DIVERSITY AND DISTRIBUTION OF SUBTIDAL SOFT-BOTTOM MACROFAUNA OF THE ISIMANGALISO WETLAND PARK, SOUTH AFRICA

by

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As the candidate's supervisor I have approved this dissertation for submission.

Supervisor: Dr D. Glassom   Signed: Date:

Abstract

There have been no previous studies describing the subtidal soft-bottom macrofaunal assemblages of the iSimangaliso Wetland Park or how they are influenced by the ecological and environmental processes associated with coral reef proximity. With South Africa having high wave energy the transportation of nutrients and organisms between the soft-bottom areas and reef habitats is probable. This transfer of resources may create ecological linkages which organisms depend on. The aim of this study was to document the species diversity, distribution and abundance of in- and epi-macrofauna in iSimangaliso Wetland Park and to relate these to depth, sediment grain size, location, reef proximity and protective status. Macrofauna were collected using an air-lift design suction sampler. The macrofauna were identified to the lowest possible taxonomic level, biomass estimates were calculated and sediment grain size was determined. A total of 5166 animals were collected and 121 macrofauna species were identified. Macrofaunal assemblages inhabiting the soft-bottom sedimentary habitat surrounding the reefs changed in species abundance and diversity with increasing distance from the reef. Lower abundances and diversity were found closest to the reefs strongly indicating that the macrofaunal assemblages were negatively affected by the reef proximity. Although reef proximity was indicated as influential, environmental gradients were found to be more important in defining community structure. Higher percentages of coarse sediments found closest to the reef edge coincided with lower abundances, biomass and species richness of macrofauna. Trends of higher abundances at the middle distance indicated hydrodynamic disturbance may be affecting near shore assemblages. Sediment grain size and hydrodynamic disturbance both appeared to be the main determinants of assemblage structure around reefs. Trophic interactions by reef associated predators were indicated by lower macrofaunal abundances recorded at close proximity to the reefs. There was no evidence for the presence of a latitudinal diversity gradient as localised environmental conditions were found to be more influential in determining soft-bottom macrofaunal community structure and distribution in the iSimangaliso Wetland Park. The presence of ecological linkages between soft-bottom macrofaunal communities and coral reefs gives insight into the important roles soft-bottom macrofauna play in the functioning of the iSimangaliso Wetland Park marine reserve. The documentation of the species diversity and distribution of macrofauna in the soft-bottom habitats will provide valuable baseline information for the future management strategies.

Keywords: Macrofauna, Soft-bottom, Ecological linkages, Spatial distribution patterns, Coral reefs

Preface

The work described in this dissertation was carried out at the University of KwaZulu-Natal, Westville. Field work was conducted at five sites in the iSimangaliso Wetland Park marine reserve from December 2012 – January 2014, under the supervision of Dr. David Glassom. This dissertation represents original work by the author and has not otherwise been submitted in any form for a degree or diploma to any other tertiary institute.

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Declaration - Plagiarism

I, Rogan Harmer, declare that:

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Chapter 1: Introduction

1.1. General overview of soft-bottom marine ecosystems and the importance of their macrofaunal communities.

Subtidal, soft-bottom marine habitats constitute the oldest and largest ecosystem on the planet (Snelgrove 1999), yet our knowledge of the benthic fauna which inhabit them is limited. Macrofauna dominate the biomass of benthic communities (Snelgrove 1998) with of global marine biodiversity at 0.3 million (Costello *et al.* 2012). Approximately 83 % of sedimentary habitats are located at depths greater than 1000 meters where environmental conditions include low temperatures, high pressure and no light (Grassle and Maciolek, 1992). Despite these extreme conditions benthic communities in deep-sea habitats have been found to be remarkably diverse (Ray and Grassle 1991, Grassle and Maciolek 1992, Gray 2002).

Coastal sediments have been sampled far more comprehensively for macrofauna than those of the deep-sea, mainly due to coastal regions being more accessible and the important role macrofauna play as bio-indicators in ecosystem monitoring (Gray 2002, Dauvin 2007, Dauvin *et al.* 2010, Muniz *et al.* 2011). With the high primary production in coastal systems substantial infaunal diversity and abundance has been found in near shore coastal sediments (Sanders 1968, Field 1970, Christie 1976, Ellingsen 2002, Gray 2002, Dauvin *et al.* 2004, Ellis and Schneider 2008, Pacheco *et al.* 2010a). Hoey *et al.* (2004) discovered higher species diversity at the shallower near shore regions of the Belgian Continental Shelf than offshore. Jayaraj *et al.* (2008) similarly found that the shallower coastal regions of the tropical eastern Arabian Sea shelf had higher abundance and diversity than the deeper regions. The infaunal composition of the shallow coastal areas along the Algerian coast were characterised by high species diversity and moderate levels of abundance (Bakalem *et al.* 2009). The variations in habitat types in the coastal sediments, specifically sedimentary characteristic and depth, are the suggested reasons for the high diversity and abundances. Due to the extent of soft-bottom habitats throughout the marine environment, the macrofaunal activities within them impact on a global scale by playing important roles in the nitrogen, carbon and sulphur cycles. They are essential in the decomposition of detritus, the cycling of nutrients, movement of energy to upper trophic levels and are a source of food for both commercially fished species and human consumption (Snelgrove 1998, Heip *et al.* 2001, Hyland *et al.* 2006, Pacheco *et al.* 2010b). They are influential in shaping the geochemical properties in marine sediments through either direct biodeposition, where feeding benthic fauna assimilate particles from the water column and deposit them as faeces into the sediment; or indirectly, where tube-structures, feeding pits or faecal mounds alter the water flow resulting in passive biodeposition or resuspension (Carey

1983, Miller *et al*. 1984, Heip *et al*. 2001). Part of the organic input to the benthic environment is a source of energy for benthic fauna and that which is not mineralised is then retained within the sediment allowing the environment to function as an important carbon sink (Haas *et al*. 2002). Through this process macrobenthos play an important role in the global ocean carbon cycle.

By studying the structure and dynamics of the benthic macrofaunal communities in soft-bottom habitats and assessing the ecological linkages they have with their neighbouring habitats we can obtain a better understanding of their significance in the marine environment. Investigating the diversity of macrofauna in marine sediments will aid in understanding their influences in ecosystem dynamics, productivity and stability (Snelgrove, 1998, Tilman 2001, Pacheco *et al*. 2010b, Nordstrom *et al*. 2010). Identifying cross-boundary linkages would help develop our understanding of one of the most important habitats of the marine environment.

1.2. The ecological linkages between neighbouring marine environments

Marine habitats are ecologically connected by migration, organism's life-history, nutrient transport and predator-prey dynamics, all of which are influential on the ecosystem's productivity and community structure (Sheaves 2009). Ecological connectivity is often associated with the movement of fauna as communities are seldom limited to within the boundaries of a specific habitat. Various studies of community structure at the boundaries between marine habitats have indicated the presence of ecological linkages between them and the different mechanisms by which they take place (Suchanek 1978, Paine 1980, Baker and Sheaves 2005, Connolly *et al*. 2005, Langlois 2005a, Martins *et al*. 2013a). For example, Baker and Sheaves (2005) discovered trophic linkages between coastal and estuarine systems through the migration of feeding predators to the estuary mouth. Connolly *et al*. (2005) showed that seagrass and epiphytic algae exported to neighbouring intertidal habitats supported valuable fisheries. Mangrove derived organic matter has been found to make a substantial contribution to the energy budget of coral reef invertebrate communities (Granek *et al*. 2009). The transfer of nutrients, either by physical environmental forces or biologically mediated through trophic interactions, can create important ecological linkages on which many organisms are dependent (Sheaves 2009). The intertidal limpet *Patella argenvillei*, along the west coast of South Africa, is dependent on subtidal kelp detritus for nourishment (Bustamante *et al*. 1995). Similarly, *Donax serra*, a South African beach clam, is reliant on imported organic materials sourced from sub-tidal kelp habitats (Soares *et al*. 1997). The degradation or loss of one habitat may therefore detrimentally affect resource availability to residents of neighbouring habitats.

In soft-bottom habitats the presence of haloes adjacent to reef structures indicates ecological linkages between the communities of the two habitats. A 'halo' is typically a result of ecological interactions such as the trans-boundary movement by foraging predators (Ogden *et al*. 1973, Fairweather 1988). Various studies have described the presence of haloes in soft-bottom habitats adjacent to reefs (Ambrose and Anderson, 1990, Posey and Ambrose 1994, Dahlgren *et al*. 1999, Barros *et al*. 2001, Langlois *et al*. 2005a, Martins *et al*. 2013a). Barros *et al*. (2001) found Syllidae polychaetes were less abundant at close proximity to the reef than further away. Similarly, Langlois *et al*. (2005a) observed density gradients for several macrofaunal species with increasing distance away from the reef's edge. Patterns of faunal abundance however, vary widely among locations and faunal groups. Numbers of large bodied fauna decreased with distance from the reefs in some cases (Dahlgren *et al*. 1999, Langlois *et al*. 2005a) while abundance of small bodied fauna increased with distance (Ambrose and Anderson 1990, Barros *et al*. 2004) or showed no consistent patterns (Langlois *et al*. 2005b). Identifying and investigating the ecological linkages signified by the presence of haloes can help attain a better understanding of benthic ecology in ecosystems associated with coral reefs.

1.3.Influences on macrofaunal community structure

Ecologists strive to obtain an understanding of the relationships between communities and the environments in which they live. In soft-bottom marine systems numerous biological and environmental processes influence macrofaunal community structure, such as, bioturbation (Dahlgren *et al*. 1999), gradients in sediment characteristics (Barros *et al*. 2004), physical disturbance (Barros *et al*. 2001), predation by reef fauna (Lindquist *et al*. 1994, Langlois *et al*. 2005a), infaunal predation (Ambrose 1990), competition (Wilson 1991) and nutrient enrichment by neighbouring reefs (Dahlgren *et al*. 1999). Through further investigations into how these processes structure soft-bottom macrofaunal communities in boundary environments an improved understanding of community dynamics can be obtained.

1.3.1 Sediment characteristics

Marine sediments are derived from a number of environmental processes, such as erosion of rocky areas, past glacial processes, wind transport, biogenic material, and riverine input (Gray 2002). Sediments interact with ocean waves and currents creating distinct differences in the size and distribution of sediments between the habitats of the deep-sea and those located on the continental shelf. Sediments across the continental shelf vary, with mean grain size changing from coarse to fine with increasing depth and distance from the shore (Bergen *et al*. 2001, Hoey *et al*. 2004, Dauvin *et al*. 2004, Martins *et al*. 2013b). Shallow coastal regions generally

experience higher wave energy than the deeper offshore regions therefore having greater amounts of coarse sediments (Gray *et al*. 1997). The much larger deep-sea sedimentary environment experience very low levels of disturbance and consist predominately of finer silt or muddy sediments (Gray *et al*. 1997, Brandes 2011).

At smaller spatial scales, specifically around reef structures, local environmental processes determine sedimentary characteristics. A reef's structure and the resultant hydrodynamic flow around it creates a gradient of coarse grained sediments and shell debris close to the reef's edge and higher percentage of finer sediments further away (Ambrose and Anderson 1990, Barros *et al*. 2001, Martins *et al*. 2013a). This gradient in the granulometric properties of the sediment can directly influence the diversity and abundance of macrofauna in the community (Gray 1974, Snelgrove and Butman 1993, Widdicombe and Austen 2001).

The spatial-temporal mosaic theory, proposed by Grassle (1989), states that infauna have the ability to respond to differences in the sediment properties either as larvae or adults seeking a more favourable habitat. Various studies support this theory. Jayaraj *et al*. (2008) found higher macrofaunal diversity in medium grain sized sediments than in areas of fine or coarse sediments on the eastern Arabian Sea continental shelf. Hoey *et al*. (2004) discovered that the variations in macrofaunal community structure on the Belgian Continental shelf coincided with the differences in the sedimentary characteristics of their habitat. Where sediments were predominantly fine and muddy the macrofauna were found at high densities and diversity whereas abundance and species diversity of communities in predominantly coarse sediments were lower. Martins *et al*. (2013a) found that gradients in sediment characteristics of coarser to finer sediments with increasing distance from a rocky reef had an influence on macrofaunal abundance and assemblage composition. Three of the eight most abundant taxa examined were found at significantly lower abundances closest to the reef. Barros *et al*. (2004) showed that macrofaunal assemblage structure varied between the micro-environments in sandy bottom habitats with greater abundances found in the troughs than on the crests of sand ripples around reefs, due to differences in micro-bathymetry and sediment properties. In False Bay however, the lamp urchin *Echinolampas crassa* was significantly more abundant on the slope of sand ripples than the trough (Thum and Allen 1975). In summary, the diversity and distribution patterns of macrofaunal communities whether over large or small spatial scales is strongly associated with the sedimentary composition of their habitat. Infaunal abundance and diversity is generally lower in coarse sediments, however, various biological and environmental factors such as predation and disturbance can further influence community structure and distribution.

1.3.2 Disturbance

Pickett and White (1985) described a disturbance as "any discrete event in time that disrupts ecosystem, community, or population structure and changes resources, substratum availability, or the physical environment". In both plant and animal communities disturbance plays a fundamental role in spatial and temporal heterogeneity (Sousa 1984, Dernie *et al*. 2003). Disturbance, whether it is physical or biological, influences the structure and distribution of macrofaunal communities in soft-bottom habitats (Wooldridge 1981, McLachlan *et al.* 1984, Widdicombe *et al*. 2000, Kruger *et al*. 2005).

Physical disturbances in soft-bottom environments are defined as temporal changes in the natural abiotic conditions from events such as a wave surge or tidal currents (Probert 1984, Hall 1994, Hall *et al*. 1994). These disturbances alter behaviour, recruitment and sediment structure in soft-bottom environments resulting in the displacement or death of resident fauna (Thistle 1981, Barry 1989, Dernie *et al*. 2003). Large scale physical disturbances in soft-bottom habitats are associated with the hydrodynamic nature of the environment. Paavo *et al*. (2011) found that in the subtidal areas of a reflective beach, macrofaunal abundance and diversity was lower than at a dissipative beach. Their findings supported the 'Wave Exclusion Hypothesis', where certain species are excluded from shallow subtidal wave dominated areas due to direct physical disturbance and sediment instability (Paavo *et al*. 2011). Similarly, DeFelice and Parrish (2001) found that infaunal diversity and abundance in the reef sediments of Hanalei Bay, Hawaii had a significantly negative correlation with exposure to wave energy.

Large scale physical disturbances generally have a far greater effect on macrofaunal communities than any biogenic disturbance (Probert 1984). Biological disturbances occur on a much smaller scale and the changes in habitat properties occur solely through biotic interactions (Brey 1991, Dernie *et al*. 2003). Bioturbation, foraging by predators or any other type of biological influence can affect sediment permeability and stability in soft-bottom environments, thus influencing the sediments' habitability and subsequently the community structure of the macrobenthos (Dahlgren *et al*. 1999, Thrush 1999, Dernie *et al*. 2003). Dahlgren *et al*. (1999) discovered high densities of bioturbating *Holothuria princeps* at close proximity to the reef and higher infaunal densities further away, suggesting that bioturbation, as a mechanism of biological disturbance, may play a role in the distribution patterns of soft-bottom infauna. The disturbance of sediments by bioturbators can bury or expose fauna, altering their susceptibility to predation (Dahlgren *et al*. 1999). In addition, foraging predators in soft sediments such as, goat fish and many rays cause small scale disturbance to the sediments further influencing

habitability (McCormick 1995). Disturbances, whether they are biological or physical, are recognized as integral elements in macrofaunal community structuring.

1.3.3 Predation

Predation plays a pivotal role in the recruitment and organisation of soft-bottom communities (Wilson 1991, Osman and Whitlatch 2004). Predation enables the transfer of energy between species and trophic levels (Wilson 1991, Barros 2005). Predator-prey interactions are thus important for energy flow through marine food webs.

From gut content analysis reef fish have been found to use soft-bottom communities as a source of nourishment (Lindquist *et al*. 1994). The cross-boundary movement of foraging reef associated predators to neighbouring soft-bottom habitats has the ability to influence the structure and spatial distribution of macrofauna (Lindquist *et al*. 1994, Barros *et al*. 2001, Langlois *et al*. 2005a, 2005b, Martins *et al*. 2013a). However, the effects of predation on soft-bottom macrofaunal assemblages around reefs are inconsistent with 'haloes' only evident for fauna greater than 4 mm body length and not the smaller sized fauna (Langlois *et al*. 2005b). Similarly, Martins *et al*. (2013a) found that reef associated predators had little influence on assemblage structure of small bodied macrofauna with populations of only one amphipod species reflecting predation pressure. Foraging by reef associated predators in soft-bottom areas adjacent to reefs can be influential in shaping infaunal assemblages of larger sized fauna. As a consequence of predation, assemblages close to the reef may thus differ from those further away (Barros *et al*. 2001). However, variations in habitat characteristics (Thrush 1999) and the environmental processes which occur in the habitat (Eriksson *et al.* 2005) can influence how predation structures benthic communities. Sediment characteristics of habitats may influence predator evasion by impacting burrowing speed (Dorgan *et al*. 2006) while physical disturbances of sandy substrate can intensify predatory pressure on macrofaunal community through increased vulnerability by exposure (Eriksson *et al.* 2005). Predation, subject to environmental characteristics and predator densities, plays an influential role in the organisation of soft-bottom macrofaunal communities around reef.

1.3.4 Latitudinal gradient

In the terrestrial environment it is the general consensus that species richness increases in number from the poles to the tropics. Although this large-scale diversity pattern, known more commonly as the latitudinal diversity gradient, has been adopted for the marine environment, its accuracy in describing diversity patterns still remains somewhat controversial (May 1994,

Ellingsen and Gray 2002). Thorson (1957) claimed that a latitudinal cline of marine diversity does exist for benthic fauna, but only with regards to epifauna and not infauna due to the temporal and spatial homogeneity of the soft-bottom environment. Bergen *et al*. (2000) investigated the relationship between benthic infaunal assemblages and depth, sediment and latitude on the continental shelf of southern California. Their study concluded that depth and sediment characteristics were the main factors which defined the benthic infaunal assemblages and that latitude played no significant role, however, their study was limited covering only two degrees of latitude. Ellingsen and Gray (2002) measured Alpha, Beta and Gamma diversity indices of soft-bottom macrofauna along the Norwegian continental shelf and found no evidence of a latitudinal gradient and similarly suggested that environmental variability had more influence on diversity. In contrast, Sanders (1968) found that there was indeed an increase in species richness towards the tropics and from the shallow coastal areas to the deep-sea. Roy *et al*. (1998) analysed the geographical ranges of 3 916 species of gastropods on the eastern Pacific and western Atlantic shelves and found a latitudinal gradient in species diversity. Roy *et al*. (2000) showed that the diversity of both epifaunal and infaunal bivalves analysed from the north-eastern Pacific shelf was associated with latitude. Crame (2000) further supported the presence of a latitudinal gradient for bivalve species however stated that there were indications of inequality between the Southern and Northern Hemisphere as diversity trends in the north tended to be more regular than in the south. In South Africa range restrictions and patterns of endemicity of coastal invertebrates, investigated by Scott *et al*. (2012), found peaks in the number endemic species coincided at recognised biogeographical borders and areas of high sampling activities. Our knowledge of biodiversity in the marine environment is far less than that of the terrestrial environment (Ellingsen and Gray 2002), making it difficult to identify the presence of a latitudinal species gradient in the marine environment (May 1994, Ellingsen and Gray 2002). Information on the benthic diversity, particularly from the African subcontinent, is lacking and it is essential for a comprehensive analysis of a latitudinal species gradient (Crame 2000, Scott *et al*. 2012).

1.3.5 Coral reefs

Coral reefs provide important environmental services on which the livelihoods of countless people are dependent (Moberg and Folke 1999, Burke *et al*. 2011, Yee *et al*. 2014). They are one of the most species diverse and productive ecosystems in the marine environment despite being situated in tropical oligotrophic conditions (Odum and Odum 1955, Muscatine and Porter 1977, Tac-An *et al*. 2013). The symbiotic relationship between zooxanthellae and corals facilitate recycling mechanisms which retain carbon and nutrients within the reef system and

allow for the seemingly paradoxical perseverance of coral reef communities in nutrient poor environments. Similarly, reef sponges take up dissolved organic matter (DOM) from the surrounding water which they convert and expel as old choanocytes. The shed sponge cells (detritus) are then consumed by reef fauna thus retaining and cycling energy and nutrients within the reef system (de Goeij *et al*. 2013). Coral reefs were originally thought of as closed systems, having high internal connectivity and very little cross-boundary flow (Odum and Odum 1955), however, they are now perceived as not only having internal connectivity but having connectivity with their neighbouring environments (Hatcher 1997). Coral reef ecosystems are then viewed as both sources and sinks of carbon and nutrients offering a more holistic understanding of coral reefs ecosystems and the ecological linkages they have with the surrounding sedimentary environment (Hatcher 1997).

Infaunal communities in sedimentary habitats surrounding coral reefs exist in an oligotrophic environment raising questions as to where they acquire nutrients. One of the main sources of carbon in reef sediments is from benthic micro- and macroalgal productivity (Heil *et al*. 2004, Gattuso *et al*. 2006, Naumann *et al*. 2012). However, coral reefs are highly productive systems and may supplement the surrounding sedimentary habitats with carbon and nutrients. Coral reefs are efficient in assimilating nutrients and zooplankton from the surrounding water, which they either retain or export as converted organic materials and organisms (Hatcher 1990, Heikoop 1997, Anthony 1999, Wild *et al*. 2005, Palardy *et al*. 2006). Transport of organic materials from the reef to adjacent sediments may support benthic communities. Wild *et al*. (2004) showed that mucus which corals release has the ability to trap suspended organic matter from the water column. This enriched coral mucus is transported to reef sediments by water movement, supplying nutrients to benthic communities. Trophic subsidies via trans-boundary fluxes of reef derived organic materials are likely to create ecological linkages which subsidise neighbouring macrofaunal communities. The import and export of energy and materials however, depend on the hydrodynamic flow and the movement of fauna between habitats (Hansen *et al*. 1992, Hatcher 1997). On high-energy coastlines the transport of nutrients and organisms between reef and soft-bottom habitats is probable and therefore it is likely that the organisms inhabiting them benefit from cross-boundary subsidies.

It is important to note that the flow of energy and nutrients between the two systems is bidirectional allowing cycling between them to occur. Alongi (1996) showed that mangroves have the ability to operate as nutrient sinks as the rate of nutrients being cycled through the systems is slowed by biological activities leading to nutrient retention. For example, sesarmid

crabs feeding on mangrove leaf litter would subsequently retain nutrients within the systems (Robertson and Daniel 1989, Sheaves 2009). Coral reefs sponges remove equal amounts of DOM from the surrounding waters in 30 min as non-symbiotic bacteria do in 30 days, thus reducing the loss of energy and nutrients from the reef system (de Goeij and van Duyl 2007, de Goeij *et al*. 2008). Similar nutrient retention and recycling processes within the soft-bottom habitats surrounding coral reefs would be beneficial in an oligotrophic environment as it would secure nutrient availability for the reef communities connected through their trophic interactions.

1.3.6 Marine protected areas

Marine protected areas (MPAs) have been advocated as a potential solution to try and mitigate the loss of resources and biodiversity due to overexploitation and increasing human activities. MPAs increase species diversity as well as the abundance and size of target species (Roberts *et al*. 2001, Unsworth *et al*. 2007, Barrett *et al*. 2007, Lester *et al*. 2009, Floros 2010). Assessment is needed whether these benefits are reflected in soft-bottom macrofaunal abundance and diversity within MPAs. Direct protection of soft-bottom habitats from anthropogenic disturbances such as, trawling and dredging, may increase the abundance and diversity of macrofauna in areas which were previously unprotected. Hyland *et al*. (2006) discovered that soft-bottom habitats within a MPA had considerably higher macrofaunal diversity than non-protected areas. However, Langlois *et al*. (2005c) showed that the indirect effects from higher predator densities within MPAs can influence macrofaunal abundance and possibly community structure. Investigating how soft-bottom communities are influenced by their protection status will aid in obtaining a better understanding of their structure and functioning within MPAs.

Often, when selecting and establishing protected areas sedimentary communities and their ecological connections to other habitats are not taken into account. Makino *et al*. (2013) discovered that when ecosystem connectivity between forested catchments and coral reefs were not incorporated models produced substantial differences in spatial planning priorities. Berkstrom *et al*. (2012) argued that only through understanding ecological connectivity between sea grass beds, mangroves and coral reef habitats by the movement of fish in the Zanzibar coastal ecosystem can effective management be achieved. Significant advances in integrating the linkages between terrestrial and marine ecosystems for spatial planning purposes have been made (Lombard *et al*. 2007, Tallis *et al*. 2008, Game *et al*. 2011, Berkstrom *et al*. 2012, Makino *et al*. 2013) however, understanding and incorporating the linkages between soft-bottom and reef systems have been overlooked. Obtaining information on soft-bottom macrofaunal

communities can help conservation planning efforts, help identify what is required for maintaining optimal conditions for the macrofaunal communities within the protected areas and contribute to the formulation of new more appropriate management plans and conservation targets where these communities are considered.

Several studies have investigated coastal soft-bottom macrofaunal communities in South Africa, (Field 1970, Christie 1976, McClurg 1988, Awad *et al*. 2002, Kruger 2005, Masikane 2011, Browne *et al*. 2013, Milne and Griffiths 2014) but few have focused on characterising the macrofaunal communities inhabiting the subtidal soft-bottom habitats of the tropical east coast. An assessment of South Africa's benthic invertebrates, for the identification of areas of high conservation priority (Awad *et al*. 2002) discovered high species richness in the south coast and low species richness in the northern east coast where the iSimangaliso Wetland Park MPA is situated. It was acknowledged however, that the low species richness was likely due to the lack of sampling and information available on the benthic communities in the region. Browne *et al*. (2013) discovered that the seagrass *Thalassodendron leptocaule* supported a high diversity of epibenthic invertebrates at Sodwana Bay in the iSimangaliso Wetland Park MPA. Milne and Griffiths (2014) similarly found high invertebrate diversity in the algal turf habitats on the coral dominant reefs at Sodwana Bay may represent a considerable portion of the total biodiversity. Supplementary sampling is needed in the under-represented areas, such as the iSimangaliso Wetland Park MPA, so as to attain a more comprehensive understanding of South Africa's soft-bottom benthic invertebrate species distribution and endemicity. An ecological assessment of the subtidal benthic communities in the iSimangaliso Wetland Park would aid in achieving this goal. System-wide assessment and monitoring of its benthic macrofaunal communities would help in assessing the functional roles benthos play with in MPA systems therefore aiding in evaluating and managing their functionality (Hyland *et al*. 2006).

1.4   Rationale for this study

There have been no previous studies describing the subtidal soft-bottom macrofaunal assemblages of the iSimangaliso Wetland Park or what influences their community structure. The iSimangaliso Wetland Park presents an opportunity for the investigation of how macrofaunal communities are influenced by the ecological and environmental processes associated with coral reef proximity. The presence of no-take areas within the iSimangaliso Wetland Park also allows for the evaluation of their importance in the management and conservation of soft-bottom macrofaunal biodiversity. Investigations into the soft-bottom macrofaunal communities of the iSimangaliso Wetland Park can assist in future spatial

conservation planning efforts and contribute in describing their biogeographical distribution patterns in South Africa.

The purpose of this study was to i) To document the species diversity, distribution and abundance of subtidal benthic macrofauna in the iSimangaliso Wetland Park and determine whether their assemblages are affected by coral reef proximity. ii) Establish if there is any relation between the distribution of macrofauna and the influences of reef proximity, sediment characteristics and latitudinal gradient. iii) Determine if differences exists between the macrofaunal assemblages located within the sanctuary zones of the iSimangaliso Wetland Park MPA and those that are not.

Chapter 2: Methods

2.1. Study Area

All sampling was conducted within the iSimangaliso Wetland Park MPA, a UNESCO World Heritage Site located on the Maputaland coast in north-eastern KwaZulu-Natal, South Africa (Fig. 1). The reserve is characterised by large areas of sandy substrate between patches of hard substrate, hosting rich coral-dominated communities. Corals extend to a depth of roughly 30 m (Schleyer and Celliers 2003). The lithology of the shelf comprises late Pleistocene beachrock and aleolianite ridges, which form the substratum for many of the coral dominated reefs in the reserve (Ramsay, 1994, 1996) No true accretive reefs are formed. The area lacks major riverine input and has heterogeneous, coarse sediment of bioclastic origin (Ramsay 1996). The shelf in this region is narrow and gradually slopes towards the edge of numerous submarine canyons between 90 - 110 m (Ramsay 1994, Hissmann *et al*. 2006). The climate is tropical to subtropical, with warm summers from November to March and an average annual rainfall of 1200 - 1300 mm (UNEP 2005). The coastline is exposed to prevailing southerly to south westerly and north easterly winds that can result in swells exceeding 6 m (SADCO data: South African Data Centre for Oceanography). In the iSimangaliso Wetland Park fringing reefs run parallel to the coastline with no lagoons being formed as the reef crests are generally $5 - 8$ m beneath the surface. Turbulence from wave action occurs in the reef and inshore regions with sediments in the surrounding sandy areas being regularly disturbed (Ramsay 1996). The coral reef community is at the southernmost limit of global coral reef distribution (Ramsay and Mason 1990). Despite being at its latitudinal limit, the reefs in the region have a rich biodiversity (Ramsay and Mason 1990, Celliers and Schleyer 2008).

2.2. Site Selection

The iSimangaliso Wetland Park MPA has been divided into three reef complexes; a southern complex incorporating Leadsman Shoal and Red Sands Reef, a central complex at Sodwana Bay and the northern complex near Kosi Bay (Fig. 1) (Riegl *et al*. 1995, Schleyer and Celliers 2005, Samaai *et al*. 2010). The entire southern complex and parts of the northern complex are sanctuary zones where all boating and fishing activities are strictly prohibited. The central complex at Sodwana Bay, however, has a strong tourism trade and SCUBA diving is allowed (Schleyer and Celliers 2005).

Five sites were selected covering the length of the park (Fig. 1) to test for the effect of latitude on macrofaunal communities and to obtain representative samples of the park's near shore macrobenthic communities. Sites were also chosen in the northern and southern sanctuary areas. Reefs of similar depth and distance from shore were selected. All the reefs selected are permanently submerged reefs and were approximately 600 – 900 m from shore. The sampling depth at each site consistently ranged between 12 – 16 m.

The Southern-most site was Red Sand Reef located in the Southern Complex and within a sanctuary zone. Two sites were selected in the Central Complex; Two-Mile Reef and Seven-Mile Reef. Their names represent the approximate distance from the Sodwana Bay launch site at Jesser Point near the Mgobozeleni estuary mouth (Fig. 1). They are both located in a non-sanctuary zone where SCUBA diving is allowed, however, fishing is prohibited on Two-Mile Reef. Rocktail Bay is located in the transition zone between the Central and Northern Complexes. This site is in a non-sanctuary zone and has no fishing or diving restrictions, although it does experience considerably less recreational activity than those at any of the Sodwana Bay sites. Saxon Reef, the Northern-most site near the Kosi Bay estuarine system, is a sanctuary zone and is part of the Northern Complex.
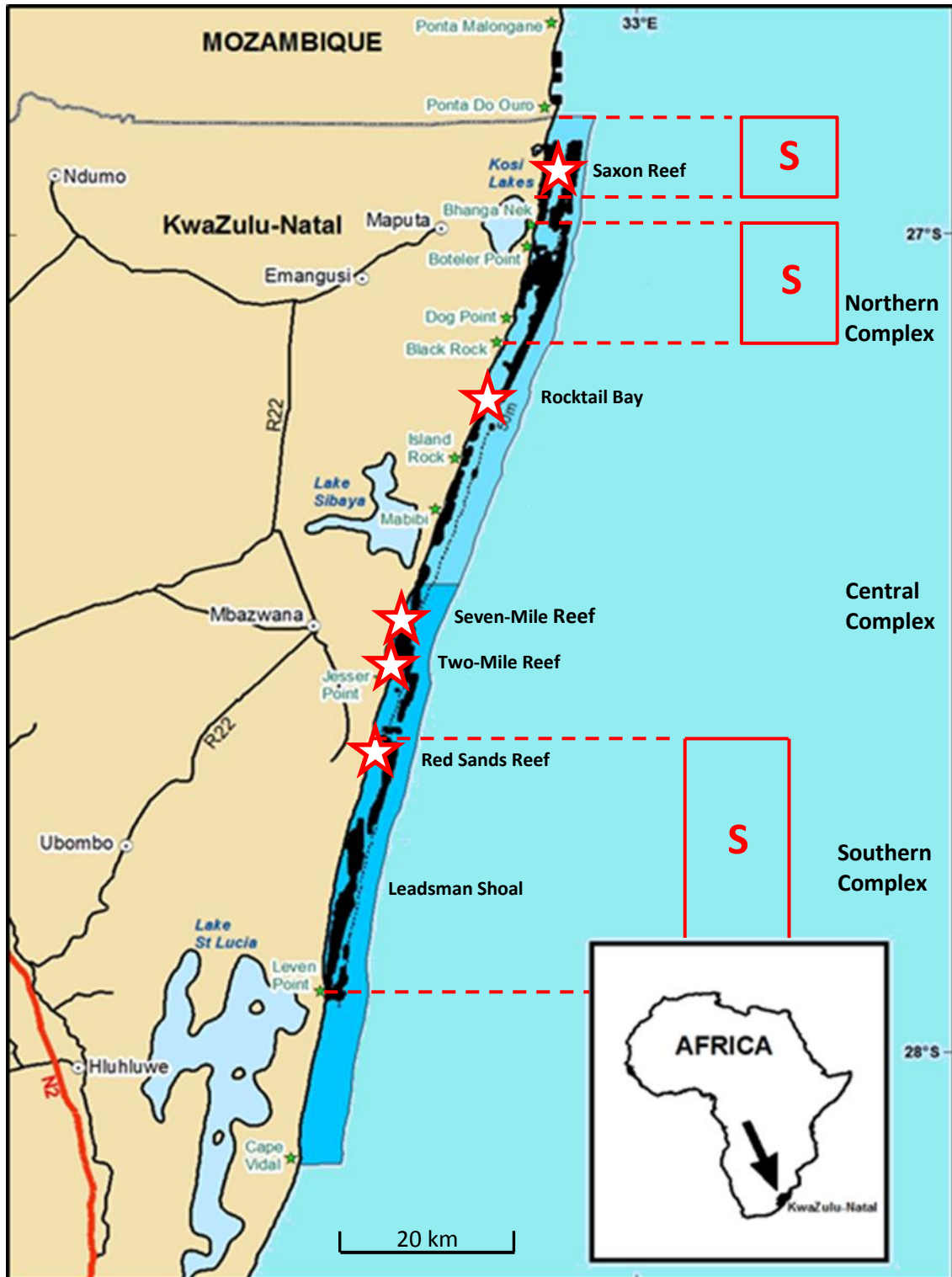
Figure 2.1. The location of the five study sites in the iSimangaliso Wetland Park MPA, KwaZulu-Natal, South Africa. Marine sanctuary zones (S) represented by stars (amended from Floros, 2010).

Table 2.1. Geographic coordinates of the sampling sites at each reef selected for this study.

Reef	Co-ordinates	
Saxon Reef	26° 92' 653" *S*	32° 88' 261" *E*
Rocktail Bay	27° 16' 399" *S*	32° 46' 514" *E*
Seven-Mile Reef	27° 26' 515" *S*	32° 42' 775" *E*
Two-Mile Reef	27° 31' 250" *S*	32° 41' 064" *E*
Red Sands Reef	27° 44' 074" *S*	32° 37' 777" *E*

2.3. Sampling Design

Sampling was carried out from December 2012 to January 2014. Eight replicate transects were conducted at each of the five sites without temporal replication. Sampling was conducted only on the near shore side on the reef due to time constraints and depth limitations when using the sampling equipment. Macrofaunal and sediment samples were taken 1 m, 200 m and 400 m along each transect starting from the near shore edge of the reef and moving in a shoreward direction. For the purpose of this study the sampled distance will be referred to as 1 m – 'near reef'; 200 m – 'middle' and 400 m – 'near shore'.

Macrofaunal samples were collected while on SCUBA using a hand-held air-lift suction sampler adapted from Barnett and Hardy (1967) (Fig. 2A). Two core samples were taken at each of the three distances along each transect. Air from a cylinder was passed through a 6 m long ridged pipe which was attached to the top of a steel core of 40 cm diameter and area (0.1256 m^2). The air that flows through the pipe expands and draws sediment and fauna upwards into a mesh bag attached to the buoyant end of the pipe (Fig. 2B). This method of sampling was preferred to a van Veen grab as the core could be placed to avoid hitting reef and the sample volume could be better controlled. It has previously been found (Christie 1976) that a diver-operated suction sampler was more efficient than a grab in collecting infaunal species in Lamberts Bay, South Africa.

Samples were taken to a depth of 30 cm and sieved through a 2 mm mesh to extract the fauna. A 2 mm mesh sieve was needed due to the large grain size of the sediment in the area. To ensure that the full size range of fauna was sampled, two additional core samples were taken at each station using a PVC pipe, 50 mm diameter and a depth of 10 cm. These core samples were sieved though a finer 500 µm mesh sieve at the laboratory. All extracted macrofauna were

bottled and labelled on the boat and analysed once ashore. A total of 96 cores were taken at each site, equating to 480 cores being collected for this study.

Once ashore all specimens collected were placed in 500 ml plastic bottles. A narcotizing agent, a solution of 7 % $MgCl_2$ and seawater, was then added to relax the specimens to aid in the identification in the laboratory. After a sedation period of two hours the sample was drained of the 7 % $MgCl_2$ and seawater solution and a fixative agent, consisting of 10 % formaldehyde buffered with sodium tetraborate (Borax) was added to the sample.

Sediment samples for analysis of carbonate percentage, total organic content (TOC) and granulometry were collected by hand while on SCUBA using a 250 ml plastic bottle. Using the plastic bottles samples were taken at each distance, along three transects, at each site. Samples were frozen once ashore and transported in a cooler box to the laboratory where they were kept frozen until analysed.
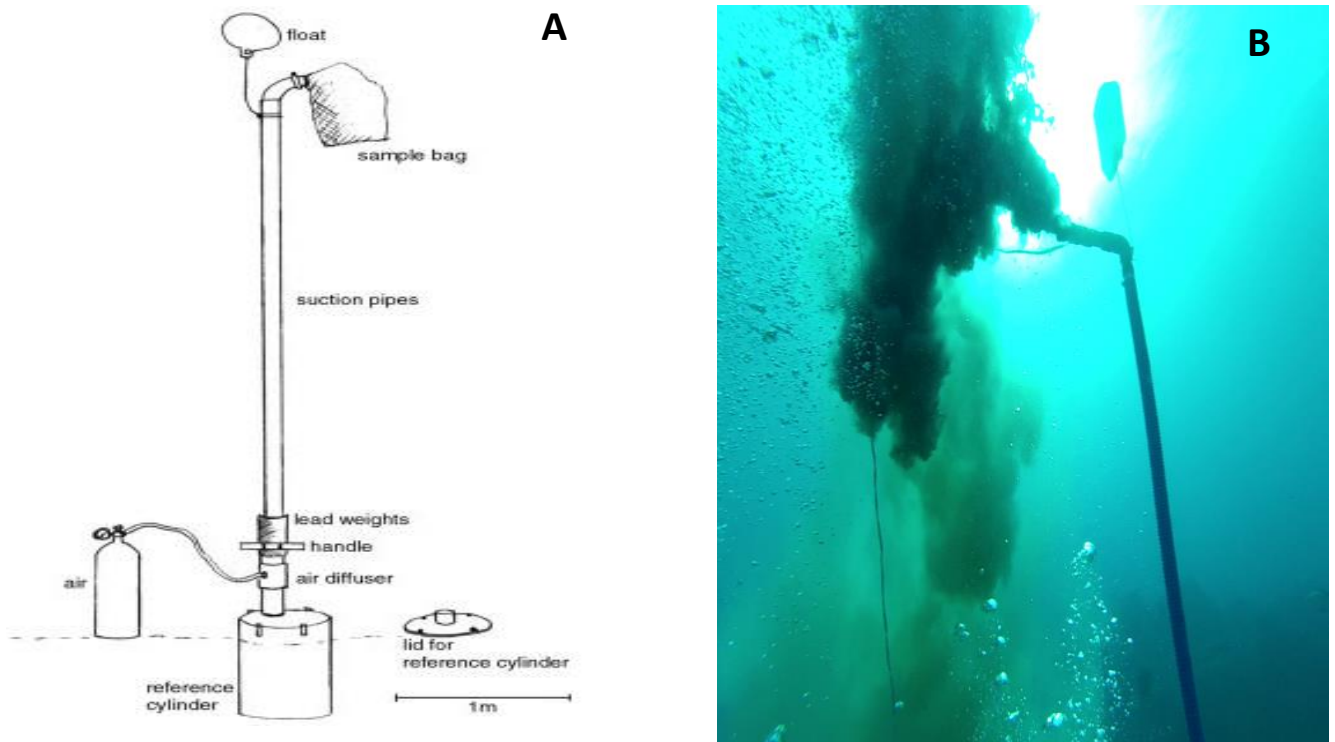

Figure 2.2. (A) Barnett and Hardy (1967) design air-lift suction sampler, (B) Sampler in operation.

2.4. Sample Processing

2.4.1. Identification

All samples were examined under either a dissecting or compound microscope. Macrofauna were carefully sorted from the sediment into broad taxonomic groups. After sorting, specimens were transferred to 100 ml plastic vials with a 70 % alcohol solution for preservation. The macrofauna were counted and then identified using the available literature: Amphipoda (Griffiths 1976), Isopoda (Kensley 1978), prawns (Kensley 1972), Gastropoda (Steyn and Lussi 1998), Bivalvia (Hurber 2010), Polychaeta (Day 1967) and Echinodermata (Clark and Rowe 1971, Clark and Courtman 1976). When species level of identification could not be obtained specimens were identified to the next highest taxonomic level (genus, family etc.). Once identified, specimens were either used for biomass determination or housed at the University of KwaZulu-Natal.

2.4.2. Biomass estimates

All specimens were weighed using a Shimadzu four decimal digital scale. Wet mass was determined after removing external fluids by placing the specimens on filter paper and allowing them to air-dry for five minutes. Specimens were then dried at 60°C for 24 h and re-weighed to determine the dry mass which was used for biomass estimates. All small specimens weighing less than 0.0001g were rounded up to 0.0001g. The contribution to total biomass of each taxon was determined.

2.4.3. Sediment analysis

To determine total organic carbon three subsamples were taken from each sediment sample collected from each distance away from the reef edge. The samples were oven dried at 60°C for 24 hours, weighed and then combusted at 450°C in a muffle furnace for 24 h. They were then reweighed and the percentage of weight lost was assumed to be equivalent to be the total organic content. Three 100 g subsamples from each sediment sample were sent to be analysed by a private company, Environmental Mapping and Surveying, for sediment grain size and calcium carbonate percentage.

2.5. Data analysis

2.5.1. Univariate analysis

All univariate analyses were performed using IBM SPSS 21. A one-way nested Analysis of Variance (ANOVA) was used to test the differences in the number of species, total abundance and biomass among reef sites and distance away from the reef. A Shannon-Wiener diversity index was used to investigate the differences in species diversity.

Shannon-Wiener's diversity index (H') (Shannon, 1949):

$$H' = -\sum p_i \left(\log p_i\right)$$

p_i is the total count of each sample signified by the ith species.

All data were tested for normality and equal variance using the Kolmogrov-Smirnov goodness of fit test and Levene's equal variance test respectively. Data were square root or log transformed if either of these criteria were not met. Post hoc analyses were performed using Tukey's HSD (honest significant difference) test for the pairwise comparison of sites and distances. A nested ANOVA was further performed on the five most abundant taxa and calculated Shannon-Wiener's diversity index.

For the sedimentary analysis, nested ANOVA's were performed on the TOC and percentage of carbonate data. Percentage carbonate and TOC did not meet the assumptions of the analysis and were arcsine transformed. Spearman's Rank correlation coefficient was used to measure the strength of the relationship between sediment grain size and site at each distance.

2.5.2. Multivariate analysis

The multivariate analysis was done using PRIMER v.6 (Plymouth Routines In Multivariate Ecological Research) (Clarke and Warwick 2001). Often species did not occur across all sites resulting in a high number of zeros in the data set. As a result, fourth root transformation of the data was required to reduce the weight of exceptionally abundant species to achieve a balance in contribution between the rarer and more common species (Field *et al.* 1982). All analyses were thus conducted using Bray-Curtis dissimilarities on fourth-root transformed abundance data.

Differences in community species composition were examined using the non-metric multi-dimensional scaling (MDS) ordination technique. This analysis places sites in a multi-dimensional plot where their orientation is based on their similarity in species composition. Sites of similar species composition are placed closer together, while those of differing composition are positioned further apart. Stress level values, which indicate the level of accuracy when converting the ordination into a two dimensional format, that are greater than 0.2

are regarded to be high (Clark and Warwick 2001). A less sensitive cluster analysis was also performed using a group average linking technique. The dendrograms further indicated the level of similarity of the macrobenthic communities across sites and distance from the reefs edge. Analysis of Similarity (ANOSIM) was also used to statistically investigate the degree of similarity in the assemblage structuring. The ANOSIM test produces a probability value (P) and an R statistic value. The R statistic, which measures the difference between assemblages, is considered to be more important than the P value as this can be influenced by the sample size (Clarke and Gorley 2006). If an R statistic value was > 0.5 the two compared sites were considered to be significantly different.

Similarity percentages routine (SIMPER) analysis was used to identify species which contributed to the Bray-Curtis similarity between samples within groups and the dissimilarity between samples from different groups (Clarke and Gorley 2006). The SIMPER analysis allows for the identification of 'indicator species' which characterise a site and the 'discriminatory species' which differentiates sites (Clarke and Gorley 2006). Indicator species contribute to the similarity in assemblages between sites by being abundant in all of the sites and having high Similarity/Standard Deviation ratio. Discriminatory species are abundant in one site and infrequent in the others and having a high Dissimilarity/Standard Deviation ratio (Clarke 1993, Clarke and Warwick 2001).

Finally, abundance biomass comparison (ABC) curves were constructed. These sequentially plot the abundance and mass of each taxon on a single set of axes. Since disturbed areas typically have few species comprising high numbers of small animals, a graph with the abundance line above that of the biomass line or with the two lines crossing at some point is a good indication of a disturbed or polluted habitat. A W-statistic represents the degree of separation between the two curves.

A sample-based rarefaction curve was created using EstimateS v.9. The rarefaction curve is a theoretical predictor model that estimates the expected number of species in an assemblage. The curve is an asymptotic species richness estimate curve based on the interpolation of a species accumulation curve (Colwell *et al*. 2004).

Chapter 3: Results

3.1. Sediment Analysis

Fine sediment (125 – 250 μm) dominated the sediment composition contributing 51 – 70 % of the total sediment mass (Table 3.1). Rocktail Bay had the highest mean percentage of fine sediments followed by Two-Mile Reef. Two-Mile Reef also had the lowest mean percentage of medium sediments. At Saxon Reef medium sediment (250 – 500 μm) was dominant. Gravel (> 2000 μm) and mud (< 63 μm) contributed little to sediment composition.

Spearman's Rank correlation revealed positive correlations in grain size among sites at each distance. At all sites the percentage of finer sediments increased with increasing distance away from the reef (Fig. 3.1). At the near reef distance Rocktail Bay had a greater percentage of medium and fine sized sediments, while Saxon Reef and Red Sand Reef had higher percentages of coarse and medium sized sediments. At the middle distance all sites showed similar sediment composition except for Saxon Reef which had higher percentages of coarse and medium sized sediments. At the near shore distance higher percentages of fine sediments occurred at all sites.

Table 3.1. Percentage contribution of different sediment particle size proportionate to the sample mass (Mean ±SE) at each site.

| Sediment Parameter	Sediment Size	Red Sands			Two-Mile		Seven-Mile		Rocktail Bay		Saxon	
		n	Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE
Gravel	> 2 mm	3	0.38	0.27	0.37	0.26	0.29	0.2	0	0.02	0.44	0.24
Very Coarse	2 -1 mm	3	1.25	0.69	1.69	1.45	0.7	0.43	0.04	0.02	1.45	0.86
Coarse	1 - 0.5 mm	3	10.49	4.7	6.98	5.03	7.58	5.15	1.43	0.19	17.18	7.26
Medium	500 - 250 µm	3	28.45	7.05	17.39	2.04	26.4	6.1	24.82	2.73	42.29	6.24
Fine	250 - 125 µm	3	51.08	10.84	68.13	7.57	58.76	9.27	70.09	2.74	36.73	10.47
Very Fine	125 - 63 µm	3	7.15	1.5	5.42	0.7	6.27	1.3	3.62	0.22	1.89	0.54
Mud	< 63 µm	3	1.19	0.11	0.01	0.01	0	0	0	0	0	0
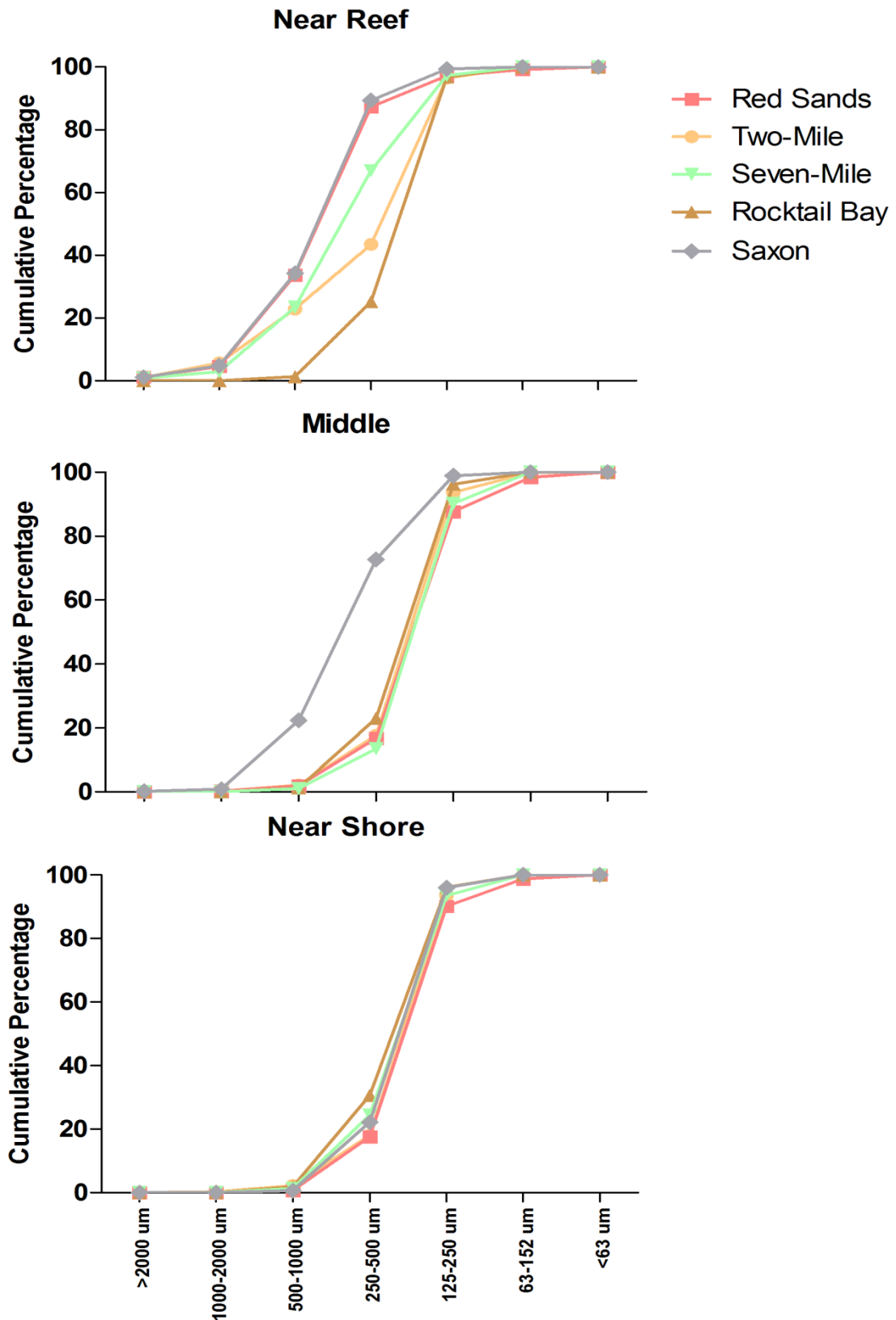
Figure 3.1. Cumulative graphs showing the spatial variability in sediment grain size composition at each distance from the reef edge of each site.
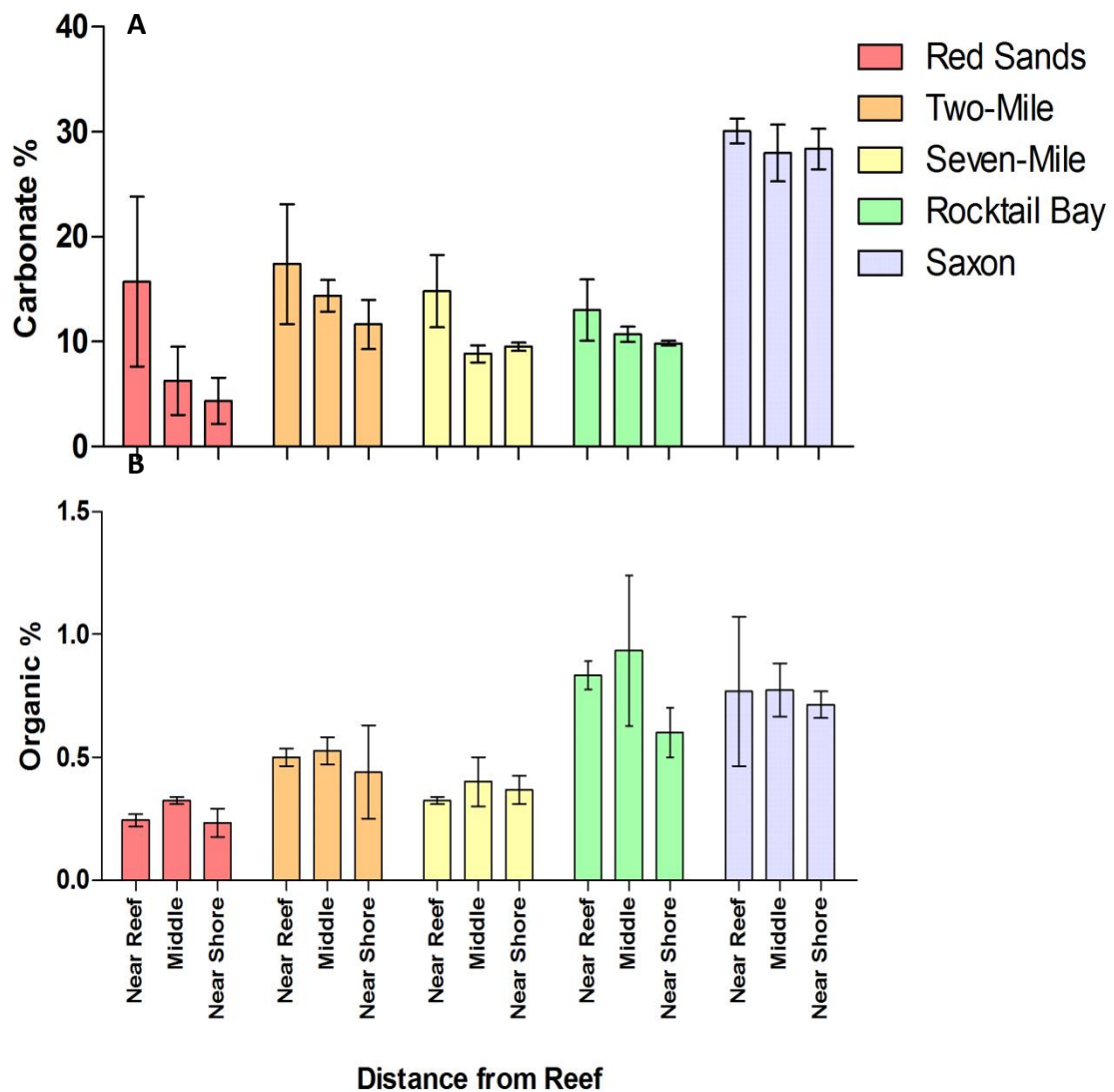
Figure 3.2. The mean (±SE) carbonate (A) and organic (B) content of sediment at each distance from the reef of each site.

The percentage of carbonate within the sediment was higher closer to the reef at all of the sites (Fig. 3.2A). At the near reef distance, Saxon Reef (31.4%) had the highest carbonate percentage of all the sites followed by Red Sands Reef (27.7%). The lowest recorded carbonate percentage was at Red Sands Reef of (5.2%) at the near shore distance. Nested ANOVA revealed significant differences between distances (Table 3.3). Post hoc Tukey analysis showed significant differences between both the 'Near Reef – Middle' and 'Near Reef – Near Shore' distances (Table 3.4).

The highest recorded organic content among the reefs was at Rocktail Bay (0.78 %) and Saxon Reef (0.75 %; Fig. 3.2B). They were followed by Two-Mile Reef (0.49 %) and Seven-Mile Reef (0.36 %), with Red Sands Reef (0.28 %) having the lowest organic content. A significant difference between sites was found (Table 3.2). Post hoc analysis comparing sites revealed significant differences between 'Saxon Reef – Red Sands' and 'Saxon Reef – Seven-Mile Reef'. Rocktail Bay was significantly different to all sites except Saxon Reef (Table 3.3). The amount of organic content was nominally higher at the middle distance at all sites. However, the pairwise comparisons of distances away from the reef indicated no significant differences among distances (Table 3.4).

Table 3.2. Nested Analysis of Variance (ANOVA) of the Organic % and Carbonate % in sediment samples.

	df	N	Organic %		Carbonate %	
			F	P	F	P
Site	4	45	40.328	0.001*	0.628	0.646
Distance	2	15	4.173	0.065	14.927	0.001*
Site*Distance	8	675	0.679	0.706	2.239	0.052

(*) = Significant

Table 3.3. Tukey's *post hoc* analysis with pairwise comparison of Organic % and Carbonate % in the sediments at each reef site.

Tukey HSD			Organic %	Carbonate %
(A) Site	(B) Site	N	P	
Two-Mile	Red Sands	3	0.431	0.564
	Rocktail Bay	3	0.048*	0.685
	Seven-Mile	3	0.475	0.667
	Saxon	3	0.189	0.401
Red Sands	Rocktail Bay	3	0.014*	0.835
	Seven-Mile	3	0.387	0.932
	Saxon	3	0.021*	0.999
Rocktail Bay	Seven-Mile	3	0.011*	1.000
	Saxon	3	0.156	0.999
Seven-Mile	Saxon	3	0.019*	0.852

(*) = Significant

Table 3.4. Tukey's *post hoc* analysis with pairwise comparison of Organic % and Carbonate % in the sediments at each distance away from the reefs edge.

Tukey HSD			Organic %	Carbonate %
(A) Distance	(B) Distance	N	P	
Near Reef	Middle	3	0.246	0.002*
	Near Shore	3	0.438	0.001*
Middle	Near Shore	3	0.239	0.335

(*) = Significant

3.2. Benthic Macrofaunal Community Analysis

3.2.1. Taxonomic composition

A total of 5166 animals were collected with 121 species, 95 genera, 69 families, 29 Orders and 20 classes being identified. The two most abundant taxa recorded across all sites were Amphipoda and Polychaeta (Fig. 3.3; Table 3. 5). Amphipoda, which mostly consisted of *Ampelisca spp*. and *Urothoe spp*, was the most abundant taxon at all the sample sites except for Rocktail Bay where the abundance of Polychaeta exceeded that of Amphipoda. Amphipoda was the next most abundant taxon at this site. Echinodermata was the third most abundant at Red Sands Reef, Two-Mile Reef and Rocktail Bay. Decapoda had the third highest abundance at Seven-Mile Reef and Isopoda at Saxon Reef. Two-Mile Reef was the only site at which Tunicata, exclusively *Molgula sp.* and Cnidaria, mostly seapens *Scytaliopsis sp.* and *Virgularia sp.* contributed more than 3 % of the community compostion.

The highest overall density occurred at Two-Mile Reef (2286 indiv. m^2), followed by Saxon Reef (1497 indiv. m^2), Seven-Mile Reef (1096 indiv. m^2), Rocktail Bay (1055 indiv. m^2) and Red Sands Reef (672 indiv. m^2). Two-Mile Reef had the highest mean abundance of all sites of benthic macrofauna at the near shore distance (1403 indiv. m^2; Fig. 3.6A). This was followed by the near reef distance at Saxon Reef (573 indiv. m^2). The lowest values at the near reef distance were at Red Sands Reef (134 indiv. m^2) and Rocktail Bay (181 indiv. m^2). Red Sand Reef, Seven-Mile Reef and Rocktail Bay showed similar trends with peaks in abundance at the middle distance. At Two-Mile Reef abundance increased with increasing distance away from the reef whereas at Saxon Reef abundance was highest at the near reef distance and lowest at the middle distance.

Overall abundance was significantly different between sites, distances and the distance within site (Table 3.9). Post hoc analysis revealed that the number of individuals varied significantly between Red Sands Reef and Two-Mile Reef and between the near reef and the near shore stations (Tables 3.10 & 3.11). Analysis of the five most abundant taxa revealed that there were significant variations between sites for Polychaeta and Decapoda (Table 3.12). Bivalvia abundance varied significantly for the nested term distance within site. Tukey's post hoc pairwise analysis revealed that Polychaeta abundance was significantly higher at Rocktail Bay than Red Sands Reef (Table 3.13). At Two-Mile Reef Decapoda abundance was significantly lower than at all other sites.

Samples at each of the three distances away from the reef edge were similarly dominated by Amphipoda and Polychaeta (Tables 3.6, 3.7 & 3.8). Excluding Rocktail Bay, Amphipoda were most abundant at all distances except for the middle distance at Saxon Reef (Table 3.7). At Rocktail Bay Polychaeta was dominant across all distances. Other taxa which were in the top four in the contribution to overall abundace at each site and distance included, Echinodermata, Bivalvia,

Decapoda, Ostracoda, Cnidaria, Ascidiacea and Isopoda. The cumulative contribution of the four most abundant taxa ranged from 80 % at the middle distance at Saxon Reef to 96 % at the near shore distance at Rocktail Bay. All the sites combined, analysis of the five taxa found no significant variations between distances (Table 3.14).
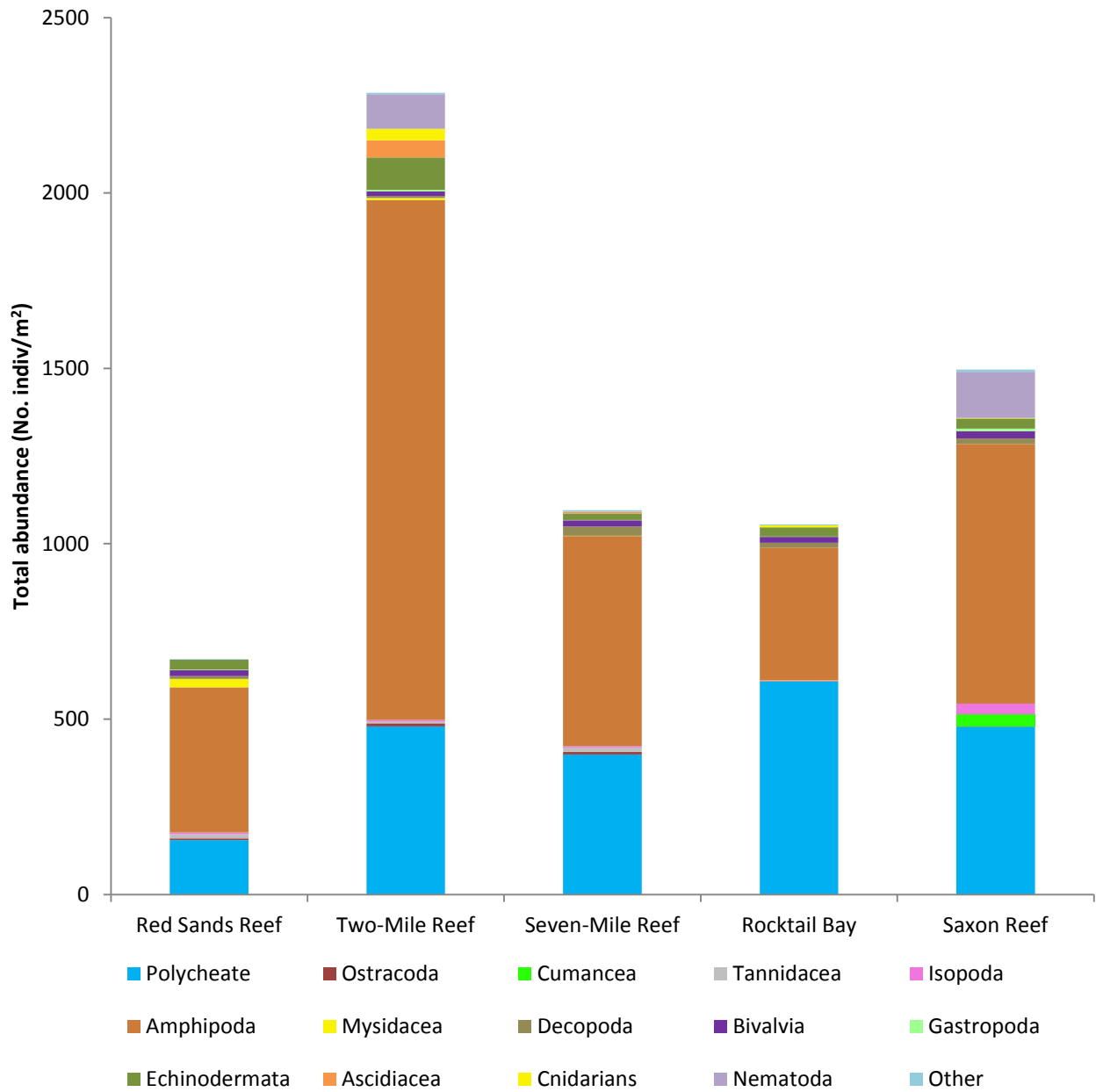
Figure 3.3. Contribution to total abundance according to taxon for each reef site

Table 3.5. Four most abundant taxa for each reef site according to their average abundance (No. indiv/m^2). Total contribution of the four taxa abundance to site is represented in percentages.

	Site														
	Red Sands			Two-Mile			Seven-Mile			Rocktail Bay			Saxon		
	Taxa	Abundance	SD	Taxa	Abundance	SD	Taxa	Abundance	SD	Taxa	Abundance	SD	Taxa	Abundance	SD
1	Amphipoda	137.88	191.39	Amphipoda	494.22	712.56	Amphipoda	199.56	251.71	Polychaeta	202.34	173.99	Amphipoda	246.71	303.65
2	Polychaeta	52.65	123.17	Polychaeta	159.78	150.07	Polychaeta	133.04	168.06	Amphipoda	126.25	200.86	Polychaeta	159.48	228.65
3	Echinodermata	9.44	16.15	Echinodermata	30.82	62.57	Decapoda	8.96	7.56	Echinodermata	8.78	8.44	Isopoda	10.11	29.49
4	Bivalvia	6.12	5.50	Ascidiacea	16.24	23.50	Echinodermata	6.13	6.88	Bivalvia	5.46	5.83	Echinodermata	9.78	14.66
Total contribution (%)	91			90			95			96			86		

Table 3.6. Four most abundant taxa at the near reef distance for the reef edge at each site according to their average abundance (No. indiv/m^2). Total contribution of the four taxa abundance to site is represented in percentages.

	Near Reef														
	Red Sands			Two-Mile			Seven-Mile			Rocktail Bay			Saxon		
	Taxa	Abundance	SD	Taxa	Abundance	SD	Taxa	Abundance	SD	Taxa	Abundance	SD	Taxa	Abundance	SD
1	Amphipoda	69.27	124.63	Amphipoda	176.91	228.11	Amphipoda	88.44	127.01	Polychaeta	101.67	129.21	Amphipoda	369.31	294.81
2	Polychaeta	38.36	92.51	Polychaeta	129.51	136.29	Polychaeta	51.29	94.53	Amphipoda	70.76	175.24	Polychaeta	107.63	186.97
3	Tanaidacea	11.44	27.84	Echinodermata	26.35	25.07	Decapoda	8.96	8.37	Decapoda	5.46	5.23	Isopoda	28.34	45.89
4	Bivalvia	5.46	5.61	Cnidaria	11.93	11.59	Ostracoda	5.47	7.15	Bivalvia	1.51	1.31	Echinodermata	20.83	20.25
Total contribution (%)	91			93			82			94			90		

Table 3.7. Four most abundant taxa at the middle distance for the reef edge at each site according to their average abundance (No. indiv/m^2). Total contribution of the four taxa abundance to site is represented in percentages.

Middle

	Red Sands			Two-Mile			Seven-Mile			Rocktail Bay			Saxon		
	Taxa	Abundance	SD	Taxa	Abundance	SD	Taxa	Abundance	SD	Taxa	Abundance	SD	Taxa	Abundance	SD
1	Amphipoda	174.92	206.61	Amphipoda	272.61	265.74	Amphipoda	88.49	271.51	Polychaeta	235.24	156.36	Polychaeta	202.34	256.17
2	Polychaeta	48.81	90.07	Polychaeta	113.12	178.65	Polychaeta	51.29	180.04	Amphipoda	206.82	175.24	Amphipoda	136.05	185.09
3	Echinodermata	14.41	25.42	Echinodermata	49.22	102.41	Bivalvia	8.95	10.85	Bivalvia	11.93	1.89	Bivalvia	5.97	5.69
4	Bivalvia	8.45	7.19	Ascidiacea	20.88	29.28	Echinodermata	8.45	9.42	Echinodermata	10.94	1.31	Echinodermata	4.47	5.77
Total contribution (%)	87			83			95			93			80		

Table 3.8. Four most abundant taxa at the near shore distance for the reef edge at each site according to their average abundance (No. indiv/m^2). Total contribution of the four taxa abundance to site is represented in percentages.

Near Shore

	Red Sands			Two-Mile			Seven-Mile			Rocktail Bay			Saxon		
	Taxa	Abundance	SD	Taxa	Abundance	SD	Taxa	Abundance	SD	Taxa	Abundance	SD	Taxa	Abundance	SD
1	Amphipoda	169.45	243.48	Amphipoda	1033.21	980.17	Amphipoda	243.19	285.35	Polychaeta	270.12	184.01	Amphipoda	234.74	357.81
2	Polychaeta	68.77	186.52	Polychaeta	236.73	89.77	Polychaeta	170.94	182.57	Amphipoda	101.17	125.56	Polychaeta	168.45	227.29
3	Echinodermata	13.92	9.74	Ascidiacea	19.39	25.27	Echinodermata	7.96	3.977	Echinodermata	13.92	9.53	Nematoda	65.78	174.06
4	Bivalvia	3.48	2.55	Cnidaria	12.43	7.81	Decapoda	6.46	7.69	Bivalvia	4.97	3.29	Bivalvia	11.43	7.01
Total contribution (%)	96			90			95			96			94		

3.2.2. Macrofaunal diversity

The site which had the highest number of species was Two-Mile Reef with 70 species. Seven-Mile Reef had the second highest number with 50 species followed by Saxon Reef (49), Rocktail Bay (45) and the lowest number of species was recorded at Red Sands Reef with 41 species. The rarefaction curve indicated that approximately 20 macrofaunal species were not collected in this study highlighting the successful sampling effort of the soft-bottom macrofaunal species in the nearshore and coral reef habitats (Fig. 3.4).

The difference in the number of species between sites and distance within site were both found to be significant (Table 3.9). Post hoc analysis comparing sites showed that Two-Mile Reef had a significantly higher number of species than all other reef sites (Table 3.10). Diversity varied significantly between sites (Table 3.9). Seven-Mile and Two-Mile Reef had the highest calculated Shannon-Wiener diversity indices of 1.44 and 1.39 respectively, while Saxon Reef had the lowest (0.992). Diversity at Saxon Reef was significantly lower than at Two-Mile Reef and Seven-Mile Reef (Table 3.10). Sanctuary sites were not found to have higher species diversity than the non-sanctuary sites. The number of unique species (species only found at one site) was highest at Two-Mile Reef (18) followed by Saxon Reef (13), Red Sands Reef (7), Seven-Mile Reef (5) and lastly Rocktail Bay (3).

At the near shore distance, Two-Mile Reef had the highest mean number of species (14 ±2 SD) (Fig. 3.6C). Trends in species diversity at each distance were similar to those of faunal abundance, but there were no significant differences in the number of species between distances (Table 3.11).

Seven-Mile Reef had the highest diversity of 0.811 at the near reef distance (Fig. 3.6D). Two-Mile Reef showed a similar trend to Seven-Mile Reef with a higher diversity closest to the reef and decreasing with distance away from its edge. However, when the distances away from the reef were compared there was no significant difference (Table 3.11).
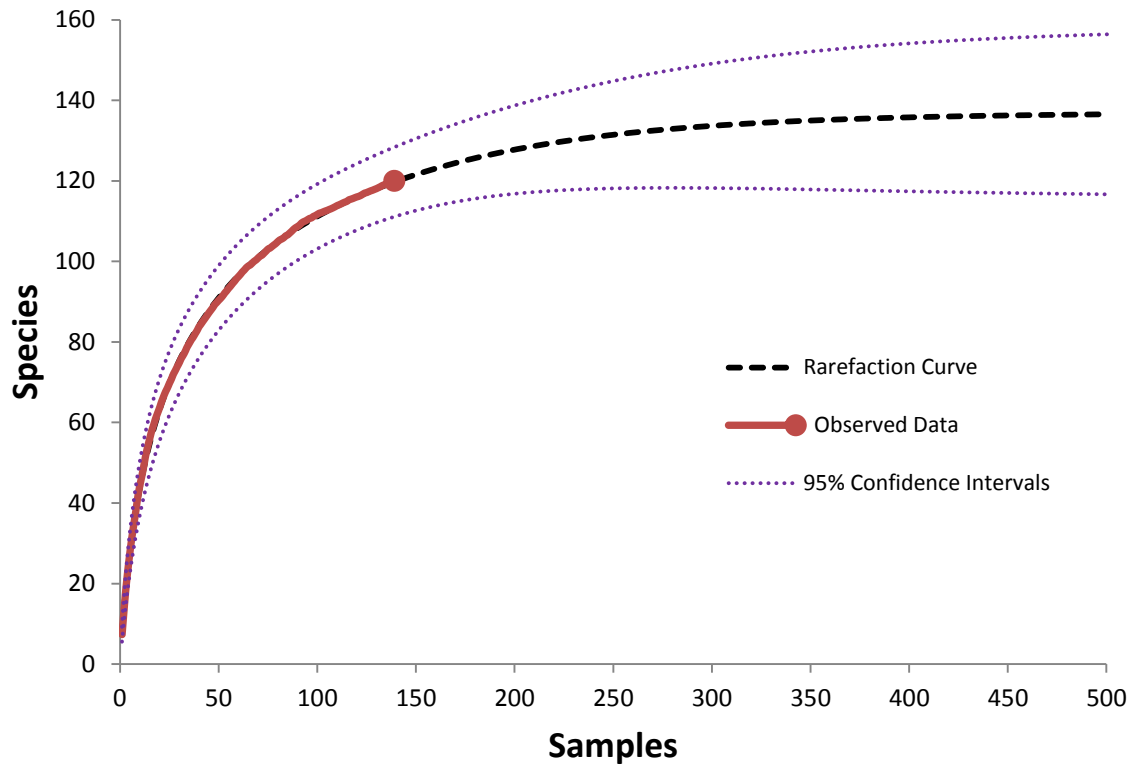
Figure 3.4. Species accumulation curve and interpolated rarefaction curve with 95% confidence intervals for species richness estimates from macrofauna recorded.

3.2.3. Community biomass estimates

At all sites Echinodermata were the dominant contributor to total biomass ranging from 50 – 88 % (Fig. 3.5). At Red Sands Reef Bivlavia and Decapoda had the next highest contribution to the total biomass after Echinodermata. The second highest contributor at Two-Mile Reef was Cnidaria which was higher than at all other sites. At Rocktail Bay the second highest contribution to the total biomass was Bivalvia followed by Decapoda and Polychaeta. At Seven-Mile Reef Decapoda and Polychaeta followed after Echinodermata. Saxon Reef, similar to Seven-Mile Reef, had a high Decapoda biomass but also had a high Gastropda biomass in comparison to the other sites.

Overall biomass was highest at Two-Mile Reef having 63.29 g.m^2. All other sites had considerably lower biomass; Saxon Reef (19.69. g.m^2), Red Sands Reef (17.78 g.m^2), Rocktail Bay (13.33 g.m^2) and Seven-Mile Reef (7.68 g.m^2). Biomass varied significantly between sites, distance and distance within site (Table 3.9). All sites, except Saxon Reef, had significantly lower biomass than Two-Mile Reef (Table 3.10).

The highest biomass recorded was at the near shore distance at Two-Mile Reef (33.28 g.m^2; Fig. 3.6B). Biomass at the near shore stations of Two-Mile Reef, Red Sands Reef and Rocktail Bay was higher than at stations further away. In contrast, Seven-Mile Reef and Saxon Reef both had greater biomass at the middle distance. Post hoc Tukey analysis revealed a significant difference in biomass between the near reef and near shore distances for all sites combined (Table 3.11).
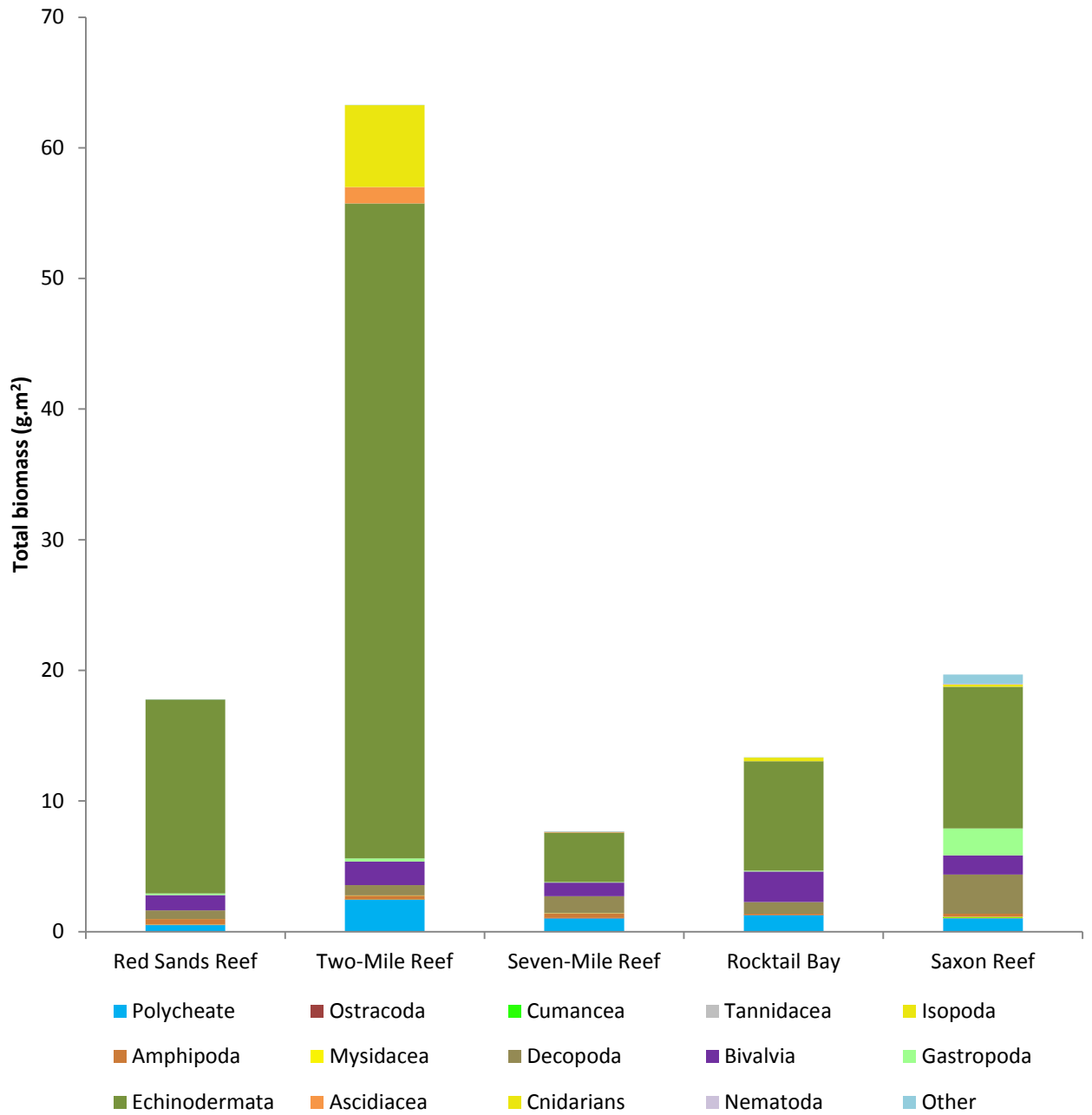
Figure 3.5. Contribution to total biomass according to taxon for each reef site.
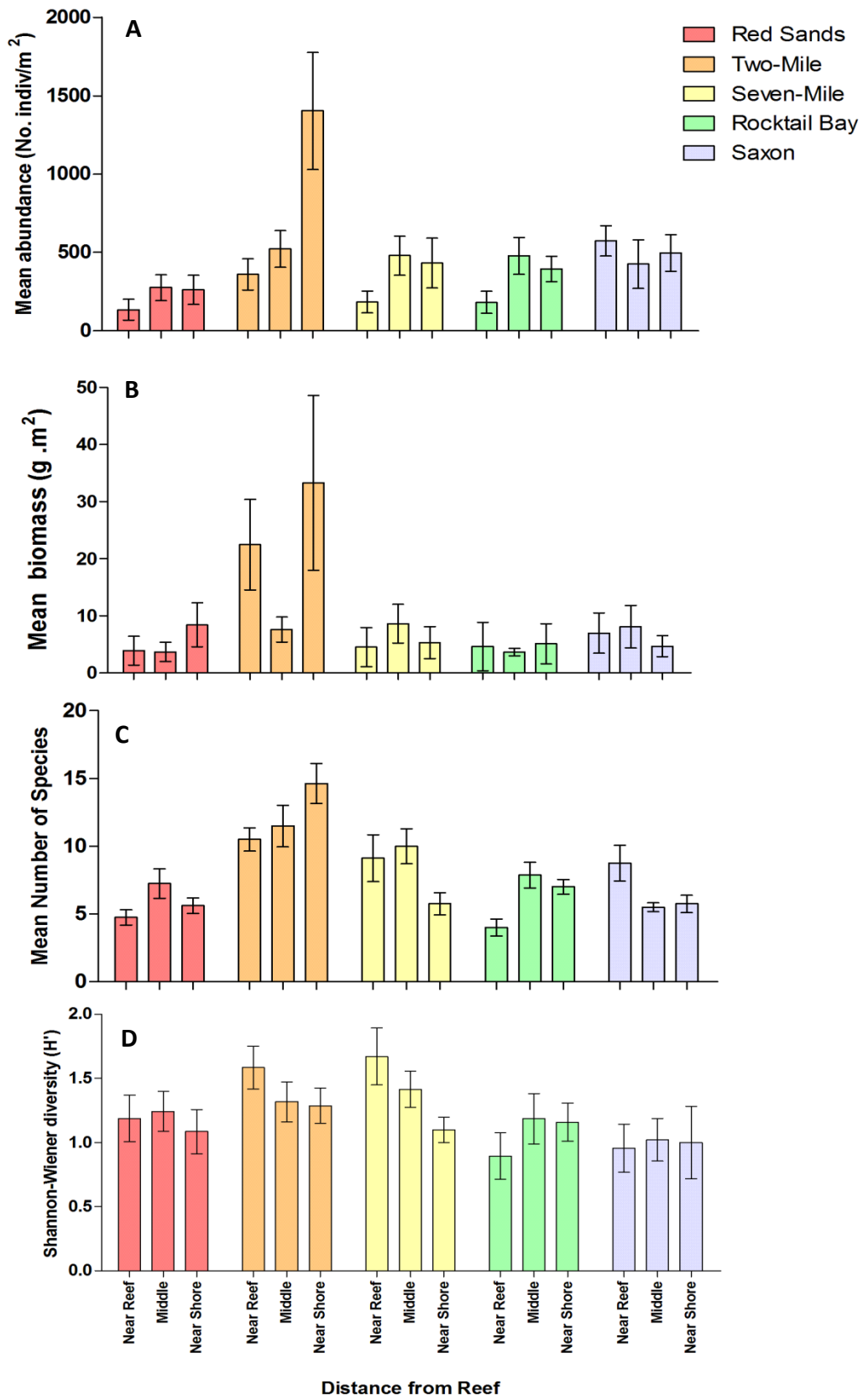
Figure 3.6. Means (±SE) for the community indices at each site and distance away from the reef. Abundance (A), Biomass (B), Number of species (C), Shannon-Wiener diversity (D).

Table 3.9. Nested Analysis of Variance (ANOVA) of the community indices.

	df	N	Abundance		Species		Biomass		S-W diversity (H')	
			F	P	F	P	F	P	F	P
Site	4	24	2.669	0.036*	16.977	<0.001*	9.114	<0.001*	3.224	0.015*
Distance	2	40	4.522	0.013*	1.779	0.174	3.851	0.024*	0.803	0.451
Site*Distance	8	960	2.573	0.013*	4.015	<0.001*	2.807	0.007*	0.935	0.491

(*) = Significant

Table 3.10. Tukey's *post hoc* analysis with pairwise comparison of community indices between sites.

Tukey HSD			Abundance	Species	Biomass	S-W diversity (H')
(A) Site	(B) Site	N		P		
Two-Mile	Red Sands	24	0.014*	<0.001*	<0.001*	0.530
	Rocktail Bay	24	0.330	<0.001*	<0.001*	0.191
	Seven-Mile	24	0.311	<0.001*	<0.001*	1.000
	Saxon	24	0.437	<0.001*	0.069	0.048*
Red Sands	Rocktail Bay	24	0.659	0.989	1.000	0.969
	Seven-Mile	24	0.682	0.053	0.997	0.538
	Saxon	24	0.540	0.838	0.224	0.728
Rocktail Bay	Seven-Mile	24	1.000	0.160	0.987	0.196
	Saxon	24	1.000	0.980	0.307	0.974
Seven-Mile	Saxon	24	0.999	0.427	0.113	0.049*

(*) = Significant

Table 3.11. Tukey's *post hoc* analysis with pairwise comparison of community indices between distances away from the reefs edge.

Tukey HSD			Abundance	Species	Biomass	S-W diversity (H')
(A) Distance	(B) Distance	N		P		
Near Reef	Middle	40	0.084	0.156	0.073	0.997
	Near Shore	40	0.013*	0.797	0.032*	0.455
Middle	Near Shore	40	0.741	0.447	0.941	0.41

(*) = Significant

Table 3.12. Nested Analysis of Variance (ANOVA) of the five most numerically abundant taxa.

	df	N	Polychaeta F	Polychaeta P	Amphipoda F	Amphipoda P	Echinodermata F	Echinodermata P	Bivalvia F	Bivalvia P	Decapoda F	Decapoda P
Site	4	24	3.81	0.007*	0.829	0.51	1.298	0.28	2.048	0.1	6.945	<0.001*
Distance	2	40	2.64	0.077	1.365	0.261	0.034	0.967	1.064	0.352	1.44	0.246
Site*Distance	8	960	1.19	0.313	1.245	0.284	1.361	0.237	2.304	0.033*	0.594	0.779

(*) = Significant

Table 3.13. Tukey's *post hoc* analysis of the five most abundant taxa between sites.

Tukey HSD			Polychaeta	Amphipoda	Decapoda	Echinodermata	Bivalvia
(A) Site	(B) Site	N			P		
Two-Mile	Red Sands	24	0.244	0.691	0.003*	0.961	0.066
	Rocktail	24	0.236	0.289	0.003*	1.000	0.034*
	Seven-Mile	24	0.993	0.959	<0.001*	0.421	0.173
	Saxon	24	0.914	0.742	0.023*	0.990	0.553
Red Sands	Rocktail	24	<0.001*	0.979	0.952	0.951	0.996
	Seven-Mile	24	0.119	0.964	0.956	0.228	0.997
	Saxon	24	0.828	1.000	0.787	0.835	0.842
Rocktail Bay	Seven-Mile	24	0.481	0.690	0.386	0.545	0.958
	Saxon	24	0.064	0.934	0.981	0.997	0.669
Seven-Mile	Saxon	24	0.745	0.984	0.183	0.766	0.963

(*) = Significant

Table 3.14. Tukey's *post hoc* analysis with pairwise comparison of the five most abundant taxa between distances away from the reefs edge.

Tukey HSD			Polychaeta	Amphipoda	Decapoda	Echinodermata	Bivalvia
(A) Distance	(B) Distance	N			P		
Near Reef	Middle	40	0.178	0.299	0.986	0.793	0.881
	Near Shore	40	0.157	0.405	0.900	0.675	0.635
Middle	Near Shore	40	0.438	0.972	0.951	0.977	0.190

(*) = Significant

3.2.4. Multivariate analysis of macrofaunal communities

The nested ANOSIM indicated a significant degree of dissimilarity between Two-Mile Reef and all other sites (Table 3.15). Saxon Reef and Rocktail Bay were the only other sites which were significantly different from one another, however, the Global R-statistics did show an overall significant dissimilarity between sites. The MDS ordination supported the ANOSIM results with Two-Mile Reef forming a separate cluster (Fig. 3.7A). Although there is an overlap between sites, grouping of Red Sands Reef, Rocktail Bay and Saxon Reef were observed in the MDS plot. The Global R-statistic for distance indicated no significant differences between them (Table 3.16). This was further supported by the MDS ordination plot which showed no distinctive grouping in distance away from the reefs edge (Fig. 3.7B). The 'protective status' of the sites was overlaid in the MDS ordination plot and two distinct grouping became evident with the two sanctuary sites, Red Sands Reef and Saxon Reef, showing separate clustering to the non-sanctuary sites (Fig. 3.7C). ANOSIM analysis did indicated similarity between these Red Sands Reef and Saxon Reef with a low R-statistic value, however, these sites showed no significant differences to the other sites.

Table 3.15. Results of nested analysis of similarity (ANOSIM). Global R = 0.539. Significance of Global R <0.002. R-statistics >0.5 were considered to be significant.

Pairwise Tests	R Statistic	Significance Level
Two-Mile - Red Sands	0.778*	0.1
Two-Mile - Rocktail Bay	0.741*	0.1
Two-Mile - Seven-Mile	0.630*	0.1
Two-Mile - Saxon	1*	0.1
Red Sands - Rocktail Bay	0.333	0.3
Red Sands - Seven-Mile	0.444	0.2
Red Sands - Saxon	0.120	0.1
Rocktail Bay - Seven-Mile	0	0.7
Rocktail Bay - Saxon	0.519*	0.1
Seven-Mile - Saxon	0.407	0.1

(*) = Significant

Figure 3.7. Non-metric multidimensional (MDS) ordination plots of forth root transformed abundance data illustrating groupings according on site (A), distance (B) and protective status (C).

Red Sands Reef

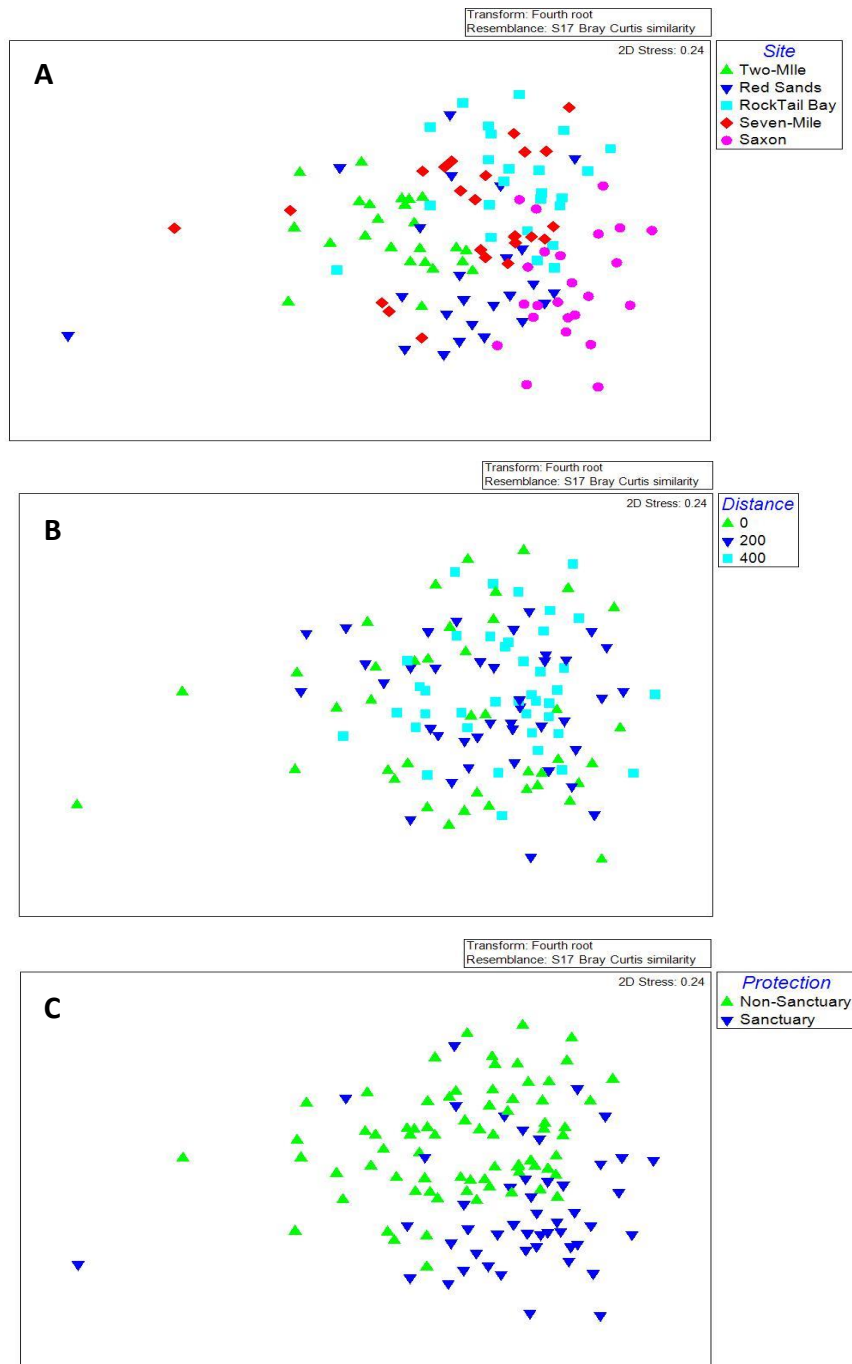## Two-Mile Reef

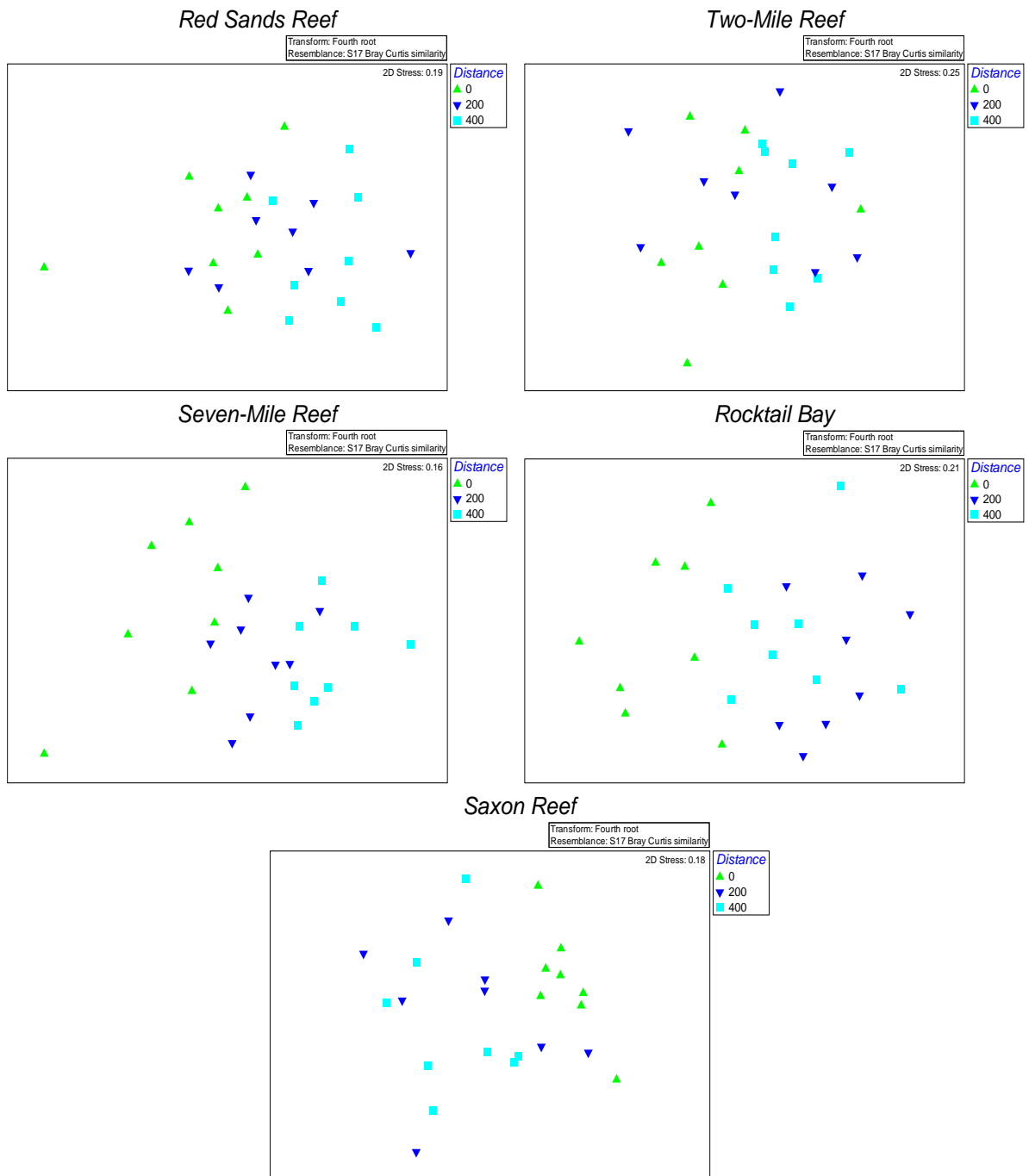## Seven-Mile Reef

Rocktail Bay

Saxon Reef

Figure 3.8. Non-metric multidimensional (MDS) ordination plots of forth root transformed abundance data illustrating groupings according the three sampled distances away from the reef at each site.

ANOSIM analysis comparing distances at each individual site indicated significant differences between stations at Seven-Mile Reef , Rocktail Bay and Saxon Reef (Table 3.16). MDS ordination plots produced for each site supported the ANOSIM (Fig. 3.8). Seven-Mile Reef showed distinct separate clustering between the near reef and the near shore distances. Similar patterns between the ANOSIM results and MDS ordination plots were observed for Rocktail Bay and Saxon Reef.

Table 3.16. Results of analysis of similarity (ANOSIM) pairwise comparisons of faunal abundance at varying distance from the reef for each site. Global R = 0.269. Significance of Global R <0.001. R-statistics >0.5 were considered to be significant.

Site	Pairwise Tests	R Statistic	Significance Level
Red Sand Reef	Near Reef - Middle	0.007	0.445
	Near Reef – Near Shore	0.381	0.001
	Middle – Near Shore	0.136	0.083
Two-Mile Reef	Near Reef - Middle	0.041	0.335
	Near Reef – Near Shore	0.333	0.001
	Middle – Near Shore	0.026	0.345
Seven-Mile Reef	Near Reef - Middle	0.308	0.001
	Near Reef – Near Shore	0.673*	0.001
	Middle – Near Shore	0.092	0.156
Rocktail Bay	Near Reef - Middle	0.671*	0.001
	Near Reef – Near Shore	0.362	0.002
	Middle – Near Shore	0.027	0.361
Saxon Reef	Near Reef - Middle	0.263	0.008
	Near Reef – Near Shore	0.641*	0.001
	Middle – Near Shore	0.077	0.226

(*) = Significant
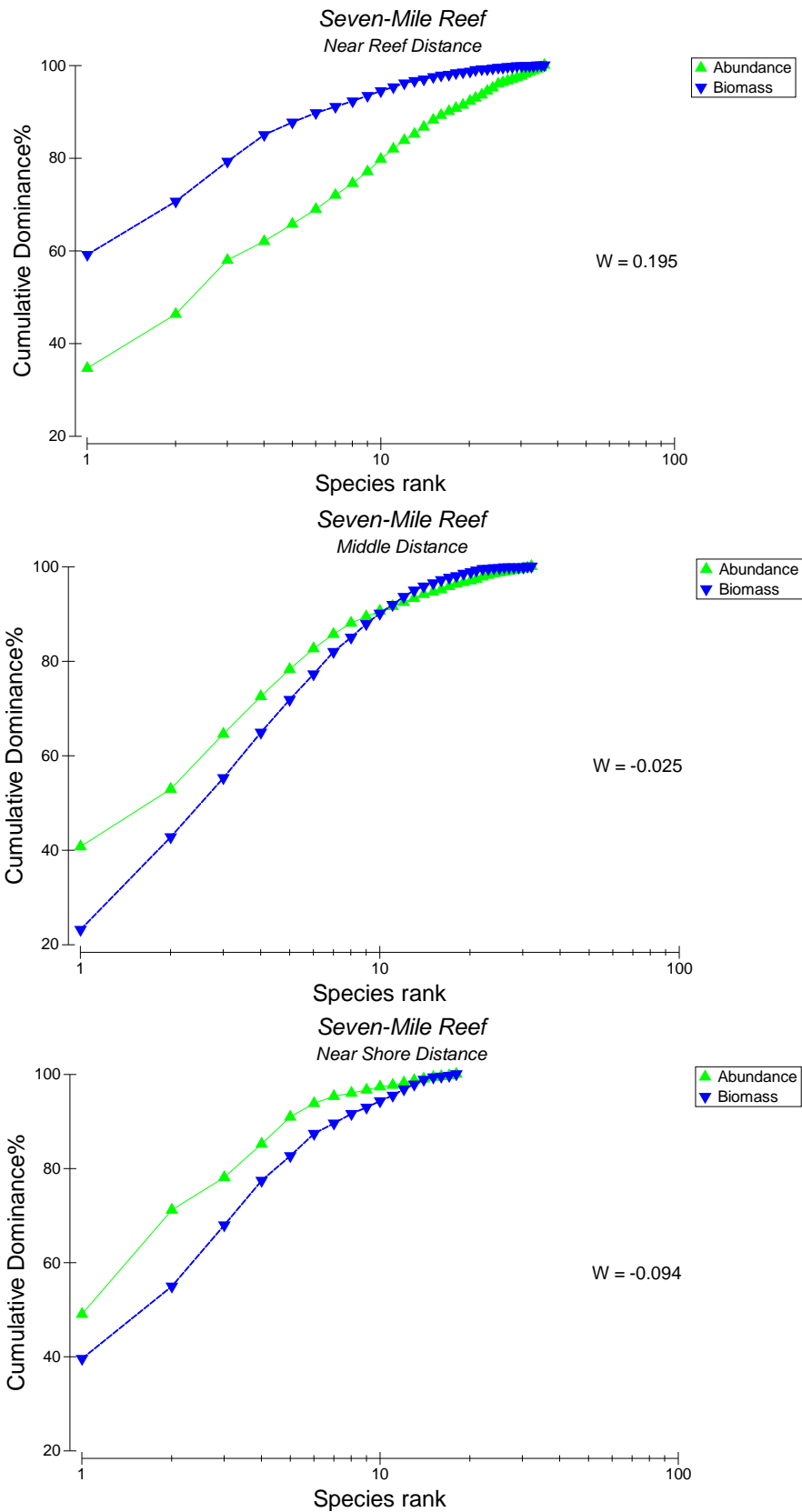
Figure 3.9. Abundance biomass comparison (ABC) plots for the macrobenthic species at each distance at Seven-Mile Reef.
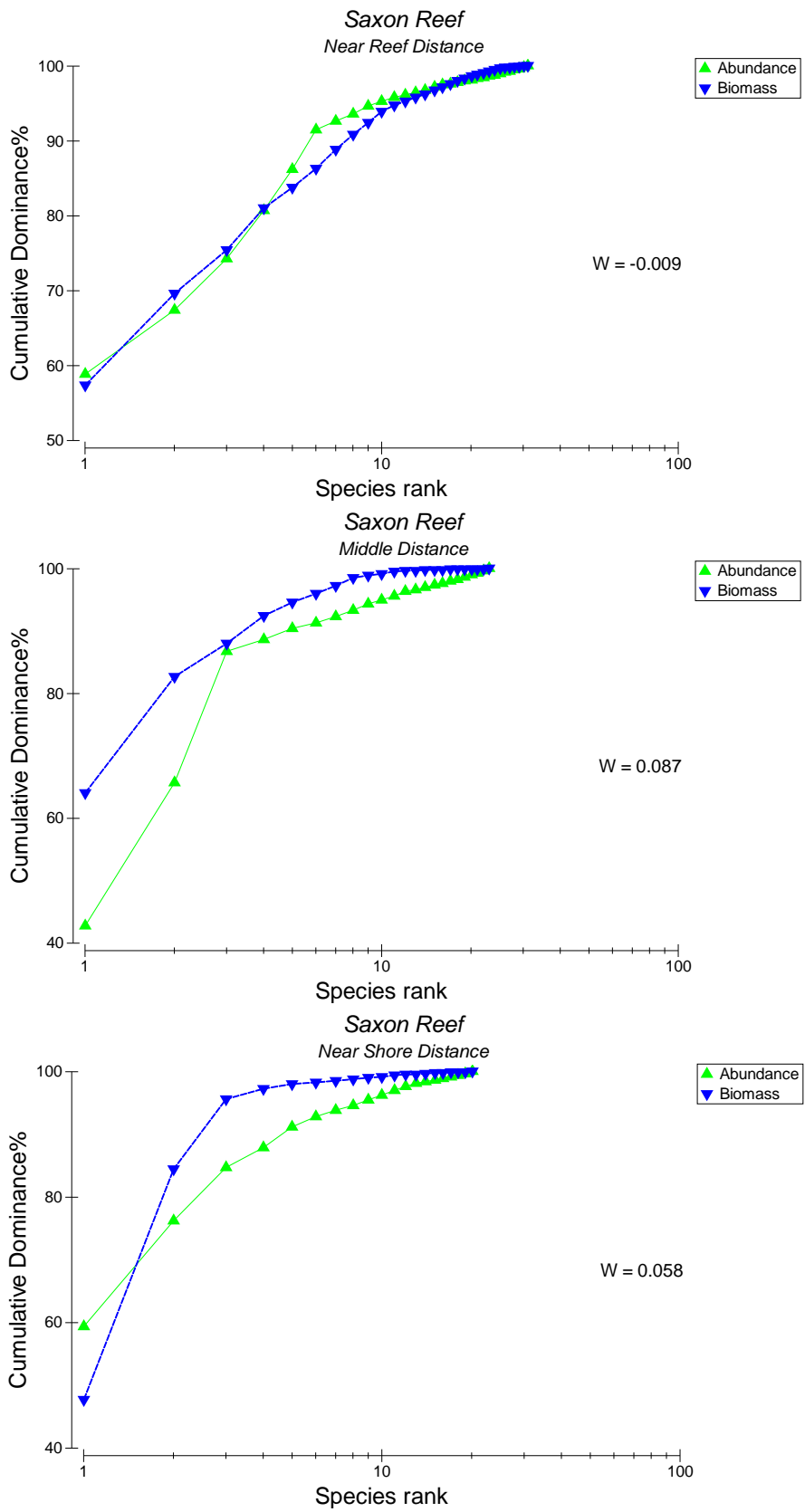
Figure 3.10. Abundance biomass comparison (ABC) plots for the macrobenthic species at each distance at Saxon Reef.

Abundance Biomass Comparison curves give an indication of the level of disturbance on benthic communities. Seven-Mile Reef and Saxon Reef were the only sites where disturbance was indicated by the curves. The ABC plots for each distance at Seven-Mile Reef showed interesting results with the near reef distance indicating no disturbance (Fig. 3.9). This was supported by the high W-statistic (W = 0.195) indicating a large degree of separation between the two curves. Disturbance was shown at the near shore distance with the abundance curve located above the biomass curve indicating few species and a high number of small animals. Similarly, at the middle distance the abundance curve was located above the biomass curve, however, the curves intercepted high on the graph signifying the presence of numerous smaller sized fauna but only a moderate level of disturbance. At the near reef and near shore distances of Saxon Reef moderate levels of disturbance were similarly shown (Fig. 3.10). At the near shore distance however, curves intercepted low on the graph and indicated the occurrence of numerous larger sized species. The middle distance did not indicate any disturbance.

3.2.5. Indicator and discriminator species for sites

Samples collected from Two-Mile Reef had higher average similarity in species composition than among samples at other sites (Table 3.17). Five taxa contributed 52.69 % to the average similarity. Indicator species were the ascidian *Molgula sp.* the amphipods *Ampelisca miops*, *Urothoe elegans* and the polychaete *Diopatra neapolitana capensis*. *Molgula sp.* and *A. miops* had the highest Sim / SD value and were more consistently found throughout the samples. These taxa are therefore considered to be the most reliable indicator species for Two-Mile Reef. Indicator species contribute to the similarity in assemblages between sites by being abundant in all of the sites and having high Sim /SD values.

Table 3.17. SIMPER analysis showing taxa which contributed ~ 90 % to the similarity at Two-Mile Reef. Taxa are arranged in their order of contribution to the average similarity.

Site: Two-Mile Reef

Average similarity: 26.84

Taxa	Av.Abund	Av.Sim	Sim/SD	Contrib(%)	Cum(%)
Molgula sp	2.52	4.88	1.07	18.18	18.18
Ampelisca miops	1.76	3.64	1.05	13.58	31.75
Urothoe elegans	2.27	2.21	0.42	8.24	39.99
Diopatra neapolitana capensis	1.34	2.06	0.54	7.68	47.67
Cerianthid sp 1	1.17	1.35	0.55	5.02	52.69

The five leading indicator species contributed 73.92 % to the average similarity of 20.63 % at Red Sands Reef (Table 3.18). The bivalve *Sunetta bruggeni,* Polychaete sp 1, *U. elegans*, Amphipod sp 1 and the brittlestar *Ophionephthys lowelli* contributed most to the similarity *U. elegans* had the highest average abundance, however, the low Sim / SD value indicated that it was not consistently found throughout the site. Due to its greater Sim / SD value, *S. bruggeni* is considered to be the most reliable indicator species for Red Sands Reef.

Table 3.18. SIMPER analysis showing taxa which contributed ~ 90 % to the similarity at Red Sand Reef. Taxa are arranged in their order of contribution to the average similarity.

Site: Red Sands Reef

Average similarity: 20.63

Taxa	Av.Abund	Av.Sim	Sim/SD	Contrib(%)	Cum(%)
Sunetta bruggeni	1.57	5.46	0.74	26.48	26.48
Polychaete sp 1	1.52	3.45	0.47	16.73	43.21
Urothoe elegans	2.15	3.41	0.41	16.53	59.74
Amphipod sp 1	1.03	1.55	0.37	7.51	67.25
Ophionephthys lowelli	0.92	1.38	0.32	6.67	73.92

Rocktail Bay had an average similarity of 20.54 % in which five taxa contributed 73.87 % (Table 3.19). The leading contributors to the average similarity were *A. miops*, *O. lowelli*, *S. bruggeni*, Polychaete sp 1 and *Ashtoret lunaris*. The most abundant species at Rocktail Bay were *O. lowelli* and *A. miops*. Even though *O. lowelli* had a lower contribution to the average similarity than *A. miops* it was considered to be the main indicator species for this site as it had the greater Sim / SD value.

Table 3.19. SIMPER analysis showing taxa which contributed ~ 90 % to the similarity at Rocktail Bay. Taxa are arranged in their order of contribution to the average similarity.

Site: Rocktail Bay

Average similarity: 20.54

Taxa	Av.Abund	Av.Sim	Sim/SD	Contrib%	Cum.%
Ampelisca miops	1.47	5.2	0.61	25.32	25.32
Ophionephthys lowelli	1.76	4.61	0.76	22.45	47.77
Sunetta bruggeni	1.21	2.1	0.49	10.24	58.01
Polychaete sp 1	1.32	2.05	0.41	9.97	67.99
Ashtoret lunaris	0.8	1.21	0.33	5.88	73.87

Seven-Mile Reef had an average similarity of 24.69 % in which five taxa contributed 60.61 % (Table 3.20). The indicator species which contributed most to similarity were *A. miops, O. lowelli*, *U. elegans*, *Scolaricia sp* and Caridea sp 3. *U. elegans* was the most abundant species, however, was not consistent enough throughout the samples collected for it to be deemed the most reliable indicator species for Seven-Mile Reef. *A. miops* was slightly less abundant than *U. elegans* but was found more consistently across Seven-Mile Reef making it a more appropriate indicator species.

Table 3.20. SIMPER analysis showing taxa which contributed ~ 90 % to the similarity at Seven-Mile Reef. Taxa are arranged in their order of contribution to the average similarity.

Site: Seven-Mile Reef

Average similarity: 24.69

Taxa	Av.Abund	Av.Sim	Sim/SD	Contrib%	Cum.%
Ampelisca miops	2.17	5.5	0.91	22.28	22.28
Ophionephthys lowelli	1.67	4.53	0.76	18.36	40.64
Urothoe elegans	2.18	2.76	0.38	11.17	51.81
Scolaricia sp	1.06	1.58	0.48	6.42	58.23
Caridea sp 3	0.97	1.57	0.42	6.37	64.61

Saxon Reef had an average similarity of 23.90 % (Table 3.21). The main contributors to similarity were *U. elegans*, Polychaete sp 1, *S. bruggeni*, *A. puncatata* and Echinoidea sp 1 with 70.86 %. The most abundant and consistently found species was *U. elegans*, making it the most reliable indicator species for Saxon Reef.

Table 3.21. SIMPER analysis showing taxa which contributed ~ 90 % to the similarity at Saxon Reef. Taxa are arranged in their order of contribution to the average similarity.

Site: Saxon Reef					
Average similarity: 23.90					
Taxa	Av.Abund	Av.Sim	Sim/SD	Contrib %	Cum.%
Urothoe elegans	3.17	7.63	0.64	31.94	31.94
Polychaete Sp 1	1.67	3.34	0.58	13.98	45.92
Sunetta bruggeni	1.01	2.28	0.43	9.55	55.46
Afrophila punctata	0.92	1.9	0.38	7.96	63.42
Echinoidea sp 1	1.19	1.78	0.36	7.44	70.86

The average dissimilarity between reef sites ranged from 80 – 90 % (Table 3.22). The macrofaunal assemblages at Two-Mile Reef and Saxon Reef were most dissimilar while Seven-Mile Reef and Rocktail Bay were least dissimilar. The average dissimilarity was generally higher when Two-Mile Reef was compared to the other reef sites. All identified discriminators had low Dissimilarity/Standard Deviation ratios indicating inconsistencies in their contribution to the difference between sites. The most reliable of these discriminating species were identified from the five taxa which contributed most to the overall average dissimilarity.

Table 3.22. Top five discriminating taxa of species composition of benthic macrofauna between reef sites. The Dissimilarity/Standard Deviation ratio indicates their consistency in the contribution to the difference between sites. The most reliable discriminating species from each site comparison is highlighted in bold.

	Two-Mile	Red Sands	Rocktail Bay	Seven-Mile
Red Sands	87.14 **Max Diss/SD: 1.34** *Urothoe elegans* (1.02) *Molgula sp* (1.3) Polychaete Sp 1 (0.98) *Urothoe sp 2* (0.71) ***Ampelisca miops* (1.34)**			
Rocktail Bay	88.16 **Max Diss/SD: 1.29** ***Molgula sp* (1.29)** *Urothoe elegans* (0.91) ***Ophionephthys lowelli* (1.17)** *Urothoe sp 2* (0.68) *Diopatra neapolitana capensis* (0.91)	85.12 **Max Diss/SD: 1.09** *Urothoe elegans* (0.88) ***Ophionephthys lowelli* (1.09)** *Ampelisca miops* (0.97) *Sunetta bruggeni* (1.04) *Scolelepis squamata* (0.72)		
Seven-Mile	85.02 **Max Diss/SD: 1.18** *Urothoe elegans* (0.98) ***Molgula sp* (1.18)** *Urothoe sp 2* (0.68) ***Ampelisca miops* (1.13)** ***Ophionephthys lowelli* (1.13)**	85.04 **Max Diss/SD: 1.27** *Urothoe elegans* (0.94) ***Ampelisca miops* (1.27)** *Ophionephthys lowelli* (1.05) *Sunetta bruggeni* (1.02) *Polydora c.f. giardi* (0.59)	80.63 **Max Diss/SD: 1.03** *Urothoe elegans* (0.85) ***Ampelisca miops* (1.03)** *Ophionephthys lowelli* (0.97) *Sunetta bruggeni* (1.00) *Scolaricia sp* (0.87)	
Saxon	89.97 **Max Diss/SD: 1.32** *Urothoe elegans* (1.13) ***Molgula sp* (1.32)** Urothoe sp 2 (0.68) *Ampelisca miops* (1.30) *Diopatra neapolitana capensis* (0.91)	83.65 **Max Diss/SD: 1.09** ***Urothoe elegans* (1.09)** *Sunetta bruggeni* (1.06) Echinoidea sp 1 (0.71) *Ophionephthys lowelli* (0.77) *Afrophila punctata* (0.73)	86.2 **Max Diss/SD: 1.16** ***Urothoe elegans* (1.03)** *Ophionephthys lowelli* (1.16) *Ampelisca miops* (1.00) *Mandibulophoxus stimpsoni* (0.83) *Sunetta bruggeni* (0.98)	84.51 **Max Diss/SD: 1.30** *Urothoe elegans* (1.02) ***Ampelisca miops* (1.30)** *Ophionephthys lowelli* (1.11) *Sunetta bruggeni* (0.93) *Polydora c.f. giardi* (0.69)

3.2.6. Indicator and discriminator species for distances

The SIMPER analysis was additionally performed to identify the indicator and discriminatory species for each distance away from the reefs edge. The average similarity closest to the reef was 13.00 % (Table 3.23). The main five taxa which contributed 54.77 % to the similarity in samples collected closest to the reefs were *U. elegans*, *A. miops*, *Diopatra neapolitana capensis*, Sipunculida sp and *S. bruggeni*. Although overall Sim / SD ratios were low the most reliable indicator species for this distance was *Diopatra neapolitana capensis*.

Table 3.23. SIMPER analysis showing taxa which contributed ~ 90 % to the similarity at the near reef distance away from the reef edge. Taxa are arranged in their order of contribution to the average similarity.

Near Reef Distance – 1 m

Average similarity: 13.00

Taxa	Av.Abund	Av.Sim	Sim/SD	Contrib%	Cum.%
Urothoe elegans	1.57	1.87	0.31	14.39	14.39
Ampelisca miops	0.99	1.76	0.34	13.57	27.96
Diopatra neapolitana capensis	1.15	1.44	0.36	11.07	39.03
Sipunculida sp	0.78	1.29	0.34	9.93	48.96
Sunetta bruggeni	0.75	0.76	0.26	5.81	54.77

At the middle distance the average similarity was 18.27 % in which the five top taxa contributed 70.56 % (Table 3.24). The top contributing taxa were *S. bruggeni*, *U. elegans*, Polychaete sp 1, *A. miops* and *O. lowelli*. *S. bruggeni* was the indicator species for this distance.

Table 3.24. SIMPER analysis showing taxa which contributed ~ 90 % to the similarity at the middle distance away from the reef edge. Taxa are arranged in their order of contribution to the average similarity.

Middle Distance – 200 m

Average similarity: 18.27

Taxa	Av.Abund	Av.Sim	Sim/SD	Contrib%	Cum.%
Sunetta bruggeni	1.5	3.38	0.65	18.5	18.5
Urothoe elegans	2.18	3.02	0.41	16.54	35.04
Polychaete sp 1	1.67	2.86	0.47	15.66	50.7
Ampelisca miops	1.25	1.82	0.5	9.96	60.67
Ophionephthys lowelli	1.17	1.81	0.47	9.9	70.56

The near shore stations had the highest average similarity in species composition (Table 3.25). The main contributing taxa to the similarity were *O. lowelli*, *U. elegans*, *A. miops*, *S. bruggeni* and *A. punctate* with 80.46 %. The top indicator species for the near shore distance was *O. lowelli*.

Table 3.25. SIMPER analysis showing taxa which contributed ~ 90 % to the similarity at the near shore distance away from the reef edge. Taxa are arranged in their order of contribution to the average similarity.

Near Shore Distance – 400 m

Average similarity: 22.47

Taxa	Av.Abund	Av.Sim	Sim/SD	Contrib%	Cum.%
Ophionephthys lowelli	1.84	5.97	0.87	26.57	26.57
Urothoe elegans	2.82	4.81	0.52	21.42	47.99
Ampelisca miops	1.54	3.96	0.67	17.62	65.61
Sunetta bruggeni	1.03	2.02	0.45	8.97	74.58
Afrophila punctata	1.16	1.32	0.3	5.89	80.46

High dissimilarities were observed among distances, ranging from 80 – 87 % (Table 3.26). The 'Near Reef - Near Shore' had the highest dissimilarity (87.08 %), whereas 'Middle – Near Shore' was least dissimilar (80.66 %). All discriminatory species had low Dissimilarity/Standard Deviation ratios indicating inconsistencies in their contribution to the difference between distances. The most reliable discriminators were identified from the five taxa which contributed greatest to the overall dissimilarity. The bivalve *S. bruggeni* was the best discriminating species between the 'Near Reef – Middle', whereas *O. lowelli* was determined to be the discriminating species for both the 'Near Reef – Near Shore' and the 'Middle – Near Shore'.

Table 3.26. Top five discriminating taxa of species composition of benthic macrofauna at each distance away from the reef edge. The Dissimilarity/Standard Deviation ratio indicates their consistency in the contribution to the difference between distances. The most reliable discriminating species from each site comparison is highlighted in bold.

	Near Reef	Middle
	86.31	
Middle	**Max Diss/SD: 1**	
	Urothoe elegans (0.91)	
	Polychaete sp 1 (0.95)	
	***Sunetta bruggeni* (1.00)**	
	Ampelisca miops (0.95)	
	Ophionephthys lowelli (0.84)	
	87.08	80.66
Near Shore	**Max Diss/SD: 1.15**	**Max Diss/SD: 1.07**
	Urothoe elegans (0.97)	*Urothoe elegans* (1.01)
	***Ophionephthys lowelli* (1.15)**	Polychaete sp 1(0.95)
	Polychaete sp 1(0.81)	***Ophionephthys lowelli* (1.07)**
	Ampelisca miops (0.99)	*Ampelisca miops* (1.06)
	Sunetta bruggeni (0.86)	*Sunetta bruggeni* (1.03)

Chapter 4: Discussion

4.1 Spatial distribution patterns

Heterogeneity at both temporal and spatial scales is a widely accepted characteristic of soft-bottom benthic communities and may be increased in the boundary zones between habitats. Variations in macrofaunal assemblages occur at both small (Cusson and Bourget 1997, Kendall and Widdicombe 1999, Barros *et al*. 2001, Barros *et al*. 2004) and large (Morrisey *et al*. 1992, Levin and DiBacco 1995) spatial scales. However patterns observed at smaller spatial scales may not persists at larger scales as localised influences such as, patches of organic content and environmental disturbances, coupled with differing species succession rates creates uneven distributions in soft-bottom macrofaunal communities (Grassle and Sanders 1973, Grassle 1989, Pacheco *et al*. 2010a, Alves *et al*. 2014).

In the sandy area adjacent to the reefs in the iSimangaliso Wetland Park, spatial variability of the macrofaunal assemblages was indicated by significant differences in abundance and biomass with reef proximity. At all sites, excluding Saxon Reef, lowest abundances were recorded closest to the reef. This strongly indicated that the macrofaunal assemblages were negatively affected by the presence of reefs. No consistent patterns in macrofaunal biomass were observed in relation to reef proximity. Although sites did not share similar trends in biomass with increasing distance significant differences were found between the assemblages closest to the reef and those furthest away. The lack of consistent patterns may be attributed to the inconsistencies in the occurrence of large sized fauna in samples such as, gastropod *Phalium glaucum* and echinoderm *Echinodiscus bisperforatus*.

Patterns of lower macrofaunal abundances at close proximity to the reefs supported results of Posey and Ambrose (1994) where significantly greater abundances of infauna were found 75 m away from the reefs edge than at 1 m. Similarly, Ambrose and Anderson (1990) found that infaunal abundance increased with distance. In contrast, Barros *et al*. (2001) found no consistent trends in abundance with increasing distance. However, sampling in their study was done at a small spatial scale, only ranging from 1 – 11 m from the reef. It therefore did not account for possible heterogeneity further away from the reef, but gives a useful indication of the minimal extent of the reef's influence on neighbouring soft-bottom macrofaunal assemblages.

Trends of higher abundances at the middle distance of Red Sands Reef, Seven-Mile Reef and Rocktail Bay indicated that not only reef proximity influences macrofaunal abundance but that hydrodynamic disturbance may be affecting them near to shore as well. Patterns of species

diversity with increasing distance from the reef were similar to the abundance patterns observed at each site. There were however, no significant differences when comparing distance and the number of species or the S-W diversity indices. The peaks in abundance and number of species at the middle distance of these sites produce a parabolic pattern that resembles a 'Mid Domain Effect' (Pindea and Caswell 1998) with higher macrofaunal abundance and diversity between environmental boundaries. Although Pindea and Caswell's (1998) Mid Domain model was applied to species diversity patterns over large depth ranges rather than small scale spatial patterns the concept of influential environmental boundary conditions is evident. Decreases in abundance at the near shore distance may be related to greater intensities of wave surge and thus frequent sediment disturbance.

Despite the overall significant difference in abundance with reef proximity none of the five most abundant taxa varied significantly in abundance among distances from the reef edge, however, abundances were generally lower closest to the reef. Davis *et al* (1982) found similar results when investigating the effects of artificial reefs on adjacent soft-bottom macrofaunal assemblages. They found no significant relationship between the infaunal taxonomic groups and distance but did find evidence of reduced abundances of certain macrofaunal species close to the reef. In this study, crustaceans were found to be more abundant closer to the reef than further away which was likely associated with gradients of coarse to fine sediment with increasing distance from the reef. Crustacean abundances are generally higher in coarse than fine sediment (Jones 1984) explaining contrasting patterns in relation to reef proximity. SIMPER analysis identified the amphipod *U. elegans* as an indicator species for the near reef distance. In contrast, echinoderms were more abundant at the middle and near shore distances while the brittle star *O. lowelli* was the top indicator species for the near shore distance. Martins *et al*. (2013a) found significant increases in the abundance of bivalve *E. castenea* and polychaete *S. filicornis* at greater distances away from the reef. However, in their study an unknown ostracod species showed contrasting results with significantly high abundances closest to the reef. Furthermore, Langlois *et al*. (2005a) found increases in the abundance of several invertebrate species with increasing distance but also observed reverse patterns in the hermit crab *P. novaezelandiae*. The contrast in abundance patterns suggests that certain infaunal species are affected differently by small scale biological and environmental conditions and processes associated with reef proximity.

Significant differences in the number of species and in the S-W diversity index between the reefs suggested large scale spatial variation. Pairwise comparisons however, revealed Two-Mile

Reef as the only site significantly different to all other sampled sites. There was thus no clear latitudinal diversity gradient. However, the latitudinal scale in this study was restricted to within the boundaries of the park covering 26° 51' – 28° 8' degrees latitude and further investigations covering greater latitudinal spatial scales may reveal differences in diversity. Expansion of the study site northwards to include the reef habitats of the neighbouring southern Mozambique MPA would increase the spatial scale for the identification of the presence of a latitudinal species gradient. Two-Mile Reef's significantly greater number of species than all other sites was likely due to localised physical and ecological factors such as the proximity of the Mgobozeleni estuary mouth, an embayment formed by Jesser Point and the possible reduced predation pressure. Blanchard and Feder (2013) found that variations in macrofaunal assemblages over multiple spatial scales were strongly associated with localised environmental gradients in habitat complexity and food availability. Bergen *et al*. (2000) similarly found that depth and sedimentary characteristics were more influential than latitudinal gradient in determining infaunal community structure. Localised environmental conditions of the reefs in the iSimangaliso Wetland Park were indicated to be important drivers in macrofaunal assemblage structure and abundance patterns around reefs in the near shore soft-bottom habitats.

4.2. What drives macrofaunal assemblage patterns around reefs?

4.2.1. Disturbance

South Africa has a high energy coast line and thus near shore fringing reefs and their neighbouring soft-bottom systems are subjected to continuous hydrodynamic disturbances. Since patterns in macrofauna distribution are associated with hydrodynamic disturbance (Riddle 1988, Netto *et al*. 1999, Dernie *et al*. 2003, Austen and Widdicombe 2006) and sediment characteristics (Gray 1974, Etter and Grassle 1992, Bergen *et al*. 2000, Ellingsen, 2002, Anderson 2008) the high levels of physical disturbance and the predominantly larger grained sedimentary characteristics of iSimangaliso Wetland Park would result in sediments being frequently turned over, thus being influential in macrofaunal community structure and distribution patterns.

Direct physical disturbance on macrofauna can influence assemblage structure by either, limiting recruitment (Crimaldi *et al*. 2002), increasing physiological stress (Probert 1984) changing predator-prey interactions (Eriksson *et al*. 2005) or influencing feeding efficiency (Ward and Shumway 2004). The hydrodynamic forces which govern the micro-bathymetry of the sediment surrounding reefs may through direct physical disturbance influence the abundance and diversity of the macrofaunal assemblages. Macrofaunal abundance and diversity in the

iSimangaliso Wetland Park decreased substantially from the middle to the near shore. The near shore was subjected to considerable wave swell and surge which may affect infaunal assemblages. For example, species diversity was greater in sediments which were stable than those of mobile sandbars at Aldabra Atoll (Hughes and Gamble 1977) and species richness increased with decreasing wave disturbance on a high energy beach (Oliver *et al*. 1980). Furthermore, DeFelice and Parrish (2001) found that infaunal abundance and diversity had clear negative relationships with the exposure to wave energy around a fringing reef. The level of disturbance at each distance from the reefs was not quantified in this study, however, increased turbulence was noted at the nearshore region when sampling. The comparison of the abundance and biomass curves of the macrofaunal assemblages at the near shore distance of both Seven-Mile Reef and Saxon Reef indicated disturbance. Furthermore, larger bodied macrofauna are generally more resilient to direct physical disturbance than smaller sized macrofauna (Olafsson *et al*. 1994). Relatively larger echinoderms *E. cordatum, E. bisperforatus* and *A. irregularis pontoporeus* were found at greater abundances further away from the reefs' edge where hydrodynamic forces appeared to be greater. It therefore seems likely that the lower faunal abundance and diversity found furthest from the reef is linked to the increase in wave turbulence experienced there.

In shallow soft-bottom systems natural physical disturbances from waves and currents, and biological disturbances such as, bioturbation by fauna are common (Hall *et al*. 1994). However, a majority of studies investigating the soft-bottom macrofaunal communities near coral reefs have been conducted in lagoons and back-reef areas which are relativity protected from wave swell and surge (Jones *et al*. 1990, 1992, Hansen *et al*. 1992, Schlacher *et al*. 1998, Frouin 2000, Hernandez-Guevara *et al*. 2008). In soft-bottom habitats that are exposed to low levels of physical disturbance biological disturbances, such as bioturbation, can become influential in structuring macrofaunal communities (Jones *et al*. 1990, 1992, Lindquist *et al*. 1994). Bioturbation reworks the sediments altering sedimentary properties and therefore affects macrofaunal assemblage structure (Probert 1984). Dahlgren *et al*. (1999) found correlations between higher density of *Holothuria princeps* and lower infaunal densities closest to the reef. The influence of biological disturbances on assemblage structure and distribution was not explicitly investigated in this study. It is possible that they do have some influence on near reef macrofaunal communities in the iSimangaliso Wetland Park, however, where physical disturbances are high and frequent the influences of biological disturbances would become less significant. It is thus unlikely that the effects of biological disturbances would outweigh those of the physical in the structuring the soft-bottom macrofaunal assemblages surrounding the coral

reefs of iSimangaliso Wetland Park. However, further investigations identifying what biological disturbances occur in the soft-bottom habitats and assessing their impacts on macrofaunal communities is needed.

4.2.2. Sedimentary characteristics

Numerous studies have shown that macrofauna have a direct relationship with the sedimentary characteristics of their environment (Gray 1974, Etter and Grassle 1992, Bergen *et al*. 2000, Ellingsen 2002, Thrush *et al*., 2003, Anderson 2008). Higher percentages of coarse sediments found closest to the reef edge coincided with lower abundances, biomass and species of macrofauna within the iSimangaliso Wetland Park. The gradient of coarse to fine sediments with increasing distance away from the reef follows general granulometric patterns around natural and artificial reef structures (Ambrose and Anderson 1990, Barros *et al*. 2001, Barros *et al*. 2004, Martins *et al*. 2013a). Hydrodynamic forces keep fine sediments in suspension and deposit coarse sediment near the reefs edge. As sediment grain size is a determining factor in macrofaunal distributions and assemblage structure (Gray 1974) the presence of the reef would indirectly influence neighbouring soft-bottom communities (Barros *et al*. 2004, Martins *et al*. 2013a). Barros *et al*. (2004) found that soft-bottom communities were partly governed by the hydrodynamic forces which alter the micro-bathymetry of the surrounding sediments creating deeper and wider ripples marks closer to the reef. The gradient in the percentage of calcium carbonate with increasing distance away from the reef observed in the iSimangaliso Wetland Park is also likely a result of the hydrodynamic flow around reefs which deposits the coarse carbonate remains of fauna such as, shell debris near the reef's edge.

Two-Mile Reef had the highest abundance, biomass and species richness of all sites, which may be explained by its sediment grain size characteristics. Sediments from Two-Mile Reef had a high composition of fine sediments and low amounts of medium grained sediments. These sedimentary characteristics are likely associated with the localised physiographic features of the coastline. The inshore region of Two-Mile Reef is partly protected from ocean swell and current by the presence of the reef and an embayment formed by Jesser Point. Outflow of fine sediments from the Mgobozeleni estuarine system at Jesser Point directly in to the bay would explain the high percentages of fine sediments as there would be limited sediment transport out of the system. At the near reef distance Two-Mile Reef had a higher composition of fine sediments and lower amounts of medium grained sediments than other sites. The higher percentages of fine sediment at the near reef distance corresponded with higher macrofaunal abundance and species than other sites at the same distance. Similarly, the patterns in abundance

and species richness in relation to reef proximity at Saxon Reef coincided with those of sediment grain size. The relative uniformity in abundance and species richness with increasing distance observed at Saxon Reef may be associated with the generally higher percentages of larger grained sediments found across all distances. The homogeneity in sediment characteristics would explain the lack of distinctive community patterns with increasing distance. Unlike Two-Mile Reef the inshore region of Saxon Reef is exposed to ocean swell and current which may prevent sedimentary gradients forming and prevent fine sediments settling from the nearby Kosi Bay estuarine system. The lack of similarity, indicated by the ANOSIM analysis, between the macrofaunal assemblages of Saxon Reef - Rocktail Bay and Saxon Reef - Two-Mile Reef may be due to its higher percentage of coarse sediments. Rocktail Bay and Two-Mile Reef both had high percentages of fine sediments while Saxon Reef had the lowest. Furthermore, Red Sands Reef and Saxon Reef had the highest percentage of coarse sediments in comparison to the other sites and the ANOSIM analysis indicated the greatest similarity in assemblage structure between them. Jones (1984) found that crustacean abundance in reef sediments was lower in fine sediments. Crustaceans were found to be most abundant at Saxon Reef and Red Sands Reef, particularly the amphipod *U. elegans*, brachyuran *A. punctata* and anomuran Paguroidae sp 1. In contrast, Rocktail Bay was the only site in which polychaetes made up over 50 % of the community. Polychaete densities have been found to be generally higher in fine sediments than coarse sediments (Knox 1977, Etter and Grassle 1992). The corresponding patterns between community structure and sediment grain size indicates the direct relationship macrofauna have with the sedimentary characteristics of their environment. It is improbable that sediment grain size is the sole determining factor in the abundance and structure of macrofaunal communities found surrounding reefs. However, the degree of its influence as demonstrated here is substantial.

4.2.3 Cross-boundary subsidies

Apart from the granulometric composition, organic content in the sediment can similarly influence macrofaunal distribution and diversity (Bolam *et al*. 2004, Austen and Widdicombe 2006, Martins *et al*. 2013a). Variations of sediment organic content with increasing distance away from the reefs in the iSimangaliso Wetland Park were similar to the patterns in abundance and species diversity of macrofauna. Although there was no overall significant difference with regards to distance, marginally higher amounts of organic contents were recorded at the middle distances. It is possible that reef derived organic matter is transported by wave surge and accumulates in the middle distance rather than near the reef , however, further investigation in to the hydrodynamic movement of detritus through the study area is needed to substantiate this.

The similarity in patterns indicated that organic content may be one of the factors driving macrobenthic assemblage structure around the reefs in iSimangaliso Wetland Park. Rossi and Underwood (2002) suggested that detritus, which can accumulate in the soft-bottom areas adjacent to reefs, may explain infaunal assemblage patterns with regards to reef proximity. Norkko and Bonsdorff (1996) proposed that benthic communities respond to the presence of particulate organic matter through shifts in their trophic structure from predominantly suspension feeders to detritivores. Martins *et al*. (2013a) supported this, finding a significantly greater abundance of detritus feeding ostracods closest to the reef while more filter feeding bivalves were found further away. However, no consistent patterns in abundance of specific functional groups with increasing distance away from the reefs were observed in this study, possibly due to overall low organic content and relative evenness in the amount at each distance.

Ecological linkages from reef derived kelp detritus and the neighbouring intertidal and beach communities have been shown (Griffiths and Stenton-Dozey 1981, Griffiths *et al*. 1983, Duggins *et al*. 1989, Bustamante *et al*. 1995, Soares *et al*. 1997, Savage *et al*. 2012) however, there is a lack of similar studies investigating the cross-boundary subsidies between tropical coral reef systems and the soft-bottom environment. The mechanisms which create spatial patterns in macrofaunal assemblages around coral reefs are not yet fully understood, partly due to the lack of holistic cross boundary ecosystem studies on coral reefs. Coral reefs are connected with neighbouring systems through the export and import of nutrients and organisms (Hatcher 1997). The transfer of particulate organic matter from reef systems to adjacent soft-bottom habitats has been suggested as one of the possible drivers of macrofaunal assemblage patterns around reefs (Hatcher 1983, Alongi 1989, Hansen *et al*. 1992). Dahlgren *et al*. (1999) found greater densities of a deposit feeding holothurian (*Holothuria princeps*) closest to the reef's edge suggesting reef productivity may enrich neighbouring soft-bottom habitats with reef-derived organic matter. Wild *et al*. (2004) showed how coral mucus enriched with pelagic-derived organic matter is transported to reef sediments potentially subsidising benthic communities. As the reefs in iSimangaliso Wetland Park experience relatively high levels of physical disturbance by wave action, the exchanges between the soft-bottom and coral reef systems may be substantial. Parkinson (2012) using stable isotope analysis, found a high degree of trophic connectivity between the inshore and the deeper offshore habitats at Sodwana Bay. Stable isotope signatures indicated that benthic fauna found offshore utilised organic matter sourced from inshore production. The evidence of trophic connectivity between the offshore and inshore habitats makes it highly probable that within the inshore environment soft-bottom habitats adjacent to the reefs would have high interconnectedness. The trophic connections

created by nutrient exchanges may influence macrofaunal distribution and diversity, which would explain the patterns observed adjacent to the reefs. Whether trophic connectivity exists at smaller spatial scales within the iSimangaliso Wetland Park and the possible influence on macrofaunal distribution and community structure is not yet know and is a subject of an ongoing study.

Among sites in this study, Rocktail Bay had the highest recorded organic content. Considerable algal cover was observed on the reef in comparison to other sites and the cross-boundary transfer of algal detritus from the reef to the soft-bottom habitats is likely to occur due to the hydrodynamic nature of the area as previously mentioned. Rocktail Bay was the only site where polychaetes were found at higher abundances than amphipods. Higher abundances of *Capitella spp.*, a non-selective deposit feeder, were found at Rocktail Bay. *Capitella spp.* occurs at higher abundance in organic rich sediments (Tsutsumi 1990, Tsutsumi *et al.* 1990). The greater organic content together with the finer composition of sediments at Rocktail Bay is more than likely the reason for the observed dominance of polychaetes.

The presence of Mgobozeleni and Kosi Bay estuarine systems near Two-Mile Reef and Saxon Reef respectively, may explain the unique assemblage patterns observed in relation to reef proximity. Estuaries are highly productive (Nixon *et al.* 1986) and their outflow transports nutrients, organic matter and organisms to the near shore systems which can potentially influence the structure of soft-bottom macrofaunal communities through increased productivity of the system. Studies have shown increases in primary and secondary productivity in coastal waters due to estuarine outflow (Grimes and Kingsford 1996, Lohrenz *et al.* 1999, Levin *et al.* 2001, Dagg *et al.* 2004, Smith 2006, Schlacher *et al.* 2009, McKenzie *et al.* 2010), however, few studies have shown linkages to increases in macrobenthic productivity (Herman *et al.* 1999, Nixon and Buckley 2002, Savage *et al.* 2012). Savage *et al.* (2012) found that estuarine outflow subsidised suspension feeding bivalve populations in neighbouring coastal sediments and in doing so had an indirect influence on the assemblage structure of the soft-bottom macrofaunal communities. It is therefore possible that the cross-boundary subsidies of organic matter into the Two-Mile Reef and Saxon Reef soft-bottom systems from their neighbouring estuaries results in the contrasting assemblage patterns.

4.2.4. Predation

Predation by reef associated fauna on neighbouring soft-bottom macrofaunal communities was not explicitly investigated in this study. The limited knowledge on the behaviour and life history of soft-bottom macrofauna and their predators makes it difficult to evaluate the effects predation

has on soft-bottom macrofaunal assemblages around reefs. The effects of the environmental gradients of sediment grain size and hydrodynamic disturbance on macrofaunal assemblages in iSimangaliso Wetland Park may outweigh those of predation. Furthermore, due to the heterogeneity of soft-bottom macrofaunal communities over small spatial scales establishing links to predation intensity can be challenging. Nonetheless, assemblage patterns did suggest that predation may have some influence on macrofaunal community organisation. Lower macrofaunal abundances, biomass and diversity closest to the reef may be partly due to heightened predatory pressure by reef associated fauna.

Predation by reef associated fauna has been indicated as an influential factor in the organisation of soft-bottom macrofaunal communities (Lindquist *et al*. 1994, Langlois *et al*. 2005, 2006, Martins *et al*. 2013a). For example, gut contents indicate that reef fish communities may be supported by preying on soft-bottom fauna (Lindquist *et al*. 1994). During sampling predatory reef fish, such as the goatfish, *Parupeneus sp*, were regularly observed foraging in the soft-bottom areas adjacent to the reefs in the iSimangaliso Wetland Park. Langlois *et al*. (2005a) found evidence of reef associated predatory pressure with higher densities of bivalves *D. subrosea* and *M. striata* in non-protected areas where reef associated predator densities were lower. Sea pen, *Stylatula elongate* densities in soft-bottom areas adjacent to artificial reefs have been found to be significantly reduced by foraging reef associated fishes (Davis *et al*. 1982). Two-Mile Reef had the greatest abundance and diversity of sea pens. This may be due to reduced level of predation by reef associated fishes at Two-Mile Reef in comparison to the other sites. Lower abundances of reef fish has been documented on Two-Mile Reef than on reefs located in the sanctuary zones of iSimangaliso Wetland Park (Floros 2010). Currie *et al*. (2012) concluded that the partially protected areas in MPA's, specifically those in the iSimangaliso Wetland Park, do not ensure the protection of reef fish communities as diver disturbance, fishing for pelagic species and illegal fishing activities undermine their effectiveness. Since fishing is prohibited on Two-Mile Reef the high intensity of recreational diving on the reef was recognised as the reason for the lower fish abundances (Floros 2010). The reduced predation pressure due to lower fish abundance on Two-Mile Reef may thus explain the greater abundance of sea pens in the adjacent soft-bottom areas and the overall greater abundance, biomass and diversity of macrofauna at Two-Mile Reef and at the near reef distance.

Although few studies have investigated the effects of infaunal predation in subtidal soft-bottom habitats it has been shown to significantly influence infaunal densities (Ambrose 1984, 1991, Desroy *et al*. 1998). Ambrose (1984) found through the exclusion of the predatory polychaete

Glycera dibranchiata from the intertidal soft-bottom assemblages in the Maine estuary, the density of its prey, another predatory polychaete *Nereis virens* increased. Predatory polychaetes, *Glycera sp*. and *Diopatra sp.* were found throughout the samples collected from iSimangaliso Wetland Park, however, were most abundant at the near reef distance of Two-Mile Reef. Predators such as these have the ability to influence the temporal and spatial distribution of their prey. The responses of the prey populations to infaunal predatory pressure can influence community distributions patterns (Ambrose 1991) which may explain the lower abundances recorded closest to the reef.

4.2.5. Protective Status
Marine reserves, as an experimental tool, provide the opportunity for the comparison between soft-bottom macrofaunal assemblages of protected and non-protected regions. The protective status of a reef and its faunal communities may influence the neighbouring soft-bottom communities due to ecological linkages. Apart from the direct protection of a soft-bottom system from anthropogenic disturbances such as, dredging or trawling, there may be indirect effects which can result in differences in the structure of macrofaunal communities. Pinnegar *et al*. (2000) suggested that marine reserves offer an opportunity to investigate the indirect effects of fishing on benthic assemblages in soft-bottom systems, including their top down regulation by reef associated predators shown by Shears and Babcock (2002). Langlois *et al*. (2005c) further showed that high predator densities in a marine reserve decreased the survivorship of their prey, numerous infaunal bivalve species. Hyland *et al*. (2005) found that the infaunal assemblages within the Gray's Reef National Marine Sanctuary were highly diverse and suggested that sanctuaries play an important role as source of recruitments for non-protected areas. The ecological assessment of the soft-bottom systems in the iSimangaliso Wetland Park MPA in relation to their protective status would help ascertain a better understanding of the trophic interaction which occurs across the reef and soft-bottom boundaries and how the macrofaunal communities are characterised.

There was indication that the macrofaunal assemblages in the sanctuary areas in the iSimangaliso Wetland Park differed from other areas, however, it was not statistically supported by univariate analysis. Non-metric multidimensional scaling, using 'protection status' as a defining factor showed sample grouping between the macrofaunal assemblages of the non-sanctuary and sanctuary reefs. This indicated similarities in the assemblage structure of the sanctuaries despite each sanctuary site being separated by all other sites in this study. In support of this, Saxon Reef had the lowest average dissimilarity to Red Sands Reef and from the

SIMPER analysis they shared three of the top five indicator species, *S. bruggeni*, Polychaete sp 1 and *U, elegans*. The similarities in assemblage structure between the sanctuary sites and higher dissimilarities with non-sanctuary sites may indirectly be associated with the protection status of the coral reefs. Langlios (2005c) discovered that protection of a reef indirectly resulted in differences in the infaunal community structure when compared to non-protected areas. Since reef fish communities within the sanctuary areas of the iSimangaliso Wetland Park have higher abundances and diversity in comparison to non-sanctuary areas (Floors 2010) the differences in predatory pressure on soft-bottom macrofauna would results in differences in their community structure. Protective status would thus indirectly influence soft-bottom macrofaunal community structure adjacent to reefs. The protective status together with the previously mentioned greater percentages of coarser sediments at Saxon Reef and Red Sands Reef may explain the similarities in their macrofaunal assemblages. Further investigation however, is required as no strong conclusions on the influence of protection status on the soft-bottom macrofaunal communities can be made. Whether protection of the reefs adequately protects the surrounding soft-bottom habitats is not known. It is however best not to assume that the protection of the reef would indirectly provide adequate protection of soft-bottom habitats. Soft-bottom communites of the iSimangaliso Wetland Park have ecological importance beyond that of the coral reefs. The cycling of nutrients, movement of energy to upper trophic levels and decomposition of detritus by soft-bottom macrofauna in the iSimangaliso Wetland Park is essential for the functioning of system. Assessment of their importance in the marine reserve is needed in order to establish if macrofaunal communities should be separately addressed in conservation efforts and suitable sites for protecting them be designated, irrespective of the reefs presence.

4.3. General Summary

The aim of this study was to document the species diversity, distribution and abundance of macrofauna in iSimangaliso Wetland Park and to relate these to depth, sediment grain size, location, reef proximity and protective status. The results indicated that the macrofaunal assemblages inhabiting the soft-bottom sedimentary habitat surrounding the reefs change in species abundance and diversity with increasing distance from the reef. The gradients in the environmental dynamics, as a consequence of the reefs presence were influential in defining community structure. Sediment grain size and physical hydrodynamic disturbance appear to be the main determinants of assemblage structure around reefs. Hydrodynamic forces create a gradient of coarse to fine sediments with increasing distance away from the reef indirectly influencing macrofaunal abundance and diversity. Similarly, direct physical disturbance of

sediments and macrofauna by wave action at the near shore distance further influenced community structure. The assemblage patterns observed with increasing distance corresponded with the physical environmental changes rather than the reefs ecological influences. It is however, likely that cross-boundary nutrient subsidies and predatory pressure from the reef do play underlying roles in macrofaunal distribution and assemblage structure. There was no evidence for the presence of a latitudinal diversity gradient, however, this study was limited to within a degree of latitude and further investigations over a greater latitudinal scale may reveal different results. There was an indication that protection status may indirectly influence the structure of soft-bottom macrofaunal communities around reefs. Trophic interactions by reef associated predators and their level of intensity partial to the reefs protection status was indicated as an influential factor. However, further investigation into the predator-prey relationships reef and soft-bottom communities share is needed as ecological linkages between them are highly likely and through these linkages macrofaunal assemblages are characterised. Consequently, soft-bottom macrofaunal assemblages in proximity to reef systems are defined by a combination of various environmental and ecological forces which are closely associated with reefs.

Assessment of the macrofauna within the soft-bottom habitats of the iSimangaliso Wetland Park was limited to the near shore side of the reefs due to depth, time and logistical constraints. Soft-bottom macrofaunal communities exhibit temporal variations in assemblage structure and abundance patterns (Morrisey *et al*. 1992, Bone and Klein 2000, Reiss and Kroncke 2005, Labrune *et al*. 2007). In this study, sampling was spread over more than a year but the community patterns observed and their correlations with the investigated factors imply that there was little seasonal effect on macrofaunal diversity and abundance. However, future long term monitoring of the subtidal soft-bottom macrofaunal assemblages in the iSimangaliso Wetland Park would help identify temporal variations in macrofaunal community structure and succession processes which would assist in the identification and assessment of the ecological linkages they share with neighbouring systems. Further studies investigating the soft-bottom communities located in the offshore region of the reef would help provide a more holistic view of macrofaunal diversity and abundance patterns. Infaunal diversity on the deeper seaward side of the reefs may be higher as fauna would be subjected to lower levels of hydrodynamic disturbance than those on the near shore side. The reduced disturbance would allow for a more reliable assessment of the effects of reef proximity and the cross-boundary ecological linkages reef and soft-bottom systems may share. Investigating the ecological links and nutrient cycling between the reef, soft-bottom and estuarine systems, using isotope analysis, would further aid in

obtaining a comprehensive understanding of the important roles soft-bottom macrofauna play in the ecosystem. To strive towards the better management of our marine ecosystems it is essential to understand the importance of soft-bottom communities and the relationships they share with neighbouring systems. The designation of the sanctuary areas within the iSimangaliso Wetland Park MPA was primarily based on coral distribution and diversity with soft-bottom communities was not taken into consideration. This research will provide valuable baseline information on the diversity and distribution of soft-bottom macrofauna in the iSimangaliso Wetland Park. It will not only benefit future management of soft-bottom habitats and sanctuary areas in the iSimangaliso Wetland Park but further add to the collective knowledge on macrofaunal species biogeographical distribution.

In conclusion, localised environmental and ecological processes are more important in defining soft-bottom macrofaunal community around coral reefs in the iSimangaliso Wetland Park MPA than their latitudinal positioning or protective status. Furthermore, the macrofaunal community patterns observed in this study support the concept that coral reefs do indeed influence the structure of macrofaunal assemblages inhabiting the neighbouring soft-bottom areas. However, due to the multiple ecological facets associated with coral reefs there are still many questions on how they influence macrofaunal communities.

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Appendix 1: iSimangaliso Wetland Park Species List

Table 5.1. List of benthic macrofaunal species collected from the sub-tidal sandy bottom habitats of iSimangaliso Wetland Park.

Phylum	Class	Order	Family	Species
Annelida				
	Polychaeta	Eunicida	Eunicidae	*Marphysa macintoshi*
	Polychaeta	Eunicida	Onuphidae	*Diopatra neapolitana capensis*
	Polychaeta	Eunicida	Onuphidae	*Onuphis eremita*
	Polychaeta	Eunicida	Onuphidae	*Onuphis* sp 2
	Polychaeta	Phyllodocida	Glyceridae	*Glycera natalensis*
	Polychaeta	Phyllodocida	Glyceridae	*Glycera* sp 1
	Polychaeta	Phyllodocida	Nephtyidae	*Nephtys capensis*
	Polychaeta	Phyllodocida	Nephtyidae	*Nephtys* sp.
	Polychaeta	Phyllodocida	Nereididae	*Nereis pelagica*
	Polychaeta	Phyllodocida	Sigalionidae	*Euthalenessa oculata*
	Polychaeta	Phyllodocida	Sigalionidae	*Sigalion capensis*
	Polychaeta	Phyllodocida	Sigalionidae	*Sigalion* sp 1
	Polychaeta	Phyllodocida	Sigalionidae	*Sigalion* sp 2
	Polychaeta	Phyllodocida	Sigalionidae	*Sthenelais* sp 1
	Polychaeta	Phyllodocida	Syllidae	*Haplosyllis spongicola*
	Polychaeta	Terebellida	Cirratulidae	*Cirriformia tentaculata*
	Polychaeta	Terebellida	Cirratulidae	*Timarete punctata*
	Polychaeta	Terebellida	Flabelligeridae	*Pherusa* sp
	Polychaeta	Polychaeta	Capitellidae	Capitellidae Sp.
	Polychaeta	Polychaeta	Capitellidae	*Notomastus aberans*
	Polychaeta	Polychaeta	Opheliidae	*Ophelina acuminata*
	Polychaeta	Polychaeta	Opheliidae	*Polyophthalmus pictus*
	Polychaeta	Polychaeta	Orbiniidae	Orbiniidae sp 1
	Polychaeta	Polychaeta	Orbiniidae	*Scolaricia* sp 1
	Polychaeta	Polychaeta	Maldanidae	*Euclymene natalensis*
	Polychaeta	Polychaeta	Maldanidae	*Euclymene* sp 1
	Polychaeta	Polychaeta	Maldanidae	*Euclymene* sp 2
	Polychaeta	Polychaeta	Paraonidae	*Paraonis* sp
	Polychaeta	Polychaeta	Paraonidae	*Aricidea* sp 1
	Polychaeta	Spionida	Spionidae	*Polydora c.f. giardi*
	Polychaeta	Spionida	Spionidae	*Scolelepis squamata*
	Polychaeta	Terebellida	Pectinariidae	*Pectinaria* sp 1
	Echiura	Echiuroidea	Echiuroidea	Echiuroidea sp 1
Arthropoda				
	Malacostraca	Amphipoda	Ampeliscidae	*Ampelisca miops*
	Malacostraca	Amphipoda	Ampeliscidae	*Ampelisca brachyceras*

Malacostraca	Amphipoda	Ampeliscidae	*Ampelisca palmata*
Malacostraca	Amphipoda	Urothoidae	*Urothoe elegans*
Malacostraca	Amphipoda	Urothoidae	*Urothoe* sp 2
Malacostraca	Amphipoda	Platyischnopidae	*Indischnopus herdmani*
Malacostraca	Amphipoda	Pontogeneiidae	*Paramoera capensis*
Malacostraca	Amphipoda	Phoxocephalidae	*Mandibulophoxus stimpsoni*
Malacostraca	Amphipoda	Photidae	*Photis* sp 1
Malacostraca	Amphipoda	Lysianassidae	*Lysianassa ceratina*
Malacostraca	Amphipoda	Ampithoidae	*Ampithoe* sp 1
Malacostraca	Amphipoda	Ampithoidae	*Ampithoe* sp 2
Malacostraca	Amphipoda	Dexaminidae	*Polycheria atolli*
Malacostraca	Amphipoda	Ingolfiellidae	*Ingolfiella berrisfordi*
Malacostraca	Amphipoda	Caprellidae	*Pseudaeginella tristanensis*
Malacostraca	Cumacea	Cumacea	Cumacea sp
Malacostraca	Decapoda	Matutidae	*Ashtoret lunaris*
Malacostraca	Decapoda	Leucosiidae	*Afrophila punctata*
Malacostraca	Decapoda	Albuneidae	*Albunea paretii*
Malacostraca	Decapoda	Brachyura	Brachyura sp 1
Malacostraca	Decapoda	Paguridae	*Pagurus* sp 1
Malacostraca	Decapoda	Caridea	Caridean prawn sp 1
Malacostraca	Decapoda	Caridea	Caridean prawn sp 2
Malacostraca	Decapoda	Caridea	Caridean prawn sp 3
Malacostraca	Decapoda	Caridea	Caridean prawn sp 4
Malacostraca	Decapoda	Caridea	Caridean prawn sp 5
Malacostraca	Decapoda	Caridea	Caridean prawn sp 6
Malacostraca	Isopoda	Cirolanidae	*Natatolana pilula*
Malacostraca	Isopoda	Cirolanidae	*Cirolana sp 1*
Malacostraca	Mysida	Mysidae	*Gastrosaccus longifissura*
Malacostraca	Stomatopoda	Squillidae	*Squillidae sp 1*
Malacostraca	Tanaidacea	Tanaid	Tenaid sp 1
Malacostraca	Tanaidacea	Tanaid	Tenaid sp 2
Ostracoda	Myodocopida	Ostracod	Ostracod sp
Pycnogonida	Pantopoda	Ammotheidae	*Nymphopsi*s sp
Pycnogonida	Pantopoda	Ammotheidae	*Achelia* sp

Cnidaria

Anthozoa	Ceriantharia	Cerianthidae	Cerianthid sp 1
Anthozoa	Ceriantharia	Cerianthidae	Cerianthid sp 2
Anthozoa	Ceriantharia	Cerianthidae	Cerianthid sp 3
Anthozoa	Scleractinia	Caryophylliidae	*Caryophyllia* sp
Anthozoa	Pennatulacea	Veretillidae	*Lituaria* sp
Anthozoa	Pennatulacea	Veretillidae	*Cavernularia* sp 1 - possiably *Cavernularia capitata*
Anthozoa	Pennatulacea	Veretillidae	*Veretillum* sp 1 - possiably *Veretillum leloupi*
Anthozoa	Pennatulacea	Virgulariidae	*Virgularia* sp 1

	Anthozoa	Pennatulacea	Virgulariidae	*Virgularia* sp 2
Chordata				
	Ascidiacea	Stolidobranchia	Molgulidae	*Molgula* sp 1
Echinodermata				
	Asteroidea	Paxillosida	Astropectinidae	*Astropecten irregularis pontoporeus*
	Echinoidea	Spatangoida	Loveniidae	*Echinocardium cordatum*
	Echinoidea	Spatangoida	Loveniidae	*Lovenia elongata*
	Echinoidea	Echinoidea	Echinoidea	Echinoidea sp 1
	Echinoidea	Clypeasteroida	Astriclypeidae	*Echinodiscus bisperforatus*
	Ophiuroidea	Ophiurida	Amphiuridae	*Amphipholis similis*
	Ophiuroidea	Ophiurida	Amphiuridae	*Amphipholis squamata*
	Ophiuroidea	Ophiurida	Amphiuridae	*Amphioplus (Lymanella) hastatus*
	Ophiuroidea	Ophiurida	Amphiuridae	*Ophionephthys lowelli*
	Ophiuroidea	Ophiurida	Ophiactidae	*Ophiactis carnea*
Mollusca				
	Bivalvia	Veneroida	Donacidae	*Donax bipartitus*
	Bivalvia	Veneroida	Donacidae	*Donax burnupi*
	Bivalvia	Veneroida	Veneridae	*Grafrarium pectinatum alfredense*
	Bivalvia	Veneroida	Veneridae	*Sunetta bruggeni*
	Bivalvia	Veneroida	Veneridae	*Pitar abbreviatus*
	Bivalvia	Veneroida	Veneridae	*Tivela dunkeri*
	Bivalvia	Veneroida	Veneridae	*Tivela transversa*
	Bivalvia	Veneroida	Veneridae	*Tivela rejecta*
	Cephalopoda	Teuthida	Teuthida	Teuthida sp 1
	Cephalopoda	Octopoda	Octopodidae	*Amphioctopus marginatus*
	Gastropoda	Gastropoda	Fissurellidae	*Macroschisma africanum*
	Gastropoda	Gastropoda	Phasianellidae	*Tricolia capensis*
	Gastropoda	Littorinimorpha	Cassidae	*Phalium glaucum*
	Gastropoda	Littorinimorpha	Naticidae	*Mammilla simiae*
	Gastropoda	Neogastropoda	Conidae	*Conus augur*
	Gastropoda	Neogastropoda	Conidae	*Conus betulinus*
	Gastropoda	Neogastropoda	Conidae	*Conus zeylanicus*
	Gastropoda	Neogastropoda	Nassariidae	*Bullia diluta*
	Gastropoda	Neogastropoda	Nassariidae	*Bullia similis*
	Gastropoda	Neogastropoda	Olividae	*Oliva tremulina*
	Gastropoda	Pleurobranchomorpha	Pleurobranchaeidae	Pleurobranchaea sp 1
	Gastropoda	Pleurobranchomorpha	Pleurobranchaeidae	Pleurobranchaea sp 2
	Polyplacophora	Chitonida	Chitonidae	*Chiton* sp 1
Nematoda	Nematoda	Nematode	Nematode	Nematode sp 1
Platyhelminthes	Platyhelminthes	Platyhelminthes	Platyhelminthes	Flatworm sp 1
Sipuncula	Sipuncula	Sipunculid	Sipunculid	Sipunculid sp 1