed the highest CI during September throughout the different zones (Figure 17b). During September adults of *M. galloprovincialis* in the mid- and high shore zones of Dolphin Beach and Long Beach had higher condition indices compared to those in the low shore zone. Generally *M. galloprovincialis* had a higher CI during all the seasons and within all the intertidal zones compared to *P. perna* at both beaches.

4.6 Condition Indices of *Perna perna* and *Mytilus galloprovincialis* juveniles

There was no significant differences in the condition indices of *Perna perna* and *Mytilus galloprovincialis* for the different seasons (Bonferroni, $p = 1$). There was also no significant seasonal differences in the condition indices of *P. perna* and that of *M. galloprovincialis* between different zones ($p = 0.928$ and $p = 0.084$, respectively).

Since there were no juveniles, no condition indices were calculated for *P. perna* during January and May at Long Beach (Figure 20a). The highest CI for *P. perna* was during May at Dolphin beach throughout the intertidal zones (Figure 20a).



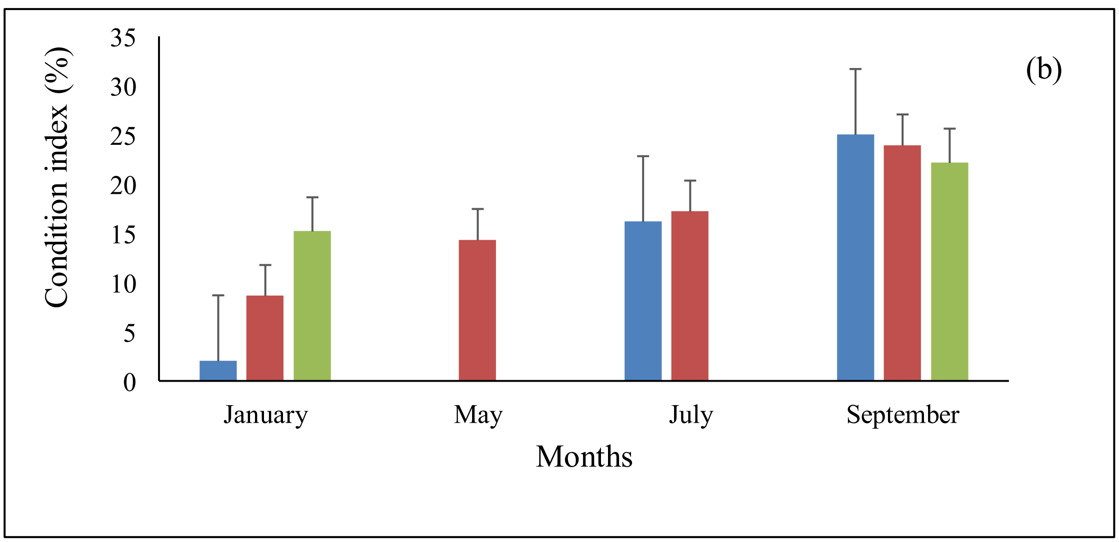


Figure 17: Mean Condition index (+SE) of (a) *P. perna* (adults) and (b) *M. galloprovincialis* (adults) at Long Beach (Low shore zone– blue; Mid shore zone – red; High shore zone – green)

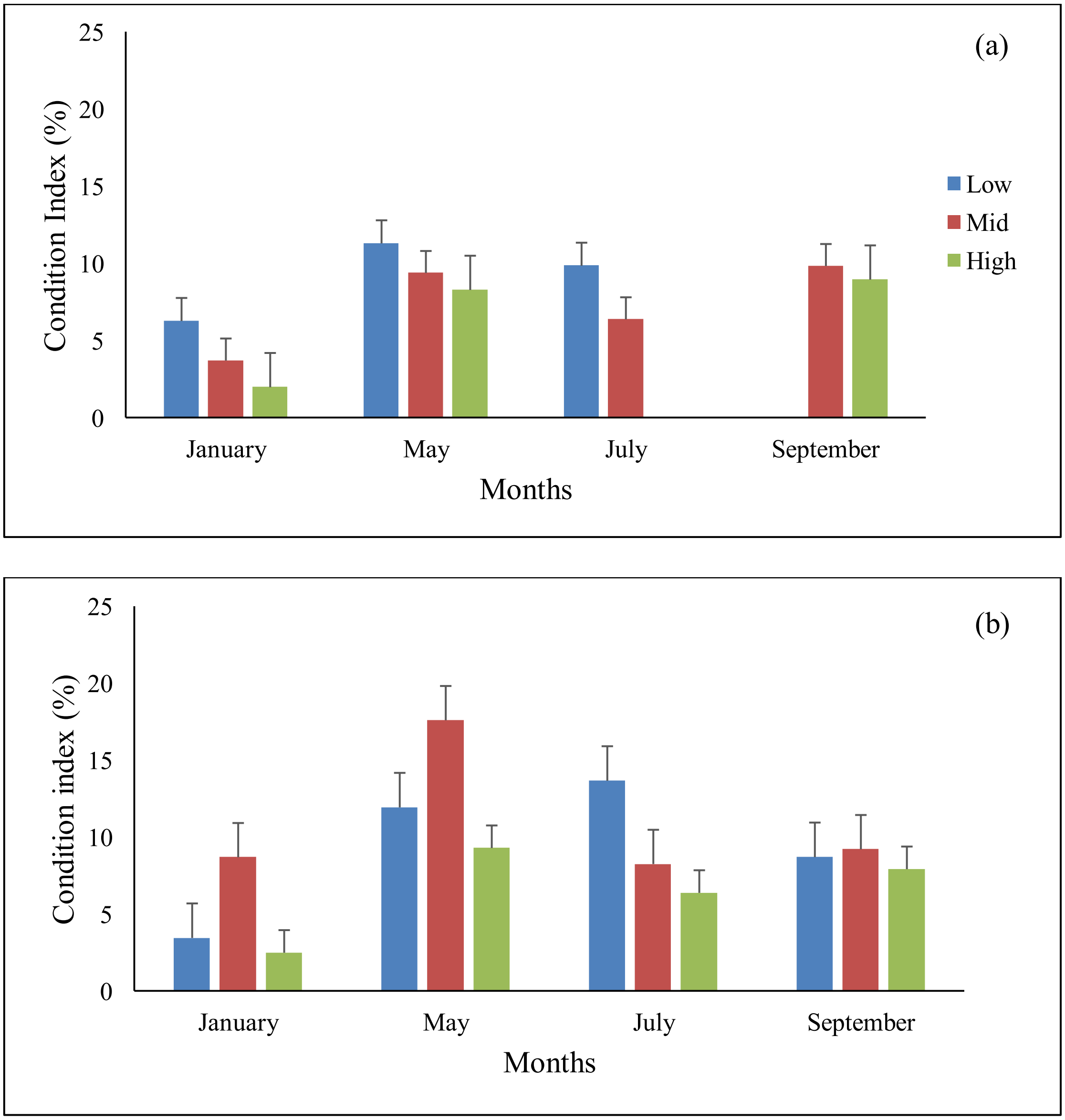


Figure 18: Mean Condition index (+SE) of (a) *P. perna* (adults) and (b) *M. galloprovincialis* (adults) at Dolphin Beach (low – blue; mid – red; high – green)

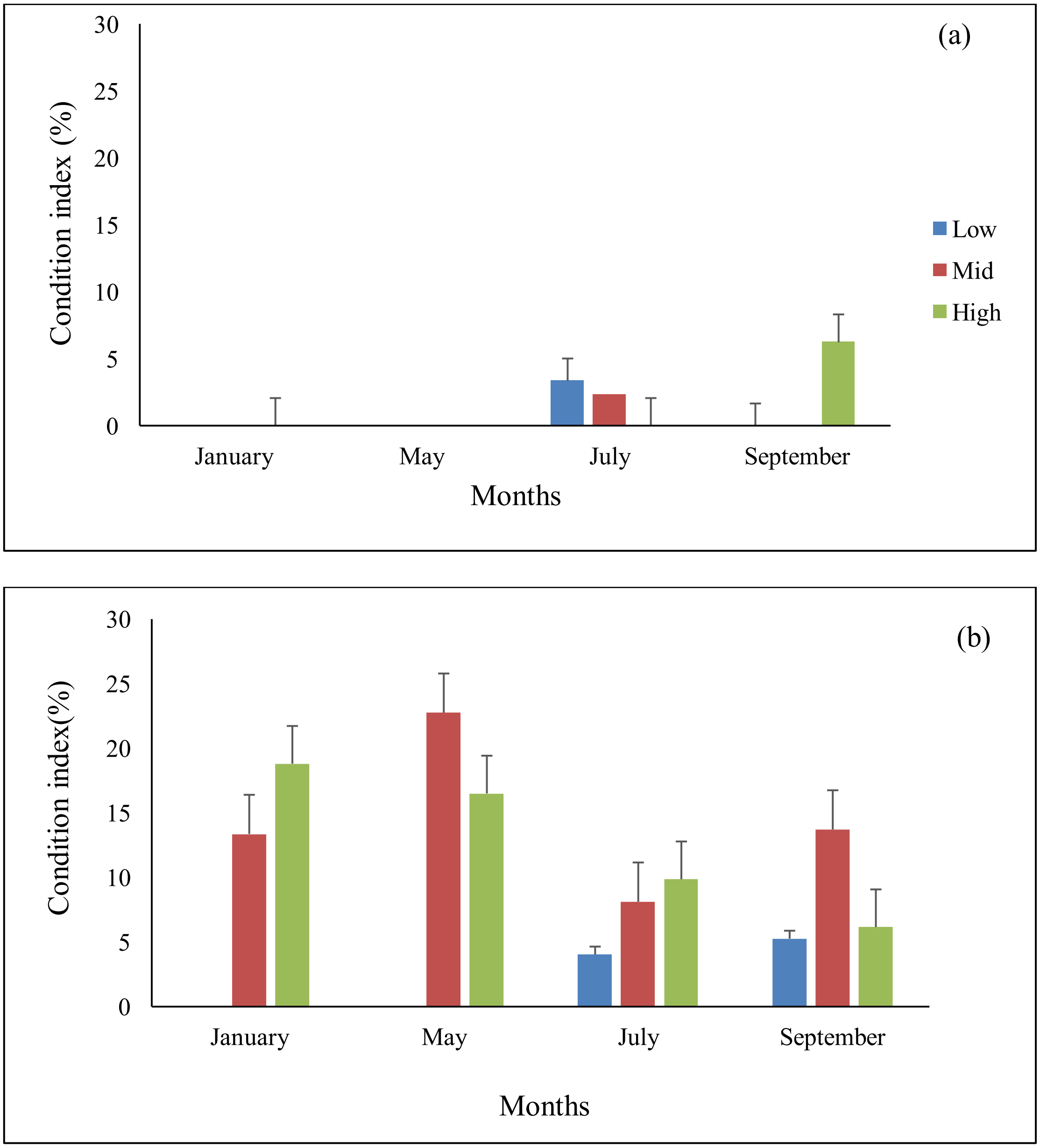


Figure 19: Mean Condition index (+SE) of (a) *P. perna* (juveniles) and (b) *M. galloprovincialis* (juveniles) at Long Beach (low – blue; mid – red; high – green)

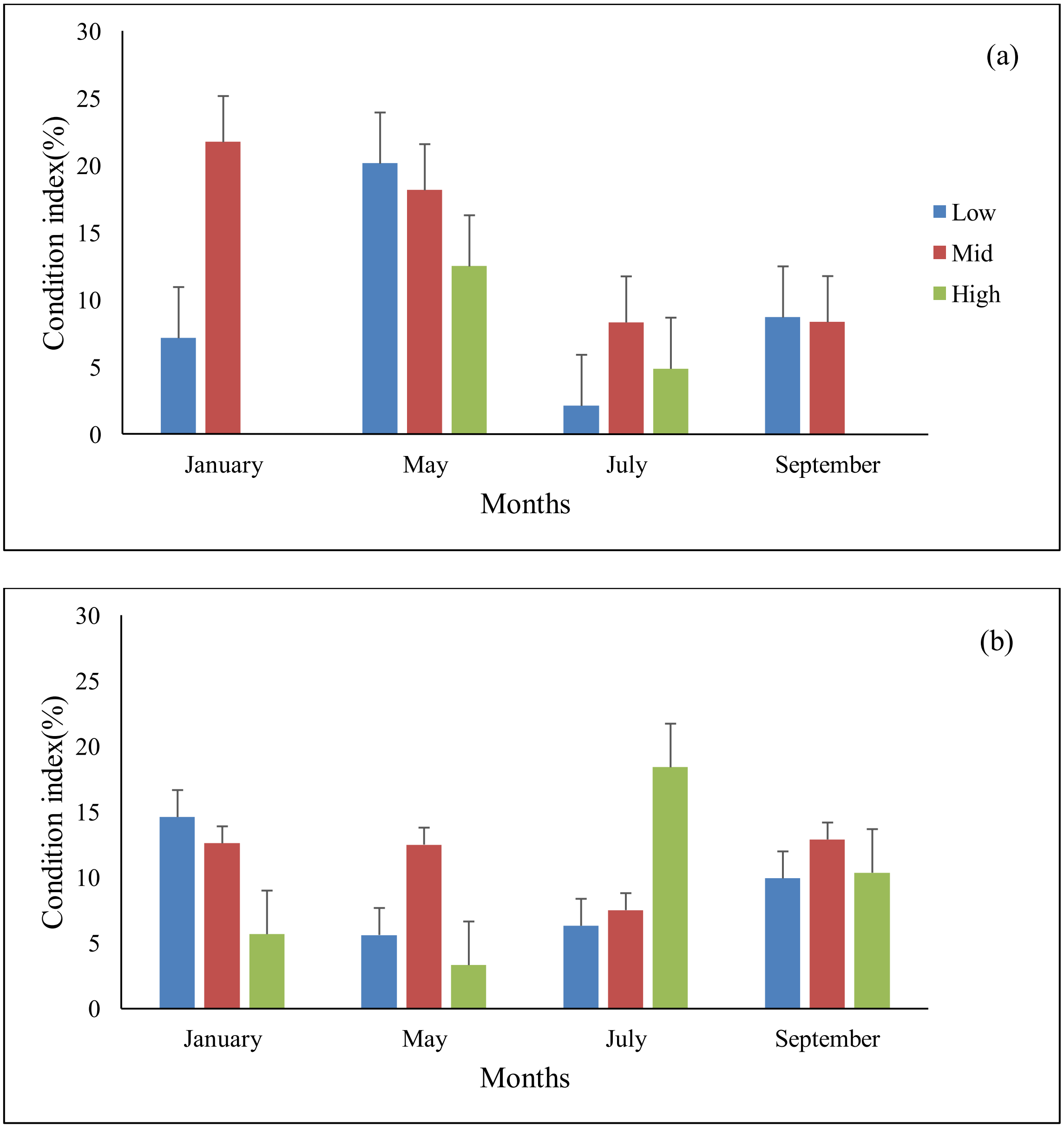


Figure 20: Mean Condition index (+SE) of (a) *P. perna* (juveniles) and (b) *M. galloprovincialis* (juveniles) at Dolphin Beach (low – blue; mid – red; high – green)

Chapter 5

Discussion

This study focussed on recruitment patterns and population structure of the indigenous mussel *Perna perna* and the alien mussel *Mytilus galloprovincialis* on the central Namibian coast. It is different from most of the previous studies conducted on the Namibian coast (Harris et al., 1998; Hammond & Griffiths, 2006; Reaugh-Flower et al., 2010, 2011) since it focussed on small-scale, localised patterns. Furthermore, there exists no data base that allows for the assessment of potential impact of *M. galloprovincialis* on indigenous mussel species. Hence, this study provides a baseline that can be utilised to accumulate data on the status of these two species in future to allow for monitoring.

5.1 Recruitment Patterns

Seasonal differences exist in the average ambient temperature on the central Namibian coast. During 2014 the average air temperature during summer (January) was 20.1°C, and decreased during autumn (May) to 15°C, winter (July) to 13.1°C and in spring (September) it was 13.9°C (http://www.namibiaweather.info). In addition inter-annual variability also exists within the Benguela ecosystem due to upwelling events and warm events (Bartholomae & van der Plas, 2007). This study was conducted only over a period of one year capturing four seasons and therefore it did not measure any possible inter-annual variation. Thus, although the seasonal recruitment on the central Namibian coast are discussed here, it is important to keep in mind that any patterns only reveal a snapshot over one year.

This study found that recruitment of *Perna perna*, varied significantly between the different months of sampling, while no seasonal variation in recruitment of *Mytilus galloprovincialis* was observed during 2014. Recruitment of *P. perna* was the highest during January and September. A study on the south coast of South Africa found that recruitment for *P. perna* occurs throughout the year and peaks from January to April (McQuaid & Lindsay, 2007). The difference in findings with results from the current study can be explained by different environmental conditions existing on the South coast of South Africa compared to the Namibian coast (Reaugh-Flower et al., 2011). Studies conducted on sites along the Namibian coast by Reaugh-Flower et al. (2011) found that season did not contribute as strongly as year on recruitment of *P. perna* and *M. galloprovincialis*. The current study therefore contradicts the findings of Reaugh-Flower et al. (2011) as far as *P. perna* is concerned, but agrees with their findings on recruitment of *M. galloprovincialis*. This demonstrates the importance of long term monitoring to capture and explain seasonal variation as well as inter-annual variability in recruitment.

McQuaid & Phillips (2007) observed that spawning of *P. perna* peaks in winter with the primary settlement taking place during April and between September and November. Primary settlement takes place into filamentous algae and only later the larvae will settle on another substrate. Several studies (Erlandsson et al., 2006; Bownes, 2005) have reported initial larval settlement on filamentous algae and growth up to 2 mm before they migrate into mussel beds. It is essential that future investigations on the Namibian coast incorporate elements of larval settlement into recruitment studies.

Reaugh-Flower et al. (2011) reported that recruitment for both *P. perna* and *M. galloprovincialis* were not synchronised on Long Beach South, but was synchronised on Long Beach North (Reaugh-Flower et al. 2011). These two locations are approximately 2-4 km apart and their finding demonstrates that differences in recruitment patterns can occur on a small scale. Similar results were found in the current study, since recruitment patterns on Dolphin Beach and Long Beach, which are 2 km apart, were significantly different. This implies that it is essential to conduct small scale studies when investigating the impacts of alien species on the Namibian coast.

The findings of the current study are in agreement with the study of Bownes and McQuaid (2006) on the south coast of South Africa, since they also found that recruitment of *P. perna* occurs during spring and summer. The higher temperatures during summer and spring can be one of the reasons for the timing of recruitment for *P. perna* as it is considered a warm water species (Bownes and McQuaid, 2006). *M. galloprovincialis* is considered more a cold temperate species and can tolerate temperatures between 17 and 20°C for growth of larvae (Anestis et. al, 2007). During summer months it is most likely that *P. perna* is a stronger competitor for space and might restrict the settling of *M. galloprovincialis*. During winter months *M. galloprovincialis* might be the stronger competitor for space (Bownes, 2005).

Based on the abundance of recruits, recruitment of *P. perna* occurs in the low shore zone, while recruitment of *M. galloprovincialis* occurs in the mid shore zone. This can again be explained by the morphological and physiological differences between the two species. At the middle zone the wave action is less and exposure to desiccation greater, while on the lower zone wave action is considered stronger (Steffani & Branch, 2003; Erlandsson et al., 2006). This could also be from the stronger byssal attachment of *P. perna* (Erlandsson et al., 2006) and the higher tolerance of *M. galloprovincialis* to desiccation (Robinson et al., 2007; Rius & McQuaid, 2009). Steffani & Branch (2003) and Erlandsson et.al. (2006) explains this by a higher mortality of *M. galloprovincialis* recruits on the low shore zone because of weaker attachment strength and possibly also predation. The wider shell as well as the weaker byssal attachment could possibly explain the zonation of the two species (Zardi, et.al. 2006).

5.2 Population Structure

Juveniles of *Perna perna* displayed no significant difference between the different intertidal zones, while for *Mytilus galloprovincialis* the abundance of juveniles was significantly different between the different zones. Juvenile abundance also exhibited significant seasonal differences for *M. galloprovincialis,* but not for *P. perna*. This may be explained in the mid shore zone by competition and in the low shore zone by predation results in juvenile abundance of *M. galloprovincialis* to be seasonal (Steffani & Branch, 2003). Another reason could be that favourable conditions such as availability of food, which is mainly attained during favourable upwelling conditions, were present during time of settlement (McQuaid et al., 2000).

M. galloprovincialis juveniles were abundant throughout the year at Dolphin Beach and Long Beach, while *P. perna* juveniles were present in high numbers only at Dolphin Beach and not at Long Beach. However, this was not the case for Shipwreck, as only a few juveniles could be found throughout the year.

The abundance of *P. perna* adults displayed a significant difference between all the shore zones (low, mid and high). They were more abundant on the low shore zone, while *M. galloprovincialis* was significantly more abundant on the mid- and high shore zones. Several studies confirmed this finding, as *P. perna* maintained spatial dominance on the lower shore and *M. galloprovincialis* on the upper shore (Hockey & Van Erkom Schurink, 1992; Bownes & McQuaid, 2006; Rius & McQuaid, 2006). This can be attributed to the stronger byssal threads of *P. perna* in comparison to the weaker attachment strength of *M. galloprovincialis* (Erlandsson et al., 2006; Zardi et al., 2006). Since wave action is stronger at the low shore zone compared to the mid and upper shore zones (Zardi et.al.,2006) the stronger byssal threads of *P. perna* allows them to better cope with the stronger wave action in the low shore zone. McQuaid et al. (2000) found that densities of adults and juveniles of *P. perna* were significantly affected by tidal height, the numbers will decrease towards the high shore zone.

McQuaid and Lindsay (2007), found that the number of adult *P. perna* were more abundant than the juveniles, which is in agreement with the results of the current study. However, for *M. galloprovincialis* adults were less abundant than juveniles. This is possibly because adults provide suitable settlement areas for juveniles in the form of byssal threads and in multi layered mussel beds as was observed at Dolphin Beach.

Adults on the mid- and high shore zones occurred in clumps rather than on continuous beds and juveniles were part of these clumps.

At Long Beach the number of *P. perna* adults were lower than the adults for *M. galloprovincialis,* especially on the mid shore zone. Since the two species co-exist in the mid shore zone it can be that *M. galloprovincialis* is a better competitor for space and together with its ability to tolerate desiccation for longer periods (Van Erkom Schurink, 1992) it can be more successful on the mid shore zone. *P. perna* occupied more the lower shore zone due to its lower tolerance towards desiccation and *M. galloprovincialis* occupied the mid and high shore zones as it is more tolerant towards emersion and desiccation (Hockey & Van Erkom Schurink, 1992).The low abundance of *P. perna* in the high shore zone can be explained by low recruitment rates of individuals that were unable to survive (Bownes, 2005).

5.3 Condition Indices of *Mytilus galloprovincialis* and *Perna perna*

The condition indices of Bivalves exhibit seasonal variation in terms of water temperature, food availability and the reproductive cycle (Gosling, 2003). Seasonal patterns should reveal the best time for harvesting and marketing.

This study found that there was a significant seasonal difference in the condition index (CI) of adult *Perna perna* between the different shore zones, but not for the CI of adult *Mytilus galloprovincialis*. The CI of *P. perna* in the lower zone was high and exceeded 25%. As the lower zone is covered with water for longer periods, the feeding time where mussels feed will be longer compared to the feeding time in the high shore zone, which is exposed for longer periods. Steffani and Branch (2003a) also explained the higher CI of *M. galloprovincialis* on semi-exposed sites, where stronger currents and waves are experienced, by the greater food availability at such sites due to higher water and hence, plankton influx.

Rius & McQuaid (2006) found higher CI values for *P. perna* than *M. galloprovincialis* in the low- and mid- zones, but no significant differences in the high zone. Thus *P. perna* performed better than *M. galloprovincialis* in the low shore zones, while *M. galloprovincialis* performed better in the high shore zone.

The maximum CI values for adults were obtained during September for both *M. galloprovincialis* and *P. perna* on all the shore zones at Long Beach and Dolphin Beach. Yildiz et al. (2006) in his study conducted on the coast of Chile also found that during September the meat content of *M. galloprovincialis* was the best before spawning takes place between September and October. Robinson et al. (2008) also reported that *M. galloprovincialis* has two spawning seasons along the south coast that are in agreement with results from reported form Yildiz et al. (2006). These spawning seasons are between March and April as well as September and October (Van Erkom Schurink & Griffiths, 1991). There is a need to conduct spawning studies of both mussel species on the Namibian coast and investigate possible effects on the condition index of the mussels.

Condition indices for juveniles of *P. perna* and *M. galloprovincialis* showed no differences between seasons as well as between the intertidal zones. However, it is important to note that the sample size for assessing the CI of juveniles was relatively small and could have affected the data analysis.

Chapter 6

Conclusions and Recommendations

6.1 Conclusions

This study was only a snap shot over a one year period of the population structure and recruitment patterns of *Mytilus galloprovincialis* and *Perna perna* along the central coast of Namibia. Considerable spatial and temporal variation in both recruitment patterns and population structure of the two species were studied.

The seasonal recruitment of *P. perna* observed in this study appeared to be more or less consistent with previous reports for the south coast of South Africa. Recruitment of *P. perna* occurs in summer, while recruitment of *M. galloprovincialis* occurs throughout the year. In the low shore zone the higher recruitment rates of *P. perna* observed during summer indicated a better competitive advantage over *M. galloprovincialis*.

The two most important scales of variation in terms of the distribution and abundance of *P. perna* and *M. galloprovincialis* were between the different shore zones (low, mid and high) and between the different sampling sites (Long Beach, Dolphin Beach and Shipwreck). *P. perna* showed greater abundance on the low shore zone and *M. galloprovincialis* on the mid- and high shore zone. Both species indicated co-existence on the mid shore zone. Overall, mussel abundance of both species was higher at Dolphin Beach and Long Beach than at Shipwreck. Results indicated that recruitment patterns are very localized and specific for each sampling site. It is therefore essential to perform small-scale studies when investigating recruitment patterns of mussels on the Namibian coast.

The high abundance of *Mytilus galloprovincialis* found at Dolphin Beach and Long Beach is alarming and there is a need for management strategies to protect the indigenous mussel *P. perna* at these sites. Furthermore, the spawning periodicity and patterns for these mussels should be determined.

The condition index, which relates flesh weight to shell weight, was significantly higher for *P. perna* on the low shore zone, while for *M. galloprovincialis* it was significantly higher in the mid- and high shore zones. The condition indices for *P. perna* and *M. galloprovincialis* were significantly higher in September compared to other months. Since, the condition index is an indication of the optimum time for harvesting, it is recommended that, as in the case of Chile, the harvesting time should be September when the flesh weight relative to shell weight is the maximum. The biggest seasonal difference found in condition indices of both species was on the low shore zone.

Currently it is difficult to conclude if there is a possible invasion of *M. galloprovincialis* on the central coast of Namibia, since this study does not capture inter-annual variation. However, the abundant recruits of *M. galloprovincialis* at Dolphin Beach observed during this study, might be a sign of possible invasion which needs to be monitored. Although the numbers of *M. galloprovincialis* were clearly higher than the numbers of *P. perna* at all the sites, one study will not be enough to make such a conclusion.

6.2 Recommendations

Monitoring of population structure and recruitment patterns should be an on-going process on all the rocky shores of Namibia. Long term studies will be the only solution to really test the hypothesis that *Mytilus galloprovincialis* can outcompete and replace *Perna perna* on the Namibian coasts. Recruits should be measured individually so that a distinction can be made between primary and secondary recruits to accurately determine the recruitment rates of both species. Mortality rates should also be included in future studies to test the hypothesis that *M. galloprovincialis* are limited by post settlement effects on the lower shore.

The effects of environmental factors on these mussels should be investigated in more detail in order to substantiate the effects of physical parameters on the biological state o relationships better.

Further studies would be necessary to confirm these results and to corroborate that the situation found on South African shores could be extrapolated to the whole of the Namibian shore.

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Appendices

Appendix 1: Seasonal recruitment patterns of *Perna perna*

Seasonal Recruitment *Perna perna*			
Season	Ship Wreck	Long Beach	Dolphin Beach
January	0.02	0.95	1.34
May	0.04	0.08	0.48
July	0.24	0.72	0.84
September	0.08	0.66	1.28

Appendix 2: Seasonal recruitment patterns of *Mytilus galloprovincialis*

Seasonal Recruitment *Mytilus galloprovincialis*			
Season	Ship Wreck	Long Beach	Dolphin Beach
January	0.01	0.86	1.35
May	0.31	1.29	5.73
July	0.55	0.77	5.12
September	0.24	1.12	3.88

Appendix 3: Table Class and Zone distribution of sampling sites

Long Beach		Zone: Lower	Zone: Middle	Zone: Upper	**Total**
P. perna	recruits	1009	507	229	**1745**
M. galloprovincialis		1402	1564	688	**3654**
	juveniles	15	45	1	**61**
		183	593	590	**1366**
	adults	95	26	6	**127**
		110	354	227	**691**
		1119	578	236	**1933**
	Total	1695	2511	1505	**5711**

Dolphin Beach		Zone: Lower	Zone: Middle	Zone: Upper	Total
P. perna	recruits	1956	1534	434	**3924**
M. galloprovincialis		4254	9821	2005	**16080**
	juveniles	423	153	4	**580**
		212	1057	223	**1492**
	adults	104	35	6	**145**
		141	436	196	**773**
Total	*P. perna*	2483	1722	444	**4649**
		4607	11314	2424	**18345**

Shipwreck		Zone: Lower	Zone: Middle	Zone: Upper	Total
P. perna	recruits	390	109	26	**525**
M. galloprovincialis		895	626	31	**1552**
	juveniles	4	1	0	**5**
		2	1	0	**3**
	adults	37	98	17	**152**
		42	82	24	**148**
Total	*P. perna*	431	208	43	**682**
		939	709	55	**1703**

Appendix 4: Population Structure *P. perna* & *M. galloprovincialis* Long Beach

Long Beach January 2014				
		Low	Mid	High
Perna	Recruits	0.615	1.287	1.115
	Juveniles	0.005	0.14	0
	Adults	0.105	0.006	0
Mytilus	Recruits	0	1.37	1.83
	Juveniles	0.003	0.827	1.71
	Adults	0.003	0.967	0.39
Long Beach May 2014				
		Low	Mid	High
Perna	Recruits	0.123	0.0667	0,015
	Juveniles	0	0	0
	Adults	0.043	0.027	0
Mytilus	Recruits	1.818	0.817	0.985
	Juveniles	0	0.77	1.095
	Adults	0	0.79	0.525
Long Beach July 2014				
		Low	Mid	High
Perna	Recruits	1.36	0.32	0.01

	Juveniles	0.033	0.003	0
	Adults	0.053	0.013	0.01
Mytilus	Recruits	1.17	0.767	0.01
	Juveniles	0.438	0.347	0.12
	Adults	0.203	0.213	0.18
Long Beach September 2014				
		Low	Mid	High
Perna	Recruits	0.425	0.007	0.005
	Juveniles	0	0.007	0.005
	Adults	0.038	0.04	0.025
Mytilus	Recruits	0.518	1.695	0.615
	Juveniles	0.018	0.033	0.025
	Adults	0.07	0.08	0.04

Appendix 5: Population Structure *P. perna* & *M. galloprovincialis* Dolphin Beach

January Dolphin Beach					
January		Low	Mid	High	
Perna	Recruits	1.284	1.907	0.605	
	Juveniles	0.78	0.11	0	
	Adults	0.158	0.027	0.01	
Mytilus	Recruits	0.71	1.98	2.025	
	Juveniles	0.286	1.15	0.335	
	Adults	0.1	0.48	0.27	
May Dolphin Beach 2014					
May		Low	Mid	High	
Perna	Recruits	0.084	1.28	0.25	
	Juveniles	0.012	0.393	0.005	
	Adults	0.028	0.063	0.015	
Mytilus	Recruits	1.126	15.637	2.375	
	Juveniles	0.006	1.637	0.315	
	Adults	0.016	0.597	0.325	
Dolphin Beach July 2014					
July		Low	Mid	High	
Perna	Recruits	0.584	1.39	0.64	

	Juveniles	0.052	0.003	0.015	
	Adults	0.022	0.02	0	
Mytilus	Recruits	3.102	9.53	3.53	
	Juveniles	0.12	0.667	0.395	
	Adults	0.14	0.31	0.285	
Dolphin Beach September 2014					
September		Low	Mid	High	
Perna	Recruits	1.96	0.537	0.675	
	Juveniles	0.002	0.003	0	
	Adults	0	0.007	0.005	
Mytilus	Recruits	3.57	5.59	2.095	
	Juveniles	0.012	0.06	0.07	
	Adults	0.026	0.067	0.1	

Appendix 6: **Population Structure *P. perna* & *M. galloprovincialis* Shipwreck**

Shipwreck January 2014				
January		Low	Mid	High
Perna	Recruits	0.043	0	0
	Juveniles	0	0	0
	Adults	0.028	0.026	0.01
Mytilus	Recruits	0.03	0	0
	Juveniles	0	0	0
	Adults	0.05	0.042	0
	Shipwreck May 2014			
May		Low	Mid	High
Perna	Recruits	0.022	0.05	0.05
	Juveniles	0	0	0
	Adults	6	0.036	0.03
Mytilus	Recruits	0.033	0.754	0.073
	Juveniles	0	0.002	0
	Adults	0.003	0.028	0.02
	Shipwreck July 2014			
July		Low	Mid	High
Perna	Recruits	0.42	0.138	0.033
	Juveniles	0.003	0.002	0.000

	Adults	0.012	0.044	0.017
Mytilus	Recruits	1.097	0.24	0.007
	Juveniles	0.003	0	0
	Adults	0.012	0.026	0.01

Shipwreck September 2014				
September		Low	Mid	High
Perna	Recruits	0.165	0.03	0.003
	Juveniles	0	0	0
	Adults	0.012	0.09	0
Mytilus	Recruits	0.332	0.258	0.023
	Juveniles	0	0	0
	Adults	0.005	0.068	0.01

Appendix 7: Condition Indices of *P. perna* and *M. galloprovincialis*

Condition index *Perna perna* (Adults)			
Long Beach	Zones		
Seasons	Low	Mid	High
January	6.8	17.5	
May	23.88	8.95	
July	11.76	7.23	0
September	25.2	23.35	16.96

Condition index *Perna perna* (Adults)			
Dolphin Beach	Zones		
Seasons	Low	Mid	High
January	6.29	3.73	2
May	11.32	9.4	8.3
July	9.87	6.4	
September		9.85	8.97

Condition index Perna perna (Juveniles)			
Long Beach	Zones		
Seasons	Low	Mid	High
January		0	0
May			
July	3.36	2.36	0
September	0		6.25

Condition index *Perna perna* (Juveniles)			
Dolphin Beach	Zones		
Seasons	Low	Mid	High
January	7.16	21.75	
May	20.15	18.17	12.5
July	2.12	8.33	4.88
September	8.7	8.35	

Appendix 8: Multivariate Tests comparisons

Multivariate Tests[a]

Species	Effect		Value	F	Hypothesis df	Error df	Sig.
Perna	Intercept	Pillai's Trace	.983	94.282[b]	5.000	8.000	.000
		Wilks' Lambda	.017	94.282[b]	5.000	8.000	.000
		Hotelling's Trace	58.926	94.282[b]	5.000	8.000	.000
		Roy's Largest Root	58.926	94.282[b]	5.000	8.000	.000
	Species	Pillai's Trace	.000	.[b]	.000	.000	.
		Wilks' Lambda	1.000	.[b]	.000	10.000	.
		Hotelling's Trace	.000	.[b]	.000	2.000	.
		Roy's Largest Root	.000	.000[b]	5.000	7.000	1.000
	Season	Pillai's Trace	1.889	3.399	15.000	30.000	.002
		Wilks' Lambda	.032	3.735	15.000	22.486	.002
		Hotelling's Trace	8.617	3.830	15.000	20.000	.003
		Roy's Largest Root	6.502	13.005[c]	5.000	10.000	.000
	Zone	Pillai's Trace	1.481	5.130	10.000	18.000	.001
		Wilks' Lambda	.028	8.040[b]	10.000	16.000	.000
		Hotelling's Trace	16.857	11.800	10.000	14.000	.000
		Roy's Largest Root	15.681	28.226[c]	5.000	9.000	.000
	Species * Season	Pillai's Trace	.000	.[b]	.000	.000	.
		Wilks' Lambda	1.000	.[b]	.000	10.000	.
		Hotelling's Trace	.000	.[b]	.000	2.000	.
		Roy's Largest Root	.000	.000[b]	5.000	7.000	1.000
	Species * Zone	Pillai's Trace	.000	.[b]	.000	.000	.
		Wilks' Lambda	1.000	.[b]	.000	10.000	.
		Hotelling's Trace	.000	.[b]	.000	2.000	.
		Roy's Largest Root	.000	.000[b]	5.000	7.000	1.000
	Season * Zone	Pillai's Trace	1.658	.992	30.000	60.000	.496
		Wilks' Lambda	.045	1.324	30.000	34.000	.213
		Hotelling's Trace	7.993	1.705	30.000	32.000	.070
		Roy's Largest Root	6.342	12.684[c]	6.000	12.000	.000
	Species * Season * Zone	Pillai's Trace	.000	.[b]	.000	.000	.
		Wilks' Lambda	1.000	.[b]	.000	10.000	.
		Hotelling's Trace	.000	.[b]	.000	2.000	.
		Roy's Largest Root	.000	.000[b]	5.000	7.000	1.000
Mytilus	Intercept	Pillai's Trace	.946	28.205[b]	5.000	8.000	.000
		Wilks' Lambda	.054	28.205[b]	5.000	8.000	.000
		Hotelling's Trace	17.628	28.205[b]	5.000	8.000	.000
		Roy's Largest Root	17.628	28.205[b]	5.000	8.000	.000
	Species	Pillai's Trace	.000	.[b]	.000	.000	.
		Wilks' Lambda	1.000	.[b]	.000	10.000	.
		Hotelling's Trace	.000	.[b]	.000	2.000	.
		Roy's Largest Root	.000	.000[b]	5.000	7.000	1.000
	Season	Pillai's Trace	1.239	1.408	15.000	30.000	.206
		Wilks' Lambda	.114	1.795	15.000	22.486	.102
		Hotelling's Trace	4.848	2.155	15.000	20.000	.055
		Roy's Largest Root	4.194	8.388[c]	5.000	10.000	.002
	Zone	Pillai's Trace	1.101	2.207	10.000	18.000	.069
		Wilks' Lambda	.133	2.780[b]	10.000	16.000	.033
		Hotelling's Trace	4.733	3.313	10.000	14.000	.020
		Roy's Largest Root	4.326	7.786[c]	5.000	9.000	.004
	Species * Season	Pillai's Trace	.000	.[b]	.000	.000	.
		Wilks' Lambda	1.000	.[b]	.000	10.000	.
		Hotelling's Trace	.000	.[b]	.000	2.000	.
		Roy's Largest Root	.000	.000[b]	5.000	7.000	1.000
	Species * Zone	Pillai's Trace	.000	.[b]	.000	.000	.
		Wilks' Lambda	1.000	.[b]	.000	10.000	.
		Hotelling's Trace	.000	.[b]	.000	2.000	.
		Roy's Largest Root	.000	.000[b]	5.000	7.000	1.000
	Season * Zone	Pillai's Trace	1.729	1.057	30.000	60.000	.417
		Wilks' Lambda	.068	1.082	30.000	34.000	.410
		Hotelling's Trace	4.899	1.045	30.000	32.000	.450
		Roy's Largest Root	3.291	6.581[c]	6.000	12.000	.003
	Species * Season * Zone	Pillai's Trace	.000	.[b]	.000	.000	.
		Wilks' Lambda	1.000	.[b]	.000	10.000	.
		Hotelling's Trace	.000	.[b]	.000	2.000	.
		Roy's Largest Root	.000	.000[b]	5.000	7.000	1.000

a. Design: Intercept + Species + Season + Zone + Species * Season + Species * Zone + Season * Zone + Species * Season * Zone

b. Exact statistic

c. The statistic is an upper bound on F that yields a lower bound on the significance level.

Appendix 9: Bonferroni Test Analysis – Shore Zones

Multiple Comparisons

Bonferroni

Species	Dependent Variable	(I) Zone	(J) Zone	Mean Difference (I-J)	Std. Error	Sig.	95% Confidence Interval Lower Bound	95% Confidence Interval Upper Bound
Perna	Recruit L	Lower	Middle	-.0012	.02576	1.000	-.0729	.0704
			Upper	.0346	.02576	.614	-.0370	.1062
		Middle	Lower	.0012	.02576	1.000	-.0704	.0729
			Upper	.0358	.02576	.569	-.0358	.1074
		Upper	Lower	-.0346	.02576	.614	-.1062	.0370
			Middle	-.0358	.02576	.569	-.1074	.0358
	Recruit L	Lower	Middle	.0052	.02934	1.000	-.0763	.0867
			Upper	.0355	.02934	.749	-.0461	.1170
		Middle	Lower	-.0052	.02934	1.000	-.0867	.0763
			Upper	.0303	.02934	.967	-.0513	.1118
		Upper	Lower	-.0355	.02934	.749	-.1170	.0461
			Middle	-.0303	.02934	.967	-.1118	.0513
	Recruit L	Lower	Middle	.0253*	.00422	.000	.0135	.0370
			Upper	.0295*	.00422	.000	.0178	.0413
		Middle	Lower	-.0253*	.00422	.000	-.0370	-.0135
			Upper	.0043	.00422	.999	-.0075	.0160
		Upper	Lower	-.0295*	.00422	.000	-.0413	-.0178
			Middle	-.0043	.00422	.999	-.0160	.0075
	Recruit L	Lower	Middle	.0433	.13624	1.000	-.3354	.4220
			Upper	.6440*	.13624	.001	.2653	1.0227
		Middle	Lower	-.0433	.13624	1.000	-.4220	.3354
			Upper	.6007*	.13624	.003	.2220	.9794
		Upper	Lower	-.6440*	.13624	.001	-1.0227	-.2653
			Middle	-.6007*	.13624	.003	-.9794	-.2220
	Recruit L	Lower	Middle	-.0937	.33569	1.000	-1.0267	.8394
			Upper	.1997	.33569	1.000	-.7334	1.1327
		Middle	Lower	.0937	.33569	1.000	-.8394	1.0267
			Upper	.2933	.33569	1.000	-.6397	1.2264
		Upper	Lower	-.1997	.33569	1.000	-1.1327	.7334
			Middle	-.2933	.33569	1.000	-1.2264	.6397
Mytilus	Recruit L	Lower	Middle	-.0755	.04721	.408	-.2067	.0557
			Upper	-.0174	.04721	1.000	-.1487	.1138
		Middle	Lower	.0755	.04721	.408	-.0557	.2067
			Upper	.0580	.04721	.727	-.0732	.1893
		Upper	Lower	.0174	.04721	1.000	-.1138	.1487
			Middle	-.0580	.04721	.727	-.1893	.0732
	Recruit L	Lower	Middle	-.1794*	.04798	.008	-.3128	-.0460
			Upper	-.1149	.04798	.101	-.2483	.0184
		Middle	Lower	.1794*	.04798	.008	.0460	.3128
			Upper	.0645	.04798	.612	-.0689	.1978
		Upper	Lower	.1149	.04798	.101	-.0184	.2483
			Middle	-.0645	.04798	.612	-.1978	.0689
	Recruit L	Lower	Middle	-.1160*	.02062	.000	-.1733	-.0587
			Upper	-.0587*	.02062	.044	-.1160	-.0014
		Middle	Lower	.1160*	.02062	.000	.0587	.1733
			Upper	.0573	.02062	.050	-.0001	.1146
		Upper	Lower	.0587*	.02062	.044	.0014	.1160
			Middle	-.0573	.02062	.050	-.1146	.0001
	Recruit L	Lower	Middle	-.3826	.21801	.314	-.9885	.2234
			Upper	.0069	.21801	1.000	-.5991	.6128
		Middle	Lower	.3826	.21801	.314	-.2234	.9885
			Upper	.3895	.21801	.298	-.2165	.9954
		Upper	Lower	-.0069	.21801	1.000	-.6128	.5991
			Middle	-.3895	.21801	.298	-.9954	.2165
	Recruit L	Lower	Middle	-.4499	.17507	.074	-.9365	.0367
			Upper	-.3522	.17507	.202	-.8387	.1344
		Middle	Lower	.4499	.17507	.074	-.0367	.9365
			Upper	.0977	.17507	1.000	-.3889	.5843
		Upper	Lower	.3522	.17507	.202	-.1344	.8387
			Middle	-.0977	.17507	1.000	-.5843	.3889

Based on observed means.
The error term is Mean Square(Error) = .123.

*. The mean difference is significant at the .05 level.

Appendix 10: Bonferroni Tests – Seasonal comparisons *Perna perna*

Multiple Comparisons

Bonferroni

Species	Dependent Variable	(I) Season	(J) Season	Mean Difference (I-J)	Std. Error	Sig.	95% Confidence Interval	
							Lower Bound	Upper Bound
Perna	Recruit L	January	May	.0822	.02975	.103	-.0116	.1760
			July	.0376	.02975	1.000	-.0562	.1314
			September	.0539	.02975	.572	-.0399	.1477
		May	January	-.0822	.02975	.103	-.1760	.0116
			July	-.0446	.02975	.957	-.1384	.0492
			September	-.0283	.02975	1.000	-.1221	.0655
		July	January	-.0376	.02975	1.000	-.1314	.0562
			May	.0446	.02975	.957	-.0492	.1384
			September	.0163	.02975	1.000	-.0775	.1101
		September	January	-.0539	.02975	.572	-.1477	.0399
			May	.0283	.02975	1.000	-.0655	.1221
			July	-.0163	.02975	1.000	-.1101	.0775
	Recruit L	January	May	.0339	.03388	1.000	-.0729	.1407
			July	.0516	.03388	.922	-.0552	.1584
			September	.0579	.03388	.679	-.0489	.1647
		May	January	-.0339	.03388	1.000	-.1407	.0729
			July	.0177	.03388	1.000	-.0891	.1245
			September	.0240	.03388	1.000	-.0828	.1308
		July	January	-.0516	.03388	.922	-.1584	.0552
			May	-.0177	.03388	1.000	-.1245	.0891
			September	.0063	.03388	1.000	-.1005	.1131
		September	January	-.0579	.03388	.679	-.1647	.0489
			May	-.0240	.03388	1.000	-.1308	.0828
			July	-.0063	.03388	1.000	-.1131	.1005
	Recruit L	January	May	.0004	.00488	1.000	-.0149	.0158
			July	.0125	.00488	.148	-.0029	.0279
			September	.0127	.00488	.137	-.0026	.0281
		May	January	-.0004	.00488	1.000	-.0158	.0149
			July	.0121	.00488	.175	-.0033	.0275
			September	.0123	.00488	.162	-.0031	.0277
		July	January	-.0125	.00488	.148	-.0279	.0029
			May	-.0121	.00488	.175	-.0275	.0033
			September	.0002	.00488	1.000	-.0152	.0156
		September	January	-.0127	.00488	.137	-.0281	.0026
			May	-.0123	.00488	.162	-.0277	.0031
			July	-.0002	.00488	1.000	-.0156	.0152
	Recruit L	January	May	-.2160	.15732	1.000	-.7119	.2800
			July	-.0164	.15732	1.000	-.5124	.4795
			September	-.6774*	.15732	.006	-1.1734	-.1814
		May	January	.2160	.15732	1.000	-.2800	.7119
			July	.1995	.15732	1.000	-.2964	.6955
			September	-.4615	.15732	.075	-.9574	.0345
		July	January	.0164	.15732	1.000	-.4795	.5124
			May	-.1995	.15732	1.000	-.6955	.2964
			September	-.6610*	.15732	.007	-1.1570	-.1650
		September	January	.6774*	.15732	.006	.1814	1.1734
			May	.4615	.15732	.075	-.0345	.9574
			July	.6610*	.15732	.007	.1650	1.1570
	Recruit L	January	May	-.2449	.38762	1.000	-1.4670	.9771
			July	-.1884	.38762	1.000	-1.4105	1.0336
			September	-.0915	.38762	1.000	-1.3136	1.1305
		May	January	.2449	.38762	1.000	-.9771	1.4670
			July	.0565	.38762	1.000	-1.1655	1.2785
			September	.1534	.38762	1.000	-1.0687	1.3754
		July	January	.1884	.38762	1.000	-1.0336	1.4105
			May	-.0565	.38762	1.000	-1.2785	1.1655
			September	.0969	.38762	1.000	-1.1252	1.3189
		September	January	.0915	.38762	1.000	-1.1305	1.3136
			May	-.1534	.38762	1.000	-1.3754	1.0687
			July	-.0969	.38762	1.000	-1.3189	1.1252

Appendix 11: Bonferroni Tests – Seasonal Comparisons *Mytilus galloprovincialis*

Mytilus	Recruit L	January	May	-.0440	.05452	1.000	-.2158	.1279
			July	-.0377	.05452	1.000	-.2096	.1342
			September	-.0389	.05452	1.000	-.2107	.1330
		May	January	.0440	.05452	1.000	-.1279	.2158
			July	.0063	.05452	1.000	-.1656	.1781
			September	.0051	.05452	1.000	-.1668	.1770
		July	January	.0377	.05452	1.000	-.1342	.2096
			May	-.0063	.05452	1.000	-.1781	.1656
			September	-.0011	.05452	1.000	-.1730	.1707
		September	January	.0389	.05452	1.000	-.1330	.2107
			May	-.0051	.05452	1.000	-.1770	.1668
			July	.0011	.05452	1.000	-.1707	.1730
	Recruit L	January	May	.0470	.05540	1.000	-.1277	.2217
			July	.1069	.05540	.465	-.0677	.2816
			September	.2169*	.05540	.012	.0422	.3915
		May	January	-.0470	.05540	1.000	-.2217	.1277
			July	.0600	.05540	1.000	-.1147	.2346
			September	.1699	.05540	.059	-.0048	.3446
		July	January	-.1069	.05540	.465	-.2816	.0677
			May	-.0600	.05540	1.000	-.2346	.1147
			September	.1099	.05540	.423	-.0647	.2846
		September	January	-.2169*	.05540	.012	-.3915	-.0422
			May	-.1699	.05540	.059	-.3446	.0048
			July	-.1099	.05540	.423	-.2846	.0647
	Recruit L	January	May	.0000	.02381	1.000	-.0751	.0751
			July	.0391	.02381	.759	-.0360	.1141
			September	.0988*	.02381	.008	.0238	.1739
		May	January	.0000	.02381	1.000	-.0751	.0751
			July	.0391	.02381	.759	-.0360	.1141
			September	.0988*	.02381	.008	.0238	.1739
		July	January	-.0391	.02381	.759	-.1141	.0360
			May	-.0391	.02381	.759	-.1141	.0360
			September	.0598	.02381	.164	-.0153	.1348
		September	January	-.0988*	.02381	.008	-.1739	-.0238
			May	-.0988*	.02381	.008	-.1739	-.0238
			July	-.0598	.02381	.164	-.1348	.0153
	Recruit L	January	May	.0477	.25174	1.000	-.7460	.8413
			July	-.1054	.25174	1.000	-.8990	.6883
			September	-.0191	.25174	1.000	-.8128	.7745
		May	January	-.0477	.25174	1.000	-.8413	.7460
			July	-.1530	.25174	1.000	-.9467	.6407
			September	-.0668	.25174	1.000	-.8604	.7269
		July	January	.1054	.25174	1.000	-.6883	.8990
			May	.1530	.25174	1.000	-.6407	.9467
			September	.0862	.25174	1.000	-.7074	.8799
		September	January	.0191	.25174	1.000	-.7745	.8128
			May	.0668	.25174	1.000	-.7269	.8604
			July	-.0862	.25174	1.000	-.8799	.7074
	Recruit L	January	May	.0695	.20215	1.000	-.5678	.7068
			July	-.0265	.20215	1.000	-.6638	.6108
			September	-.0726	.20215	1.000	-.7099	.5647
		May	January	-.0695	.20215	1.000	-.7068	.5678
			July	-.0960	.20215	1.000	-.7333	.5413
			September	-.1421	.20215	1.000	-.7794	.4953
		July	January	.0265	.20215	1.000	-.6108	.6638
			May	.0960	.20215	1.000	-.5413	.7333
			September	-.0461	.20215	1.000	-.6834	.5912
		September	January	.0726	.20215	1.000	-.5647	.7099
			May	.1421	.20215	1.000	-.4953	.7794
			July	.0461	.20215	1.000	-.5912	.6834

Based on observed means.
The error term is Mean Square(Error) = .123.

*. The mean difference is significant at the .05 level.

Appendix 12: Bonferroni Tests- Population Structure and Condition Index Seasonal comparisons of *Perna perna*.

Multiple Comparisons

Bonferroni

Species	Dependent Variable	(I) Season	(J) Season	Mean Difference (I-J)	Std. Error	Sig.	95% Confidence Interval Lower Bound	95% Confidence Interval Upper Bound
Perna	Recruits	January	May	.83233	.330197	.161	-.20867	1.87334
			July	.41817	.330197	1.000	-.62284	1.45917
			September	.53400	.330197	.791	-.50701	1.57501
		May	January	-.83233	.330197	.161	-1.87334	.20867
			July	-.41417	.330197	1.000	-1.45517	.62684
			September	-.29833	.330197	1.000	-1.33934	.74267
		July	January	-.41817	.330197	1.000	-1.45917	.62284
			May	.41417	.330197	1.000	-.62684	1.45517
			September	.11583	.330197	1.000	-.92517	1.15684
		September	January	-.53400	.330197	.791	-1.57501	.50701
			May	.29833	.330197	1.000	-.74267	1.33934
			July	-.11583	.330197	1.000	-1.15684	.92517
	Juveniles	January	May	.10417	.102522	1.000	-.21905	.42739
			July	.15483	.102522	.941	-.16839	.47805
			September	.16967	.102522	.743	-.15355	.49289
		May	January	-.10417	.102522	1.000	-.42739	.21905
			July	.05067	.102522	1.000	-.27255	.37389
			September	.06550	.102522	1.000	-.25772	.38872
		July	January	-.15483	.102522	.941	-.47805	.16839
			May	-.05067	.102522	1.000	-.37389	.27255
			September	.01483	.102522	1.000	-.30839	.33805
		September	January	-.16967	.102522	.743	-.49289	.15355
			May	-.06550	.102522	1.000	-.38872	.25772
			July	-.01483	.102522	1.000	-.33805	.30839
	Adults	January	May	.00105	.012087	1.000	-.03706	.03916
			July	.03133	.012087	.141	-.00677	.06944
			September	.03183	.012087	.131	-.00627	.06994
		May	January	-.00105	.012087	1.000	-.03916	.03706
			July	.03028	.012087	.166	-.00782	.06839
			September	.03078	.012087	.154	-.00732	.06889
		July	January	-.03133	.012087	.141	-.06944	.00677
			May	-.03028	.012087	.166	-.06839	.00782
			September	.00050	.012087	1.000	-.03761	.03861
		September	January	-.03183	.012087	.131	-.06994	.00627
			May	-.03078	.012087	.154	-.06889	.00732
			July	-.00050	.012087	1.000	-.03861	.03761
	CIAdults	January	May	-4.2550	2.81386	.938	-13.1262	4.6162
			July	-1.4933	2.81386	1.000	-10.3645	7.3779
			September	-16.7417*	2.81386	.000	-25.6129	-7.8705
		May	January	4.2550	2.81386	.938	-4.6162	13.1262
			July	2.7617	2.81386	1.000	-6.1095	11.6329
			September	-12.4867*	2.81386	.005	-21.3579	-3.6155
		July	January	1.4933	2.81386	1.000	-7.3779	10.3645
			May	-2.7617	2.81386	1.000	-11.6329	6.1095
			September	-15.2483*	2.81386	.001	-24.1195	-6.3771
		September	January	16.7417*	2.81386	.000	7.8705	25.6129
			May	12.4867*	2.81386	.005	3.6155	21.3579
			July	15.2483*	2.81386	.001	6.3771	24.1195
	CIJuveniles	January	May	-3.6517	4.80483	1.000	-18.7998	11.4964
			July	1.3100	4.80483	1.000	-13.8381	16.4581
			September	.9350	4.80483	1.000	-14.2131	16.0831
		May	January	3.6517	4.80483	1.000	-11.4964	18.7998
			July	4.9617	4.80483	1.000	-10.1864	20.1098
			September	4.5867	4.80483	1.000	-10.5614	19.7348
		July	January	-1.3100	4.80483	1.000	-16.4581	13.8381
			May	-4.9617	4.80483	1.000	-20.1098	10.1864
			September	-.3750	4.80483	1.000	-15.5231	14.7731
		September	January	-.9350	4.80483	1.000	-16.0831	14.2131
			May	-4.5867	4.80483	1.000	-19.7348	10.5614
			July	.3750	4.80483	1.000	-14.7731	15.5231

Appendix 13: Bonferroni Tests- Population Structure and Condition Index Seasonal comparisons of *Mytilus galloprovincialis*

Mytilus	Recruits	January	May	-2.36783	2.179676	1.000	-9.23966	4.50399
			July	-1.69900	2.179676	1.000	-8.57082	5.17282
			September	-1.02800	2.179676	1.000	-7.89982	5.84382
		May	January	2.36783	2.179676	1.000	-4.50399	9.23966
			July	.66883	2.179676	1.000	-6.20299	7.54066
			September	1.33983	2.179676	1.000	-5.53199	8.21166
		July	January	1.69900	2.179676	1.000	-5.17282	8.57082
			May	-.66883	2.179676	1.000	-7.54066	6.20299
			September	.67100	2.179676	1.000	-6.20082	7.54282
		September	January	1.02800	2.179676	1.000	-5.84382	7.89982
			May	-1.33983	2.179676	1.000	-8.21166	5.53199
			July	-.67100	2.179676	1.000	-7.54282	6.20082
	Juveniles	January	May	.19133	.235917	1.000	-.55244	.93510
			July	.48067	.235917	.386	-.26310	1.22444
			September	.79217*	.235917	.034	.04840	1.53594
		May	January	-.19133	.235917	1.000	-.93510	.55244
			July	.28933	.235917	1.000	-.45444	1.03310
			September	.60083	.235917	.154	-.14294	1.34460
		July	January	-.48067	.235917	.386	-1.22444	.26310
			May	-.28933	.235917	1.000	-1.03310	.45444
			September	.31150	.235917	1.000	-.43227	1.05527
		September	January	-.79217*	.235917	.034	-1.53594	-.04840
			May	-.60083	.235917	.154	-1.34460	.14294
			July	-.31150	.235917	1.000	-1.05527	.43227
	Adults	January	May	.00000	.087565	1.000	-.27606	.27606
			July	.14650	.087565	.721	-.12956	.42256
			September	.30450*	.087565	.027	.02844	.58056
		May	January	.00000	.087565	1.000	-.27606	.27606
			July	.14650	.087565	.721	-.12956	.42256
			September	.30450*	.087565	.027	.02844	.58056
		July	January	-.14650	.087565	.721	-.42256	.12956
			May	-.14650	.087565	.721	-.42256	.12956
			September	.15800	.087565	.578	-.11806	.43406
		September	January	-.30450*	.087565	.027	-.58056	-.02844
			May	-.30450*	.087565	.027	-.58056	-.02844
			July	-.15800	.087565	.578	-.43406	.11806
	CIAdults	January	May	-2.0883	2.90933	1.000	-11.2605	7.0839
			July	-3.5183	2.90933	1.000	-12.6905	5.6539
			September	-.6667	2.90933	1.000	-9.8389	8.5055
		May	January	2.0883	2.90933	1.000	-7.0839	11.2605
			July	-1.4300	2.90933	1.000	-10.6022	7.7422
			September	1.4217	2.90933	1.000	-7.7505	10.5939
		July	January	3.5183	2.90933	1.000	-5.6539	12.6905
			May	1.4300	2.90933	1.000	-7.7422	10.6022
			September	2.8517	2.90933	1.000	-6.3205	12.0239
		September	January	.6667	2.90933	1.000	-8.5055	9.8389
			May	-1.4217	2.90933	1.000	-10.5939	7.7505
			July	-2.8517	2.90933	1.000	-12.0239	6.3205
	CIJuveniles	January	May	.8117	3.36767	1.000	-9.8055	11.4289
			July	1.8850	3.36767	1.000	-8.7322	12.5022
			September	1.2067	3.36767	1.000	-9.4105	11.8239
		May	January	-.8117	3.36767	1.000	-11.4289	9.8055
			July	1.0733	3.36767	1.000	-9.5439	11.6905
			September	.3950	3.36767	1.000	-10.2222	11.0122
		July	January	-1.8850	3.36767	1.000	-12.5022	8.7322
			May	-1.0733	3.36767	1.000	-11.6905	9.5439
			September	-.6783	3.36767	1.000	-11.2955	9.9389
		September	January	-1.2067	3.36767	1.000	-11.8239	9.4105
			May	-.3950	3.36767	1.000	-11.0122	10.2222
			July	.6783	3.36767	1.000	-9.9389	11.2955

Based on observed means.
The error term is Mean Square(Error) = 34.024.

*. The mean difference is significant at the .05 level.

Appendix 14: Bonferroni Tests- Population Structure and Condition Index shore zones comparisons of *Perna perna.*

Multiple Comparisons

Bonferroni

Species	Dependent Variable	(I) Zone	(J) Zone	Mean Difference (I-J)	Std. Error	Sig.	95% Confidence Interval	
							Lower Bound	Upper Bound
Perna	Recruits	Lower	Middle	-.04500	.285959	1.000	-.83982	.74982
			Upper	.39000	.285959	.593	-.40482	1.18482
		Middle	Lower	.04500	.285959	1.000	-.74982	.83982
			Upper	.43500	.285959	.462	-.35982	1.22982
		Upper	Lower	-.39000	.285959	.593	-1.18482	.40482
			Middle	-.43500	.285959	.462	-1.22982	.35982
	Juveniles	Lower	Middle	.02813	.088787	1.000	-.21866	.27491
			Upper	.10738	.088787	.749	-.13941	.35416
		Middle	Lower	-.02813	.088787	1.000	-.27491	.21866
			Upper	.07925	.088787	1.000	-.16753	.32603
		Upper	Lower	-.10738	.088787	.749	-.35416	.13941
			Middle	-.07925	.088787	1.000	-.32603	.16753
	Adults	Lower	Middle	.06241*	.010467	.000	.03332	.09151
			Upper	.07238*	.010467	.000	.04328	.10147
		Middle	Lower	-.06241*	.010467	.000	-.09151	-.03332
			Upper	.00996	.010467	1.000	-.01913	.03906
		Upper	Lower	-.07238*	.010467	.000	-.10147	-.04328
			Middle	-.00996	.010467	1.000	-.03906	.01913
	CIAdults	Lower	Middle	1.2050	2.43688	1.000	-5.5682	7.9782
			Upper	8.8388*	2.43688	.010	2.0655	15.6120
		Middle	Lower	-1.2050	2.43688	1.000	-7.9782	5.5682
			Upper	7.6337*	2.43688	.026	.8605	14.4070
		Upper	Lower	-8.8388*	2.43688	.010	-15.6120	-2.0655
			Middle	-7.6337*	2.43688	.026	-14.4070	-.8605
	CIJuveniles	Lower	Middle	-2.1838	4.16110	1.000	-13.7494	9.3819
			Upper	2.2325	4.16110	1.000	-9.3332	13.7982
		Middle	Lower	2.1838	4.16110	1.000	-9.3819	13.7494
			Upper	4.4163	4.16110	.928	-7.1494	15.9819
		Upper	Lower	-2.2325	4.16110	1.000	-13.7982	9.3332
			Middle	-4.4163	4.16110	.928	-15.9819	7.1494

Appendix 15: **Bonferroni Tests- Population Structure and Condition Index shore zones comparisons of *Mytilus galloprovincialis***

Mytilus	Recruits	Lower	Middle	-3.25100	1.887655	.332	-8.49769	1.99569
			Upper	-.26088	1.887655	1.000	-5.50756	4.98581
		Middle	Lower	3.25100	1.887655	.332	-1.99569	8.49769
			Upper	2.99013	1.887655	.418	-2.25656	8.23681
		Upper	Lower	.26088	1.887655	1.000	-4.98581	5.50756
			Middle	-2.99013	1.887655	.418	-8.23681	2.25656
	Juveniles	Lower	Middle	-.64425*	.204310	.025	-1.21212	-.07638
			Upper	-.41313	.204310	.198	-.98100	.15475
		Middle	Lower	.64425*	.204310	.025	.07638	1.21212
			Upper	.23112	.204310	.840	-.33675	.79900
		Upper	Lower	.41313	.204310	.198	-.15475	.98100
			Middle	-.23112	.204310	.840	-.79900	.33675
	Adults	Lower	Middle	-.36488*	.075833	.001	-.57565	-.15410
			Upper	-.16000	.075833	.170	-.37078	.05078
		Middle	Lower	.36488*	.075833	.001	.15410	.57565
			Upper	.20488	.075833	.058	-.00590	.41565
		Upper	Lower	.16000	.075833	.170	-.05078	.37078
			Middle	-.20488	.075833	.058	-.41565	.00590
	CIAdults	Lower	Middle	-4.7300	2.51956	.255	-11.7330	2.2730
			Upper	.7188	2.51956	1.000	-6.2843	7.7218
		Middle	Lower	4.7300	2.51956	.255	-2.2730	11.7330
			Upper	5.4487	2.51956	.154	-1.5543	12.4518
		Upper	Lower	-.7188	2.51956	1.000	-7.7218	6.2843
			Middle	-5.4487	2.51956	.154	-12.4518	1.5543
	CIJuveniles	Lower	Middle	-7.2775	2.91649	.084	-15.3838	.8288
			Upper	-5.4138	2.91649	.264	-13.5200	2.6925
		Middle	Lower	7.2775	2.91649	.084	-.8288	15.3838
			Upper	1.8637	2.91649	1.000	-6.2425	9.9700
		Upper	Lower	5.4138	2.91649	.264	-2.6925	13.5200
			Middle	-1.8637	2.91649	1.000	-9.9700	6.2425

Based on observed means.
The error term is Mean Square(Error) = 34.024.

*. The mean difference is significant at the .05 level.