SPATIAL VARIABILITY OF MACRO-BENTHIC INVERTEBRATE ASSEMBLAGES IN THE KOGELBERG REGION, FOCUSING ON THE BETTY’S BAY MARINE PROTECTED AREA

by

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DECLARATION

I, Taryn Joy Joshua, declare that the contents of this dissertation represent my own unaided work, and that the dissertation has not previously been submitted for academic examination towards any qualification. Furthermore, it represents my own opinions and not necessarily those of the Cape Peninsula University of Technology.

______________________________  __________________________
Signed                      Date
“I dedicate my thesis to my close friends and family, especially my Mom, Vanessa, and my Dad, Trevor, who encouraged and supported me throughout my years of studying and allowed me to achieve my dream of becoming a conservationist…”
ABSTRACT

There is large variation in the patterns of biological diversity in the ocean. This variation is a result of the range in combinations of physical and biological interactions which exist in the marine environment. The South African marine environment supports a diversity of marine ecosystems in which species richness and endemism have been found to be high (33 % endemism). The high diversity of organisms promotes the maintenance of healthy and ecologically stable ecosystems. The diversity of life in the oceans however, is under threat as a result of numerous natural and anthropogenic threats such as over-fishing, over-extraction of marine resources, ocean acidification, to name a few.

Marine Protected Areas (MPAs) have been implemented throughout the world to address the threats facing the marine environment. Marine Protected Areas are considered the most effective tool at protecting marine ecosystems and play a key role in marine Ecosystem Based Management (EBM). Marine Protected Areas also offer the added benefit of providing areas in which research can be conducted, more specifically in the area of conservation, MPAs have been declared for either fisheries management purposes, biodiversity conservation, or for management of conflict between competing users. The Betty’s Bay MPA is located within the Kogelberg Biosphere Reserve (KBR) on the south-west coast of South Africa. The MPA was established in 1990 as the H.F Verwoerd Marine Reserve (re-proclaimed as the Betty’s Bay MPA in 2000) to protect, among others, the endangered African penguin (*Spheniscus demersus*), abalone (*Haliotis midae*) and the west coast rock lobster (*Jasus lalandii*). To date, few studies have been conducted within the area and as a result, knowledge of the sessile macro-benthic flora and invertebrate fauna of the Betty’s Bay MPA is sparse. The paucity of information of the macro-benthos creates a barrier for informed management decisions of the MPA, as well as a proposal to expand the MPA boundary.

To aid in an assessment of and provide information on the macro-benthic flora and invertebrate fauna assemblage patterns and diversity within the area, a spatial photo-quadratic survey was conducted in November 2012 and January 2013. A photo-quadrat of 0.33 m² was used to survey the MPA and outside its boundary at two depth categories (10 m – 15 m and 20 m – 25 m). Representative samples of specimens were randomly collected within the sampling stations to create a database of the species occurring within the area and in so doing, aid in species identification and verification during photo-quadrat analysis. A total of 881 viable (clear with focal frame correctly positioned) photographs from 10 sampling stations were analysed using a grid overlay of 10 x 10 (100) points per photograph. A 10 x 10 grid was used to allow for percentage cover and individual (for non-colonial species) or...
colony (for colonial species) abundance estimates of faunal organisms, to be calculated simultaneously. Organisms occurring under each point of the grid were identified and the individual or colony abundance of faunal species and percentage cover per species for each sample was recorded. Species accumulation curves and a rarefaction model, the Morgan-Mercer-Flodin (MMF) Model, were used to assess the sampling effort and provide the number of faunal species estimated to be within the study area, respectively. Uni- and multivariate statistical procedures were used to analyse percentage cover estimates from photo-quadrats and compare the floral, sessile and semi-motile macro-benthic community structure along a spatial and bathymetric gradient within the study area.

The univariate indices selected for analyses and interpretation of percentage cover data included species richness (S), percentage cover (%), Pielou's evenness index (J') and the Shannon-Wiener diversity index (H'). Data met the assumptions for parametric tests and multi-effects Analysis of Variances (ANOVAs) were conducted to assess whether depth or location had a greater effect on variances of species diversity, richness and percentage cover between samples. Cluster and ordination analyses were used for multivariate comparisons.

Results showed that species accumulation curves for the study area did not reach an asymptote and a higher estimated than observed faunal species richness was calculated for the area, suggesting that sampling effort was not sufficient. Despite this, species accumulation curves indicated that 140 to 168 photographs per station (curves began levelling off at this amount) were enough to obtain an adequate estimate of species richness within the study area. This suggests that too few photographs were collected for most stations. However despite this, 76% of the faunal species estimated to occur within the study area were recorded, indicating that the area was adequately sampled.

The mean species richness measured $S = 15.49 \pm 4.55$ SD, $n = 881$ samples and the mean species diversity was average ($H' = 2.21 \pm 0.48$ SD, $n = 881$ samples) within the study area. The mean percentage cover of benthic organisms in the area was $78.03 \% \ (\pm 11.80 \%, n = 881$ samples). In addition, the area appears to be fairly even with a mean evenness of 0.88 ($\pm 0.07$ SD, $n = 881$ samples), indicating that the percentage coverage of individuals was well distributed amongst the species within the area.

The multi-effects ANOVAs revealed that location had a greater effect on the variances of samples for species diversity and species richness than depth. Upon further investigation it was found that the species richness and diversity of samples inside the MPA were significantly higher ($p < 0.001$) than that outside the MPA. No significant differences in
percentage cover were found to occur between locations (p > 0.05), however the mean percentage cover of most taxa was higher outside the MPA. This difference between diversity inside and outside the MPA could be as a result of a number of factors. Habitat heterogeneity, found to be high in previous studies conducted in the Betty’s Bay area, may be an example of one of such factor. Findings suggest that the MPA is potentially fulfilling its management objective of biodiversity conservation for the species included in this particular study.

Depth was the primary factor affecting percentage cover within the study area, with deep samples having significantly lower (p < 0.01) percentage cover estimates than shallower samples. The multivariate analysis as well as an Analysis of Similarity (ANOSIM) using depth as a factor, also indicated differences in communities. Algae dominated (i.e. had the greatest percentage cover) areas in the shallow-reaches. The percentage cover of Porifera, Bryozoa and other sessile filter- and suspension-feeders increased with increasing depth, thus, revealing a community shift similar to other subtidal assemblages on hard substrata. It was concluded that macro-benthic assemblages within the Betty’s Bay area are mainly influenced by depth.

Colonial taxa such as Cnidaria and Algae were dominant in the study area. Dominant species in the area included the cnidarian species *Eudendrium* spp 1 and algal species *Leptophyllum foveatum*, *Jania adhaerens*, *Rhodophyllis reptans* and *Rhodymenia obtusa*. The dominance of Algae in relation to other taxonomic groups in the area is important to monitor as it may influence the settlement of benthic invertebrate macro-fauna and increase the abundance and distribution of epifauna and infauna, for example, *Eudendrium* spp 1. It is also important to prioritize the effective monitoring and management of the increased abundance of the carnivorous west coast rock lobster, *Jasus lalandii* which reduces herbivore abundance and causes a subsequent increase in Algae.

Further investigations of benthic invertebrates within the study area, which take environmental variables and habitat heterogeneity into account, need to be conducted in order to establish whether the differences in diversity observed during this study can be linked to protection. Should the significant differences be a result of protection within the MPA, managers should consider expanding the MPA or, failing that, converting the MPA to a Category 1 or "no-take" MPA as population fluctuations in exploited organisms, may affect populations of other unexploited species. The expansion of the MPA or conversion to a Category 1 MPA may ensure that the marine benthic biodiversity within the area is well-conserved. Moreover, a monitoring programme examining both biotic and abiotic factors should be implemented within the area. Within the monitoring programme, managers should
attempt to have organisms identified to genus level at the very least. A monitoring programme of this nature would aid managers to be more informed and proactive and implement an ecosystems-based approach to management.
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CHAPTER 1: INTRODUCTION

1.1 Marine biodiversity and macro-benthic species distribution

Marine biodiversity can be defined as the diversity of life in the ocean (Heip et al. 1998, Sala and Knowlton 2006) where a range of different physical features such as water motion/oceanography, substrate, light, temperature and nutrient availability exists (Valentine 2009). Marine biodiversity may also include diversity in ecosystem structure. The diversity in marine ecosystem structure is reflected in the distribution and patterns of abundance within land/seascapes, habitats, populations and communities (Thrush and Dayton 2002, Belanger et al. 2012). Marine biodiversity also includes functional ecosystem components such as the mechanisms responsible for driving biological interactions between species, their environment and processes (Thrush and Dayton 2002). The biological interactions which exist in the ocean include competition, predation and mutualism as well as trophic structure, patchiness and endemism (Thorne-Miller 1999). The combinations of the various physical and biological processes and interactions determine the biodiversity patterns and diversity of organisms within the ocean resulting in a high variation of life (Thorne-Miller 1999, Pinnegar et al. 2000, Belanger et al. 2012).

Differences in diversity within the ocean may occur on a small scale between individuals within a species or populations or on a much larger scale between entire communities or ecosystems (Heip et al. 1998, Sala and Knowlton 2006, Valentine 2009). The large variation in the physical and biological processes which exist in certain parts of the ocean may have resulted in a higher phyletic diversity within the ocean compared to terrestrial and fresh water environments (Widdicombe and Somerfield 2012). There are over 35 known phyla which occur in the ocean, 14 of which are solely marine (Briggs 1994). Of the 14 marine phyla, most are benthic (May 1988, Widdicombe and Somerfield 2012). Benthic organisms are defined as organisms living on or within the benthic sediments of an aquatic environment (Benham et al. 2003).

Within benthic ecosystems, biodiversity estimates are lower in the shallower coastal regions than in the deeper, open ocean (Gray et al. 1997, Thorne-Miller 1999). Gray (2001), in a review on depth-related diversity gradients of coastal and deep-sea benthic species, questioned this bathymetric related diversity hypothesis. Although the deep sea has high species richness estimates, it is unclear whether or not these richness estimates are in fact higher than all coastal areas (Gray 2001). However, regardless of whether or not communities differ in diversity with increasing depth, depth-related differences in community structure are almost always evident (Garrabou et al. 2002).
In general, environmental changes with changes in depth play an important role in the structure of marine communities and their diversity (Kingsford and Battershill 1998, Gray 2000, 2001, Lombard et al. 2004, Cleary et al. 2005, Celliers et al. 2007, Blamey and Branch 2012). Garrabou et al. (2002) found that with increasing depth, communities become more complex, and that the dynamics and seasonal variation within communities decrease. A number of environmental factors such as light penetration, water movement, temperature, nutrient availability and sedimentation are also influenced by depth (Thorne-Miller 1999, Garrabou et al. 2002, Clearly et al. 2005, Celliers et al. 2007). The range of depth in which benthic taxa, whether sessile or motile, are recorded is related to their tolerance of these environmental gradients (Clearly et al. 2005). For example, a study on North West Pacific gastropods and North East Atlantic Algae reported that fluctuations in temperature, salinity and nutrients decreased with depth (Harley et al. 2003). This study, found that temperature was the most important variable determining the distribution of these taxonomic groups (Harley et al. 2003). Temperature has demonstrable effects on the physiology and physical fitness of marine organisms and affects both bathymetrical and latitudinal ranges of marine benthic species (Harley et al. 2003, Belanger et al. 2012). Harley et al. (2003) also found that deeper-dwelling species were more vulnerable to environmental changes in temperature, nutrient availability and salinity (over shorter periods of time) than species in shallower water where greater environmental change exists (Harley et al. 2003).

The distributions of organisms in benthic ecosystems are also affected by the availability of light and water movement. Within the shallow photic zone (0 m to approximately 10 m depth), there is a constant supply of light and turbulence which decreases as the deeper photic zone (15 m - 30 m depth) is approached (Garrabou et al. 2002, Celliers et al. 2007). As a result, shallower-reaches (0 m to approximately 10 m depth) are often dominated by Algae (due to the light penetration) while the abundance of sessile filter-feeders such as poriferans and ascidians increase with depth (Kingsford and Battershill 1998, Lombard et al. 2004, Celliers et al. 2007). This pattern of decreasing Algae and increasing sessile filter-feeder abundance with increasing depth was observed by Celliers et al. (2007) off the east coast of South Africa. In the south-west coast of southern Africa, Blamey and Branch (2012) found both an increasing floral and faunal diversity with increasing depth (up to 20 m depth).

In South Africa, depth variation (i.e. changes in biotic and abiotic processes with changes in depth), benthic community structure and large-scale variation in habitats have all been considered in the defining of marine bioregions and ecosystems (Lombard et al. 2004). Lombard et al. (2004) utilised South African bioregions, which are defined according to the variability of biological process (such as spawning sites, migration routes etc.) as well as biogeography, in a spatial marine biodiversity assessment. During the assessment,
emphasis was placed on the importance of the variation in community structure associated with depth (Lombard et al. 2004). It is also important to take the abiotic processes into account which may influence the marine benthos, such as current systems and upwelling regions as well as biogeography, geology, substrate, connectivity the coast (Lombard et al. 2004, Sink et al. 2011a). Taking this information into account and utilising greater technologies and research available, Sink et al. (2011) extensively built on the habitat classification and mapping of Lombard et al. (2004) indicating the heterogeneity within the oceans surrounding the South African coast as well as the importance of a greater knowledge base.

1.2 Marine Biodiversity in Southern Africa

As a result of its long coastline (3 650 km long (Lombard et al. 2004)) encompassing a range of different oceanographic regimes, South Africa has a high diversity of marine and coastal systems (Lutjeharms et al. 2001, Wynberg 2002) resulting in a high diversity of marine organisms (Gibbons et al. 1999, Griffiths et al. 2010). The current system around the South African coast consists of warm temperate water being transported by the Agulhas Current southwards along the east coast of South Africa (Lutjeharms 2006) and the cooler Benguela Current which flows northwards along the west coast (Shannon 1985). The Benguela Current is an upwelling region with inshore wind-driven upwelling cycles regulated by local weather systems and lasting 5 - 10 days at a time (Shannon 1985, Shannon and Nelson 1996). Upwelling can be defined as the blowing of equator-ward and offshore-directed winds across the sea surface, which causes surface waters to be replaced by cooler, nutrient rich waters from below (Garvine 1971, Schumann et al. 1982).

Due to the intense upwelling, the west coast of South Africa is an area of high productivity (Shannon 1985, Jarre et al. 2015). In comparison to the west coast, the east coast of South Africa is an area of lower productivity (Wynberg 2002). Unlike productivity, marine species richness (for most taxa) around the coast of South Africa follows an increasing gradient from the colder water of the Atlantic Ocean in the west to the warmer, more tropical water of the Indian Ocean in the east (Gibbons and Hutchings 1996, Awad et al. 2002, Acuña and Griffiths 2004, Samaai 2006, Griffiths et al. 2010). For example, Gibbons et al. (2010) found an increasing trend in species richness of Hydrozoa from the west to the east coast of Southern Africa. Peaks in species richness and endemcity of some taxa occur in the transitional area in the temperate south and south-west where there is a mixing of the warm and cool ocean waters (Gibbons and Hutchings 1996, Griffiths et al. 2010). Many species such as anemones (Acuña and Griffiths 2004), sponges (Samaai 2006), octocorals, chitons, polychaetes and ascidians (Awad et al. 2002) as well as seaweed (Bolton and Stegenga...
2002) were found to be more diverse on the south and south-west coasts of southern Africa. Griffiths et al. (2010) further reported that many range-restricted species, which are species with range distributions of 300 km or less, were found at overlaps of biogeographical boundaries.

The geographical location of South Africa’s coasts in relation to the oceanographic systems surrounding the country, provide an explanation for the country's reported high marine species richness and endemism levels (Gibbons et al. 1999, Griffiths et al. 2010, Scott et al. 2012). Marine species richness in South Africa was reported to be approximately 13 000 species, with an estimate of 4 233 species being endemic (Griffiths et al. 2010). A possible reason for the high levels of endemism of South African marine species may be attributed to a lack of research in surrounding countries where many species are yet to be discovered (Griffiths et al. 2010). Despite this, the high endemism levels and high marine species richness as well as the distribution of marine species around the coast of South Africa is important to consider when managing the marine resources (Emanuel et al. 1992).

1.3 The role of, and threats to, marine biodiversity

High marine species diversity results in greater stability within ecosystems (Thorne-Miller 1999). Biodiversity affects the functioning of ecosystems as rates of nutrient cycling and energy flow are affected by species composition (Tilman et al. 1997, Naeem 2008). The greater the diversity of marine organisms performing their individual functional roles, the greater the ability for ecological processes to be regulated (Valentine 2009). For example, higher macroalgal species diversity results in an increased opportunity for photosynthesis and reduction of carbon dioxide (Thorne-Miller 1999).

The biodiversity of marine species has implications for the provision of marine ecosystem services such as food security, recreation, recycling of pollutants, protection from coastal erosion, climate regulation (Sala and Knowlton 2006), medicinal products and building materials such as sand (Thorne-Miller 1999). Many fisheries are reliant on the vast diversity of marine biota provided by the ocean (Griffiths et al. 2010). According to Worm and Lotze (2009), changes in marine biodiversity may also be used as indicators of global climate change and variation, especially warming. Biodiversity, and the roles with which it is associated, is thus important for the sustainability of human existence. Despite this, human activity is the primary reason for the loss of biodiversity through, for example, the unsustainable use of marine resources (Kim and Bryne 2006).

As a result of the large number of threats to the marine environment, much of the existing biodiversity within the ocean is being lost without it ever being discovered (Kochzius and Nuryanto 2008, Costello et al. 2010). The current knowledge of what is in the oceans, its biomass and biodiversity, is both limited as well as insufficient to sustainably maintain ocean resources (Norse 1995, Kim and Bryne 2006, Naeem 2006, Sala and Knowlton 2006). It can therefore be said that the paucity of knowledge of life within the oceans, whether globally (Alexander et al. 2011) or locally (Gibbons et al. 1999, Griffiths et al. 2010, von der Heyden 2011) is perhaps one of the greatest threats to marine biodiversity.

Globally, there is extensive patchiness in sampling with large gaps in sampling effort and taxonomy (Costello et al. 2010). Knowledge gaps have a negative effect on the reliable representation of organisms in an area and thus promote erroneous conclusions on the conservation value of a site (Mazaris et al. 2008). Gibbons et al. (1999) stated that although marine species richness in South Africa is suggested to be quite high, much of the studies also seem to be patchy and many taxa remain undescribed. Costello et al. (2010) estimated the percentage of undescribed marine species in South Africa to be 38 %. South Africa is reported to possess 10 % of the global total of marine fauna but, only 4 % of this has been recorded or described (Gibbons et al. 1999, Samaai 2006, Griffiths et al. 2010). With approximately 31 % of known South African marine species being endemic (Gibbons et al. 1999, Awad et al. 2002, Griffiths et al. 2010), many more endemic species may be undiscovered. With regards to known marine biodiversity, Europe has the greatest wealth of knowledge of marine biodiversity within their country (Griffiths et al. 2010). In order to match these standards, South Africa would need to increase the number of described marine species by an estimated 7590 species (Griffiths et al. 2010). However, in comparison to other developing countries, South Africa has a relatively extensive knowledge for some marine fauna (Griffiths et al. 2010).
Knowledge gaps regarding marine biodiversity are important to address as the ecological processes which regulate populations cannot be fully understood unless the abundance of organisms, together with their patterns of distribution, is well documented (Underwood et al. 2000). Much of the ocean remains unsampled as a result of sampling constraints such as the amount of time spent at sea and the cost of hiring vessels and crew (Widdicombe and Somerfield 2012). In South Africa, although the coastal zone is fairly well sampled (Awad et al. 2002), much of the sampling is pre-1980 and 99% of these samples do not exceed depths of 1000 m and 83% are from less than 100 m (Griffiths et al. 2010).

1.4 Marine Protected Areas

The gaps in the knowledge of the biodiversity of marine organisms are especially concerning because species’ abundances are affected by increased human-induced changes on marine species’ biodiversity (Naeem 2006). Where environmental disturbances were the main drivers of change in marine biodiversity, human-induced changes (such as changes due to over-fishing, pollution etc.) have become more prominent (Sala and Knowlton 2006, Griffiths et al. 2010). One such change is in organism biomass which can have diverse effects on ecosystem functioning, as interactions between organisms can influence patterns of distribution, abundance, survivorship and growth of organisms in marine ecosystems (Kingsford and Battershill 1998, Naeem 2006). The ocean environment was once considered too large for human activities to significantly affect the structure and function of marine ecosystems (NRC 2001). A greater appreciation for the conservation of the marine environment has since, increased the global desire to reduce human-induced changes (Kelleher 1996, Roberts et al. 2006). This increased appreciation is brought upon by greater access of the public and scientists to the marine realm through, for example, research, outreach and access to information. Fisheries managers, most of whom in the past focused primarily on increasing the yield of a single species with disregard for the consequences thereof, also seem to be following a similar trend in the appreciation of the ocean environment with regards to the management of most fisheries (Bohnsak and Ault 1996, Pikitch et al. 2004).

The management of marine resources was, in the past, species specific and ignored the spatial heterogeneity of marine systems and as a result, the policies that were put in place to protect habitats and species often failed to do so (NRC 2001). There is thus a global recognition that traditional single-species management practices are inadequate to ensure sustainable exploitation and conservation of biodiversity, and scientists are moving towards more holistic approaches such as ecosystem-based management (EBM) (Pikitch et al. 2004, Babcock et al. 2005, Crowder and Norse 2008, Fletcher et al. 2010). Ecosystem-based
management ensures that conservation priorities are placed on ecosystems rather than on
the target species, thereby sustaining healthy marine ecosystems (Pikitch et al 2004). Protected areas, such as Marine Protected Areas (MPAs), have been established as an implementation tool for EBM approaches (NRC 2001, Halpern et al. 2010, Grantham et al. 2011). In particular, MPAs have been recognised as the foundation on which other tools for marine species management can be built by providing protection and increasing the restoration capacity of marine ecosystems (Gell and Roberts 2003).

By applying protection to entire marine ecosystems, MPAs maintain ecosystem functioning in an undisturbed state (Attwood et al. 1997a) as well as relieve the environment of high levels of stress (NRC 2001). According to Agardy et al. (2011), MPAs are arguably the most effective tool in existence for the combat of over-exploitation and habitat degradation. Marine Protected Areas also allow populations of exploited fish and/or invertebrate populations to recover with the assurance of adequate compliance as well as the implementation of the EBM approach (Attwood et al. 1997b, Pikitch et al. 2004). The solvent nature of the ocean ensures the dispersal of dissolved materials and biota from one ecosystem to another, allowing organisms to live out different stages of their life-cycles in different ecosystems, while under the protection of MPAs (Attwood et al. 1997b, Kingsford and Battershill 1998, NRC 2001, Thorne-Miller 1999). Therefore, the possible spill over effects of productivity of both fauna and flora, adult and juvenile, across protected area boundaries is an important benefit of species protection within MPAs (Agardy 1994, Bohnsack and Ault 1996, Boersma and Parrish 1999, Pikitch et al. 2004, Agardy et al. 2011).

Although MPAs are able to adequately provide for fishery and ecosystem objectives to be fulfilled within South Africa, the criteria for the selection and management strategies of MPAs often differed substantially (Turpie 2000). The establishment of an MPA to protect representative biodiversity and habitats of certain species may fail to adequately protect other species as well as the habitats in which they live if interactions between protected species, habitats and communities are not fully understood (Mills et al. 1993). Ecosystem integrity within MPAs, if managed in isolation, is vulnerable to the exploitation occurring outside these areas (Cicin-Sain and Belfiore 2005, Turpie et al. 2009). The reliance on MPAs to counteract the loss of biodiversity is only part of the solution to limiting the threats to marine biodiversity (Jennings 2009, Agardy et al. 2011) and has its shortcomings. These shortcomings are often include an ecologically insufficient design, for example the area is too small and poorly designed to fulfil management objectives (Agardy et al. 2011). Agardy et al. (2011) states that many MPAs are also inappropriately managed, the area may fail due to degradation in the surrounding areas and some MPAs only appear to be offering protection, when in fact, no protection is being offered. Another common disadvantage of MPAs,
especially those containing large no-take areas, is displacement of fishing activities, which places more pressure on surrounding environments (NRC 2001, Jennings 2009, Agardy et al. 2011). While many off-shore areas remain unprotected, many MPAs have failed (Agardy et al. 2011, Grantham et al. 2011). The failure of these MPA’s is mainly due to poor planning, a lack of local support and non-compliance (Agardy et al. 2011, Grantham et al. 2011). For more sustainable and effective EBM, especially within coastal areas, greater integrated management areas and plans are necessary (Bohsack and Ault 1996, Gray et al. 1997, Babcock et al. 2005). These are often achieved through informed marine spatial planning and zoning for multi-use to reduce user conflicts (Babcock et al. 2005, Douvere 2008). Monitoring and evaluation of MPAs are also imperative to ensure that objectives are being met and allow managers to learn from mistakes (NRC 2001). Informed ecosystem management is important as ecosystems are constantly changing (Boero and Bonsdorff 2007). Changes in ecosystem processes may have adverse effects on the economy and the aesthetic environment (Bolam et al. 2002). Within marine ecosystems, rare species may become abundant and abundant species may become rare and species are constantly moving between ecosystems, whether permanently or temporarily (Boero and Bonsdorff 2007). Hence, MPAs could be an important research tool in the assessment and monitoring of ecosystems by allowing for studies of ecosystems inside MPAs and comparing results of these studies to that outside the MPA (Andersen 1995).

In South Africa, MPAs have been established to assist in the management of marine resources (Lombard et al. 2004, Grantham et al. 2011). The Marine Living Resources Act (MLRA) (Act 18 of 1998) is just one of the legislations which have been put in place to assist in the marine resource management in South Africa. The Act states that MPAs are proclaimed to ensure the protection of marine biodiversity, habitats and ecosystems, as well as to facilitate better fisheries management and to reduce user-conflicts. The socio-economic well-being of many South Africans is dependent, whether directly or indirectly, on marine biodiversity (Tunley 2009). Therefore MPAs are needed to assist in limiting the over-exploitation of South Africa’s marine living resources which is considered one of the primary threats to marine biodiversity in the country (Lombard et al. 2004, Grantham et al. 2011). Attwood et al. (2000) further stated that the main function of MPAs is to preserve the natural state of marine communities.

South Africa’s coastline is reported to be well protected, relative to the rest of the world, however there are still shortfalls within the management of MPAs (Hockey and Branch 1997, Tunley 2009, von der Heyden 2009). The current MPA network in South Africa consists of 23 protected areas, situated across a range of bioregions and encompassing 0.42 % of the mainland of South Africa’s marine territory (Figure 1.1) (Sink et al. 2011a). Of these 23,
seven (0.17 %) are “no-take” MPAs with no form of extractive use being permitted within them, nine offer some form of extractive use and the remaining seven contain both “no-take” areas and areas where extraction is permitted (Sink et al. 2011a). Many of South Africa’s MPAs were not selected based on predetermined objectives similar to those all over the world (Agardy et al. 2003). Many are small and inadequately policed (Griffiths 2005), the overall distribution of MPAs was not well planned (Hockey and Branch 1997) and the connectivity of the distinctive habitats within each bioregion was not ensured (von der Heyden 2009), thereby not enabling the effective protection of the biota surrounding South Africa’s coasts.

Various MPAs within South Africa were established for the protection of economically and ecologically important species (Attwood et al. 1997a) and many areas where MPAs have been placed were often not adequately surveyed, with regards to habitats and resources, (Götz et al. 2013). For example, often, the protection of an endangered species (such as Haliotis midae Linnaeus, 1758) was a strong motivation for the proclamation of an MPA, with the main requirement for its placement being that the MPA offered adequate protection to this species (Attwood et al. 1997a, Griffiths 2005). Protection itself may however contribute to a community shift in marine benthic communities (Parravincini et al. 2013) as populations of protected predators may indirectly affect populations of grazers and abundance of Algae within protected areas (Babcock et al. 2010).

The situation with regards to lack of protection of marine resources and ecosystems is considerably worse away from the coastline, where no offshore MPAs are in place to specifically protect the deep water benthic habitats (Sink et al. 2011b). Only a few of the coastal MPAs extend far enough offshore to protect the sub-photic habitats below 70 meters (Solano-Fernandez et al. 2012). Consequently, South Africa’s existing MPA network does not offer adequate protection to all shelf habitat types, with an estimated 40% of the habitats receiving no protection at all (Sink et al. 2011a).

To address this, a no-take MPA expansion strategy has been developed which aims to protect 15% of the offshore shelf environment and 25% of the coastal or inshore environment (Government of South Africa 2010). However, there is a poor understanding of the importance of MPAs for fisheries and biodiversity conservation in South Africa, and for the expansion objectives to be met and accepted, South Africa needs to improve the science base for MPAs through coordinated and standardised monitoring and research (Sink et al. 2011b, Solano-Fernandez et al. 2012).

1.5 The Kogelberg Region
In the south-western Cape, the marine component of the Kogelberg Biosphere Reserve (KBR) promotes the protection of marine biodiversity in this area. The KBR was the first proclaimed Biosphere Reserve in South Africa designated by the United Nations Educational and Scientific Organisation (UNESCO) under the Man and Biosphere programme (Tunley 2009, Clark and Heydorn 2014). The marine component of the area expands over 24 500 ha, encompassing 79 km of coast and extends to three nautical miles (5.6 km) offshore (Turpie et al. 2009). The marine section of the KBR is situated within the Agulhas Bioregion which extends from Cape Point to the Mbashe River in the south of Africa (Lombard et al. 2004) (Figure 1.2). The area supports commercial fisheries such as line fish, west coast rock lobster (*Jasus lalandii* (H. Milne Edwards, 1837)) and kelp (*Ecklonia maxima* (Osbeck) Papenfuss, 1940) as well as subsistence fisheries from two neighbouring towns, namely Hawston and Kleinmond (Turpie et al. 2009). The economic and ecological value of this area is important to the local and regional economy as well as the livelihood of the community (Turpie et al. 2009). Knowledge of ecosystem functioning and community structure in the area is essential, to provide managers with more information as well as promote the sustainable use and conservation of marine ecosystems within the KBR (Vanderklift et al. 1998, Babcock et al. 1999).

The Betty’s Bay Marine Protected Area (hereafter referred to as “the MPA”) is located within the KBR (Turpie et al. 2009). The MPA is productive and supports a high diversity of invertebrates, fish and algae as well as two populations of red data species (those species listed on the International Union for Conservation of Nature and Natural Resources’ (IUCN) list of threatened species) namely the African penguin (*Spheniscus demersus* (Linnaeus 1758)) and the bank cormorant (*Phalacrocorax neglectus* (Wahlberg, 1855)) (Tunley 2009). The MPA was established (as the H.F. Verwoerd Marine Reserve) in 1981 to protect these species as well as abalone (*H. midae*), the over exploited west coast rock lobster (*J. lalandii*) and line fish species such as geelbek (*Atractoscion aequidens* (Cuvier, 1830)) (Tunley 2009).

The rich biodiversity within the MPA may be at risk as a result of a distribution shift of *J. lalandii* from the west coast, as an increase in the abundance of this species has been reported in the area (Tarr et al. 1996, Day and Branch 2000, Mayfield and Branch 2000, Cockcroft and Hutchings 2008, Blamey et al. 2010, Blamey and Branch 2012). Lobster catch rates on the west coast of southern Africa decreased from 60 % to < 10 % during the late 1980’s and early 1990’s (Cockcroft and Hutchings 2008). At the same time, total lobster catches in the southern region increased from 18 % to 60 %, this has severe implications to ecological functioning, diversity patterns and communities, representative benthic biodiversity, fisheries and other marine resources (Cockcroft and Hutchings 2008).
A number of studies have shown that an increase in the population of *J. lalandii* may result in a decrease in benthic community diversity (Day and Branch 2000, Mayfield and Branch 2000, Blamey et al. 2010, Blamey and Branch 2012). The most recent study by Blamey et al. (2010) attributed an increase in sessile benthic invertebrates and the decline of 99.3 % of herbivores, to the increase in *J. lalandii* in the MPA (Blamey et al. 2010). Therefore, although the MPA offers partial protection to *J. lalandii*, the effects on the ecosystem due to its increase in abundance, appears to be detrimental (Babcock et al. 1999). More research on the benthic communities and their interactions within the Betty’s Bay area is, therefore, essential.

Investigations are being made into the expansion of protected areas within the KBR and surrounding areas within the Agulhas bioregion, to ensure that marine conservation targets for the region are met (Clark and Lombard 2007, Sink et al. 2011a). Lombard et al. (2004) stated that, in the south-western Cape, Category 2 MPAs (MPAs in which extraction, of some form, is allowed e.g. shore-angling) be re-proclaimed as Category 1 MPAs (No-take MPAs in which no form of extraction of marine living resources is allowed) in order to ensure that conservation targets of protection status for shallow (spring low to approximately 10 m depth) and deep (up to 30 m depth) photic zones be met. The Betty’s Bay MPA, as a Category 2 MPA, falls within this category requiring greater reef protection (Sink et al. 2011a). The shallow photic zone of the MPA is vulnerable to extraction of marine living resources from abalone poaching, over-exploitation by shore anglers and the removal of intertidal organisms (Lombard et al. 2004). The accumulation of fishing gear and tackle left behind by shore-anglers also poses a threat to the marine environment in this area (Lombard et al. 2004).

To date, very little information is available on the sessile macro-benthic flora and invertebrate fauna of the Betty’s Bay MPA. Because of the shifts in benthic biodiversity, due to an increase in the abundance of *J. lalandii*, as well as the possibility of an expansion and conversion of the MPA to category 1 status, the need for more research of the MPA has been identified. This study will contribute to a better understanding of the marine benthic community structure and marine species in the area, and the results can assist in the implementation of an expansion and monitoring programme for the Betty’s Bay MPA.

### 1.6 Objectives of the study

#### 1.6.1 Main Aim
The aim of the study was to examine the sessile and semi-motile macro-benthic community and to describe the species diversity and spatial patterns of the macro-benthic assemblages in the Betty’s Bay area, within the KBR.

1.6.2 Objectives

- To describe the macro-benthic assemblages within the Betty’s Bay area of the KBR.
- To describe the spatial distribution patterns of macro-benthic organisms, in relation to depth and location (inside and outside the Betty’s Bay MPA).

1.7 Thesis outline

Chapter 1 is the introductory chapter and provides a literature review on marine biodiversity (including the roles of and threats to marine biodiversity) and benthic species distribution both globally and within South Africa. The literature review also provides information on marine protected areas and background information on the Betty’s Bay MPA. Chapter 1 also outlines the specific objectives of this study.

Chapter 2 provides a description of the study area, materials and methods and statistical analyses used.

Chapter 3 describes the results which include sampling effort, patterns of species diversity and community structure as well as a description of the community and floral and faunal composition.

Chapter 4 provides the discussion and interpretation of the results obtained. This includes a discussion on species accumulation curves, species composition, diversity indices and community structure, as well as depth and location comparisons.

Chapter 5 concludes the thesis and makes general recommendations.
Figure 1.1: Map of South Africa showing the position of MPAs (Sink et al. 2011a)
Figure 1.2: Map of South Africa, indicating the inshore and offshore marine bioregions (Data source: Sink et al. 2011a)
Chapter 2: MATERIALS AND METHODS

2.1 Study Area

Sampling was conducted on the south-west coast of South Africa, adjacent to the town of Betty's Bay and within the KBR which contains the Betty's Bay MPA (Figure 2.1).


The biogeographic location of the Betty’s Bay MPA situated on the western end of the Agulhas bioregion (Lombard et al. 2004), is oceanographically diverse due to the dynamics of the current systems surrounding it (Lutjeharms et al. 2001, Lutjeharms 2006). These current systems are complex due to the mixing of warm temperate water diverging from eddies of the Agulhas Current, from the east coast and the interaction with cooler water of the Benguela Current from the west (Shannon 1985, Shannon and Nelson 1996, Lutjeharms et al. 2001, Lutjeharms 2006). In addition to these complex current systems, wind-induced upwelling events (predominantly in spring and summer) and the mixing of warm and cool water, adds to the diversity and creates a productive environment within the study area (Gibbons and Hutchings 1996).

The reefs within the KBR and the Agulhas bioregion are classified as warm temperate reefs and are considered to have a more heterogeneous community structure than the inshore zones of the South-western Cape and Natal bioregions (Sink et al. 2011a). The subtidal geology of the area is defined as Agulhas Inshore Reef (Sink et al. 2011a).

2.2 Field Sampling

Self-Containing Underwater Breathing Apparatus (SCUBA) diving limits the amount of time that can be spent sampling benthic substrates due to air constraints at certain depths. In an effort to assess the community and diversity patterns of the benthic invertebrate fauna and flora in the study area, a rapid area assessment technique, photographic sampling, was used (Preskitt et al. 2004). Rapid area assessments such as, photographic sampling, decrease
time spent in the field and are relatively non-destructive, allow a record of photographs to be kept and a large volume of data can be recorded, including species abundance, density and percentage cover (Foster et al. 1991, Kingsford and Battershill 1998, Preskitt et al. 2004). It is for these reasons that the photographic sampling technique, as adopted by Olbers et al. (2008) in Aliwal Shoal, was used for this survey. The investigation presented here is a baseline study of the macro-benthic flora and sessile and semi-motile fauna in the Betty’s Bay area and the photographs could be stored in a database for further research of the area.

A two day sampling trip was conducted on the 6 - 7 November 2012. During photograph sorting after the November sampling trip, it was discovered that many of the photographs were unclear and were unusable for analysis. It was therefore decided that another sampling trip was required. Sampling was completed on the 24 - 25 January 2013, which is still within the upwelling season (i.e. during spring and summer) in the region (Gibbons and Hutchings 1996). A team consisting of two divers using SCUBA photographed the benthos at each station with a Canon G12/10 camera in an underwater housing (Figure 2.2). The focal frame was standardized to a photo-quadrat size of 0.33 m². During each dive, a diver using a swim reel, swam a 50m transect line along a randomly generated bearing and collected sample specimens of representative species along the way. A second diver swam along the same transect line, following the first diver, and collected photo-quadratic samples by placing the photo-quadrat at random intervals along the swim line. Photo sampling was limited to 30 minutes per dive and photographs were stored digitally on the camera’s Storage Device (SD card). The representative samples of species collected were frozen and labelled for identification in the laboratory.

2.3 Sampling Stations

An attempt was made to identify rocky reefs, on which sampling stations were randomly selected, based on low resolution bathymetric and reef data from the Marine Component of the National Biodiversity Assessment of South Africa (Sink et al. 2011a). However, the data used and the location of reefs differed in situ and the echo sounder of the research vessel (a semi-inflatable boat) was used to randomly locate reefs, within the correct depth range and close to the GPS co-ordinates of the pre-selected stations. Ten sampling stations were pre-selected, six inside the MPA and four outside the MPA (two on either side situated on rocky reefs closest to the border of the MPA, approximately 1.5 km to 2 km from the MPA boundary). These stations were pre-selected for depth, a shallow depth range (10 m - 15 m) and a deep depth range (20 m – 25 m). The shallow depth range was positioned to occur on rocky reefs within the area and the deep depth zone was selected to be on rocky reefs as deep as possible within diving depth restrictions (30 m) (Figure 2.3).
During the four day sampling period 12 dives were undertaken of which 10 were successful (completed sampling periods) and were selected as sampling stations. The 10 sampling stations were given unique sampling station numbers according to the month, “JAN” for January and “NOV” for November, the dive station number, 01-06, the depth, “D” for deep and “S” for shallow and the location “IW” where “I” is inside the MPA and “W” is to the west, “OE” where “O” is outside the MPA and “E” is to the east and “M” is middle (Table 2.1 and Figure 2.3). One of the stations pre-selected to occur outside of the MPA was positioned on a sand bar instead of a rocky reef and after a thorough survey of the area, a rocky reef could only be found just inside the border of the MPA. This station was therefore reclassified as an inside station, however the station name, “JAN05_SOE”, remained the same to avoid confusion with other stations. During analyses, sampling station names were shortened by omitting sampling date and station number. Global Positioning System (GPS) co-ordinates were recorded at the drop down points of divers for record and mapping purposes.

### 2.4 Sample Analysis

The samples collected in the field were identified, to species level where possible, by means of appropriate field guides (e.g. King 2000, Branch et al. 2010), taxonomic literature (e.g. Samaai and Gibbons 2005, Florence et al. 2007) and others verified by South African experts (Porifera - Dr Samaai, Department of Environmental Affairs (DEA); Ascidia – Dr Parker-Nance, Nelson Mandela Metropolitan University (NMMU) and Bryozoa – Dr Florence, Iziko South African Museum). The samples were labelled with unique numbers and dive information, photographed (Figure 2.4) and preserved in 96 % ethanol. A species list was constructed from the identified samples and used as a reference collection during the identification of species in the photo-quadrats.

All photo-quadrats collected in the field which were clear, (with the focal frame i.e. quadrat boarders, correctly positioned within the frame of the photograph) were analysed and each photograph was treated as a sample within a sampling station. The number of samples (n) per station differed due to many of the collected photographs not being clear enough for the reliable identification of species (Table 2.1). A total of 881 photo-quadrats were analysed. Each organism was identified and the individuals’ total abundance, for non-colonial species, or colony abundance, for colonial species (with the exception of algae), were recorded for each photo-quadrat by means of photographic point-sampling (Foster et al. 1991). Percentage cover was recorded for all species, by means of the same photo-quadratic points (Foster et al. 1991). This methodology is commonly used in estimating species diversity and community structure of the marine benthos (Kohler and Gill 2005). Coral Point Count with
Excel extensions (CPCe version 3.6 Copyright © National Coral Reef Institute 2001 - 2009), was used to create overlay points in a uniform grid of 10 rows by 10 columns (100 points) (Figure 2.5). All organisms visible to the naked eye or the substrates occurring under points were identified and recorded i.e. point-count representation (Table 2.2). The use of 100 points allows for percentage cover per species and abundance estimates (per non-colonial species or colony) to be calculated simultaneously (Foster et al. 1991), thus limiting observer bias and allowing for faster processing. Percentage cover was obtained by recording and summing the number of recordings of each represented species within the sample i.e. the number of individual points out of 100 for each species occurring in the sample. As no measure of scale was used in the field, a scale bar was added to the photo-quadrats during photo-analysis (Figure 2.5). The full scale measured 0.33 m and the intervals measure 0.03 m.

In cases where individuals could not be identified to species level, they were identified to genus and these individuals were given a unique species number (per genus), for example *Clathria* spp 1. Higher taxon surrogates are commonly used in studies where sufficient effort, resources and expertise are not available (Grelle et al. 2002, Cardoso et al. 2004, Mazaris et al. 2008). Genus richness has been found to be the most significantly reliable surrogate for species richness in biodiversity studies when species data are not available (Grelle et al. 2002, Cardoso et al. 2004, Mazaris et al. 2008). In cases where organisms could not be identified to genus level, mainly due to lack of clarity of the photos and the inability to identify key features, they were identified to the organisms’ highest taxonomic surrogate used within this study i.e. taxonomic group. Each of these organisms was assigned a unique number, per taxonomic group, for example Mollusca spp 1. This approach is considered acceptable to use when not all species identifications are available and to make conclusions regarding the spatial distribution of biodiversity (Cardoso et al. 2004).

Although all species were recorded, only sessile and semi-motile benthic species and flora were used for statistical analysis as this study focussed on benthic invertebrates. In this study, semi-motile species refers to all species that are slow moving or cannot voluntarily detach themselves from the benthos and actively swim.

2.5 Statistical Analysis

2.5.1 Statistical packages and programmes

Data was recorded and descriptive statistics and graphs produced using Microsoft Excel (Copyright © Microsoft 2010). Plymouth Routines in Multivariate Ecological Research
(PRIMER V6 Copyright © PRIMER-E Ltd. 2012) was used for univariate and multivariate analysis of the data. Data was tested for equal variances using SigmaXL V7.04 (Copyright © SigmaXL Inc. 2001 - 2014). STATISTICA V7 (Copyright © StatSoft Inc. 1984 - 2013) was used to test the distribution of data as well as for univariate analyses (such as ANOVAs). Data were randomised, without replacement and running means were calculated for species richness using EstimateS V9.1.0 (Copyright © Colwell 1994 - 2013). CurveExpert 1.4 (Copyright © Hyams 1995 - 2009) was then used to extrapolate and fit models to the observed data, produced by EstimateS.

2.5.2 Data analysis

The total percentage cover of organisms per species, per sample (percentage cover was used as a measure of abundance) was recorded and this data matrix was used in PRIMER V6 to obtain the diversity indices per sample using the DIVERSE function (Krebs 2014, Wijewardene et al. 2014). Many parametric statistical tests rely on the assumptions that samples are collected randomly from populations that are normally distributed and have equal variances (Cochran 1947, Box 1953, Zar 1999, Clark and Gorley 2006). Therefore, because the diversity indices were statistically analysed to obtain significant results, the graphic distribution of these data was examined (Reimann and Filzmoser 1999). Significant tests of normality and homogeneity of variances are often more sensitive to non-normality and deviations in variance than the parametric tests themselves (McGuinness 2002). Despite this, the Levene’s statistical test was used to test for the homogeneity of sample variances of diversities at the various locations and depths, separately (Townend 2002, Stat Soft 2005). The Levene’s Test results were not significantly different indicating that sample variances were equal (Townend 2002, Stat Soft 2005). The large sample size allowed for the graphical checking of the distribution of data (Townend 2002). The results obtained from the DIVERSE analysis were graphically checked for normal distribution using normality histograms in STATISTICA V7. These graphical tests indicated that data was normally distributed (Appendix A).

As the distribution of data was normal, sample variances were revealed to be equal and data was biological and not environmental, it was considered unnecessary to normalise data (Clarke and Gorley 2006). However, during multivariate analyses in PRIMER V6, percentage cover data was fourth root transformed to limit the skewing of data by rare or dominant species recorded within the study area (Clarke and Gorley 2006). The Bray-Curtis Similarity Index was used to construct all similarity matrices (on fourth root transformed data) within this study. The Bray-Curtis Similarity Index was used as it seems to obey most natural biological theories when other coefficients do not (Clarke and Gorley 2006).
The unequal number of samples per station may have resulted in erroneous conclusions during descriptive and multivariate analyses of the total values for variables per station. It is for this reason that the mean per station was used to compare between variables such as species richness, percentage cover, diversity and evenness and during multivariate analyses when stations were compared. The mean is the central tendency of data as a measure of the number of samples collected (Sokal and Rohlf 1995, Zar 1999).

A 95% significance level was used i.e. p-values of < 0.05, in the interpretation of statistical analysis. The standard error of the mean was used to illustrate the error margin in the estimation of the population mean (Townend 2002), when comparing between populations at the different depth and locations, separately. The standard deviation, which indicates the amount of deviation between individual sample values from the mean of a population (Townend 2002), was used when reporting on the means of any given variable i.e. species richness, diversity etc.

### 2.5.3 Sampling effort

To determine whether sampling effort was sufficient for statistical, univariate and multivariate analyses, species accumulation curves were plotted. Species accumulation curves are used to record the cumulative number of species obtained as a function of the cumulative sampling effort extended during the sampling period (Gotelli and Colwell 2001). PRIMER V6 was utilised to produce species accumulation curves indicating $S_{obs}$ which is the total number of species observed in the samples (Chazdon et al. 1998). Species accumulation curves were produced by plotting the number of samples against the number of species, using the percentage cover data matrix. Curves were produced for the percentage cover data of all samples, separately for each depth (i.e. a curve for deep and a curve for shallow samples), as well as separately for each location (i.e. a curve for samples inside the MPA and a curve for samples outside the MPA, separately). A species accumulation curve was also produced for each individual station.

EstimateS 9.1.0 was used to calculate running species richness means of faunal species, against the number of individuals per sample sequentially, by randomising without replacement (Colwell 2013). Only faunal species were used to obtain the expected species richness, as no accurate measure of algal abundance is possible, however, individuals or colony abundance of faunal species may be measured. Samples were randomised without replacement such that the sequence converged to the total observed species richness per dataset, with algal species removed (i.e. all abundance, deep, shallow, inside, outside and
The complete sequence obtained was then utilised to compute rarefaction curves by fitting models to the observed data using non-linear regression in CurveExpert (Hyams 2010). The rarefaction curve is based on the number of individuals recorded per sample and it provides a prediction of the total number of faunal species expected to occur within the study area as sampling effort increases (Colwell and Coddington 1994, Gotelli and Colwell 2001). The rarefaction curve also allows for meaningful comparisons of diversity to be made (Gotelli and Colwell 2010). The sigmoidal Morgan-Mercer-Flodin (MMF) Model, with the equation: \( y = \frac{a + bx + c + dx^d}{b + dx^d} \), was found to best apply to the data (Hyams 2010). The MMF model was considered appropriate for the data as it produces an “S”-shaped rarefaction curve (Hyams 2010). The “S”-shaped curve starts at a fixed point, increasing the growth rate until an inflection point is reached thereafter decreasing the growth rate as an asymptotic value is approached (Hyams 2010). The asymptote of the curve provided an indication as to the total number of faunal species in the area, as a measure of the sampling effort (Chazdon et al. 1998) i.e. whether or not sampling effort was sufficient to obtain an adequate representation of the faunal species in the area to realise the objectives set out for the study. The coefficients “a, b, c and d” in the MMF model list the parameter values (Hyams 2010) and are calculated during the computation of the rarefaction curve. The rarefaction curve was computed to obtain the “c” parameter value which provides the expected species richness. The model was applied to the species’ abundance data of all samples, deep and shallow samples, inside and outside MPA samples and generic data, with algal species removed.

The correlation coefficient (r) was used to establish whether or not the number of individuals counted and the faunal species richness increased interdependently of each other as they were recorded per sample (Zar 1999, Clarke and Warwick 2001). An r-value between the range -1 and 0 indicates data that is negatively correlated and a value between 0 and 1 is presented by positively correlated data (Clarke and Warwick 2001). A strong positive correlation between the data (i.e. \( r = \) closer to 1 than 0) indicates that the number of individuals counted and faunal species richness are interdependent of each other and the use of this data would provide a good indication as to the required sampling effort in the area (Anderson and Walsh 2013).

### 2.5.4 Diversity Indices

The results of the DIVERSE function in PRIMER V6 provided species richness (S), evenness (\( J' \)) and species diversity (\( H' \)) for each sample (using percentage cover data). Species richness refers to the total number of species within an area (Gray 2000). The number of species alone is not enough to describe the assemblages within the study area as the number of individuals sampled per species may vary (Gray 2000). Therefore, species
richness was considered in conjunction with species diversity within the area to provide indications of patterns in the KBR (Gray 2000).

The Shannon-Wiener index of species diversity was selected as a diversity index during this study (Clarke and Gorley 2006). This index is calculated as: 
\[ H' = -\sum_{i=1}^{S} p_i \log p_i \]
where \( p_i \) is the proportion of each species in the sample and \( S \) is total number of species collected (Gray 2000, Magurran 2004, Clarke and Gorley 2006). The Shannon-Wiener index was used as it incorporates the number of species as well as the proportion of individuals distributed among each species, within the calculation (Gray 2000). This index is also the most commonly used index in biodiversity studies (Gray 2000). In this study, percentage cover is used to calculate \( H' \) as a measure of abundance to account for colonial species and algae (Krebs 2014, Wijewardene et al. 2014).

Evenness provides an indication of how abundances or measures of abundance, such as percentage cover are partitioned among species (Heip et al. 1998, Gray 2000) and was calculated using Pielou’s evenness index: 
\[ J' = \frac{H'}{H_{max}'} \]
where \( H' \) = number derived from Shannon-Wiener index and \( H_{max}' \) = highest value scored with Shannon-Wiener index (Magurran 2004, Clarke and Gorley 2006). Evenness measures between 0, which indicates communities with low evenness, and 1, which indicates high evenness (Routledge 1980, Alatalo 1981, Stirling and Wilsey 2001). A low evenness normally indicates that species within the study area have patchy distributions, whereas a high evenness indicates that the percentage covers of species are equally distributed (Smith and Wilson 1996).

Box plots of the means and standard error of the species diversity of the samples inside and outside of the MPA as well as plots of the means and standard error of deep and shallow samples (produced in STATISTICA V7) were used to graphically illustrate differences as well as the variations between samples.

Independent observations, from randomly collected samples, were made and data was shown to be normally distributed (Appendix A) with equal sample variances. Therefore as all assumptions for a parametric test were met, an Analysis of Variance (ANOVA), was considered appropriate to use for statistical analyses (Townend 2002). The ANOVA was considered appropriate as it is robust to the slight deviations of normality and unequal sample variances (Cochran 1947, Underwood 1981, Zar 1999). An ANOVA test allows for more defined observations of trends in the study area to be made, by analysing the variances of individual samples, as opposed to groupings (StatSoft Inc. 2005). A multi-effects ANOVA was used for analyses as this test analysis the variances of samples while
simultaneously assessing the effects of each factor (i.e. depth and location) on the variance (Shaw and Mitchell-olds 1993). Multi-effects ANOVAs were conducted on the species richness, diversity and percentage cover, with depth and location as the effects (i.e. three separate ANOVAs). The results of the ANOVAs were interpreted to establish whether sample variances were more significantly different in terms of species richness, diversity and abundance between the two depths or between the two locations or if both factors had an effect on the significant differences. Following the results of the multi-effects ANOVAs, a post-hoc test was conducted on the factor found to have a significant effect on sample variances. A Tukey Honest Significant Difference (HSD) test for unequal sample sizes (as there were an unequal number of samples per location as well as per depth) was utilised as a post-hoc comparison of the means per factor. This post-hoc test was used to indicate whether the mean species diversity, richness and abundance were significantly different from each other for depth or location. The Tukey HSD test is regarded as the best test to detect differences between samples of unequal size (StatSoft Inc. 2005).

To test for significant differences between the diversity of sampling stations, a one-way ANOVA was performed on the diversity of all samples, within the stations. The Tukey Honest HSD test for unequal sample sizes was used for the post-hoc comparison of the means of species diversities per station to determine whether they were significantly different from each other (StatSoft Inc. 2005).

2.5.5 Assemblage structure

Similarity matrices of fourth root transformed percentage cover of each species per sample as well as the mean percentage cover per station were constructed to determine similarities between samples and sampling stations (Clarke and Gorley 2006, Celliers et al. 2007).

Multi-Dimensional Scaling (MDS) ordinations were employed on the similarity matrix of the percentage cover of each species per sample to determine and observe, more visually, the apparent similarities or differences in groupings (Clarke and Gorley 2006). Depth and location were used as factors (separately) to indicate whether natural groupings in community structure occurred between deep and shallow stations and between stations inside and outside the MPA. These ordinations produced high stress levels (Stress: 0.3). The stress level indicates how accurately the ordination represents the similarity in terms of distance between the data (Clarke and Gorley 2006). Multi-Dimensional Scaling ordinations with lower stress levels (<0.05 to <0.1) more accurately represent the distances than those with higher stress levels (>0.2 to >0.3) (Clarke and Warwick 2001, Clarke and Gorley 2006). Higher stress levels often occur as a result of a high number of samples and may result in
misinterpretation of the data (Clarke and Warwick 2001). Multi-Dimensional Scaling ordinations were then employed on the similarity matrix of the mean percentage cover per station (i.e. 10 samples as opposed to 881 samples) to lower the stress level (Stress: 0.05) and for more accurate interpretation.

Cluster analyses were performed on the mean percentage cover similarity matrix of the stations and dendrograms were constructed. Cluster analysis allows one to observe natural groupings of samples in such a way that more similar samples are generally grouped together and separated from samples in different groups (Clarke and Warwick 2001). Separate dendrograms were constructed for location and depth to indicate whether natural groupings of data occurred between the two depths and between the two locations.

Natural groupings of data obtained within the study area from the MDS and cluster analyses provided an indication as to similarities between stations, in terms of depth and location. The groupings of data provide a visual indication as to the assemblage structure within the area to accompany statistical results obtained.

A one-way Analysis of Similarity (ANOSIM) was calculated on the similarity matrix of the sampling stations mean percentage cover, to calculate a Global R-value (or R-statistic). The Global R reflects the differences observed between sites while contrasting these differences amongst replicates within sites and usually falls between 0 and 1 (Clarke and Warwick 2001). The R-statistic was calculated to test for similarity between sampling stations inside and outside the MPA as well as deep and shallow sampling stations. The ANOSIM allows for the testing of the null-hypothesis that there are no significant differences in assemblages at different depths or locations (Clarke and Gorley 2006). Should the calculated R-value be approximately 0, similarities between sampling stations and among samples within sampling stations would be considered, generally, the same and the null hypothesis would be accepted (Clarke and Warwick 2001). An R-value closer to 1 indicates a significant difference in similarity between sampling stations, but not within sampling stations (Clarke and Warwick 2001).

To determine which species were most responsible for the similarity within and the dissimilarity between depth and locations, separately, a Similarity Percentage (SIMPER) procedure was performed on fourth root transformed percentage cover per species (Gray 2000).

**2.5.6 Floral and Faunal Composition**
Managers within the area may have enough expertise to identify organisms to genus level and, should that be the case, it is important to assess whether this will be sufficient for analysis. In order to achieve this, the species were grouped into genera to calculate the percentage cover per genera for further analysis of the community.

Species were further placed into their respective higher taxonomic group to calculate the species richness and the percentage cover per taxonomic group within the community. The use of higher taxonomic groups allows for patterns in the composition of assemblages to be revealed within the area (Bremner et al. 2003). Represented higher taxonomic groups were the Algae, Annelida, Ascidia, Arthropoda, Bryozoa, Cnidaria, Echinodermata, Mollusca and Porifera. Algae rather than Protista was used as a taxonomic grouping because Algae was the only group within this phylum that was recorded during the study. Graphs of the mean individual (for non-colonial species) or colony (for colonial species) abundance (± SD) and species richness (± SD) for each taxonomic group, per sample within each depth and location were constructed, to illustrate the differences in the number of species and abundance between taxonomic groups per depth and location.

The total percentage cover per taxonomic group was calculated by summing the average percentage cover of each species within the respective groups and represented graphically. As the percentage cover of rock and sand were also included in the examination of photographs, the sum of the percentage cover of all taxonomic groups did not equal 100 %.

A similarity matrix of fourth root transformed data of the total percentage cover for each genus as well as that for each taxonomic group, per sample, was constructed. Multi-Dimensional Scaling (MDS) ordinations were employed on these similarity matrices to indicate whether natural groupings, with regards to genera and taxonomic groups, occurred between samples, using depths and locations (separately) as factors. For a more accurate and interpretable representation of similarities with regards to both genera and taxonomic groups, MDS ordinations were also employed on the similarity matrices of both the mean percentage cover per genus and per taxonomic group, per sampling station (constructed on fourth root transformed mean percentage cover per genus and taxonomic group, per sampling station data). Depth and location (separately) were used as factors to indicate whether natural groupings occurred with regards to both genera and taxonomic groups.

Cluster analyses were performed on the similarity matrices of the mean percentage cover of the genera and taxonomic groups per station to construct dendrograms for each factor (i.e. depth and location) to test for natural groupings of assemblages between both genera and taxonomic groups and depth and location, separately.
To determine which taxonomic groups were most responsible for the similarity within and the dissimilarity between depth and locations, separately, a SIMPER procedure was performed on fourth root transformed data of the mean percentage cover per taxonomic group, per sample. Results obtained from the SIMPER procedure provided an indication of which taxonomic groups were most dominant and/or rare between depth and location groupings. A SIMPER procedure was also performed on fourth root transformed data of the mean percentage cover per genera, per sample. The SIMPER procedure was used to obtain the genera most responsible for similarity within and dissimilarity between depth and locations, separately.

A higher taxon approach, i.e. the use of higher taxonomic groupings such as orders, phyla, genera etc. instead of species, is useful during monitoring as it assists in the reduction of costs, expertise required and time spent during species identification (Williams and Gaston 1994, Cardoso et al. 2004). Although helpful for rapid area assessments, higher taxon approaches when surveying are not always sufficient for all areas. Therefore, in order to determine if the use of genera or higher taxonomic groups during monitoring would provide sufficient information for monitoring to inform management decisions within the Betty’s Bay area, a RELATE routine, in PRIMER V6 was used. The RELATE routine allows for the testing of the null hypothesis that there is not a relationship between multivariate patterns among the independently-derived resemblance matrices of the percentage cover of each species per sample and total percentage cover of genera per sample, as well taxonomic group total percentage cover per sample (Clarke and Gorley 2006). The measurement derived from the RELATE routine is the rank correlation coefficient \( \rho \) (or Rho-value) and measures between -1 and 1, as with the correlation coefficient i.e. the closer the value is to 1, the higher the correlation between the two sets of data and vice versa (Clarke and Gorley 2006).
Table 2.1: Sampling stations ("S"- Shallow, “D”- Deep, “O”- Outside, “I”- Inside, “M”- middle, “E”- East and “W”- West) with the number of samples, dates, depths and locations in the Betty’s Bay Marine Protected Area in the Kogelberg Biosphere Reserve, South Africa

<table>
<thead>
<tr>
<th>Dive station</th>
<th>Sampling station</th>
<th>Number of samples (n)</th>
<th>Date</th>
<th>GPS-coordinates</th>
<th>Depth</th>
<th>Location</th>
</tr>
</thead>
<tbody>
<tr>
<td>JAN01_DOW</td>
<td>DOW</td>
<td>86</td>
<td>January 2013</td>
<td>34°22'54&quot;S, 18°53'19&quot;E</td>
<td>Deep-22 m</td>
<td>Outside-west</td>
</tr>
<tr>
<td>JAN02_DIW</td>
<td>DIW</td>
<td>54</td>
<td>January 2013</td>
<td>34°22'56&quot;S, 18°53'57&quot;E</td>
<td>Deep-22 m</td>
<td>Inside-west</td>
</tr>
<tr>
<td>NOV03_DM</td>
<td>DM</td>
<td>90</td>
<td>November 2012</td>
<td>34°22'12&quot;S, 18°55'21&quot;E</td>
<td>Deep-23.2 m</td>
<td>Middle</td>
</tr>
<tr>
<td>NOV04_DOE</td>
<td>DOE</td>
<td>54</td>
<td>November 2012</td>
<td>34°21'55&quot;S, 18°56'33&quot;E</td>
<td>Deep-23.1 m</td>
<td>Outside-east</td>
</tr>
<tr>
<td>NOV07_SIE</td>
<td>SIE</td>
<td>168</td>
<td>November 2012</td>
<td>34°21'44&quot;S, 18°55'22&quot;E</td>
<td>Shallow-10.2 m</td>
<td>Inside-east</td>
</tr>
<tr>
<td>NOV05_SOW</td>
<td>SOW</td>
<td>107</td>
<td>November 2012</td>
<td>34°22'39&quot;S, 18°53'09&quot;E</td>
<td>Shallow-13 m</td>
<td>Outside-west</td>
</tr>
<tr>
<td>JAN03_SIW</td>
<td>SIW</td>
<td>140</td>
<td>January 2013</td>
<td>34°22'18&quot;S, 18°54'07&quot;E</td>
<td>Shallow-11.9 m</td>
<td>Inside-west</td>
</tr>
<tr>
<td>JAN04_SM</td>
<td>SM</td>
<td>62</td>
<td>January 2013</td>
<td>34°21'40&quot;S, 18°54'56&quot;E</td>
<td>Shallow-10.8 m</td>
<td>Middle</td>
</tr>
<tr>
<td>JAN05_SOE</td>
<td>SOE</td>
<td>44</td>
<td>January 2013</td>
<td>34°21'34&quot;S, 18°56'07&quot;E</td>
<td>Shallow-10.7 m</td>
<td>Inside-east</td>
</tr>
<tr>
<td>JAN06_DIE</td>
<td>DIE</td>
<td>76</td>
<td>January 2013</td>
<td>34°22'00&quot;S, 18°56'01&quot;E</td>
<td>Deep-19 m</td>
<td>Inside-east</td>
</tr>
</tbody>
</table>
Table 2.2: The point-count representation and respective explanations utilised during photo-quadratic analysis

<table>
<thead>
<tr>
<th>Point-count representation</th>
<th>Explanation</th>
</tr>
</thead>
<tbody>
<tr>
<td>Macro-benthic organisms (MBO)</td>
<td>All species including vertebrate, invertebrate, sessile, semi-motile and motile which can be seen with the naked eye</td>
</tr>
<tr>
<td>Sand</td>
<td>Point fell on bare sand</td>
</tr>
<tr>
<td>Rock</td>
<td>Point fell on bare rock</td>
</tr>
<tr>
<td>Unclear</td>
<td>Item below point blurred or indistinguishable</td>
</tr>
<tr>
<td>Shadow</td>
<td>Shadow over item below point</td>
</tr>
<tr>
<td>Quad</td>
<td>Point fell on quadrat border</td>
</tr>
</tbody>
</table>
Figure 2.1: Map showing the location of the study area (indicated by ⊙), within (a) the Kogelberg Biosphere Reserve and (b) the Agulhas Bioregion, South Africa
Figure 2.2: SCUBA diver, within the study area, with photo-quadrat utilised for image capturing (Photo by: Marco Worship 2012)
Figure 2.3: Map showing the location of sampling stations ("S"- Shallow, "D"- Deep, "O"- Outside, "I"- Inside, "M"- middle, "E"- East and "W"- West) within the study area in the Kogelberg Biosphere Reserve, south-west Africa
Figure 2.4: Photographed representative specie’s sample showing unique sample number and dive information
Figure 2.5: Photo-quadrat showing a grid overlay of 100 points in the CPCe programme and scale-bar (For all photo-quadrats, full scale = 0.33 m and the intervals = 0.03 m)
Chapter 3: RESULTS

A total of 30 624 individuals were identified and recorded from 881 analysed photo-quadrats (samples) and a species list of 250 species was compiled (Appendix B, Table 1), of which 241 were sessile and semi-motile species and were used for the analyses within this study. The five most commonly recorded species per taxonomic group were recorded and examples presented as they appeared in the photo-quadrats (Appendix C, Figures a-i). The mean percentage cover of benthic organisms for all samples was 78.01 % (± 11.79 SD, n = 881 samples), rock measured 8.04 % (± 14.80 SD, n = 881 samples) and sand was 11.52 % (± 11.27 SD, n = 881 samples) (Table 3.1).

The highest mean percentage cover of benthic organisms (88.85 % ± 5.37 SD, n = 44 samples), in the sampled area, was calculated for sampling station SOE (Table 3.1). The deep, outside station DOW had the lowest mean percentage cover of benthic organisms (71.55 % ± 15.26 SD, n = 86 samples), but the highest of sand (18.82 % ± 14.45 SD, n = 86 samples) (Table 3.1). The highest mean percentage cover of rock was calculated for station DIW (38.65 % ± 8.54 SD, n = 55 samples) and the lowest for station SM (0.05 % ± 0.25, n = 62 samples). Station DIW had the lowest mean percentage cover of sand in the study area (0.26 % ± 1.48 SD, n = 55 samples).

3.1 Sampling Effort

Species accumulation curves (indicating Sobs) of all data (Figure 3.1), individual station data (Appendix D, Figures a-j) as well as data, separated by depth (deep and shallow) (Appendix D, Figures k-l) and location (inside and outside the MPA) (Appendix D, Figures m-n), did not reach an asymptote. Although the species curves for all individual stations did not reach an asymptote, the species accumulation curves of stations SIE (n = 168 samples) (Appendix D, Figure 2f) and SIW (n = 140 samples) (Appendix D, Figure 2g) appear to be levelling off.

A fitted extrapolation curve, the sigmoidal MMF curve, provided a much higher estimated faunal species’ richness (237 species) than the observed faunal species richness (180 species) for the area (Table 3.2). This indicates that close to 76 % of the total number of faunal species estimated to occur within the study area was sampled. The difference between observed and estimated faunal species richness was not more than 95 species (Genera data) for all data groupings and the estimated species richness for faunal species occurring in samples outside of the MPA measured only 29 species more than observed species richness (Table 3.2). The correlation coefficient measured 1 for deep, shallow, inside and outside curves and 0.999 for genera and all species curves (Table 3.2) indicating that
species richness and the number of faunal individuals counted per sample were interdependent of each other and therefore provided a good indication for the required sampling effort.

### 3.2 Diversity Indices

Diversity indices were calculated on the percentage cover of species per sample to determine diversity. Where necessary for descriptions of results between stations, the means of the respective variables being compared were used to standardise between stations as there were an unequal number of photographs per station. The mean species richness of samples within the study area was 15.49 species (± 4.55 SD, n = 881 samples) and the mean percentage cover measured 78.03 % (± 11.80 SD, n = 881 samples) (Table 3.1). The mean evenness for all the samples was high and measured 0.81 (± 0.11 SD, n = 881 samples) (Table 3.3). The species diversity mean for all the samples was 2.21 (± 0.48 SD, n = 881 samples) (Table 3.3).

The inside, shallow station SOE had the highest mean percentage cover (88.89 % ± 5.37 SD, n = 44 samples) and the deep, inside station DOW had the lowest mean percentage cover (71.57 % ± 15.24 SD, n = 86 samples) (Table 3.3). The highest mean species richness (16.94 species) was recorded at stations DM (± 3.67 SD, n = 90 samples) and SIW (± 4.72 SD, n = 140 samples) and the lowest was recorded for station DOE (12.02 species ± 3.50 SD, n = 54 samples) (Table 3.3). The inside, shallow station SOE had the highest mean species diversity (2.34 ± 0.33 SD, n = 44 samples) and the lowest mean species diversity was calculated for station DOE (1.88 ± 0.46 SD, n = 54 samples) (Table 3.3). Mean evenness was high and the highest mean evenness ($J'$ = 0.84) was calculated for station SOE (± 0.07 SD, n = 44 samples) (Table 3.3). Station DOE had the lowest mean evenness ($J'$ = 0.76 ± 0.12 SD, n = 54 samples) (Table 3.3).

Inside stations possessed the highest means of the diversity indices ($H'$, $S$) and the box plots of means and standard errors of diversities of samples inside the MPA and those outside, revealed no overlap in the standard errors of the mean between the two locations (Figure 3.2a). A large difference between the standard error of the mean of deep samples and of shallow samples was also revealed (Figure 3.2b).

The multi-effects ANOVAs conducted indicated that location had a greater effect on sample variances of species richness ($F_{1, 637.4} = 32, p < 0.001$) and diversity ($F_{1, 5.47} = 24.18, p < 0.001$) than depth. The post-hoc tests conducted with location as a factor indicated that the mean species richness and diversity of samples outside the MPA ($S = 14.05$ species ± 4.22
SD samples and $H' = 2.07 \pm 0.47$ SD, n = 247 samples) were highly significantly lower ($p < 0.001$) than that of stations inside the MPA ($S = 16.05 \pm 4.55$ SD and $H' = 2.26 \pm 0.48$ SD, n = 634). Depth had a greater effect on the variances in percentage cover within samples ($F_{1, 761} = 5.9$, $p < 0.05$) and the post-hoc test of the percentage cover ANOVA conducted with depth as a factor indicated that the mean percentage cover of deep samples ($\% = 76.89$ individuals $\pm 12.68$ SD) were significantly lower ($p < 0.05$) than that of shallow samples ($\% = 78.81$ individuals $\pm 11.09$ SD).

The ANOVA of the species diversity between stations revealed only one significant difference in species diversity amongst shallow stations, namely between station SM and SIW. With the exception of the deep station DIW, significant differences in species diversity were found amongst most deep stations, and the deep outside station DOE, was significantly different to all except three stations (Table 3.4).

### 3.3 Assemblage Composition

The MDS ordination of the percentage cover of each species per sample (2D stress: 0.29) (Figure 3.3), MDS ordination of the mean percentage cover per species per sampling station (2D stress: 0.07) (Figure 3.4) and cluster analysis of the mean percentage cover per species per station (Figure 3.5) revealed no natural groupings in species of stations at different locations. An ANOSIM between the mean species percentage cover of inside and outside stations (Global $R = -0.06$) also did not reveal any significant differences. Although the cluster analysis was permutated with location as a factor, it revealed much stronger groupings associated with depth (Figure 3.5).

The MDS ordination (2D stress: 0.29) of the percentage cover per species per sample revealed that the deep and shallow sites grouped separately, with some overlap between them (Figure 3.6). The MDS ordination (2D stress: 0.07) (Figure 3.7) and cluster analysis of the mean percentage cover per sampling station (grouped according to depth) provided a greater representation of two communities as the deep and shallow stations grouped separately at $\approx 62\%$ similarity, (Figure 3.8). An ANOSIM between the two depths produced a Global $R$-value of 0.96 indicating a significant difference between the deep and shallow samples, but not within deep and shallow samples.

The SIMPER procedures performed on the percentage cover data revealed higher dissimilarity than similarity in the percentage cover of species between stations according to both depth and location variables.
The SIMPER procedures for total percentage cover per species indicated low similarities within stations inside (25.23 % similarity) and outside (28.25 % similarity) the MPA. The species most responsible for the community structure of the stations inside and outside the MPA in terms of percentage cover were Leptophytum foveatum Chamberlain & Keats, 1994 (Algae) (29.96 % contribution to similarity within outside and 23.69 % contribution within inside stations), Eudendrium Ehrenberg, 1834 species 1 (spp 1) (Cnidaria) (18.53 % contribution to similarity for outside and 8.15 % contribution for inside stations) and Jania adhaerens J.V.Lamouroux, 1816 (Algae) (11.49 % contribution to similarity for outside and 10.58 % contribution for inside stations) (Figure 3.9a and 3.9b). Eudendrium spp 1 (2.89 % contribution), Plumularia setacea (Linnaeus, 1758) (Cnidarian) (2.59 % contribution), J. adhaerens (2.46 % contribution), Rhodophyllis reptans (Suhr) Papenfuss, 1956 (Algae) (2.42 % contribution) and Rhodymenia obtusa (Greville) Womersley, 1996 (Algae) (2.31 % contribution) were most responsible for the high dissimilarity (76.46 % dissimilarity) between stations inside and outside the MPA (Figure 3.9c).

In the SIMPER of the total percentage cover of species between deep and shallow stations, the species that contributed the most to the similarity within deep stations (27.24 % similarity) were L. foveatum (27.21 % contribution), Eudendrium spp 1 (18.93 % contribution) and J. adhaerens (9.14 % contribution) (Figure 3.10a). Similarity within shallow stations (27.80 %) was contributed to by L. foveatum (21.90 %) and J. adhaerens (11.03 %) (Figure 3.10b). Eudendrium spp 1 (3 % contribution), R. reptans (2.51 % contribution) and P. setacea (2.42 % contribution) were most responsible for dissimilarity between deep and shallow stations (78.23 % dissimilarity between deep and shallow stations) (Figure 3.10c).

3.4 Floral and Faunal Composition

Algae had the highest mean percentage cover of the sampled area (41.97 % ± 21.07 SD, n = 881) and Porifera the second highest (13.11 % ± 13.85 SD, n = 881) (Figure 3.11). Arthropoda (0.0 % ± 0.06 SD, n = 10) and Mollusca (0.14 % ± 0.74 SD, n = 881) had the lowest mean percentage cover in the sampled area (Figure 3.11).

With the exception of Algae (mean % = 44.59 % ± 22.04 SD inside the MPA, n = 634 samples and mean % = 32.25 % ± 16.56 SD outside, n = 247 samples) and Mollusca (mean % = 0.16 % ± 0.82 SD inside the MPA and N = 0.10 % ± 0.47 SD outside) the mean percentage cover of taxonomic groups, was highest outside the MPA (Figure 3.12a). Algae (mean % = 50.27 % ± 19.26 SD in shallow samples, n = 521 and mean % = 29.96 % ± 17.49 SD in deep samples, n = 360), Echinodermata (mean % = 2.44 % ± 5.13 SD in deep samples and mean % = 2.59 % ± 6.17 SD in shallow samples), Mollusca (mean % = 0.08 %
± 0.45 SD in deep samples and mean % = 0.18 % ± 0.88 SD in shallow) and Arthropoda which were absent in the deep samples, were higher in the shallow than the deep samples and the remaining taxonomic groups had a higher, relative, mean percentage cover in the deep samples (Figure 3.12b).

The total number of species of Porifera (S = 61), Algae (S = 61), Ascidia (S = 38) and Cnidaria (S = 32) were the highest in the sampled area and Arthropoda (S = 1) had the lowest number of species (Table 3.5). With the exception of Porifera (mean $S = 3.22 \pm 2.15$ SD inside the MPA and mean $S = 2 \pm 1.47$ SD outside) and Cnidaria (mean $S = 2.21 \pm 1.54$ SD inside the MPA and mean $S = 1.66 \pm 1.17$ SD outside), as well as Mollusca and Arthropoda which both had equal mean species richness inside and outside the MPA, mean species richness was higher outside than inside the MPA (Figure 3.13a). With the exception of Algae (S = 44 in deep and S = 55 in shallow) and Cnidaria (S = 29 in deep and S = 15 in shallow), the number of species within the taxonomic groups did not show great differences between depths (Figure 3.13b).

The MDS ordination of the percentage cover per genus, per sample, regardless of the factor (i.e. depth or location) (Figure 3.14) revealed the same natural groupings of data as that of the percentage cover per species, per sample (Figure 3.3 and Figure 3.6). The cluster analysis (Figure 3.15) and MDS ordinations (Figure 3.16) of the mean percentage cover per genus, per station, regardless of the factor (i.e. depth or location) also revealed the same natural groupings as that of the mean percentage cover per species, per station (Figure 3.4, Figure 3.5, Figure 3.7 and Figure 3.8).

Dominant genera were obtained for the taxonomic groups found to be contributing the most to community structure within the studied area. A dominant genus is one which occurred across the study area and was among the highest contributors to the percentage cover within the respective dominant taxonomic groups. The dominant genera are *Leptophytum*, *Jania* and *Rhodymenia* for Algae with *Leptophytum* completely dominating the area with a much higher mean percentage cover than all other dominant algal genera (Figure 3.17a) Dominant cnidarian genera were *Eudendrium*, *Plumaria* and *Isozoanthus* Carlgren in Chun, 1903 (Figure 3.17b). *Eudendrium* showed much higher mean percentage cover in deep stations and stations inside and outside of the MPA (Figure 3.17b).

The cluster analyses of the mean percentage cover per taxonomic group, per station, indicated natural groupings of data (Figure 3.18). Stations DOW, SIW and SOE grouped separately from other stations (at approximately 87.70 %), regardless of the factor (i.e. depth or location) (Figure 3.18). The MDS ordinations for the mean percentage cover per
The SIMPER procedure for similarity tests of mean percentage cover of each taxonomic group, per sample, between locations indicated a high similarity within both the inside stations (89.58 % similarity) and the outside stations (91.83 % similarity) (Table 3.6). The taxonomic groups that contributed the most to the similarity within samples outside and inside the MPA were Algae (23.07 % contribution within the MPA and 28.70 % contribution outside the MPA), Cnidaria (14.90 % contribution inside and 16.40 % contribution outside the MPA) and Porifera (17.23 % contribution inside and 17.23 % contribution outside the MPA) (Table 3.6). Echinodermata (20.85 % contribution), Annelida (13.43 % contribution) and Cnidaria (13.01 % contribution) contributed the most to the low dissimilarity between locations which measured 9.21 % (Table 3.6). Ascidia (9.92 % contribution) and Porifera (9.18 % contribution) had the lowest contributions to dissimilarity between locations (Table 3.6).

A SIMPER of the mean percentage cover per taxonomic group, per sample, between deep and shallow stations showed that the groups that contributed the most to the high similarity within deep sites (92.19 % similarity between deep stations) were Algae (20.78 % contribution), Cnidaria (16.79 % contribution) and Porifera (18.78 % contribution) (Table 3.6). Algae (25.26 % contribution), Cnidaria (14.23 % contribution) and Porifera (16.62 % contribution) also made the greatest contribution to the high similarity in percentage cover of taxonomic groups within shallow sites (90.30 % similarity between shallow stations) (Table 3.6). The low dissimilarity between deep and shallow sites (10.46 % dissimilarity) was mainly attributed to Echinodermata (16.69 % contribution to dissimilarity), Cnidaria (14.98 % contribution to dissimilarity) and Algae (14.21 % contribution to dissimilarity). Mollusca (7.62 % contribution) made the lowest contributions to dissimilarity in percentage cover per taxonomic group between deep and shallow samples (Table 3.6).

To summarise, there was high similarity within depths and within locations in the total percentage cover per taxonomic group. Algae, Cnidaria and Porifera were most responsible for characterising similarity within the study area. Echinodermata contributed the most to
dissimilarity at all sites. Dissimilarity between locations and between depths were low. Mollusca made minimal contributions and Arthropoda made no contribution to the similarity within and dissimilarity between samples within the study area.

The similarity matrix of the percentage cover per species and of the percentage cover per genera, per sample, were revealed to have a significant relationship (Rho = 0.895) by the RELATE routine. The RELATE routine between the similarity matrix of the percentage cover of all species and the percentage cover of the taxonomic groups, per sample, produced an Rho-value of 0.38 which indicated that these two data sets were not significantly related (Rho-value = closer to 0 than 1).
Table 3.1: Percentage cover (%) means and standard deviations of benthic species, rock and sand, per station ("S"- Shallow, “D”- Deep, “O”- Outside, “I”- Inside, “M”- middle, “E”- East and “W”- West), as well as for all samples collected within the study area

<table>
<thead>
<tr>
<th>Station</th>
<th>Benthic Species</th>
<th>Rock</th>
<th>Sand</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Mean</td>
<td>SD</td>
<td>Mean</td>
</tr>
<tr>
<td>DOW</td>
<td>71.55</td>
<td>15.26</td>
<td>1.17</td>
</tr>
<tr>
<td>DIW</td>
<td>81.67</td>
<td>9.06</td>
<td>38.65</td>
</tr>
<tr>
<td>SIW</td>
<td>78.40</td>
<td>9.46</td>
<td>32.66</td>
</tr>
<tr>
<td>SM</td>
<td>80.90</td>
<td>11.85</td>
<td>0.05</td>
</tr>
<tr>
<td>SOE</td>
<td>88.85</td>
<td>5.37</td>
<td>1.04</td>
</tr>
<tr>
<td>DIE</td>
<td>75.91</td>
<td>12.82</td>
<td>0.20</td>
</tr>
<tr>
<td>DM</td>
<td>80.37</td>
<td>9.84</td>
<td>0.29</td>
</tr>
<tr>
<td>DOE</td>
<td>76.04</td>
<td>12.01</td>
<td>0.85</td>
</tr>
<tr>
<td>SOW</td>
<td>83.49</td>
<td>10.30</td>
<td>0.13</td>
</tr>
<tr>
<td>SIE</td>
<td>72.75</td>
<td>10.13</td>
<td>1.03</td>
</tr>
<tr>
<td>All samples</td>
<td>78.01</td>
<td>11.79</td>
<td>8.04</td>
</tr>
</tbody>
</table>
Table 3.2: Estimations of the species richness of sessile and semi-motile macro-benthic faunal species using an extrapolation of an MMF Model: \( y = \frac{(a*b+c*x^d)}{(b+x^d)} \) of a plot of species accumulation of sample data

<table>
<thead>
<tr>
<th>Sigmoidal Growth model parameters</th>
<th>( r )</th>
<th>Estimated species richness</th>
<th>Observed species richness</th>
<th>Total</th>
<th>Percentage of estimated</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Inside samples</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>( a = -20.29 )</td>
<td>1</td>
<td>221</td>
<td>168</td>
<td></td>
<td>76 %</td>
</tr>
<tr>
<td>( b = 38.23 )</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>( c = 220.88 )</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>( d = 0.54 )</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><strong>Outside samples</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>( a = -6.33 )</td>
<td>1</td>
<td>167</td>
<td>138</td>
<td></td>
<td>83 %</td>
</tr>
<tr>
<td>( b = 88.60 )</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>( c = 167.41 )</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>( d = 0.70 )</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><strong>Deep samples</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>( a = -38.54 )</td>
<td>1</td>
<td>237</td>
<td>154</td>
<td></td>
<td>65 %</td>
</tr>
<tr>
<td>( b = 18.86 )</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>( c = 236.77 )</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>( d = 0.42 )</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><strong>Shallow samples</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>( a = -16.91 )</td>
<td>1</td>
<td>198</td>
<td>142</td>
<td></td>
<td>72 %</td>
</tr>
<tr>
<td>( b = 38.16 )</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>( c = 198.48 )</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>( d = 0.53 )</td>
<td></td>
<td></td>
<td></td>
<td></td>
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</tr>
<tr>
<td><strong>Genera-all data</strong></td>
<td></td>
<td></td>
<td></td>
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</tr>
<tr>
<td>( a = -35.47 )</td>
<td>1</td>
<td>219</td>
<td>124</td>
<td></td>
<td>57 %</td>
</tr>
<tr>
<td>( b = 12.16 )</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>( c = 218.75 )</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>( d = 0.32 )</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><strong>All data</strong></td>
<td>0.999</td>
<td>237</td>
<td>180</td>
<td></td>
<td>76 %</td>
</tr>
<tr>
<td>( a = -13.62 )</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>( b = 40.12 )</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>( c = 236.99 )</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>( d = 0.51 )</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>
Table 3.3: Summary table showing the mean and standard deviation of species richness (S), evenness (J') and diversity (H'(Loge)) for all stations ("S"- Shallow, “D”- Deep, “O”- Outside, “I”- Inside, “M”- middle, “E”- East and “W”- West), as well as all samples collected within the study area

<table>
<thead>
<tr>
<th>Station</th>
<th>S</th>
<th>SD</th>
<th>J'</th>
<th>SD</th>
<th>H'(Loge)</th>
<th>SD</th>
</tr>
</thead>
<tbody>
<tr>
<td>Die</td>
<td>16.53</td>
<td>3.91</td>
<td>0.83</td>
<td>0.08</td>
<td>2.31</td>
<td>0.37</td>
</tr>
<tr>
<td>Diw</td>
<td>15.91</td>
<td>5.49</td>
<td>0.79</td>
<td>0.14</td>
<td>2.16</td>
<td>0.59</td>
</tr>
<tr>
<td>Dm</td>
<td>16.94</td>
<td>3.67</td>
<td>0.82</td>
<td>0.09</td>
<td>2.31</td>
<td>0.38</td>
</tr>
<tr>
<td>Doe</td>
<td>12.02</td>
<td>3.50</td>
<td>0.76</td>
<td>0.12</td>
<td>1.88</td>
<td>0.46</td>
</tr>
<tr>
<td>Dow</td>
<td>13.34</td>
<td>4.18</td>
<td>0.79</td>
<td>0.10</td>
<td>2.02</td>
<td>0.47</td>
</tr>
<tr>
<td>Sie</td>
<td>15.30</td>
<td>4.52</td>
<td>0.83</td>
<td>0.10</td>
<td>2.25</td>
<td>0.48</td>
</tr>
<tr>
<td>Siw</td>
<td>16.94</td>
<td>4.72</td>
<td>0.83</td>
<td>0.10</td>
<td>2.32</td>
<td>0.48</td>
</tr>
<tr>
<td>Sm</td>
<td>14.06</td>
<td>5.20</td>
<td>0.77</td>
<td>0.14</td>
<td>2.03</td>
<td>0.62</td>
</tr>
<tr>
<td>Soe</td>
<td>16.45</td>
<td>3.35</td>
<td>0.84</td>
<td>0.07</td>
<td>2.34</td>
<td>0.33</td>
</tr>
<tr>
<td>Sow</td>
<td>15.65</td>
<td>4.02</td>
<td>0.80</td>
<td>0.11</td>
<td>2.20</td>
<td>0.44</td>
</tr>
<tr>
<td>All samples</td>
<td>15.76</td>
<td>4.55</td>
<td>0.82</td>
<td>0.11</td>
<td>2.24</td>
<td>0.49</td>
</tr>
</tbody>
</table>
Table 3.4: The one-way ANOVA result, of the post-hoc comparison of means, using the Tukey Honest Significance Difference (HSD) Test, for unequal sample sizes, of the species diversity of sampled stations in Betty's Bay. Significant differences and the mean diversity per station are indicated (“S”- Shallow, “D”- Deep, “O”- Outside, “I”- Inside, “M”- middle, “E”- East and “W”- West)

<table>
<thead>
<tr>
<th>Mean diversity</th>
<th>DIE</th>
<th>DIW</th>
<th>DM</th>
<th>DOE</th>
<th>DOW</th>
<th>SIE</th>
<th>SIW</th>
<th>SM</th>
<th>SOE</th>
<th>SOW</th>
</tr>
</thead>
<tbody>
<tr>
<td>DIE</td>
<td>2.31</td>
<td>2.16</td>
<td>2.31</td>
<td>1.88</td>
<td>2.02</td>
<td>2.25</td>
<td>2.32</td>
<td>2.03</td>
<td>2.35</td>
<td>2.20</td>
</tr>
<tr>
<td>DIW</td>
<td>0.82</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
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</tr>
<tr>
<td>DM</td>
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<td>0.8</td>
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<td></td>
<td></td>
</tr>
<tr>
<td>DOE</td>
<td>0</td>
<td>0.65</td>
<td>0</td>
<td>0</td>
<td></td>
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<td></td>
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</tr>
<tr>
<td>DOW</td>
<td>0</td>
<td>0.88</td>
<td>0</td>
<td>0</td>
<td>0.88</td>
<td></td>
<td></td>
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</tr>
<tr>
<td>SIE</td>
<td>1</td>
<td>0.99</td>
<td>1</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>SIW</td>
<td>1</td>
<td>0.72</td>
<td>1</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0.95</td>
<td></td>
<td></td>
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</tr>
<tr>
<td>SM</td>
<td>0.04</td>
<td>0.93</td>
<td>0.03</td>
<td>0.80</td>
<td>1</td>
<td>0.24</td>
<td>0.02</td>
<td></td>
<td></td>
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</tr>
<tr>
<td>SOE</td>
<td>1</td>
<td>0.69</td>
<td>1</td>
<td>0</td>
<td>0.04</td>
<td>0.99</td>
<td>1</td>
<td>0.06</td>
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</tr>
<tr>
<td>SOW</td>
<td>0.92</td>
<td>1</td>
<td>0.86</td>
<td>0.02</td>
<td>0.25</td>
<td>1</td>
<td>0.66</td>
<td>0.62</td>
<td>0.91</td>
<td></td>
</tr>
</tbody>
</table>

Key
- p < 0.001
- p < 0.01
- p < 0.05
Table 3.5: Total species richness per taxonomic group represented within the study area

<table>
<thead>
<tr>
<th>Taxonomic Group</th>
<th>Total</th>
</tr>
</thead>
<tbody>
<tr>
<td>Algae</td>
<td>61</td>
</tr>
<tr>
<td>Annelida</td>
<td>10</td>
</tr>
<tr>
<td>Arthropoda</td>
<td>1</td>
</tr>
<tr>
<td>Ascidia</td>
<td>38</td>
</tr>
<tr>
<td>Bryozoa</td>
<td>18</td>
</tr>
<tr>
<td>Cnidaria</td>
<td>32</td>
</tr>
<tr>
<td>Echinodermata</td>
<td>4</td>
</tr>
<tr>
<td>Mollusca</td>
<td>16</td>
</tr>
<tr>
<td>Porifera</td>
<td>61</td>
</tr>
</tbody>
</table>
Table 3.6: SIMPER results indicating the taxonomic groups that are most responsible for similarity within and dissimilarity between samples within the study area (with regards to depth and location, separately). The SIMPER was performed on fourth root transformed data using the Bray-Curtis similarity matrix.

<table>
<thead>
<tr>
<th>Phylum</th>
<th>Contribution to similarity (%)</th>
<th>Contribution to dissimilarity (%)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Location</td>
<td>Depth</td>
</tr>
<tr>
<td>Algae</td>
<td>23.07</td>
<td>22.70</td>
</tr>
<tr>
<td>Bryozoa</td>
<td>13.06</td>
<td>11.23</td>
</tr>
<tr>
<td>Echinodermata</td>
<td>9.04</td>
<td>7.18</td>
</tr>
<tr>
<td>Porifera</td>
<td>17.23</td>
<td>18.69</td>
</tr>
<tr>
<td>Average</td>
<td>89.58</td>
<td>91.83</td>
</tr>
</tbody>
</table>
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Chapter 4: DISCUSSION

The primary aim of the study was to provide baseline information on the sessile and semi-motile macro-benthic communities in the Betty's Bay area, within the KBR. In order to accomplish this, the diversity indices, species diversity, richness and abundance as well as the spatial patterns of these organisms, that is the assemblage structure were investigated. This information will assist managers within the KBR in making more informed decisions regarding the management of the MPA as well as during the proposed expansion process.

4.1 Sampling Effort

The measurement of species richness within an area is predominantly sensitive to the size of the sample (Gotelli and Colwell 2010, Chao et al. 2014). It was therefore important to establish whether or not the sampling effort was sufficient during the study to enable a proper analysis of the results obtained. A good measure of sampling effort is investigating the asymptote of a species accumulation curve which provides the total number of species in the area as a measure of the sampling effort (Chazdon et al. 1998). The absence of an asymptote as evident in all the graphs presented (Figure 3.1 and Appendix D), together with a higher predicted estimate for species richness (Table 3.2), imply that the sampling effort was inadequate. However, according to Chazdon et al. (1998), the lack of an asymptote may also be indicative of a heterogeneous area, whereas the asymptote of a species accumulation curve largely describes species richness within homogenous assemblages (Chazdon et al. 1998).

As a result of the sampling method and the number of viable photographs available per station, a different number of samples were analysed per station. The species accumulation curves produced indicated that 140 (Appendix D, Figure 2g) to 168 (Appendix D, Figure 2f) photographs per station were enough to obtain a good estimation of species richness. Fewer photographs (n = 44 to n = 107) provided much lower observed than estimated species richness estimates, thus illustrating how sensitive species richness is to sample size and the amount of rare species within an assemblage (Gotelli and Colwell 2010, Chao et al. 2014). This sensitivity often results in biodiversity surveys being incomplete as many species remain undetected (Gotelli and Colwell 2010, Chao et al. 2014). Subtidally, as with this study which included SCUBA diving, sampling is difficult and often labour intensive with very little understanding as to the extent of a habitat or assemblage as boundaries cannot be determined as easily as on land (Gray 2000, Chao et al. 2009, Valentine 2009, Gotelli and Colwell 2010, Colwell et al. 2012, Chao et al. 2014). Therefore, it may be said that a greater number of photographs were required per station (i.e. between 140 and 168 photo-quadrats).
within this study. Despite this, close to 76% of the total species estimated to occur within the area were sampled and 75% of the total species in an area is the level considered by Foggo et al. (2003) to represent a well sampled area.

The distribution of species in the sampled area also plays a role in the estimation of species richness (Chazdon et al. 1998). A greater number of randomly distributed species within an assemblage as well as a high evenness, results in a faster growth of accumulation curves (Chazdon et al. 1998, Gotelli and Colwell 2010). The fast growth means that a larger number of new species are discovered per individual counted than if species and their abundances have a patchy distribution (Chazdon et al. 1998, Gotelli and Colwell 2010). High evenness also suggests that there is a low number of dominant and/or rare species within the area (Smith and Wilson 1996, Heip et al. 1998, Magurran 2004). In this study, the fast growth rate of the species accumulation curve produced for the study area (Figure 3.1), together with the high mean evenness (mean $J' = 0.81$) and low number of species dominating the area with large percentages, suggests that species are randomly distributed within the study area. Further indicating the heterogeneity of the subtidal benthic community within Betty’s Bay area as stated in previous studies (Blamey et al. 2012) and may be as a result of increased productivity during the upwelling season (Gibbons and Hutchings 1996).

Many biodiversity studies, even the more comprehensive ones, are often not extensive enough to reveal the total species richness of an assemblage (Gotelli and Colwell 2010). A greater number of samples and sampling stations would have been preferred within this study, however, the challenges of time and effort required to achieve this, did not permit it. A high correlation coefficient ($r = near 1$) was obtained between species richness and the number of individuals counted and a high percentage of species estimated to be within the area was recorded. Therefore, although the sampling effort extended during this study did not approach an asymptotic value and the estimated species richness was calculated to be higher than the observed species richness, it may not be entirely indicative of insufficient sampling. The sampling restrictions, such as dive restrictions (duration, depths, required conditions etc.) and challenges faced, such as the bathymetry data proving unreliable in situ together with the heterogeneity of the area (Blamey et al, 2012), added to the difficulty of collecting data on all species represented within the sampled area (Gotelli and Colwell 2010).

### 4.2 Diversity Indices

The percentage cover (%), species richness ($S$), diversity ($H'$) and evenness ($J'$) of the organisms recorded within the study area may be used to describe the assemblage patterns within the KBR (Gray 2000). As the Shannon-Wiener index has such a narrow range (1.5 to
it can be said that the species diversity of the area (area mean \( H' = 2.21 \pm 0.48 \text{ SD, n = 881 samples} \)) was fairly average. Most of the diversity and numerical measurements included in this study indicated statistically significant differences between the various sites. For example, the macro-benthic assemblages in the Betty's Bay area showed higher diversity, species richness and percentage cover inside of the MPA, especially within the deeper stations. The higher diversity may be as a result of increased protection within the MPA, but may also be due to a number of other factors, such as the habitat heterogeneity or the influences of environmental variables for example changes in pH, turbidity or light intensity. However, no measure of environmental variables was made during this study. The area was found to have high habitat heterogeneity by Blamey et al. (2012) and more diverse habitats may support more distinctive species assemblages, increasing diversity within an area (Gotelli and Colwell 2010). The study was conducted during the reported upwelling period within the study area, which may influence the findings with regards to higher diversity and productivity as a result of increased nutrient availability (Gibbons and Hutchings 1996).

Within the study area, the location of samples had a greater effect between the variances of species diversity and richness of samples than depth. This result, as well as the significantly higher mean diversity and species richness of stations inside the Betty's Bay MPA, should be further investigated as changes in assemblages and/or diversity of species are often used as indicators of the impact a reserve or protected area has on an ecosystem (NRC 2001). Götz et al. (2013) stated that, before measuring the effectiveness of an MPA using cross-boundary comparisons (i.e. between areas inside and outside of the MPA), it is important to establish that all differences found may be due to the same attributes, for example rates of exploitation. Baseline studies of habitat, seasonality and other environmental factors within and around the MPA to be assessed should be completed prior to the cross-boundary comparison in order to ensure this (Götz et al. 2013). It is therefore important that these results be further tested with regards to differences in habitats or other environmental factors to assess whether protection within the MPA was the cause for the significant differences.

The higher percentage cover of benthic organisms (Table 3.1) in shallow stations compared to deeper stations could be as a result of greater nutrient availability and more physical disturbance by wave action and inshore currents (Garrabou et al. 2002). The environmental variability in the shallower reaches may result in many organisms having faster growth and reproduction rates (Garrabou et al. 2002). The faster growth and reproduction rates of these species allow them to occupy more space enabling them to out-compete slower growing organisms (Underwood 2000, Garrabou et al. 2002). As a result, diversity in the shallower-reaches could be reduced (Garrabou et al. 2002). Many studies, both around the coast of
South Africa (Celliers et al. 2007, Blamey and Branch 2012) as well as internationally (Garrabou et al. 2002, Balata and Piazzi 2008), found that benthic organisms in shallower marine environments were less diverse than in deeper environments. This does not seem to be the case within the study area. While percentage cover was significantly lower in deeper samples within the study area, location had a greater effect on species diversity than depth. However, the standard error of the mean of species diversity between deep samples was higher than that of shallow samples, indicating a greater variance in species diversity within the deep samples.

Deep stations were also responsible for the highest and lowest mean diversities, species richness and evenness within the study area (Table 3.3), further indicating the variability between these stations. Blamey and Branch (2012) found a similar increasing trend in heterogeneity in species composition with depth, in the area. The high significant differences in diversity between the deep stations DOE and DOW to almost of the other stations as well as the low values of species richness and abundance calculated for these stations, could explain the significantly higher species richness, percentage cover and diversity found for stations inside of the MPA compared to those outside of the MPA. The higher percentage cover of sand in these two deep stations compared to the rest may indicate a different habitat type which supports fewer macro-benthic species than stations dominated by hard substrata (Thrush and Dayton 2002).

4.3 Assemblage Structure

Detailed studies at a community level are required to make informed decisions regarding the organisation of marine benthic assemblages in sublittoral marine environments (Garrabou et al. 2002). Community-level studies are especially necessary in areas known to have a heterogeneous community structure such as the warm temperate reefs of the Agulhas bioregion where the study area is situated (Sink et al. 2011a). Multivariate analyses, such as MDS ordinations, allow for the community composition within an assemblage to be investigated, and are required to be accurately interpreted for relevant decisions to be made. The high stress values produced by the MDS ordinations of both depth (Figure 3.6) and location (Figure 3.3) percentage cover data matrices suggests that the data points are close to being arbitrarily placed, which could result in misleading interpretation (Clarke and Warwick 2001). The high stress levels may be as a result of the high number of samples used as too many samples do not allow for distances, and therefore similarities, between samples to be accurately represented when using an MDS ordination (Clarke and Warwick 2001). When the mean percentage cover per station was used a much lower stress level was produced, providing a better ordination. This allowed for the similarities between the
sampling stations to be accurately interpreted for further analyses (Clarke and Warwick 2001).

The ANOSIM of the mean percentage cover for locations, which produced a Global R-value that was not significant, and the lack of definite natural groupings of communities inside and outside the MPA, could be interpreted to suggest that protection within the MPA does not have a significant effect on community composition in the area. However, this is not conclusive as the lack of groupings could also be as a result of a number of factors such as differences in habitat or other environmental factors, which are not necessarily related to added protection. The much stronger clustering of groupings associated with depth, as opposed to location (Figure 3.5), suggested that depth differences have a stronger influence on community structure than whether these organisms are inside or outside the MPA.

The influence of depth was further revealed in almost all of the multivariate analyses of data permuted using depth as a factor (Figures 3.6-3.8, Figure 3.16b and Figure 3.20b), including the ANOSIM, which revealed that mean percentage cover per species per sample were also significantly different between depths. Differences in community composition with depth were also previously found by Blamey and Branch (2012) within and around the study area. During the study it was found that kelp communities reduced with depth, whilst understorey algal communities became increasingly diverse with depth (Blamey and Branch 2012). In a study of sublittoral reefs in the Mediterranean, Garrabou et al. (2002) also found that the species composition and abundance of shallow and deep water assemblages of macro-algae differed greatly from each other. Garrabou et al. (2002) found a similar distinctiveness in community composition with changes in depth gradients on sublittoral reefs in the Mediterranean. It was suggested by Garrabou et al. (2002) that the structuring of assemblages according to depth gradients on all sublittoral rocky reefs, are similar. The similarity was suggested as environmental changes with changes in depth are common in many sublittoral habitats (Garrabou et al. 2002). While depth may not necessarily be described as an ecological factor contributing to the distribution of marine benthic organisms within the study area, the important abiotic factors influenced by changes in depth play a large role, as benthic organisms are distributed according to their tolerance levels of these abiotic factors (Garrabou et al. 2002, Harley et al. 2003, Clearly et al. 2005, Celliers et al. 2007). Species composition may be influenced by the degree of light penetration, water movement, temperature, nutrient availability and sedimentation (Thorne-Miller 2009, Garrabou et al. 2002, Harley et al. 2003, Clearly et al. 2005, Celliers et al. 2007).

The above-mentioned abiotic factors may be further influenced by the physical characteristics of the ocean environment surrounding the area (Lombard et al. 2004, Sink et
al. 2011a). The area surrounding the study area is affected by physical characteristics such as diverse current systems (Lutjeharms et al. 2001, Lutjeharms 2006) and the study area experiences seasonal variability brought on by upwelling events (Gibbons and Hutchings 1996). The presence of two distinct groupings as an apparent result of depth within this study area, at a multi-taxon level, adds to a greater knowledge of the reef dynamics and benthic species distribution in the Betty’s Bay area. This therefore enables managers to create relevant and holistic, scientifically-based, conservation strategies that are not restricted to a single species or taxonomic group (Clearly et al. 2005).

4.4 Floral and Faunal Composition

When species data are not available for analyses in biodiversity studies, genus richness has been suggested as a reliable surrogate (Grelle et al. 2002, Cardoso et al. 2004, Mazaris et al. 2008). The use of genus richness as a surrogate for species, as opposed to taxonomic groups, has also been revealed as suitable within the study area. It was further revealed by the RELATE statistic (Rho = 0.895), as well as the similarity in the cluster analyses and MDS ordinations of generic and all species percentage cover, that genus richness is a suitable surrogate for species richness. Generic percentage cover would have been redundant to use in conjunction with species percentage cover for further investigation within this study. Therefore, taxonomic group data was further investigated. Taxonomic group analyses allowed for the patterns in assemblage structure illustrated above to be investigated and discussed further based on the characteristics portrayed by each group (Bremner et al. 2003).

Algae and Cnidaria played the largest role in the similarity within the area in terms of taxonomic groups and as well as the species responsible for similarity. The high percentage cover of Algae within the study area may, as shown in previous studies (Tarr et al. 1996, Day and Branch 2000, Blamey et al. 2010, Blamey and Branch 2012), be a result of the relatively low abundance of herbivorous species such as abalone (Haliotis midae) and the smooth turban shell (Turbo cidaris cidaris Gmelin, 1791), and the Cape sea urchin (Parechinus angulosus (Leske, 1778)) which was unrepresented in photo-quadrats, within the study area. The lack of representation of the Cape sea urchin is cause for concern and should be further investigated as other studies within the area had previously found that these species were declining. The low abundance could also be attributed to the study method used, however, Blamey et al. (2010) and Blamey and Branch (2012) also found a decrease in herbivorous species in the Betty’s Bay area. The high percentage cover of Algae and low abundance of herbivorous species in this area may also be attributed to the reduction of herbivores, due to an increase in the West Coast rock lobster (Jasus lalandii) population (Tarr et al. 1996, Day
and Branch 2000, Mayfield and Branch 2000, Blamey et al. 2010, Blamey and Branch 2012). It may be said that *J. lalandii* has caused a trophic cascade within the area. This is when predatory interactions involve three trophic levels i.e. carnivores cause the suppression of herbivores which in turn results in an increase in plant biomass (Mazaris et al. 2008). However, this should be further tested as this study did not measure the abundance of motile species, such as *J. lalandii* nor functional groupings such as the abundance of herbivorous species and no historical data was consulted during this study. It is for this reason that the high percentage cover of Algae, relative to other taxonomic groups, within this area cannot, conclusively, be attributed to the west coast rock lobster diminishing herbivorous species. Other factors such as upwelling, currents, topography, sediments etc. which could affect species distribution and settlement may play a role and should be further investigated (Garrabou et al. 2002, Celliers et al. 2007). The low percentage cover of Arthropoda recorded during this study may be attributed to the mobility of species within this taxonomic group as most arthropods are motile (Brose and Martinez 2004). An assessment of arthropods would also require a much greater sampling intensity for all species within the area to be sampled (Brose and Martinez 2004).

Götz et al. (2009a) conducted a similar study in the Goukamma MPA on the south coast of South Africa. During the study, benthic taxa were also compared between protected and exploited sites. The study revealed that a higher percentage cover of Porifera was found inside the MPA, with a lower percentage cover of Algae and Crinoidea (Echinodermata), and it was found that Bryozoa dominated areas outside the MPA (Götz et al. 2009a). Götz et al. (2009a) were able to almost conclusively attribute the higher abundances of Porifera and Crinoidea to their location outside of the MPA, through a survey of oceanographic factors by regularly taking water, temperature and turbidity measurements. Within the study area, however, Porifera had a higher percentage cover in areas outside of the MPA, but lower species richness in samples outside the MPA. However, as previously mentioned, these results cannot be attributed, conclusively, to the location of samples. It would be beneficial to conduct further research into the benefit of the Betty’s Bay MPA for benthic taxa, as many of the taxonomic groups were found to have a higher percentage cover and species richness outside of the MPA (Figure 3.12a and Figure 3.13a, respectively).

The higher mean percentage cover of Algae in the shallower-reaches and the increase of Porifera, Bryozoa and other sessile filter- and suspension-feeders with increasing depths (Figure 3.12b) may be responsible for the similarity within deep and shallow stations (Table 3.6) and the two groupings of the taxonomic groups at the different depths (Figure 3.19). These findings are similar to results found in other studies (Kingsford and Battershill 1998, Celliers et al. 2007). The differences in the floral and faunal composition between the two
depths within the study area, may be as a result of light penetration (Celliers et al. 2007). Non-phototrophic species (i.e. those not directly dependent on light for productivity e.g. elegant feather stars) are able to out-compete phototrophic species (i.e. those reliant on light for productivity e.g. sea fans containing zooxanthellae) as the degree of light penetration decreases with depth (Steneck 1986, Celliers et al. 2007, Götz et al. 2009a). Götz et al. (2009a) found a similar decrease in Algae percentage cover with increasing depth in Goukamma, on the south coast of South Africa. In a similar study in an MPA on a rocky reef in Brazil, Parravincini et al. (2013) also found Algae and Porifera to be the most species rich groups. This high species richness is important as these taxa, together with ascidians, are habitat formers for other species and Algae are an important cover on subtidal reefs (Kingsford and Battershill 1998). The large contribution of filter-feeders in the deeper depths is also of importance as these groups assist in the maintenance of healthy marine ecosystems (van Soest et al. 2012) by assisting in the improvement of water quality (Ostroumov 2005). Filter-feeders absorb and filter the microscopic organisms in water providing a link between the nutrients of the open ocean and the benthic environment (van Soest et al. 2012). Other organisms and the ecosystem as a whole are therefore able to benefit from the functioning of filter-feeders as filter-feeders filter large volumes of water, with particles of differing sizes, and only assimilate the few nutrients required for the filter-feeding organism, releasing the remainder (Ostroumov 2005).

Colonial species, such as sponges (van Soest 2007) which are more resilient than non-colonial species such as molluscs, normally have a much larger percentage cover, as they occupy more space within an area (Kingsford and Battershill 1998). The relatively high percentage cover of sponges within the study area is evidence of this. Sponges have an important function and also make up a large component of marine benthic communities due to the numerical abundance, biomass dominance and longevity of these colonial species (Arntz et al. 2006, van Soest 2007, Bell 2008). Porifera are an important food source and efficient filter-feeders (van Soest et al. 2012). Sponges contribute to organic production through symbiotic relationships with species that are nitrogen-fixers (van Soest et al. 2012). Many species within this taxonomic group are important bio-eroders able to successfully compete with other sessile benthic invertebrates and certain groups of sponges are able to bind loose substrate material into stable surfaces (van Soest et al. 2012). Samaai et al. (2010) reported a decrease in species richness within Porifera, with increasing depth in the iSimangaliso Wetland Park, KwaZulu Natal. Despite the differences in geographic location, this also seems to be the case in the study area where the mean species richness of sponges was higher in the shallower reaches. In this study, the entire study area would be considered within one depth range, namely the deep sub-photic zone which, according to Samaai et al. (2010), is between 10 and 30 m, therefore also providing a possible
explanation for the lack of an increase in poriferan species richness with an increase in depth within the study area.

Thinly encrusting coralline algae, such as *L. foveatum*, are among the most abundant organisms in the marine environment that are able to inhabit hard substrata within the photic zone as well as great depths (Steneck 1986). Due to the two-dimensional method of primary growth, *L. foveatum* is able to occupy large areas and compete for space through interference (Steneck 1986), as well as reduce overgrowth and competition through the regeneration of its margins (meristematic, or growth, cells are present near the margins of the algae) (Keats and Maneveldt 1994). The imbricate surface of *L. foveatum*, which is as a result of regeneration of the thallus margins at the surface, enables this thinly encrusting coralline to grow at a much faster rate than, and often over, thicker encrusting coralline algae enabling it to dominate more space (Keats and Maneveldt 1994). Herbivory is the main disturbance to encrusting coralline algae (Steneck 1986). Therefore, the possible reduction of herbivory in the area, due to the reduction of grazers (Blamey et al. 2010, Blamey and Branch 2012), together with the ability of this species to compete for space, regenerate, fast growth and growth form (Steneck 1986, Keats and Maneveldt 1994), plays a role in the success of *L. foveatum* in this area. The high percentage cover of *J. adhaerens* in the study area may be explained by the morphology of this species. *Jania adhaerens* is a calcareous species of macroalgae, and is thus high in calcium carbonate (Littler and Littler 1980, Hata and Kato 2002). The calcareous nature of this species allows it to combat predation as most herbivorous species will find little nutritional value and very little energy in the calcareous skeleton (Littler and Littler 1980, Hata and Kato 2002). This species is also less reliant on light for photosynthesis and is thus, not restricted to the phototrophic zone (Littler and Littler 1980).

Eight of the 32 cnidarian species recorded in the study area, were sea anemones. Acuña and Griffiths (2004) reported that 49 species of sea anemone were recorded along the entire coast of Southern Africa, eight of which were recorded in this study (*Anthopleura michaelseni* (Pax, 1920); *Anthostella stephonsoni* Carlgren, 1938; *Anthothoe chilensis* (Lesson, 1830); *Corynactis annulata* (Verrill, 1867); *Halacampa capensis* Carlgren, 1938; *Isanthus capensis* Carlgren, 1938; *Preactis millardae* England in England & Robson, 1984 and *Pseudactinia flagellifera* (Hertwig, 1882)). Considering the fairly small size of the study area in comparison to the rest of the coast, it can be said that the recorded species richness of sea anemones are fairly high, a finding in accordance with Acuña and Griffiths’ (2004) statement that it is apparent that anemones are more diverse on the south-west coast. Most cnidarians exhibit a life-cycle organised into the succession of three main stages, namely the planula, hydroid and medusa stages (Boero et al. 1992). This life-cycle, termed the alteration of generations or metagenesis (Boero et al. 1992), allows for greater distribution of this group (Kingsford
and Battershill 1998, Gibbons et al. 1999), which, together with upwelling which increases productivity (Gibbons and Hutchings 1996), could have resulted in the high representation of *Eudendrium* spp 1 within the area. The bushy hydroid, *Eudendrium* spp 1, is an important attached epifauna which provides food and shelter for many organisms (Collie et al. 2000). In a study in which sites disturbed by benthic trawling was compared with sites that were undisturbed, Collie et al. (2000) found that bushy hydroids and bryozoans were more numerous within undisturbed sites than disturbed sites. The high percentage cover and higher contribution of this species within the study area, in comparison to other represented species, is therefore of great importance and should be further investigated as this species had a higher contribution to similarity within inside and deep stations than outside stations and shallow stations (Figure 3.9 and 3.10).

Echinoderms played a higher role in the dissimilarity of samples within the study area, compared to that of other taxonomic groups, (Table 3.6). The mean abundance of echinoderms was between 1.20 and 1.40, indicating at least one individual per sample, despite the low number of species (four). The large representation of this taxonomic group within the study area can be explained by the diversity of the Phylum Echinodermata and the various life-styles portrayed within, and variety of habitats inhabited by this group (Uthicke et al. 2009). Even though this taxonomic group was not represented by many species within the study area three, of the five echinoderm Classes (Ophiuroidea, Crinoidea, Asteroidea, Holothuroidea and Echinoidea) were represented, indicating the diversity of this group (Pawson 2007). The represented species and their respective classes were *Amphiura capensis* Ljungman, 1867 from the Class: Ophiuroidea, *Comanthus wahlbergi* (Müller, 1843) and *Tropiometra carinata* (Lamarck, 1816) from the Class: Crinoidea and *Austrofromia schultzei* (Döderlein, 1910) from the Class: Asteroidea.

Within the study area, Bryozoa was most responsible for the higher similarity within deep samples than within shallow samples and a large dissimilarity between these samples (Table 3.6). Bryozoans are mostly suspension-feeding organisms which feed by the movement of body parts, such as cilia, creating a small current from which the animal picks particles and small organisms (Hunt 1925, Shunatova and Otrovsky 2001). Bryozoan are therefore less reliant on light and on wave action for feeding and are able to out-compete those taxonomic groups which are more reliant on these factors enabling Bryozoa to increase in cover and abundance at greater depths (Kingsford and Battershill 1998, Celliers et al. 2007). It is also apparent that Bryozoa were more successful inside the MPA as this taxonomic group made a higher contribution to similarity within samples inside of the MPA (Table 3.6). This is different to Götz et al. (2009a) who found Bryozoa in greater representation outside of the Goukamma MPA. The difference in distribution may however, be due to various factors such
differing habitats, ocean characteristics, upwelling etc. which should be further tested. Bryozoa also played a larger role in the dissimilarity between samples at the two locations (Table 3.6), compared to other taxonomic groups. This may be due to the higher variation in percentage cover of Bryozoa relative to the groups mean percentage cover (mean percentage cover = 4.44 ± 6.91 % i.e. large standard deviation) together with the higher contribution of Bryozoa to similarity within samples inside of the MPA or possibly patchiness in distribution as a result of differing biotic and/or abiotic factors.

In addition to the above mentioned indigenous flora and fauna, alien and cryptogenic species were also found within the study area. Many alien species have been accidentally introduced around the coast of South Africa through ships’ ballast water for example, often causing the displacement of indigenous species (Wynberg 2002). In the study area, few alien (Ascidian species: Clavelina lepadiformis (Müller, 1776) and Diplosoma listerianum (Milne Edwards, 1841)) and some cryptogenic (bryozoan species: Bugula neritina (Linnaeus, 1758), cnidarian species: Obelia dichotoma (Linnaeus, 1758) and arthropod species: Amphibalanus amphitrite (Darwin, 1854)) species (Robinson et al. 2005), were found. The low number of alien and cryptogenic species corresponds with Awad et al. (2002) and Scott et al. (2012) who stated that there is a high level of endemism and restricted species in the South-western Cape. The low number of alien and cryptogenic species may also be explained by the distance of the study area from any large harbours sheltered lagoons or estuaries where most alien species are restricted to (Robinson et al. 2005).
Chapter 5: CONCLUSION AND GENERAL RECOMMENDATIONS

The study has revealed that the Betty's Bay area is heterogeneous in terms of represented species and macro-benthic organisms are distributed spatially according to depth. The community shift with increasing depth, which was revealed, concurs with the literature as well as previous studies conducted in and around the Betty's Bay area (Blamey et al. 2010, Blamey and Branch 2012). Thus, indicating a system similar to other similar subtidal benthic communities located on hard substrata.

The inclusion of the Betty's Bay MPA within the Kogelberg Biosphere Reserve, ensures the connectivity of the coastal, inshore and offshore zones within this area. However this inclusion may not be enough to ensure the MPAs integrity to preserve the biodiversity within the area. This study revealed that diversity and species richness was higher in areas inside the MPA, whilst stations outside the MPA had a higher percentage cover for most taxa. The difference between the diversity inside and outside of the MPA indicated that the MPA is potentially conserving biodiversity on rocky reefs within the Kogelberg Region. The significant difference and lower measurements at deep stations on either side of the MPA should be investigated.

Managers and stakeholders should consider expanding the protected area to include the rocky reefs situated outside the MPA, and in so doing, protect it from increased utilisation and the degradation of biodiversity. During the proposal for the seaward extension of the Goukamma MPA, Götz et al. (2009b) suggest that simple adjustments may be possible at many of South Africa's MPAs in order to achieve fishery and conservation goals. The extension to the Goukamma MPA was proposed to include greater areas of reef habitats for the increased protection of fish eggs and sessile macro-benthic invertebrate larvae (Götz et al. 2009b). Expansion of the Betty's Bay MPA will allow for increased reef protection, as proposed for the Goukamma MPA, and possibly increase the diversity within the area.

The high presence of Algae in the area can influence the settlement of other organisms which could result in a much higher epifaunal and infaunal distribution and reduction of macro-fauna abundance in the area (Kingsford and Battershill 1998). *Eudendrium* spp 1, a cnidarian with a high percentage cover in this area, is evident of this fact. While the Betty’s Bay MPA seems to be functioning in terms of maintaining biodiversity within the Kogelberg Region, the protection of carnivorous and/or scavenging species such as *J. lalandii* within it can result in the loss of biodiversity over time. *J. lalandii* was found by Blamey et al. (2010) to be reducing herbivore abundance within the Betty’s Bay area through predation, and revealed negative consequences for the benthic biodiversity as a result. It is therefore
essential that a monitoring programme be implemented to allow for more effective management of the benthic community within the Kogelberg Region (Tunley 2009) and that further studies are conducted which compare historical and current biodiversity research within the area.

Monitoring of an MPA and surrounding areas enable managers to evaluate changes, which are important for determining the effectiveness, improve design and providing progress reports to stakeholders (NRC 2001). The objectives of an MPA will determine what needs to be monitored. Monitoring programmes should include categories such as the structure of the marine environment, habitat maintenance or recovery, indicators of water quality or environmental degradation and socio-economic attributes or impacts such as the effect of the MPA on the surrounding communities (NRC 2001). It is suggested that a monitoring programme be put in place for the benthic community of the Kogelberg Region. The monitoring programme of the benthic community should be standardised, representative of the area and able to be replicated and compared across sites of differing protection (NRC 2001) and should include sampling sessions throughout the year and not only within the upwelling period. When comparing across protected area boundaries, it is important to measure environmental factors as well in order to determine whether these factors do not differ across sites as differing environmental factors may be the cause for the differing diversities (Götz et al. 2013).

Should a similar method be employed for macro-benthic monitoring or further studies within the area, it is suggested that sites remain fixed, including a greater number of sites outside of the MPA i.e. a more balanced sampling design. The photo-quadratic method, whilst rapid, has its downfalls in that many smaller species may be missed and only the surface layer is included in the survey. Many photographs may be unclear or some species may be missed or incorrectly identified, by an inexperienced eye, due to unclear areas in photographs. It is for this reason and the heterogeneity of the area that a large number of photo-quadrats, no less than 168, should be collected per site. A high resolution camera should be used to ensure that photographs are clear enough for the visual identification of benthic organisms, as this proved a challenge for the identification of some species. A scale bar should also be incorporated into the quadrat design to further assist with organism identification. Photo-quadrats should be collected annually as the effects of changes to benthic communities are cumulative with time therefore, temporal comparisons are necessary to provide evidence of changes which may take place (Schleyer et al. 2008). The photo-quadrats will serve as a permanent means of monitoring community structure, much like that of fixed-point photography in terrestrial environments. A combination of percentage cover, for colonial
species and Algae, as well as individual abundance, for non-algal/colonial species, should be recorded and analysed separately.

A higher taxon approach may be utilised during analysis of photo-quadrats to reduce costs, expertise required and time spent (Williams and Gaston 1994, Cardoso et al. 2004). It is suggested that managers identify macro-benthic organisms to at least generic level as this was revealed to be the most ideal surrogate for species within the study area. Indicator groups, such as macroalgae, which are taxonomically and ecologically well known and documented, can be easily surveyed and identified, can also be used by to monitor the benthic environment within the Betty’s Bay area (Gladstone 2002). Managers would especially need to monitor the percentage cover of L. foveatum which is currently in high abundance in the area and limits the settlement of other species, as well as the abundance of herbivore species in the area.

As suggested during this baseline study, a survey of only sessile and semi-motile species is not conclusive enough for decision making in the management of the MPA and surrounding areas. Therefore should a monitoring programme be implemented within the area, it would need to be more comprehensive and include in-depth, ecosystem-based research of the marine environment within the Kogelberg Region. This would include the assessment of environmental variables such as water quality etc. as well as motile species and non-benthic environments and communities because the structure of all communities is variable with space and time and each community responds differently to physical and biological factors (Pinnegar et al. 2000). Therefore, decisions should not be based on single species or communities as this may result in negative implications elsewhere in the ecosystem. It is thus necessary and imperative that an ecosystem approach to the management be implemented during any adaption or modifications and species management of this MPA (Blamey et al. 2010). On-going research is necessary within the area and other studies which include environmental factors should accompany the results obtained from this particular study.
REFERENCES


Figure 1: A histogram showing the distribution of variances within groups, of (a) percentage cover (%) and (b) species richness (S) data, depicting the consistency of data with the assumptions for parametric tests.
Figure 2: A histogram showing the distribution of variances within groups of species diversity (H’) data, depicting the consistency of data with the assumptions for parametric tests.
## APPENDIX B – FULL SPECIES LIST

Table 1: Full species list

<table>
<thead>
<tr>
<th>Taxonomic group and Scientific name</th>
<th>Naming Authority (WoRMS database; Downloaded 21 July 2015)</th>
<th>Common name</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>ALGAE</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Acrosorium acrospermum</td>
<td>(J.Agardh) Kylin, 1938</td>
<td>Plain acrosorium</td>
</tr>
<tr>
<td>Algae spp 1</td>
<td></td>
<td>Algae spp 1</td>
</tr>
<tr>
<td>Amphiroa bowerbankii</td>
<td>Harvey, 1849</td>
<td>Nodular coralline</td>
</tr>
<tr>
<td>Axillariella constricta</td>
<td>(Kützing) Gruber, 1896</td>
<td>Constricted axils</td>
</tr>
<tr>
<td>Bifurcariopsos capensis</td>
<td>(Areschoug) Papenfuss</td>
<td>Upright wrack</td>
</tr>
<tr>
<td>Botryocarpa prolifer</td>
<td>Greville, 1830</td>
<td>Black spot</td>
</tr>
<tr>
<td>Botryoglossum platycarpum</td>
<td>(Turner) Kützing, 1843</td>
<td>Botryoglossum</td>
</tr>
<tr>
<td>Brown algae spp 6</td>
<td></td>
<td>Brown algae spp 1</td>
</tr>
<tr>
<td>Calliblepharis fimbriata</td>
<td>(Greville) Kützing, 1843</td>
<td>Eyelid-weed</td>
</tr>
<tr>
<td>Caulerpa holmesiana</td>
<td>G.Murray, 1891</td>
<td>Feathery caulepra</td>
</tr>
<tr>
<td>Champaia compressa</td>
<td>Harvey, 1838</td>
<td>Compressed champia</td>
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<tr>
<td>Cladophora capensis</td>
<td>(C.Agardh) De Toni, 1889</td>
<td>Cape cladophora</td>
</tr>
<tr>
<td>Cladophora spp 1</td>
<td>Kützing, 1843</td>
<td>Cladophora spp 1</td>
</tr>
<tr>
<td>Desmaresia firma</td>
<td>(C.Agardh) Skottsberg, 1907</td>
<td>Acid weed</td>
</tr>
<tr>
<td>Dictyopteris ligulata</td>
<td>(Suhr) O.C.Schmidt, 1938</td>
<td>Smooth-tongued dictyopteris</td>
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<tr>
<td>Dictyopteris serrata</td>
<td>(Areschoug) Hoyt, 1920</td>
<td>Serrated dictyopteris</td>
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<td>Dictyota spp 1</td>
<td>J.V.Lamouroux, 1809</td>
<td>Intricate dictyota</td>
</tr>
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<td>Ecklonia maxima</td>
<td>(Osbeck) Papenfuss, 1940</td>
<td>Sea bamboo</td>
</tr>
<tr>
<td>Encrusting coralline algae spp 1</td>
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<td>Encrusting coralline algae spp 1</td>
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<td>Exallosorus harveyanus</td>
<td>(Pappe ex Kützing)</td>
<td>Multi-fanned zonaria</td>
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<td>Gelidium abbottiorum</td>
<td>R.E.Norris, 1990</td>
<td>Abbott's jelly-weed</td>
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<td>Gelidium capense</td>
<td>(S.G.Gmelin) P.C.Silva, 1987</td>
<td>Cape jelly-weed</td>
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<td>Grateloupa capensis</td>
<td>O.De Clerck, 2005</td>
<td>Tattered-rag weed</td>
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<td>Green algae spp 1</td>
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<td>Green algae 1</td>
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<tr>
<td>Green algae spp 2</td>
<td></td>
<td>Green algae 2</td>
</tr>
<tr>
<td>Gymnogongrus spp 1</td>
<td>Martius, 1833</td>
<td>Fine gymnogongrus</td>
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<tr>
<td>Heydrichia woelkerlingii</td>
<td>R.A.Townsend, Y.M.Chamberlain &amp; Keats, 1994</td>
<td>Velvety coralline crust</td>
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<tr>
<td>Hymenena venosa</td>
<td>(Linnaeus) C.Krauss, 1846</td>
<td>Veined oil-weed</td>
</tr>
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<td>Hypnea ecklonii</td>
<td>Suhr, 1836</td>
<td>Straight-tipped hypnea</td>
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<tr>
<td>Hypnea viridis</td>
<td>Papenfuss, 1947</td>
<td>Iridescent hypnea</td>
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<tr>
<td>Jania adhaerens</td>
<td>J.V.Lamouroux, 1816</td>
<td>Finely forked coralline</td>
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<td>Jania cultratum</td>
<td>(Harvey) J.H.Kim, Guiry &amp; H.-G.Chi, 2007</td>
<td>Arrowhead coralline</td>
</tr>
<tr>
<td>Kentrophora natalensis</td>
<td>(J.Agardh) S.M.Wilson &amp; Kraft, 2001</td>
<td>Plectrum weed</td>
</tr>
<tr>
<td>Laminaria pallida</td>
<td>Greville, 1848</td>
<td>Split-fan kelp</td>
</tr>
<tr>
<td>Leptophyllum foveatum</td>
<td>Y.M.Chamberlain &amp; D.W.Keats, 1994</td>
<td>Thin coralline crust</td>
</tr>
<tr>
<td>Leptophyllum spp 1</td>
<td>W.H.Adey, 1966</td>
<td>Thin coralline crust 2</td>
</tr>
<tr>
<td>Lobophora variegata</td>
<td>(J.V.Lamouroux) Womersley</td>
<td>Lobe-fan</td>
</tr>
</tbody>
</table>
**Martensia elegans**
Hering, 1841

**Martensia flabelliformis**
Harvey ex J.Agardh, 1863

**Pachymenia carnosa**
(J.Agardh) J.Agardh, 1876

**Pachymenia cornea**
(Kützing) Chang, 1970

**Plocamium beckeri**
F.Schmitz ex Simons, 1964

**Plocamium corallorhiza**
(Bory de Saint-Vincent, 1834

**Plocamium rigidum**
Kützing, 1849

**Plocamium suhrii**
(Lyngbye) P.C.Silva, 1987

**Portieria homemannii**
(C.Agardh) Falkenberg, 1897

**Pterosiphonia cloiophylla**
(M.A.Pocock, 1953

**Red algae spp 1**

**Red algae spp 2**

**Red algae spp 3**

**Red algae spp 4**

**Rhodomelopsis africana**
(J.Agardh) Kylin, 1938

**Rhodophyllis reptans**
(A.Agardh) Womersley, 1996

**Rhodymenia capensis**
(Leuckart) P.C.Silva, 1952

**Rhodymenia natalensis**
(Montagne) M.J.Wynne, 2011

**Rhodymenia obtusa**
Kützing, 1849

**Rhodymenia pseudepalmata**
(Linnaeus) Huisman & R.A.Townsend, 1993

**Sonderophycus capensis**
Berkeley, 1835

**Spyridia cupressina**
(Quatrefages, 1848)

**Tayloriella tenebrosa**
(Teuscher, 1874)

**Tricleocarpa fragilis**
(Linnaeus) Daudin, 1800

**ANNELODA**

**Filograna implexa**
Berkeley, 1835

**Golfingia capensis**
(Teuscher, 1874)

**Gunnarea gaimardi**
(Quatrefages, 1848)

**Polychaete spp 1**

**Protula bispinalis**
(Savigny, 1822)

**Pseudopotamilla reniformis**
(Bruquére, 1789)

**Sabella spallanzani**
(Gmelin, 1791)

**Serpula vermicularis**
Linnaeus, 1767

**Spirorbis spp 1**

**Thelepus spp 1**

**ARTHROPODA**

**Amphibalanus amphitrite**
(Darwin, 1854)

**Guinsea chabrus**
(Linnaeus, 1758)

**Jasus lalandii**
(H. Milne Edwards, 1837)

**ASCIDIA**

**Aplidiopsis tubiferus**
Linnaeus, 1767

**Aplidium flavolineatum**
F. Monniot, 2001

**Aplidium pantherinum**
(Sluit, 1898)

**Aplidium spp 1**

**Ascidia incrassata**
Heller, 1878

**ex E.C.Oliveira, 1977**

**elegant net fan**

**Camouflaged net fan**

**Red-rubber weed-no holes**

**Red-rubber weed-holes**

**Becker's Plocamium**

**Coral plocamium**

**Rigid plocamium**

**Suhr's Plocamium**

**Little hands**

**Red feather-weed**

**Red algae 1**

**Red algae 2**

**Red algae 3**

**Red algae 4**

**Rhodomelopsis**

**Roseleaf**

**Cape wine-weed**

**Stalked roseweed**

**Broad wine-weed**

**Palmate roseweed**

**Red fan-weed**

**Untidy spyridia**

**Tayloriella**

**Tricleocarpa**

**Filigreed coral-worm**

**Common peanut worm**

**Cape reef-worm**

**Polychaete spp 1**

**Red fanworm**

**Gregarious fanworm**

**Pencil worm**

**Operculate fanworm**

**Spiral fanworms**

**Tangleworms**

**Striped barnacle**

**Cape rock crab**

**West coast rock lobster**

**Aplidiopsis tubiferis**

**Aplidium flavolineatum**

**Aplidium pantherinum**

**Aplidium spp 1**

**Ascidia incrassata**
Ascidia spp 1
Ascidian spp 1
Ascidian spp 2
Atriotheca spp 1
Botryllus elegans
Botryllus gregalis
Botryllus magnicoecum
Botryllus meandrius
Botryllus spp 1
Botryllus spp 2
Clavelina lepadiformis
Didemnum spp 1
Didemnum spp 2
Didemnum spp 3
Didemnum spp 4
Diplosoma listerianum
Eudistoma spp 1
Euherdmania divida
Gynandrocarpa placenta
Lissoclinum spp 1
Polyandrocarpa spp 1
Pseudodistoma spp 1
Pseudodistoma spp 2
Pseudodistoma spp 3
Pycnoclavella filamentosa
Pycnoclavella narcissus
Pyura herdmani
Styela plicata
Sycosoa spp 1
Sycosoa arborescens
Trididemnum cerebriforme
Trididemnum spp 1
Trididemnum spp 2

**BRYOZOA**

Adeonella conspicua
Adeonella pluscula
Alcyonidium rhomboidale
Bicellariella bonsai

Bryozoan spp 1
Bryozoan spp 2
Bryozoan spp 3
Bugula dentata
Bugula flabellata
Bugula neritina
Chaperia spp 1
Gigantopora polymorpha
Jellyella tuberculata

Linnaeus, 1767
Kott, 1983
(Quoy & Gaimard, 1834)
(Sluiter, 1898)
(Hartmeyer, 1912)
(Sluiter, 1898)
Gaertner, 1774
Gaertner, 1774
(Müller, 1776)
Savigny, 1816
Savigny, 1816
Savigny, 1816
(Smilne Edwards, 1841)
Caullery, 1909
Monniot, Monniot, Griffiths & Schleyer, 2001
(Quoy, 1834)
Verrill, 1871
Michaelsen, 1904
Michaelsen, 1924
Michaelsen, 1924
Michaelsen, 1924
Kott, 2005
Kott, 2005
(Drasche, 1884)
(Lesueur, 1823)
Lesson, 1832
Hartmeyer, 1912
Hartmeyer, 1913
Della Valle, 1881
Della Valle, 1881
Hayward & Cook, 1983
Hayward, 1888
O'Donoghue, 1924
Florence, Hayward & Gibbons, 2007
(Lamouroux, 1816)
(Thompson, in Gray, 1848)
(Linnaeus, 1758)
Jullien, 1881
(Busk, 1884)
(Bosc, 1802)
Crevice ascidian
Ascidian spp 1
Ascidian spp 2
Atriotheca sp
Seaweed ascidian
Variable ascidian
White-ringed ascidian
Meandering ascidian
Botryllus spp 1
Botryllus spp 2
Bell ascidian
Didemnum spp 1
Didemnum spp 2
Didemnum spp 3
Didemnum spp 4
Gossamer Ascidian
Eudistoma spp 1
Elephant's ears
Lissoclinum spp 1
Polyandrocarpa spp 1
Pseudodistoma spp 1
Pseudodistoma spp 2
Pseudodistoma spp 3
Pycnoclavella filamentosa
Choir boys
Herdmann's redbait
Styela plicata
Sycosoa spp 1
Fan Ascidian
Brain ascidian
Trididemnum spp 1
Trididemnum spp 2

Forked false coral
Adeonella pluscula
Soft false coral
Bonsai bush bryozoan
Bryozoan spp 1
Bryozoan spp 2
Bryozoan spp 3
Dentate moss animal
Fan-shaped moss animal
Fouling moss animal
Scrolled false-coral
Staghorn false-coral
Membranous lace animal
Laminopora jellyae
Margaretta levinseni
Membranipora rustica
Menipea crispa
Reteporella lata

**CNIDARIA**
Aglaophenia pluma
Alcyonium fauri
Amphisbetta operculata
Anthopleura michaelseni
Anthostella spp 1
Anthostella stephensonii
Anthothoe chilensis
Balanophyllia bonaespei
Corynactis annulata
Ectopleura crocea
Eleutherobia variabile
Eudendrium spp 1
Eunephthya thyrsoides
Eunicella papillosa
Eunicella tricornata
Halicampa capensis
Homophyton verrucosum
Hydroid spp 1
Isanthus capensis
Isozoanthus capensis
Leptogorgia palma
Lytocarpia formosa
Macrorhynchia filamentosa
Obelia dichotoma
Parasphaerasclera valdiviae
Parazoanthus spp 1
Plumularia setacea
Preactis millardae
Pseudactinia flagellifera
Sertularella arbuscula
Stylaster nobilis
Thuiaria articulata

**ECHINODERMATA**
Amphiura capensis
Austrofromia schultzei
Comanthus wahlbergii
Tropiometra carinata

**MOLLUSCA**
Argobuccinum pustulosum
Bivalve spp 1
Bivalve spp 2

Pore-plated false-coral
Cactus bush bryozoan
Rustic lace animal
Curled lace moss animal
Lacy false-coral 2
Toothed feather-hydroid
Purple soft-coral
Wiry hydroid
Crevic anemone
Dwarf spotted anemone
Violet-spotted anemone
Striped anemone
Cup coral
Strawberry anemone
Tubular hydroid
Variable soft coral
Bushy hydroid
Cauliflower soft coral
Nipped sea fan
Sinus sea fan
Burrowing anemone
Warty sea fan
Hydroid spp 1
Ring-tentacle anemone
Cape Zoanthid
Palmate sea fan
Rusty feather hydroid
Smoky feather-hydroid
Thin-walled Obelia
Valdivian soft-coral
Cape Zoanthid 2
Plumed hydroid
Hedgehog anemone
False plum anemone
Planar hydroid
Noble coral
Jointed Hydroid

**ECHINODERMATA**
Amphiura capensis
Austrofromia schultzei
Comanthus wahlbergii
Tropiometra carinata

**MOLLUSCA**
Argobuccinum pustulosum
Bivalve spp 1
Bivalve spp 2

Pustular triton
Bivalve spp 1
Bivalve spp 2

Ljungman, 1867
Ljungman, 1867

Hooked brittle star
Equitailed brittle star

Equitailed brittle star
Granular starfish

Granular starfish
Common feather star

Common feather star
Elegant feather star
Burupena lagenaria
Burupena papyracea
Clionella spp 1
Haliotis midae
Janolus capensis
Janthina janthina
Mollusc spp 1
Mollusc spp 2
Mollusc spp 3
Nucella squamosa
Octopus spp 1
Octopus vulgaris
Sepia tuberculata
Turbo cidaris cidaris
Turritella carinifera

PORIFERA
Aaptos aaptos
Aplysilla rosea
Axinella spp 1
Callyspongia spp 1
Coelosphaera spp 1
Clathria dayi
Clathria hooperi
Clathria spp 1
Clathria spp 2
Clathria spp 3
Clathria spp 4
Clathria Thalysias oxitoxa
Cliona celata
Crambe acuata
Echinoclathria dichotoma
Geodia littoralis
Guitarra flamencca
Haliclona spp 1
Haliclona spp 2
Haliclona spp 3
Haliclona spp 4
Haliclona spp 5
Haliclona spp 6
Haliclona spp 7
Haliclona stilensis
Hymeniacidon perlevis
Hymeniacidon spp 1
Hymeniacidon spp 2
Ircinia arbuscula
Ircinia spp 1
Ircinia spp 2

Variable burnupena
Papery burnupena
Clionella spp
Abalone
Cape silvertip nudibranch
Violet snail
Mollusc spp 1
Mollusc spp 2
Mollusc spp 3
Scaly dogwhelk
Common octopus 1
Common octopus
Cuttlefish
Smooth turban shell
Threaded screw-shell

Aaptos aaptos
Aplysilla rosea
Cup sponge
Callyspongia sp 1
Coelosphaera spp 1
Broad bladed tree sponge
Nodular sponge
Clathria spp 1
Clathria spp 2
Clathria spp 3
Clathria spp 4
Clathria Thalysias oxitoxa
Boring sponge
Stellar sponge
Tree sponge
Grey wall sponge
Tar Sponge
Haliclona spp 1
Haliclona spp 2
Haliclona spp 3
Haliclona spp 4
Haliclona spp 5
Haliclona spp 6
Haliclona spp 7
Encrusting turret sponge
Crumb-of-bread sponge
Hymeniacidon spp 1
Hymeniacidon spp 2
Black stink sponge
Ircinia spp 1
Ircinia spp 2
Isodictya ectyofibrosa
(Lévi, 1963)
Fanned kelp sponge
Isodictya frondosa
(Lévi, 1963)
Lissodendoryx spp 1
Lissodendoryx spp 2
Lissodendoryx spp 3
Lissodendoryx tenuatensis
Mycale spp 1
Mycale spp 2
Mycale spp 3
Myxilla spp 1
Petrosia Strongylophora vulcaniensis
Polymastia littoralis
Polymastia spp 1
Polymastia spp 2
Polymastia spp 3
Psammocinia spp 1
Psammoclema spp 1
Psammoclema spp 2
Psammoclema spp 3
Psammoclema spp 4
Spheciospongia spp 1
Stelletta agulhana
Suberites globosus
Suberites spp 1
Suberites spp 2
Tedania tubulifera
Tethya aurantium
Tethya rubra
Tethya spp 1
Tethya spp 2
VERTEBRATA
Clinus superciliosus
Fish spp 1
Halidesmus scapularis
Haploblepharus pictus
Scartella emarginata
(Linnaeus, 1758)
Super klipfish
(Günther, 1872)
Fish spp 1
(Günther, 1861)
Snakelet
(Teleos, 1863)
Dark shyshark
(Teleos, 1863)
Maned Blenny
(Teleos, 1863)
Figure 1: Dominant Algae species as identified in the photo-quadrats (a) *Caulepra holmesiana*; (b) *Jania adhaerens*; (c) *Leptophytum foveatum*; (d) *Rhodophyllis reptans* and (e) *Rhodymenia obtusa*
Figure 2: Dominant annelid species as identified in the photo-quadrats (a) Golfinigia capensis; (b) Gunnarea gaimardi; (c) Polychaete spp 1; (d) Spirorbis spp 1 and (e) Thelepsus spp 1
Figure 3: Dominant arthropod species as identified in the photo-quadrats (a) *Amphibalanus amphitrite*; (b) *Jasus lalandii* and (c) *Guinusia chabrus*
Figure 4: Dominant ascidian species as identified in the photo-quadrats (a) *Botryllus gregalis*; (b) *Didemnum* spp 1; (c) *Euherdmania divida*; (d) *Clavelina lepadiformis* and (e) *Tridemnum cerebriforme*
Figure 5: Dominant bryozoan species as identified in the photo-quadrats (a) *Bugula flabellata*; (b) *Bugula neritina*; (c) *Gigantopora polymorpha*; (d) *Margaretta levenseni* and (e) *Menipea crispa*
Figure 6: Dominant cnidarian species as identified in the photo-quadrats (a) *Aglaophenia plumula*; (b) *Balanophyllia bonaespei*; (c) *Eudendrium spp* 1; (d) *Isozoanthus capensis* and (e) *Plumularia setacea*.
Figure 7: Dominant echinoderm species as identified in the photo-quadrats (a) *Amphiura capensis*; (b) *Austrofromia schultzei*; (c) *Comanthus wahlbergii*; and (d) *Tropiometra carinata*
Figure 8: Dominant mollusc species as identified in the photo-quadrats (a) *Burnupena lagenaria*; (b) *Burnupena papyracea*; (c) *Haliotis midae*; (d) *Janolus capensis* and (e) *Janthina janthina*
Figure 9: Dominant Porifera species as identified in the photo-quadrats (a) *Crambe acuata*; (b) *Guitarra flamenca*; (c) *Haliclona stilensis*; (d) *Hymeniacidon perlevis* and (e) *Tethya spp*.
APPENDIX D – SPECIES ACCUMULATION CURVES

Figure 1: Species accumulation curves indicating $S_{obs}$ for stations DIE (a); DIW (b); DM (c) and DOE (d)
Figure 2: Species accumulation curves indicating Sobs for stations DOW (e); SIE (f); SIW (g) and SM (h)
Figure 3: Species accumulation curves indicating Sobs for stations SOE (i) and SOW (j) as well as shallow (k) and deep (l) samples.
Figure 4: Species accumulation curves indicating Sobs for inside (m) and outside (n) samples