EFFECTS OF HABITAT PATCH SIZE AND ISOLATION ON THE POPULATION STRUCTURE OF TWO SIPHONARIAN LIMPETS

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Abstract

Habitat fragmentation is a fundamental process that determines trends and patterns of distribution and density of organisms. These patterns and trends have been the focus of numerous terrestrial and marine studies and have led to the development of several explanatory hypotheses. Systems and organisms are dynamic and no single hypothesis has adequately accounted for these observed trends. It is therefore important to understand the interaction of these processes and patterns to explain the mechanisms controlling population dynamics.

The main aim of this thesis was to test the effect of patch size and isolation on organisms with different modes of dispersal. Mode of dispersal has previously been examined as a factor influencing the effects that habitat fragmentation has on organisms. Very few studies have, however, examined the mode of dispersal of marine organisms because it has long been assumed that marine animals are not directly influenced by habitat fragmentation because of large-scale dispersal. I used two co-occurring species of siphonariid limpets with different modes of dispersal to highlight that not only are marine organisms affected by habitat fragmentation but that they are affected in different ways. The two species of limpet, *Siphonaria serrata* and *Siphonaria concinna*, are found within the same habitat and have the same geographic range along the South African coastline, however, they have different modes of dispersal and development.

The effect of patch size on organism density has been examined to a great extent with varied results. This study investigated whether habitat patch size played a key role in determining

population density and limpet body sizes. The two species are found on the eastern and southern coasts of South Africa were examined across this entire biogeographic range. Patch size was found to have a significant effect on population density of the pelagic developer, *S. concinna*, but not the direct developing *S. serrata*. Patch size did play a role in determining limpet body size for both species. *S. concinna* body size was proposed to be effected directly by patch size whilst *S. serrata* body size was proposed to be affected indirectly by the effects of the *S. concinna* densities. The same patterns and trends were observed at five of the seven examined regions across the biogeographic range. The trends observed for *S. concinna* with respect to patch size conform to the source-sink hypothesis with large habitat patches acting as the source populations whilst the small habitat patches acted as the sink populations.

Many previous studies have focused on the effects of habitat patch size at one point in time or over one season. I tested the influence of habitat patch size on the two species of limpets over a period of twelve months to determine whether the trends observed were consistent over time or whether populations varied with time. *S. concinna* showed a consistently significant difference between small and large patches; whilst *S. serrata* did not follow a consistent pattern. The mode of dispersal for the two limpets was used to explain the different trends shown by the two species. This examination allowed for the determining of source and sink populations for *S. concinna* through the examination of fluctuations in limpet body sizes and population densities at small and large habitat patches over twelve months. The direct developing *S. serrata* trends could not be explained using source-sink theory, as populations were independent from one another. *S. serrata* demonstrated body size differences at small and large patches which, may be explained by interspecific and intraspecific competition.

Habitat isolation is known to play an important role in determining the structure of assemblages and the densities of populations. In this study the population density of the pelagic developing *S. concinna* showed a weak influence of degree of isolation whilst that of the direct developing *S. serrata* did not, which may be because of habitat patches along the South African coastline not having great enough degrees of isolation. The population size-structure was influenced directly influenced by isolation for *S. concinna*, whilst the different population size structure for *S. serrata* may be explained by assemblage co-dependence. The mode of dispersal showed effects on the relationship of population density and population size-structure with habitat size and isolation.

This study indicates the importance of investigating patterns and processes across a range of spatial and temporal scales to gain a comprehensive understanding of factors effecting intertidal organisms.

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Chapter 1

General Introduction

Ecological understanding is based on the examination of the geographical distributions and densities of organisms (Turner, 1989; Levin, 1992; Boyce and McDonald, 1999). To be able to fully understand patterns and trends in the density and distribution of organisms, the determination of theories by which assemblages and ecosystems are organised must be quantified within and across systems (Levin, 1992). Pattern and scale are unavoidably intertwined as organisms interact and respond to their surrounding environment in different ways and at different scales (Levin, 1992; Lawton, 1999; Underwood, 2000 Turner *et al*., 2001; Coleman *et al*., 2006).

1.1 The importance of spatial patterning:

Landscape ecology emerged in the 1980s offering new concepts, theories and methods that all emphasise the importance of spatial patterning (Turner *et al.,* 2001). The term landscape refers to the landform and vegetation elements that contain and influence the ecological dynamics of a system (Wright, 1974; Turner, *et al.,* 2001). Landscape ecology is motivated by the desire to understand the development of patterns and processes in ecological systems (Urban *et al*., 1987). It places emphasis on the interaction between spatial pattern and ecological processes and essentially combines the spatial approach of a geographer with the functional approach of an ecologist (Turner *et al.,* 2001). Much importance is placed on spatial pattern and spatial scale in landscape ecology but it must be noted that an important factor that affects the development of ecological patterns and dynamics is that of time (Urban *et al*., 1987; Levin, 1992; Crowe, 1999).

Fine-scale observations are very often not true representations of the larger scale and generalizations cannot be used therefore to accurately predict what will be found at a landscape at a certain time (Urban *et al.,* 1987; Turner e*t al.,* 2001; Coleman *et al*., 2006). The problem comes with trying to define the boundaries of scale within landscapes. This is because ecosystems are not static, meaning that boundaries are often seen as fuzzy and constantly changing (Urban *et al.,* 1987; Levin, 1992; Turner *et al.,* 2001). Not only is the defining of the boundaries a common problem, but it is often found that processes happen at more than one scale (Urban *et al.,* 1987). This suggests that landscape ecology does not define specific scales that should be utilised when examining ecosystems; rather emphasis is placed on identification of the appropriate scale for the study in question (Urban *et al.,* 1987; Levin, 1992; Turner *et al.,* 2001). This is not to say that scale is specific to landscape ecology; many other areas utilise scale as a vital part of understanding systems. However, landscape ecology highlights the importance of scale and raised awareness to how vital scale is in understanding patterns and trends in ecology (Turner *et al*., 2001). There are many examples of considerable variation in densities of single species at different spatial scales and when linked with organism interconnectedness the two dictate the structure of assemblages (Underwood and Chapman, 1998). This has led to the idea that a system needs to be studied as a whole and possibly at several different scales to be fully understood and to resolve pattern complexity and dynamics (Urban *et al.,* 1987; Levin, 1992; Underwood and Chapman, 1998; Turner *et al.,* 2001, Coleman *et al.,* 2006; Burrows *et al*., 2009).

1.2 Habitat fragmentation:

Landscapes can be seen as matrices of suitable and unsuitable habitat patches (Fahrig and Merriam, 1985; 1994). The size and isolation of the patch and the type of surrounding habitat all

play major roles in determining whether a species will be present and the structure of assemblages (Fahrig and Merriam, 1985; Andrén, 1994; Fahrig and Merriam, 1994; Anderson 1999). The process that determines patch size, isolation and surrounding habitat is known as habitat fragmentation and most species live in habitat patches within fragmented landscapes (Krauss *et al*., 2003). The process of habitat fragmentation involves the reduction of size and dividing of larger habitats into smaller and isolated discontinuous habitat patches (Fahrig and Merriam, 1985; Andrén, 1994; Turner *et al.*, 2001, Franklin *et al.*, 2002; Krauss *et al*., 2003). Habitat fragmentation happens through natural processes, such as weathering of rock or fire, (Andrén, 1994; Fahrig and Merriam, 1994; Wright, 1974; Pickett and Thompson, 1978) and through increased expansion and intensification of human land use (Andrén, 1994; Fahrig and Merriam, 1994; Haila, 2002). The role that humans are playing in habitat fragmentation is seen to be dominant in many systems (Franklin *et al.*, 2002). Although human influence is dominant, the results from natural and human induced habitat fragmentation are more often than not seen in a negative light (Franklin *et al.*; 2002, Weins, 1994; Goodsell *et al*., 2007).

There are three major components of habitat fragmentation: (1) the loss of the original habitat; (2) the reduction of habitat patch size; and (3) the increase in isolation of patches (Andrén, 1994; Franklin *et al.*, 2002). All three components are known to affect species richness and population density (Andrén, 1994; Wilcox and Murphy, 1985; Krauss *et al*., 2003), increasing the likelihood of species extinction (Simberloff and Abele, 1982; Wilcox and Murphy, 1985). To address this concern, methods and theory about the effects of habitat fragmentation on assemblages have been developed using the theory of Island Biogeography (MacArthur and Wilson, 1967; Andrén, 1994). The theory of Island Biogeography assumes that suitable habitat patches are isolated from one another by hostile habitat and thus populations living in different patches are isolated from one another (MacAthur and Wilson, 1967; Diamond, 1975; Andrén, 1994). The theory of Island

Biogeography proposes that if a large habitat patch is split up into several smaller sized patches the population density of existing organisms will remain the same throughout all patches (MacArthur and Wilson 1967). Conversely, extremely small patches may have lower densities than larger patches because they might not be able to reach carrying capacity due to high extinction rates, resulting in a positive relationship between population density and patch size within some size ranges (Andrén, 1994; Hoover *et al.*, 1995; Ehrlen and Eriksson, 2000; Melbourne, 2004). The theory of Island Biogeography assumes that suitable habitat patches are separated from one another by inhospitable habitat (MacArthur and Wilson, 1967; Diamond, 1975). This inhospitable surrounding matrix has often been neglected and is seen as a barrier, but it affects the connectedness of matrices as not all surrounding habitats are impassable (Gustafson and Gardener, 1996; Joly *et al*., 2001; Jonsen *et al*., 2001; Cronin, 2003; Tanner, 2006).

Fragmentation generally leads to the creation of smaller sized patches (Connor and McCoy, 1979; Andrén, 1994). The Random Sample hypothesis, which can also be applied to individual species, assumes that population size is linked to proportion of suitable habitat in the landscape (Connor and McCoy, 1979; Andrén, 1994; Fahrig and Merriam, 1994; Hanski, 1994; Ehrlen and Eriksson, 2000; Dethier, 2003). To link habitat fragmentation with either Island Biogeography or the Random Sample hypothesis it is important to note that more often than not the islands considered are patches within a landscape and not islands surrounded by a completely hostile environment (Andrén, 1994; Gustafson and Gardener, 1996; Joly *et al*., 2001; Jonsen *et al*., 2001; Cronin, 2003; Tanner, 2006). As both natural and anthropogenic habitat fragmentation disturb the connectivity of a landscape, the extent of the disturbance affects the spatial configuration of the fragments and whether the organisms have the ability to disperse between patches (Goodesell *et al.,* 2007). If the surrounding landscape is habitable, although not ideal, distribution patterns may be better explained using landscape ecology approaches through

examination over different spatial and temporal scales (Turner *et al.*, 2001, Haila, 2002). Franklin *et al.* (2002) takes this argument further in stating that the affect of fragmentation of a habitat is in fact the "simplest form of heterogeneity" (Franklin *et al.*, 2002 : 23), creating areas of habitat and non-habitat and whether the creation of the habitat matrix itself will influence organism survival. A large proportion of terrestrial studies ignore the effects that the surrounding landscape has on population densities and species richness. They focus on patch size and isolation, while it has been found that different species respond to the surrounding landscape in different manners and at different scales (Haila, 2002; Krauss *et al.*, 2003). The effects of fragmentation will not be uniform for all species, the ability to adapt to the new patch size and ability to move between patches will greatly influence a population's chance of survival (Andrén, 1994; Franklin *et al*., 2002). For example a higher degree of fragmentation could lead to a greater quality of habitat for edge dwellers, whilst decreasing quality for interior species (Hoover, 1995; Bender *et al.*, 1998, Franklin *et al.*, 2002). A decline in population size is linearly related to the proportion of original habitat lost when the habitat is initially fragmented (Diamond, 1975; Andrén, 1994; Fischer, 2007). Patch area and isolation may not initially affect population size, but, at some point they will play a role in defining population size (Andrén, 1994). It is important to note that it is not only area and isolation that play a role in population survival and that the quality of the habitat after fragmentation is of great importance (Franklin *et al.*, 2002).

The degree of isolation of habitat patches has been linked to species richness, with an increase in isolation leading to a decrease in species richness (Macarthur and Wilson, 1967; Diamond, 1975; Krauss *et al*., 2003). In fragmentation studies, the degree of isolation is generally determined by the nearest suitable habitat patch or distance to nearest occupied patch or source patch. It may be more accurate to look at concentric isolation, determining the degree of isolation from all

surrounding patches and taking their sizes into account (Vos and Stumpel, 1995). The ability of organisms to move among patches determines whether and to what degree they are affected by isolation (Possingham and Roughgarden, 1990; Goodsell *et al*., 2007). Therefore once again the connectivity of habitat patches and the type of surrounding habitat play a critical role as to whether organisms can find and move to isolated patches (Gustafson and Gardener, 1996; Jonsen *et al*., 2001; Tanner, 2006).

Natural habitat fragmentation occurs in many linear landscapes, such as along rivers, coastlines and the tops of mountains. In these landscapes, habitat patches are often small and isolated from one another by other natural habitat patches (Goodsell *et al.,* 2007). Little is known about the effects of marine habitat fragmentation, and it is assumed that marine organisms respond to fragmentation in a similar fashion as terrestrial plants and animals that disperse through air or in other dispersive manners (Goodsell *et al*., 2007). These assumptions can only be made about planktonic developers and even then many marine organisms have very brief planktonic phases and often have no control of their movements, relying on oceanic currents to return them to the coastal environment (Possingham and Roughgarden, 1990; Roberts and Hawkins, 1999; Goodsell *et al*., 2007). This indicates that marine populations are not as connected as once thought and that they are affected by isolation, patch size and the surrounding patch matrix (Eggleston *et al*., 1999; Goodsell *et al*., 2007). Eggleston *et al.* (1999) suggests that a matrix comprised of many small suitable habitat patches will increase the probability that pelagic larvae will encounter suitable habitat rather than fewer large patches. It is important to note that in Eggleston *et al.* (1999) population densities were high when there were many small patches within the landscape matrix and that isolated patches were not taken into account. Kim and DeWreede (1996) found, however, that small habitat patches had fewer barnacles than larger patches conforming to common understanding of habitat fragmentation. Due to different

findings, two main approaches to studying fragmentation have emerged (Fischer and Lindenmayer, 2007). The first is the species-oriented approach which investigates the responses that individual species have to a range of processes. The second is the pattern-oriented approach which focuses on landscape patterns and their correlation with measures of species densities and richness. The two are highly complementary for understanding and managing fragmented landscapes, but in both cases it is difficult to identify all species and their influencing processes in individual studies (Fischer and Lindenmayer, 2007).

A growing body of evidence suggests that dispersal is important in setting the mean densities and patterns of fluctuations of many natural populations (Holt, 1985). Population survival is based on the colonisation-extinction relationship and if new recruits do not make it to suitable habitat patches then the likelihood of local extinctions increase (Andrén, 1994; Ehrlen and Eriksson, 2000; Hanski *et al*., 2000; Kinlin and Gaines, 2003 Melbourne, 2004). Therefore, it is pertinent to investigate whether organisms with different modes of dispersal have different responses to habitat patch size and degree of isolation. This is particularly true for marine systems as the variation in dispersal ability and mobility determine whether species can continue to exist within a system (Possingham and Roughgarden, 1990; Goodsell *et al*., 2007; Coleman *et al*., 2009). Although coastal marine systems are linear environments and it is often believed that patterns and trends found within them cannot be extrapolated to explain terrestrial trends and patterns; with the introduction of mode of dispersal as a key influencing factor linked to habitat fragmentation marine trends and patterns could ultimately be used to explain terrestrial systems.

1.3 This study:

Different species respond to their environment at different spatial and temporal scales (Jonsen and Fahrig, 1997). This study examined this by investigating by looking at two species of limpet with differing dispersal modes. The two species were selected because they are extremely similar except for mode of dispersal and for regional populations to survive the ability to disperse between patches is vital (MacArthur and Wilson, 1967; Diamond, 1975; Andrén, 1994; Fahrig and Merriam, 1994; Jonsen and Fahrig, 1997; Melbourne, 2004). Intertidal limpets are a convenient group in which to examine population dynamics as they exhibit great plasticity, and show a variety of developmental modes among closely related species (Creese, 1981; Chambers and McQuaid, 1994) Two intertidal pulmonate limpets were selected for examination to determine whether their differing modes of dispersal played a pertinent role in determining the effects that habitat fragmentation have on organisms. The two limpets that were selected were the direct developing, *Siphonaria serrata* (Fischer), and the pelagic developing, *Siphonaria concinna* (Sowerby), which are co-occurring species commonly found on the east and south coasts of South Africa (Chambers and McQuaid, 1998). Siphonariid species are herbivores that are found within the intertidal zone on rocky shores in the southern hemisphere, most commonly in the Indian Ocean (Chambers & McQuaid, 1994, Younge 1952, Hubendick, 1947). *S. serrata* and *S. concinna* are small limpets with a shell length of up to 25 mm (Chambers & McQuaid, 1994). As described by Chamber and McQuaid (1994) the outer shell of *S. serrata* is grey or brown in colour and ribbed. The ribs are a lighter colour and often produce spines giving the ribs a rough texture. *S. concinna* are a paler grey colour than *S. serrata* and the juveniles often have blue flecks on the outer shell that are not found on *S. serrata* juveniles. They too have ribs on the outer shell but *S. concinna* shells have smaller ribs in between the ribs reaching the apex (Chambers & McQuaid, 1994).

These two species have similar geographical distributions and morphologies and are both found within the mid littoral zone, but have differing developmental characteristics (Chambers & McQuaid, 1994, Hodgson, 1999). *S. serrata* are direct developers with larvae that develop on the substratum on which the egg masses are laid. Whereas *S. concinna* are planktonic developers; once hatched the planktotrophic larvae move into the water column where they develop before returning to the rocky shore approximately two months later to develop into adults (Chambers & McQuaid, 1994). The reason for studying two species with different modes of development is that the pelagic developers rely on external factors such as wind, currents and wave action to return the larvae to the rocky shore (Possingham and Roughgarden, 1990). Therefore, population survival will be highly dependent on whether recruits can find and land on suitable habitat patches (Diamond, 1975; Possingham and Roughgarden, 1990; Levin, 1992; Andrén, 1994; Eggleston, 1999). The role of (1) patch size, (2) isolation, and (3) temporal patterns are all important in the understanding of fragmentation. In this study, the three were examined to highlight the different responses of organisms with different modes of dispersal to natural habitat fragmentation.

Chapter 2

Effect of habitat patch size on the densities and population size-structure of two limpet species

2.1 Introduction:

2.1.1 The importance of scale:

Explaining the variability in ecological processes is a key task for ecologists because organisms are extremely variable in space and time (Lawton, 1999, Underwood, 2000, Coleman e*t al.,* 2006). An essential issue in ecology is the scale-dependent distribution and density patterns of organisms and the identification of the processes that underlie these patterns (Kareiva 1987, Levin 1992, Eggleston *et al.,* 1999). In the last decade, there has been growing interest in the trends and patterns that organisms demonstrate at large spatial scales (Noda *et al.,* 2009). This is because large scale processes are thought to influence the patterns and densities of species across large distances and understanding these patterns is one of the main goals of ecology (Holt, 1985, Underwood *et al*., 2008). To be able to understand these ecological patterns fully, it is necessary to conduct field experiments over different spatial scales. It has been found that experiments at fine scales often do not capture all of the processes occurring within the system and therefore cannot be extrapolated to explain large scale processes and large scale experiments are often too broad to include fine scale processes (Urban *et al.,* 1987, Turner *et al.,* 2001, Levin, 1992). This has lead to an increase in ecological studies over varying distances in all landscapes (Worm *et al*., 2002).

2.1.2 The role of patch size:

Spatial aspects of the environment can influence the structure of assemblages (Anderson, 1999). An important spatial factor that can determine the presence and density of a species is that of habitat patch size (Anderson, 1999). Changes in the structure of a landscape will alter the ability of organisms to disperse (Jonsen and Fahrig, 1997). Not only the isolation and connectivity of patches but most importantly the structure and size of habitat patches play a major role in determining the density of a population (van Dorp and Opdam, 1987; Jonsen and Fahrig, 1997). Patch size is often determined by the process of habitat fragmentation, which can be both a natural and human induced process (Wright, 1974; Pickett and Thompson, 1978; Andrén, 1994; Haila, 2002). Most habitats are fragmented to one degree or other because they are defined by the spatial pattern of the landscape.

The process of fragmentation generally leads to a matrix of differing habitat patches within a single landscape. Some landscapes have, however, a higher tendency to be naturally fragmented than others, such as along rivers, coasts and mountain tops/ridges, as they are linear and encompass a matrix of small patches of different habitat types (Goodsell *et al.,* 2007). Regardless of whether the spatial patterns are because of fragmentation or occur naturally, they are in most cases labelled as fragmented habitats because they are not seen as a single continuous patch of homogeneous habitat (Eggleston *et al*., 1999).

Patch dynamics models may be a more representative way to approach fragmented landscapes. The patch dynamics models identify patches as gaps in a uniform landscape placing no thresholds on location, size or persistence (Levin and Paine, 1974). Patch dynamics has been

named the most appropriate model to use in naturally fragmented landscapes and has been widely adopted when describing rocky shore assemblages (Underwood, 2000). The problem comes when defining the patch, this is because each system is different (Levin and Paine, 1974) and patch studies should be carried out at various scales to understand all patterns and dynamics (Urban *et al.,* 1987; Levin, 1992; Turner *et al.,* 2001). This has been attempted in this mensurative experiment where the entire geographic South African range of two species was sampled, but each region was treated as a separate study and then regions were compared to determine whether there is an overall patch size pattern across the entire bio-geographic range.

Patch size is said to affect organisms to different degrees depending on their mobility (Possingham and Roughgarden, 1990). This study looks specifically at two species of limpet, *Siphonaria serrata* and *Siphonaria concinna*. The species are extremely similar except for their modes of dispersal; both lay benthic egg masses, but *S. serrata* is a direct developer, whilst *S. concinna* is a pelagic developer (Chambers and McQuaid, 1994). Looking at their regional distribution this study aims to determine whether population density patterns are influenced by habitat patch size. Individual body sizes is seen as an important reaction to patch size, as it is often seen that species density is directly related to the size of animals (Blackburn *et al.,* 1990, Bender *et al.,* 1998, Andrén, 1994).

Two predictions were made about the densities of limpets in each region. It was predicted that the densities of limpets at small habitat patches would be different to the densities of limpets at large habitat patches. Furthermore, limpet size distribution would be different at small and large habitat patches.

2.2 Methods:

2.2.1 Study sites:

S. serrata and *S. concinna* have the same geographical range and are found between Kosi Bay and Cape Point on the eastern / southern shores of South Africa (see Figure 2.1). To get a full understanding of the patterns of distribution and therefore the effects that patch size have on the two limpets, sampling across the entire geographic range was necessary (Sink *et al*., 2005).

Seven geographical regions were selected to measure densities and sizes of both species of siphonariids. At each of the seven sites, four large and four small rock patches were selected. The rock patches were selected using aerial photographs, geographical information systems and Google Earth to ensure they fitted the definition of large and small sites (small patches $\leq$ 20m in length and large patches $\geq$ 100 m in length). The rock patches were determined to be suitable if they were non-boulder rock patches situated in the midshore. Each rock patch was measured along the maximum length of the patch because both species are edge dwellers and therefore the linear dimension of the rock / sea interface provides a good representation of the siphonariid habitat. The classifications of large and small habitat patches were determined through a preliminary study (see Appendix).The preliminary study provided observations that were used to form the hypothesis to test the effects that habitat patch size had on limpet densities, which was that in patches less than 20 metres and patches greater than 100 meters there would be a clear pattern of limpet densities and size-frequency distributions displayed across the coast of South Africa. Four small and four large sites were selected from each of the following areas: False Bay, Brenton-on-Sea, The Tsitsikamma National Park, Kenton-on-Sea, Dwesa National Park, Silaka National Park and Kwa-Zulu Natal, from west to east respectively (Figure 2.1).

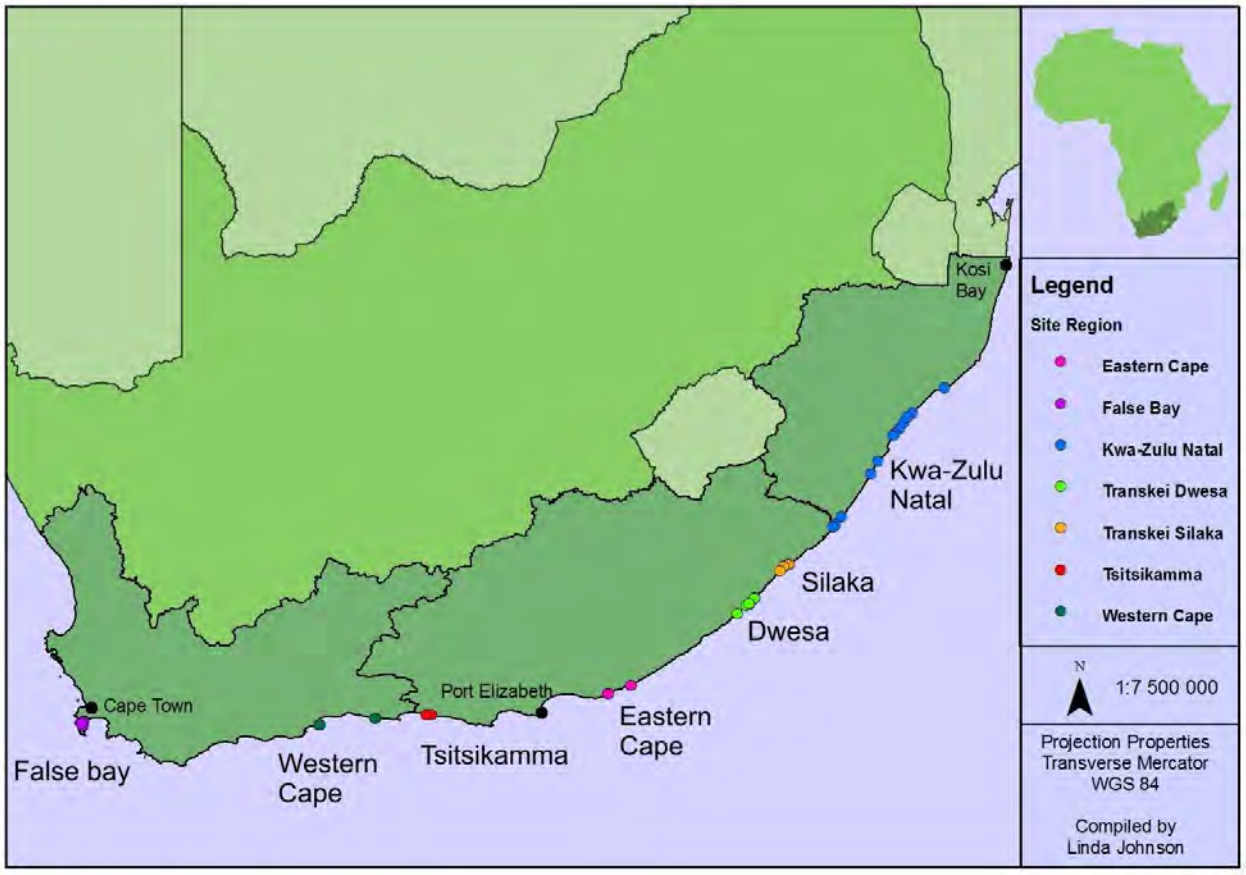


Figure 2.1: Regional sites along the southern and eastern coast of South Africa

All sites were selected based on the size of the patch of rock and whether both species of limpet were present. The type of rock and rock structure were not uniform across regions. A description of each region can be found below. An attempt was made to intersperse small and large patches in all regions.

False Bay

The sites in False Bay were located between Simon's Town (southern-most site) and Muizenberg (northern-most site; Figure 2.2). The small sites within this region consisted of irregular basalt patches separated by sand. Large patches were not continuous stretches of rock but were clusters

of large basalt stable boulders that were not broken up by patches of sand and were therefore assumed to form continuous habitat.

Western Cape

Two of the large and two of the small Western Cape sites were located in Mossel Bay (Figure 2.3). These sites were similar to the False Bay sites, where the small patches were stable individual basalt boulders separated by sand whilst the large patches were clusters of stable boulders. The remaining two small patches and two large patches were located in Brenton on Sea (Figure 2.3). The small patches were irregular stable sandstone boulders separated by sand patches while the large patches were evenly sloping sandstone platforms.

Tsitsikamma

The eight Tsitsikamma sites lie within the Tsitsikamma Marine Protected Area (Figure 2.4). The reserve is predominantly rocky shore and this made the determination of small patches difficult. Instead of being separated by stretches of sand, patches were defined as individual rock patches separated by pebble stretches. The large patches were angular sheets of basalt while the small patches were stable basalt boulders.

Eastern Cape

Half, two large and two small, of the Eastern Cape sites were located in Kenton on Sea whilst the other half of the sites were located at Riet River (Figure 2.5). All of the large patches were evenly sloping sandstone platforms. The small sites consisted of irregularly shaped stable sandstone boulders and all sites were separated by stretches of sand.

Dwesa

The eight sites sampled at Dwesa were either inside or just outside the Dwesa Marine Protected Area (Figure 2.6). Like the Tsitskamma MPA, the Dwesa region is predominantly basalt with very few stretches of sand. Both small and large patches were basalt platforms separated by either sand or pebble stretches.

Silaka

The sites selected for sampling in this region were either within or near to the Silaka National Park (Figure 2.7). As with Dwesa and Tsitsikamma, this stretch of coastline was mainly rock and therefore large and small sites were separated with either stretches of sand or stretches of pebbles. Large sites were basalt platforms while small sites were stable basalt boulders.

Kwa-Zulu Natal

The sites selected along the Kwa-Zulu Natal coastline lie between Port Edward (western-most site) and Richards Bay (eastern-most site; Figure 2.8). Small sites were stable boulders while large sites were either continuous platforms or clusters of rock.

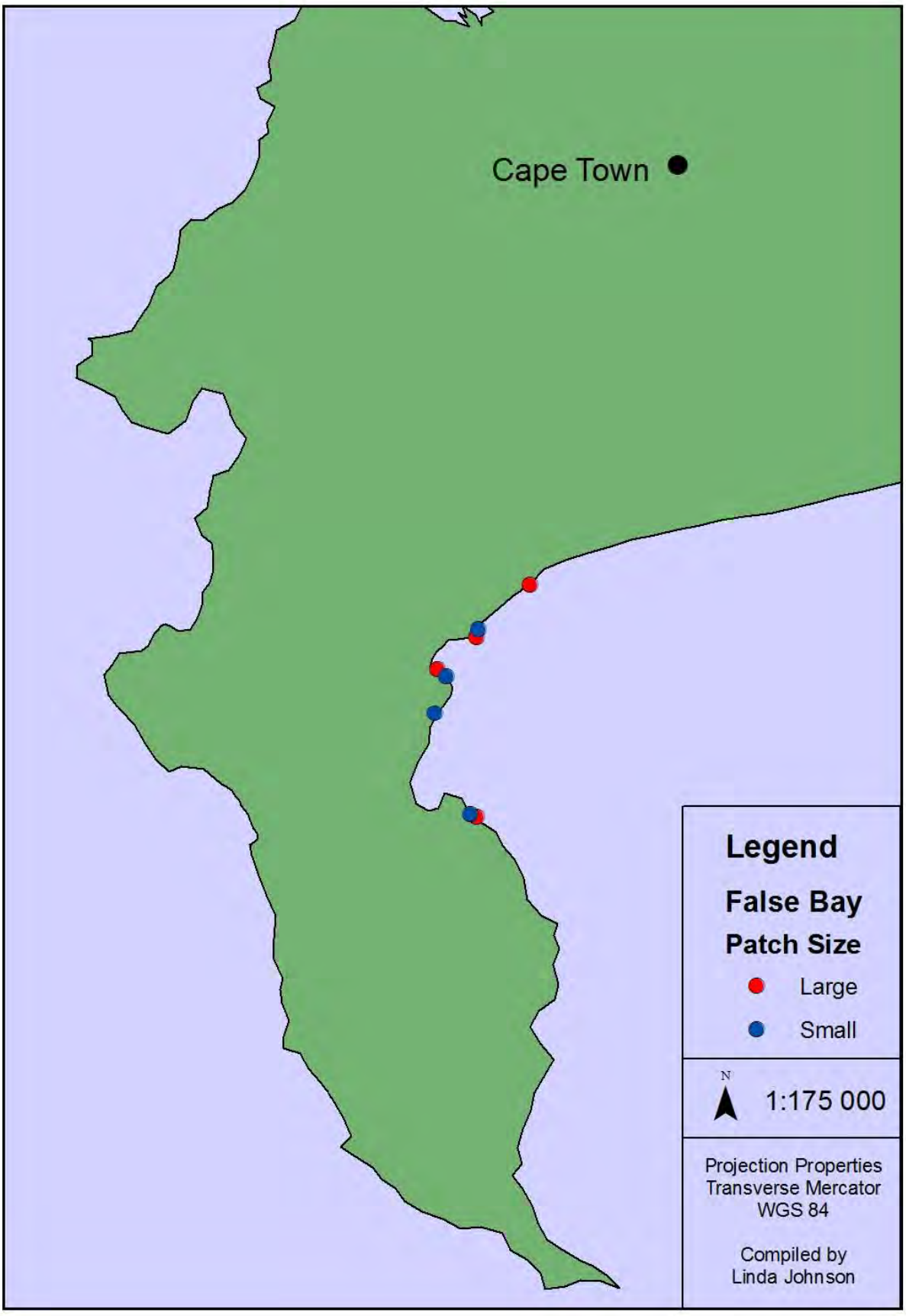


Figure 2.2: Large and small sites sampled in False Bay

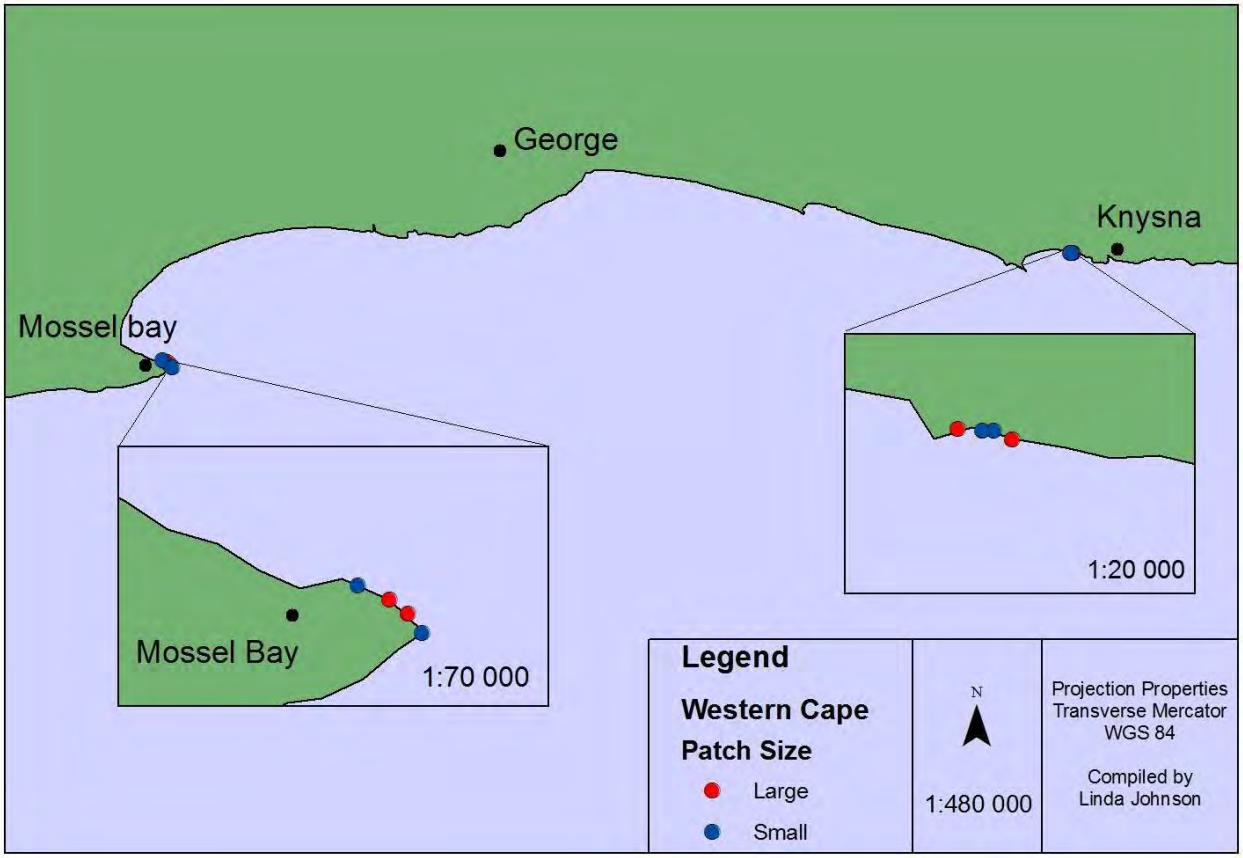


Figure 2.3: Large and small sites sampled in the Western Cape

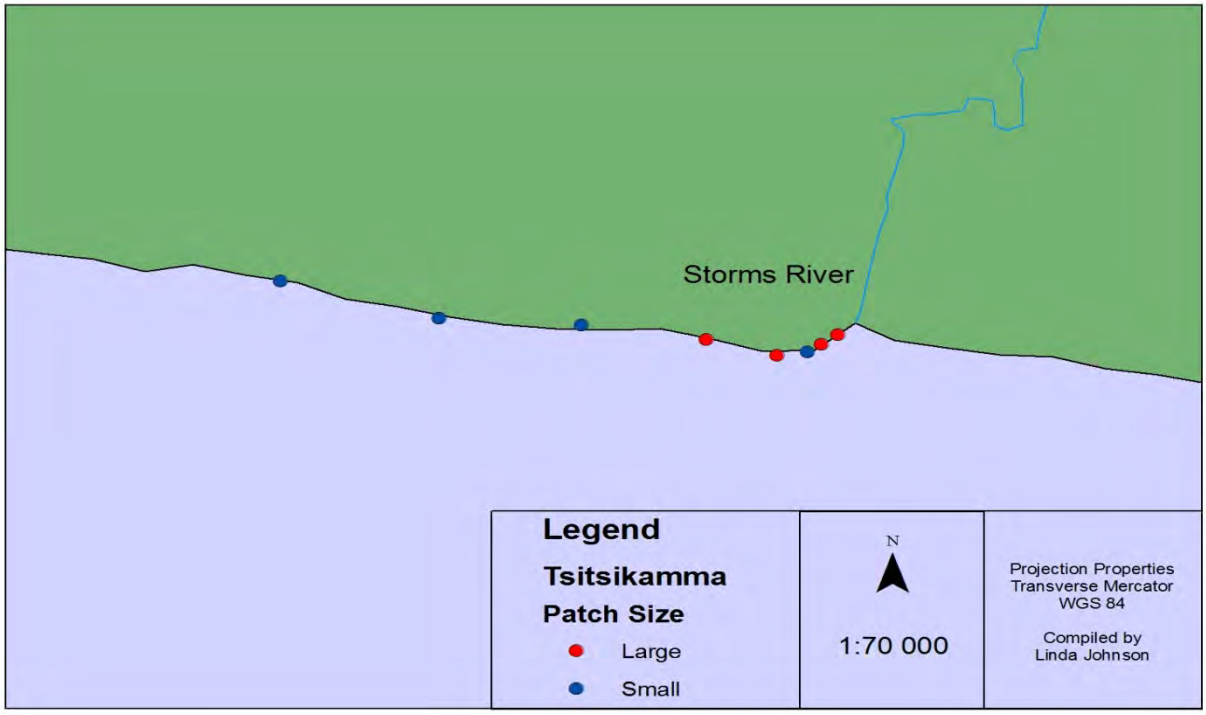


Figure 2.4: Large and small sites sampled in Tsitsikamma

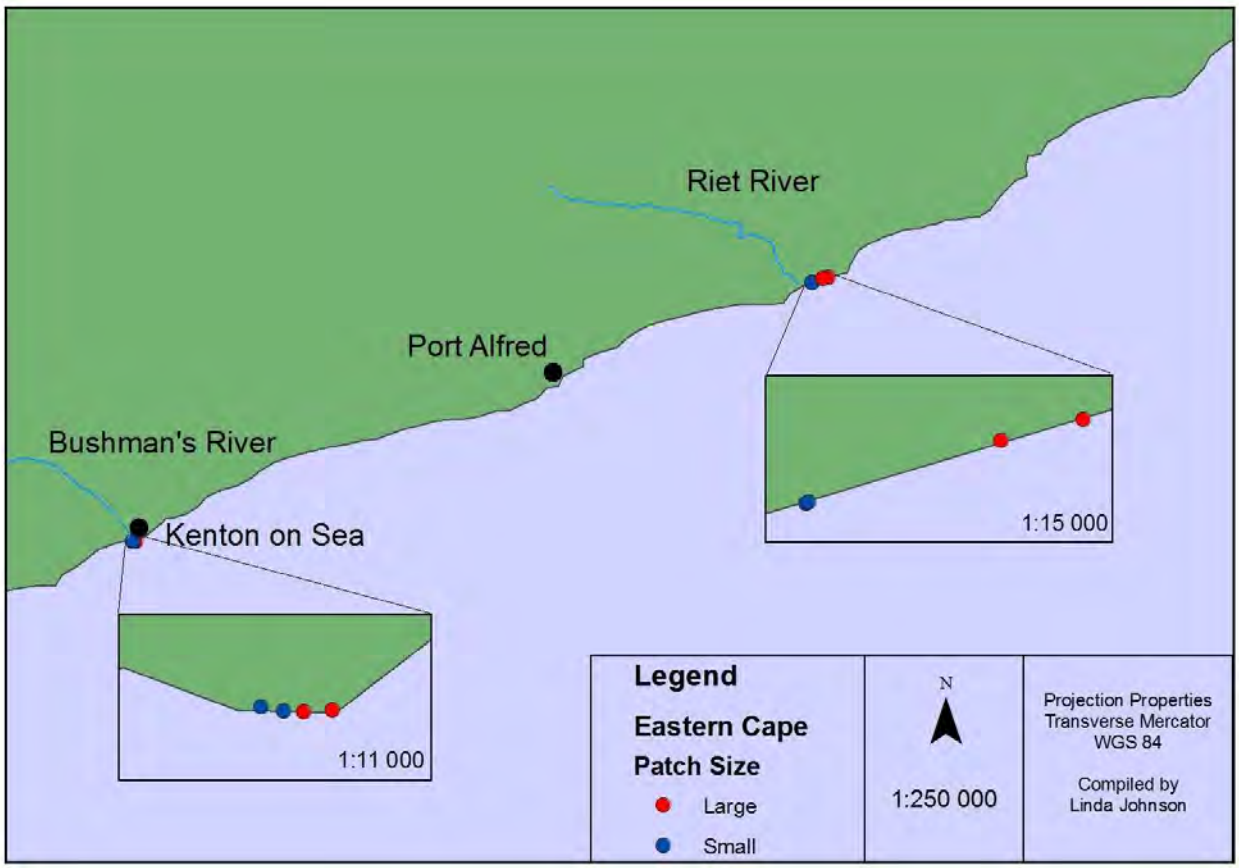


Figure 2.5: Large and small sites sampled in the Eastern Cape

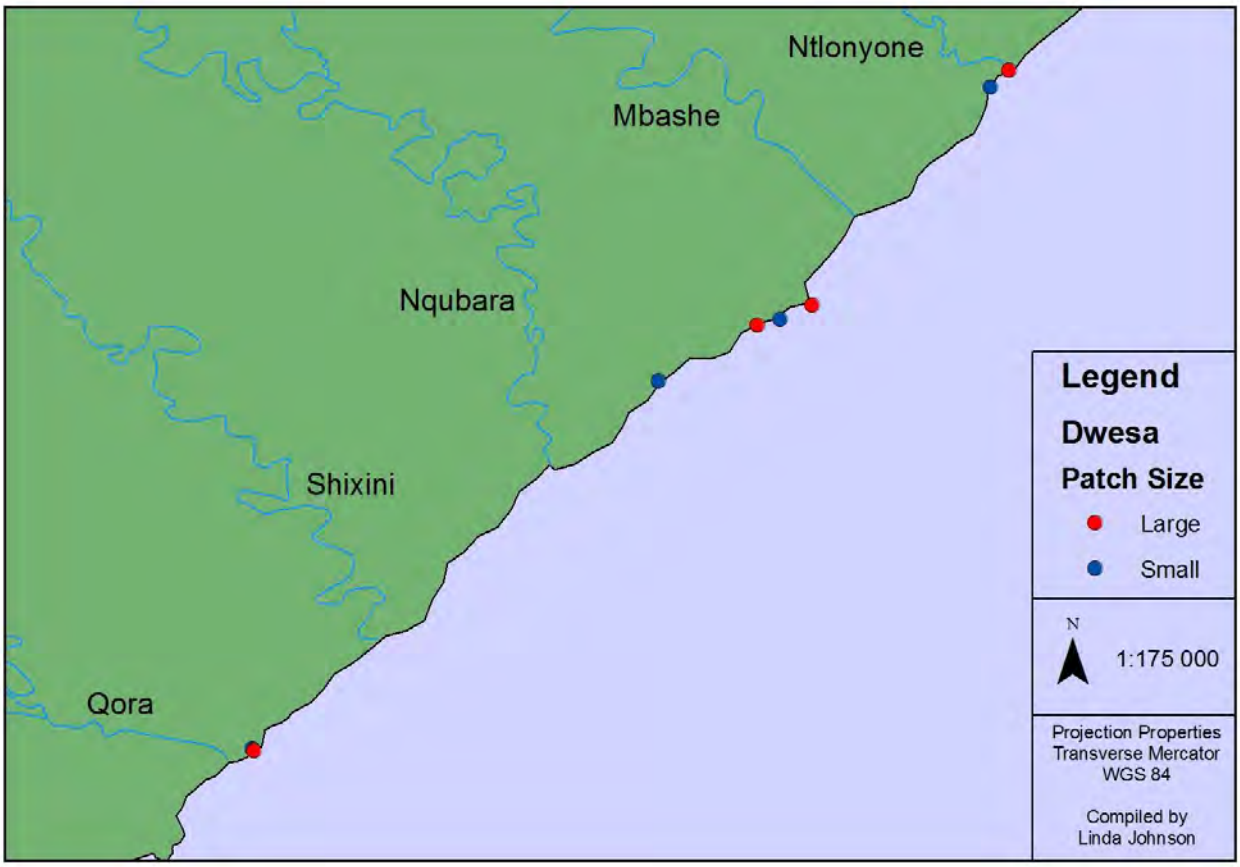


Figure 2.6: Large and small sites sampled in Dwesa

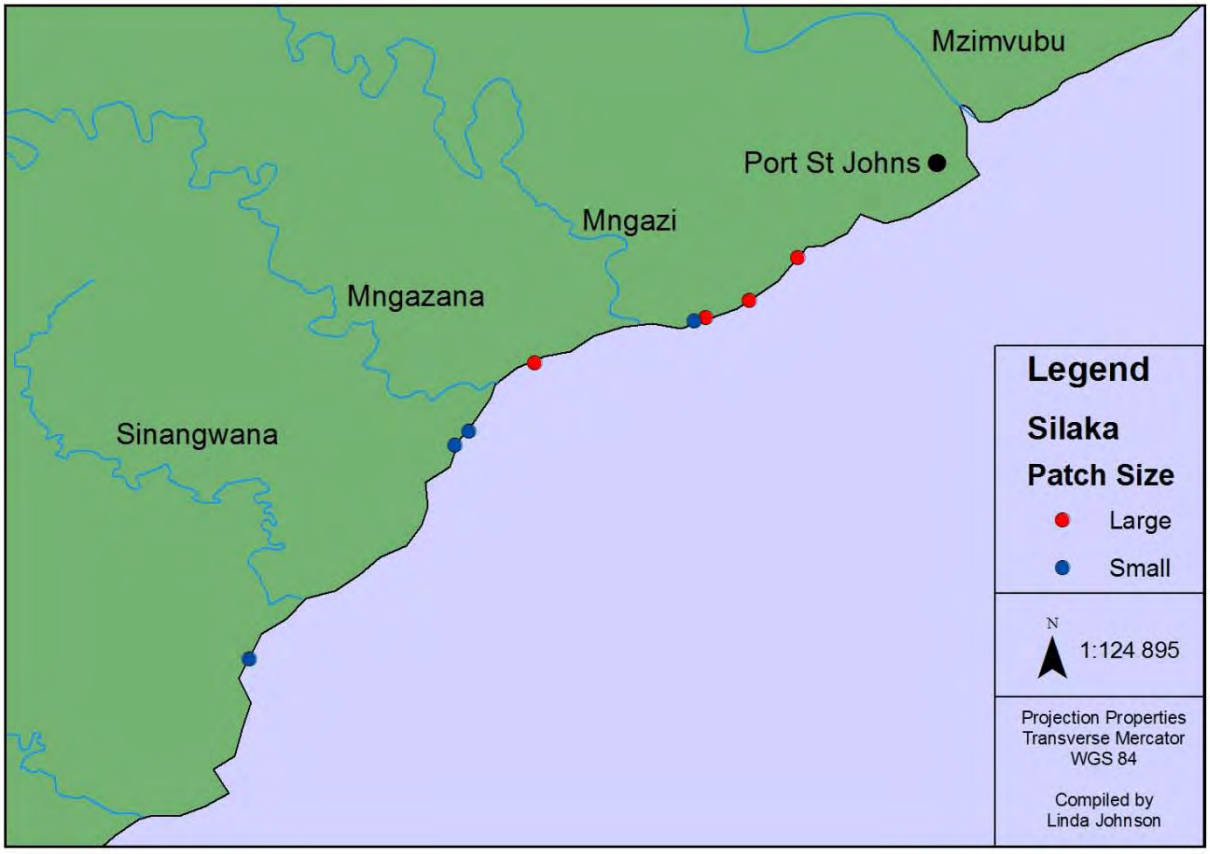


Figure 2.7: Large and small sites sampled in Silaka

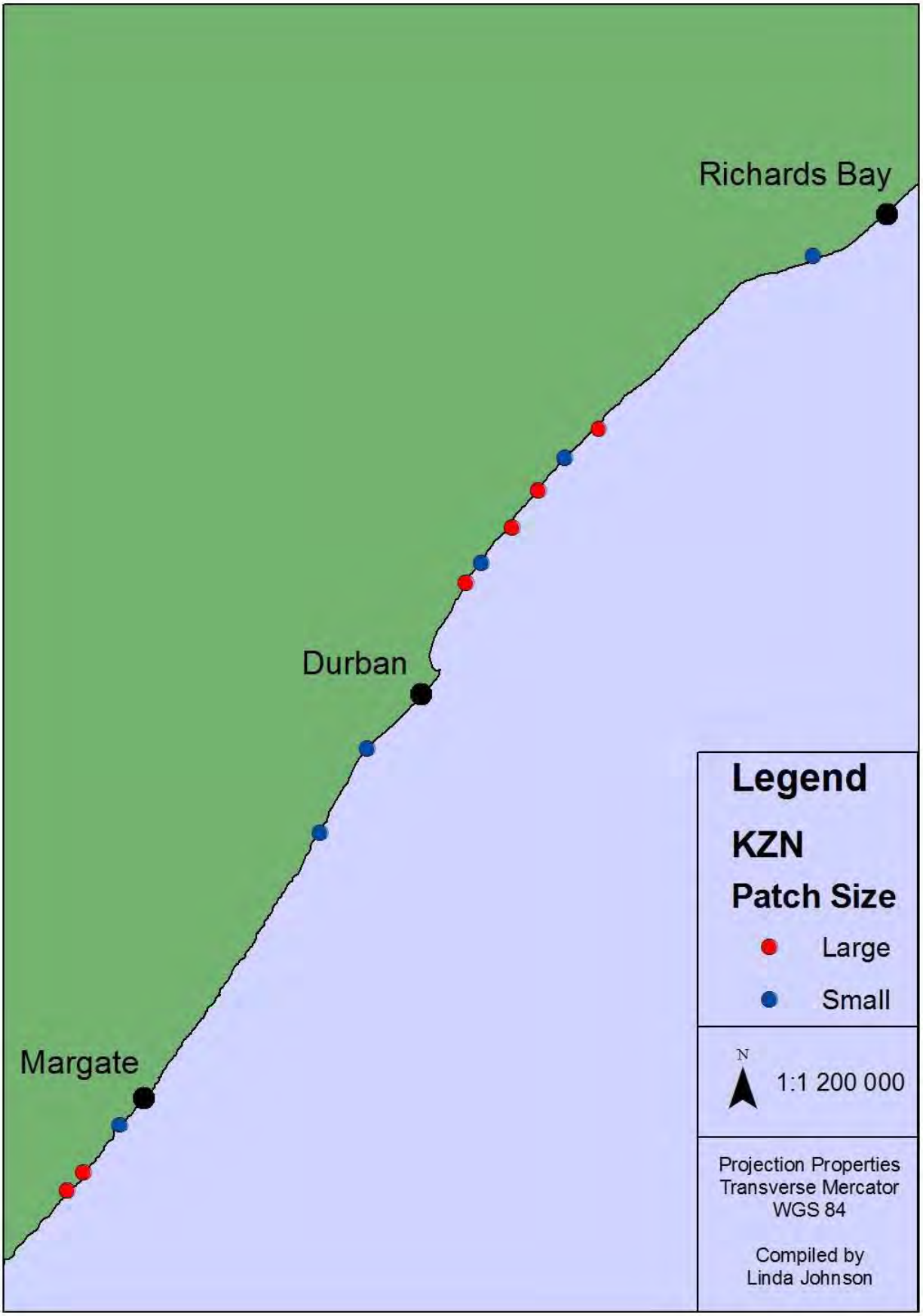


Figure 2.8: Large and Small sites sampled in Kwa-Zulu-Natal

2.2.2 Sampling process and statistical analysis:

After site selection, once-off sampling of the two limpet species was carried out. Sampling was carried out during spring low tides, between the months of August 2009 and May 2010. Each rock patch was sampled using a 50 cm by 50 cm quadrat. At each patch, six replicate quadrats were haphazardly placed for each species. Each species was sampled in separate quadrats to maintain independent estimates of the two populations. Within each quadrat individual limpets were measured along the longest axis of the shell using vernier callipers. Before analysis, Cochran's tests were carried out to ensure that there was homogeneity of variances between data in each region. To test the aforementioned hypotheses, the numbers of limpets at each shore were compared with a three-factor analysis of variance (ANOVA) comparing shore, rock patch size and species. Prior to analyses, data were tested for homogeneity of variances with Cochran's *C*-test. The data for many analyses did not did not require transformation and for those that did, few required the same transformation to create homogeneous variances. Therefore, in order to make simple comparisons among regions, none of the data were transformed. The violation of homogeneity of variances was not considered to be a problem because ANOVA is relatively robust to heterogeneous variances for large designs such as this (Underwood, 1997). When source of variation were found to be significant Student-Newman-Keuls (SNK) tests were used to determine the direction of difference with respect to the hypotheses of interest.

To test the hypotheses about the size structure of limpets, in each region the sizes of all limpets were grouped into size classes, according to rock patch size, and size-frequency distributions were compared between small and large patches using chi-squared contingency tests using the following five size classes; 1) 1 – 4 mm, 2) 5 – 9 mm, 3) 10 – 14 mm, 4) 15 – 19 mm and 5) 20 –

24 mm. To examine the differences between regions, the four small and four large patches were pooled for each region and the size classes from each region were compared using chi-squared contingency tests (χ^2).

2.3 Results:

2.3.1 Comparison of limpet densities at small and large patches:

Five of the seven regions showed very similar responses to the different habitat patch sizes (Figure 2.9). In all regions, except Silaka and Tsitsikamma, there was a clear difference between densities of *S. concinna* at small and large patches. As predicted, there were fewer *S. concinna* at small patches than at large patches. In the five regions there was a higher density of *S. serrata* than *S. concinna* at small patches while at large patches there were high densities of both species. Whilst, in Silaka and Tsitsikamma no significant relationship was found between patch size and species at both large and small patches (Table 2.2). The difference between the density of *S. concinna* at small and large sites is clearly illustrated by the above graphs and the ANOVAs in Table 2.1 show the same results of a significant relationship between patch size and species density for the five remaining regions. Kwa-Zulu Natal and the Western Cape showed significant differences in limpet densities and patch sizes for both species while the Eastern Cape, False Bay and Dwesa regions showed this difference only for *S. concinna* (SNK $P < 0.01$). Species densities differed significantly and site for Silaka and Tsitsikamma but there are no other significant relationships at these two sites (Table 2.2).

Table 2.1: ANOVA of untransformed data for the number of limpets per quadrat for *S. concinna* and *S. serrata* within seven regions throughout the limpets' biogeographic range.

Seven regions each with large and small habitat patches, each with four sites nested in either large or small $n = 6$ replicate quadrats per site. All variances were heterogeneous (Cochran's C test, $P < 0.05$).

* $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$

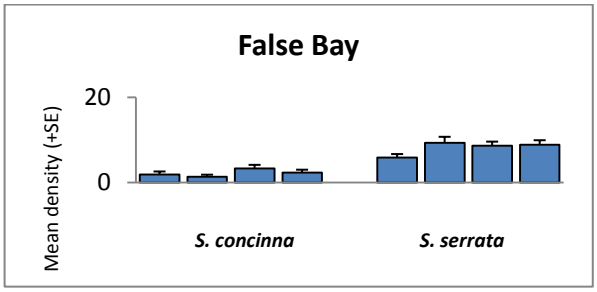
Source	df	M.S.		*F*	
a) False Bay					
Size	1	43.03		9.08	*
Site (Size)	6	4.74		22.93	***
Species	1	0.12		0.16	
Size x Species	1	0.11		0.14	
Species x Site (Size)	6	0.74		3.58	**
Residual	80	0.21			
Total	95				
b)Western Cape					
Size	1	48.48		9.75	*
Site (Size)	6	4.97		5.39	***
Species	1	6.08		6.59	*
Size x Species	1	5.93		6.43	*
Species x Site (Size)	6	0.79	†		
Residual	80	0.93	†		
Total	95				
1-Pooled data	86	0.922			
c) Tsitsikamma					
Size	1	18.71		7.87	*
Site (Size)	6	2.38		4.55	*
Species	1	9.87		7.63	**
Size x Species	1	0.00		0.00	
Species x Site (Size)	6	1.29		2.47	*
Residual	80	0.52			
Total	95				

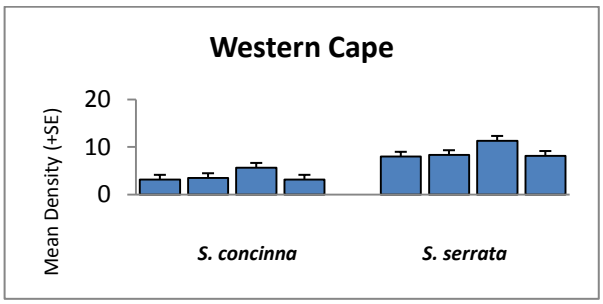
Table 2.1 continued

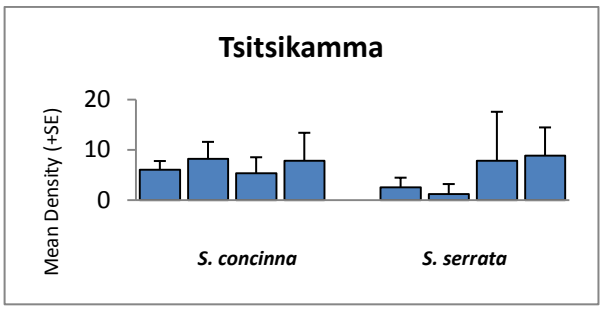
Source	df	M.S.		*F*	
Size	1	42.97		95.68	***
Site (Size)	6	0.45		2.13	
Species	1	1.09		1.61	
Size x Species	1	0.94		1.39	
Species x Site (Size)	6	0.68		3.22	**
Residual	80	0.21			
Total	95				
e) Dwesa					
Size	1	58.91		157.19	***
Site (Size)	6	0.37		1.68	
Species	1	0.01		0.01	
Size x Species	1	0.05		0.04	
Species x Site (Size)	6	1.21		5.46	***
Residual	224	0.22			
Total	239				
f) Silaka					
Size	1	44.53		126.07	***
Site (Size)	6	0.35		2.40	*
Species	1	2.57		4.09	
Size x Species	1	0.44		0.70	
Species x Site (Size)	6	0.63		4.25	**
Residual	224	0.15			
Total	239				
g) KZN					
Size	1	15.80		16.04	**
Site (Size)	6	0.99		6.17	***
Species	1	9.11		57.02	***
Size x Species	1	3.32		20.77	***
Species x Site (Size)	6	0.16	†		
Residual	80	0.16	†		
Total	95				
1-Pooled data	86	0.15			

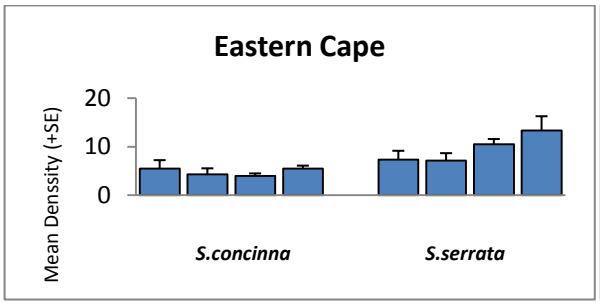
† Denotes post hoc pooling, $P > 0.25$. New *F* ratios are given for those tested against the pooled term.

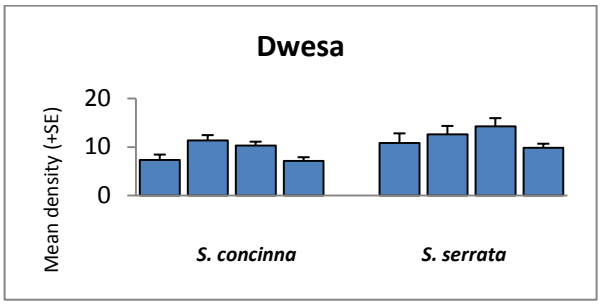
Small Patches



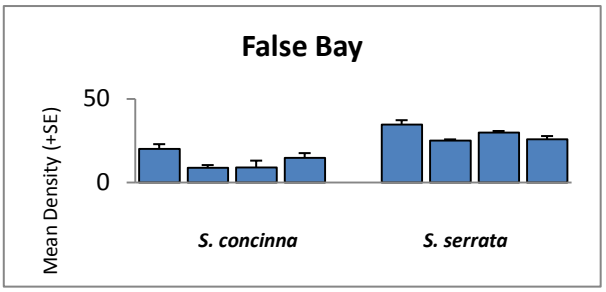


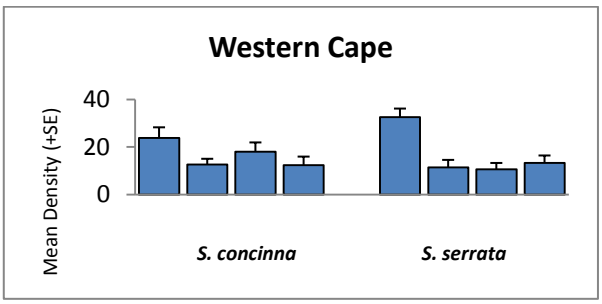


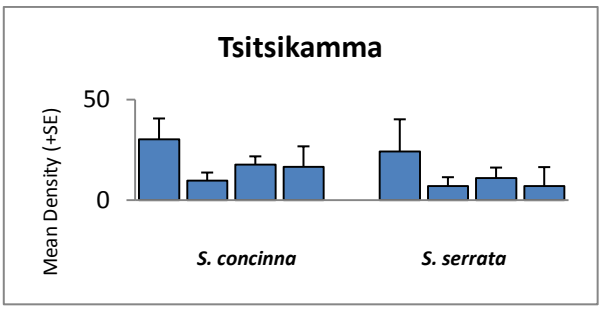


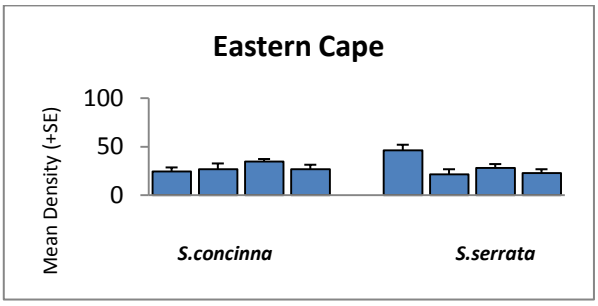


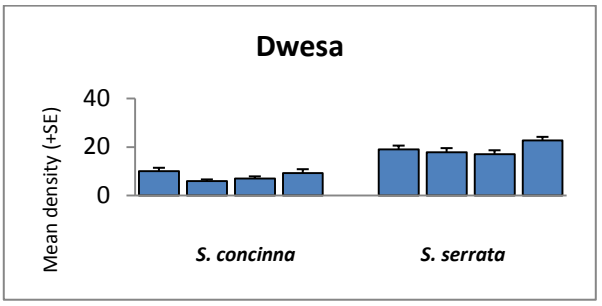
Large Patches











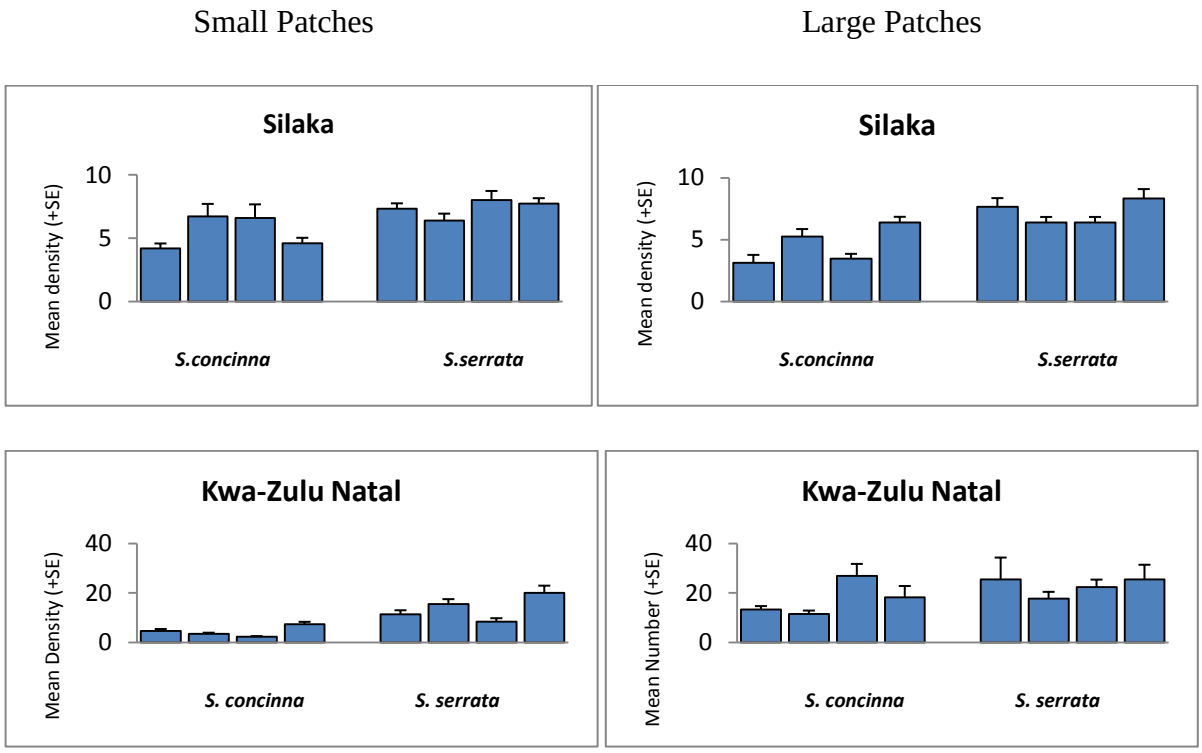


Figure 2.9: The mean (+SE) species density in small and large patches. Each bar represents the mean density of limpets at each site that was sampled.

2.3.2 Investigation of limpet size-structure at small and large patches:

The two species showed very similar responses to patch size with reference to size frequencies within each region (Figure 2.10). The size structure differed for *S. concinna* in all regions: False Bay ($\chi^2 = 68.9$, df = 2, $P < 0.05$), Western Cape ($\chi^2 = 59.3$, df = 2, $P < 0.05$), Tsitsikamma ($\chi^2 = 9.8$, df = 2, $P < 0.05$), Eastern Cape ($\chi^2 = 138.4$, df = 2, $P < 0.05$), Dwesa ($\chi^2 = 64.5$, df = 2, $P < 0.05$), Silaka ($\chi^2 = 56.3$, df = 2, $P < 0.05$) and Kwa-Zulu Natal ($\chi^2 = 11.9$, df = 2, $P < 0.05$). The pattern was similar for *S. serrata* where size structure differed between small and large patches in all regions: False Bay ($\chi^2 = 159.3$, df = 2, $P < 0.05$), Western Cape ($\chi^2 = 60.3$, df = 2, $P < 0.05$), Tsitsikamma ($\chi^2 = 33.4$, df = 2, $P < 0.05$), Eastern Cape ($\chi^2 = 393.0$, df = 2, $P < 0.05$), Dwesa ($\chi^2 = 43.5$, df = 2, $P < 0.05$), Silaka ($\chi^2 = 16.2$, df = 2, $P < 0.05$) and Kwa-Zulu Natal ($\chi^2 = 6.1$, df = 2, $P < 0.05$).

In False Bay, Eastern Cape, Dwesa and Kwa-Zulu Natal *S. concinna* had a greater proportion of large limpets at small patches than at large patches, where there were more small individuals. In Tsitsikamma and Silaka there was a high proportion of small *S. concinna* individuals at small patches than large patches. In the Western Cape there was an even size distribution of *S. concinna* at large patches while at small patches the majority of *S. concinna* were found within size class 3. *S. serrata* had a higher proportion of large individuals at small patches than at large patches at False Bay, Western Cape, Tsitsikamma, Eastern Cape, Dwesa and Kwa-Zulu Natal. Whilst in Silaka there was, once again, a higher proportion of small *S. serrata* at small patches than at large patches (Figure 2.10). Size frequencies of limpets also differed among regions (*S. concinna* $\chi^2 = 2019.8$, df = 30; *S. serrata* $\chi^2 = 8288.5$, df = 30). The effect of patch size was therefore greater for *S. serrata* because there were a greater number of larger individuals at small patches while densities remained high.

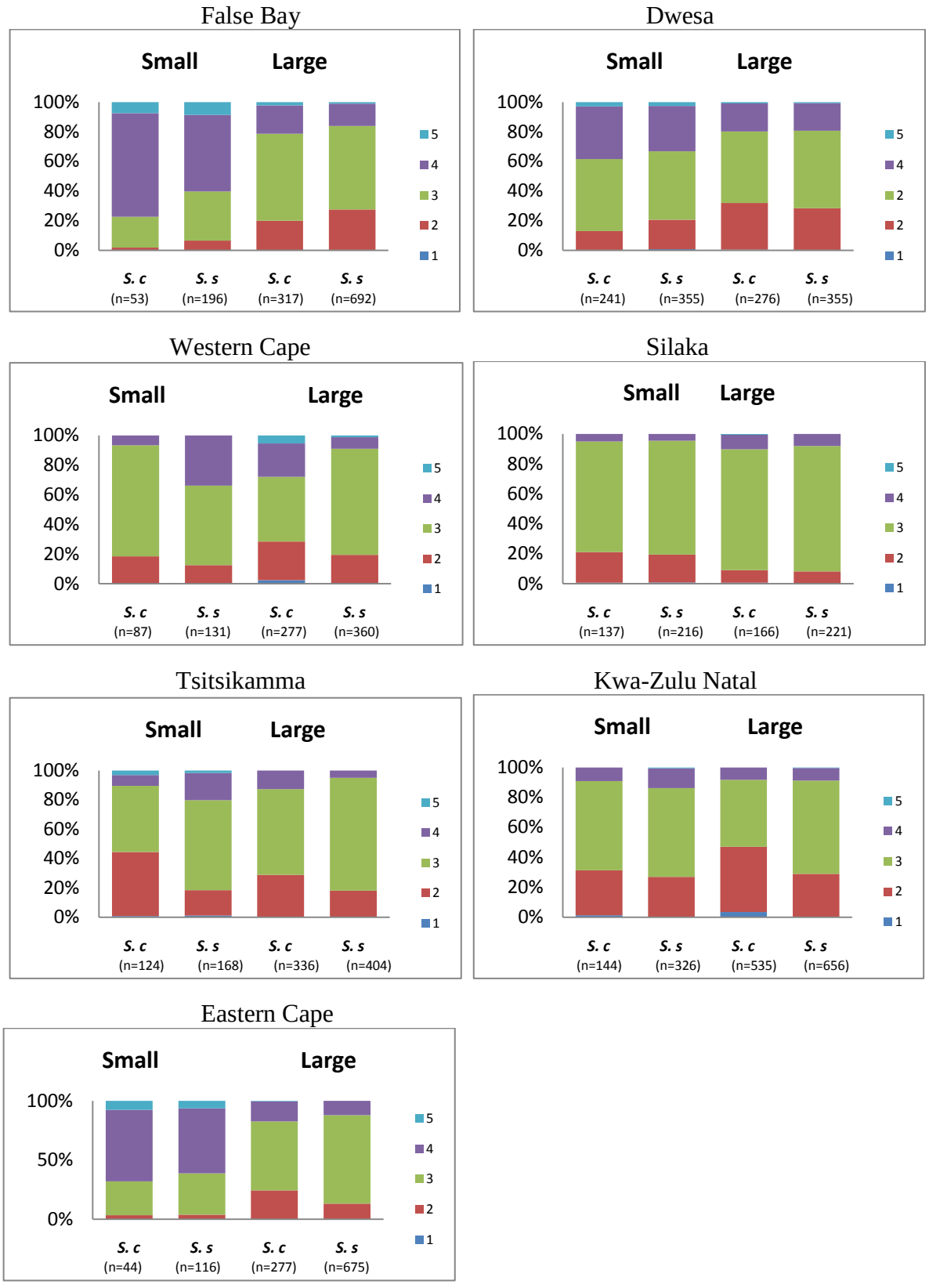


Figure 2.10: Size-class proportions of *S. concinna* (*S. c*) and *S. serrata* (*S. s*) in small and large patches. 1) 1 – 4 mm, 2) 5 – 9 mm, 3) 10 – 14 mm, 4) 15 – 19 mm, 5) 20 – 24 mm.

2.4 Discussion:

The effect of habitat patch size was clearly different for the two species of limpet. It was found that across the entire biogeographic range there was a lower density of *S. concinna* at small patches than at large patches and that there was no significant difference between densities of *S. serrata* on different sized patches. Distribution patterns of species in naturally fragmented habitats are often found to be nested and it is assumed that the smaller the habitat patch, the smaller the population that will survive (Atmar and Patterson, 1993, Anderson, 1999). As such inevitably the pattern between species and area has dominated fragmentation research (Haila, 2002). The argument is not easily refuted as the majority of experiments display some degree of species impoverishment or population decline (Whitcomb *et al*., 1981; van Dorp and Opdam, 1987; Kim and DeReede, 1997; Haila, 2002; Krauss *et al*., 2003). Local population declines must be balanced by recruitment, thus the colonisation of habitat patches by dispersal of organisms over the landscape is vital for the survival of regional populations (Jonsen and Fahrig, 1997, Fahrig and Merriam, 1994, Hanski, 1994) and in reality the probability of a habitat patch being colonized is directly linked to the size of that patch (van Dorp and Opdam, 1987). It is assumed that mortality rates do not directly depend on habitat patch size but rather on other factors such as food supply and competition (Zannette, 2000).

The effect of habitat patch size is species-specific and therefore organisms react to the process of habitat fragmentation in different ways. For example, Krauss *et al*. (2003) found that habitat specialists are affected by patch size to a greater degree than habitat generalists. The studies carried out by Andrén (1994) and Bender *et al*. (1998) show that mobility and mode of dispersal may not be important in the extent to which a species reacts to patch size when looking at a variety of animals including: birds, insects and mammals. None of the studies examined by these

two papers looked at the reaction of marine organisms to habitat patch size. The effect of patch size on pelagic developing marine organisms was examined by Possingham and Roughgarden (1990). The results for terrestrial organisms completely contradict the findings of the present study which agree with the patterns observed by Possingham and Roughgarden (1990) indicating that species with complex lifestages are affected by patch size, implying that mode of dispersal does have an effect on population density.

S. concinna population densities were considerably lower at small patches than at large patches. The majority of *S. concinna* individuals may be larger because recruits rely on water movement to transport them to suitable habitat patches and it is therefore recruits stand have a higher chance of reaching a suitable patch if it is a large stretch of rock than if it is a small patch of rock surrounded by unsuitable habitat. Although this finding is apparent for this experiment, it has been argued that the more fragmented the landscape the higher the population density will be. This may be true for seagrass habitats, as found by Eggleston *et al.* (1999), where it was easier for propagules to find small habitat patches in a highly fragmented matrix of suitable patches but it depends on the connectivity of the habitats and whether organisms have the ability to control their movement (Eggleston *et al*., 1999, Goodsell *et al*., 2007). In the case of *S. concinna,* larvae depend on currents and wave action to transport them between patches and therefore the chance of finding a small patch is lessened unless in a highly fragmented landscape where patches are close together (Possingham and Roughgarden, 1990, Eggleston *et al*., 1999, Goodsell *et al*., 2007). This pattern is illustrated by Eggleston *et al.* (1999) where many small seagrass habitats in an area increased the probability of settlement of grass shrimp and mobile crustaceans such as isopods. Thomas *et al.,* (1992) found, in a study on butterflies, that the effect that fragmentation has on a population depends on the degree of fragmentation and the composition of the landscape matrix; finding the same density and settlement patterns as Eggleston *et al.* (1999) in

landscapes made up of numerous small suitable patches. The results for landscapes with a significantly lower number of suitable small habitat patches within the matrix were similar to the results of this study, where the *S. concinna* densities were considerably lower at small patches than at large patches. This may be because larvae have no control of their movement and if a landscape matrix is made up of a few small patches, such as was found in this study, the probability of a larvae being carried to a small patch is significantly lower than it would be in a matrix with a high number of small patches.

The densities for both limpet species indicate that the idea that in small patches, there is a high proportion of edge habitat which should result in high densities of edge dwelling organisms. Both limpet species are found along the edge of suitable habitat patches, yet neither species experienced an increase in population density at small patches. Hoover *et al*. (1995), Bender *et al*. (1998) and Cronin (2003) found that an increase in small suitable habitat patches was directly related to an increase in edge dwelling organisms in both terrestrial and marine systems. However, once again, these studies discuss landscapes with a high number of small patches within a matrix. Although small habitat patches do have high proportions of edge habitat, there is clearly no link, for limpet species, to an increase in population density. A possible reason for this is that as *S. concinna* have a pelagic development stage they rely on currents and wind to move them to the small habitat patch, which is often less likely than landing a large patch (Possingham and Roughgarden, 1990).

The two species of limpet showed remarkably similar responses in size structure to patch size. As predicted, at small habitat patches there was a greater proportion of larger limpets whereas at large habitat patches there was a higher proportion of smaller limpets. This was not uniform

across all regions but the majority of regions did follow this pattern. Damuth (1981, 1987) showed, through various studies, ranging from viruses to trees, that as population density increases there will be a decrease in body size of the individuals within the population. It was suggested that this relationship was uniform for all organisms (Damuth 1981; 1987). Brown and Maurer (1986, 1987) argue that not all organisms will follow this trend and they found that many species of birds in North America live in low density communities but they do not have the larger body sizes predicted from Damuth's theory. They do not completely discredit the theory but it is suggested that the relationship is much less steep than Damuth (1981) suggests (Blackburn *et al.*, 1990, Blackburn *et al*., 1993). As shown in the above results, there is a clear relationship between species body size and density for *S. concinna* but this relationship was not as clear for *S. serrata* in all regions. The results for *S. serrata* show that the animals were larger at small habitat patches however; density was not significantly lower in small patches at all regions, contradicting the relationship put forward by Damuth (1981).

The relationship between body size and patch size can further be related to predation. Small habitat patches, are often refuges for organisms (Keough, 1984). With lower levels of predation, at small patches it is possible that individuals are given the opportunity to live longer and therefore have larger body sizes which was observed for both limpet species. However, it is possible that the size of the patch is not what determines the level of predation but rather the size of the prey population that determines whether there will be a high level of predation. Connell and Anderson (1999) demonstrated this with the example of predatory fish species, finding that the patch size did not have an effect on the rate of predation and rather the fish responded to large numbers of prey. It is probably not likely that this argument holds true in the case of this study as because the size of the prey population is often determined by the size of the habitat patch, as was found with the *S. concinna* at small patches. However, it has been found that large

numbers of predator species are often abundant in areas with relatively low numbers of prey. This has been related to the fluidity of water, such that although there are low numbers of adults there may be a high rate of transport of larvae to the area which then acts as the main food source to the predators (Barkai and Branch, 1988, McQuaid *et al*., 1999). In an examination of rock lobster diets Barkai and Branch (1988) found that a high proportion of the lobster diet was made up of barnacles which were not well established in the area suggesting that the lobster fed on the newly recruited barnacles so rapidly that they were unable to establish a strong community and that is why population densities remained low. This could be used to explain the low numbers of small limpets at small patches, suggesting that because they are being preyed upon before settlement or as they attempt to settle densities of the species remains low. However, this may not be the case for siphonariids because siphonariid species often show strong chemical defence against predation and therefore the likelihood of fish predation is relatively low (McQuaid *et al*., 1999).

The low numbers of small limpets could be related to high rates of post-settlement mortality and it has been found that the adult population size is very often limited by recruitment rather than larval supply (Hunt and Scheibling, 1997). Survival rate of settlers is often very low and in the case of barnacles up to 87 % of settlers die within the first 48 hours reducing the number of possible recruits hugely (Young, 1991, Hunt and Scheibling, 1997). Post-settlement mortality can be caused by a number of factors but the most common is delayed metamorphosis which results in a decline in body condition and often leads to juveniles settling on substrata that are not suitable and therefore there is a higher chance of mortality (Pechenik, 1990, Hunt and Scheibling, 1997). As it is less likely that *S.concinna* larvae will be transported to small patches as they are harder to find it can be assumed that there is a higher chance of poor body condition making them more vulnerable to post-settlement mortality. It is extremely difficult to measure

post-settlement mortality rates as settlers are often extremely small and therefore it is not known if this is the reason why low numbers of small limpets were found at small patches however, it is likely that this is a limiting factor contributing to lower densities of *S.concinna* at small patches than in large patches.

This study showed clear differences in the densities and population size-structure of two species of limpets, and this was pattern was consistent across multiple regions along the South African coastline. The observed patterns may be due to a variety of interacting processes influencing recruitment and post-recruitment effects. It is likely the observed differences may in part be due to differences in their mode of development but further experimentation is required to test this hypothesis.

Chapter 3

Testing the temporal generality of differences between small and large patches

3.1 Introduction:

The relationship between how assemblages change over time and landscape structure is important in understanding and predicting the effects that natural processes, such as habitat fragmentation, have on organisms (Boulinier, 1998; Turner *et al.*, 2001). Two of the most significant characteristics of any assemblage are their spatial (see Chapter 2) and temporal variability which arise from a variety of biotic and physical processes (Gaston and McArdle, 1994; Wiernasz and Cole, 1995; Dye, 1998). These processes vary on time scales that often follow an apparent pattern and because of this, discovering temporal patterns of variation in communities is difficult (Menge and Olson, 1990; Crowe, 1999). Assemblage level studies are made even more difficult by the fact that each species responds to spatial and temporal environmental heterogeneity in a different way (Fransworth and Ellison, 1996; Crowe, 1999). This implies that studying temporal variability could be easier if investigations were carried out on individual species rather than for an entire assemblage to understand the growth and persistence of a population (Dunning 1992).

Variability of a population is determined through local losses of organisms and the recruitment of new individuals (Ims *et al.*, 2004), both of which vary temporally. They are very often seasonal and can be influenced to a great extent by many other factors (Dye, 1998), particularly

when referring to dispersal modes, habitat thresholds and resource abundance (Underwood and Skilleter, 1996; Eggleston *et al*., 1999; Kong and Ang, 2004; Goodsell *et al*., 2007). The variability of births and deaths ultimately controls the stability and structure of a population (Bouliner, 1998). Recruits joining a population determine structuring, often seasonally, through inter-annual recruitment cycles and seasonal limits on dispersal capabilities (Kay and Keough, 1981; Wiernasz and Cole, 1995; Austen *et al*., 2002). Marine organisms with pelagic life stages can display strong seasonal fluctuations because of the influence that fluctuations in ocean temperatures and currents have on larvae (Possingham and Roughgarden, 1990; Austen *et al*., 2002). A combination of limited dispersal and local variation in reproductive output may limit the number of recruits arriving at a site (Roughgarden *et al*., 1988; Wiernasz and Cole, 1995). If recruits are limited in density or localized in their distribution then populations become extremely variable over both time and space (Wiernasz and Cole, 1995).

The effects that patch size has on the density and size-distribution of two species of limpet across multiple regions were investigated through the study in Chapter 2. This chapter takes the results from Chapter 2 and examines whether the patterns that were found across the coast of South Africa are consistent through time. Due to the nature of this study only one region of the seven could be selected and examined. In a twelve month observational study of two different patch sizes the following predictions were tested:

1. Population density would be lower at small patches than in large patches for *S. concinna* over a twelve month period. Furthermore, similar densities of *S. serrata* were predicted in small and large patches over the same period.

2. Populations of both species in small patches would have a greater proportion of larger individuals than small individuals while limpet populations in large patches would have the opposite.

3.2 Methods:

As it is the centre of distribution for both species, the Eastern Cape sites were selected from the regional study for the temporal study.

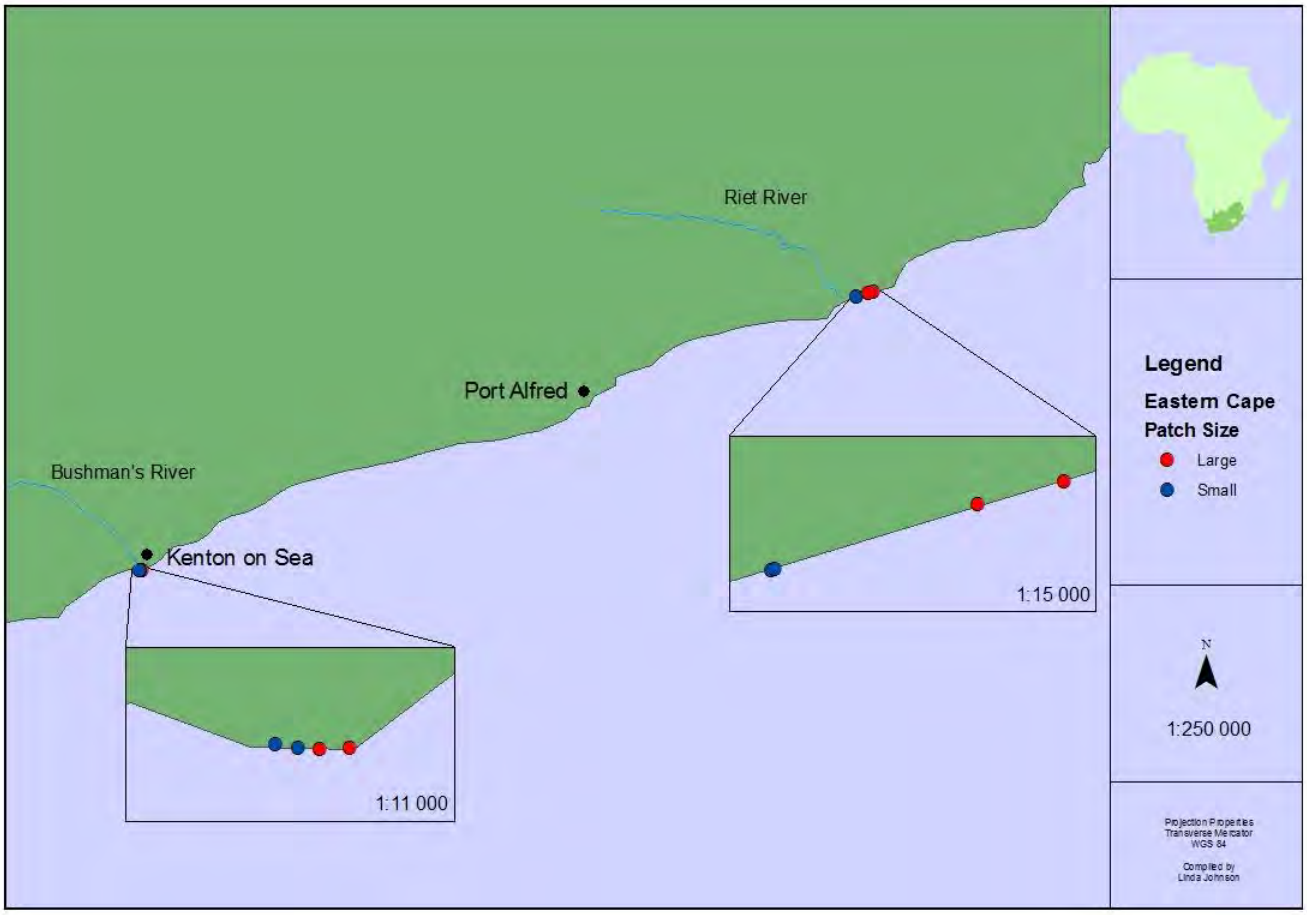


Figure 3.1: Eastern Cape large and small sampling sites

The sites sampled for this study were selected from the study carried out in chapter two. It was decided that as the Eastern Cape sites were the most central to both species biogeographic range it would be the most suitable region to carry out the temporal study. As mentioned in Chapter 2 four sites were selected from Riet River and four sites were selected from Kenton on sea and at each two of those sites were small and two were large (see Chapter 2 and Appendix for classification of small and large patches).

Once the sites were selected, monthly sampling was carried out to determine densities and sizes of the two limpet species *Siphonaria serrata* and *Siphonaria concinna*. Monthly monitoring took place during spring low tides for a total of twelve months, starting in June of 2009 and ending in May of 2010. Sampling was carried out using the same methods as in the Regional Study (see Chapter 2) where each rock patch was sampled using a 50 cm by 50 cm quadrat. At each patch, six replicate quadrats were haphazardly placed for each species. Each species was sampled in separate quadrats to maintain independent estimates of the two populations. Within each quadrat, each individual limpet was measured along its longest shell axis of the shell using vernier callipers. Prior to analyses, data were tested for homogeneity of variances with Cochran's *C*-test. The data for many anaylses did not did not require transformation and for those that did, few required the same transformation to create homogeneous variances. Therefore, in order to make simple comparisons among regions, none of the data were transformed. The violation of homogeneity of variances was not considered to be a problem because ANOVA is relatively robust to heterogeneous variances for large designs such as this (Underwood, 1997). When sources of variation were found to be significant Student-Newman-Keuls (SNK) tests were used to determine the direction of difference with respect to the hypotheses of interest.

As in the previous chapter, size of the limpets was seen as an important factor in determining distribution patterns at large and small patches. To test if the proportions of sizes of limpets within small and large patches changed over time, in each month the sizes of all limpets were grouped, according to rock patch size, and size-frequency distributions were compared between small and large patches using chi-squared contingency (χ^2) tests using the following five size classes: 1) 1 – 4 mm, 2) 5 – 9 mm, 3) 10 – 14 mm, 4) 15 – 19 mm and 5) 20 – 24 mm.

3.3 Results:

3.3.1 Comparison of densities:

There appeared to be very similar densities of both species in large patches (Figure 3.2). Results indicate that there was a significant effect of patch size for ten of the twelve months for *S. concinna* (Table 3.1). The remaining two months showed a significant effect of site for *S. concinna*. In small patches, there were significantly fewer *S. concinna* compared to the large patches (Figure 3.2, SNK $P < 0.05$). *S. serrata* densities were significantly different between small and large patches in five of the twelve months (Table 3.1). Six months showed a significant difference among the different sites rather than patch size and in August there was no significant effect of patch size, location or site (Table 3.1).

Looking at the entire twelve month period both species showed the same density patterns as observed in Chapter 2 where *S. concinna* had significantly lower densities at small patches than at large patches (Figure 3.2, SNK $P < 0.05$). *S. serrata* showed similar population densities at both small and large patches throughout the twelve month period (Figure 3.2).

Table 3.1: Summary of ANOVAs comparing densities of *Siphonaria serrata* and *S. concinna* between small at large patches at 2 sites nested in each of 2 locations (Riet River and Kenton-On-Sea), n = 6 replicate quadrats for each species at each site. The table displays the significant ($P < 0.05$) source of variation for each species and month. NS indicates no significant difference. (Cochran's *C* test, $P < 0.05$)

Month	*S. serrata*	*S. concinna*
June	Size	Size
July	Site (Location x Size)	Site (Location x Size)
August	NS	Size
September	Size	Size
October	Site (Location x Size)	Size
November	Site (Location x Size)	Size
December	Site (Location x Size)	Size
January	Size	Size
February	Size	Size
March	Site (Location x Size)	Site (Location x Size)
April	Size	Size
May	Site (Location x Size)	Size

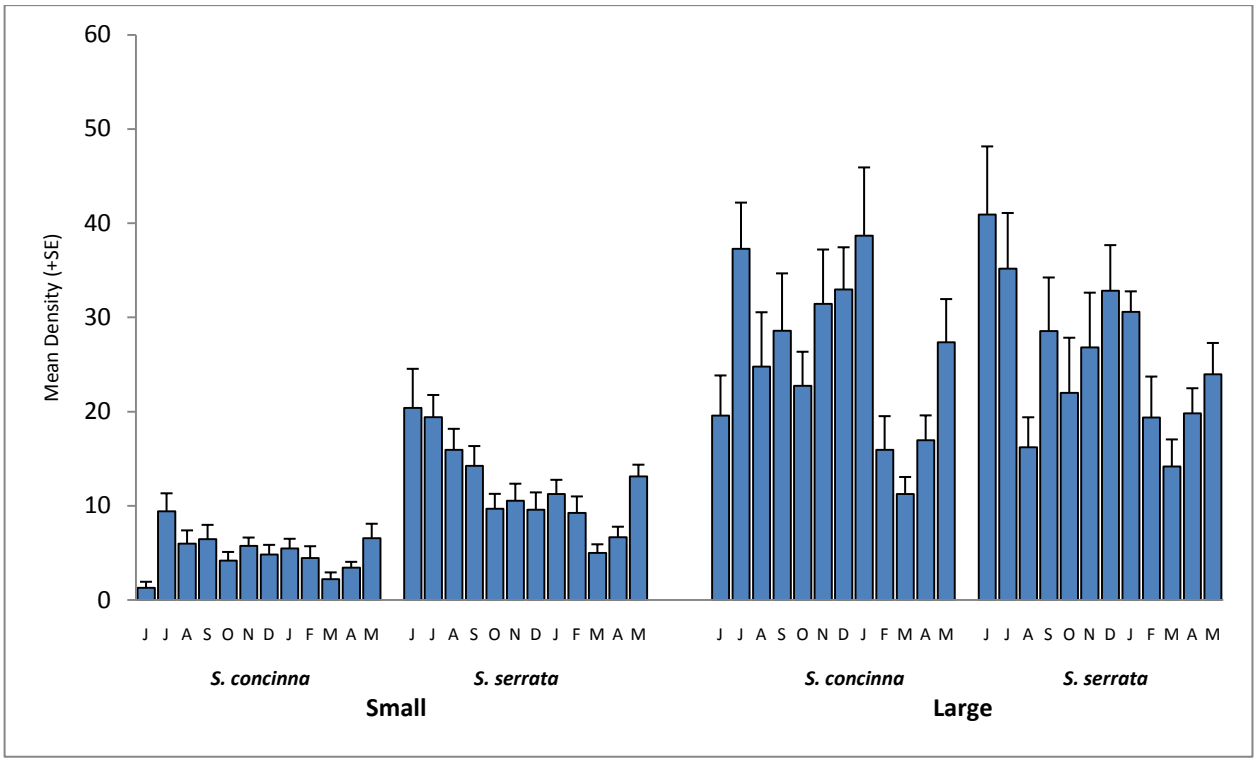


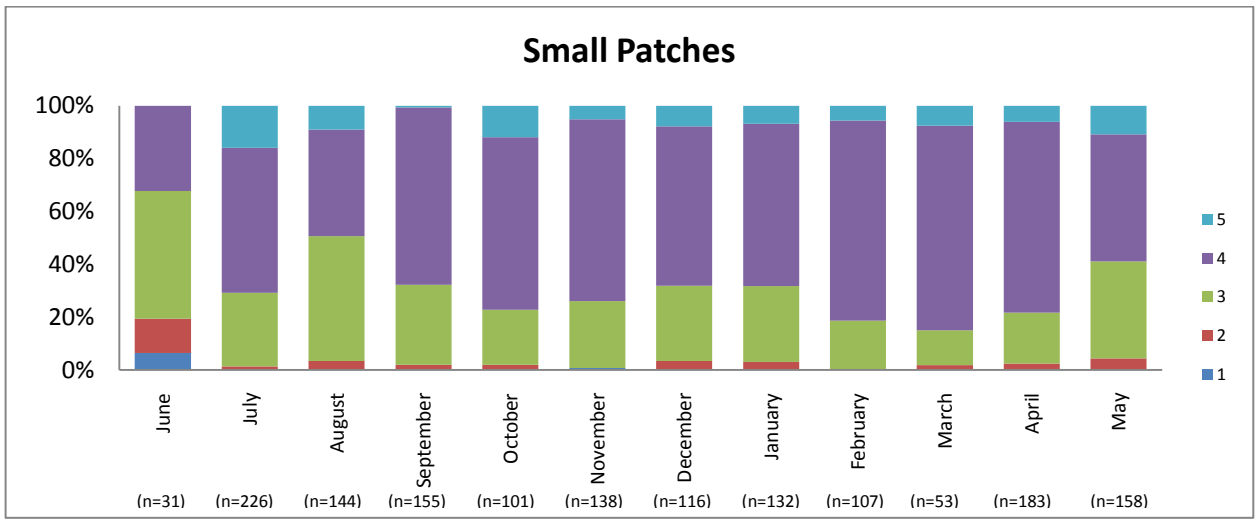
Figure 3.2: Mean (+SE, n=6) monthly density of *S. concinna* and *S. serrata* at small and large patches. Each bar represents the mean density of limpets measured at either small or large patches for each month for each species.

3.3.2 Investigation of size-structure at small and large patches:

Size class distribution for *S. concinna* (Figure 3.3) at small patches was relatively consistent over the twelve month period except for months June and August, with a higher proportion of smaller limpets (classes 1 - 3) than larger limpets (classes 4 and 5) indicating significant changes over the twelve months (χ^2 = 192.7, df = 44, P < 0.001). In May there was a higher proportion of smaller limpets than the remaining months, however over 50 % of the limpets found at small patches were larger than 10 mm in length. Size class 4 was the dominant class for the remaining months with more than 50 % of limpets sampled being in this class.

Significant fluctuations of population size classes were found at large patches over the twelve month period (χ^2 = 446.4, df = 44, P < 0.001). The large patches also illustrated relatively consistent size class distribution over the twelve month period. The distribution was a more bell shaped distribution with size class 3 being the predominant size class in each month. There were very few size class 1 individuals with no month recording more than 0.9 % of the sampled population smaller than 0.5 mm in length. Size class 5 individuals were equally rare at large patches with the exception of August and February which both had over 4 % of the sampled population greater than 20 mm in length.

Comparing the size-structure in the two patch sizes we see that there is a difference between size frequency distribution in small or large patches in every month (χ^2 = 639.1, df = 77, P < 0.001). There was a clear difference in the size class with the most limpets within it at each patch size in all months except June where the majority of limpets were in classes 1, 2 and 3.



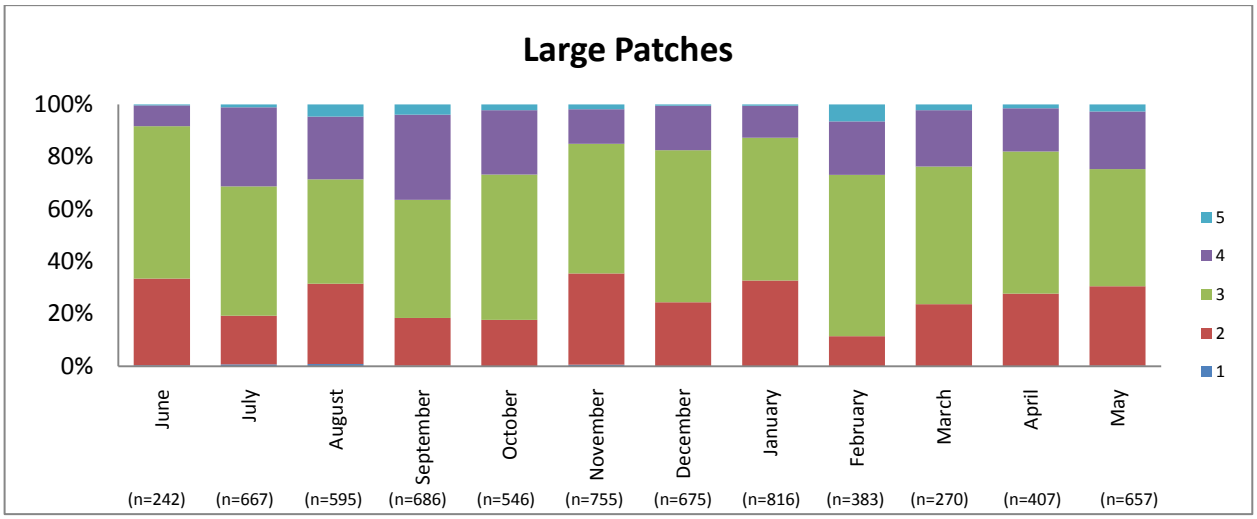


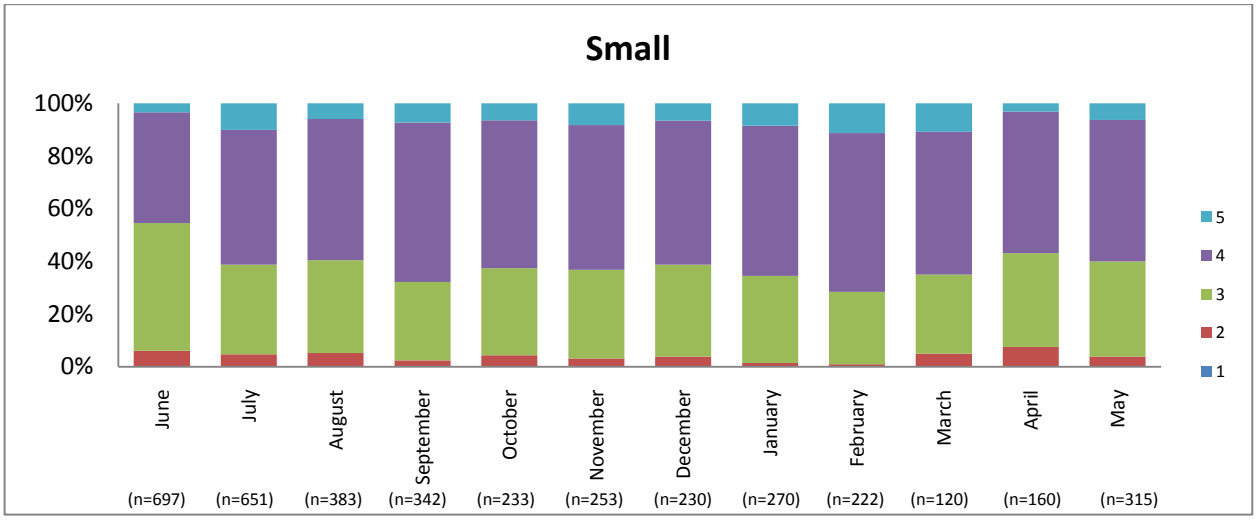
Figure 3.3: Size class distribution for *S. concinna* at small and large patches over the twelve month period. Each size class is represented by the proportion of the population that it represents. 1) 1 – 4 mm, 2) 5 – 9 mm, 3) 10 – 14 mm, 4) 15 – 19 mm, 5) 20 – 24 mm.

Similar to the distribution of *S. concinna*, the *S. serrata* size frequency distribution (Figure 3.4) was predominantly characterised by larger limpets, size classes 4 and 5, at small patches. This was true for all months except for the month of June where the majority of limpets measured were found to be from class 3 (49%). Similar size frequencies were observed in October, November and December where all classes had approximately the same proportions of limpets in each size class. At small patches a significant difference was observed between the size classes at each month ($\chi^2 = 131.6$, df = 44, $P < 0.001$).

At large patches the majority of limpets measured were small, with a low proportion of large individuals. Approximately 75 % of limpets measured each month were found in size classes 2 and 3. January was found to have the highest proportion of small limpets (87 %) and July having the lowest proportion of small limpets (67 %). Throughout the twelve months very low proportions of classes 1 and 5 were found. The highest proportion of class 1 limpets was

measured in August, 0.8 %, and the highest proportion of class 5 limpets was measured in February, 6.5 % of the total number measured (Figure 3.3). There was a significant difference among proportions of the different size classes ($\chi^2 = 547.4$, df = 44, $P < 0.001$).

Clear differences were observed between small and large patches throughout the twelve month sampling period ($\chi^2 = 931.7$, df = 77, $P < 0.001$). As with *S. concinna*, the *S. serrata*, distributions indicated a dominance of large limpets at small patches and a dominance of small limpets at large patches.



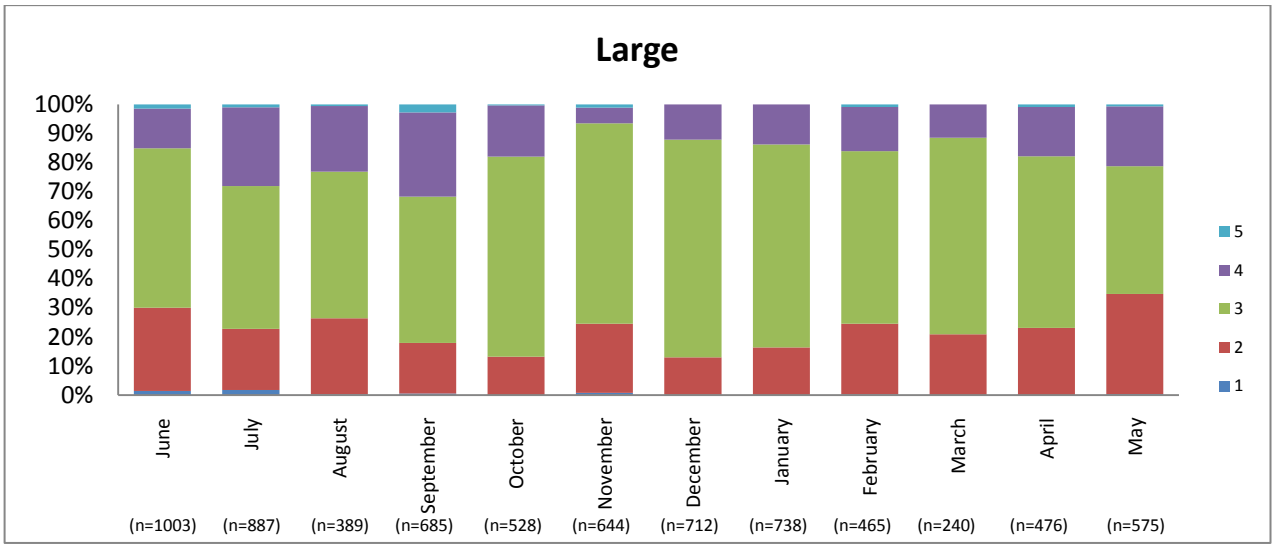


Figure 3.4: Size class distribution for *S. serrata* at small and large patches over the twelve month period. Each size class is represented by the proportion of the population that it represents. 1) 1 – 4 mm, 2) 5 – 9 mm, 3) 10 – 14 mm, 4) 15 – 19 mm, 5) 20 – 24 mm.

3.4 Discussion:

Over the entire twelve month period *S. concinna* showed low population densities at small habitat patches whilst retaining high densities at large patches. This finding conforms with the predictions made at the beginning of this chapter. This pattern has often led to the assumption that a low level of recruitment suggests that the population is not reproducing (Hoover *et al*., 1995). However it cannot be assumed that because small patches show small proportions of new *S. concinna* recruits that these populations are not reproducing. It could be quite the opposite situation where although these populations have high levels of reproduction and dispersal they have extremely low levels of recruitment. For example, Kadmon and Shmida (1990) studied plant population dynamics and found that the smaller grass populations reproduce and disperse seeds but the population depends on external propagules to survive, indicating that small habitat patches support populations that reproduce but do not attract sufficient individuals for survival. There is also the argument of post-recruitment mortality which is often a problem in areas that

are seen as less suitable habitat for settlement and in cases where larval body condition is poor because of spending too long in the water column (Hunt and Sheibling, 1997). The large patches had a significantly greater density of *S. concinna* throughout the twelve month period. With greater densities in the large patches indicate that the local populations have the ability to sustain themselves (Watkins and Sutherland, 1995). Although it is possible that settlers may not originate from the large patch it is more likely that the settlers in the water column will be transported to suitable large patches as they are easier to locate. A possible reason for recruit survival is that recruits are often safer at large patches because they are often less vulnerable to wave action, over exposure to the sun and predation as there is more likely to be areas to shelter in (Hunt and Sheibling, 1997). However, very high numbers of recruits can place the animals in a stressed situation because there may be high levels of competition for food and space. If this is the case, recruits may suffer from post-settlement mortality because they are unable to control their energy usage in stressful conditions, which can ultimately lead to death (Baker and Mann, 1992; Hunt and Sheibling, 1997).

A possible physical factor limiting densities of *S. concinna* is that of habitat patch size. Possingham and Roughgarden (1990) found that in marine systems the size of a suitable habitat affected the population growth of species with complex life stages. This argument is supported by the findings of Hunt and Scheibling (1997) who state that recruits have a higher chance of mortality if settling on a less suitable patch. This supports the results for the pelagic developer, *S. concinna*, and suggests that the lower densities of *S. concinna* found at small patches were because habitat patch size influencespopulation growth. The effect of patch size as a limiting factor for *S. concinna* was consistent through time as small patches consistently had significantly lower densities. Furthermore, there was no indication of population growth of this species over the twelve month period. Large suitable patches may be easier for recruits to find (Possingham

and Roughgarden, 1990), explaining why there are higher proportions of small *S. concinna* at large patches. This being said, there does not appear to be a trend of population growth at large patches; instead population density appeared to fluctuate randomly across the twelve months. It must therefore be emphasised that dispersal along with settlement and extinction processes are integral factors influencing fluctuations in local population size (Karlson, 2006).

As *S. serrata* are direct developing limpets, most the above possible explanations for their patterns of size-structure and densities over time cannot be applied. This is because the adult limpets do not move very much and are unlikely to emigrate to other populations, while recruits do not spend time in the water column and therefore remain within the same population into which they are born making them less vulnerable to wave action and poor body condition (Hunt and Scheibling, 1997). Size class analysis for *S. serrata* showed that smaller patches had larger limpets; this could be related to competition and food availability. The studies done by Bustamante *et al*. (1995) and Huston and Wolveton (2009) indicate that limpet body size is directly related to food availability. This effects of recruitment on size structure are not apparent in this study because the implication of lower limpet densities increasing food supplies at small patches should result in high levels of recruits and high proportions of small limpets, which is clearly not the case. It would also imply that at large patches with high densities, there would be low levels of recruitment because of limited food resources. At all large patches, high densities of both species were identified, which implies increased inter-specific and intra-specific competition for resources. In terms of intraspecific competition; the higher proportions of small limpets at large patches could be due to the fact that smaller limpets have greater competitive capabilities than large limpets (Marshall and Keough, 1994).

The results drawn from the spatial study (Chapter 2) were clearly consistent over a twelve month period. There were lower densities of *S. concinna* at smaller habitat patches and *S. serrata* had similar densities at all patches. All populations showed fluctuations in densities across the twelve month period indicating that a variety of factors may influence their densities over time. *S. concinna* found at small patches were the most stable populations in terms of numbers and this suggests that there was little recruitment and low mortality over the study period.

Chapter 4

The effect of isolation on the densities and population size-structure of two limpet species

4.1 Introduction:

Most organisms live in fragmented landscapes; habitable areas are located within matrices of discrete habitat patches and are defined by their size and isolation from other patches (Krauss *et al*., 2003). The effect of the spatial arrangement of suitable habitats on organisms depends on several interacting factors: habitat patch size, proportion of habitat in the matrix and the distance between suitable patches (Andrén, 1994; Turner *et al*., 2001; Russell *et al*., 2005). The distance between suitable habitat patches characterises the degree of isolation that assemblages are exposed to (Diamond, 1975). The way in which organisms react to isolation depends on their ability to move between patches, suggesting that organisms will react to isolation in a species-specific manner (Bowman *et al*., 2002; Russell *et al*., 2005). A general assumption has been that organisms with greater migration abilities can disperse more easily and therefore the distance between patches may have a reduced effect on these organisms (Russell *et al*., 2005). Mobility is not the only significant factor when considering the effects of isolation; the connectivity of the landscape is important (Dethier, 2003). The landscape surrounding the suitable habitat will either be a boundary between patches or can provide corridors for the movement of organisms between patches (Turner *et al*., 2001; Dethier, 2003). When the surrounding habitat is inhospitable and acts like a boundary / barrier, isolation becomes an important influencing factor when considering population dynamics (Turner *et al*., 2001).

It has been proposed that when patches are near together it is more likely that animals will encounter neighbouring habitats (Kareiva, 1985). Therefore, a landscape matrix of many suitable patches that are close together will lead to a high density of organisms (Eggleston, 1998; Eggleston *et al*., 1999). This has been refuted by Virnstein and Curran (1986) and Russell *et al*. (2005) who argue that habitat patches with a high degree of isolation will receive recruits more rapidly because in a landscape with relatively few suitable patches animals will settle at the first available patch. The problem here is that it is assumed that all organisms control their movements; many organisms, both marine and terrestrial, depend on external forces such as wind or water movement for their dispersal. This implies that there is a higher probability of propagules finding a matrix of patches close together than of finding highly isolated patches (Possingham and Roughgarden, 1990; Goodsell *et al*., 2007).

To determine the effects that isolation will have on populations, one must consider that each species reacts to isolation in a distinctive manner and therefore the reactions of individual species should to be examined at varying scales. The degree of isolation is most often defined by the distance to the nearest suitable habitat patch or the nearest occupied habitat patch or source patch. This study uses the first approach where the degree of isolation was defined by the closest suitable habitat patch as has been done for a variety of organisms (e.g. birds: Van Dorp and Opdam 1987; amphibians: Laan and Verboom 1990; butterflies: Thomas *et al.* 1992). The distance between patches and the components of the surrounding habitat matrix pose a physical barrier to organisms. When this is linked with the organism's migratory and dispersal abilities, one can successfully determine the effect that isolation of habitat patches has on local populations.

This study takes a linear landscape, the Kwa-Zulu Natal coastline in South Africa, and compares how differing degrees of isolation of rocky shores affect the population density and size structure of two limpet species, *S. concinna* and *S. serrata*. The two limpet species were selected because they are very similar in distribution, body size and grazing preferences but have different developmental modes (see General Introduction). It was hypothesised that at different degrees of isolation different densities of limpets would be found. Second, it was hypothesised that the size structure of limpets would be different at the different degrees of isolation.

4.2 Methods:

The two species of *Siphonaria* occur on rock patches that are separated by sand. The distance between the rock patches varies along the South African coastline and to understand the influence that these sand barriers have on the two species, isolation must be examined at all degrees possible. The KwaZulu-Natal coast of South Africa has the longest stretches of sandy beaches, compared to the rest of the beaches within the two species' geographical range and this is the reason why it was selected to be the area of study for the isolation experiment. Sites were classified as close, near and far with the degrees of isolation interspersed as much as possible. The very far sites were all located in the northern-most section of the region, as this was the only area where there was a high degree of isolation of rocky shores.

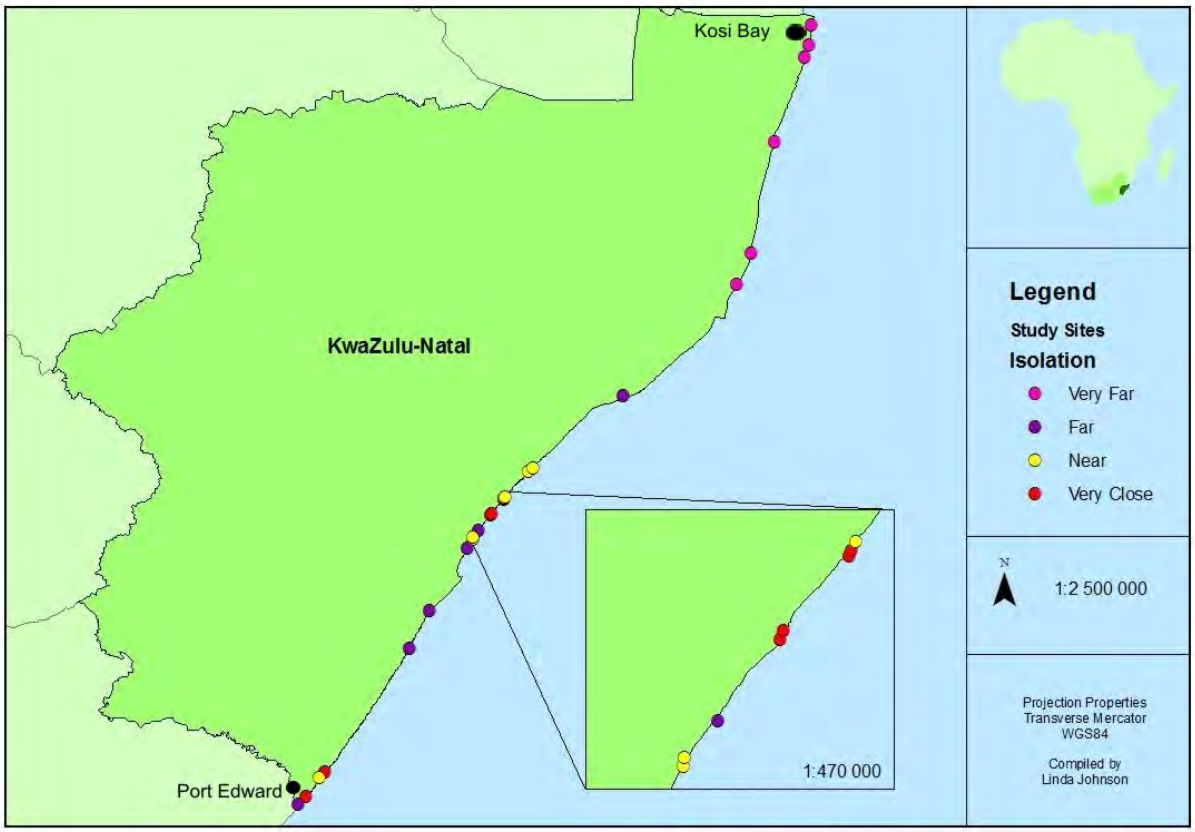


Figure 4.1: Location of isolation study sites in Kwa-Zulu Natal

To determine the degree of isolation patches of rock, the lengths of sandy beaches on either side of each patch were measured. As the lengths of sand on either side of the rock patch were not equal, the degree of isolation was defined by the shortest length of sand. Measurement of sand was first carried out using aerial photographs, geographical information systems and Google Earth. This was then followed up by ground truthing, at the close sites tape measures were used to get more accurate distances. A total of 24 rock patches were selected. These were split into four groups of six patches, depending on how isolated they were: close, near, far and very far (Table 4.1). The determination of the four degrees of isolation was done in an arbitrary fashion to try to cover all accessible isolated patches. To ensure that patch size did not act as a confounding factor to the results of this study each degree of isolation comprised both small

rock patches and large rock patches, as defined in Chapter 2. The distances used for the degree of isolation are displayed in the following table.

Table 4.1: Measurements of degree of isolation

Degree of Isolation	**Length of Sand (m)**
Close	1 - 20
Near	100 – 300
Far	1 000 – 2 500
Very Far	3 000 +

Rock patches were selected along the eastern coast of South Africa between Kosi Bay and Port Edward (Figure 4.1). Sampling of the two species of limpets was carried out during spring low tides. The first hypothesis, concerning the density of limpets, was tested using the same method of sampling as in Chapters 2 and 3. On each rock patch, six haphazardly placed 50 cm by 50 cm quadrats were sampled for each species along the length of each patch. Within each quadrat, each limpet was measured along the longest axis of the shell using vernier callipers.

To test whether isolation had an effect on the densities of limpets, a three-factor analysis of variance (ANOVA) testing the effect of degree of isolation, rock patch and species was carried out. Isolation was fixed, orthogonal and had four levels, site was nested in isolation and species was orthogonal and fixed with two levels and n = 6 quadrats. No single transformation was found to satisfy the assumption and therefore a violation of homogeneity of variances was not considered to be a problem because ANOVA is relatively robust to heterogeneous variances for large designs such as this (Underwood, 1997). When variation in analyses was found to be significant, Student-Newman-Keuls (SNK) tests were used to explore the differences. To test the

hypothesis about the size-structure of the limpets, all individuals of each species were grouped according to degree of isolation, and size-frequency distributions were compared between very close, near, far and very far patches using chi-squared contingency tests and the following five size classes; 1) 1 – 4 mm, 2) 5 – 9 mm, 3) 10 – 14 mm, 4) 15 – 19 mm and 5) 20 – 24 mm. To determine the differences between degrees of isolation the six very close, six near, six far and six very far patches were pooled and the size classes from each region were compared using chi-squared contingency tests (χ^2).

4.3 Results:

4.3.1 Species density with isolation:

The two species appeared to show similar responses to very close and near degrees of isolation but at far and very far degrees of isolation responses appeared to differ between the two species (Figure 4.2). The ANOVA (Table 4.2) showed a significant interaction between species and site but not between species and isolation and sites appear to be very variable. There were greater densities of *S. serrata* than *S. concinna* at far and very far patches (SNK $P < 0.01$), while at the close and near patches densities of the two species were not significantly different. Although there appeared to be fewer *S. concinna* on very isolated patches (Fig 4.2), there was no significant effect of degree of isolation for *S. concinna* (Table 4.2).

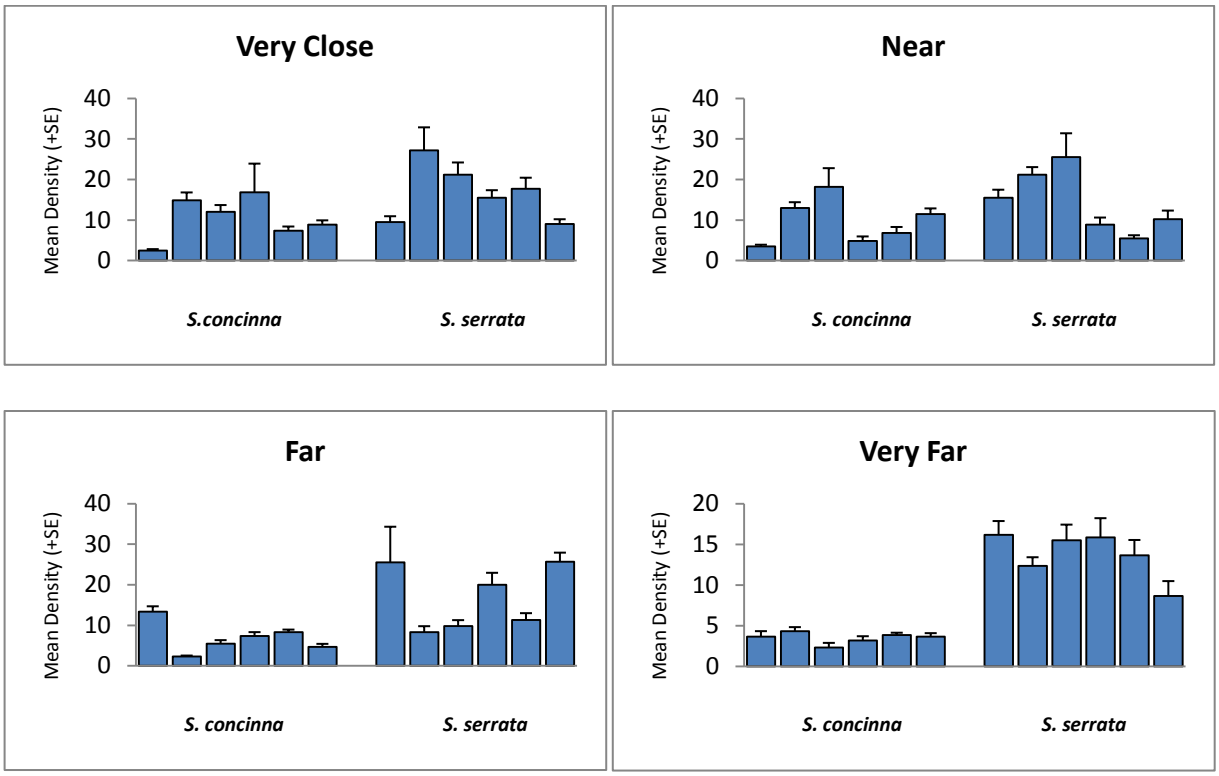


Figure 4.2: Mean density (+SE, n = 6) of *S. concinna* and *S. serrata* at very close, near, far and very far degrees of isolation. Each bar representing the mean density of limpets measured at each site.

Table 4.2: ANOVA of untransformed data for the number of limpets per quadrat for *S. concinna* and *S. serrata* at different degrees of isolation. Four different degrees of isolation which are fixed, site was nested in isolation and was random, *n* = 6 replicate quadrats per site. Variances were heterogeneous (Cochran's *C* test, $P < 0.05$).

* $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$

Source	df	M.S.	*F*	
Isolation	3	2.51	0.96	
Site (Isolation)	20	2.60	18.67	***
Species	1	0.05	0.03	
Isolation x Species	3	0.73	0.43	
Species x Site (Isolation)	20	1.71	12.26	***
Res	240	0.14		
Tot	287			

4.3.2 Analysis of the size-structure of limpets at different degrees of isolation:

The size structure differed for both species among the different degrees of isolation (*S. concinna* $\chi^2 = 114.8$, df = 6, $P < 0.001$; *S. serrata* $\chi^2 = 62.8$, df = 6, $P < 0.001$). There was a greater proportion of small *S. concinna* at less isolated patches and as the isolation increased, the population shifted to be made up of larger individuals. Patches with a very close degree of isolation had a higher proportion of size class 1 and 2 than any other degree of isolation (Figure 4.3 and 4.4). The patches with near, far and very far degrees of isolation had the majority of *S. concinna* individuals in size classes 3 and 4 with very far having the highest proportion of size class 4 (Figure 4.3 and 4.4). The distribution of *S. serrata* was fairly independent and remained similar at all of the degrees of isolation, with size class 3 having the highest proportion of individuals within it (Figure 4.4). Very close and very far degrees of isolation had high proportions of size class 2 while near and far had high proportions of class 4. There was a significant difference between the limpet size class distribution for both species at the different degrees of isolation ($\chi^2 = 242.6$, df = 14, $P < 0.001$). They had very similar size class distributions at medium and large degrees of isolation but they differed at very close and very far degrees of isolation. *S. concinna* had a higher proportion of size class 2 than *S. serrata* at very close degrees of isolation, whilst the majority of *S. serrata* individuals were found of size class 3 at very close degrees of isolation. At very far degrees of isolation the majority of *S. serrata* individuals were within size classes 2 and 3 whilst for *S. concinna* had the majority were within classes 3 and 4.

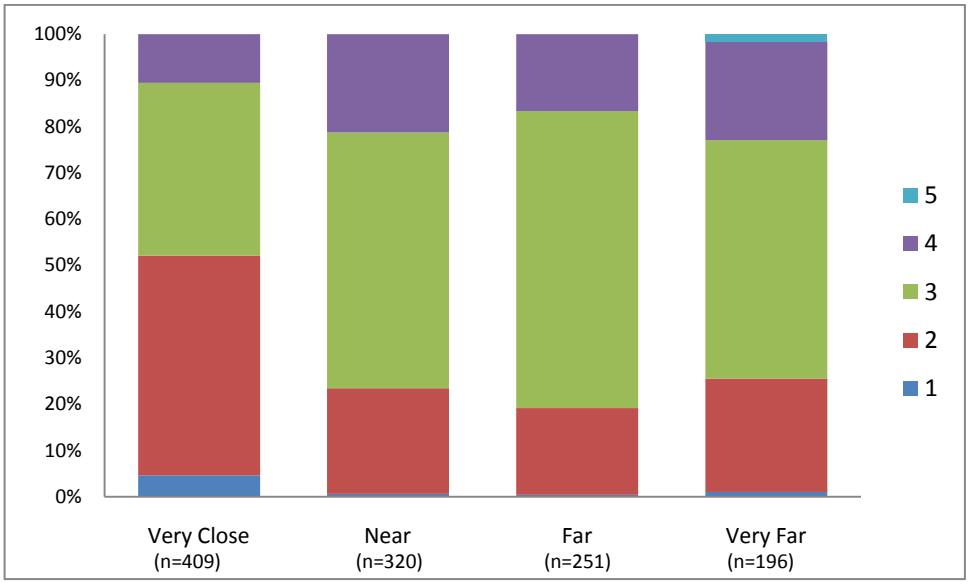


Figure 4.3: Size class distribution of *S. concinna* at each degree of isolation. 1) 0 – 4 mm, 2) 5 – 9 mm, 3) 10 – 14 mm, 4) 15 – 19 mm, 5) 20 – 24 mm.

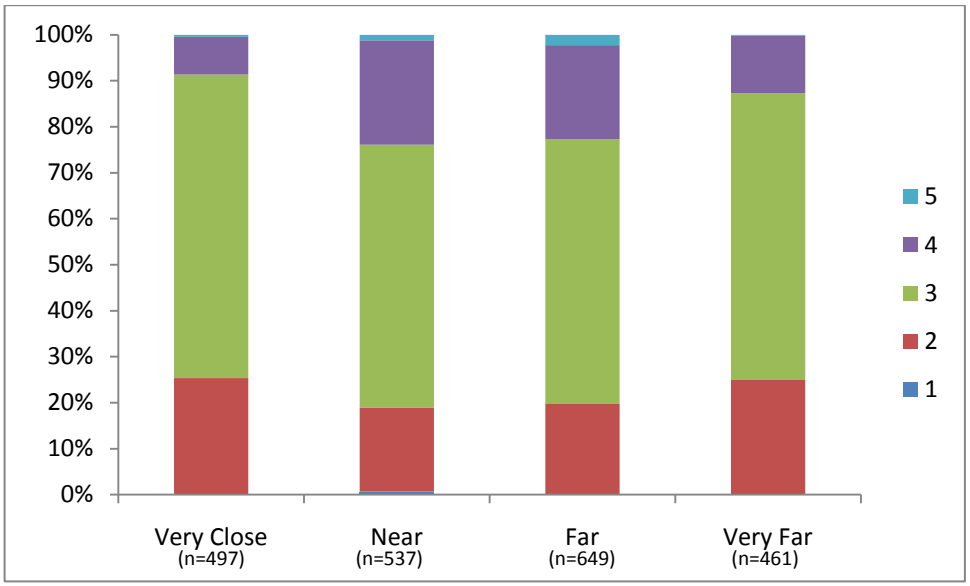


Figure 4.4: Size class distribution of *S. serrata* at each degree of isolation. 1) 0 – 4 mm, 2) 5 – 9 mm, 3) 10 – 14 mm, 4) 15 – 19 mm, 5) 20 – 24 mm.

4.4 Discussion:

Different patterns of density were observed across the different degrees of isolation. *S. serrata* was clearly not affected by the degree of isolation as they were found at all patches and their densities did not vary significantly among the four degrees of isolation. *S. concinna* showed a response to the different degrees of isolation (Fig 4.2). However, the differences seen between densities and degree of isolation were not statistically different. It is possible that the pattern observed in Figure 4.2, where population density appears to decrease with degree of isolation, is a trend that would continue if the degree of isolation could be increased. Underwood and Chapman (2006) emphasise the importance of scale when examining patterns of distribution and density of intertidal organisms. This is particularly true for *S. concinna* as the water column can transport larvae great distances and it is possible that in the case of the South African coastline the degree of isolation of any patch was not great enough to show a significant response by *S. concinna*.

Possingham and Roughgarden (1990) state that the more isolated the habitat patch the less likely it is to be colonized because recruits cannot locate suitable habitat patches. Thus, an increase in isolation leads to lower rates of recruitment, resulting in smaller populations. This is because recruits are less likely to be capable of moving great distances to find suitable patches to settle in, which leads to higher death rates than settlement rates (Keough, 1985; Vos and Stumpel, 1995, Watkins and Sutherland, 1995). In the case of this study limpets from both species were found at all sites indicating that the degree of isolation that limpets were exposed to was not great enough to pose an absolute barrier. It can be assumed that populations that are not well separated might exhibit spatial dependence because of localized ecological processes and therefore illustrate similar population trends (Underwood and Chapman, 1996). If the study had

been on a greater scale with higher degrees of separation then the patterns that were beginning to emerge by *S. concinna* may have mirrored the findings that have been illustrated by several studies, in both aquatic and terrestrial systems, where it was found that the more isolated the patch the less likely it was to be colonised and the lower population density would be (e.g. Birds: van Dorp and Opdam, 1987; Amphibians: Laan and Verboom, 1990; Butterflies: Thomas *et al*., 1992; Krauss *et al*., 2003). This suggests that if higher degrees of isolation were observed, the emerging patterns would have lead to a significant difference because the higher degree of isolation, the lower the probability that larvae will reach unoccupied patches (Keough, 1985; Vos and Stumpel, 1995).

Russell *et al.* (2005) found that the greater the mobility and dispersal of an organism, the less effect isolation will have on population density and occurrence of that organism. This appears to be the case for *S. concinna* as it is considered the more mobile of the two species. However, *S. concinna* has very little to no control of its movements as larvae within the water column and so does not have the ability to actively seek out suitable habitat patches giving it very weak control over its dispersal (Diamond, 1975; Possingham and Roughgarden, 1990; Goodsell *et al*., 2007). The relationship between power of dispersal and colonisation is addressed by the theory of Island Biogeography and by using the Incidence Function (Diamond, 1975). A highly fragmented landscape made up of a large number of closely linked suitable habitat patches, as shown by Eggleston *et al*. (1999), will be colonised at a high rate as organisms move easily between patches because there is a high probability that they will find the nearby patches. The further apart the suitable habitat patches are from one another the less likely that organisms will successfully move between suitable habitat patches, indicating that distance is a barrier force (Diamond, 1975; Keough, 1985; Hanski, 1994; Coleman and Kelaher, 2009). In an examination

of algal distribution in Australia, Coleman and Kelaher (2009) indicated that the distance between patches was the most pertinent factor influencing the successful movement of propagules between suitable habitat patches. If distance is linked with the dispersal capability of an organism then the likelihood of extinction and extirpation can be determined (Coleman and Kelaher, 1999; Roberts and Hawkins, 1999). Therefore organisms with low dispersal capabilities and limited control of their movements are highly vulnerable to extinction and extirpation when suitable habitat patches are far apart (Roberts and Hawkins, 1999, Russell *et al.*, 2005).

The densities of *S. serrata* did not differ significantly with the degree of isolation. As this species is a direct developer that does not rely of currents and wind to return propagules to rock patches, it can be assumed that if it is found at a patch, it should be able to keep population densities high and relatively stable (Thomas *et al.*, 1992; Krauss *et al.*, 2003; Karlson, 2006). Looking at the size class data it can be seen that there are very little difference in size structure at the different degrees of isolation. The possibility of predation limiting the size-structure of limpets is clearly illustrated in the results for *S. serrata* as at every site the dominant size class are class 3 (10 – 14 mm) and very few limpets are found to be larger than 19 mm in length. This coupled with avian predators preferring to prey on large limpets (Frank, 1982; Wootton, 1993) would suggest that there would be a higher proportion of smaller limpets than large limpets.

As *S. concinna* populations depend on the settlement of new recruits to ensure that local populations survive, one can examine the size class data to determine whether new recruits are reaching isolated patches. This was found at near and far degrees of isolation but surprisingly extra large degrees of isolation showed a bell-shape size class distribution with all size classes being represented. This suggests that at near and far patches recruitment events had not taken place, whilst they had at very far patches. The results at the very far patches can be explained

through the example given by Russell *et al*. (2005) who found that if a suitable habitat patch was found settlement would take place. The limited size class distribution for *S. concinna* at near and far degrees of isolation can be linked back to the dispersal capabilities of an organism, suggesting that they have limited capabilities and rely heavily on currents and wind to deliver propagules to rock patches (Roberts and Hawkins, 1999; Russell *et al*., 2005; Coleman *et al*., 2009). The majority of limpets, for both species, found at near and far degrees of isolation were of size class 3 (10 – 14 mm) with very few limpets of any other size within these patches. Possible reasons for finding limpets of class 3 (10 – 14 mm) at near and far degrees on isolation can be linked to food availability, competition and predation (Kelaher and Cole, 2005). Predation may be a significant factor in most cases as major predator species prefer to eat larger limpets which would result in a population of smaller limpets (Frank, 1982; Wootton, 1993). Although this is unlikely as Siphonariids show strong chemical defence and therefore predators are not likely to feed on these two limpet species (McQuaid *et al*., 1999). The availability of food and the prospect of inter and intra specific competition influence the size structure of a population, and as mentioned in Chapter 3, smaller limpets are better competitors than large limpets at high densities often resulting in populations made up of smaller limpets (Marshall and Keough, 1994).

Recruitment and mortality determine population density and survival; coupled with distance between patches, recruitment can be a limiting factor for pelagic developers (Hunt and Scheibling, 1997, Karlson, 2006). However, in the case of this study it appears that although there were differences between densities of limpets at the different degrees of isolation the differences were not significant. Based on the results of this study it can be concluded that isolation is not an important factor affecting the densities of the two species. The effects can, however, be seen due to the differences between species in their population structure.

Chapter 5

General Discussion

Landscapes are patchy environments because of processes such as habitat fragmentation, which have varying influences on organisms. It is these processes that produce an environmental patchwork which often exerts a powerful influence on the distribution and density of organisms (Weins, 1976; Fahrig and Merriam, 1994; Turner *et al.*, 2001). Most systems are complex and three dimensional making them difficult to study. There are, however, linear systems such as river courses, mountain ranges and coastal zones, which are easier to examine as they are essentially two dimensional (Goodsell *et al.*, 2007). These two dimensional systems provide the ideal opportunity for investigating patterns and processes such as the way that organisms with different modes of dispersal react to patch size and isolation. Marine systems are particularly important because it has frequently been assumed that marine organisms will not be affected by habitat fragmentation because they have the ability to disperse among fragmented patches through pelagic larvae (Possingham and Roughgarden, 1990; Goodsell *et al*., 2007). Many marine organisms are direct developers or have a very short pelagic phase making them sensitive to patch size and isolation indicating that marine systems are not as connected as was once thought (Goodsell *et al*., 2007). The response of marine organisms to fragmentation is similar to that of terrestrial plants with dispersive propagules and animals that disperse through air (Goodsell *et al*., 2007). As this is the case, marine organisms are good indicator organisms for illustrating population patterns and trends associated with habitat fragmentation.

Population density should increase as the size of the habitat patch increases (Atmar and Patterson, 1993; Andrén, 1994; Turner *et al*., 2001) and population densities should decrease with greater degrees of isolation (Diamond, 1975; Hanski, 1994; Coleman *et al*., 2009). This appears to be true for the pelagic developer, *S. concinna* when looking at patch size but not the degree of isolation. The direct developer, *S. serrata*, did not exhibit these trends and instead population densities remained relatively constant at the different patch sizes and different degrees of isolation. Chapters 2 and 3 demonstrated that the population density of *S. serrata* in small patches was greater than populations of *S. concinna* in small patches. As there was a link between population density and the decrease in habitat patch size, it could therefore be assumed that the density of both species populations should be lower at small patches (Hastings and Wolin 1989). This was not the case because the density of the population of *S. serrata* in small patches was the same as in large patches. A possible explanation for this trend is that in small patches the density of *S. concinna* is low because settlers are not transported to suitable patches or suffer from post-settlement mortality (Possingham and Roughgarden, 1990, Hunt and Scheibling, 1997) as discussed in Chapter 2. This could possibly decrease the pressure on algal food supplies which are commonly found to be low in small patches (Raffaelli and Hawkins, 1999; Zanette *et al*., 2000). The decreased pressure leads to increased growth of algae and with this growth there is a greater supply of food for the limpets (Raffaelli and Hawkins, 1999). If there was an increase in supply of food this could have led to a higher density of *S. serrata* at small patches. As food supply acts as a control on population size and the growth of the population, an increase in algal supply could very possibly have resulted in no significant difference in population density between patch sizes for *S. serrata*. This links to community co-dependence where a change in one species can, directly or indirectly, result in a change in another species living in the same environment (Wootton, 1993). Although estimates of the two species were sampled independently they occupied similar habitat and this has allowed for their

comparison. In this case it is possible that changes in densities of *S. concinna* indirectly increased the density of *S. serrata* at small patches allowing the density of *S. serrata* to be similar across all habitat sizes.

Similarly, when referring to the density of either limpet at differing degrees of isolation, there was no significant difference in density for any degree of isolation (Chapter 4). MacArthur and Wilson's (1963; 1967) theory of Island Biogeography states that, with increasing degrees of isolation of habitat patches, there should be a decrease in population size, which was not found. *S. concinna* showed an emerging trend of density decreasing with increased isolation, however, this was not statistically significant and it has been assumed that because of larval transport in the water column, it is extremely likely that the degree of isolation examined was not great enough to greatly hinder the successful transport and settlement of *S. concinna*. *S. serrata* showed no emerging trend and the densities observed could be possibly be explained by Levin's (1992) model of metapopulations, which states that the extinction and colonization of habitat patches are independent from their spatial locations (Levin, 1992). This implies that the distance between patches does not affect population densities at all. This implies that the populations of *S. serrata* were all part of a larger interconnected metapopulation (Hanski, 1994), which is highly improbable as the dispersal of *S. serrata* is localised as it is direct developing and dispersal can only be achieved by adult movement, or by rafting of adults or egg masses (Johannesson and Johannesson, 1995). Rafting and adult movement very rarely takes place and when it does, a very low number of founding organisms move to colonize a habitat patch (Johannesson and Johannesson, 1995). Very little is known about this form of dispersal (Underwood and Chapman, 1992). It is believed to be a rudimentary form of dispersal that for direct developers, depends on water movement (Underwood and Chapman, 1992; Johannesson and Johannesson, 1995; Goodsell *et al*., 2007). The theory of metapopulations could be applied to *S. concinna* and it is

much more likely that their populations are connected as the larvae do move through the water column but once again they depend on the movement of water and this ultimately determines the connectivity of the populations at different habitat patches. This suggests that each population could be connected but with little proof that rafting has taken place it can be assumed that populations are effectively separate. As each site was assumed to be a separate population of *S. serrata* it is clear that if they successfully reproduce so that populations should be able to grow until they reach carrying capacity. This goes back to the idea that small patches will have low population densities and as the *S. concinna* densities were considerably lower at small patches than at large, there was a greater carrying capacity for *S. serrata* populations and therefore *S. serrata* densities were higher than *S. concinna* densities across all small patches.

It is possible that the extent of fragmentation examined was inappropriate for both species. The effect of fragmentation varies from one species to the next and each species is affected at different observational scales as is seen from the emerging trend shown by *S. concinna* and not by *S. serrata* (Fahrig and Merriam, 1994, Blanchard and Bourget, 1999). It must therefore be acknowledged that the scale of fragmentation which was examined may not have been great enough to display possible effects of habitat fragmentation. As the South African coastline does not possess vast degrees of isolation of habitat patches it is is possible that the habitat fragmentation along the coast of South Africa is not sufficient to result in an effect on densities of either species. Even though the two species appear to be extremely similar, their different mode of dispersal is an important factor that determines the scale at which isolation and patch size influence their densities. To fully understand the distributional patterns displayed by any organism the correct scale for study needs to be selected (Underwood and Chapman, 1996). In this case an appropriate scale was selected for the patch size studies; however, the lack of

significant differences in the isolation experiment may have resulted from the isolated patches not being far enough apart from one another.

The three experimental chapters investigated patch size and isolation separately, which may have limited the results found in this study because the two are inherently linked. Within highly fragmented landscapes, where habitat patches are small and distances between patches are not great, it has often been found that population densities are high because there is an increased edge effect and movement of organisms between patches is relatively easy (Eggleston *et al.*, 1999; Fischer and Lindenmayer, 2007). Irrespective of their size, the further patches are from each other, the lower the population density will be because it is more difficult to move between patches (MacArthur and Wilson, 1967; Diamond, 1975; Keough, 1985; Possingham and Roughgarden, 1990; Hanski, 1994; Ehrlen and Eriksson, 2000; Coleman *et al*., 2009). It is possible that when larvae encounter a suitable patch, whether it is small in size or highly isolated, it will be colonized rapidly resulting in a relatively high population density (Russell *et al*., 2005). Although population density was not found to be high at highly isolated patches, the pattern of recruitment was found in Chapter 4 was of highly isolated patches displaying a high proportion of small *S. concinna.* This indicated that recruitment had taken place, while the middle two degrees of isolation had mainly larger *S. concinna,* implying no recent recruitment. Although Russell *et al*. (2005) predict high densities at highly isolated patches because of recruitment, low recruit numbers and population densities are not unheard of at highly isolated patches as the majority of larvae only travel short distances (Possingham and Roughgarden, 1990; Kinlin and Gaines, 2003). The remaining minority can be transported great distances and when they finally do come across a suitable habitat patch they will colonise it resulting in low densities of recruits (Kinlin and Gaines, 2003).

Dispersal and recruitment act as stabilising forces in populations with high death rates (Hastings and Wolin, 1989). It is therefore of great importance to understand the spatial structure of populations across their entire biogeographic range in order to be able to predict whether local populations are at risk of becoming extinct (Hastings and Wolin, 1989; Ehrlen and Eriksson, 2000; Kinlin and Gaines, 2003). Population size and regional distribution are limited by larval availability, which in turn is limited by the availability of suitable habitat (Hastings and Wolin, 1989; Ehrlen and Eriksson, 2000). Hastings and Wolin (1989) state that an increase in patch size will lead to a decrease in the probability of extinction as population growth potential has increased. Populations may, however, fail even if there is suitable habitat available because of limitations of larval distribution (Possingham and Roughgarden, 1990; Ehrlen and Eriksson, 2000)

The majority of habitat fragmentation studies examine the relationship between population density and patch size with very few of them examining the effects over more than two seasons (Andrén, 1994). This study investigated the spatial and temporal distributions ensuring that the patterns observed were not once-off phenomena and represented consistent population trends. Although time constraints only allowed a twelve month investigation of population densities at small and large patches the variability of these populations was clearly indicated through density changes over the twelve months. Chapter 2 tackled the regional patterns of fragmentation but it only took a snap shot of population densities at the time of sampling. From the temporal study, Chapter 3, the results found by Chapter 2 were supported. Chapter 3 clearly illustrates that over time population densities remained high at large patches for both species and confirmed that it was at small patches that the discrepancy lay. The spatio-temporal link is pertinent for

understanding patterns and processes within systems (Levin, 1992; Bouliner, 1998; Turner *et al*., 2001). The temporal variability of populations is inherently linked to extinction and colonisation processes (Kay and Keough, 1981; Bouliner, 1998; Dye, 1998; Ims *et al*., 2004). When dealing with an organism with a dispersal mode that depends highly on external factors one cannot neglect the fact that population trends and patterns will fluctuate greatly over time.

Mobility and dispersal ability are key traits that determine the effect that habitat fragmentation has on a species. *S. concinna* is considered the more mobile of the two species examined but was the species that was more affected by patch size and isolation. This clearly indicates that organisms will respond to habitat fragmentation in different ways and at different scales. It is therefore vital to recognise and determine these unique responses to be able to understand the underpinning factors that influence population dynamics at any given time within a landscape.

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Appendix

Preliminary Study

A preliminary study was carried out to determine the appropriate sizes of habitat patches for examining the effects of small and large patches on population density in Chapter 2 and Chapter 3.

6.1 Methods:

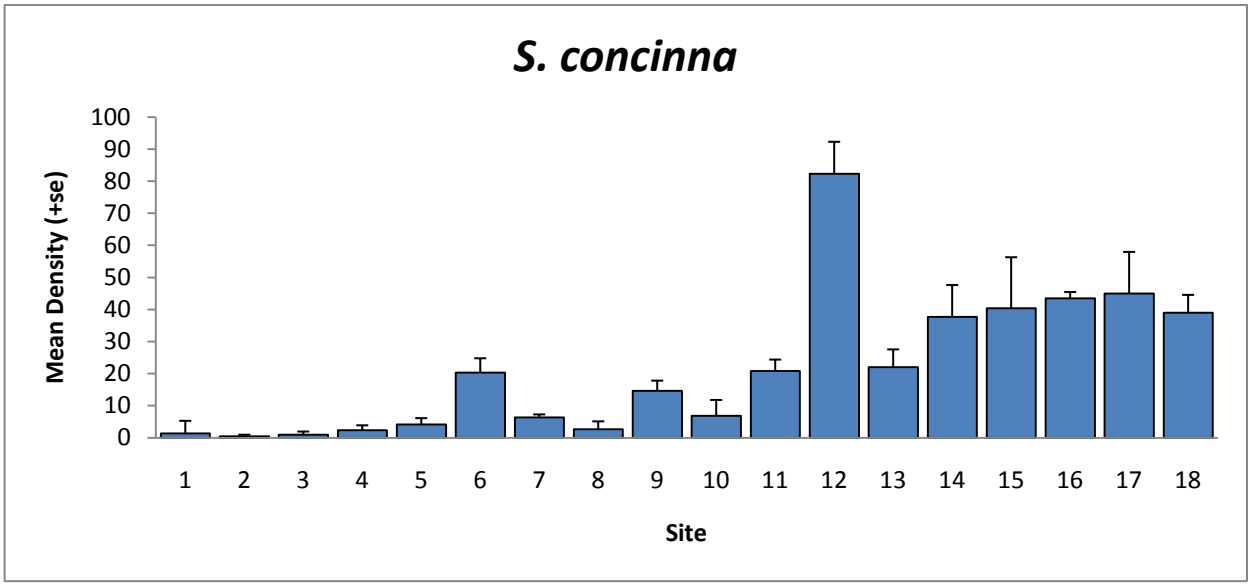
To determine the appropriate habitat sizes that should be considered large and small 18 sites were selected along the Eastern Cape coastline of South Africa. The 18 sites were selected based on their size and whether the two limpet species, *S. concinna and S. serrata*, were present. The 18 sites ranged in perimeter from 8 m to 253 m, with an even distribution of lengths between the two.

After site selection, once-off sampling of the two limpet species was carried out during spring low tides in April and May of 2009. Each rock patch was sampled using a 50 cm by 50 cm quadrat. At each patch, three replicate quadrats were haphazardly placed for each species. Each species was sampled in separate quadrats to maintain independent estimates of the two populations. Within each quadrat individual limpets were measured along the longest axis of the shell using vernier callipers. Before analysis, Cochran's Tests were carried out to ensure that

there was homogeneity of variances between data in each region. The numbers of limpets for each species at each shore were compared with single-factor analyses of variance (ANOVA).

6.2 Results:

There was a great deal of variability in limpet densities for *S. concinna* across the range of patch sizes. The ANOVA (Table 6.1) indicated that there was a significant difference between sites and when the figure below was examined it was clear that the greatest differences were between the smallest and the largest sites. The smallest three sites had the lowest densities; sites 4, 5, 7 and 8 had considerably low densities. Sites 6, 9, 10, 11 and 13 had fairly low densities and site 12 had the highest density of *S. concinna*. Sites 14 to 18 had similarly high densities with very little variance. The *S. serrata* showed a significant difference between sites (Table 6.1), but the mean densities did not vary greatly throughout the 18 sites. The 18 sites did not show a trend of increasing or decreasing density with patch size for *S. serrata* whereas, *S. concinna* show a clear trend of increase in density with increasing habitat patch size.



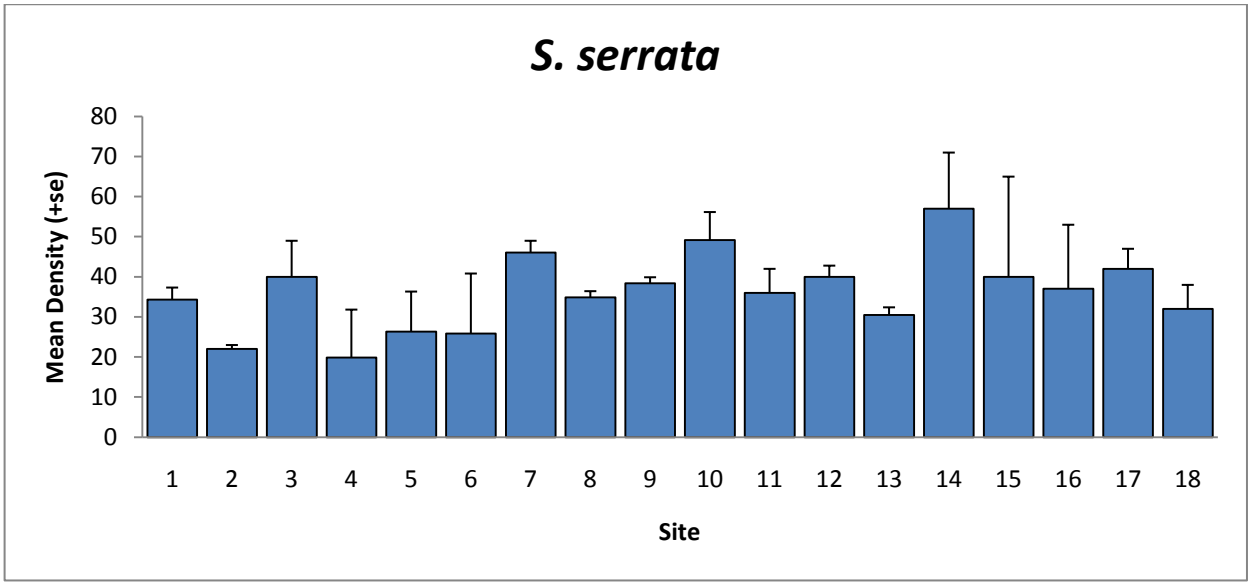


Figure 6.1: Average density of limpets at each site ranging from smallest patch to largest patch

Table 6.1: ANOVA of untransformed data for the number of limpets per quadrat for *S. concinna* and *S. serrata* within 18 sites of different lengths.

18 patches all of different lengths, n = 3 replicate quadrats per site. All variances were heterogeneous (Cochran's C test, $P < 0.05$).

* $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$

Source	df	M.S.	F	
S. concinna				
Site	17	20.42	9.21	***
Residual	36	2.21		
Total	53			
S. serrata				
Site	17	8.56	2.45	**
Residual	36	3.49		
Total	53			

6.3 Conclusions drawn:

From the findings above it was decided that as the greatest difference in densities of *S. concinna* lay between the smallest and the largest patches. The patches found between these showed a great deal of variability. As there was no obvious trend of increase or decrease for *S. serrata* densities it was decided that patch size would be defined based on *S. concinna* findings. This meant that small patches would be defined as habitat patches that were ≤ 20 m in length and large patches were defined as habitat patches that were ≥ 100 m in length.