TESTING THE EXISTENCE AND DIRECTION OF "SPILL-OVER" OF MUSSEL RECRUITS BEYOND THE BOUNDARIES OF MARINE PROTECTED AREAS

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Abstract

Landscape ecology helps in predicting the influence of habitat fragmentation on populations. Marine protected areas (MPAs) are expected to create areas of good quality patches and so improve connectivity among shores. MPAs are believed not only to protect adult populations, but also to enhance recruitment both within MPAs and on surrounding exploited shores, therefore improving their ability to recover from overexploitation. As such, MPAs are a preferred management tool for the conservation of natural populations. Although MPAs have been demonstrated to enhance adult abundances, little work has been done on their ability to provide so called "spill-over" of recruits nor has the generality of the influence of MPAs been investigated in a single region with multiple control sites.

The Transkei region, on the east coast of South Africa, and the intertidal mussel, *Perna perna*, offer an ideal system to test the generality of the influence of MPAs on surrounding shores, due to the presence of multiple MPAs and exploited control sites. Patterns of adult abundance were surveyed at four MPAs and two comparably sized exploited control sites. Adult abundances were, in general, found to be higher within MPAs than at exploited control sites, with adult abundances decreasing towards the edge of MPAs and decreasing even more on the outside shores.

To simplify the sorting procedure for samples of mussel recruits, a new method using fractionated elutriation was devised and tested. This new method was found to be more accurate, although not statistically significant but also substantially more time consuming. The increase in accuracy although not statistically significant could be biologically significant, especially when looking at low numbers. This new method could, therefore, be very useful especially when is low.

Recruitment was estimated over three months during the main reproductive season at two of the MPAs and at appropriate control sites. I predicted that recruitment patterns would mirror the patterns found in adult abundances and that there would be directionality in patterns of recruitment, with northern sites having greater recruitment due to the direction of near-shore ocean currents. Contrary to this, there were no correlations between adult abundance and recruitment for any of the months or sites, with no clear spatial pattern of recruitment in any of the three months. There was, however, a slight trend of greater recruitment at northern sites. To explain the lack of consistency in recruitment and adult abundances, wind data were used to examine the near-shore surface currents in this area, with theoretical surface currents showing similar patterns to those observed for recruitment.

From a landscape perspective, the good patches created by MPAs supply recruits to the surrounding matrix but the low quality of habitat in the matrix prevents rehabilitation. The quality of the matrix must therefore be first improved by reseeding these shores. These results emphasise that while MPAs may function in protecting adult abundances, their influence on supplying recruits and hence recovery of near-by exploited shores may be overestimated. This lack of influence on near-by exploited shores highlights the need for re-seeding of shores in conjunction with suitable management plans.

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Chapter 1

General Introduction

1.1 Landscape Ecology

Landscape ecology examines the interacting effects of ecological processes and spatial patterns on one another (Turner 1989). The term ‘landscape’ is used in several different ways. Forman and Gordon (1981) define a landscape as a kilometre-scale wide area where a cluster of interacting ecosystems is repeated in similar form and these landscapes can vary considerably. Broadly, a landscape is any heterogeneous area over any spatial scale (Turner 1989). Landscapes are usually described as having three main components: patches, the surrounding matrix and dispersal routes or corridors by which animals move through the matrix (Forman and Gordon 1981, Wiens 1997). Previously patches were described as gaps or ‘empty spaces’ within a habitat (Paine and Levin 1981). More recently, patches have been identified as areas of homogenous hospitable habitat surrounded by a dissimilar inhospitable matrix, with patches being connected by corridors that are made up of lower quality hospitable habitat that allow dispersal. Simply, a patch is effectively an area of habitat surrounded by the matrix of non-habitat which provides resistance to migration of animals (Hanski 1999, Goodsell and Connell 2002). Populations occupy a mosaic of habitat patches that vary in quality (Watkinson and Sutherland 1995), and these patches are not closed but part of an integrated, dynamic mosaic, with materials constantly being exchanged between the patches within the matrix and through corridors (Levin and Paine 1974).

Landscapes are often categorised as continuous or fragmented (Fahrig 2003). The process whereby a large amount of habitat (continuous landscape) is transformed into a number of smaller patches isolated from and surrounded by each other is termed habitat fragmentation (Wilcove *et al.* 1986). Habitat fragmentation has more recently also been defined as a landscape-scale process that includes both the separation and loss of habitat (Fahrig 2003). The process of fragmentation results in unequal effects on habitat pattern: a decrease in the size of patches, increase in the number of patches, increase in the size of the matrix and therefore an increase in isolation of patches, and a reduction in hospitable habitat. Not all of these processes necessarily occur at the same time (Fahrig 2003), but fragmentation nevertheless leads to an overall increase in ecosystem patchiness.

Patchiness can be anthropogenically or naturally derived (Wiens 1995). Keough (1984) proposed that there are two distinct types of patchiness: isolated and non-isolated patches, referred to as type 1 and 2 patches respectively (Connell and Keough 1985, Sousa 1985). Any single patch surrounded by a matrix can be both these kinds of patches but, the way in which the patchiness was created is an important defining characteristic. Type 1 patches are often anthropogenically created and are patches of distinct habitat surrounded by unsuitable space, while type 2 patches are areas of habitat that were surrounded by similar hospitable habitat which was then cleared by disturbance, either natural or human induced, and thus freed from resources. Patchiness in fragmented habitats is usually characterised by type 2 patchiness (Keough 1984, Connell and Keough 1985, Sousa 1985).

Patchiness in fragmented landscapes fits well in the ‘source-sink’ model, where some patch populations act as a source of colonists for other patches, the sinks, which depend on these sources for persistence (Pullium 1988). Source populations are those for which reproduction exceeds mortality, with surplus individuals dispersing to sink populations where mortality exceeds local reproduction (Watkinson and Sutherland 1995, Dias 1996, Diffendorfer 1998). Sinks will be patches of poorer quality, and will yield a demographic deficit (natality < mortality), these are usually areas where there is little or no recruitment and where the adult abundance and biomass are low (Watkinson and Sutherland 1995). Such patches would not be viable habitats in the absence of immigration (Watkinson and Sutherland 1995, Diffendorfer 1998). Source habitats will be patches of good quality and will yield a demographic excess (natality > mortality) (Dias 1996). A common feature of source-sink models is the extreme difference in quality between these two types of patches. There is either density-dependent or density-independent dispersal with some form of constraint on this dispersal. These models also assume that within source habitats there is density-dependant population regulation. Source-sink theory may be helpful in understanding species spatial distributions and dispersal patterns across heterogeneous, fragmented landscapes (Diffendorfer 1998).

1.2 Disturbance and its effect on landscapes

Space is the primary limiting resource for many rocky shore assemblages (Dayton 1971, Paine and Levin 1981). Local disturbances frees up space by removing organisms, thereby renewing this limiting resource (Paine and Levin 1981). The intermediate disturbance hypothesis states that species richness will be highest at intermediate levels of disturbance, with both large and small disturbances as well as frequent and infrequent disturbances causing a reduction in species richness (Connell 1978). Traditionally, it has been considered that disturbances increase environmental heterogeneity by constantly interrupting natural succession and by allowing random colonisation, which leads to local differentiation or patchiness (Levin and Paine 1974). More recently, it has become accepted that landscapes are heterogeneous and fragmented, being composed of patches of different habitats (den Boer 1981, Andrewartha and Birch 1984, Fahrig and Merriam1994), with spatial structure of the landscape becoming more defined as disturbance increases (Forman and Gordon 1981). Disturbance causes changes in the spatial structure of a landscape, and this change is driven by the spatial relationships among the landscape components including patches, matrix and corridors (Fahrig and Merriam 1994). Such landscape modification will include habitat loss, degradation, sub-division and isolation (Goodsell and Connell 2002, Fischer and Lindenmeyer 2007). Habitat loss rarely occurs by itself but rather is usually linked with habitat sub-division and habitat isolation (Liu *et al.* 2001).

Disturbances affect patches in five different ways (Forman and Gordon 1981, Fahrig 2003). First, disturbances will generally result in reduced patch size (Paine and Levin 1981). Patch size has been shown to influence local population persistence (Fahrig and Merriam 1994). Individual species have minimum patch size requirements and smaller patches generally contain fewer species than larger patches (Fahrig 2003). Thus, patch size is an important determinant of species diversity with smaller patch size leading to lower diversity of species (Forman and Gordon 1981). Second, disturbances could change the shape and amount of edge in a patch and, by so doing, change population dynamics within the patch itself so that two patches with the same area but differing edge sizes may have different population dynamics (Fahrig and Merriam 1994). Thirdly, patch isolation is usually linked to patch number and configuration. Less fragmented landscapes will have fewer patches that are generally further away from one another and thus more isolated. Patch isolation is a measure of the lack of suitable habitat in the landscape surrounding the patch, with many studies showing a negative effect of patch isolation on species richness (Fahrig 2003). The actual distance between patches is an important measure of potential for patch interactions (Forman and Gordon 1981). Increases in distance between patches will likely cause a reduction in patch introductions due to an increase in the size of the matrix. Larger or more persistent disturbances are likely to cause greater isolation and therefore a reduction in species richness. Fourth, disturbance affects the overall quality of the patch and fifth, the number and configuration of patches (Forman and Gordon 1981, Fahrig 2003).

1.3 Marine protected areas: artificial patches of coastal landscapes

Marine protected areas (MPAs) have been proposed as a way of conserving marine populations and combating habitat loss and declining biodiversity mainly produced by human disturbance or exploitation. MPAs are meant to help in the preservation of habitat, reduction of exploitation and rehabilitation of near-by shores by acting as source populations (Hastings and Botsford 1999, Airame *et al.* 2003, Gell and Roberts 2003, Halpern and Warner 2003, Halpern 2003, Roberts *et al.* 2003, Shanks *et al.* 2003, Gaylord *et al.* 2005). Despite the recent increase in interest in MPAs and their role in fisheries and conservation, MPAs have not been examined in a landscape context.

Following the definition of remnant patches and type 2 patches in landscape ecology, MPAs in essence fit these descriptions. A remnant patch is a patch that is left undisturbed after the surrounding area has been disturbed (Foreman and Gordon 1981, Fahrig 2003). Strictly speaking MPAs are not true remnant patches, but become remnant patches due to the fact that they are protected and eventually the unprotected areas become disturbed. The main difference is that remnant patches are what are left after disturbance, whereas MPAs are protected patches after which the surrounding areas usually become disturbed and thus freed from resources, or artificially created remnant patches similar to previously described type 2 patches. In this context, the matrix is formed by the surrounding exploited shores and the ocean itself. An important difference between the terrestrial and marine environments is the corridors. Terrestrial corridors are usually fixed in position and quality within the matrix and can either impede or assist movement. These corridors are part of a two-dimensional configuration and the organisms often have a choice as to which corridor, if any, to use. The exceptionally strong difference between the land and sea makes marine corridors unlike any corridors, including wind, in the terrestrial system. For sessile/sedentary adults the corridors overlap with the matrix, but while these corridors are non-habitat for adult benthos, they are essential habitat for larvae which depend on them for survival. For larvae, the corridors are a moving patch and although at large scales seem fixed, they continually change at smaller scales. This fluid environment allows for three-dimensional movement and often the larvae have little or no control on their movement within this fluid corridor. The same corridor can then both assist and impede movement and often switches between the two functions depending on environmental conditions. The application of terrestrial landscape components to the marine environment will change with landscape systems, scale and the organism. In this thesis I consider the whole MPA as a patch with the areas around MPAs comprising the matrix.

When looking at MPAs, as patches, in the conservation of fragmented landscapes application of source-sink models is important. The MPA would essentially make up the source while the surrounding shores will be sinks. The surrounding shores are usually areas where the adult abundance and biomass is low and where there is little or no recruitment (Watkinson and Sutherland 1995) due to exploitation and are therefore considered to be sinks. This reduction in the quality of the habitat leads to mortality being greater than natality at these shores. This exploitation therefore makes them unviable in the absence of immigration. This essentially makes the MPAs the source populations as they are of greater quality. It is also important to consider whether proposed areas for MPAs fall within natural source or sink habitats, if MPAs are established in natural sink habitat they will be less effective (Crowder *et al.* 2000, Lipcius *et al.* 2001).

1.4 Connectivity among MPAs and the matrix

Connectivity is a vital element in determining the position of patches and the surrounding matrix and hence landscape structure (Taylor *et al.* 1993) with the inverse also being applicable. Connectivity can be looked at from a genetic or demographic view point, here I concentrate on the latter. There are multiple definitions of connectivity, looking at biological relationships (functional connectivity), physical relationships (structural connectivity), or how these bio-physical relationships interact at different scales (landscape connectivity versus metapopulation connectivity) (see Moilanen and Hanski 2001, Tischendorf and Fahrig 2001, Kadoya 2009 for discussion). Because of these multiple definitions, there is no generally accepted single definition of connectivity (Kadoya 2009). Landscape connectivity is defined as the "degree to which the landscape facilitates or impedes movement among resource patches" (Taylor *et al.* 1993: 571). Connectivity here is seen as a property of the entire landscape with movement through the landscape depending on the movement of individual organisms through the matrix. This differs from metapopulation connectivity where connectivity is seen as a property of a patch, not the entire landscape, with distance being the most important determinant of connectivity (Tischendorf and Fahrig 2001, Moilanen and Hanski 2001, Kadoya 2009). The movement of individuals through a landscape can be seen as a consequence of their movement through patches and between patches and thus there should not be major differences between landscape and metapopulation connectivity (Wiens 1997). The use of landscape or metapopulation connectivity depends on the heterogeneity of the landscape and the relative spatial scale of the organisms movement (Kadoya 2009). Recently, for marine systems, population connectivity and reproductive population connectivity have been proposed as more meaningful measures of connectivity (Pineda *et al*. 2007). Population connectivity is essentially the bio-physical movement of organisms from one population to another geographically separated population (Hastings and Harrison 1994, Botsford *et al.* 2001, Cowen *et al.* 2007, Pineda *et al.* 2009), while for reproductive population connectivity, juveniles moving between sub-populations must survive, grow, mature and reproduce (Pineda *et al.* 2007). Simply put, connectivity is the degree to which movement, mainly dispersal, is allowed to occur by the multiple bio-physical characteristics of the organism interacting with the environment at any given scale and can be both qualitative and quantitative. Ignoring direct development and self recruitment, the rate of movement and local extinctions determines the survival of populations (Fahrig and Merriam 1985, Gaines *et al.* 2007).

Some of the major factors that influence marine connectivity and thus local population dynamics are dispersal and the interaction between organisms and local landscape structure (Van Dorp and Opdam 1987, Bond *et al.* 2000, Kadoya 2009, Pineda *et al.* 2009). The movement of larvae between two points is termed transport. Dispersal differs from transport because it implies movement from a natal to a settlement site (Gerrodette 1981, Nathan and Muller-Landau 2000, Pineda *et al*. 2007). Dispersal and recruitment are complex processes determined by many factors operating over multiple spatio-temporal, covering micro-scale to meso-scale processes (Connell 1985, Nakaoka 1993, Eckman 1996, Letcher *et al.* 1996, Nathan *et al*. 2005, Sponaugle *et al.* 2006, Pineda 2007, Pineda *et al*. 2009).

In marine intertidal species, there is a wide array of different developmental modes and dispersal strategies (Levin and Bridges 1995). Omitting direct developers for simplification, recruitment is influenced by four main processes: (1) larval pool processes, (2) larval transport, (3) settlement processes and (4) post-settlement processes (Pineda *et al.* 2009). Larval transport and dispersal are influenced by a complex interaction of many oceanographic factors, such as: wind induced flows (McQuaid and Phillips 2000), moving in the cross-shore or along-shore direction with cross shore transport being considered the most relevant to population connectivity (Pineda *et al.* 2007), up/downwelling (Shanks and Brink 2005, Morgan *et al.* 2009) and tidal bores (Pineda 1991). The behavioural interaction of larvae with these physical processes adds to the complexity, with dispersal either being influenced by active behaviour, such as diel and vertical migrations or other forms of swimming (Hill 1998, Garland *et al.* 2002, Shanks and Brink 2005, North *et al.* 2008), or solely due to passive transport by these currents (McQuaid and Phillips 2000). Even with behaviour, larvae are often unable to oppose the magnitude of ocean currents and so dispersal is mostly reliant on hydrodynamics (Underwood and Keough 2001). Marine taxa are generally capable of long distance dispersal and so are capable of having a high degree of connectivity, with important implications for population structure (Carr *et al.* 2003, Kinlan and Gaines 2003).

Dispersal is particularly important for sessile/sedentary organisms which can only escape unfavourable conditions through dispersal. Dispersal, therefore, determines the scale at which species interact with their environment and respond to disturbances, with the scale and pattern of dispersal having important consequences for population distribution (Sousa 1984, Reed *et al.* 2000).

In marine systems dispersal is one of the main driving forces behind connectivity which in turn determines biological landscape structure. This connectivity may help describe the importance of MPAs as patches of coastal landscapes, as well as their importance in population distributions and population recovery.

1.5 Rationale for a study on connectivity between marine protected areas and exploited shores

MPAs are believed to protect natural populations as well as re-seed nearby shores with both adults and juveniles and thus are used around the world in an attempt to conserve natural populations (McClanahan and Mangi 2000, Airame *et al.* 2003, Branch and Odendaal 2003). Most studies have concentrated on mobile species such as fish, but very few have looked at connectivity between MPAs and the nearby shores with an emphasis on sessile/sedentary species (but see Pelc *et al.* 2009). The use of sessile/sedentary species in determining net or absolute connectivity is important because as adults they cannot move great distances and therefore dispersal will mainly dictate the connectivity between areas (Kinlan and Gaines 2003). Mussels are harvested by people around the world, and are particularly heavily exploited on the Transkei coast of South Africa (Lasiak and Dye 1989; Lasiak 1991, 1992), thus mussels form an ideal model organism to describe connectivity between protected and exploited shores.

The present study aimed to investigate the general patterns of settlement and recruitment and of adult abundances within MPAs and on exploited shores, thereby assessing the role of MPAs in the rehabilitation of denuded shores at specific scales. The use of multiple reserves and controls supplies some much needed replication, with the differing sizes and management of the MPAs increasing the generality of the results.

This thesis investigates these aims through a progression of 3 working chapters. The first part (Chapter 2) compares adult mussel cover in MPAs and exploited shores. Chapter 3 establishes spatial patterns of recruitment, and investigates the relationship between recruitment and adult cover. Specifically this chapter tested the hypothesis that recruitment would be greater within MPAs and that it will decrease as distances from MPAs increases.

Furthermore it was predicted that there would be more recruitment at northern sites than southern sites, based on predominant wind patterns in this area and how these winds are believed to drive very near shore ocean currents. The use of predominant winds and their assumed effects on ocean currents was necessary due to the lack of oceanographic data for this area, particularly the near shore region. Chapter 3 also examines local wind patterns in an attempt to describe the near shore surface currents and explain the results of the recruitment data. Chapter 4 describes a new method for sorting benthic samples with emphasis on small post recruitment stages.

1.6 Study Sites

This study was done on the southeast coast of South Africa in an area formerly known as the Transkei, where two distinct biogeographic regions overlap. The warm-temperate south coast and the sub-tropical east coast biogeographic regions overlap around Port St. Johns (Brown and Jarman 1978, Kilburn and Rippey 1982), where the northern most sites of this study were located (Fig 1). All study sites had similar aspect and topography, with irregularly shaped headlands, gently to moderately sloping shores, and moderate to heavy wave action. The shores in the northern region of the Transkei are formed of quartzitic sandstone, those in the central region are formed of sandstone while those in the southern region comprise a mixture of mudstone, dolerite and shale platforms (Hockey *et al.* 1988). Consequently, it was not possible for all study sites to be consistent in terms of biogeographic region and rock type due to the heterogenous nature of the underlying geological substrata and the positioning of the marine reserves along the Transkei coast (Brown and Jarman 1978, Hockey *et al.* 1988).

To test the effectiveness of marine reserves (with the hypothesis of greater recruitment within reserves compared to outside); the effect of distance from marine reserves (less recruitment farther away from reserves) and the effect of direction (greater recruitment north of than south of reserves), sampling was done at two marine reserves and two suitably chosen control sites. The control sites were situated south of each reserve and at a distance far enough apart so that there was 5 km between the closest reserve and control sites to ensure independence and no influence on one other (McQuaid and Phillips 2000, Cole *et al.* submitted). Six sites were chosen at each reserve location and each control location; two centre sites, a northern and southern edge site and a northern and southern outside site. The centre sites in reserves were selected as close to the centre of the reserve as possible. The centre sites at Dwesa-Cwebe were closer to the southern edge due to the inaccessibility of true centre sites. The outside sites were as close to 2 km from the edge sites as was physically possible. The Dwesa-Cwebe (32º 15'S, 28º 54'E) site encompasses a section of coastline with a linear distance of 20.1 km, while Silaka (31º 39'S, 29º 30'E) covers 5.3 km. The Dwesa-Cwebe control site (Control 1) (32º 27'S, 28º 41'E) encompassed a linear distance of 11.2 km from Mazeppa Bay to Shixini, while the Silaka control site (Control 2) (31º 44'S, 29º 23'E) covered a distance of 9.05 km from Mpande to Mngazana (Fig 1.1 and 1.2). Due to the vastly different MPA sizes, the sizes of control sites were chosen to make the controls comparable to each other as well as the MPAs. In addition to this, the two remaining MPAs in the Transkei (Fig 1.1), Mkambathi (31º 17'S, 30º 01'E) and Hluleka (31º 49'S, 29º 18'E), were surveyed during an extensive once-off survey in October 2010 to determine the generality of the effect of MPAs on adult abundances.

Due to the large difference in sizes of the reserves, the amount of rocky shore and therefore available habitat, at each site was determined using Google Earth (eye elevation of 483.71 m). Dwesa-Cwebe and Silaka have approximate shore lengths of 8.596 km and 3.015

km respectively, while Control 1 and Control 2 have approximate shore lengths of 7.033 km and 6.723 km respectively. This gives a relative amount of habitat for comparison between reserves and controls.

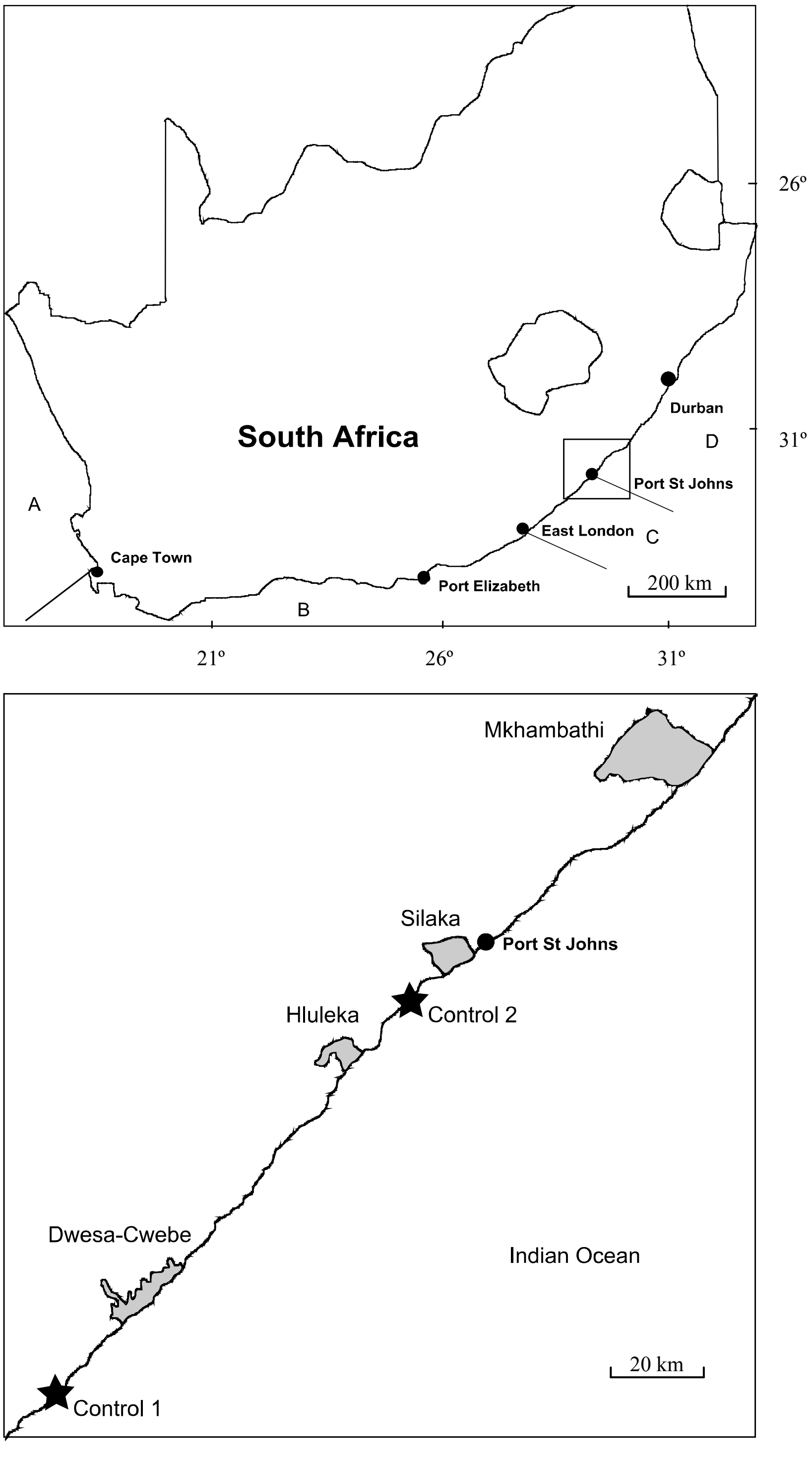


Figure 1.1 Study sites along the south-east coast of South Africa. Reserves in grey. Lines show proposed marine biogeographic provinces. (A) Cool-temperale Namaqua Province, (B) Warm-temperate South Coast Agulhas Province, (C) Proposed overlap between Warm-temperate South Coast Agulhas Province and Subtropical East Coast Province (D) Subtropical East Coast Province

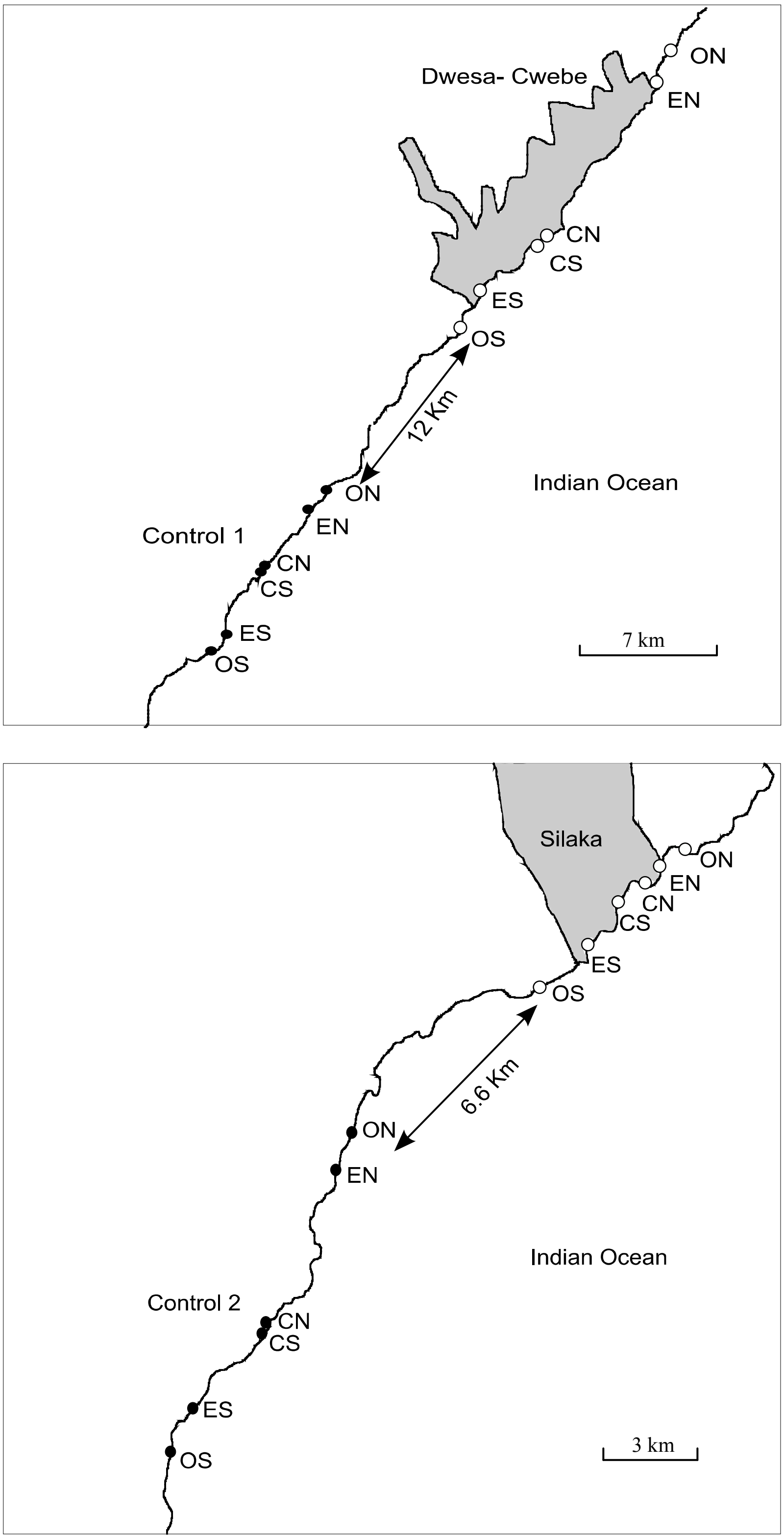


Figure 1.2 Location and relative position of study sites. N: North, S: South; O: Outside; E: Edge; C: Centre. Closed circles indicate controls sites, open circles indicate reserve sites.

1.7 Study Species

Perna perna, belongs to the family Mytilidae and is indigenous to South Africa, extending from Mozambique to the southwestern Cape (van Erkom Schurink and Griffiths 1991). This species spawns multiple times each year, most often in winter and spring (Dye *et al.* 1997, Harris *et al.* 1998, McQuaid and Phillips 2000), but spawning has also been documented in summer (Lasiak and Dye 1989). Larvae can live from two to four weeks in the water column (Lasiak 1991), with peaks in settlement occurring between September and November along the Transkei coast (Lasiak and Dye 1989).

Chapter 2

Abundance of adult mussels in marine protected and surrounding areas

2.1 Introduction

For rocky intertidal organisms, patterns of adult abundance and distribution are controlled by factors such as predation, competition and physical disturbance (Dayton 1971), as well as factors influencing settlement like larval supply (Fairweather 1991), larval behaviour and transport (Morgan 2001, Underwood and Keough 2001, Pineda 2007), and recruitment (Connell 1961, Keough and Downes 1982). Thus, the influence of all these processes should be detectable in adult populations, which are the product of interactions among these integrated effects. This is especially important for sessile/sedentary organisms where adult populations not only make up the breeding stock, but often the habitat where newly settled conspecifics tend to recruit.

Sessile/sedentary organisms provide and important example of ecological systems ideal to understand interspecific/intraspecific interactions and physical effects (see Underwood 2000 for review). Mussels play an important role ecologically (Paine 1966, Seed and Suchanek 1992, Bertness and Leonard 1997, see Gutierrez *et al.* 2003 for review) and mussel beds are of great importance to intertidal biodiversity (Seed 1996, Cole 2010). They provide unique habitat for a host of associated organisms (Petraitis 1990, Stephens and Bertness 1991, Hunt and Schiebling 1996, Seed *et al.* 2000) and are the preferred settlement habitat for mussels themselves (Lasiak and Bernard 1995, Erlandsson *et al*. 2008, Porri *et al.* unpublished data).

MPAs are thought to alter many of the processes which influence patterns of adult abundance and distribution (Branch and Odendaal 2003). First, they protect adult populations from enhanced disturbance. It has been shown that, for various taxa, adult numbers are higher inside MPAs than in surrounding areas (Halpern 2003). Numerous studies have focused on entire assemblages (Addessi 1994, Lasiak 1998), fish (Bennett and Attwood 1991, McClanahan and Mangi 2000, Murawski *et al.* 2000, Roberts *et al.* 2001, Russ *et al*. 2004, Gaylord *et al*. 2005), macroalgae (Moreno-Sutherland *et al*. 1984, Hockey and Bosman 1986), and molluscs (Castilla and Duran 1985, Keough *et al.* 1993, Wallace 1998, Petraitas and Dudgeon 1999, Foster and Hodgson 2000, Manriquez and Castilla 2001, Branch and Odendaal 2003, Beaukers-Stewart *et al.* 2005), with the general consensus that MPAs provide a protective area for the buildup of larger adult abundances. A study done in South Africa by Dye and co-workers (1997) found lower cover of the mollusc *Perna perna* at exploited sites when compared to reserves. This reduction in mussel cover through human disturbance can then weaken the mussel bed which will become more susceptible to natural disturbances such as wave exposure (McQuaid and Lindsay 2000), and predation (Steneck 1998). Second, by protecting the adult stock, there is an increase in the potential reproductive output in the area which may lead to increased connectivity within surrounding areas (Branch and Odendaal 2003). Moreover, increasing adult cover also increases the size of suitable habitat into which larvae can recruit, thus increasing the overall population survival and persistence. Knowledge of the brood stock size and how much suitable habitat there is, is vital in ecology and management because it helps in predicting the influence of exploitation on population dynamics and where populations are in general (Lipcius and Stockhausen 2002).

This Chapter describes the effect of MPAs on intertidal populations by examining adult mussel abundance in relation to protective status. This will then be used to try to understand the influence of MPAs on seeding surrounding shores and the potential scales of seeding (Chapter 3). In order to do this, surveys of adult cover of the mussel *P. perna* were undertaken at four MPAs and two exploited areas, one south of each main reserve. Due to the protection afforded by MPAs and harvesting being partially directed at the peripherals of reserves (Willis *et al.* 2001, Kellner *et al.* 2007), I tested the hypothesis that MPAs would, generally, have greater mussel cover than outside MPA areas and that the cover will decrease along a gradient from the centre to the edges, to outside.

2.2 Materials and Methods

2.2.1 Mussel Cover

To determine the adult stock of mussels within MPAs and at control sites, estimates of the abundance of adult *P. perna* were done by estimating percentage cover. Dwesa-Cwebe, Silaka and their respective control sites were sampled during once-off surveys in August and September 2009 respectively. Once-off sampling has been shown to be adequate as mussel cover is, in this area, remarkably stable in the long-term, despite small scale short-term changes (Reaugh 2005, Reaugh *et al.* in review). In addition to this, the two remaining MPAs in the Transkei, Mkambathi and Hluleka, were surveyed during an extensive once-off survey in October 2010 to determine the generality of the effect of MPAs on adult abundances (see Chapter 1, Fig 1.1). Twenty five 50 X 50 cm quadrats were haphazardly thrown, within the mussel zone, within each site. Sites were chosen approximately every 100 to 400 metres (depending on the size of reserve and when this distance was accessible and fell on rocky shores) along the shore within each MPA (see Chapter 1 for site details). The point intercept method was used to determine percentage cover of mussels within each quadrat, with 100 evenly spaced points within each quadrat.

During the survey one of the sites, Control 1 OS/Qora Mouth, was actively being harvested. This site was used for a small scale temporal study to determine the extent of exploitation. This site was surveyed during September, October, November and December 2009.

2.2.2 Data Analysis

Percentage cover of adult mussels was analysed using a four-factor analysis of variance (ANOVA). The first factor "Reserve" (2 levels; reserve or non-reserve) was fixed, factor 2 "Site" (2 levels; reserve 1, reserve 2, control 1 and control 2) was random and nested in "Reserve", factor 3 "Position" (3 levels; centre/edge/out) was fixed and orthogonal to reserve and factor 4 "Direction" (2 levels; North or South) was fixed and orthogonal to reserve and position. When a very non-significant interaction ($P > 0.25$) was found the data were pooled *post-hoc* to enable a more powerful test of main factors (Underwood 1997). For Mkambathi and Hluleka, as there were no controls, the first factor "Reserve" was removed and a three-factor ANOVA was used. All variances were heterogeneous (Cochran's test) but there were no suitable transformations to create homogeneous variances. As large, balanced ANOVAs, such as these, are relatively robust to heterogeneity of variances, untransformed data were analysed. Student-Newman-Keuls (SNK) tests were done for significant sources of variation to determine the patterns of difference relative to hypotheses of interest.

2.3 Results

For all reserves and control sites there was a significant interaction between all factors: site (nested in reserve), direction and position. At Dwesa-Cwebe, the predicted pattern was observed, with numbers decreasing from centre to out in both north and south directions (SNK; N: C>E>O; S: C>E>O, Table 2.1). The magnitude of this pattern did, however, differ with the southern edge having much higher cover than the northern edge (Fig 2.1). At Silaka, the predicted pattern was not observed, for both directions the centre sites had the greatest numbers and the edges having the lowest, with the outside sites having higher numbers than the edges. For the northern direction; the centre was greater than out which was even greater than edge, while for the southern direction the centre was equal to the out which was greater than the edge (SNK; N: C>O>E; S: C=O>E, Table 2.1). In the controls there was, as predicted, no clear pattern in adult percentage cover (Table 2.1). The control sites did, however, generally have much lower percentage cover than the sites within the reserves (Fig 2.1).

To test for generality of the patterns observed in the reserves, the additional two reserves were surveyed and analysed. Mkambathi showed a similar pattern to that predicted, with the centre being the highest and decreasing from edge to outside. It was, however, different in that the edge sites had similar cover to the centre sites for both directions (Table 2.2). Sites to the south had higher numbers than at the same positions in the north (Fig 2.2). At Hluleka a similar pattern was observed with numbers decreasing from centre to out, but with edges being the same as out sites in both directions (Table 2.2). The magnitude was also different with the centre south sites having much higher cover than the remaining sites (Fig 2.2).

Cover showed a similar pattern with the more intensive distance from centre plots for all reserves. Values were higher near the centre of reserves, albeit with a fair amount of variability, decreasing on or near the edge and again decreasing sharply outside the reserves. These plots showed no clear pattern for either control sites. These plots show that the control sites had much lower percentage cover than the reserve centers and similar cover to the sites outside reserves (Fig 2.3 – 2.5). These plots also show that Dwesa-Cwebe had a higher cover of adults, (average cover of approximately 50%), within the reserve than the other 3 reserves. Mkambathi had an average cover of approximately 25%, Silaka 20% and Hluleka 20% while the controls had approximately 15% cover at both sites.

The small scale temporal study done at Qora mouth showed a decrease in percentage cover from 38 ± 5% in September to 17.37 ± 2.21% in October and then remaining near this value for November and December 2009 (Fig 2.6).

2.4 Discussion

It was important to test empirically the theory that MPAs act as a protective area for sessile/sedentary invertebrates and that this ‘protected’ state is eroded when moving out of reserves. It was also important to determine any differences in directionality from these reserves to gain a better understanding of connectivity between the reserve and surrounding shores, and to get a better understanding of the directionality near shore ocean currents. Although MPAs have been found to have greater abundances of animals when compared to areas outside of them (Castilla and Duran 1985, Siegfried *et al.* 1985, Lasiak and Dye 1989, Lasiak 1991, Keough *et al.* 1993, Lasiak and Field 1995, Russ *et al*. 2004, Pillians *et al.* 2005), this has not been tested using a balanced multi-directional design on multiple reserves and control sites in any of these studies.

The Transkei coast of South Africa provides a suitable testing ground for replicated large scale experiments on the effectiveness of MPAs due to the presence of multiple MPAs and the surrounding areas being subjected to strong harvesting pressure on mussel beds. The common trend found in three of the four reserves, with higher abundances of mussels in the centre decreasing outward, supports the hypothesis that reserves have a generally positive effect on mussel abundance and that this effect decreases when moving out of reserves. Low adult abundances at the edges of reserves may indicate that they are not effective at conserving mussels, but more likely reflect the effects of poaching on the borders of reserves, as there are reports of harvesting on or near these boundaries.

Differences in mussel cover between sites and between reserves and controls can be linked to multiple mechanisms, ranging from larval transport and supply (Shanks *et al.* 2003, Pineda *et al.* 2009) to disturbance (Beaukers-Stewart *et al.* 2005) and habitat availability (Lasiak and Bernard 1995, Erlandsson *et al.* 2008) and exploitation (Griffiths and Branch 1997). Larval transport and supply is often a primary mechanism influencing the patterns of distribution of marine intertidal organisms and this will be discussed in detail in Chapters 3 and 4. Disturbance, both natural and human induced (exploitation), can have a large effect on marine assemblages and has been shown to cause a switch in community structure (Sousa 1979, Lasiak and Field 1995, Petraitis and Latham 1999, Underwood 1999, Airoldi *et al.* 2005). The general pattern of greater cover of mussels within the boundaries of reserves, particularly at the centre of a reserve when compared to the edges and outside sites, could therefore be due to harvesting pressure and the protection from this that reserves allow. The variability seen inside the reserve could be attributed to natural variation or possibly due to poaching (Lasiak and Dye 1989, Underwood and Kennelly 1990, Paddack and Estes 2000, Willis *et al.* 2001, Williamson *et al.* 2004). The differences between the edges when compared to the centre sites and the outside sites could be a result of harvesting being concentrated on or near the boundaries, with MPAs with similar edge cover to outside cover because of harvesting at the edge, while MPAs with higher cover at the edge than outside have no edge harvesting (Willis *et al.* 2001, Kellner *et al.* 2007), but this seems to be reserve specific. The reserves Dwesa-Cwebe and Hluleka showed a strong pattern while Mkambathi and to some extent Silaka did not. This difference in level of exploitation among MPAs is probably due to the level of policing or the distance of the edge from local populations

(Addessi 1999). The lack of any clear pattern at Silaka is probably attributable to management of the reserve as harvesting is allowed within the boundaries of the reserve. This, coupled with the fact that the shoreline around Silaka is extremely precipitous, while the rocky shores within the reserve are relatively accessible, could direct local harvesting pressure toward the reserve. The lack of any clear pattern in control sites and the relatively uniform low cover within control sites indicates that the differences between the controls and the reserves is not due to natural variability but is rather due to the effect of reserve itself.

Even though mussel cover offers time-integrated information over relatively long time periods (Reaugh *et al*. 2003), harvesting pressure can change cover very quickly and this was seen in the small scale temporal study with a rapid decrease in abundance of mussels due mainly to active harvesting. Dye *et al*. (1997) found a 75% decrease in the abundance of mussels over a 4 year period at an exploited site which they attributed to harvesting. The present study indicates that the change in abundance can be rapid, with a 50% reduction in one month. It is important to note that the adult mussel cover reached a value at which it stayed relatively constant, approximately 15%. This 'cut-off point' of mussel cover is probably due to the increased effort needed to collect the same number of mussels and this possibly makes the harvesters direct their effort elsewhere leading to no continual reduction in the number. A possible explanation for this cut-off point remaining at a constant value and not increasing may be due to the level being below that from which a population can naturally recover or that natural recovery is slow but with continual harvesting pressure there is no real recovery. This study therefore indicates that there may be a critical harvesting level after which harvesting may cease at a particular site.

Most studies on MPAs only compare sites in one direction, often believed to be linked to the main direction of dispersal. The different magnitudes of mussel cover found at northern and southern sites show that to get a clear understanding of the processes affecting exploited and protected shores a balanced, multi-directional design is needed. This study showed that reserves have a strong effect on adult cover but this effect is reserve specific and there may be a strong edge effect. Furthermore, there were distinct differences when looking at positions north and south of the reserve.

Table 2.1 Results of four-factor ANOVA comparing percentage cover estimates for Dwesa-Cwebe and Silaka (Reserves) and Control 1 and Control 2 (Controls), north and south of each site at the centre, edge and outside. Student-Newman Keuls (SNK) results showed using codes representing N: North; S: South; C: centre; E: edge; O: outside. For this and the following tables; * = $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$

Source	**d.f.**	**M.S.**	***F***	***P***
Reserve = Re	1	35167	68.37	*
Site(Reserve) = Si(Re)	2	514	2.79	>0.05
Direction = Di	1	95	0.02	>0.05
Position = Po	2	18796	3.05	>0.05
Re x Di	1	836	0.20	>0.05
Re x Po	2	11458	1.86	>0.05
Di x Si(Re)	2	4136	22.41	***
Po x Si(Re)	4	6163	33.39	***
Di x Po	2	8726	3.38	>0.05
Re x Di x Po	2	44	0.02	>0.05
Po x Di x Si(Re)	4	2584	14.00	***
Residual	552	184		
SNK	Dwesa-Cwebe N: C>E>O; S:C>E>O		Silaka N: C>O>E; S: C=O>E	
	Control 1 N:C>E=O; S: C<E=O		Control 2 N: C=O>E; S: C=O>E	

Table 2.2 Results of three-factor ANOVA of percentage cover estimates for Mkambathi and Hluleka. Student Newman Keuls (SNK) results showed using codes representing N: North; S: South; C: centre; E: edge; O: outside.

Source	**d.f.**	**M.S.**	***F***	***P***
Site = Si	1	8474	57.31	***
Direction = Di	1	3898	26.36	***
Position = Po	2	7786	52.66	***
Si x Di	1	0.70	0.00	>0.05
Si x Po	2	2836	19.18	***
Di x Po	2	783	5.30	**
Si x Di x Po	2	991	6.71	**
Residual	288	147		
SNK	Mkambathi N: C=E>O; S: C=E>O		Hluleka N:C>E=O; S: C>E=O	

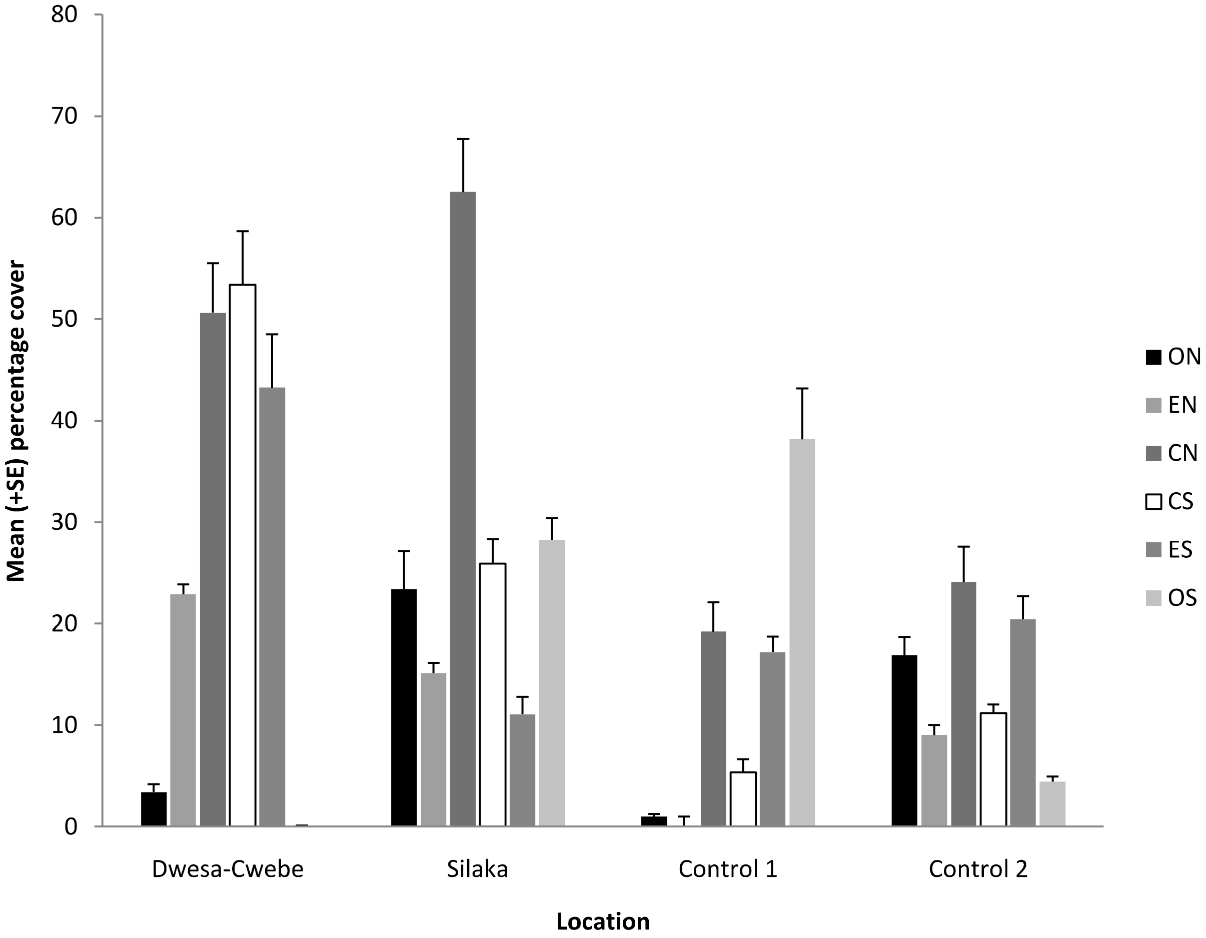


Figure 2.1 Mean (*n* = 25, + SE) percentage cover of *Perna perna* at Dwesa-Cwebe, Silaka, Control 1 and Control 2 at the 6 study locations. Key with codes representing N: North; S: South; C: centre; E: edge; O: outside.

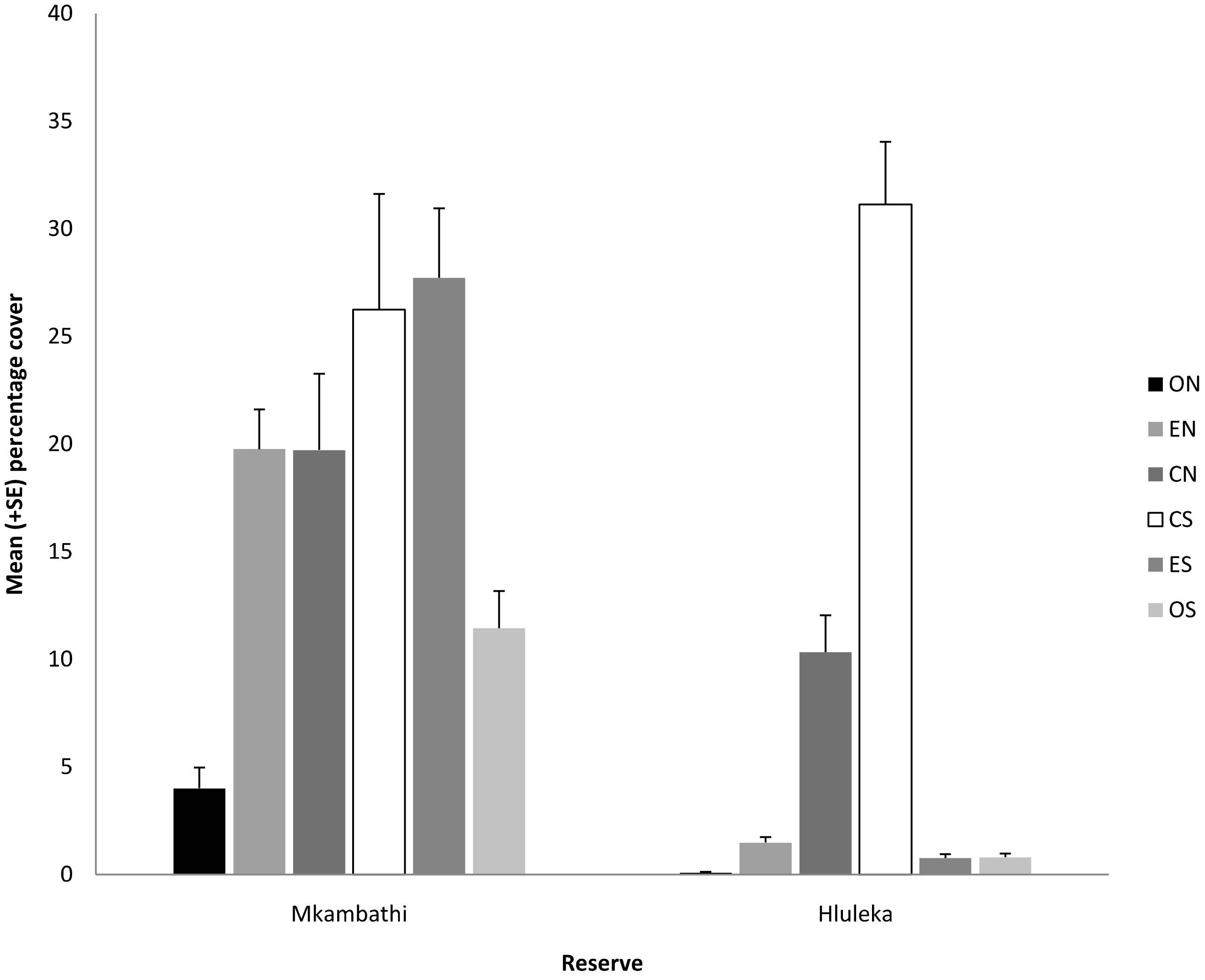


Figure 2.2 Mean (n = 25, +SE) percentage cover of *Perna perna* at Mkambathi and Hluleka at the equivalent 6 study sites. Key with codes representing N: North; S: South; C: centre; E: edge; O: outside.

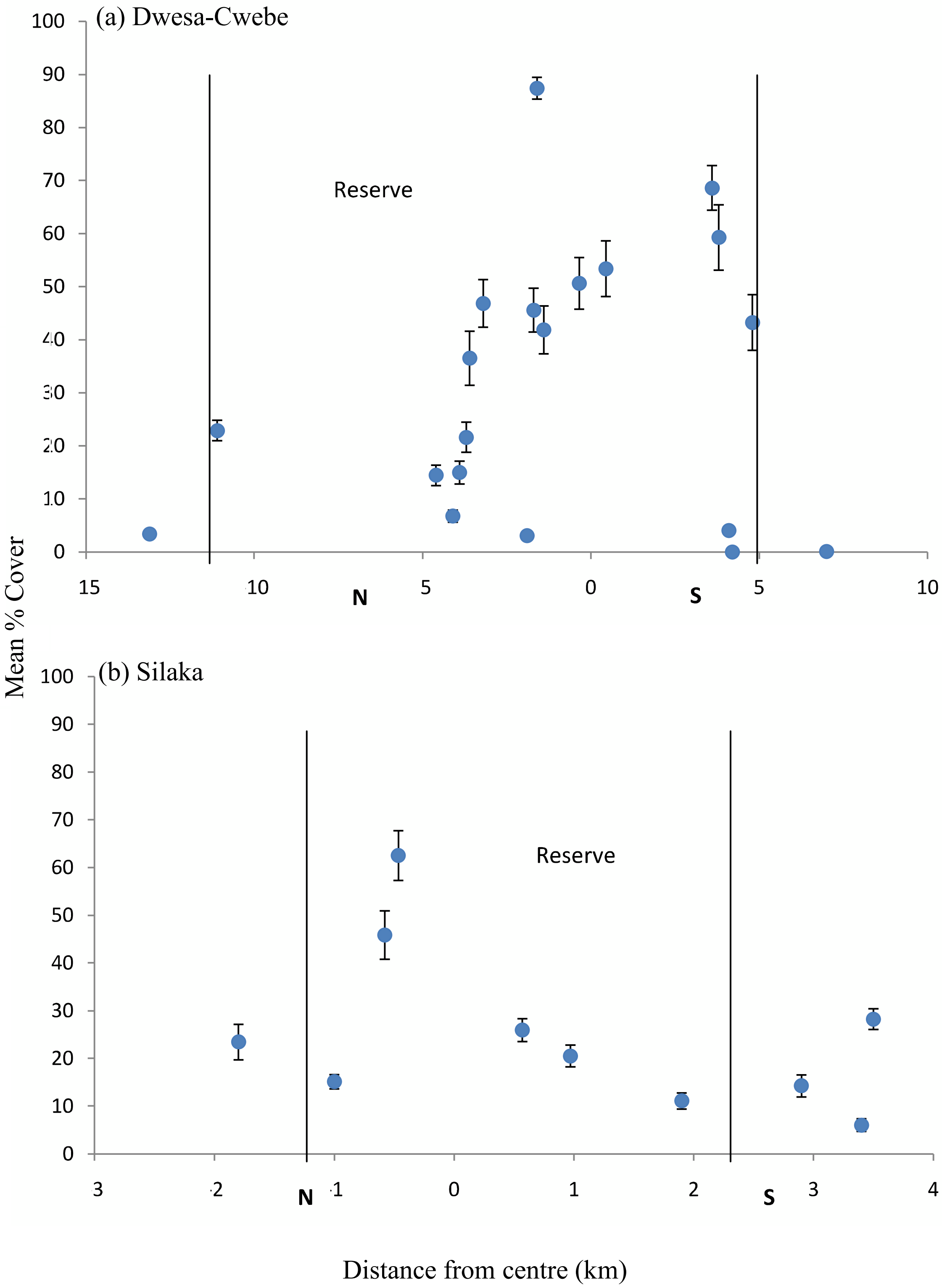
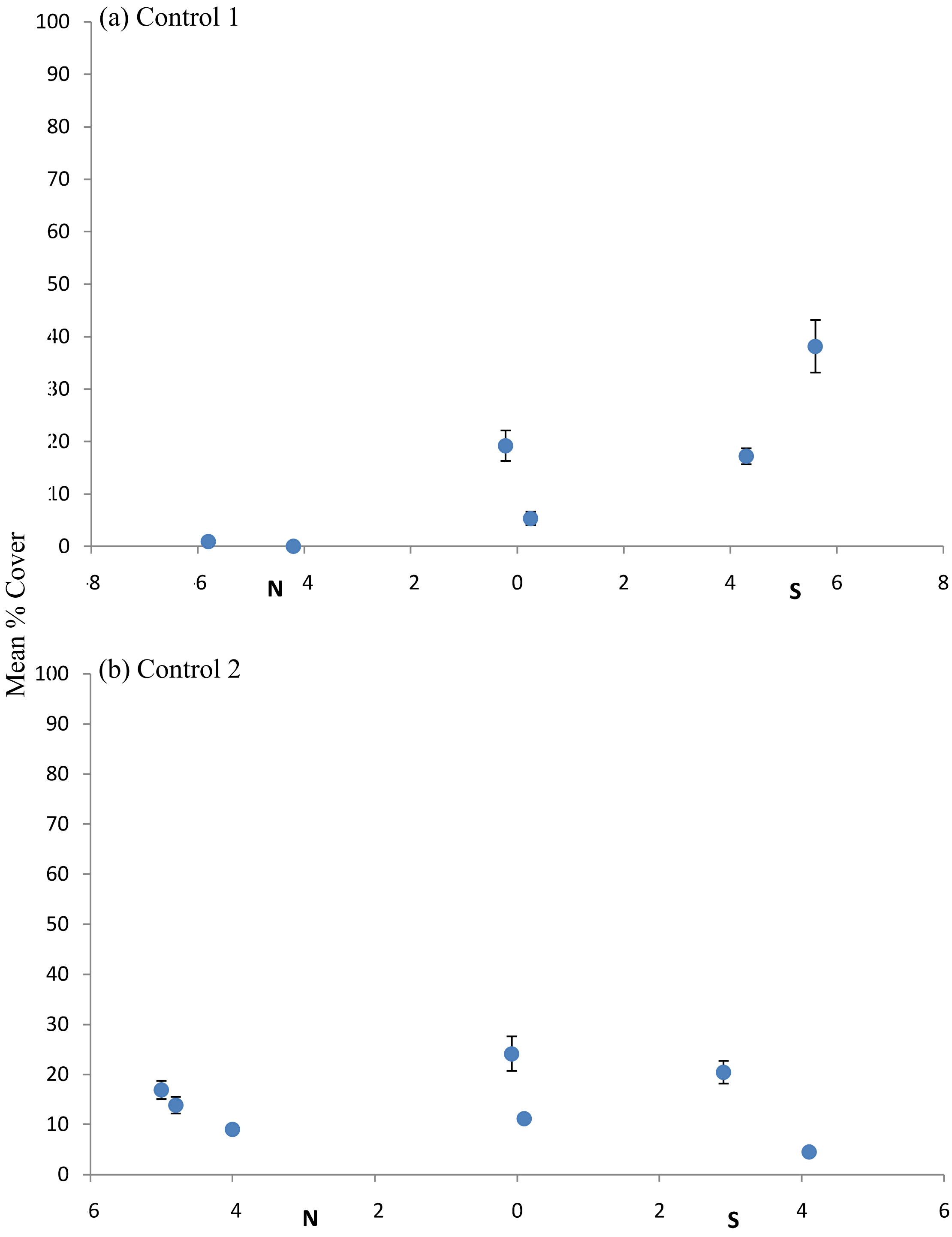


Figure 2.3 Diagrams from high resolution surveys showing mean ($n = 25$, ±SE) percentage cover of *Perna perna* at distances from the centre both north and south at (a) Dwesa-Cwebe and (b) Silaka. Lines indicate reserve edges. Gaps indicate unsuitable habitat such as sand.



Distance from centre (km)

Figure 2.4 Diagrams from high resolution surveys showing mean (n = 25, ±SE) percentage cover of *Perna perna* at distances from the centre both north and south of (a) Control 1 and (b) Control 2. Gaps indicate unsuitable habitat such as sand.

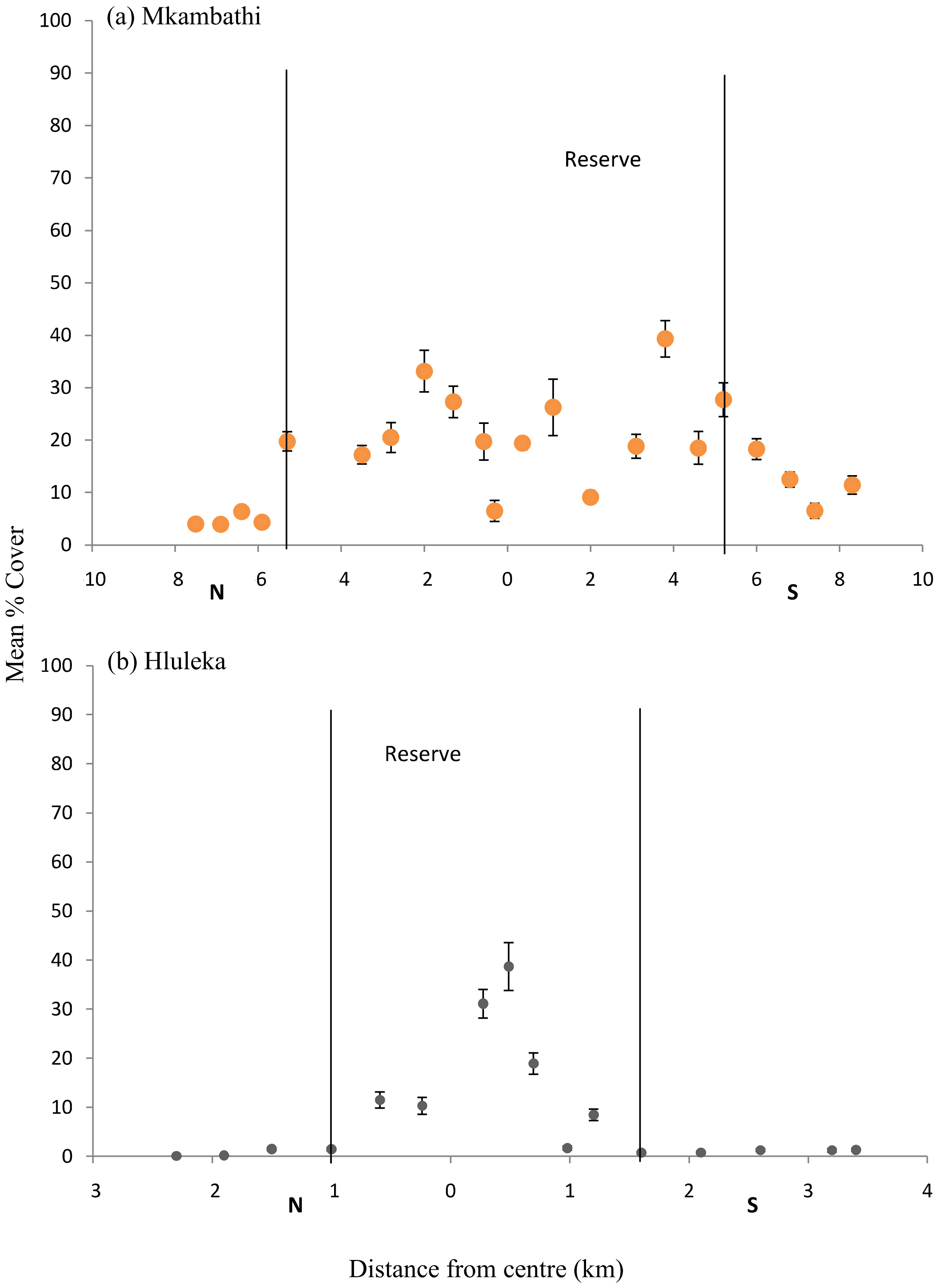


Figure 2.5 Diagrams from high resolution surveys showing mean ($n = 25$, ±SE) percentage cover of *Perna perna* at distances from the centre both north and south of (a) Mkambathi and (b) Hluleka. Lines indicate reserve edges. Gaps indicate unsuitable habitat such as sand.

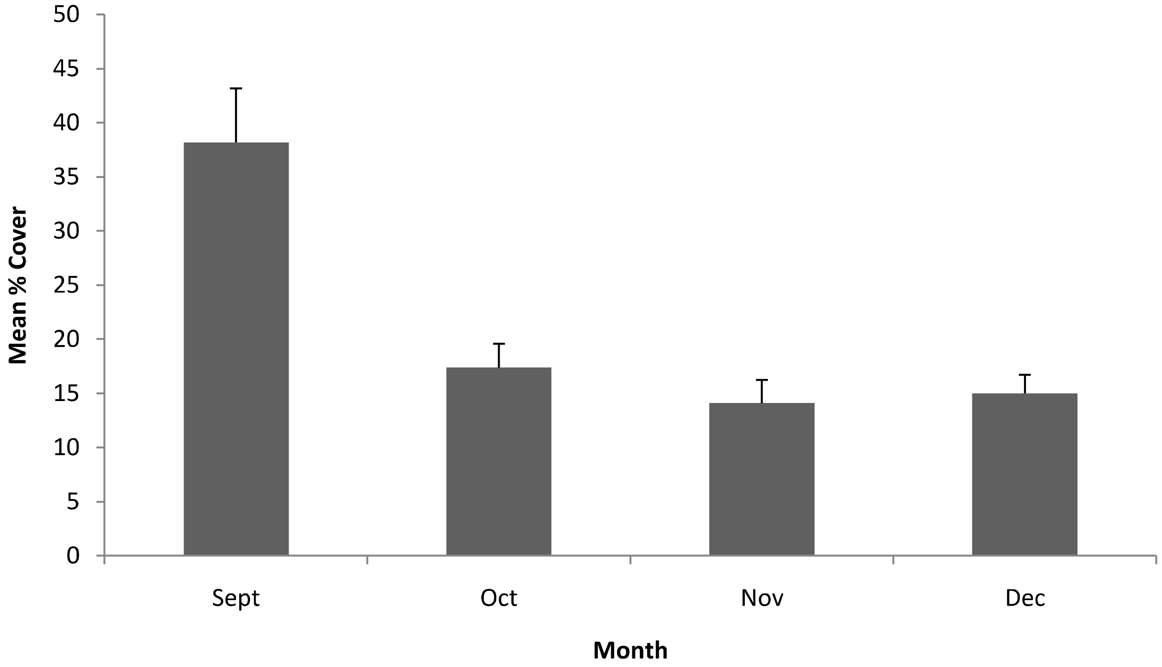


Figure 2.6 Mean (*n* = 25, +SE) percentage cover of *Perna perna* at Qora Mouth for the months; September, October, November and December 2009.

Chapter 3

Settlement and recruitment of *P. perna* in the Transkei, in proximity to protected and exploited shores

3.1 Introduction

Many sessile and sedentary marine invertebrates, including mussels, rely on their pelagic larval for dispersal. This pelagic larval stage introduces the potential for long distance dispersal and high losses of larvae. Because of this potentially long distance dispersal, and the use of pelagic larval duration as a predictor of potential dispersal distance, populations have previously been considered as 'open', resulting in weak adult-recruit relationships (Roughgarden *et al.* 1988, Caley *et al.* 1996, Swearer *et al.* 2002, Thorrold *et al.* 2002, Grantham *et al.* 2003, Largier 2003, Weersing and Toonen 2009). Recent studies have increasingly shown self-recruitment, due to retention of larvae near natal populations such larval retention and self-recruitment has been found to be more common than previously thought (McQuaid and Phillips 2000, Swearer *et al.* 2002), resulting in a re-assessment of the 'openness' of populations (see Levin 2006 for review).

Settlement of larvae and their subsequent recruitment, are considered to be two separate and distinct processes (Keough and Downes 1982). Settlement, due to its linking of pelagic and benthic life stages, is considered as one of the main processes regulating the structure and dynamics of benthic poupulations (Underwood and Fairweather 1989, Rodriguez *et al.* 1993, Caley *et al.* 1996, Hunt and Scheibling 1996, but see Pineda *et al.* 2010). Settlement is described as the return of larvae from the pelagic environment to the shore by attachment to the substratum, and this may also include metamorphosis (Keough and Downes 1982, Seed and Suchanek 1992, Rodriguez *et al.* 1993). Recruitment includes post-settlement mortality and is generally described as the number of settlers that survive a particular time or to a particular size (Keough and Downes 1982, Connell 1985, Lasiak and Barnard 1995). More meaningfully, the rate of recruitment has been defined as the rate at which juveniles join the population (Pineda 2000). In the present study only recruitment was considered. For bivalves, settlement and recruitment can be complicated by the "primary-secondary settlement hypothesis", which proposes the attachment of larvae to an initial filamentous substratum followed by detachment from this substratum, and a secondary pelagic stage followed by the attachment at a final settlement site (Bayne 1964). The primary-secondary settlement hypothesis has been supported for *Mytilus edulis* (Pulfrich 1996), but for *Perna perna* it has mainly been refuted with the assumption that the secondary pelagic stage is accidental and results in the loss of settlers (Lasiak and Bernard 1995, Erlandsson *et al.* 2008). The refutation of this idea has important implications for the survival of *P. perna* in areas where human over-exploitation has led to an alternate stable state (Lambert and Steinke 1986) with rocky shores being dominated by filamentous algae, rather than mussel beds.

Settlement can be influenced by biological and physical factors acting on pre-settlement factors such as larval quality, larval supply and the availability of habitat (Underwood and Keough 2001, Jarrett 2003, Marshall and Keough 2006), and post-settlement factors including competition, physical disturbances and predation (Caley *et al.* 1996). Crucial factors determining larval supply are large scale oceanographic and wind induced forces (Pineda 2000). These factors act directly on the larval pool and hence on a large number of larvae resulting in larval supply (Pineda 2000, Morgan 2001, Underwood and Keough 2001). Larval delivery from near-shore waters onto the intertidal and the resultant settlement of larvae are then modified by hydrodynamics including tidal bores (Pineda 1991, 1999), turbulence and wave-exposure (McQuaid *et al.* 2000, Dobretsov and

Wahl 2008), as well as larval behaviour (Hunt and Scheibling 1996). High settlement rates tend to lead to adult populations being controlled by post-settlement factors, while pre-settlement factors are likely to drive the structure of low-settlement populations (Connell 1985, Underwood and Keough 2001). Subsequently, the potential for density-dependent settlement may be an influential factor in the structuring of adult benthic populations (Connell 1985, Roughgarden *et al*. 1985).

Local hydrodynamics are amongst the main factors affecting larval supply when larvae are in surface waters. Carson *et al.* (2010) found larval movement of two species of mussels to coincide with near-shore surface currents. These hydrodynamics will determine spatial variability and potentially the resultant adult distribution (Gaines *et al*. 1985, Raimondi 1990, Gaines and Bertness 1992, Bertness *et al.* 1996, Pineda 2000). The influence of wind, in driving surface currents, can influence the delivery of larvae and this is especially important for species that are transported like passive particles such as mussels (Phillips 1994). Despite the importance of wind-driven surface currents on pelagic larval transport and delivery, very few studies have looked at the relationship between these wind forced surface currents and the population dynamics of benthic species (Commito *et al.* 1995, McQuaid and Phillips 2000, Porri 2003). It has been suggested that wind driven surface currents affect the transport of the megalopae of crabs (Shanks 1998, Shanks and Roegner 2007), with settlement of megalopae in estuaries occurring in pulses following wind events (Natunewicz and Epifanio 2001). Peaks in barnacle settlement have been found to occur following days of strong wind (Raimondi 1990).

On the coast of South Africa, wind forced inshore currents are common, with the influence of the wind decreasing with depth (Field *et al.* 1980, Roberts 1989, Goschen and Schumann 1994, Phillips 1994). The influence of wind may vary at fine scales, with local topography and near-shore thermohaline currents interacting with these wind driven currents (Goschen and Schumann 1988).

Despite the importance of settlement and recruitment for the understanding of population dynamics, very few studies have measured the influence that reserves have on supplying larvae to surrounding shores. Hockey and Branch (1994) found an exponential decline in abundances of juvenile limpets with increasing distance from a reserve in the Canary Islands, suggesting possible spill-over of larvae produced in the reserve. Studies on clams in Ucunivanua, Fiji (Tawake *et al.* 2001, 2002), on scallops in the Georges Bank, North America (Murawski *et al.* 2000), and more recently on scallops in the Gulf of California, USA (Cudney-Bueno *et al.* 2009) describe increases in larval abundances near reserves after they started being protected. Pelc *et al.* (2009) found an exponential decrease in recruitment of mussels with distance from two reserves, Dwesa-Cwebe in the Transkei and Goukamma on the southern coast, in South Africa. These authors also found no reduction in recruitment at increasing distances from the centre of the Mapelane reserve in Kwa-Zulu Natal. They attributed this effect to be due to relatively high production and the low harvesting rates outside of the reserve. The study of Pelc *et al.* (2009), only considered sites south (downstream) of the reserves and did not use control locations nor have a balanced multi-directional design. Despite these previous studies, information on the influence of reserves on supplying larvae to surrounding shores remains scarce (Sale *et al.* 2005). There is therefore a need for more studies to determine more accurately the influence of reserves on surrounding shores and to gain insight into whether spill-over is taxon of locality specific.

The present study is a balanced multi-directional design examining recruitment rates of mussels at multiple reserves and control sites. This was done during the three month peak recruitment period in an attempt to determine the generality of the influence of reserves on recruitment rates. I tested the hypotheses that: (1) recruitment rates would be greater within reserves than outside, (2) that they would decrease with distance from marine reserves, and (3) that there would be greater recruitment to the north, due to the direction of the predominant winds, rather than south of reserves as in Pelc *et al*. (2009).

3.2 Materials and Methods

3.2.1 Recruitment

To test the hypotheses in this study, monthly settlement and recruitment of *Perna perna* were examined during Austral spring and early summer (the beginning of October, November and December 2009). This period was chosen because settlement rates are usually relatively high in these seasons (Lasiak and Dye 1989, Dye and Lasiak 1997, Harris *et al.* 1998) and sites are more accessible due to lower swell during the summer months (Lasiak 1992). Sampling was done by attaching standardised units of habitat (plastic scouring pads with a diameter of 10 – 11 cm and a thickness of 2 cm) to the rocks with eye bolts. Previous studies have found that within regions (Reaugh-Flower *et al.* in press), these are suitable substrata for estimating recruitment of mussels (Menge 1992, Porri *et al.* 2006, 2007, Rilov *et al.* 2008). These collectors provide only a relative estimate of settlement and recruitment due to the differences found between them and natural substrata (Hunt and Scheibling 1996). At each site, six collectors were haphazardly placed approximately 1 m apart from each other within low shore mussel beds. Collectors were taken up and replaced during the first low tide of each month. On some occasions collectors were lost due to heavy wave action or theft. Nevertheless, a minimum of three were obtained from each site at each time, except control 2 edge south where all collectors were stolen. The collectors were preserved in 70 % ethanol and washed in the laboratory to remove mussels. Mussels were sorted using a Barnett's fluidised sand bath (see Chapter 5 for details) which assisted in separating the mussels into different size classes. The settlers (< 400 µm) and recruits (> 400 µm) (based on Bownes *et al.* 2008) were then identified, counted and measured using a dissecting microscope with a micrometer.

3.2.2 Data Analysis

During the study, densities of settlers were extremely low. For each of the three months, numbers of recruits and settlers were combined, and each month was analysed separately, with a four-factor analysis of variance (ANOVA). The first factor "Reserve" (2 levels; reserve or control) was fixed, factor 2 "Site" (2 levels; reserve 1, reserve 2, control 1 and control 2) was random and nested in "Reserve", factor 3 "Position" (3 levels; centre/edge/out) was fixed and orthogonal to reserve and factor 4 "Direction" (2 levels; North or South) was fixed and orthogonal to reserve and position. When a very non-significant interaction ($P > 0.25$) was found, the data were pooled *post-hoc* to enable a more powerful test of main factors (Underwood 1997). All variances were heterogeneous (Cochran's test) but there were no suitable transformations to create homogeneous variances. As large, balanced ANOVAs such as these, are relatively robust to heterogeneity of variances, untransformed data were analysed (Underwood 1997). Post-hoc Student-Newman-Keuls (SNK) tests were done for significant sources of variation to determine the patterns of difference relative to hypotheses of interest.

In October 2009, all of the standardised units of habitat were stolen at the Control 2 southern edge site. In order to retain the symmetrical design, all edge sites were removed from the analysis and factor 3 "Position" was reduced to 2 levels (centre and out). The decision to remove the edge sites and not the northern sites was based on the figures showing a clear directionality in settler abundance that could not be ignored.

Correlation analyses were done to determine the relationship between adult cover and recruitment rates. First, Pearson's correlation co-efficient, r, was calculated for the three months combined for the separate reserves and controls. Second, Pearson's correlation co-efficient, r, was calculated for the three months for combined reserves and combined controls. Third, Pearson's correlation co-efficient, r, was calculated for combined months for combined reserves and combined controls.

3.2.3 Estimation of dispersal direction

Wind vectors were calculated from hourly wind speed and direction data for the three months preceding the collection of larval collectors (September, October and November 2009). Hourly data on wind speed and direction for the nearest weather station (Umtata, approximately 72.4 km from the study sites) were obtained from the South African Weather Service. Wind vectors were calculated as cumulative distance per month (i.e. hourly speed multiplied by duration) and a single distance was calculated for each of the predominant wind directions (SW, SE, NW and NE). Potential larval dispersal direction and distance were then predicted using the conceptual model in Table 3.5 based on wind directionality in Figure 3.5. Wind direction is given as direction from which the wind is coming, while currents are described as the direction in which they flow.

3.3 Results

3.3.1 Recruitment

For October 2009, the predicted pattern of more recruits inside reserves and more to the north was not observed. There was a significant interaction between reserve and position. In reserves, the centre sites were equal to the outside sites (Table 3.1). For controls the outside sites had more recruits than the centre sites (Table 3.1). When comparing the reserves with controls, there was no significant difference between sites (Table 3.1). Control outside sites had more recruits than reserve outside sites but this pattern was not statistically significant (Fig. 3.1). Reserve centre sites had more recruits than the control centre sites but this was also not significant (Fig. 3.1). The highest number of recruits were found at Silaka and Control 1, while Dwesa-Cwebe had the fewest. At all sites there was very little difference in numbers of recruits between north and south sites (Fig. 3.1).

For November 2009, the predicted pattern was not observed. There was a significant interaction between the factors reserve and direction (Table 3.2). For reserves, both directions were equal, while for controls, south was greater than north (Fig. 3.2). When comparing reserves to controls, reserve north sites were greater than control north sites, while reserve south sites are equal to control south sites (Table 3.2). For all reserves and controls the numbers of recruits were similar (Fig. 3.2).

For December 2009, the predicted pattern was not observed. There was a significant interaction between all factors: site (nested in reserve), direction and position. Both reserves showed the same pattern with centre being equal to edge and outside in the north, while centre was greater than edge which was equal to outside in the south. In the controls there was, as predicted, no clear pattern in recruitment, with all sites being equal except for the Control 2 outside south site which was greater than both centre and edge south sites (Fig.

3.3). In general the differences between controls and reserves showed a higher number of recruits at centre sites in reserves, with the exception of Silaka centre north (Fig. 3.3). There was also more recruitment in southern sites (Fig. 3.3).

When comparing recruitment for the three months, recruitment decreased drastically from an average of 15 individuals per collector across all sites in October to an average of 7 individuals per collector in November and again to an average of 4 individuals per collector in December (Figs. 3.1 - 3.3). Generally there was extremely low recruitment in each of the three months with a maximum average of 15 individuals per collector.

There were no correlations between the number of recruits and adult cover in any of the combinations of months or reserves or among months and reserves (Table 3.4).

3.3.2 Estimation of dispersal direction

Monthly distance vectors for each month for each of the four main wind directions are shown in figure 3.4. Over the three month period SE winds were the predominant wind in terms of duration and strength, resulting in the greatest vector, this was followed by SW winds in September and October and by NE winds in November. NW winds were the least common and produced the smallest vectors in all three months. NE winds produce westerly flows with a slight offshore component due to the effects of Coriolis force, while SW winds produce easterly flows with a slight onshore component (Fig. 3.5). SE winds produce onshore flows with a slight westerly component due to Coriolis force, while NW winds produce offshore flows with a slight easterly component (Fig. 3.5). SW and NE winds are assumed to have the most direct effect on along shore flow and on this basis I assumed that these winds were antagonistic to each other. SE winds are assumed to then resist easterly flows and enhance westerly flows. When comparing NE and SW winds (Fig. 3.5), for each of the three months the wind data indicate a strong east current directionality for September, a weak east current direction for October and strong west current direction for November. When including for the influence of SE winds (Fig. 3.5), an overall weak east flow was assumed for September, weak west flow for October and strong west flow for November (Table 3.5).

Recruitment data indicate extremely weak west directionality in recruitment for all three months (Fig 3.1 – 3.3). This directionality is not consistent at all sites, with the controls showing stronger directionality.

3.4 Discussion

The most noticeable result of this study was the general lack of any clear recruitment pattern found at reserves or controls, with no gradient of decreasing recruitment at greater distances from reserves or clear directionality for reserves or controls. Recruitment was similar across sites with a high degree of variability among and within sites for each of the sampling months. This pattern was in direct contrast with the three main hypotheses and the findings of previous studies done on recruitment inside and at different distances from reserves (Hockey and Branch 1994), including another study done in the same study region (Pelc *et al*. 2009). This indicates that the influence of reserves in supplying recruits to nearby shores may be overestimated. In general, similar recruitment at reserve and control positions was observed for two of the three months (Figs. 3.2 – 3.3). The clearer pattern found in December 2009, with reserve centre south sites having higher recruitment than edges, which were equal to the outside, and north sites being equal, may be the result of the extremely low recruitment. Low recruitment numbers may highlight existing patterns, with high recruitment hiding this pattern due to saturation settlement (Connell 1985, Pelc *et al.* 2009). This should, however, be considered with caution as the previous months may not have been subjected to high enough recruitment to cause saturation (McQuaid and Phillips 2006). The low degree of recruitment found in this study is similar to other studies done in the same region (Harris *et al*. 1998, Reaugh 2006). *P. perna* has been found to spawn in this area from March to September (Lasiak 1986). In this study, the spawning in September may have been detected as settlement/recruitment in October. According to Lasiak (1986), these results suggest that October may be a peak recruitment month, but they also show that even in peak months recruitment may be extremely low in the Transkei.

The lack of any clear pattern in recruitment may be explained by differences in larval dynamics (production, transport and mortality) (Pineda *et al.* 2009), fine scale local hydrodynamics (coastal morphology, topography and wind) (Pineda 2000, Morgan 2001, Underwood and Keough 2001) and post-settlement mortality (natural or due to disturbance) (Caley *at al*. 1996). Settlement intensification may also influence this pattern, but is improbable due to mussels seemingly lacking active substratum choice at settlement in contrast to barnacles (Raimondi 1988). Because of the complexity of settlement and recruitment it is unrealistic to attempt to identify a single process responsible for controlling recruitment (Pineda 2009), although, looking at individual processes will help in understanding settlement and recruitment.

Reproductive output is believed to be higher within reserves, due to higher adult abundances, than in areas outside of them (Manriquez and Castilla 2001, Branch and Odendaal 2003) and this would expectedly be the case here. This study shows that this perceived increase in productivity is not reflected in settlement/recruitment patterns and this suggests that differences between settlement/recruitment in reserves and areas outside of reserves is probably not driven by the increased production within reserves.

Wind vectors for each of the four predominant winds (SW, SE, NW, NE) for each month were compared. SW and NE winds were assumed to create the largest along shore movement, due to their orientation along the coast, and to work against each other (Fig. 3.5), with SW winds producing net easterly flows and NE winds producing net westerly flows. These vectors were compared to estimate subjectively the net strength and direction of surface currents. SE winds, assumed to resist easterly flows and assist westerly flows (Fig. 3.5), were then compared to the net strength and direction of flow from SW versus NE winds to estimate the residual flow direction. NW winds made up a small proportion of the monthly wind vectors and were therefore omitted. This estimated residual flow direction was then used to predict larval dispersal direction (Table 3.5). These wind data then predict down-stream to be east for September (weak) and west for both October (weak) and November (strong).

Recent work done by Roberts *et al.* (2010), found evidence of a northeasterly-flowing counter current, approximately 1.25 - 1.5 km offshore, at certain times of the year near Port St. Johns, with a velocity ranging between 20 and 60 cm.s^{-1}. There will be complex interactions between wind driven surface currents and this thermohaline counter current. The influence of the counter current on immediately near shore waters is not known and it may not come close enough to the shore to affect on the immediately near shore waters. If this current and the wind are in opposition, then the influence of the wind will be small and downstream will be in the direction of the current, or northeast because it is much greater than wind currents.

Larvae appear to be equally mixed between surface and deep layers (Porri, pers comm). So we can hypothetically stratify the water column and assume that the upper surface layer of the water column respond to wind forcing, while larvae in the water column below the influence of the wind-driven currents respond to the counter current (see Roberts 1989). In this case, the surface wind driven currents (and the larvae within this layer) will move predominantly westwards at low rates (Table 3.5), while larvae in the water column below the influence of the wind-driven currents will then be advected to the east by the counter current. The speed of this counter current is so great that such larvae will be carried out of the study area to the east. In this case, only wind driven surface layers will result in the retention of larvae within the study area and downstream will be south. This is the same as was assumed by Pelc *et al.* (2009) but for different reasons. Near shore surface layer wind driven flow may be more meaningful when considering directionality of larvae that remain within the study region.

Recruitment data show slight suggestions of directionality, with controls seemingly showing stronger suggestions. These recruitment data suggest a zero to south flowing dispersal for September with southerly dispersal in October and November (Figs. 3.1 – 3.3). These recruitment data seem to agree with the wind derived predicted larval direction (Table 3.5). Thus, wind may be a useful although extremely speculative means of determining larval dispersal directionality in this area.

Local hydrodynamics, including topographically and wind driven larval transport, may be an explanation for the lack of any clear pattern. At larger scales (100s of km) shelf morphology, in the Transkei, is relatively homogenous, with a relatively straight coastline and narrow coastal shelf (Reaugh 2006) which is unlikely to cause drastic changes in patterns of recruitment found between and within areas. Despite this, dispersal processes influence recruitment patterns at relatively small scales (10s of meters) (Harris *et al*. 1998). At smaller scales, differential delivery may be an explanation for the variability found between and within sites a few km apart (Porri *et al*. 2006). This indicates that local hydrodynamics may have a strong influence on the pattern found in recruitment with small scale differential delivery accounting for both the lack of difference in pattern found and the high variability.

The lack of a correlation between adults and recruitment may help identify the processes acting on recruitment, i.e. pre-settlement or post-settlement processes. Recruitment was not correlated with adult cover for any of the combinations used, indicating that recruitment is not linked with adult abundances in this area. This lack of a correlation between adults and recruits was similar to previous studies done in the area (Reaugh 2006, Pelc *et al.* 2009). This suggests that when adult abundances are low the initial abundance created by recruitment may be influenced by some post-settlement/post-recruitment processes (such as biological interactions or physical disturbances) leading to the differences found in adult abundances. When investigating comparable habitats, post-settlement processes are believed to drive population structure when recruitment rates are high (Connell 1985, Minchinton and Scheibling 1991), while spatio-temporal variability is believed to determine population structure when recruitment is low (Minchinton and Scheibling 1991). Since no data for any biological interactions, such as competition and predation, were gathered during this study, it is not possible to rule out any effects of these interactions. Disturbance, mainly due to harvesting, has been shown to be greater outside of reserves than within reserves (Halpern 2003). This disturbance and the subsequent reduction in adult abundance (Chapter 2) may be crucial in explaining the lack of correlation between adults and recruits. Adult populations seem to be the ideal habitat for settlement of mussels (Lasiak and Bernard 1995, Erlandsson *et al.* 2008), and a reduction in this settlement habitat could lead to higher pre/post-settlement mortality. In mussels, this can be complicated by the primary-secondary settlement hypothesis, where mussels initially settle on filamentous algae and later have a secondary dispersal phase after which they attach to mussel beds (Bayne 1964). The initial attachment to algae may be an explanation for the similar levels of recruitment found at sites with high adult abundance and at those with low adult abundance. This initial attachment to algae and the refutation of the primary-secondary settlement hypothesis for *P. perna*, may then result in lost recruits with the increase in mortality due to ‘wasted’ settlers seemingly the most likely reason for adult abundances not being similar to the initial abundances set up by settlement/recruitment. The lack of natural recovery of exploited shores and the persistent strong difference in adult abundances found in reserves and exploited shores is, therefore, mainly a product of exploitation of the adults and the increased post-settlement mortality due to the removal of the adults resulting in a lack of primary substratum.

Recruitment limited populations are defined as "populations that are under-saturated as a result of finite larval supply and could support greater abundances given enhanced recruitment" (Doherty 1998, p 129) and adult abundance varies as a function of colonisation rate rather than post-settlement and post-recruitment processes (Doherty and Fowler 1994). Recruitment levels can therefore be a limiting factor. The lack of recruitment patterns, correlations between adult abundances and recruitment and the similar numbers of recruits found at the different sites, suggests that this area is not recruitment limited and that recruitment is not a function of local adult abundances. The data suggests that exploited shores are not recruitment limited and while it also suggests that reserves are not recruitment limited this may be due to the lack of data on adult population size structure. Reaugh-Flower *et al.* (submitted), found recruitment limitation in Dwesa-Cwebe by comparing recruitment rates to sub-adult mussel numbers, and the inclusion of sub-adults in this study may have resulted in similar findings. One possible explanation for the lack of difference in recruitment between reserves and exploited shores, is the presence of inaccessible or 'naturally protected' populations near exploited shores. For example at control 2, there is a 2.95 km stretch of rocky coast line that is relatively inaccessible within the 9.05 km control site. This stretch of inaccessible coast is of similar size to Silaka and therefore these 'naturally protected' populations could supply recruits to the exploited shores near them contributing to the lack of pattern found.

In conclusion, the lack of any clear pattern and the lack of correlation between adult abundances and recruitment seem to indicate a strong influence of localised supply and post-settlement processes. This de-coupling between adults and recruits indicates open populations in the area that I dealt with and this is important for connectivity and the persistence of local populations. Open populations allow for greater movement and exchange of individuals leading to enhanced gene flow (Nicastro *et al.* 2008). The differences in magnitude found between north and south sites may indicate the predominant direction of immediate near-shore currents and shows the importance of a multi-directional design when looking at the influence of reserves on supplying recruits to surrounding shores. This study also refutes the idea that reserves continually supply recruits to nearby shores and that there is a gradient of declining recruitment at distances from reserves. The similar levels found in recruitment between reserves and exploited shores may not be valid on shores where exploitation is high and this lack of habitat overcomes any possible spill-over from reserves.

Table 3.1 Results of a three-factor ANOVA of recruitment estimates for Dwesa-Cwebe; Silaka; Control 1 and Control 2 for October 2009. Student-Neuman Keuls (SNK) results showed using codes representing N: North; S: South; C: Centre; E: Edge; O: Outside. * indicates $P < 0.05$

Source	**d.f.**	**M.S.**	***F***	***P***
Reserve = Re	1	305	1.71	> 0.05
Site(Reserve) = Si(Re)	2	178	1.08	> 0.05
Direction = Di	1	143	0.72	> 0.05
Position = Po	1	77	0.47	> 0.05
Re x Di	1	150	0.76	> 0.05
Re x Po	1	744	4.51	*
Di x Si(Re)	2	198	1.20	> 0.05
[2]Po x Si(Re)	2	186		
Di x Po	1	346	2.10	> 0.05
Re x Di x Po	1	6	0.04	> 0.05
[1]Po x Di x Si(Re)	2	31		
[1]Residual	32	172		
[2]Pooled 1	34	163		
Pooled 2	36	165		

SNK Reserves C = Reserves O; Controls O > Controls C
Reserves O = Controls O; Reserves C = Controls C

[1,2] Denotes post-hoc pooling when $P > 0.25$. New F-ratios are given for those nested against the pooled terms (pooled 1 and pooled 2).

Table 3.2 Results of a three-factor ANOVA of recruitment estimates for Dwesa-Cwebe; Silaka; Control 1 and Control 2 for November 2009. Student-Neuman Keuls (SNK) results showed using codes representing N: North; S: South; C: Centre; E: Edge; O: Outside * indicates $P < 0.05$

Source	**d.f.**	**M.S.**	***F***	***P***
Reserve = Re	1	50	0.46	> 0.05
Site(Reserve) = Si(Re)	2	109	3.45	*
Direction = Di	1	102	3.25	> 0.05
Position = Po	2	102	1.99	> 0.05
Re x Di	1	150	4.75	*
Re x Po	2	23	0.45	> 0.05
[2]Di x Si(Re)	2	21		> 0.05
Po x Si(Re)	4	51	1.63	> 0.05
Di x Po	2	2.1	0.07	> 0.05
Re x Di x Po	2	35	1.13	> 0.05
[1]Po x Di x Si(Re)	4	10		
[1]Residual	48	33		
[2]Pooled 1	52	31		
Pooled 2	54	31		

SNK Reserves N = Reserves S; Controls S > Controls N
Reserves N > Control N; Reserve S = Control S

[1,2] Denotes post-hoc pooling when $P > 0.25$. New F-ratios are given for those tested agianst the pooled terms (pooled 1 and pooled 2)

Table 3.3 Results of a three-factor ANOVA of recruitment estimates for Dwesa-Cwebe; Silaka; Control 1 and Control 2 for December 2009. Student-Neuman Keuls (SNK) results showed using codes representing N: North; S: South; C: Centre; E: Edge; O: Outside * indicates $P < 0.05$

Source	**d.f.**	**M.S.**	***F***	***P***
Reserve = Re	1	72	2.96	> 0.05
Site(Reserve) = Si(Re)	2	24	1.85	> 0.05
Direction = Di	1	138	76.92	*
Position = Po	2	54	1.45	> 0.05
Re x Di	1	0.05	0.03	> 0.05
Re x Po	2	94	2.52	> 0.05
Di x Si(Re)	2	1.8	0.14	> 0.05
Po x Si(Re)	4	37	2.84	*
Di x Po	2	33	0.80	> 0.05
Re x Di x Po	2	68	1.64	> 0.05
Po x Di x Si(Re)	4	42	3.20	*
Residual	48	13		

SNK Dwesa-Cwebe N: C=E=O; S: C>E=O Silaka N: C=E=O; S: C>E=O
Control 1N: C=E=O S: C=E>O Control 2 N: C=E=O S: C=E=O

Table 3.4 Correlations between number of recruits and adult abundance. Combinations shown: (a) combined months (b) combined reserves (c) combined reserves and months. *r* critical, *r* observed, d.f. and significance levels are shown

(a) Combined months				
	***r* crit**	***r* obs**	**d.f.**	***P***
Dwesa-Cwebe	0.486	0.434	16	> 0.05
Silaka		-0.359		
Control 1		0.306		
Control 2		-0.145		
(b) Combined reserves				
	r crit	*r* obs	d.f.	*P*
Reserves October	0.576	-0.229	10	> 0.05
Reserves November		-0.099		
Reserves December		0.180		
Controls October		0.31		
Controls November		0.077		
Controls December		0.28		
(c) Combined Reserves and months				
	r crit	*r* obs	d.f.	*P*
Reserves	0.32	-0.077	34	> 0.05
Controls		0.162		

Table 3.5 Conceptual current strength and direction and predicted larval direction for September, October and November 2009

	Winds			
	NE vs. SW winds	SE winds	Residual Direction	Predicted larval dispersal direction
	Current Strength and Direction			
September	Strong E	Strong W	Weak E	N
October	Weak E	Strong W	Weak W	S
November	Strong W	Strong W	Strong W	S

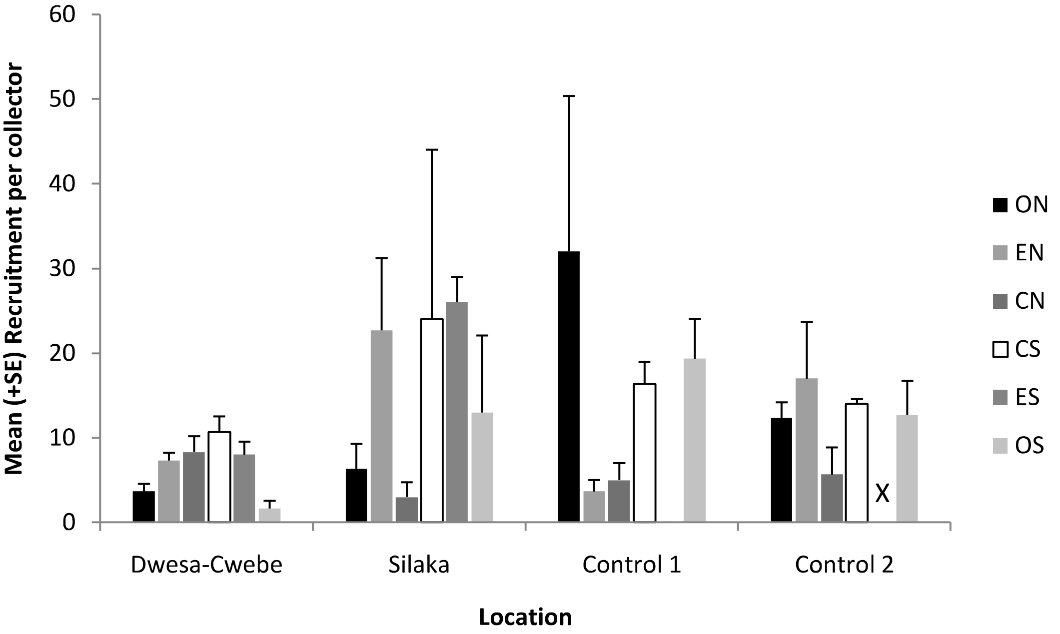


Figure 3.1 Mean (*n* = 3, +SE) recruitment of *Perna perna* at Dwesa-Cwebe, Silaka, Control 1 and Control 2 for October 2009. Key with codes representing N: North; S: South; C: centre; E: edge; O: outside. X shows missing data.

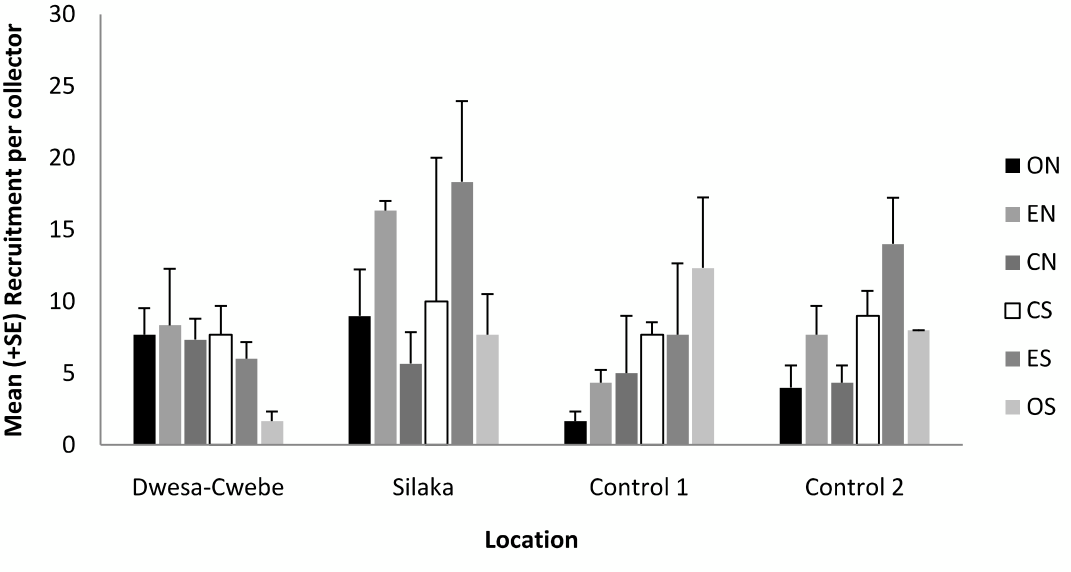


Figure 3.2 Mean (*n* = 3, +SE) recruitment of *Perna perna* at Dwesa-Cwebe, Silaka, Control 1 and Control 2 for November 2009. Key with codes representing N: North; S: South; C: centre; E: edge; O: outside.

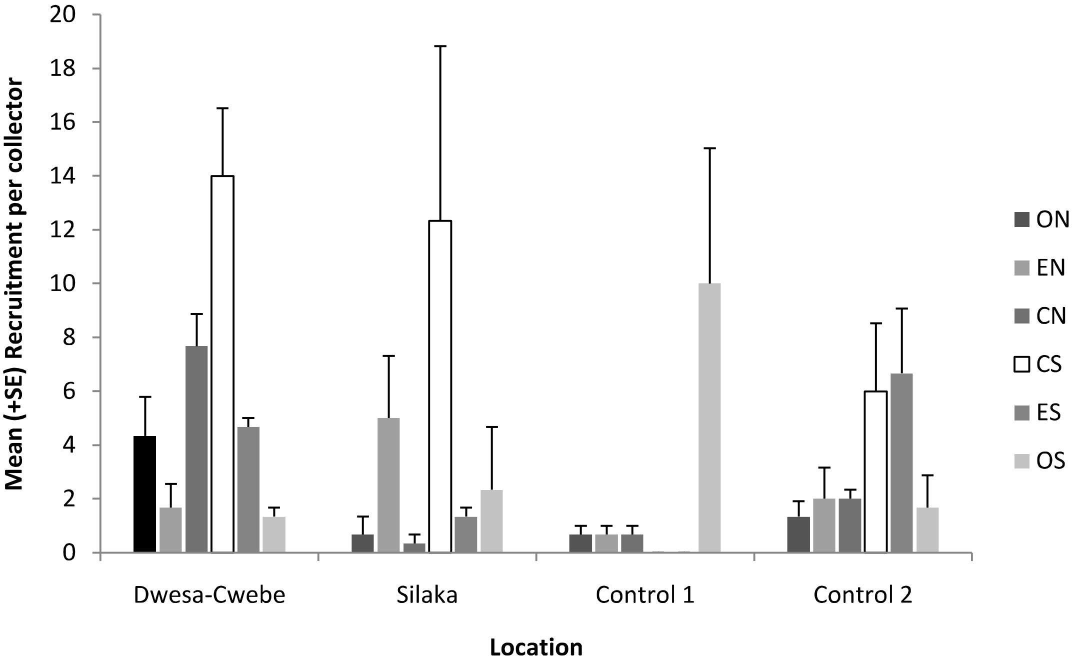


Figure 3.3 Mean (n = 3, +SE) recruitment of *Perna perna* at Dwesa-Cwebe, Silaka, Control 1 and Control 2 for December 2009. Key with codes representing N: North; S: South; C: centre; E: edge; O: outside.

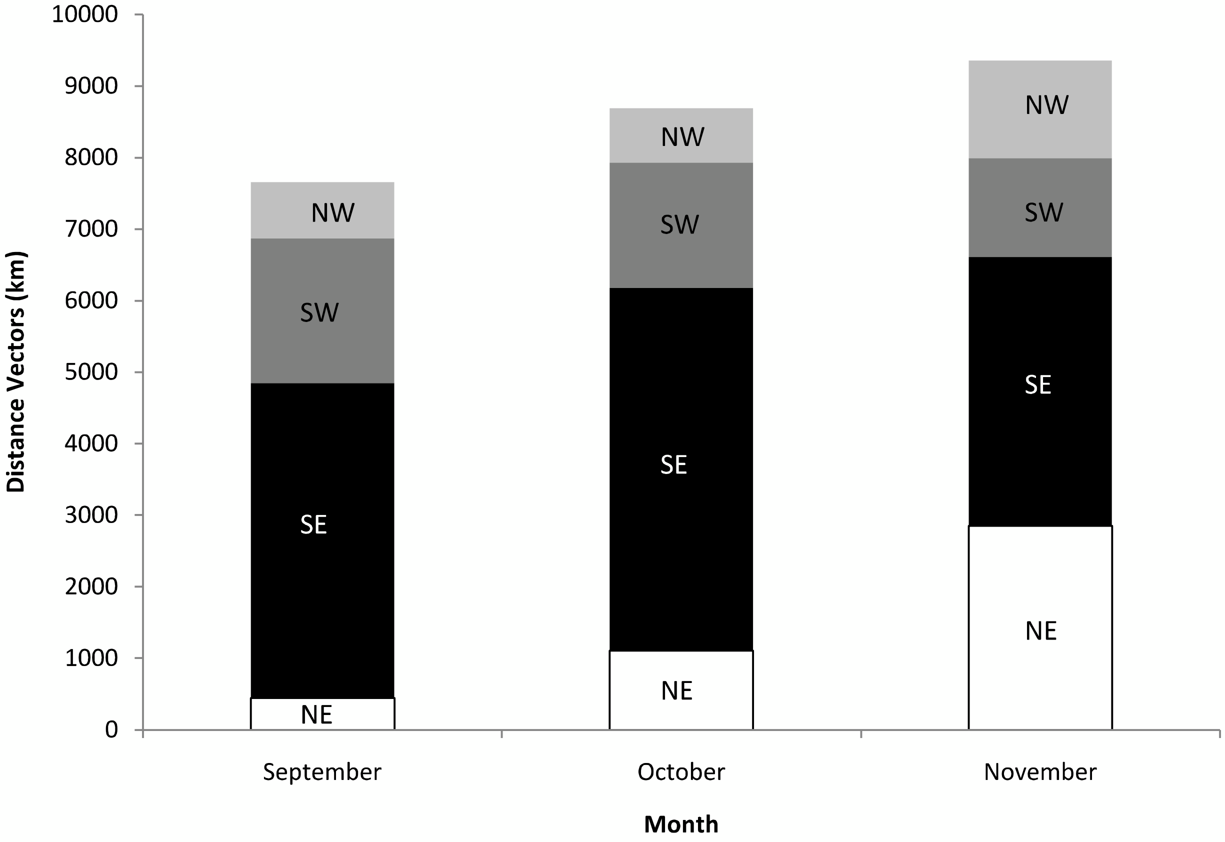


Figure 3.4 Distance vectors of the predominant winds for September, October and November 2009

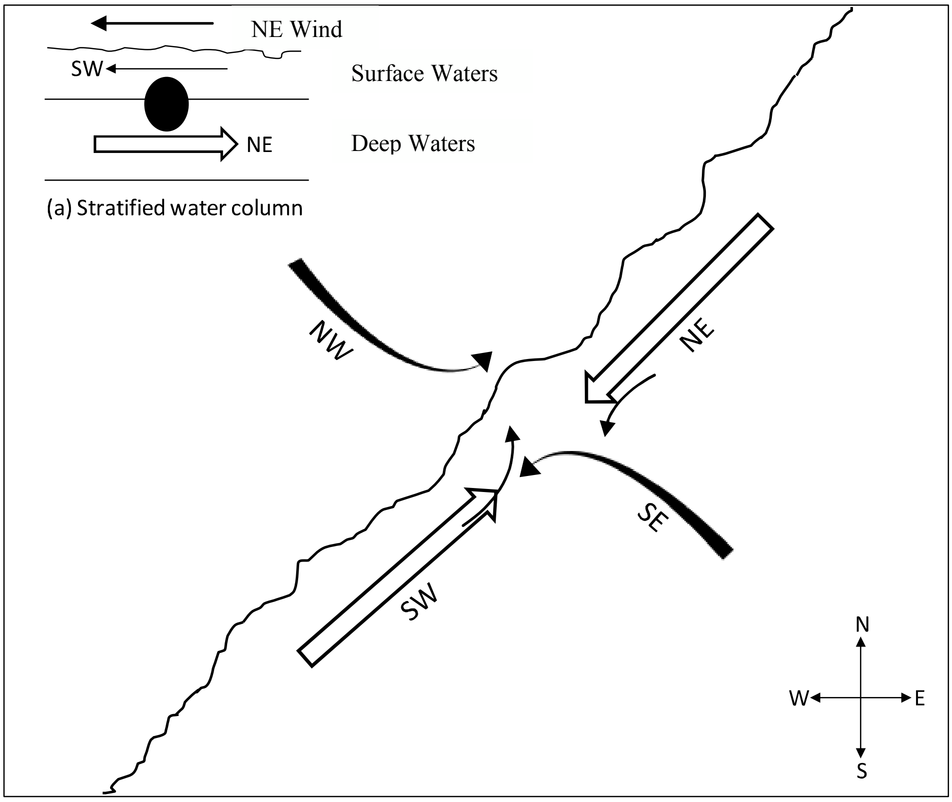


Figure 3.5 Diagramatic representation of winds along the east coast of South Africa used to derive the model in Table 3.5. Open arrows indicate winds responsible for the majority of along-shore movement. Both curved lines indicate the influence of Coriolis force. (a) Insert depicting stratified water column, indicating the hypothesised difference in movement of surface waters (wind driven) and deep waters (counter current driven) when NE winds prevail. Closed circle indicates larval distribution in the water column.

Chapter 4

An effective method for sorting benthic samples, with emphasis on small post-recruitment stages

4.1 Introduction

Analysis of benthic samples is extremely time consuming; separation of animals from sediment is difficult especially when large amounts of debris, sand and gravel are present (Worswick and Barbour 1974). The presence of sediment in samples reduces the accuracy and increases time required for sorting samples under a microscope and may lead to eye fatigue which will further reduce accuracy (Worswick and Barbour 1974, Robinson and Chandler 1993). Traditional techniques for sorting benthic organisms from sand and gravel are extremely time consuming and are inadequate (Whitman *et al.* 1983, Robinson and Chandler 1993). The labour involved in sorting can be reduced by applying a satisfactory sorting method (Hickley 1975), and this requires methodological equipment that is easy to use, quick, accurate and reliable (Been *et al.* 2007).

Elutriation is the process whereby organisms are separated from sediments by washing in a constant stream of water (Tieman and Betz 1979, Southwood *et al.* 2000). This method has been used since 1935 (Moon 1935) and is considered to be one of the only suitable methods for removing invertebrates from sediments (Cummins 1962). It relies on the sediment particles having a higher density than the invertebrates in the sediment and therefore sinking quicker than the invertebrates (Edwards 1991). This results in the separation of fauna from their sediments (Lauff *et al.* 1961). The technique is particularly appropriate for marine benthic samples (Southwood *et al.* 2000). Organisms are washed out according to their volume, weight and bodyshape and are collected on a sieve, with the separation of lighter soft bodied animals from heavier shelled animals and sediments (Pedrick 1974, Tiemen and Betz 1979, Whitman *et al.* 1983, Robinson and Chandler 1993). The removal of these organisms allows for better, quicker analysis of the samples (Lauff *et al.* 1961, Cummins 1962, Worswick and Barbour 1974). Teiman and Betz (1979), state that the quality of an elutriation method can be determined from the quantity and quality of the organisms compared to the original states.

By the use of key word searches (ISI Web of Science and Google Scholar) for elutriation, benthic samples, separation and sediment in the fields of zoology, marine and freshwater biology and oceanography, I found and assessed 13 relevant peer-reviewed articles and 2 book chapters. The majority of papers dealt with particle sizes not relevant to this study. Most of the papers, also focused on design and methods (Moon 1935, Lauff *et al.* 1961, Cummins 1962, Pedrick 1974, Worswick and Barbour 1974, Tieman and Betz 1979, Whitman *et al.* 1983, Gross 1990, Edwards 1991), and the terrestrial use of elutriation, ranging from the removal of micro-fauna, particularly nematodes from soil (Tieman and Betz 1979, Bernard and Schmitt 2005, Been *et al.* 2007), to seeds (Gross 1990). Elutriation has also been used for macrofaunal separation in fresh water streams (Cummins 1962, Hickley 1975). In marine studies, elutriation has mainly been used by sandy beach ecologists. Whitman *et al*. (1983) found very low recoveries of small molluscs (0.7 – 26 mm), while in contrast, Robinson and Chandler (1993) used a mixture of elutriation and flotation and found good recovery rates of small molluscs (0.5 – 65 mm).

One of the main difficulties in studying small molluscs is sorting them from the sediment so that they can be counted. The density of an organism seems more important than its size or shape in affecting separation from sand and gravel (Whitman *et al.* 1983). Due to their shells, molluscs have a higher density than the sediment and therefore elutriation has not been used on molluscs extensively (Whitman *et al.* 1983, Robinson and Chandler 1993). To date, elutriation has mainly been used in the separation of large sizes or individual target organisms. Most of the larger organisms (especially molluscs) have a much higher or lower density than the sediment and so they can be easily separated. The smaller the molluscs are, the closer their specific density is to that of the sediment; this is especially relevant with regard to newly recruited individuals. Robinson and Chandler (1993) proposed that for the removal of newly recruited individuals, flotation could be used, but this technique would increase the sorting time.

A new technique, adapted from multiple elutriation techniques, which uses fractionated elutriation or the use of different flow rates and sieve sizes, allows for the separation of a sample into density size classes. The different flow rates and sieve sizes separate the floating debris from the newly recruited individuals (< 0.5 mm) and larger individuals (> 0.5 mm) and this ensures the entire sample can be sorted quickly and accurately. This study tests this new method and whether it can help to simplify studies, especially those on recruitment.

4.2 Materials and Methods

4.2.1 Field Sampling

The samples used to test fractionated elutriation were the same as those collected for Chapter 3 (details of collection described in chapter 3).

4.2.2 Fractionated Elutriation Method

Sub-sampling was done by placing raw samples in the centre of a Barnett's fluidised sand bath (design notes from Southwood *et al.* 2000). These samples were then subjected to an upward current via water forced through a scintered plate at an initial low velocity of 0.05 $l.s^{-1}$ (Low flow rate) and then at a higher velocity of 0.11 $l.s^{-1}$ (High flow rate). Initial bubbling of water through the scintered plate broke up the sample which then became fluidised. The samples were subjected to each flow rate until they ran relatively clear (little sediment movement in the sand bath, approximately 5 minutes). The suspended animals and debris were collected via an over flow spout and retained through a series of sieves. For low flow rates, the sieves were placed in a graded series with mesh sizes of 500 µm and 75 µm (sub-sample treatments Low 500 and Low 75) which made it possible to separate larger floating animals and debris from the smaller sand particles and animals. For high flow rates, suspended material of the samples was retained with a 75 µm sieve only, this was done as the suspended material was all of a similar size and there was no added need to separate larger floating animals (sub-sample treatment High). After subjecting the samples to the two water pressures, the remainder of the sample retained in the Barnett's fluidised sand bath was poured through a graded series of sieves measuring 500 µm (sub-sample treatment 500), 250µm (sub-sample treatment 250) and 75 µm (sub-sample treatment 75). The sub-sample treatments were all collected and labelled.

The elutriated samples were sorted under a dissecting microscope. Treatments Low 75, High, 75 and 250 were sorted under 32x magnification, while treatments Low 500 and 500 were sorted under 10x magnification. Different magnifications were used to sort the sizes of the target organisms recovered. Pre-recruitment (< 400 µm) and post-recruitment stages (> 400 µm) of the mussel *Perna perna*, were used to determine the effectiveness of this sorting procedure.

4.2.3 Standardised samples

In order to determine the effectiveness of the technique, standardised samples were prepared and sorted using the two different techniques. Standardised samples were prepared by thorough cleaning of a field sample and counting the total number of the target species. These samples were then sorted by a newly trained individual. For comparison, the samples were sorted using both methods; elutriation and standard sorting with no elutriation, the same samples were 're-assembled' to allow the two techniques to be used without the individual knowing that the samples were the same. Both time for sorting and number of animals retrieved were recorded to analyse time to sort and accuracy. In order to reduce any bias, samples were sorted while alternating techniques to ensure that any perceived difference was not due to improvement by the individual.

4.2.4 Statistical Analysis

t-tests were done to determine differences in accuracy and time taken between the two methods and to make decisions about possible discarding of sub-sample treatments. Paired *t*-tests were done to determine if any of the sub-sample treatments could be discarded. This was done by comparing the total number of recruits in the entire sample with the total number minus the number of recruits in each of the 6 sub-sample treatments. To determine the difference in accuracy of the two methods, a paired *t*-test was used to analyse the percentage of the standardised numbers retrieved. To determine the time required using the new method, a paired *t*-test compared the time taken to sort the samples using each of the methods. Under normal circumstances, elutriation of a different sample would be done while sorting the present sample. Because of this, for the elutriated samples, an adjusted time (time used in elutriation) was used to account for the continual alternation of techniques used.

4.3 Results

The paired *t*-tests for discarding of sub-sample treatments showed no significant difference between the total number of recruits minus the sub-sample treatments Low500, Low75, High and 500 when compared to the total numbers of recruits (d.f. = 39, $P > 0.05$). There was, however, a significant difference between the total numbers and the 250 and 75 sub-sample treatments (d.f. = 39, $P < 0.05$).

There was a 9 % difference in percentage between elurtiation and non-elutriation methods, but the paired *t*-tests indicated that this was marginally non-significant (t = 2.36, d.f. = 7, $P = 0.06$). The new elutriation method had a mean accuracy of 90 % while the non-elutriation method had a mean accuracy of 81 % (Fig. 4.1).

The paired T-tests for time taken to sort the same sample showed a significant difference between the two methods, with the new elutriation method taking significantly longer than the non-elutriation method ($t = 2.36$, d.f. = 7, $P = 0.01$).

4.4 Discussion

This study shows that the new method of fractionated elutriation increases the accuracy of sorting small post recruitment stages from sand and gravel. Although not significantly more accurate than the standard method, the increase of 9 % in accuracy should not be overlooked. The separation efficiency of this new method is comparable to previous studies done using elutriation on other organisms. Whitmann *et al.* (1983), found a mean recovery of 90 % for organisms between the sizes of 0.7 - 26 mm, but also found very low recovery of molluscs. I was only able to find one paper that used elutriation exclusively on molluscs in the marine environment. Robinson and Chandler (1993), used a mixture of elutriation and floatation and proposed an accuracy of 98 – 100 % in separating a species of clam, *Mya arenaria*, (0.5 – 24 mm). The other molluscs in the study by Robinson and Chandler (1993) were in the range of 1-65 mm. These authors also proposed that for smaller individuals (<0.5 mm) only flotation should be used, but this would increase the time of sorting. No studies have been done on the use of elutriation on small post-recruitment individuals under the size of 0.5 mm. When looking at small post-recruitment individuals, the increase in accuracy is only achievable with a significant increase in time for sorting, a mean of 10 minutes per sample. The samples used to determine the difference in time were moderately 'dirty'. This amount of sediment was chosen because of logistical constraints, with 'dirtier' samples taking longer to sort. The cleaner the samples, the less effective the new elutriation method is in saving time, with the difference in time to sort being reduced with an increase in the amount of sediment. The increase in amount of sediment will also lead to a reduction in accuracy of the old non elutriation technique (Worswick and Barbour 1974) increasing the effectiveness of this technique. Despite this increase in time to sort, the advantages of the new method outweigh the disadvantages. The new method increases accuracy, which is important when sorting a large number of samples. This increase in accuracy is especially important when looking at the ability to detect differences in field studies, possibly leading to improved analysis of ecological studies (Andrew and Mapstone 1987). The new method also makes the task of sorting the sample less daunting, with smaller portions to work through instead of a single larger sample. This will reduce boredom when working through a single large sample which can lead to a decrease in accuracy. The most important aspect of this new method is that it enables samples to be sorted in their entirety as well as separating the samples into size classes, making 'cleaner' fractions. By separating the sample by size classes it is possible to sort the larger portions more thoroughly, which may contain filamentous material onto which recruits are often attached. This separation into size classes will also make identification easier and more precise as all the bivalves will be of similar size and therefore easier to distinguish from each other. Light bodied organisms, small post-recruitment individuals and larger organisms can all be separated allowing larger more complex studies to be addressed. This new method can be adjusted with different flow rates and sieve sizes, making size selected separation more precise. Small differences in accuracy may be more important when the effect size between treatments (e.g. between reserves and non-reserves) is small (*sensu* Underwood 1993).

This method, although more time consuming, can lead to more complex studies, including simultaneous investigations of multiple size classes and different animals with an increased accuracy in sorting.

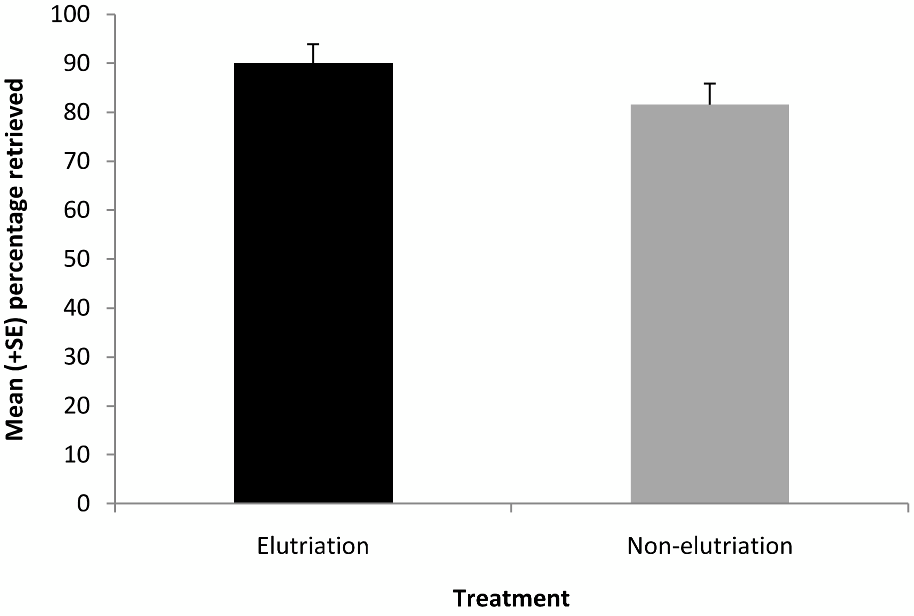


Figure 4.1 Mean (*n* = 9, +SE) percentage of a known number of individuals of *Perna perna* retrieved using two different methods.

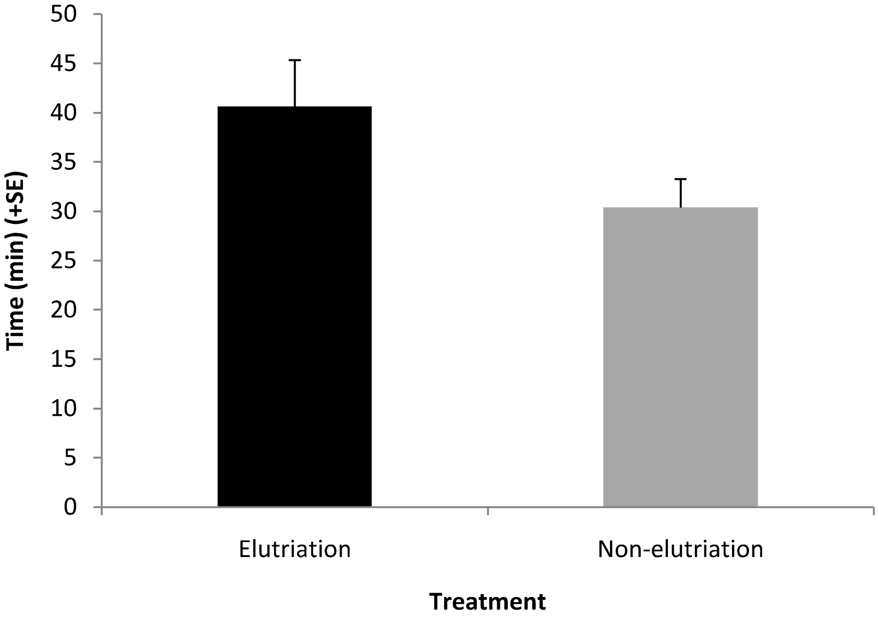


Figure 4.2 Mean (*n* = 9, +SE) time taken to sort a sample of individuals of recruited *Perna perna* using two different methods.

Chapter 5

General Discussion

This thesis offers a generalised view of the utility of MPAs in protecting adult stocks of an intertidal resource and supplying recruits to nearby exploited shores. The use of a balanced multi-directional design, with multiple MPAs and control sites (surrounding exploited shores), and the intertidal mussel *Perna perna* as a model organism, allowed an integrated view of the influence of MPAs on the distribution of mussels (landscape pattern) and recruitment of juveniles through the influence of near shore ocean currents to explain connectivity between MPAs and the exploited shores (landscape processes). The combination of investigating adult abundances and recruitment can then be used to demonstrate the relationship between pattern (adult abundance) and process (recruitment) (Turner 1989). The results lead to the identification of the relationship between MPAs and exploited shores, and the influence of MPAs on intertidal population connectivity and rehabilitation of exploited shores, further increasing our understanding of the role that MPAs play in conservation.

5.1 An integrated look at recruitment and adult abundances

When comparing recruitment and adult abundances, the lack of any clear similarity in pattern between adult abundance and recruitment suggests a de-coupling of adults and recruits in this area. The most noticeable difference in adult abundances is the sharp reduction found at areas outside of MPAs. This pattern, linked to the similar levels of recruitment found in reserves and exploited shores, indicates the possible need for adult "substratum" for successful recruitment and rehabilitation (Lasiak and Bernard 1995, Erlandsson *et al*. 2008), with the reduced adult abundances at exploited sites mainly being responsible for the lack of recovery, and hence continual low adult abundances, in these areas (Dye 1992). This difference in patterns of adult abundances and recruitment, and lack of natural recovery of exploited shores is, therefore, mainly a product of exploitation of adults and the increased post-settlement mortality due to the removal of the adults and the subsequent loss of primary substratum. Algae do make up suitable settlement habitat, but settlement on algae leads to lost recruitment because larvae cannot make the transition from this to the suitable recruitment substratum (Erlandsson *et al.* 2008). Simply, re-colonisation is delayed not because larvae do not arrive, but because larvae do not recruit due to the lack of suitable recruitment habitat. Exploitation must therefore have reduced the amount of settlement habitat below a critical level preventing recovery.

A critical level of disturbance or remaining habitat amount, termed the ‘extinction threshold’, has been predicted by theoretical studies. Below this threshold value, a population cannot sustain itself naturally and recovery becomes impossible (Johnson and Preece 1992, Fahrig 2003, Huggett 2005). This threshold value varies amongst species and regions, but if the amount of remaining habitat decreases below the threshold value, the survival probability for the given species will decrease sharply (Johnson and Preece 1992, Huggett 2005). The threshold value increases or decreases depending on the reproductive rates, the movement of individuals (Fahrig and Merriam 1992), the level of connectivity between patches, and the level of disturbance (Johnson and Preece 1992, Hanski *et al*. 2000). The spatial configuration of the landscape, driven by habitat loss and fragmentation, is linked to the movement of individuals and connectivity between patches affecting population dynamics and therefore affects the threshold value (Fahrig and Merriam 1992, Moilanen and Hanski 1998). Persistence of a given species will occur if the amount of habitat and the ability of the species to recover are greater than the threshold value for that species (Hanski and Otso 2000). Once below the threshold value, the ability of the system to recover will depend on connectivity and local hydrodymanics. Recovery potential increases with an increase in connectivity, i.e. better spatially connected areas will be able to recover even with low adult abundances (Johnson and Preece 1992). When connectivity is low, large and small scale local hydrodynamics, most importantly small scale localised retention of propagules are critical to recovery (Johnson and Preece 1992). If connectivity is low and there is little or no retention, then the system will either remain in its exploited state or collapse, leading to local extinctions.

There is little empirical evidence of this threshold value, but Robinson *et al.* (2007) found that harvesting intensities, removing more than thirty percent of adult abundance, resulted in a drastic decrease in recruitment of the mussel *Mytilus galloprovincialis* along the west coast of South Africa. Studies have proposed that harvesting levels of above thirty percent of mussels will result in an inability to maintain the population (Harris *et al.* 2003, Robinson *et al.* 2007). Removal rates of adults in the control sites of this study are well in excess of thirty percent so that control sites are probably below the critical habitat value, making natural recover impossible. Identifying a minimum habitat threshold value is important when looking at areas exposed to habitat modification through habitat loss or fragmentation and will help in developing management plans (Huggett 2005).

5.2 The influence of MPAs on patterns and processes

MPAs can have large influences on both patterns and processes in pelagic and benthic marine environments. MPAs may influence patterns by influencing population structure, and the distribution of organisms by protecting populations from exploitation and increasing adult abundances (Addessi 1994, Lasiak 1998, Foster and Hodgson 2000, Manriquez and Castilla 2001, Branch and Odendaal 2003, Halpern 2003, Beaukers-Stewart *et al.* 2005). MPAs positively influence processes by influencing settlement and recruitment, by supplying juveniles to surrounding shores through ‘spill-over’ (Hockey and Branch 1994, Dye *et al.* 1997, Williamson *et al*. 2004, Fogharty and Botsford 2007, Pelc *et al.* 2009). They also decrease immediate post-settlement mortality, by increasing the amount of suitable habitat. The increase in adult abundance within reserves creates a distinct difference in habitat between MPAs and the surrounding exploited shores resulting in an alternating pattern of high adult abundance, within MPAs, surrounded by low adult abundance. In a landscape context, the differential adult abundance pattern represents a pattern of differential quality of patches, with good quality patches surrounded by a poor quality matrix.

MPAs can also influence three major processes. First, through the increase in reproductive output (Branch and Odendaal 2003), MPAs can increase the amount of settlers arriving at surrounding shores. Second, by increasing the amount of suitable habitat, through protection of adult abundances, they can reduce post-settlement mortality linked to habitat availability, and third, by reducing post-settlement mortality they can increase recruitment. The combination of adult abundance and settlement and recruitment data can be used to demonstrate the influence of MPAs on the relationship between patterns (adult abundance) and processes (settlement and recruitment and post-settlement mortality) (Turner 1989).

The pattern of alternation of good and poor quality habitat patches observed in the present study may influence some of the processes above. The pattern may, due to the build up of adults and the subsequent higher reproductive output, encourage settlement at exploited or poor quality patches. This increase in settlement at poor quality patches could then lead to the removal of this pattern through the recovery of these shores. This pattern is, however, not able to influence post-settlement mortality, as it does not change habitat quality or availability. Thus, the pattern cannot influence recruitment at poor quality patches and so it appears that the pattern is self-sustaining with areas of high quality habitat (MPAs) continually remaining high, due to increased recruitment, while areas of low quality habitat (exploited shores) remaining low or decreasing due to low recruitment driven by post-settlement mortality. For rehabilitation of exploited shores, habitat quality and availability and post-settlement mortality are amongst the most important processes.

5.3 Landscape ecology and management of MPAs

Exploitation of natural habitats and subsequent habitat fragmentation are a major concern driving conservation efforts (Moilanen and Hanski 1998). Habitat fragmentation can be an important determinant of the size and persistence of populations due to its influence on the movement of individuals among habitat patches (Vos *et al*. 2001, Cascante *et al*. 2002, Levey *et al.* 2005). In a landscape context for MPAs to be effective, they need to be good quality patches favouring connectivity through good quality corridors. In marine systems, MPAs are a common management tool for conservation as they can have important advantages for the persistence of populations of sessile/sedentary species (Hastings and Botsford 1997). For MPAs to be an effective conservation tool and to provide benefits to surrounding shores then they must achieve two aims: (1) they must increase the adult abundance and hence reproductive capacity within the MPAs; and (2) they must supply adequate juveniles to increase adult abundances and sustainability of exploited shores outside of the MPAs (Kellner *et al.* 2007). There is considerable evidence indicating that MPAs increase adult abundances within MPAs (see Halpern 2003 for review) and, as such, they seem to be effective in achieving this aim. The present study reinforces this and indicates that MPAs make up high quality patches. There is, however, much less evidence for the second benefit. Some studies have found spill-over of recruits to surrounding shores, but few have looked at the influence of this in shaping the adult abundances on those shores. Pelc *et al.*

(2009), found decreasing settlement at greater distances from MPAs indicating a positive spill-over of recruits from reserves, but the study was limited due to the lack of replication at the appropriate scale, and the different temporal scales used for different MPAs. The present study indicates that the level at which MPAs supply juveniles to surrounding shores and their ability to help the recovery of nearby shores may be over estimated. As such, MPAs may not fulfil their second objective and may not be able to help sustainability of surrounding exploited shores. In a landscape context, MPAs may not improve connectivity and may have little influence on corridor quality.

Hastings and Botsford (1999) proposed that size and distribution of MPAs is critical in the sustainability of protected populations, and that these attributes can greatly influence the extent to which reserves influence exploited shores. While moderately spaced reserves with variable sizes (encompassing different scales of dispersal) can meet multiple needs, the success of any reserve network requires attention to the variability in dispersal (Shanks 1995, 2003, Halpern and Warner 2003), with the focus of recovery at a landscape scale and not just of the individual patch or reserve (Johnson and Preece 1992). The results of the present study indicate that for any management plan to be effective the exploited shores around the MPAs would need to be rehabilitated by re-stocking with initial adult populations (Dye and Dyantyi 2002).

The continual high levels of exploitation outside of reserves indicate that while reserves function to protect adult abundances, this increase is not translated through the export of recruits to surrounding shores due to the lack of settlement habitat and inability of settlers to move from algae to primary substratum. A combination of reserves and re-seeding of surrounding shores will be necessary to allow recovery of overexploited shores.

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