# POPULATION STRUCTURE OF ROCKY INTERTIDAL LIMPETS IN ROCK POOLS INSIDE AND OUTSIDE MARINE PROTECTED AREAS (MPAS) ON THE SOUTHEAST COAST OF SOUTH AFRICA

by

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#### ABSTRACT

Intertidal rock pools are regarded as important habitats providing protection and nursery areas for invertebrates. However, relevant to emergent rocks, little information is available on the processes governing community interactions in these microhabitats. This study investigated the effects of marine reserves over a period of 12 months from June 2011 to May 2012 on limpet diversity, density, size structure and recruitment in rock pools of reserve and non-reserve sites along the southeast coast of South Africa. Sampling was done in two reserve (Dwesa-Cwebe and Hluleka Nature Reserves) and two non-reserve (Nqabara and Presley's Bay) sites. Three areas were selected in each study site and 9 rock pools with well defined boundaries were identified (3 at low shore, mid shore and high shore).

Shannon's Diversity Index indicated greater species diversity in rock pools of nonreserve than reserve sites. Although mean densities and mean recruit densities were generally greater in rock pools of non-reserve than reserve sites, they were found to be site- and species specific. Mean and mean maximum sizes were significantly greater in rock pools of reserve than non-reserve sites. Species diversity was governed by regional differences in species distribution and independent of site exploitation. Greater sizes found inside reserve sites were attributed to protection from exploitation. These results highlight not only the importance of considering rock pools in designing marine reserves but also understanding limpet assemblages in rock pools for biodiversity management.

**Key words:** rock pool, marine reserves, limpet, diversity, density, size structure, recruitment.

### DECLARATION

I, Tabile Loqo declare that this study is my own original effort and that it has never been submitted for the award of any degree at any other university. All sources used in this study have been indicated and acknowledged by means of complete references.

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CHAPTER 1:

## **GENERAL INTRODUCTION**

#### **1.1 EXPLOITATION OF MARINE RESOURCES**

South Africa is one of the few countries whose coastline is regarded as relatively pristine (Branch, et al., 2002). The shores of southern Africa provide rich diversity of fauna and flora with over 10 000 species or 15% of known marine species worldwide and 12 % of these species are endemic (Branch, et al., 2002). This wide array of marine resources is however under pressure from commercial, subsistence and recreational exploitation due to increases in human population, especially rural communities that reside along the coast. Although there are regulations governing utilization of these marine resources, in the Eastern Cape they are rarely enforced and poorly advertised (Lasiak, 1998).

Marine resources have long been exploited by humans for subsistence, commercial and recreational use (Lasiak, 1998; Claudet, et al., 2006; Barrett, et al., 2009) and the southeast coast of South Africa is no exception. Many coastal communities rely on intertidal invertebrates to provide food as well as bait for fishing (pers. obs.). The effects of human predation have been examined in intertidal populations and communities between accessible and non-accessible areas to humans (Gell & Roberts, 2002; Airame, et al., 2003; Kaplan & Botsford, 2005; Claudet, et al., 2006; Salomon, et al., 2006; Barrett, et al., 2009; Botsford, et al., 2009; Espinosa, et al., 2009; Fenberg, et al., 2012) and harvest and collection of macroinvertebrates is one of the main human impacts on the littoral environment (Navarro, et al., 2005). These invertebrates include, among others, mussels, oysters, abalone, limpets, sea urchins and crabs depending on local distribution. Increase in the human population as well as changes in the global climate have placed tremendous pressure on populations of these marine resources and this has led to the urgent need of protecting marine organisms through "no-take" (closed off to all fishing and harvesting of marine life) Marine Protected Areas (MPAs)/Marine Reserves. MPAs have been recognized worldwide as alternative tools for the conservation of marine biodiversity as well as provision of more reliable fishery yields (Roberts & Hawkins,

2000; Ward, et al. 2001; Gell & Roberts, 2002; Roberts, et al., 2003; Rius, et al., 2006; Edgar, et al., 2007; Botsford, et al., 2009).

Consequences of human harvesting pressures include reduction in population abundance (Fenberg, et al., 2012), decreases in the mean sizes of individuals within populations (Rius & Cabral, 2004), reproductive output (Libralato, et al., 2010) as well as habitat destruction (Murray, et al., 1999; Alatah & Crowe, 2010) due to trampling and harvesting equipment. These consequences, in turn, can have indirect effects on other species as most of the target species (e.g. mussels and limpets) are occupiers of primary space and some provide a substratum for other species (Rius, et al., 2006). Coastal marine species that have a planktonic larval phase and adult lifestyles with limited mobility (or sedentary) are among the most threatened by overfishing and implementation of marine reserves will be of benefit to these species (Kaplan & Botsford, 2005). These marine reserves are increasingly considered in coastal areas as an instrument to preserve vagile fauna and habitat from the detrimental effects of fishing (Claudet, et al., 2006) and to provide greater density, biomass and size of exploited species (Lasiak, 2006) in comparison to non-reserve areas.

#### **1.2 MARINE RESERVES/MARINE PROTECTED AREAS (MPAS)**

Roberts et al. (2003) recorded well over 1300 MPAs in the world with thousands more still in the planning stages. In South Africa, 21 MPAs have been declared under the Marine Living Resources Act No. 18 of 1998 (WWF-SA). MPAs were established with the main objectives of conservation, sustainable provision for human uses and maintaining the ecological processes that underpin the functioning of marine ecosystems (Roberts, et al., 2003). These marine reserves contribute to the conservation of habitats and exploited species, while also presenting opportunities for marine research and education and providing relatively natural areas that can be compared to exploited areas in order to determine the impacts of human harvesting

on various species (Airame, et al., 2003). This allows researchers to track any changes or loss in species diversity and abundance over time.

Although there have been variations in target species' response to protection, there are many examples of marine organisms benefiting from establishment of MPAs through increases in abundance and mean sizes (Bell, et al., 1985; Cole, et al., 1990; Cole, et al., 2000; Gell & Roberts, 2003; Claudet, et al., 2006), increased ecosystem resilience (Barret,t et al., 2009), stock rebuilding (Branch & Odendaal, 2003) and enhanced recruitment of target species (Guenette, et al., 1998; Libralato, et al., 2010). Botsford et al. (2001; 2009) illustrated that a species' persistence in any single reserve depends on whether the reserve meets the average dispersal distance of that species. The maximum benefit of fully protected reserves in terms of sustainability and yield, therefore, occurs when the reserve sites (Airame, et al. 2003). MPAs, therefore, act as tools for conservation while also providing larvae and mobile adult individuals to unprotected areas (Gell & Roberts, 2003; Kaplan & Botsford, 2005; Salomon, et al., 2006; Nakin, et al., 2012).

The conservation value of a MPA depends on its ability to: (1) maximize species richness, species diversity, habitat heterogeneity and the viability of keystone species; (2) provide protection to populations with vulnerable life history stages; (3) maintain essential linkages of ecosystems, and (4) regulate the degree of human and natural threat (Kaplan & Botsford, 2005; Salomon, et al., 2006; Botsford, et al., 2009). In order to ensure efficacy of MPAs, multiple objectives must be fulfilled in their design rather than past trends of fragmented management objectives which have led to the establishment of protection based upon narrow sets of criteria resulting in not only wasted efforts but higher costs and a false sense of protection as well (Roberts, et al., 2003). Factors affecting species persistence should also be incorporated in reserve design and management (Salomon, et al., 2006). Although

some multi-species and ecosystem-based approaches exist, most MPA design and management tend to focus on conserving single species (Salomon, et al., 2006) and this approach neglects critical ecological linkages among species and between species and the environment (Airame, et al., 2003). Another essential component to MPA success is monitoring aimed at determining if objectives are met in order to inform management decisions and conservation programs (Claudet, et al., 2006; Salomon, et al., 2006).

#### **1.3 INTERTIDAL LIMPETS**

Limpets are marine gastropod molluscs characterized by a flattened conical shell and a large muscular foot (Denny, 2000). They are among heavily exploited invertebrates on the southeast coast of South Africa (Hockey & Bosman, 1986; Lasiak, 1998). They are commonly found on wave-swept rocky shores (Denny, 2000), utilizing their muscular foot for adhering to the rocky substratum as well as locomotion. Their broadly conical shell serves as protection from desiccation and predation. Intertidal limpet distribution along the rocky shores is influenced by physical factors (heating and desiccation) in the upper littoral zone while the lower littoral zone is influenced by biological factors such as predation and competition (Hobday, 1995). Limpets feed by grazing on algae that is commonly found along the rocky shores. As a result, limpets are considered as dominant intertidal grazers worldwide (Dunmore & Schiel, 2000; Davies, et al., 2006). Limpet grazing on rocky shores has been shown to control algal biomass thereby preventing wave exposed locations from being dominated by fucoid algae (Jenkins, et al., 1999; Coleman, et al., 2006). The removal of such vital grazers would, therefore, have an effect on algal assemblages of intertidal zones. Limpets, like many marine species, are broadcast spawners which deposit egg masses throughout the intertidal zone (Dunmore & Schiel, 2000; Russel & Phillips, 2009). Intertidal limpets are not only important as grazers of the rocky shores but also act as a food source for many intertidal predators. These predators include shore birds such as oystercatchers (Fletcher, 1984; Lindberg, et al., 1987; Coleman & Hockey, 2008), many fish species (Silva, et al., 2006), crabs and sea stars (Branch, 1981). Limpets are of nutritive value to humans as they are cooked and eaten in many parts of the world (Lasiak, 1992) and are also used recreationally as fishing bait (Lasiak, 1998; Espinosa, et al., 2009).

#### **1.4 ROCK POOLS**

The intertidal zone is a biologically-rich area characterized by numerous habitat types such as emergent rock and tide pools (rock pools). Tide pools form during the high tide when depressions on the rocky shore are filled with water (Branch & Branch, 1981). When the tide recedes, these pools become isolated with well-refined boundaries (Metaxas & Scheibling, 1993; Methratta, 2004). Tide pool habitats differ significantly from the emergent rock due to constant water availability throughout the tidal cycle (during both high and low tide). The physical environment of tide pools does not fluctuate as much as that of emergent substrata (Metaxas & Scheibling, 1993), as a consequence, these pools are considered as distinct habitats from the rest of the intertidal zone (Altamirano, et al., 2009; Noel, et al., 2009) with each pool differing from the next. Organisms inhabiting tide pools are similar to those on emergent rock, i.e. vascular plants, bryophytes and invertebrates such as sponges, limpets and mussels. Although there is a general similarity in biological assemblages of tide pools, several taxa, such as algae and gastropods, are more abundant in pools than emergent rock while other species, such as fucoids and barnacles, may be absent or less abundant in pools (Metaxas & Scheibling, 1993). Diversity and abundance in intertidal rock pools vary with the size of the pool, location on the rocky shore as well as structural complexity within the pool (Meager, et al., 2005). Factors affecting community structure in tide pools include herbivory (Metaxas & Scheibling, 1993), predation (Firth & Crowe, 2008), competition (Blanchette, et al., 2006), recruitment (Firth, et al., 2009), nutrient availability (Methratta, 2004) as well as physical factors such as temperature, salinity, oxygen availability and wave action (Thompson, et al., 2002; Martins, et al., 2007; Russell & Phillips, 2009). These tide pools are not only important in providing habitat, but also

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provide potential refuge from stressful environmental conditions (Metaxas & Scheibling, 1993), and act as spawning and nursery areas for mobile marine animals such as fish and crustaceans (Thompson, et al., 2002; Meager, et al., 2005). Our understanding of vital marine habitats such as tide pools is important an addressing conservation objectives of MPAs including habitat fragmentation.

#### **1.5 COMMUNITY STRUCTURE**

Assessing any variations in intertidal community structure is a key component for researchers as the presence or absence of any population may affect ecosystem functioning. In order to determine the structure of an intertidal community, it is important to understand the diversity, distribution and abundance patterns of individual populations. Farrell (1988) found that removal of important intertidal grazers such as limpets resulted in a rapid increase of sessile organisms (encrusting algae and barnacles) and upon limpet reintroduction, algal cover declined rapidly. Many studies have illustrated that intertidal community structure is strongly influenced by environmental processes (such as sea surface temperature, salinity, wave action, coastal upwelling systems and intertidal landscape), biological processes (such as intra- and inter-specific competition, food availability and predation) (Farrell, 1988; Bustamante & Branch, 1996; Broitman, et al., 2001; Blanchette, et al., 2006; O'Connor, et al., 2006; Gingold, et al., 2010) and recreational as well as subsistence harvesting by humans (Farrell, 1988; Lasiak, 1998; Broitman, et al., 2001).

Temporal and spatial variability in intertidal recruitment is determined by temperature, adult abundance on the rocky shore as well as the oceanographic process of offshore Ekman transport (Broitman, et al., 2001; Blanchette, et al., 2006; Smith, et al., 2009). In the rocky shores of California, Blanchette et al. (2006) have illustrated the existence of a positive correlation between invertebrate recruitment rate and surface sea temperature (SST), with higher recruitment rates

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where sea temperature was warmer and this was attributed to wind-driven surface circulation in the area. Some intertidal invertebrate populations have shown an increase in individual fecundity with an increase in body size (Espinosa, et al., 2009). The preference of larger sized individuals by harvesters, therefore, may produce a negative effect on intertidal limpet recruitment.

#### **1.6 AIMS & OBJECTIVES**

While numerous studies have been conducted on community structures of intertidal limpets (Hockey & Branch, 1984; Farrel, 1988; Hobday, 1995; Chelazzi, et al., 1998; Jenkins, et al., 1999; Dunmore & Schiel, 2000; Coleman, et al., 2006; Davies, et al., 2006), most research tends to focus on limpet distribution along the emergent rock (Coleman, et al., 1999; Menconi, et al., 1999; Denny, 2000; Dunmore & Schiel, 2003; Navarro, et al., 2005; Blanchette, et al., 2006; Lasiak, 2006; Coleman & Hockey, 2008; Firth & Crowe, 2008; Guerry, 2008; Firth, et al., 2009), and few studies provide information on limpet community structure in tide pools (Metaxas & Scheibling, 1993; Underwood & Skilleter, 1996; Methratta, 2004; Noel, et al., 2009; Atalah & Crowe, 2010). No studies have been done to compare community structures of intertidal limpets in rock pools of restricted MPAs (reserves) and accessible non-reserve sites on the southeast coast of South Africa.

This study, therefore, investigated marine reserve effects on diversity, density, size structure and recruitment of intertidal limpets in rock pools along the southeast coast of South Africa. An assessment and understanding of population structures in reserve and non-reserve areas is essential in tracking any losses of intertidal invertebrate populations due to human exploitation and in evaluating MPAs and their role of ensuring sustainable ecological health, economic benefits as well as livelihoods provided by marine ecosystems.

### **1.7 STUDY SITES**

In the Transkei coast along the Eastern Cape Province of South Africa, sampling was done in four sites, two Reserves (R) and two adjacent non-Reserves (NR) (Fig 1). Reserve sites were Dwesa-Cwebe Nature Reserve (32°15'36"S 28°53'42"E) and Hluleka Nature Reserve (31°49'29.7"S 29°18'7.5"E) and both are 'no take' Marine Protected Areas governed by the Eastern Cape Parks & Tourism Agency (Fig 1). Two non-reserve sites adjacent to the MPAs were also identified, Ngabara and Presley's Bay (Fig 1). The east coast of Southern Africa is influenced by a subtropical Natal province (in which Hluleka and Presley's Bay are located), extending from southern Mozambique to just south of Durban, and a warm Agulhas province (in which Dwesa and Ngabara are located) which stretches from Dwesa to Cape point (Bustamante & Branch, 1996). Although both regions fall into the east coast, oceanographic conditions as well as habitat heterogeneity differ greatly between the two regions. Geological substrata found in the southern region (Dwesa and Ngabara) comprises either shale or mudstone, while in the central region (Hluleka and Presley's Bay), unmetamorphosed sandstone is prevalent (Lasiak, 1998). Harvesting intensity also differs greatly between the two regions (Lasiak, 1998), and this may lead to differences in invertebrate populations.



Fig. 1: Map showing the location of study sites

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### **1.8 LAYOUT OF THE THESIS**

Chapter 1 gives general information about limpets and reviews literature on intertidal community structure.

Chapter 2 outlines sampling design of the study and provides a general overview of study sites and statistical analysis.

Chapter 3 highlights effects exploitation on diversity and density of intertidal limpets in rock pools of reserve and non reserve sites, in order to determine whether protection by MPAs has any effect on diversity as well as distribution of these intertidal invertebrates.

In chapter 4 effects of human disturbances on limpet size structures are presented. Harvesting of intertidal invertebrates is informed by both species and size, therefore, it is important to determine whether there are any differences (that are a result of harvesting) in limpet size structures of reserve and non-reserve sites. In order to investigate these potential differences in size, a comparison of mean and mean maximum sizes in rock pools found inside and outside MPAs was made.

Chapter 5 compares differences in limpet recruitment between rock pools of reserve and non-reserve sites. This chapter assesses whether MPAs act as sources of larvae to rock pools of adjacent non-reserve sites, and as a result, intertidal limpet recruitment inside and outside MPAs was monitored throughout the study.

Chapter 6 concludes the thesis with a general discussion.

CHAPTER 3:

**POPULATION DENSITY AND DIVERSITY** 

### **2.1 INTRODUCTION**

Studying the intertidal zone is important in trying to define biotic and physical factors that have an effect on the population structure of intertidal communities (Benedetti-Checchi, 2006). An assessment of MPA effectiveness in protecting diversity and density of marine biota is a key component in addressing human impacts to biodiversity. Community structures of intertidal rock pools are influenced by factors such as temperature, salinity (Russell & Phillips, 2009), nutrient availability (Methratta, 2004), and interactions with other species (Firth & Crowe, 2008; Blanchette, et al., 2006). Although there are a number of environmental stressors in tidal pools, e.g. extreme temperature, salinity and limited oxygen availability (Russell & Phillips, 2009), these microhabitats also act as nurseries for many intertidal species, provide refuge from wave action and desiccation (Firth, et al., 2009) and facilitate the advancement of a species up a shore (Firth & Crowe, 2008).

Diversity within a population is crucial for species survival, especially those that inhabit variable environments (such as the rocky shores) and those that are subject to anthropogenic changes (Fauvelot, et al., 2009). Diversity within a population also has an effect on the productivity, growth and stability as well as interspecific interaction within community and ecosystem-level processes (Firth & Crowe, 2008). According to Gingold et al. (2010), habitat disturbance and structurally complex environments yield high species diversity in some species, as disturbance leads to species-specific mortality which may allow dominance of the inferior species. Decreases in limpet diversity and density, therefore, can lead to the dominance of intertidal algae since limpets are the primary grazers on rocky shores. The resulting changes in space occupancy can have negative implications for a number of species, e.g. there be a decline in the settlement of sessile fauna while remaining organisms are likely to become overgrown or smothered by macroalgae (Lasiak, 1998). Investigating intertidal limpet density is essential in determining community structure, as any variability in a population can have an influence on community processes such as reproduction, competition and predation on the rocky shores (Lasiak, 2006). While the removal of limpets on the rocky shores may have a positive effect on algal populations, ecosystem services provided by limpets (such as controlling algal biomass) will no longer be available, thus altering settlement of organisms such as barnacles as well as movement and feeding of other macroinvertebrates along the shore. Understanding and documenting the scales of variability in intertidal invertebrate density will help to focus attention on the importance of different ecological processes that determine these patterns observed (Bayer-Girald, et al., 2010).

Coastal natural resources have been subject to intense human disturbances during the past decades (Navarro, et al., 2009), and community structures can be used to track any losses in intertidal populations due to human exploitation. Studies of the effects of conservation on rocky intertidal invertebrate communities have focused on differences in mean densities, percentage cover, biomass or size of organisms inside and outside reserves (Lasiak, 2006). These studies, however, tend to focus on limpet distribution on emergent rock (Menconi, et al., 1999; Navarro, et al., 2005; Blanchette, et al., 2006; Lasiak, 2006; Firth & Crowe, 2008), as well as rock pools (Underwood & Skilleter, 1996; Noel, et al., 2009; Atalah & Crowe, 2010) and little or no studies have been done on comparison of intertidal limpet distribution in rock pools of reserves and non reserves.

The aim of this chapter was to investigate the effects of protection by MPAs on diversity and density of intertidal limpets in rock pools. Such information will be useful in the conservation of these limpet species and in dealing with habitat fragmentation in intertidal zones. In order to understand the processes that drive diversity and density in rock pools, the following hypotheses were tested in this chapter:

- There will be no variation in diversity of limpets found in rock pools of reserve and non-reserve sites; and
- There will be no variation in species density of limpets in rock pools of reserve and non-reserve sites.

#### **2.2 MATERIALS AND METHODS**

#### 2.2.1 Sampling procedure

Sampling was conducted in four sites, two marine reserves (R), Dwesa-Cwebe and Hluleka Nature reserves, and two non-reserve sites (NR), Nqabara and Presley's Bay, over a period of 12 months (June 2011 to May 2012) (Fig. 1 in Chapter 1). Within each study site, three areas (approximately 100m apart) were identified and labelled as follows: Dwesa (D) = D1, D2, D3; Nqabara (N) = N1, N2, N3; Hluleka (H) = H1, H2, H3; Presleys (P) = P1, P2, P3. In each area within each site, 9 rock pools (approximately 20m apart and spread across the intertidal zone from mid-low to high shore), with well-defined boundaries, were selected as sampling sites for this study (i.e. 9 rock pools per area x 3 areas = 27 rock pools/study site).

In each rock pool in reserve and non-reserve sites, three random throws of a square quadrat (25 x 25cm) were conducted and individual limpets within each quadrat were identified (using a magnifying glass and a field guide book), counted and recorded every month. Intertidal limpet diversity in each rock pool was measured in terms of the number of different species found within the quadrats. The limpet density was determined by identifying, counting and recording the number of individuals in each quadrat monthly.

#### 2.2.2 Statistical analysis

A 4-way ANOVA was used to test the effect of month, reserve, site and area on mean density of limpet species. Prior to the use of ANOVA, data were tested for normality and homogeneity of variances using Cochran's and Kolmogorov-Smirnov tests (Underwood, 1997; Zar, 2010), respectively. No transformation of data was necessary. Intertidal limpet diversity (represented as H) was compared among sites as well as between reserve and non-reserve sites using Shannon's Diversity Index. Evenness of the community (represented by E) as well as species dominance (represented by D) within sites were also compared using Simpson index. Similarities in sites that share common species were tested using Bray-Curtis similarity measures

using PRIMER (version 6). Cluster and ordination by non-metric multidimensional scaling (MDS) were used to detect any differences among sites and between reserve and non-reserve sites.

#### 2.3 RESULTS

#### 2.3.1 Diversity

A total of 11 different intertidal limpet species were recorded in all the four study sites (Table 1). Species diversity was greater in rock pools of reserve than nonreserve sites (Table 2). Dwesa, a reserve site, had the highest total of 10 out of 11 species and Hluleka, another reserve site, had the lowest total number of species recorded (6 out of 10 species) (Table 2). Shannon's Diversity Index (H) indicated greater species diversity in rock pools of non-reserve than reserve sites (Table 2). Ngabara, a non-reserve site, had the highest diversity index while Hluleka, a reserve site, had the lowest (Table 2). Simpson's Index (E) showed greater evenness of species distribution in rock pools of non-reserve sites (Table 2). Ngabara (NR) recorded greater species evenness and Dwesa (R) had the least (Table 2). Simpson's Index also indicated greater species dominance (D) in rock pools of reserve than non-reserve sites (Table 2). Species dominance was highest in Hluleka (R) and lowest in Presley's Bay (NR) (Table 2). Cluster and MDS ordinations showed two study areas (within sites), Dwesa 1 (D1) and Presley's Bay 2 (P2), which had the greatest percentage similarity (Fig. 3), while Hluleka 3 (H3) and Nqabara 3 (N3) differed greatly when compared to other study areas (Fig. 3). Area H3 had the least number of species identified (4 out of 11), whereas N3 had the most recorded number of species (9 out of 11).

#### 2.3.2 Density

Reserve status and site had no significant effect (p > 0.05) on mean density of intertidal limpets in rock pools of reserve and non-reserve sites (Table 3). Month had a significant effect (p < 0.05) on mean density of one (*Cellana capensis*) out of 11 species and the interaction of month and reserve had a significant effect (p < 0.05) in one (*Siphonaria serrata*) out of 11 total species (Table 3). Significant area effects (p < 0.05) were found in seven limpet species, *C. capensis, S. concinna, S. serrata, H. concolor, S. longicosta, H. pruinosus* and *S. granularis* (Table 3).

Dwesa (a reserve site) had the highest recorded total limpet density and Presley's Bay (a non-reserve site) was the lowest (Table 1). Out of 11 total species recorded throughout this study, only five species were common in all study sites, namely Cellana capensis, Siphonaria concinna, S. serrata, Helcion concolor and Scutellastra longicosta (Table 1). Dendrofissurella scutellum was recorded in three out of four sites (D, N, P), while species such as Scutellastra pica and S. argenvillei were both recorded in only one out of the four study sites (D) (Table 1). Dwesa, a reserve site, had greater mean densities for five limpet species (H. concolor, D. scutellum, C. oculus, S. pica and S. argenvillei), while Ngabara, a non-reserve site, recorded greater mean densities for four limpet species (S. serrata, C. oculus, S. granularis and *H. pruinosus*) (Table 1). Although mean density of *Cellana capensis* was greater in rock pools of non-reserve sites for six out of 12 months (Fig. 2), significant differences existed in two out of 12 months (Fig. 3). Higher densities of this species were recorded from September 2011 to January 2012 in all four study sites. The highest and lowest mean diversities of C. capensis which were recorded in reserve sites were 5 – 8 individuals per m<sup>-2</sup> and in non-reserve sites 5 – 10 individuals per m<sup>-2</sup> <sup>2</sup> (Fig. 2). Only a few numbers of *Cymbula oculus* were observed in two of the four study sites (D, N), throughout this study (Table 1).

#### 2.3.3 Cluster Analysis

Cluster analysis and MDS grouping based on similarity across study sites indicated three groupings with two major sub-divisions of the sampling sites (Fig. 3): Cluster 1 includes five study areas, D1, D2, D3, P1 and P2, which shared 80% similarity (Fig.3a). Cluster 2 also includes five study areas, H1, H2, N1, N2 and P3, which had percentage similarity 78% (Fig. 3a). Cluster 3 consisted of two study sites, H3 and N3, which had similarity among sites of 65% (Fig. 3a). Percentage similarity between Clusters 1 and 2 ranged at 76% while similarity among all three clusters was 60% (Fig. 3a). MDS ordination illustrated similar grouping of areas (Fig. 3b), with Dwesa and Presley's Bay having the most similar areas (D1 and P2) ranging at 92% (Fig. 3a).

Species	Dwesa (R)	Hluleka (R)	Nqabara (NR)	Presleys Bay (NR)
Cellana capensis	5	8	7	6
Siphonaria concinna	2	2	2	4
Siphonaria serrata	1	2	3	3
Helcion concolor	4	1	1	1
Scutellastra longicosta	1	1	1	1
Dendrofissurella scutellum	2	0	1	1
Cymbula oculus	1	0	1	0
Helcion pruinosus	0	1	3	1
Scutellastra granularis	1	0	2	1
Scutellastra pica	1	0	0	0
Scutellastra argenvillei	3	0	0	0

**Table 1:** Mean limpet density (m<sup>-2</sup>) recorded in the four study sites.

**Table 2:** Diversity indices of intertidal limpet species found among the four studysites and in reserve (R) and non-reserve sites (NR)

Diversity Index	Sites				Reserve / Non-reserve sites	
	Res	serves	Non	Non-reserves		
	Dwesa	Hluleka	Nqabara	Presley's	R	NR
Number of species	10	6	9	8	11	9
Shannon-Wiener (H)	1.058	0.572	1.19	1.01	0.822	1.134
Evenness (E)	0.288	0.295	0.365	0.343	0.207	0.345
Dominance (D)	0.462	0.736	0.444	0.425	0.603	0.427



**Fig. 2.** Mean (±SE) density of *C. capensis* in rock pools of reserve (R) and non-reserve (NR) sites throughout the study period (\* = months with significant differences).



Fig. 3a. Dendrogram based on Bray-Curtis percentage similarity index for all study sites (Dwesa = D1, D2, D3; Nqabara = N1, N2, N3; Hluleka = H1, H2, H3; Presley's Bay = P1, P2, P3)



Fig. 3b. MDS ordination based on Bray-Curtis similarity index for all study sites (Dwesa = D1, D2, D3; Nqabara = N1, N2, N3; Hluleka = H1, H2, H3; Presley's Bay = P1, P2, P3)

## **Table 3:** Results of the 4-way ANOVA based on mean density of intertidal limpet

Source of variation	SS	Df	MS	F	р
a) <i>Cellana capensis</i>					-
Month	2179.44	11	198.13	4,434	***
Reserve	111.97	1	111.97	0.118	0.76
Month * Reserve	266.09	11	24.19	0.541	0.85
Site (Reserve)	1893.4	2	946.7	1.145	0.37
Area (Reserve * Site)	6632.33	8	9829.04	22.162	***
Error	36885.07	1781	20.71		
b) <i>Siphonaria concinna</i>					
Month	74.87	11	6.806	1.0356	0.45
Reserve	360.2	1	360.2	2.041	0.29
Month * Reserve	71.45	11	6.496	0.988	0.49
Site (Reserve)	353.02	2	176.51	1.258	0.34
Area (Reserve * Site)	1130.02	8	141.25	22.902	***
Error	7938.85	1782	4.455		
c) Sinhonaria corrata					
Month	25.612	11	2 328	1 6973	0 14
Pesenve	30 44	1	30 444	2 2342	0.14
Month * Reserve	39 235	11	3 566	2.2372	*
Site (Reserve)	35 312	2	17 656	0.6472	0.55
Area (Reserve * Site)	222.46	8	27 807	16 2841	***
Frror	2339.02	1782	1 312	10.2011	
	2333.02	1/02	1.512		
d) Helcion concolor					
Month	29,245	11	2.6586	1.07976	0.42
Reserve	0.514	1	0.5141	0.06039	0.83
Month * Reserve	17.90	11	1.6280	0.66120	0.76
Site (Reserve)	17.02	2	8.5129	2.09759	0.17
Area (Reserve * Site)	25.62	8	3.2033	2.35296	*
Error	1804.24	1782	1.0124		
e) Scutellastra longicosta			0.04540	0.55660	0.01
Month	0.499	11	0.04542	0.55663	0.84
Reserve	0.130	1	0.13012	0.25844	0.66
Month * Reserve	0.425	11	0.03865	0.4/3/0	0.90
Site (Reserve)	1.00/	2	0.50351	2.82359	0.11
Area (Reserve * Site)	1.321	<u>8</u>	0.16517	2.52273	т Т
Error	120.796	1/82	0.06778		
f) Dendrofissurella scutellum					
Month	0.1647	11	0.01497	0.79155	0.65
Reserve	0.0472	1	0.04723	4.1741	0.18
Month * Reserve	0.1986	11	0.01805	0.95421	0.51
Site (Reserve)	0.0226	2	0.01132	0.53529	0.61
Area (Reserve * Site)	0.1849	8	0.02312	1.16414	0.33
Error	22.000	1782	0.01234		
g) C <i>ymbula. Oculus</i>					
Month	0.04716	11	0.00428	1.29926	0.29
Reserve	0.00725	1	0.00725	0.51627	0.55
Month * Reserve	0.02511	11	0.00228	0.69178	0.73
Site (Reserve)	0.02808	2	0.01404	5.52232	0.15
Area (Reserve * Site)	0.03625	8	0.00453	0.82253	0.58
Error	8.14814	1782	0.00457		
		1	1	1	1

## species.

## Table 3 continued

Source of variation	SS	Df	MS	F	D
				_	
h) Helcion pruinosus					
Month	9.292	11	0.8447	1.0797	0.42
Reserve	8.296	1	8.2960	0.8191	0.46
Month * Reserve	8.287	11	0.7534	0.9629	0.51
Site (Reserve)	20.257	2	10.1289	1.8566	0.22
Area (Reserve * Site)	45.615	8	5.7019	6.1101	***
Error	676.885	1782	0.3898		
i) <i>Scutellastra granularis</i>					
Month	2.338	11	0.21254	0.96871	0.50
Reserve	0.825	1	0.82498	0.84752	0.45
Month * Reserve	2.326	11	0.2115	0.96396	0.50
Site (Reserve)	1.946	2	0.97344	1.04566	0.39
Area (Reserve * Site)	7.864	8	0.98303	3.52832	***
Error	525.946	1782	0.29530		
j) <i>Scutellastra argenvillei</i>					
Month	0.00569	11	0.00051	0.94811	0.52
Reserve	0.00072	1	0.00072	0.99063	0.42
Month * Reserve	0.00569	11	0.00051	0.94811	0.52
Site (Reserve)	0.00145	2	0.00072	1.06643	0.40
Area (Reserve * Site)	0.00591	8	0.00074	1.23800	0.28
Error	0.90909	1782	0.00051		
k) <i>Scutellastra pica</i>					
Month	0.08006	11	0.00727	1.01281	0.47
Reserve	0.00773	1	0.00773	0.99635	0.42
Month * Reserve	0.08006	11	0.00727	1.01289	0.47
Site (Reserve)	0.01553	2	0.00776	0.86777	0.46
Area (Reserve * Site)	0.07252	8	0.00906	1.32037	0.24
Error	8.000	1782	0.00448		
## 2.4 DISCUSSION

Diversity in a community is an important component as productivity, growth and stability of a community are dependent on its diversity (Fauvelot, et al., 2009). Shannon's Diversity Index indicated greater diversity in rock pools of non-reserve than reserve sites. Variation of limpet diversity existed not only within Marine Protected Areas but also between reserve and non-reserve sites. There were regional differences in the distribution of limpet species, as species such as Cymbula oculus, Scutellastra pica and Scutellastra argenvillei were found in two out of four study sites (Table 1), Ngabara and Dwesa which are located at the southern region of the southeast coast (Lasiak, 1998). Rock pools found in sites of the southern region had higher diversity than Hluleka and Presley's Bay which are found at the central region (Lasiak, 1998). Study sites of the southern region were approximately 50km apart from the central region which could possibly account for the greater diversity indices observed in the former. Underwood & Chapman (1996) explained that samples closer together in space are more similar to each other than those farther apart because of responses of organisms to patchy habitats or other organisms.

Differences in habitat type, exploitation (Lasiak, 1998), food availabity, predation (Espinosa et al. 2009) and nearshore oceanographic conditions (Blanchette, et al., 2006) may also contribute to differences in assemblages. Predation has been illustrated to affect intertidal invertebrate diversity, as greater predation on one species (by shore birds, crabs and starfish) may lead to competitive superiority of another leading to higher productivity (Menge & Sutherland, 1976; Coleman & Hockey, 2008). This means in any community, limpets that are better equipped to defend against predation (through the use of homing scars, camouflage and mucus secretion) tend to thrive more than those that cannot defend themselves adequately (Iwasaki, 1993).

The observed significant differences in limpet diversity indices of reserve and nonreserve sites can be attributed to human exploitation. Intensity of exploitation is governed by species (Navarro, et al., 2005), size (Lasiak, 2006), and regional differences (Cole et al. 2011). The central region was found to be highly populated in comparison to the southern region; consequently, harvesting is more intense in the central than southern region (Lasiak, 1998). The rarely exploited siphonarids (S. concinna and S. serrata), for example, were more prevalent in all areas of nonreserve than reserve sites while the heavily exploited *H. concolor* had greater densitiy at Dwesa, a reserve site. Similarly, Lasiak (1998) found variability in limpet diversity between the south and central regions of the southeast coast and attributed that not only to regional differences in geological substrata but also exploitation intensity between the two regions. Regional differences in limpet diversity, which were observed during this study, may also be due to limits in species distribution, e.g. S. argenvillei is commonly distributed in shores of the western and southern coast and its density decreases as one moves up the east coast of southern Africa (Branch, et al., 2002).

Although limpet diversity varied significantly between rock pools of reserve and nonreserve sites, there were also significant differences in areas. MDS ordinations showed two areas within sites which had the least percentage similarity (H3 and N3) in comparison to other areas of the study. Rock pools found in H3 recorded the least mean limpet density throughout this study, while those of N3 had the highest mean density in comparison to all other areas. This can be attributed to heterogeneity of the substratum as these were the two areas with the most structurally complex habitats in terms of patterns in rock formation (Espinosa, et al., 2011). N3 was structurally distinct to all other study areas in Nqabara as there was greater density of macroalgae and macroinvertebrates than any other study area in the site. This area also contained the biggest and deepest tide pools of this study which may have contributed to greater mean diversity (pers. obs.). H3 on the other hand, consisted of a surface area that is corrugated rather than flat. This may have contributed to small diversity observed in this area, as intertidal limpets require smooth surfaces to adhere to in order to prevent desiccation when exposed during low tide. Investigating intertidal community structure in areas of the Antarctic, Waller (2008) also found higher species diversity in localities that were more structurally complex (between cobbles and underneath boulders) due to impacts caused by ice, wave exposure and trampling.

Results of this study indicated that month had a significant effect on mean density of one (*C. capensis*) of 11 species investigated. This difference in temporal variation may be attributed to differences in predation intensity, competition (Lasiak, 2006) and reproduction (Gray & Hodgson, 2003) throughout the year. Gray & Hodgson (2003) described two spawning periods in a year (summer and autumn) for patellid limpets found in the southeast coast. This may explain months with significant differences in mean density of *C. capensis* throughout this study. Lasiak (2006) also found significant differences in limpet density of exploited and unexploited sites with greater variation inside marine reserves, and attributed this variation to recruitment and mortality rates on the differences in limpet density within sites located in southern (Dwesa and Nqabara) and central region (Hluleka and Presley's Bay), were also observed, as the limpets *S. granularis, S. pica and S. argenvillei* had greater densities in rock pools of the southern region.

Area had a significant effect on mean density in seven out of 11 species during this study (Table 3). This indicated that differences in limpet density are inter-site and species-specific and variation exists at both small and large scales. Similarly, Underwood & Chapman (1996) found that variation in patterns of intertidal invertebrate density can occur from small scales of about 50cm for many species. Small-scale variation in limpet density may be attributed to differences in the types of substrates available in reserve and non-reserve sites (Lasiak, 2006) as well as behavioural responses of limpets to the habitat (Underwood & Chapman, 1996; Navarro, et al., 2005). Lasiak (2006) also found small-scale variation in intertidal

invertebrate density, and suggested that this variation was due to each species responding in a different way to ecological processes operating at spatial scales. Study sites along the rocky shores of Dwesa and Nqabara (south region) are characterized by shale or mudstone whereas sites in Hluleka and Presley's (central region) consist of unmetamorphosed sandstone (Lasiak, 1998). Variations at large scales, on the other hand, are caused by differences in recruitment and mortality (Underwood & Chapman, 1996), competition within populations (Boaventura, et al., 2003), predation (Barrett, et al., 2009; Coleman & Hockey, 2008) and nearshore oceanographic conditions (Blanchette, et al., 2006).

Habitat complexity has been shown not only to have a great effect on intertidal invertebrate diversity, but also on density (Underwood & Chapman, 1996; Navarro, 2005; Lasiak, 2006). Greater variation in limpet densities can be observed in areas where exploitation has led to habitat disturbance (Lasiak, 2006). Subsistence gatherers tend to focus harvesting to certain reachable areas within the shore which leads to greater limpet density in other areas of the shore. Other factors that may have contributed to variation in intertidal limpet density in this study were competition within intertidal populations and communities (Underwood & Chapman, 1996; Underwood, 2000) within rock pools, differences in predation intensity in rock pools found inside and outside marine reserves (Coleman & Hockey, 2008; Barrett, et al., 2009), physical processes such as wave action (Bustamante & Branch, 1996; Blanchette, et al., 2006) as well as differences in recruitment and mortality (Underwood & Chapman, 1996; Lasiak, 2006).

In conclusion, limpet diversity was significantly greater in non-reserve than reserve sites (Table 2). Significant area effects indicated small to large scale variation in mean species density. Variations in limpet density were species- and site-specific, while variations in limpet diversity were driven by regional differences.

**CHAPTER 4:** 

**POPULATION SIZE STRUCTURE** 

## **3.1 INTRODUCTION**

Intertidal invertebrate exploitation depends on the species and size of the individual removed (Rius, et al., 2006; Espinosa, et al., 2009). This has led to a global decline of marine organisms and has triggered a worldwide demand for changing the way coastal and ocean resources are managed (Angulo-valdes & Hatcher, 2010). Reserve sites act as a management option for marine conservation (Branch & Odendaal, 2003), fisheries (Claudet, et al., 2006), and other human uses of the oceans (Narvarte, et al., 2006). There are many documented examples where fished species have benefited from protection (Buxton & Smale, 1989; Bennett & Attwood, 1991; Francour, 1994; Chapman & Kramer, 1999; Paddack & Estes, 2000; Airame, et al., 2003; Branch & Odendaal, 2003; Gell & Roberts, 2003; Willis, et al., 2003; Claudet, et al., 2006; Libralato, et al., 2010), in particular through increases in mean size and abundance. Size structures have also been used to track losses of large individuals from populations, which are often the target of exploitation by humans (Espinosa, et al., 2009). Body size is considered to be one of the most important traits of an organism as it correlates with many aspects of its biology (Fernberg & Roy, 2008), including feeding intensity (Hobday, 1995) as well as reproductive output (Kido & Murray, 2003).

Variations in size distributions inside and outside MPAs may be attributed to the differences in predation pressure due to human harvesting. Studies have shown about 39 species of marine invertebrates which are known to have been subjected to size-selective harvesting pressure for decades and this has led to a reduction in mean body sizes of many intertidal invertebrates (Fernberg & Roy, 2008). In intertidal communities, the removal of larger sized grazers such as limpets can lead to increased abundance of smaller grazers (Kido & Murray, 2003), barnacles and other sessile organisms (Boaventura, et al., 2003). Kido & Murray (2003) assessed mean shell lengths of *Lottia gigantea* populations between accessible and non-accessible areas, and found smaller mean and maximum shell lengths in areas where human visitation and collection pressure was greater.

Size classes are an important component in community analysis as they are used in determining community structure. As important as size structure is to biodiversity, however, little research has been conducted to examine how different size structures influence community structure (Mc Kindsey & Bourged, 2001; Cruz et al., 2010). Size structure in a community can be used to assess effects of predation (Hobday, 1995), density and abundance (Hobday, 1995; Kido & Murray, 2003), competition (Boaventura et al. 2003) as well as reproductive quality (Branch, 1975; Fernberg & Roy, 2007). Factors affecting intertidal limpet size structures on the other hand are physical conditions such as temperature, salinity and wave action (Hobday, 1995), density-dependent growth rates and competition (Boaventura et al., 2003) as well as reproductive guality (Branch, 2003) as well as size-specific predation including human harvesting (Kido & Murray, 2003; Fernberg & Roy, 2008; Espinosa et al., 2009).

This chapter investigated differences in intertidal limpet sizes across two reserve and two non-reserve sites on the southeast coast of South Africa. Two main hypotheses tested were: (1) There will be no significant variations of mean sizes in each species of intertidal limpets in rock pools of reserve and non-reserve sites; (2) There will be no significant differences in mean maximum sizes of intertidal limpets in rock pools of reserve and non-reserve sites.

## **3.2 MATERIALS & METHODS**

## 3.2.1 Sampling procedure

Sampling was done in four sites, two reserves (Dwesa-Cwebe and Hluleka Nature reserves) and two non-reserves (Nqabara and Presley's Bay) over a period of 12 months from June 2011 to May 2012 (Fig 1, Chapter 1). In each study site 27 rock pools, with well defined boundaries, were identified (see Chapter 1) and sampling occurred in these pools throughout the study (27 rock pools per study site x 4 sites = 108 rock pools). Within each rock pool, three random throws of a square quadrat (25 x 25cm) were done and limpet individuals found inside were identified (using a magnifying glass and a field guide book), counted, measured to the nearest 0.05 mm using Venier calipers and recorded every month in reserve and non-reserve sites. Mean maximum sizes were determined for each species by recording the 10 largest individuals monthly.

## 3.2.2 Statistical analysis

A 4-way nested analysis of variances (ANOVA) was used to test the effect of month, reserve, site and area on mean size and mean maximum size of limpet species. Prior to the use of ANOVA, data were tested for normality and homogeneity of variances using Cochran's and Kolmogorov-Smirnov tests (Underwood, 1997; Zar, 2010), respectively. No transformation of data was necessary. Size frequencies of mean and mean maximum sizes between reserve and non-reserve sites were compared and plotted using histograms. Gaussian Kernel density Estimation was used to test data for normal distribution prior to plotting histograms (Silverman, 1986).

## 3.3 RESULTS

11 different limpet species were recorded and measured during this study (*Cellana capensis, Siphonaria concinna, Siphonaria serrata, Helcion concolor, Bendofissurella scutellum, Cymbula oculus, Scutellastra longicosta, Helcion pruinosus, Scutellastra granularis, Scutallastra argenvillei* and *Scutellastra pica*) with only five being common in rock pools of all four study areas (*C. capensis, S. concinna, S. serrata, H. concolor and S. longicosta*).

## 3.3.1 Mean size

Analysis of variance (ANOVA) results indicated that month (M) had a significant effect (P < 0.05) on mean sizes of eight (*C. capensis, S. concinna, S. serrata, H. concolor, S. longicosta, H. pruinosus, S. granularis* and *S. pica*) out of 11 total species (Table 4). Reserve status (R) had a significant effect (P < 0.05) on mean sizes of one (*C. capensis*) out of 11 species (Table 4). Site also had a significant effect on mean sizes of one (*H. concolor*) out of 11 species and area (A) had a significant effect (P < 0.05) on mean sizes of all 11 species recorded (Table 4). The interaction of month and reserve (M x R) had significant effects on mean sizes of five limpet species (*C. capensis, D. scutellum, H. pruinosus, S. granularis* and *S. pica*).

#### 3.3.1.1 Cellana capensis

Mean sizes were significantly greater in rock pools of reserve than non-reserve sites in all the 12 months sampled (Fig. 4a).

#### 3.3.1.2 Dendrofissurella scutellum

Mean sizes of *D. scutellum* were significantly greater in rock pools of reserve than non-reserve sites (Fig. 4). Significant differences in mean sizes were recorded for three (July, February and April) out of 12 months (see asterisk Fig. 4d).

## 3.3.1.3 Helcion pruinosus

Although greater mean sizes were found in rock pools of non-reserve than reserve sites, significant differences existed in three (August, December and April) of the 12 months (see asterisk in Fig. 4b).

## 3.3.1.4 Scutellastra granularis

Non-reserve sites recorded greater mean sizes in 11 out of 12 months (Fig. 4). Significant differences were observed in three out of 12 months, namely August, November and February (see asterisk in Fig. 4e). *Scutellastra granularis* was observed in only two (Dwesa and Nqabara – southern region) of the four study sites.

## 3.3.1.5 Scutellastra argenvillei

Mean sizes of this species were greater in reserve than non-reserve sites, with significant differences existing in only one out of 12 months (see asterisk in Fig. 4c).

## 3.3.1.6 Scutellastra pica

Significant differences in mean sizes of this species existed in only one of 12 months (November) (see asterisk in Fig. 4f).

## 3.3.2 Mean maximum size

ANOVA results also indicated that reserve status had no significant effect (p > 0.05) on mean maximum sizes of limpet species (Table 5). Month (M) had a significant effect (P < 0.05) on mean maximum sizes of nine (*C. capensis, S. concinna, S. serrata, H. concolor, S. longicosta, B. scutellum, H. pruinosus, S. granularis* and *S. pica*) out of 11 species, while site had a significant effect (P < 0.05) on mean size of

one (*H. concolor*) species (Table 5). Area (A) had significant effects (P < 0.05) on mean maximum sizes of eight limpet species (*C. capensis, S. concinna, S. serrata, S. longicosta, C. oculus, H. pruinosus, S. granularis* and *S. pica*) (Table 5) along the southeast coast of southern Africa. The interaction of month and reserve (M x R) had significant effects on mean maximum sizes of eight limpet species (*C. capensis, S. granularis* and *S. pica*).

## 3.3.2.1 Cellana capensis

Significant differences in mean maximum sizes of limpets in rock pools in reserve and non reserve sites existed for 11 out of 12 months, with greater mean maximum sizes recorded in reserve sites (Fig. 5a).

# 3.3.2.2 Siphonaria concinna

Although mean maximum sizes for *S. concinna* were greater in rock pools of nonreserve than reserve sites in nine out of 12 months, significant differences existed in two out of 12 months (see asterisk in Fig 5b).

## 3.3.2.3 Siphonaria serrata

Mean maximum sizes of *S. serrata* were greater in rock pools of non- reserve than reserve sites for 11 out of 12 months. Significant differences, however, existed in three (August, October and March) of the 12 months sampled (see asterisk in Fig. 5c).

# 3.3.2.4 Helcion concolor

*Helcion concolor* had higher mean maximum sizes in rock pools of reserve sites than non-reserve sites (Fig. 5d). This species showed significant differences in mean maximum sizes for three (August, January and February) out of 12 months (Fig. 5d).

# 3.3.2.5 Dendrofissurella scutellum

Mean maximum sizes of *D. scutellum* were significantly greater in rock pools of reserve than non-reserve sites (Fig. 5g). Significant differences in mean maximum sizes were recorded for three (July, February and April) out of 12 months (Fig. 5).

# 3.3.2.6 Helcion pruinosus

Although greater mean maximum sizes were found in rock pools of non-reserve than reserve sites (Fig. 5e) throughout the 12 months sampled, significant differences existed in three (August, December and April) of the 12 months (see asterisk in Fig. 5e).

# 3.3.2.7 Scutellastra granularis

Non-reserve sites recorded greater mean maximum sizes for seven out of 12 months (Fig. 5f). Significant differences in mean maximum sizes, however, were observed in two out of those seven months, namely November and February (see asterisk in Fig. 5f).

# 3.3.2.8 Scutellastra pica

Only three individuals belonging to this species were recorded at Dwesa (a reserve site), with shell lengths ranging from 27mm to 44mm. Significant differences in

mean maximum sizes of this species existed in one out of the 12 months sampled November (see asterisk in Fig. 5h).

## 3.3.1 Size frequency distribution

#### 3.3.1.1 Cellana capensis

Size frequency distribution for *C. capensis* indicated high numbers of larger individuals in reserves rather than non-reserve sites (Fig. 6a). Two peaks (15mm and 20mm) were prevalent (Fig. 6a) and there were more large-sized limpets inside reserves than non-reserves. The largest recorded individual of this species in rock pools of reserve and non-reserve sites was 42.5mm and 38.5mm, respectively. The histogram representing size classes of this species indicated a bimodal pattern with modes at 15mm and 20mm in both reserve and non-reserve sites (Fig. 6a).

#### 3.3.1.2 Siphonaria concinna

There were greater frequencies of smaller sized individuals in rock pools of nonreserve (with higher numbers of this species ranging within the size class of 12 to 16mm) than reserve sites (which illustrated greater frequencies from the size class of 16mm to 24mm and upwards) (Fig. 6b). Reserve sites showed a bimodal pattern in size frequency distribution of *S. concinna,* with modes occurring in the same size class, 12mm and 15mm (Fig. 6b). Non-reserve sites had a multimodal pattern which was indicated by modes ranging from 12mm to 20mm (Fig. 6b)

#### 3.3.1.3 Siphonaria serrata

Smaller sized individuals were more common in rock pools of non-reserve sites (Fig. 6c), while reserve sites recorded greater frequencies of larger size classes (from 24mm upwards). Limpets between 15mm and 20mm had the highest frequency in both reserve and non-reserve sites (Fig. 6c). Reserve sites indicated a bimodal

pattern (12mm and 15mm) in size frequency distribution pattern of this species, whereas non-reserve sites had unimodal distribution (15mm) (Fig. 6c).

## 3.1.3.4 Helcion concolor

Size frequencies for *H. concolor* illustrated more large-sized individuals (from 30mm upwards) in rock pools found inside MPAs (Fig. 6d). Non-reserve sites, however had greater frequencies of limpets ranging from 20mm to 25mm (Fig. 6d). Size frequency distribution illustrated a unimodal pattern in reserve sites (20mm) and a bimodal pattern in non-reserve sites (20mm and 35mm) (Fig. 6d).

## 3.1.3.5 Scutellastra longicosta

Although there were few individuals recorded throughout the study, greater frequencies of larger sized individuals (from 30mm upwards) were found in rock pools of non-reserve sites (Fig. 6e). A bimodal frequency distribution pattern was observed in rock pools of reserve sites (15mm and 40mm) for this species, while non-reserve sites were unimodal (35mm to 40mm) (Fig. 6e).

## 3.1.3.6 Dendrofissurella scutellum

There were more smaller-sized individuals (16mm – 20mm) in rock pools of nonreserve sites with a peak in frequency of this size class, while all individuals recorded in rock pools of reserve sites ranged from 17mm – 35mm (Fig. 6f). The size frequency distribution for *D. scutellum* was multimodal in reserve sites with modes at 15mm to 20mm, 25mm and 30mm to 35mm (Fig. 6f). Non-reserve sites showed equal distribution of size frequencies for this species (Fig. 6f).

# 3.1.3.7 Helcion pruinosus

Greater frequencies of larger sized individuals for *Helcion pruinosus* were recorded in rock pools of non-reserve than reserve sites (Fig. 6g). Reserve sites had greater frequencies of individuals ranging between 11mm and 15mm while non-reserve sites had peaks in size classes ranging from 16mm to 20mm (Fig. 6g). Size frequency distributions in reserve sites indicated a bimodal pattern with modes at 10mm and 15mm, while non-reserve sites indicated multimodal patterns with modes at 10mm, 15mm, 20mm and 23mm (Fig. 6g).

Table 4: Result	ts of the 4-way AN	OVA based	on mean siz	ze estimates	of the intertidal
limpet species (	* = P<0.05, ** =	P<0.01, ***	* = P<0.00	1).	

Source of variation	SS	Df	MS	F	р
a) Cellana.capensis					
Month	2458	11	2235	28.407	***
Reserve	5857	1	5857	19.044	*
Month * Reserve	2009	11	183	2.3201	*
Site (Reserve)	6594	2	329	0.398	0.68
Area (Reserve * Site)	7576	8	9463	120.281	***
Error	73417	9332	79		
b) Siphonaria concinna					
Month	6828.9	11	620.8	18.613	***
Reserve	1305.4	1	1305.3	0.0985	0.78
Site (Reserve)	26055	2	13027.5	2.805	0.12
Area (Reserve * Site)	4190.6	8	5238.3	157.062	***
Error	311742	9347	33.35		
c) Siphonaria serrata					
Month	1017	11	92.46	5.888	***
Reserve	1287	1	1287.0	1.4846	0.35
Site (Reserve)	1710.4	2	855.1	0.4372	0.66
Area (Reserve * Site)	1765.35	8	2206.6	140.523	***
Error	146748	9345	15.7		
d) Helcion concolor					
Month	593.25	11	53.932	6.4518	***
Reserve	106.87	1	106.874	0.2239	0.68
Month * Reserve					
Site (Reserve)	941.49	2	470.745	13.071	*
Area (Reserve * Site)	316.67	8	39.584	4.7354	***
Error	78132.1	9347	8.359		
e) Scutellastra longicosta					
Month	181.86	11	16.5325	1.9704	*
Reserve	43.85	1	43.849	0.1004	0.78
Month * Reserve	95.43	11	8.675	1.350	0.41
Site (Reserve)	936.03	2	468.016	3.2503	0.92
Area (Reserve * Site)	1308.74	8	163.592	19.5173	***
Error	782534	9336	8.381		
f) Dendrofissurella scutellum					
Month	10.612	11	0.9647	1.0869	0.37
Reserve	0.65	1	0.6551	0.2305	0.68
Month * Reserve	18.332	11	1.6665	1.8776	*
Site (Reserve)	5.97	2	2.9856	1.5481	0.26
Area (Reserve * Site)	10.632	8	2.0791	2.3425	*
Error	8287	9337	0.8875		

# Table 4 (continued)

Source of variation	SS	Df	MS	F	р
g) C. oculus					
Month	14.26	11	1.2964	0.80059	0.64
Reserve	21.17	1	21.1654	0.86653	0.45
Month * Reserve	14.79	11	1.3449	0.83053	0.61
Site (Reserve)	52.2	2	26.1034	3.45921	0.08
Area (Reserve * Site)	67.23	8	8.4031	5.18903	***
Error	15120.4	9337	1.6194		
h) H. pruinosus					
Month	192.96	11	17.542	5.795	***
Reserve	835.9	1	835.99	0.883	0.45
Month * Reserve	96.29	11	8.754	2.892	***
Site (Reserve)	2031.7	2	1015.87	2.266	0.17
Area (Reserve * Site)	4100.0	8	512.50	169.315	***
Error	28259.6	9336	3.027		
i) S. granularis					
Month	98.546	11	8.908	12.090	***
Reserve	135.34	1	135.345	1.098	0.40
Month * Reserve	119.21	11	10.837	14.626	***
Site (Reserve)	264.56	2	132.280	1.518	0.28
Area (Reserve * Site)	796.54	8	99.568	134.373	***
Error	6917.82	9336	0.741		
j) S. argenvillei					
Month	0.7565	11	0.6877	1.8876	0.04
Reserve	0.1532	1	0.1532	1.58045	0.33
Month * Reserve	0.7565	11	0.06877	1.88761	0.36
Site (Reserve)	0.2028	2	0.10138	1.50633	0.27
Month * Site (Reserve)					
Area (Reserve * Site)	0.0742	8	0.07177	1.96997	*
Month * Area (Reserve*Site)					
Error	340.101	9335	0.03643		
k) S. pica					
Month	15.21	11	1.38283	3.77148	***
Reserve	3.445	1	3.4450	0.83188	0.46
Month * Reserve	15.21	11	1.3828	3.77148	***
Site (Reserve)	8.838	2	4.419	2.095	0.18
Month * Site (Reserve)					
Area (Reserve * Site)	18.890	8	2.36123	6.43992	***
Month * Area (Reserve*Site)					
Error	3423.46	9337	0.36665		

**Table 5:** Results of the 4-way ANOVA based on mean maximum size estimates of the intertidal limpet species (\* = P < 0.05, \*\* = P < 0.01, \*\*\* = P < 0.001).

Source of variation	SS	Df	MS	F	р
a) Cellana Capensis					-
Month	7300.9	11	663.7	14.588	***
Reserve	8471.4	1	8471.4	4.324	0.17
Month * Reserve	2211.5	11	201	4.418	***
Site (Reserve)	3917.6	2	1958	0.7117	0.52
Area (Reserve * Site)	22039	8	2755	60.553	***
Error	630.58	1386	45.5		
b) Siphonaria concinna					
Month	15707	11	1427.9	33.8553	***
Reserve	3602	1	3602	0.3739	0.60
Month * Reserve	4111	11	373.8	8.8624	***
Site (Reserve)	19270	2	9635	3.7779	0.07
Area (Reserve * Site)	20453	8	2556	60.6190	***
Error	58035	1376	42.2		
c) Siphonaria serrata					
Month	13146.6	11	1195.1	29.5757	***
Reserve	2934.3	1	2934.3	6.2914	0.13
Month * Reserve	1894.8	11	172.2	4.2628	***
Site (Reserve)	932.8	2	466.4	0.1961	0.83
Area (Reserve * Site)	19042.9	8	2380.3	58.9045	***
Error	56049.4	1387	40.4		
d) Helcion concolor					
Month	2749.7	11	249.98	5.1993	***
Reserve	257.4	1	257.42	0.1555	0.73
Month * Reserve	1537.9	11	139.81	2.9519	***
Site (Reserve)	3310.4	2	1655.22	23.7337	***
Area (Reserve * Site)	559.5	8	69.94	1.4547	0.17
Error	65724.7	1367	48.08		
a) Scutellastra longicosta					
Month	2550.89	11	231.89	1 6793	***
Reserve	2350.85	1	231.65	0.15400	0.73
Month * Reserve	696.2	11	63.29	1 2771	0.73
Site (Reserve)	3144.4	2	1572.2	4,4089	0.05
Area (Reserve * Site)	2909.7	8	363.71	7,3391	***
Error	67201.7	1356	49.55		
f) Dendrofissurella scutellum					
Month	121.55	11	11.0503	2.0169	*
Reserve	19.40	1	19.402	2.1495	0.28
Month * Reserve	159.37	11	14.4889	2.645	**
Site (Reserve)	18.06	2	9.0329	0.884	0.45
Area (Reserve * Site)	82.59	8	10.3243	1.8845	0.06
Error	7423.5	1355	5.4786		
g) Cymbula oculus					
Month	157.1	11	14.287	1.3440	0.19
Reserve	83.6	1	83.604	0.9268	0.44
Month * Reserve	158.7	11	14.432	1.3577	0.19
Site (Reserve)	180.7	2	90.358	3.5875	0.08
Area (Reserve * Site)	204.1	8	25.524	2.40112	*
Error	14403.8	1355	10.630		

Source of variation	SS	Df	MS	F	р
h) Helcion pruinosus					
Month	458.74	11	41.70	3.3793	***
Reserve	1473.12	1	1473.12	0.7583	0.48
Month * Reserve	367.2	11	33.88	2.7055	**
Site (Reserve)	3889.3	2	1944.66	2.3925	0.15
Area (Reserve * Site)	6652.1	8	831.51	67.3790	***
Error	16598.5	1345	12.34		
i) Scutellastra granularis					
Month	262.09	11	23.826	7.6699	***
Reserve	111.52	1	111.521	0.9487	0.43
Month * Reserve	288.10	11	26.191	8.4310	***
Site (Reserve)	235.34	2	117.674	1.0078	0.41
Area (Reserve * Site)	955.26	8	119.408	38.4378	***
Error	4178.28	1345	3.106		
j) Scutellastra argenvillei					
Month	2.564	11	0.23309	0.9395	0.50
Reserve	0.318	1	0.3184	1.0354	0.42
Month * Reserve	2.564	11	0.2331	0.9395	0.50
Site (Reserve)	0.615	2	0.3076	1.0624	0.39
Area (Reserve * Site)	2.323	8	0.2905	1.1709	0.31
Error	333.696	1345	0.24809		
k) Scutellastra pica					
Month	75.08	11	6.82613	2.83636	**
Reserve	7.31	1	7.31058	1.03598	0.42
Month * Reserve	75.08	11	6.82613	2.83636	**
Site (Reserve)	14.12	2	7.06194	0.95604	0.42
Area (Reserve * Site)	60.02	8	7.50296	3.1176	**
Error	3236.94	1345	2.40665		

# Table 5 (continued)



**Fig. 4a-f.** Mean sizes (±SE) of the limpet species in rock pools of reserve and non-reserve sites (\* = Months with significant differences)



**Fig. 5.** Mean maximum sizes (±SE) of the limpet species in rock pools of non-reserve and reserve sites (\* = Months with significant differences).



**Fig. 6a.** Size frequency distribution of *Cellana capensis* in rock pools of reserve (R) and non-reserve sites (NR)



**Fig. 6b.** Size frequency distribution of *Siphonaria concinna* in rock pools of reserve (R) and non-reserve sites (NR)



**Fig. 6c.** Size frequency distribution of *Siphonaria serrata* in rock pools of reserve (R) and non-reserve sites (NR)



**Fig. 6d.** Size frequency distribution of *Helcion concolor* in rock pools of reserve (R) and non-reserve sites (NR)



**Fig. 6e.** Size frequency distribution of *Scutellastra longicosta* in rock pools of reserve (R) and non-reserve sites (NR)



**Fig. 6f.** Size frequency distribution of *Dendrofissurella scutellum* in rock pools of reserve (R) and non-reserve sites (NR)



**Fig. 6g.** Size frequency distribution of *Helcion pruinosus* in rock pools of reserve (R) and non-reserve sites (NR)

## 3.4 DISCUSSION

Month had a significant effect on mean sizes of eight out of 11 species and this study highlighted significant differences in mean sizes of six species, namely *C. capensis, D. scutellum, H. pruinosus, S. granularis, S. pica* and *S. argenvillei.* Greater mean sizes were found in rock pools of reserve sites for four (*C. capensis, D. scutellum, S. pica* and *S. argenvillei.*) out of the species stated above. Territorial limpets such as S. longicosta (Nakin et al., 2012), which had greater mean sizes in non-reserve sites, are usually solitary and surrounded by tufts of brown algae which act as a food source and possibly shelter the individual from predators (pers. obs.).

The observed greater mean sizes in reserve than non-reserve sites can be attributed to protection from human harvesting. Adjacent non-reserve sites on the other hand, experience higher predation pressure from humans as they are not protected and harvesting of these intertidal invertebrates (in both rock pools and emergent rock) occurs daily with harvesters collecting bigger sized individuals. Branch and Odendaal (2003) compared populations of the limpet Cymbula oculus inside and outside MPAs and found that individuals inside MPAs were 30-50% larger thereby emphasizing the importance of these 'no-take' reserve sites for base line studies on harvesting effects. Similarly, in this study, mean and mean maximum sizes for C. oculus were 50% greater in reserve than non-reserve sites. Similarly, Rogers-Bennet et al. (2013) observed dramatic declines in population sizes due to exploitation of red abalone in a MPA merely three years after it was open to fishing. Differences in limpet body size may also be attributed to density-dependent growth rates with faster growth occurring in areas where density is lower (Hobday, 1995). In areas where there are greater densities of smaller sized individuals (e.g. non-reserve sites), competition for space and food increases (Boaventura et al., 2003) in comparison to areas with low densities which provide room for growth.

Significant differences were found in mean maximum sizes of eight out of 11 limpet species (C. capensis, S. concinna, S. serrata, H. concolor, D. scutellum, H. pruinosus, S. granularis, and S. pica) and mean maximum sizes were greater in rock pools of reserve than non-reserve sites for four of the species stated above (C. capensis, H. concolor, D. scutellum, and S. pica). Scutellastra granularis, H. pruinosus, S. concinna and S. serrata, on the other hand, illustrated greater mean maximum sizes in the latter. Intertidal rock pools which were sampled during this study indicated larger-sized limpets inside MPAs than in adjacent non-reserve sites for some species. Larger limpet sizes in reserve sites can be attributed predation by humans on larger individuals in non-reserve sites, while smaller mean sizes in non-reserve areas is attributable to greater competition between smaller sized and larger sized individuals in these sites. Small-sized limpets have small radulae which are more efficient and can remove algae much closer to the rock (Hobday, 1995), therefore large limpets would be outcompeted in areas such as non-reserves where there are greater densities of small-sized limpets. Similarly, Espinosa et al., (2009) found larger sized individuals of the limpet *Patella ferruginea* in sites that were 'under custody' (marine reserves) when compared to easily accessible sites and foraging by humans was the most probable explanation. These results are similar to numerous studies sites (Kido & Murray 2003, Fenberg & Roy 2008) which have also found larger sized invertebrates in reserve than non-reserve sites and highlight the negative effects exploitation poses on some intertidal invertebrate size structures.

In conclusion, the hypotheses of no variation in limpet sizes were disproven as greater mean and mean maximum sizes were found in rock pools of reserve than non-reserve sites for some species. Site, area and species-specific effects in limpet size structure were instead observed as mean and mean maximum sizes were significantly affected by sites and areas. These results, therefore, indicated that marine reserve effects on limpet population size structure in rock pools are speciesspecific. CHAPTER 5:

# **POPULATION RECRUITMENT**

## **4.1 INTRODUCTION**

Intertidal molluscs, which are the main target taxa for artisanal fisheries (Cole et al., 2011), are of nutritive value to humans (Lasiak, 1992) and are collected recreationally as fishing bait because of their large muscular foot (Espinosa et al., 2009). These intertidal grazers play a major role in structuring the intertidal zone communities (Branch & Odendaal, 2003) by maintaining distribution of other organisms within the habitat (Davies et al., 2006) due to their efficient grazing (Chelazzi et al., 1998). Reproduction in limpets is by means of broadcast spawning (Dunmore & Schiel, 2000) and they play an important role in controlling algal biomass (Coleman et al., 2006) as they feed on microalgae attached on the rocky substrate (Lasiak, 1993).

Enormous interest has been raised by the ability of MPAs to improve species conservation and potentially fisheries yields through larval export (spillover) as well as adult and juvenile export (Gruss et al., 2011). These MPAs provide the opportunity to inform fisheries' managers about natural growth and mortality rates (Barrett et al., 2009) of intertidal organisms as well as structural and functional features of marine food webs (Libralato et al., 2010) and reproductive outputs of marine organisms (Kido & Murray, 2003). Key interest for conservationists lies on the amount of spillover offered by reserves to non-reserve sites without significantly reducing the protection offered by MPAs to intertidal populations (Gruss et al., 2011). This is because the size of spill-over relative to populations outside the reserves is important as managers rely on such information to determine the size and extent of future reserves (Cole et al., 2011).

The intertidal zones are characterized by numerous habitat types, some of which are irregular patches of rock pools (tidal pools). These rock pools may serve to provide refuge (Martins et al., 2007) from wave action, high temperatures and act as nurseries for many intertidal species (Firth et al., 2009). Analysis of these patchy,

isolated habitats, such as intertidal pools, is a key requisite in order to inform management of current and future marine reserves.

Recruitment is a key component of population structure and dynamics (Espinosa et al., 2011), and factors affecting intertidal limpet recruitment include environmental processes such as sea surface temperature (Broitman et al., 2001) and coastal upwelling (Hoffmann et al., 2012). Habitat complexity (Espinosa et al., 2011), survival of larvae post spawning (Mandal et al., 2010), distribution of adult individuals as well as predation (Bohn et al., 2013) also have an effect on limpet recruitment. While investigating recruitment of intertidal invertebrates along the west coast of South Africa, Hoffmann et al. (2012) found spatial variation which was attributed at large scales to differences in upwelling intensity along the study sites, while small scale variation was due to behavioural responses in selection of settlement sites.

In this chapter, the effects of Marine Protected Areas (MPAs) on intertidal limpet recruitment were investigated. Removal of bigger-sized individuals by harvesters can lead to reduced fecundity in a population (Espinosa et al., 2009). On the assumption that marine reserves provide protection from exploitation, the hypothesis of greater mean recruit density in rock pools of reserve than non-reserve sites was tested. A comparison of the distribution patterns of limpet recruits in rock pools both inside and outside marine reserves was made.

# **4.2 MATERIALS & METHODS**

# 4.2.1 Sampling procedure

Sampling was done in four sites, two reserve (Dwesa-Cwebe and Hluleka Nature reserves) and two non-reserve sites (Nqabara and Presley's Bay) over a period of 12 months (June 2011 – May 2012) (Fig. 1 in Chapter 1). In each study site 27 rock pools, with well defined boundaries, were identified and sampling occurred in these pools throughout the study (27 rock pools per study site x 4 sites = 108 rock pools).

Within each rock pool, three random throws of a square quadrat (25 x 25cm) were conducted and limpet recruits found inside were identified (using a magnifying glass and a field guide book), counted and recorded every month in non-reserve and non-reserve sites. Recruits of these limpets were defined as those that were greater than 2mm and less that 10mm.

# 4.2.2 Statistical analysis

A 4-way nested analysis of variances (ANOVA) was used to test the effect of month, reserve, site and area on mean recruitment of the limpet species. Prior to the use of ANOVA, data were tested for normality and homogeneity of variances using Cochran's and Kolmogorov-Smirnov tests, respectively (Underwood, 1997; Zar, 2010). No transformation of data was necessary.

## 4.3 RESULTS

ANOVA results showed no significant differences (p > 0.05) in mean recruit density of *Helcion concolor, Scutellastra granularis and Helcion Pruinosus* between rock pools of reserve and non-reserve sites (Table 6). However, significant differences (P < 0.05) existed in the recruitment of *Cellana capensis, Siphonaria concinna* and *Siphonaria serrata* (Table 6).

#### Cellana capensis

Area and interaction of Month and Reserve (M x R) had significant effects (p < 0.05) on mean recruit density of *Cellana capensis* (Table 6). Month, reserve and site had no significant effect on mean recruit density of this species (Table 6). There were more months (seven out of 12) with higher mean recruit densities in rock pools of non-reserve than reserve sites (Fig. 7a), significant differences, however, existed in three out of 12 months (Fig. 7a).

#### Siphonaria concinna

Month, reserve and site had no significant effect (P > 0.05) on mean recruit density of *Siphonaria concinna* (Table 6). Area as well as the interaction of Month and Reserve (M x R) had significant effects (p < 0.05) on mean recruit density of this species (Table 6). Although there were more months (eight out of 12 months) with higher mean recruit densities in rock pools of non-reserve than reserve sites (Fig. 7b), significant differences were recorded in only three out of 12 months (Fig. 7b).

#### Siphonaria serrata

While area had a significant effect (p < 0.05) on mean recruit density of *Siphonaria serrata,* month, reserve and site had no significant effect (p > 0.05).

# Helcion concolor

ANOVA results indicated that month, reserve, site and area had no significant effect (P > 0.05) on mean recruit density of *Helcion concolor* in rock pools of reserve and non-reserve sites (Table 6).

# Helcion Pruinosus

Month, reserve and site had no significant effect (P > 0.05) on mean recruit density of *Helcion pruinosus* (Table 6). However, area had a significant effect (P < 0.05) on mean recruit density of this species (Table 6). Nqabara, a non-reserve site, had greater mean recruit density of this species in area of site N3 than those of N1 and N2.

# Scutellastra granularis

Month, reserve, site and area had no significant effect (P > 0.05) on mean recruit density of *Scutellastra granularis* in rock pools of reserve and non-reserve sites (Table 6).

**Table 6:** Results of the 4-way ANOVA based on recruit density of selected intertidal limpet species (\* = P < 0.05, \*\* = P < 0.01, \*\*\* = P < 0.001).

Source of variation	SS	df	MS	F	Ρ
a) <i>Cellana capensis</i>					
Month	216.8	11	19.709	2.112	0.24
Reserve	41.76	1	41.768	1.126	0.37
Month * Reserve	102.63	11	9.331	3.202	***
Site (Reserve)	75.82	2	37.912	2.599	0.14
Area (Reserve * Site)	118.15	8	14.77	5.069	***
Error	5495.2	1886	2.914		
b) <i>Siphonaria concinna</i>					
Month	91.53	11	8.322	1.071	0.46
Reserve	60.06	1	60.062	10.059	0.02
Month * Reserve	85.45	11	7.769	2.271	**
Site (Reserve)	4.23	2	2.119	0.096	0.90
Area (Reserve * Site)	178.41	8	22.302	6.52	***
Error	6450.78	1886	3.4203		
c) <i>Siphonaria serrata</i>					
Month	0.72	11	0.066	1.157	0.41
Reserve	0.123	1	0.123	1.456	0.43
Month * Reserve	0.622	11	0.057	0.497	0.96
Site (Reserve)	0.272	2	0.136	0.515	0.62
Area (Reserve * Site)	2.137	8	0.267	2.344	*
Error	214.987	1886	0.11399		
d) Helcion concolor					
Month	0.0419	11	0.00381	0.893	0.57
Reserve	0.0007	1	0.0007	0.1687	0.70
Month * Reserve	0.0469	11	0.0042	1.6493	0.08
Site (Reserve)	0.0057	2	0.0029	1.1053	0.38
Area (Reserve * Site)	0.0207	8	0.0026	0.999	0.43
Error	4.8773	1886	0.00258		
e) Helcion pruinosus					
Month	0.0186	11	0.0169	1.0001	0.5
Reserve	0.0045	1	0.0045	1.6544	0.28
Month * Reserve	0.0186	11	0.0017	1.6475	0.08
Site (Reserve)	0.0048	2	0.0023	1.069	0.39
Area (Reserve * Site)	0.01801	8	0.0023	2.1906	*
Error	1.9385	1.886	0.00102		

# Table 6 continued

Source of variation	SS	df	MS	F	Ρ
f) <i>Scutellastra granularis</i>					
Month	0.3158	11	0.0287	1.00001	0.5
Reserve	0.0358	1	0.0359	1.22366	0.33
Month * Reserve	0.3158	11	0.0287	1.54087	0.11
Site (Reserve)	0.0428	2	0.02142	1.12078	0.37
Area (Reserve * Site)	0.153	8	0.0191	1.02651	0.41
Error	35.142	1886	0.01863		





**Fig. 7.** Mean (± SE) recruit density of (a) *Cellana capensis* and (b) *Siphonaria concinna* in rock pools of reserve and non-reserve sites (\* = Months with significant differences).
## 4.4 DISCUSSION

The results showed that recruitment of selected intertidal limpet species in rock pools were independent of site exploitation. Month, reserve and site had no significant effect on mean recruitment of the limpet species in rock pools of reserve and non-reserve sites. Therefore, the hypothesis of greater recruit densities in rock pools inside marine reserves was not supported as mean recruit density was highest in non-reserve than reserve sites. Results of this study indicate temporal variation in the recruitment of two out of six species. These significant differences during some months may be attributed to reproductive cycles of these limpet species. Espinosa et al. (2011) recorded temporal variation in mean recruitment of the endangered limpet *Patella ferruginea* and attributed this to reproductive cycles of patellid limpets which are determined by seasonal cues (recruits settle in spring and early autumn). Similarly results of this study illustrate greater mean recruit density in rock pools of non-reserve sites during spring and autumn months.

Increased recruit densities outside "no take" MPAs can be attributed to greater predation inside reserves in comparison to human exploitation outside reserves (which is governed by size and species). Due to protection from exploitation by marine reserves, there are greater densities of intertidal limpets inside marine reserves as well as higher predator abundance and this can lead to higher predation on vulnerable limpet recruits inside reserves. According to Boaventura et al. (2003), mortality of small limpets is greater when large limpets, which are superior competitors, are present. Barrett et al., (2009) also found significant decline of selected intertidal invertebrate species inside marine reserves than outside. Similarly, rock pools provide refuge to not only limpets but other marine organisms which may predate on smaller limpets (juveniles). Increased predation on juveniles following increased predator abundance could account for the observed decline of sub-legal sized abalone in marine reserves (Barrett, et al., 2009). Changing prey abundance and/or availability greatly affects foraging by predators (Coleman & Hockey, 2008),

meaning that intensity of predation in rock pools of reserve sites will be greater than non-reserve sites due to high density of prey (limpets).

Results of this study also indicated that effects of protection by MPAs on recruitment of these limpet species were area- and species-specific. This was illustrated by the significant effect of area on mean recruit density of four out of six species. These findings suggest spatial variation in recruitment of these species at scales of 100m apart and that protection of these limpets could be according to zones rather than general. Bohn et al. (2013) also observed spatial variation in mean recruit densities of *Crepidula fornicate* and attributed these differences between sites to geographical features of the areas.

Non-reserve sites differ in that intertidal limpets are mainly targeted by humans. Artisanal exploitation of intertidal species has a long and well-documented history in the Transkei region of South Africa (Nakin et al., 2012), and differences in the intensity of exploitation have been found to be governed by species, size (Lasiak, 2006), and regional differences (Cole et al., 2011). Large limpets are specifically targeted at non-reserve sites, as juveniles are too small to be eaten.

In conclusion, limpet mean recruit density was significantly greater in rock pools of non-reserve than reserve sites in some months for some species. Observed temporal variations and area effects on mean recruit density of limpet species indicate that recruitment in rock pools of reserve and non-reserve sites is species-specific. CHAPTER 5:

**GENERAL DISCUSSION** 

Understanding ecology of habitats such as tide pools informs management decisions on other isolated habitats such as islands and reserves. Variations in population structures of rock pools are influenced by physical factors such as temperature (Thompson et al., 2002; Steinarsdottir et al., 2003), salinity, oxygen (Methratta, 2004) and wave action (Noel et al., 2009). Differences found in limpet density, diversity, size structure and recruitment during this study can be attributed to regional, site as well as area differences in these physical factors. Thompson et al. (2002) reviewed rocky shore community structure and described how elevated temperatures in these microhabitats can lead to species becoming stressed. Increases in temperature can also lead higher salinity concentration in rock pools which may greatly affect diversity and density of organisms that cannot tolerate such conditions in rock pools. Differences in temperature have been shown to lead to migration by crustaceans in and out of rock pools depending on the seasons of the year (Steinarsdottir et al., 2003). Noel et al. (2009) assessed grazing dynamics in rock pools and found variations in the grazing activity of *Patella vulgata* which were attributed to site differences in wave exposure.

Significant differences in diversity of intertidal organisms may be controlled by factors such as of food availability/preference (Mieszkowska & Lundquist, 2011), predation (Firth & Crowe, 2008), exploitation intensity (Robinson, et al., 2008) as well as substrate heterogeneity (Meager et al., 2005). While studying interactions between the limpet *Patelloida latistrigata* and intertidal algae, Jernakoff (1985) suggested a preference by the limpet for some algal species over others. This was informed by the tendency of limpets, in areas where it was possible, to move away from macroalgae-rich patches in order to pursue the more preferred microalgae. Similarly, Mieszkowska & Lundquist (2011) found significant differences in intertidal limpet diversity at small spatial scales in New Zealand and not only attributed this to environmental characteristics such as thermal tolerances, but also to different grazing preferences among species. Consoli *et al.* (2013) on the other hand found greater species diversity in reserve than non-reserve sites when investigating marine

reserve effects on fish assemblages. Greater diversity of fish in reserve areas was found to be linked to protection from exploitation by marine reserves.

Although greater diversity was recorded in non-reserve than reserve sites, results of this study indicated no significant effect (P > 0.05) by marine reserve status on the diversity of intertidal limpets. Limpet diversity was independent of site exploitation but rather governed by regional differences in the distribution of these herbivores along the southeast coast (rock pools found in study sites along the southern region, Dwesa and Nqabara, had greater limpet diversity than those in the study sites of the central region, Hluleka and Presley's Bay). Similarly, Villamor & Becerro (2012) found no significant differences in diversity of fish and benthic species found in reserve and non-reserve sites along the Mediterranean coast. Differences in diversity were independent of site exploited but rather attributed to the different geographical locations of the study areas.

Results of this study also showed area effects in diversity of intertidal limpets and this may be due to differences in substrate/habitats along the study sites. Intertidal areas in Dwesa and Nqabara (southern region), which recorded the highest diversity indices, are composed of mainly flat-surfaced rock (pers. obs.) which favours the ability of limpets to adhere to the rock in order to avoid desiccation during low tide. Hluleka and Presley's Bay, on the other hand, are composed of more complex and uneven rock formations (pers. obs.) which may lead to difficulty in attaching to the rock for less adapted limpets; This may be a possible explanation for lower diversity indices recorded in these two sites. Similarly, Gingold et al. (2010) described a positive relationship between habitat complexity and species diversity and attributed this to more niches provided by structurally complex habitats in comparison to those that are less complex.

Results of this study indicated no significant effect (p > 0.05) by marine reserve status on mean density of intertidal limpets. Exploitation seems to have an effect on intertidal limpet density of some species as rarely exploited species such as Siphonaria concinna and Siphonaria serrata were more abundant in rock pools of non-reserve sites, while the heavily exploited Helcion concolor had greater densities in rock pools of reserve sites. This shows that intertidal limpet density in rock pools is species-specific as results of this study illustrated greater density of heavily exploited species in rock pools of reserve than non-reserve sites. Mean density of intertidal limpets in rock pools of reserve and non-reserve sites may have been influenced by exploitation (Consoli et al., 2013), habitat complexity (Navarro, 2005) as well as predation intensity (Coleman & Hockey, 2008; Barrett et al., 2009). Similarly, Consoli et al. (2013) found greater density of heavily exploited fish species in reserve than non-reserve sites, while the least exploited species had mean densities that were independent of site exploitation. These results of higher densities in marine reserve sites were attributed to protection from exploitation by MPAs. Robinson et al. (2008) also showed that exploitation can alter community structures considerably. This was indicated by resultant increases in grazer (limpet) abundance following the removal of mussels on the rocky shore. Habitat complexity has also been shown not only to have a great effect on intertidal invertebrate diversity, but density as well (Underwood & Chapman, 1996; Navarro, 2005; Lasiak, 2006). Stamoulis & Friedlander (2013) illustrated that significant differences in fish densities between reserve and non-reserve sites were governed by differences in habitat complexity rather than protection from exploitation. Silva et al. (2008) have shown that predation is an important factor in controlling intertidal limpet abundance as it accounted for more than 50% reduction in limpet density during the study. Therefore, the greater limpet density that was found in non-reserve than reserve sites in this study may be attributable to high predator abundance inside MPAs as reserves not only provide protection to prey but also predators such as small crabs and fish species which eat these limpets.

The hypothesis of no variation in mean and mean maximum sizes of limpets was not supported, as mean and mean maximum sizes were significantly greater in rock pools of reserve than non-reserve sites for some species during this study. Reserve sites were also found to have greater densities of larger-sized limpets than nonreserve sites where smaller sized individuals were prevalent. Consoli et al. (2013) also found greater densities of larger sized fishes in areas which were inside MPAs than outside and attributed this to protection from exploitation. These results are consistent with the variation in limpet density which was observed between reserve and non-reserve sites of this study. In non-reserves sites (Ngabara and Presley's Bay) smaller mean and mean maximum sizes were recorded for a majority of the common species, whereas in reserve sites (Dwesa and Hluleka) greater mean and mean maximum sizes were apparent. This can be attributed to greater competition due to the high density of intertidal limpets in non-reserve sites. High densities of intertidal invertebrates lead to more competition for space and food (Hobday, 1995), rather than room for growth which is provided by less dense reserve areas. Competition in microhabitats such as tide pools has been shown to vary with body size. Arakaki & Tokeshi (2012) found that smaller individuals of gobies found in tide pools would tend to avoid areas within the pool which had greater abundance of larger individuals due to competitive interactions.

Results of this study indicated high mean and mean maximum sizes inside protected areas than outside for some species, which showed that intertidal limpet size structures are greatly affected by exploitation. These results have implications for reserve management, as a decrease in mean and mean maximum sizes within a population leads to a decrease in the reproductive output as well (Branch & Odendaal, 2003; Kido & Murray, 2003). Quality of larvae, especially in broadcast spawners, increases with age (Gaylord et al., 2005; Fenberg & Roy, 2008), therefore, the bigger the mean maximum sizes of a population leads to better quality larval output. Removal of larger-sized individuals by harvesters in non-reserve sites could also lead to a possible decrease in the reproductive output of that

species as fecundity continues to increase with age and size in many marine species (Gaylord et al., 2005). The size and quality of larvae of some exploited marine organisms has been shown to be positively correlated with maternal length and age (Fenberg & Roy, 2008). Branch (1975) also concluded that decreases of about 20mm in shell length can result in as much as 90% reduction of gonadal production in the limpet *Patella concolor*. This can have a negative effect on broadcast spawners, such as limpets, as they require high concentrations of gametes in order for fertilization to occur (Kido & Murray, 2003). While reproductive output of the limpet *Cymbula oculus* was found to be a staggering 80-fold higher in unexploited than exploited sites, recruitment was three times higher in the latter (Branch & Odendaal, 2003). This led to the conclusion that MPAs supply recruits to adjacent sites (Branch & Odendaal, 2003; Espinosa et al., 2009).

Recruitment was recorded for six intertidal limpet species (Cellana capensis, Siphonaria concinna, Siphonaria serrata, Helcion pruinosus, Helcion concolor and Scutellastra granularis) in rock pools of reserve and non-reserve sites during this study, and results indicated greater mean recruit density in rock pools of nonreserve sites for C. capensis, S. concinna, H. pruinosus and S. granularis and greater mean recruit density in reserve sites for *S. serrata* and *H. concolor*. Marine reserves, therefore, had no significant effect on mean recruitment of intertidal limpets as rock pools found in Ngabara (a non-reserve site) had the greatest number of recruits while rock pools in Dwesa (a reserve site) had the least. This variation which was observed between reserve and non-reserve sites may be attributed to greater predation intensity experienced by juvenile individuals in rock pools of reserve sites (Barrett et al., 2009). MPAs provide protection to a number on marine organisms, some of which are predators to intertidal limpet species (e.g. crabs, starfish, etc). This, therefore, leads to high predation pressure on the more vulnerable juvenile limpets that are not yet able to defend themselves adequately (by attaching to the substrate) in comparison to bigger-sized individuals found in rock pools of reserve sites. In non-reserve sites, on the other hand, the most prevalent predator is human harvesters who tend to collect larger-sized individuals. This could be a possible explanation for the greater mean recruit density recorded in non-reserve sites as well as the smaller mean and mean maximum sizes in these sites. Similarly, Silva et al. (2008) found that smaller limpets were more vulnerable to predation as predators such as small crabs and fish tend to target smaller sized individuals in a population due to less resistance offered by these small limpets during dislodging.

In conclusion, exploitation of marine resources continues to be a detrimental factor to conservation endeavours and MPAs are important in addressing these human impacts. Findings of this study recorded species-specific responses by intertidal limpets to exploitation as great variation was observed in limpet diversity, density, size structure and recruitment between rock pools of reserve and non-reserve sites. These results indicate the importance of MPAs in conserving these important intertidal invertebrate populations and that a regional, species-specific approach may be considered for future reserve design and management along the southeast coast of South Africa.

Long-term sampling of intertidal limpet density, diversity, size and recruitment is further recommended before general conclusions are made. Further investigation into the effects of marine reserves on predation and competition of these limpets in rock pools is also recommended. This will help in understanding the major processes affecting intertidal community structure at small and large temporal and spatial scales as well as long term responses of intertidal limpets to exploitation.

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