



BIODIVERSITY SURVEY TOWARDS CONSERVATION
OF
SUBTIDAL REEF HABITATS
IN
KWAZULU NATAL:
BIOGEOGRAPHY AND DEPTH PATTERNS



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ABSTRACT

Subtidal reef communities in KwaZulu-Natal (KZN), South Africa are poorly known. This lack of knowledge is problematic as the biodiversity of these reefs may be severely impacted and inadequately conserved. This study documents and describes subtidal benthic communities occurring on reefs at four depth categories along the whole length of the coast. A distinct difference between northern reefs from those in the south and central parts of the province emerged with substantiating evidence of a discrete biogeographic separation at Cape St Lucia. Pairwise ANOSIM tests found no significant differences in community composition of reefs along a depth range of 10 m to 30 m at nine localities in KZN. However, differences among localities were significant at both regional ($R = 0.607$, $P = 0.1\%$) and local ($R = 0.792$, $P = 0.1\%$) scales. In the north, trends in species assemblages and functional groupings revealed a higher percentage cover of fauna (mainly corals) at shallower depths and a greater coverage of algae on deeper reefs. In the southern localities algae dominated shallower reefs while filter-feeding epifauna were more prevalent at deeper depths. Species richness, evenness and diversity were highest at 10 m in the northern coral-dominated region while in the central/south region diversity peaked in the intermediate depth zone (15 – 25 m). Appropriate measures to conserve representative habitats in each biogeographic zone are necessary. Further research to assess biodiversity at a finer scale, as well as the establishment of long-term monitoring to quantify natural variability and human effects, are required.

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1. INTRODUCTION

The critical protection and conservation of the remnant natural ecosystems of the world is non-negotiable. Global pressure of demands from an ever escalating human population are felt everywhere, including South Africa. In an attempt to solve this, the Convention on Biological Diversity aims to commit signatory countries to sustainable utilization of biodiversity for posterity, and nations are tasked with making inventories and assessing the status of their natural systems (UNCED, 1992). South Africa is a signatory to this Convention sparking the need for assessments to identify and prioritise key areas and to establish conservation reserve networks in the country (Pressey et al., 1993; Margules et al., 1994).

The South African Marine Living Resources Act of 1998 provides the imperative to conserve the marine environment and manage the long-term utilization of the country's marine resources. To meet the objectives of the Act, it is essential to document and define marine biodiversity and natural resources. Biological diversity is the variety of life and its processes, and includes the variety of living organisms, the genetic differences among them and the communities and ecosystems in which they occur (Global Biodiversity Strategy, 1992).

Previously, studies in the marine realm focused mainly on single species, especially commercially important ones, rather than on ecosystems that encompass community and habitat diversity as well as species interactions (Zacharias and Roff, 2000). Modern fishing technology has left no part of the earth's ocean inaccessible and has increased vulnerability of natural systems to anthropogenic pressures (Zacharias and Roff, 2000). The global depletion of fish stocks has, however, sparked concern about the status of

marine ecosystems and a need to understand the patterns and processes that govern them (NRC, 1999; Pauly et al., 2002). Thorough scientific knowledge of the fundamental requirements of a viable ecosystem is essential to informing urgent conservation measures to mitigate climate and human-induced pressures and maintain the provision of ecosystem goods and services (Duarte, 2000; Jackson, 2005). The absence of this information could lead to the cascading devastation to species, communities and habitats (Jackson, 2005). Understanding species composition and patterns in their distribution or their biogeography is the foundation to understanding ecological processes and crucial to the effective conservation of biodiversity.

Patterns in Biogeography

Analysis of species distribution, or biogeography, is defined as a science that attempts to discover or explain biological variety over space and time (Cox and Moore, 1998). Each biogeographic region is characterised by distinct sets of habitats, environmental conditions and mixes of plant and animal species particular to that part of the world (Cox and Moore, 1998). The divisions between these different regions are governed by physical and climatic conditions (e.g. temperature, nutrient supplies, light availability and oceanic current movements) (Agardy, 1994). There are, however, frequently no clear boundaries between regions but rather areas of overlap in which there is an intermingling of species, creating biogeographic transition zones (Agardy, 1994).

The boundaries of biogeographic regions or provinces around the entire coast of southern Africa correspond closely with oceanographic conditions and are dominated by the contrasting Agulhas and Benguela currents (Lutjeharms et al., 2000). The west coast is influenced by the cold, relatively slow-moving Benguela current that drifts

northwards, and is characterised by upwelling (Branch and Griffiths, 1988). On the east coast, the warm fast-flowing Agulhas current is approximately 100 km wide, more than a kilometre deep and moves rapidly down the south-east coast (Shannon, 1985). Between these two extremes, the Agulhas deflects away from the coastline along the south coast, and conditions are intermediate between those of the west and east coasts (Shannon, 1985). Three broad biogeographic regions were recognized by Stephenson (1944; 1947) for the intertidal zone along the SA coastline i.e. the cool-temperate West Coast, the warm-temperate South Coast and the subtropical East Coast. Upwelling on the west coast and its virtual absence on the east coast has resulted in a productivity gradient around southern Africa (Shannon, 1985), linked to large-scale differences in biomass and community composition (Bustamante and Branch, 1996).

Research to identify biogeographic regions in South Africa has included presence-absence data collected for certain species (Stephenson, 1944; 1947), intertidal biomass patterns (Bustamante and Branch, 1996), marine vegetation distribution (Bolton and Stegenga, 2002), and distribution patterns of fish (Turpie et al., 2000). However, confusion still exists about the precise location of biogeographic regions in KwaZulu Natal (KZN). Jackson (1976) proposed three zones: between Mozambique and Leven Point (north of Cape Vidal); from Leven Point to Durnford Point (south of Richards Bay); and between Durnford Point and Port Edward. Studies on intertidal and inshore invertebrates by Emmanuel et al. (1992) found only one break just north of Durban and a biogeographic zone that extended into southern Mozambique. More recently analysis of intertidal community data by Sink et al. (2005) did not confirm this break at Durban but instead found a distinction between northern and southern KZN, with a division at Cape Vidal Point. This was further substantiated through seaweed distributional studies

undertaken by Bolton et al. (2004) who proposed a biogeographic division between St Lucia and Sodwana Bay.

The identification of biogeographical regions is important to attain adequate and representative conservation of all aspects of biodiversity. Within each biogeographic region, representative habitats can be conserved through the establishment of marine protected areas (Roberts et al., 2003). To achieve this, it is essential to first determine and obtain a sound knowledge of where biogeographic regions occur, including their boundaries and areas of overlap. Concern has been expressed that not all biogeographic areas are adequately protected in South Africa (Hockey and Buxton, 1989). For example, representative habitats in southern KwaZulu-Natal are poorly represented in formally established marine reserves. Among other reasons, this area is important because of the high endemism of commercial and recreational linefish that utilize it as a spawning and nursery ground (Mann pers. comm.).

Conservation of Marine Biodiversity

As the value of marine biological diversity is recognized, the ecosystems that harbor this diversity are fast becoming degraded (Hughes et al., 2003). New thinking about how to conserve coastal areas has resulted in protected-area models that incorporate principles of landscape ecology, biogeography, adaptive and ecosystem management and zoning in protected-area plans (Agardy, 1994; Ward and Hegerl, 2003). Species represented in distinct marine biogeographic zones require formalized protection which can be obtained through the establishment of marine reserves or marine protected areas (MPAs). These are areas permanently protected from all extractive use or subjected to controlled extractive use and have gained widespread attention as an innovative

mechanism for conserving biodiversity while also contributing to the maintenance of healthy sustainable fisheries (Kenchington et al., 2003). They also provide opportunities for tourism and revenue generation, recreation, education, research and subsistence requirements (Hockey and Branch, 1997; Kenchington et al., 2003).

Studies on the effectiveness and impacts of MPAs in achieving biodiversity conservation and fisheries management have found that MPAs increase biomass, density, size and diversity of species living within their boundaries (PISCO, 2002; Halpern, 2003). Protection from exploitation particularly from fishing extends the life-span of fish, thus increasing their size (Bennett and Attwood, 1991; PISCO, 2002; Halpern, 2003). The recovery of habitats as a result of protection facilitates the proliferation of fauna and flora providing plentiful prey species for predators (Halpern, 2003; Roberts and Hawkins, 2000). These are factors that augment the resilience and productivity of ecosystems securing the continued supply of ecosystem goods and services (Duarte, 2000). MPAs also help to replenish adjacent areas through export or spillover effects (Holland and Brazee, 1996).

The siting and location of MPAs are important in achieving their required conservation goals. Populations of migratory species become vulnerable to exploitation when juveniles concentrate on nursery grounds and adults aggregate at breeding and spawning sites. MPAs should thus be designed to protect multiple habitats and different species' life-stage requirements (Roberts et al., 2001; Hastings and Botsford, 2003). The positioning of MPAs should also be influenced by oceanic processes such as current flow and temperature which determine the flow of nutrients and larvae transportation and influence underlying biogeographic patterns (Hastings and Botsford, 2003;

Lubchenco et al., 2003). Maximised protection of all habitats within biogeographic regions can be achieved via networks of MPAs that are connected by larval dispersal and juvenile and adult migration (Roberts et al., 2001; Botsford et al., 2003; Lubchenco et al., 2003).

There are currently 62 MPAs in South Africa with varied sizes, conservation objectives and effectiveness. Some have been established as sanctuaries for single species protection, while others are too small and therefore unable to operate as true MPAs, or are ineffective due to the lack of enforcement of regulations. Nevertheless, these reserves contribute to 19 percent protection of the linear length of South Africa's coastline although the total area involved still falls far short of meeting the target of 20 percent agreed upon at the World Parks Congress in 2003 and does not consider habitat distribution and representation.

Three MPAs have been established in KZN: (1) the northern 150 km of the province is housed within the Maputaland and St Lucia MPAs which are part of the Greater St Lucia Wetland Park World Heritage Site. These combined MPAs fall within the tropical east coast biogeographic region and are zoned for varying degrees of utilization, including wilderness areas prohibiting all forms of extractive and non-extractive use with the exception of research. (2) The newly proclaimed Aliwal Shoal MPA is situated south of Durban and stretches ~20 km along the coastline and 7 km out to sea. Two major reef complexes are incorporated within this MPA and the area is zoned to curb user-conflict. (3) The Trafalgar Marine reserve was established to protect marine fossils found in the rocky intertidal. The small stretch of coastline (6 km) set aside for this

MPA extends 500 m offshore and protects diverse coastal and marine habitats. This reserve together with the Aliwal Shoal MPA provides some degree of protection to the subtropical and warm-temperate regions of the province.

Conservation of reef ecosystems

Marine reserves provide protection to a range of habitats including coral and rocky reefs. These habitats are important systems that sustain many bottom-dwelling species and communities (Loya, 1972; 1978; Menge and Farrell, 1989; Menge and Olson, 1990; Menge et al., 1999). Reef ecosystems perform a key role in providing sustenance and refugia for benthic organisms (Levin and Hay, 1996), which in turn provide nourishment to other reef-dwelling and pelagic species contributing to a cycle of energy flow and interdependence between pelagic and benthic systems (Menge et al., 1999). However, both coral and rock-reef habitats are under worldwide threat from fishing and trawling, recreational activities such as diving (Hawkins and Roberts, 1993; Davis and Tisdell, 1995; Walters and Samways, 2001), snorkelling (Allison, 1996), boating (Alison, 1996; Medio et al., 1997), pollution and eutrophication (Grigg, 1994), human economic development (Hoffman, 2002), invasive alien infestation (Rogers, 1990; Roberts, 1993), and increases in sea surface temperature as a result of climate change (Meesters and Bak, 1993). Understanding the pattern and community composition of reef habitats at appropriate spatial and temporal scales will aid our understanding of mechanisms that drive this ecosystem and help to identify areas that require specific management and conservation action (McClanahan et al., 1997).

KwaZulu-Natal (KZN), a province on the north-east coast of South Africa, has an extensive subtidal reef system that extends mainly along the continental shelf within the

200 m isobath (Garratt, 1984). The dominant consolidated bedform on the shelf is aeolianite and beachrock that were formed when sands from the partially exposed continental shelf were subjected to weathering during the Pleistocene (Ramsay, 1994). During this period, sea-level was at least 100 m below present, and after submersion these rock forms provided the geological setting for present day reefs (Ramsay and Mason, 1990; Ramsay, 1994). Their prevalence in depths of 10 to 200 m thus provides a structural basis for community settlement and formation. The northern subtropical region of KZN sustains a remnant coral-reef population which is the southernmost distribution of corals in the western Indian Ocean (Schleyer, 1999). Moving south into the warm-temperate and cool-temperate seas, coral dominance is replaced by that of algae and other suspension- and demersal-feeding epifauna on more rocky reefs (Ramsay, 1994; personal observation).

The reef fishery in KZN is under severe pressure with many species currently on the threatened or endangered species list (Mann-Lang et al., 1997). The exact locations of most reefs on the KZN coast are unknown and little information exists on the abundance and composition of associated species. Users such as commercial and recreational fishers and spearfishermen often possess knowledge about reef localities. However, their knowledge is often not willingly imparted. The urgent need for sound scientific knowledge and conservation protection of reef habitats in KZN has incited an evaluation of reefs within the province to determine their distribution and biodiversity. The aim is to acquire a better understanding of reef ecosystems, to highlight those areas that appear stressed, threatened or possess sensitive species or habitats, and finally to take appropriate steps to conserve representative reefs.

Reef Biodiversity Study

A project to achieve the above aims has been undertaken by Ezemvelo KwaZulu-Natal Wildlife (EKZNW) and comprises both mapping and biodiversity surveys of reefs in the deep subtidal zone i.e. between 10 m and 30 m deep. It is part of a larger programme funded by the National Research Foundation (NRF), Pew Fellowship and WWF-SA to develop a Systematic Conservation Plan for the marine environment of KZN. Spatial biological data are required for systematic conservation planning analyses, including physical mapping of ecosystems and habitats and surveys of biological communities and species. These data are concurrently being sourced for rocky habitats in the intertidal (Sink, 2001; Harris, pers. comm.) and shallow subtidal reefs (Porter, current PhD project).

The reef biodiversity study reported here began in 2003 and ran intensively for two years. The focus area was the deep photic zone (as classified by the South African National Spatial Biodiversity Assessment, Lombard et. al., 2004) i.e. from a depth of 10 - 30 m, since this depth range follows the contours of the old shoreline and anecdotal reports claimed that this range has a high concentration of hard-bottom substrates (EKZNW unpubl. data). Reefs within this depth range could also be accessed easily by means of SCUBA-diving. This study has involved biological sampling of reefs along the KZN coast to determine species abundance and community structure. Three methods of biodiversity data collection were used, namely line-intercept and quadrat transects to collect data on benthic sessile species cover and abundance, and belt transects to assess abundance of mobile invertebrates on the reef.

My thesis aims to examine the biogeographic biodiversity patterns of benthic epifauna and epiflora and to determine the effects of depth on biological community structure on reefs along the KZN coastline. The following key questions are addressed:

1. Are there significant differences in community structure between regions, localities and depth categories?
2. Are there patterns in community structure and species composition with differences in depth at regional and local scales?
3. What are the depth patterns of functional groups? How does depth influence the abundance of each group?
4. Are there biogeographic differences in community structure?
5. What is the percentage cover of algae, fauna and sand at each depth? Are there obvious patterns?
6. Do species richness, evenness and diversity differ with changes in depth?

2. METHOD

2.1. STUDY SITE

The survey was carried out along the 640-km coastline of KwaZulu-Natal from the Mozambique border in the north to the southern border with the Eastern Cape Province. The continental shelf is ~3 km wide north of Cape St Lucia, then expands to ~45 km in the central part of the province and narrows again to around 11 km in the south (Garratt, 1984; Ramsay, 1994). The Agulhas is the major current running southwards parallel to the coast. Sea surface temperatures are cooler in the south than the north, although *in situ* temperature data are lacking and therefore accurate measures of temperature cannot be provided. Nine localities were selected spanning the whole KZN province and their GPS positions along the coast are provided in Table 1.

Table 1: GPS positions of the nine localities surveyed in KZN. All reefs sampled were located within 10 km of these points.

LOCALITY	GPS POSITIONS (Degrees, minutes, seconds)	
Kosi Bay	26° 55' 35.000" S	32° 53' 16.500" E
Sodwana Bay	27° 31' 00.666" S	32° 41' 0.098" E
Cape Vidal	27° 48' 00.170" S	32° 37' 0.550" E
Cape St Lucia	28° 30' 36.360" S	32° 25' 1.920" E
Prince's Grant	29° 20' 37.320" S	31° 23' 25.860" E
Umhhlali	29° 25' 59.160" S	31° 18' 18.600" E
Umkomaas	30° 15' 00.721" S	30° 49' 00.535" E
Sizela	30° 24' 48.840" S	30° 41' 11.520" E
Port Edward	31° 06' 549" S	30° 11' 609" E

2.2. SAMPLING DESIGN

A hierarchical sampling design was devised to sample representative reef ecosystems in KwaZulu-Natal. The 640 km coastline was divided into twelve ~50 km sections (Fig. 1). In each section, one locality was chosen. Distances between localities spanned 10-50 km. Within each locality two sites 1 km apart were selected. At Site 1 four depth categories ranging from 10 m to 30 m were chosen and at Site 2 one depth category (15 - 20 m) was sampled. The additional site at the 15 - 20 m depth zone (Site 2) was chosen to provide replication to investigate patterns of biogeography along the coast and because results from interviews with users revealed a greater occurrence of reef at this depth (EKZNW unpubl. data). Data from Site 2 were not used in this thesis but will in the future be utilized for more detailed analyses of biogeography.

Localities were grouped into three regions: north, central and south based on their geographical distribution along the coastline. The eventual intention is to sample reefs at all 12 localities, however it proved difficult to find reef especially within the stipulated depth categories at all localities. For this reason three localities, namely Manzengwenya, Richards Bay North and Durban, were omitted from this analysis and only three depth categories could be sampled at Sizela since it lacked reef at 20 - 25 m.

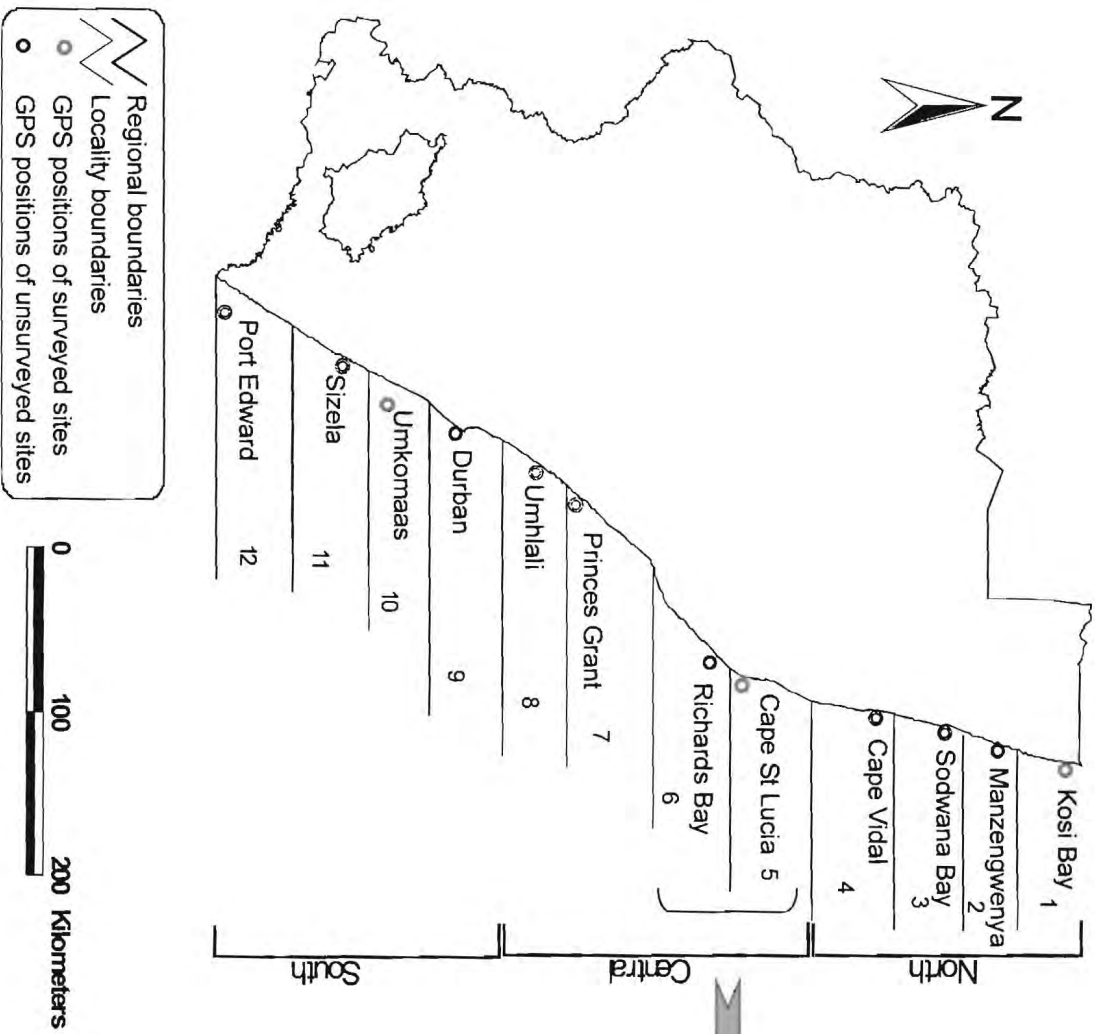
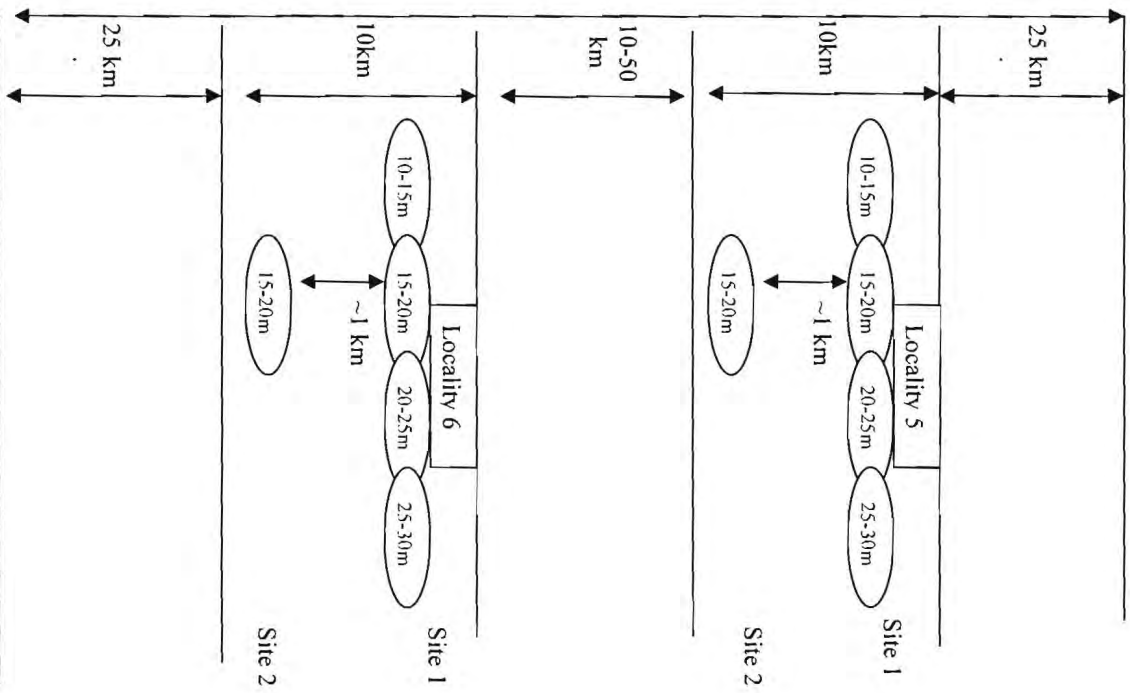


Figure 1: Hierarchical sampling design for reef habitats in KwaZulu-Natal



2.3. BENTHIC SURVEYS

2.3.1. Sessile invertebrates

Two sampling methods to assess benthic species cover were carried out within each depth category at each site and at each locality. These were:

a). *Line-Intercept Transect Method*

The line-intercept method was chosen because it is simple to apply. The methodology was taught to conservation managers who assisted in the data collection but who do not possess formal scientific training. It was also selected to reduce observer bias that may result from methods that rely on more subjective estimation of quantitative species cover (Loya, 1978; Risk et al., 2001).

At each locality and each depth range, three 10-m-long line transects were used to sample cover of benthic sessile organisms. Weighted ropes were placed parallel to the shoreline at least 5 m apart on reef flats that had a relatively high profile, i.e. rose >1 m above the sand. Only flat surfaces of reef were sampled since topography in gullies, cracks, crevices and vertical ledges is complex and difficult to sample (Loya, 1972) and was beyond the scope of this initial baseline study.

Benthic sessile organisms were scored by recording the length of transect line occupied by each species as they appeared beneath the tape measure, thereafter converted to a percentage cover by equating the 10-m length to 100 percent (after Loya, 1978). Species were identified underwater to the lowest taxonomic group possible. In most instances

organisms were given a descriptive name and a sample was collected for later expert identification.

b). Quadrat Method

Five quadrats (0.5 m x 1 m) were sampled alongside each of two of the line transects for primary percent cover of benthic epifauna. This method was used to assess benthic cover in conjunction with the line intercept transects. It was felt that the line transects may not provide a sufficient description of benthic community structure given the small area covered (equivalent to only 0.2 m² per transect). The quadrat was placed alongside the line and rolled to cover a total distance of 5 m. Only 10 quadrats were sampled at each depth as this was the maximum number that could be sampled at the deepest depth (30 m) on a single dive (~20 min). Sampling time also depended on the complexity of species assemblages present on the reef. Quadrat data were collected only by divers formerly trained in scientific data collection.

2.3.2. Mobile invertebrates

A belt transect 2 m wide that ran along the line transect was carried out to count numbers of mobile invertebrates. This was done on all three lines at each depth. Data were collected particularly to quantify indicator species, i.e. those species (rock lobsters, clams, cowries, tritons, hermit crabs, featherstars etc.) whose presence or absence on the reef indicate some measure of the health status of the reef (following method used in ReefCheck; Hodgson, 1999; www.reefcheck.com). However, their abundance was so low that they seldom influenced community composition. Invertebrate organisms were

identified *in situ* if possible, or were otherwise collected and preserved in 70% ethanol to be identified later by taxonomists.

2.4. DATA ANALYSIS

Only data from the line-intercept transect sampling were used in my thesis, as the quadrat dataset remains incomplete. Multivariate analyses (PRIMER 5.0 software, Plymouth Marine Laboratory, Clarke and Warwick, 1994) were used to examine patterns in community structure and species composition with depth. To test the null hypotheses that no significant differences existed within and between replicates, depth categories, localities and regions, ANOSIM (Analysis of Similarities) tests were used to calculate the test statistic R value (and its significance, P) as an indicator of the degree of dissimilarity between samples. Multidimensional scaling (MDS) plots and cluster hierarchies were performed on fourth-root transformed and standardised data using PRIMER 5.0 (Clarke and Warwick, 1994). The percentage contribution of each species to the similarity and dissimilarity within and between sites was identified using SIMPER (Similarity Percentage Breakdown; Clark and Warwick, 1994). For these analyses the full dataset was used, incorporating data from three transects at four depth categories for each of the nine localities.

To determine within-site variability, that is similarity between depth categories and replicates within a locality, MDS plots and cluster hierarchies were performed only on the dataset for each individual locality.

2.4.1. Taxonomic Classification and Functional Groups

In total, 265 faunal taxa, 63 algal taxa and seven substrate categories were recorded in this study. When it was not possible to identify species, they were given a descriptive code, e.g. 'SP-enc white' (sponge encrusting white). Unidentified algae were assigned into broad groups of red, green and brown as well as foliose or encrusting growth forms. I classified seven different substrate types comprising abiotic (sand, rock, sand plus rock and rubble), biotic ('scuz' – a mixture of biotic and abiotic granules) and mixed substrates (sand plus low mix turf, and rock plus low mix turf).

The 328 taxa encountered in the full dataset were later pooled into 19 functional groups (Table 2) since not all organisms were identified to species level and patterns in functional group distribution were explored. Thereafter, percentage cover of functional groups was calculated for each depth at each locality.

Table 2: List of functional groups including substrate types used in the analyses

FUNCTIONAL GROUPS	DESCRIPTION
<i>Substrate Type</i>	
Mixed Substrate	Sand + Rock (bare); Rock + Low mix turf
Abiotic substrate	Sand, Rock (bare), rubble
Biotic substrate	Fine biotic granules
<i>Algae</i>	
Algae encrusting	Encrusting algae < 1 mm high
Low mix turf	Mix of different species of algae 1 mm – 5 mm
Med mix turf	Mix of different species of algae 5 mm – 10 mm
Algae foliose	> 10 mm
<i>Fauna</i>	
Anemone	
Ascidian	Solitary and colonial
Bryozoa	Upright and encrusting
Echinoderm	Seastars, brittle stars
Octocoral	Sea pens, sea fans
Hard Coral	
Soft Coral	
Hydroid	
Sponge	
Worm	Tubeworms
Zoanthid	

2.4.2. Species Diversity

Diversity was assessed by calculating cumulative species richness (S), Pielou's Evenness (J') and Shannon-Weiner Diversity (H') indices. Cumulative species richness is the number of species for a given number of individuals. Evenness is the measure of the distribution of species and ranges from 0 (marked dominance) to approximately 1 (indicating an equal spread of species). Shannon-Weiner diversity measure considers both species richness and evenness. Each diversity measure describes a different component of community diversity (Clarke and Warwick, 1994). These indices were estimated for each depth at each locality to determine trends or patterns of similarity among localities and among depth categories.

3. RESULTS

3.1. COMMUNITY STRUCTURE

Data were first analysed to identify general trends in community composition with respect to the factors 'region', 'locality' and 'depth', thus allowing recognition of patterns at these different scales. Thereafter data for individual localities were analysed separately to assess differences within and among localities. Species were later pooled into 19 functional groups to explore patterns of functional group distribution at each depth.

3.1.1. Regions

A pairwise ANOSIM test confirmed that on average the three regions (north, central and south) were dissimilar to each other ($R = 0.607$, $P = 0.1\%$; Table 3). The northern region was dissimilar to the south ($R = 0.718$, $P = 0.1\%$) and central ($R = 0.778$, $P = 0.1\%$) regions while the central and southern regions showed less dissimilarity ($R = 0.224$, $P = 0.1\%$) to each other.

Table 3: Results of a Pairwise ANOSIM test between North, Central and South regions. Average R value is 0.607, $P = 0.1\%$.

Groups	R	Significance%
North, Central	0.718	0.1
North, South	0.778	0.1
Central, South	0.224	0.1

A percentage breakdown in similarity between regions using the full dataset revealed a clear distinction in species composition between the north and south (89.67% dissimilar) and north and central (89.43% dissimilar) regions (SIMPER analysis, Table

4). This was due to the presence of soft corals (*Lobophytum spp* and *Sinularia spp*), hard corals (mainly *Montipora spp*) and a high cover of sand in the north. The south and central regions were also highly dissimilar (average 84.32% dissimilarity) owing to the presence of coralline algae, *Dictyota sp*, *Vidalia serrata* and *Halimeda sp* in the south and the absence of these species in the central region (Table 4). The central and southern regions were also characterised by a high occurrence of filterfeeders (e.g. sponges, gorgonians, ascidians and bryozoans) that were present in both regions but were in greater abundance in the central than southern region.

Three large clusters comprising (1) the northern localities, (2) central plus southern localities, and (3) Cape St Lucia emerged from the Bray-Curtis and MDS analyses (Figs 2 and 3). These groups were more than 80% dissimilar and contradicted the *a priori* classification of localities into distinct north, central and south regions. Localities that overlapped between southern and central regions were Prince's Grant (C), Sizela (S) and Umkomaas (S). Cape St Lucia (C) formed an outlier and was >90% different to the rest of the localities (Figs 2 and 3).

Table 4: SIMPER analysis of taxa contributing to the first 40% of cumulative dissimilarity between North (N), Central (C) and Southern (S) regions (Bray-Curtis dissimilarity, standardised data, fourth root transformed). Av.Abund = average % cover; Diss = average dissimilarity of a taxa between sites; Diss/SD = ratio of mean/standard deviation of dissimilarity as a measure of spread or consistency of dissimilarity; Contrib % = % contribution to dissimilarity between sites; Cum. % = cumulative contribution to dissimilarity.

Species	Functional Group	Av. Abund N	Av. Abund C	Diss	Diss/SD	Contrib%	Cum.%
<i>Lobophytum</i> spp	Soft coral	10.7	0.0	4.6	3.1	5.1	5.1
<i>Simularia</i> spp	Soft coral	9.7	0.2	4.3	2.7	4.8	9.9
<i>Montipora</i> spp	Hard coral	7.8	0.0	3.4	1.6	3.8	13.7
Sand	Sand	4.9	12.9	3.0	1.1	3.4	17.1
Low mix turf	Algae	24.6	26.9	3.0	1.1	3.4	20.5
<i>Favites</i> spp	Hard coral	2.5	0.0	2.3	1.2	2.6	23.0
Hydroid unid.	Hydroid	0.2	3.0	2.1	1.1	2.4	25.4
<i>Favia</i> spp	Hard coral	1.7	0.0	2.0	1.2	2.2	27.6
<i>Sarcophyton</i> spp	Soft coral	3.5	0.0	1.8	0.8	2.0	29.6
<i>Echinopora hirsutissima</i>	Hard coral	3.7	0.0	1.8	0.8	2.0	31.6
Rock	Abiotic substrate	4.4	3.2	1.7	0.6	1.9	33.5
<i>Platygyra</i> spp	Hard coral	1.6	0.0	1.7	1.0	1.9	35.4
<i>Acabaria rubra</i>	Gorgonian	0.0	2.3	1.6	0.8	1.8	37.2
<i>Policarpa</i> sp	Ascidian	1.4	0.4	1.5	0.9	1.7	38.9
<i>Diplosoma</i> sp	Ascidian	2.1	0.0	1.4	0.7	1.6	40.4
		Av. Abund N	Av. Abund S				
<i>Lobophytum</i> spp	Soft coral	10.7	0.0	4.5	3.1	5.1	5.1
<i>Simularia</i> spp	Soft coral	9.7	0.0	4.3	2.9	4.8	9.9
<i>Montipora</i> spp	Hard coral	7.8	0.0	3.4	1.6	3.8	13.7
Sand	Sand	4.9	14.5	3.2	1.2	3.5	17.3
Low mix turf	Algae	24.6	20.0	2.7	1.1	3.0	20.3
<i>Favites</i> spp	Hard coral	2.5	0.0	2.3	1.2	2.5	22.8
<i>Favia</i> spp	Hard coral	1.7	0.0	1.9	1.2	2.2	24.9
<i>Sarcophyton</i> spp	Soft coral	3.5	0.2	1.8	0.8	2.0	27.0
<i>Echinopora hirsutissima</i>	Hard coral	3.7	0.0	1.8	0.8	2.0	28.9
Coralline algae unid.	Algae	0.0	4.3	1.7	0.8	1.9	30.9
<i>Dictyota</i> sp	Ascidian	0.0	5.2	1.7	0.6	1.9	32.8
<i>Platygyra</i> spp	Hard coral	1.6	0.0	1.7	1.0	1.9	34.6
Rock	Abiotic substrate	4.4	1.9	1.5	0.6	1.7	36.3
<i>Policarpa</i> sp	Ascidian	1.4	0.2	1.5	0.9	1.6	37.9
<i>Amphiroa bowerbankii</i>	Algae	0.0	3.9	1.4	0.6	1.6	39.5
<i>Diplosoma</i> sp	Ascidian	2.1	0.0	1.4	0.7	1.5	41.1
		Av. Abund C	Av. Abund S				
Sand	Sand	12.9	14.5	3.4	1.2	4.0	4.0
Low mix turf	Algae	26.9	20.0	3.1	1.2	3.7	7.7
Hydroid unid.	Hydroid	3.0	1.1	2.2	1.1	2.6	10.3
Coralline algae unid.	Algae	0.0	4.3	1.8	0.8	2.2	12.5
<i>Dictyota</i> sp	Ascidian	0.0	5.2	1.8	0.6	2.1	14.6
<i>Acabaria rubra</i>	Gorgonian	2.3	0.3	1.7	0.8	2.1	16.6
<i>Amphiroa bowerbankii</i>	Algae	1.1	3.9	1.7	0.7	2.0	18.6
<i>Mycale (Carmia) toxifera</i>	Sponge	2.0	1.6	1.6	0.7	1.9	20.6
<i>Ircinia</i> sp	Sponge	1.1	1.0	1.6	0.9	1.9	22.5
<i>Ircinia arenosa</i>	Sponge	1.0	0.4	1.4	0.8	1.7	24.1
<i>Peyssonnelia</i> sp	Algae	1.0	1.0	1.4	0.7	1.6	25.7
Low mix turf + sand	Mixed substrate	0.6	4.6	1.3	0.5	1.6	27.3
Rock	Abiotic substrate	3.2	1.9	1.3	0.5	1.5	28.8
Sponge wall unid.	Sponge	0.0	1.3	1.3	0.6	1.5	30.3
Encrusting coralline unid.	Algae	2.5	0.9	1.2	0.5	1.5	31.8
Gorgonian orange unid.	Gorgonian	0.9	0.2	1.2	0.7	1.4	33.2
<i>Schizoretepora tessellata</i>	Bryozoa	1.8	0.1	1.1	0.6	1.3	34.5
<i>Halichondria</i> sp	Sponge	0.5	0.6	1.1	0.7	1.3	35.9
<i>Cliona</i> sp	Sponge	0.7	2.3	1.0	0.5	1.2	37.1
<i>Psammoclema</i> sp	Sponge	1.3	0.2	1.0	0.6	1.2	38.3
<i>Vidalia serrata</i>	Algae	0.0	1.5	1.0	0.5	1.2	39.4
<i>Halimeda</i> sp	Algae	0.0	1.1	1.0	0.6	1.2	40.6

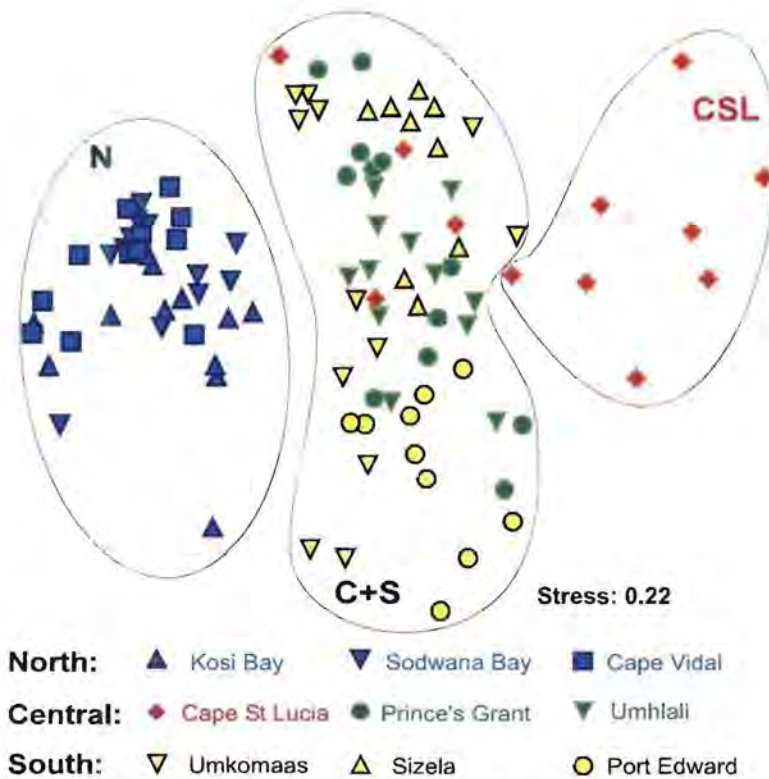


Figure 3: Multidimensional ordination plot representing distribution of transects by locality. Localities have been circled into north (N), central and south (C+S) and Cape St Lucia (CSL) with the latter forming an isolated cluster. Note the overlap between central and southern groups.

A simpler analysis carried out on the three groupings identified from the Bray-Curtis results i.e. North, Central + South and Cape St Lucia produced a high average dissimilarity between these groups (Table 5). The functional groups contributing the highest percentage average dissimilarity between Cape St Lucia and the southern and central localities were low mix turf and sand.

A greater dominance of soft and hard corals was found in the northern region than the central and southern regions (Fig. 4). Foliose algae were less abundant in the north and central regions but high in the south. Filterfeeders (sponges, worms, hydroids, bryozoans, and ascidians) were more abundant in the central and southern regions as opposed to the north (Fig. 4). Low mix turf was present in all regions but had the highest overall cover in the central region at 10 – 20 m depth intervals.

Table 5: SIMPER analysis of taxa contributing to the first 40% of cumulative dissimilarity between North (N), Central and Southern (C+S) regions, and Cape St Lucia (CSL) as identified by the cluster analysis (Bray-Curtis dissimilarity, standardised data, fourth root transformed). Abbreviations as in Table 3.

Species or Substrates	Functional Group	Av.Abund N	Av.Abund CSL	Average dissimilarity = 93.02			
				Av.Diss	Diss/SD	Contrib%	Cum.%
<i>Lobophytum</i> spp	Soft coral	10.73	0.00	4.38	3.03	4.71	4.71
<i>Sinularia</i> spp	Soft coral	9.70	0.00	4.19	2.83	4.51	9.22
Low mix turf	Algae	24.55	22.12	3.53	1.35	3.80	13.02
<i>Montipora</i> spp	Hard coral	7.83	0.08	3.21	1.56	3.45	16.47
Hydroid unid.	Hydroid	0.19	3.62	2.61	1.39	2.81	19.28
<i>Favites</i> spp	Hard coral	2.50	0.00	2.20	1.21	2.36	21.64
Worm unid.	Worm	0.00	13.63	2.15	0.69	2.32	23.96
Sand	Sand	4.94	2.53	2.11	0.92	2.27	26.22
<i>Psammoclema</i>	Sponge	0.10	3.76	1.97	0.93	2.12	28.35
<i>Favia</i> spp	Hard coral	1.71	0.00	1.88	1.15	2.02	30.36
		Av.Abund N	Av.Abund C+S	Average dissimilarity = 88.78			
<i>Lobophytum</i> spp	Soft coral	10.73	0.00	4.59	3.13	5.17	5.17
<i>Sinularia</i> spp	Soft coral	9.70	0.11	4.33	2.76	4.88	10.05
<i>Montipora</i> spp	Hard coral	7.83	0.00	3.48	1.64	3.92	13.97
Sand	Sand	4.94	16.06	3.32	1.18	3.74	17.70
Low mix turf	Algae	24.55	24.01	2.70	1.07	3.05	20.75
<i>Favites</i> spp	Hard	2.50	0.00	2.30	1.22	2.59	23.34
<i>Favia</i> spp	Hard	1.71	0.01	1.96	1.16	2.20	25.54
<i>Sarcophyton</i> spp	Soft coral	3.53	0.09	1.83	0.81	2.07	27.61
<i>Echinopora</i>	Hard coral	3.66	0.00	1.77	0.79	2.00	29.61
Rock	Abiotic	4.42	3.19	1.73	0.65	1.95	31.55
		Av.Abund CSL	Av.Abund C+S	Average dissimilarity = 87.72			
Low mix turf	Algae	22.12	24.01	3.70	1.35	4.22	4.22
Sand	Sand	2.53	16.06	3.27	1.17	3.72	7.95
Hydroid unid.	Hydroid	3.62	1.79	2.44	1.28	2.78	10.73
Worm unid.	Worm	13.63	0.07	2.30	0.71	2.62	13.35
<i>Psammoclema</i> sp	Sponge	3.76	0.12	2.08	0.95	2.37	15.72
Ascidian complex	Ascidian	1.72	0.00	1.82	1.04	2.08	17.80
<i>Hymeniacidon</i>	Sponge	2.45	0.24	1.80	0.99	2.05	19.85
<i>Schizoretepora</i>	Bryozoan	3.78	0.38	1.60	0.74	1.82	21.67
<i>Acabaria rubra</i>	Octocoral	0.65	1.52	1.46	0.79	1.66	23.33
Sponge enc.	Sponge	1.10	0.09	1.32	0.76	1.51	24.84
<i>Ircinia</i> spp	Sponge	0.33	1.20	1.30	0.77	1.48	26.32
<i>Haliclona</i> spp	Sponge	0.88	0.32	1.27	0.86	1.45	27.77
<i>Placospongia</i>	Sponge	3.10	0.04	1.22	0.52	1.39	29.15
<i>Ircinia arenosa</i>	Sponge	0.33	0.83	1.18	0.70	1.34	30.50

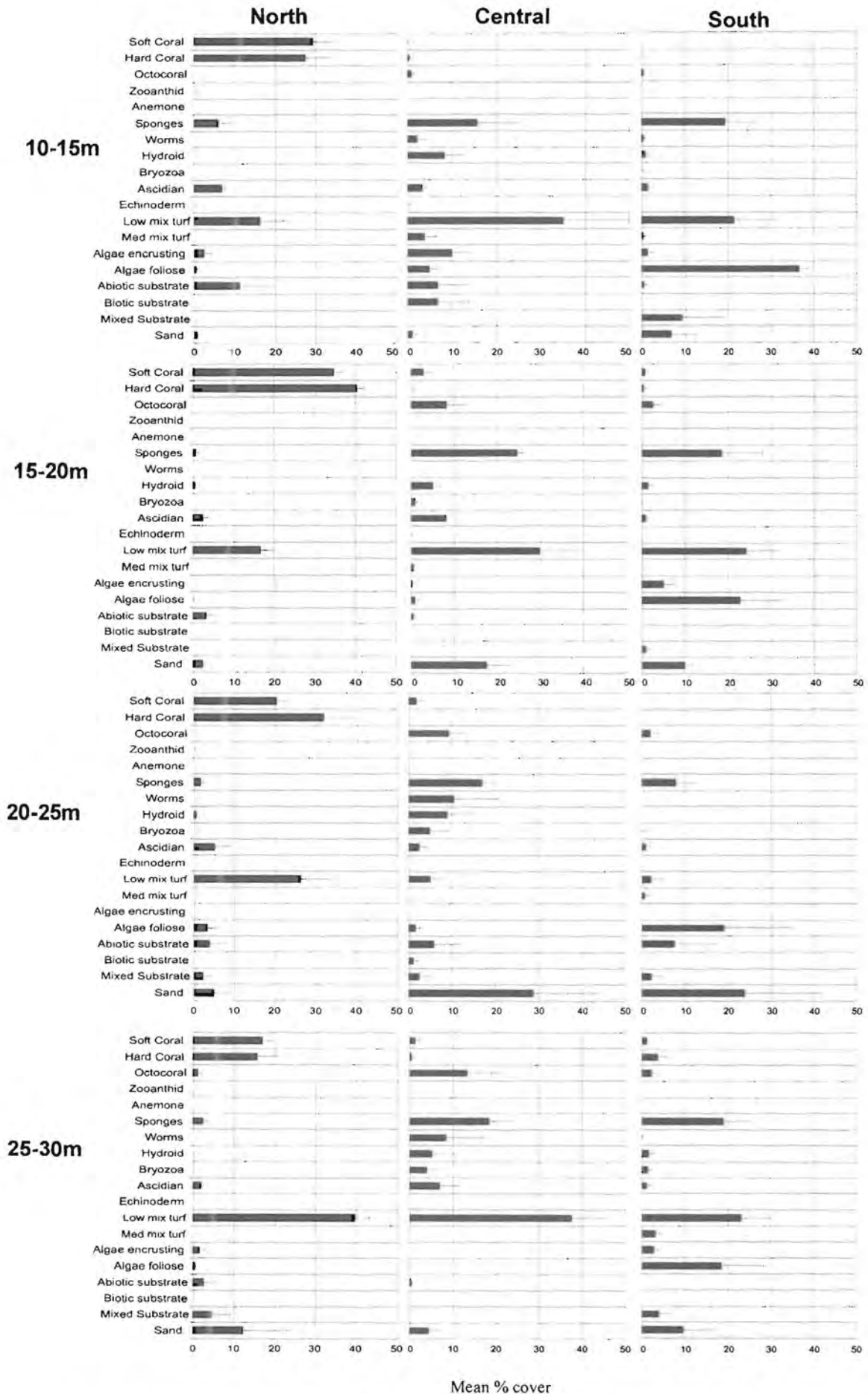


Figure 4: Mean percentage cover of the faunal and algal functional groups and substrates encountered at each depth. Localities are grouped into North, Central and Southern regions.

3.1.2. Localities

Multivariate analyses of community structure revealed distinct groupings of communities by the factor 'locality'. In the majority of cases, all samples from a particular locality clustered together, irrespective of depth (Figs. 2 and 3). The three localities in the north (Kosi Bay, Sodwana Bay and Cape Vidal) revealed a low dissimilarity to each other (Table 6). This is mainly attributed to the shared presence of hard and soft corals with the highest contributing species being *Simularia* spp, *Lobophytum* spp, *Montipora* spp and *Platygyra* spp (for detailed results refer to Appendix 2). The presence of 'low mix turf' also contributed to this. The average dissimilarity between the remaining sites was higher than between the northern three and ranged from 74.7% between Prince's Grant and Umhlali to 93.7% between Cape Vidal and Cape St Lucia (Table 6). Once again this was attributed to the presence of corals in the north, and algae and filterfeeders at Cape St Lucia and the rest of the southern localities.

The two localities where species composition was most different from each other were Cape Vidal and Cape St Lucia (93.7% average dissimilarity) even though these sites occur geographically adjacent to each other. Cape Vidal was however, most similar to its northern neighbouring site (Sodwana Bay), with an average dissimilarity of 55.4% (Table 6), due to the high percentage abundance of corals and low mix turf. Localities south of Cape Vidal comprised very low percentage cover of corals and a greater coverage of algae and filterfeeders.

Table 6: Results of SIMPER analysis with percentage dissimilarity between localities. Details of contributing species are provided in Appendix 2.

LOCALITIES	Kosi Bay	Sodwana Bay	Cape Vidal	Cape St Lucia	Prince's Grant	Umhlali	Umkomaas	Sizela	Port Edward
Kosi Bay		62.9	63.2	93.5	88.2	85.7	87.8	89.3	89.1
Sodwana Bay			55.4	91.9	86.9	86.1	89.4	86.9	90.1
Cape Vidal				93.7	90.0	88.8	91.2	89.4	93.3
Cape St Lucia					87.1	84.2	90.9	86.8	89.7
Prince's Grant						74.7	83.6	81.0	84.0
Umhlali							81.6	78.2	81.7
Umkomaas								79.3	87.2
Sizela									85.8
Port Edward									

3.1.3. Depth Categories

To determine if dissimilarities between depth categories existed along the latitudinal gradient, i.e. from north to south, and whether community composition at shallower depths was distinct from that at deeper depths, depth categories were compared across all localities. An ordination plot did not reveal definite relationships among samples taken at particular depths and a cluster dendrogram revealed no distinct clustering of different depth-category groups (Figs. 5 and 6). Similarity between depth categories within a locality was prevalent whereas dissimilarity between localities was a feature. An ANOSIM test carried out among depth zones averaged across regions produced almost no significant differences between depth categories (at $R = 0.154$, $P = 0.1\%$) (Table 7a) while comparisons of regions averaged across depth zones confirmed a high dissimilarity between the north and central ($R = 0.792$, $P = 0.1\%$) and north and southern ($R = 0.792$, $P = 0.1\%$) regions (Table 7b). The central and southern regions were less dissimilar with an R value of 0.264, but even this was significant ($P = 0.1\%$).

Table 7: Two-way crossed ANOSIM test for differences between a) depth categories averaged across regions and b) regions averaged across all depth categories.

a). Depth Categories		R	Significance (%)
10 - 15 m	15 - 20 m	0.144	0.8
10 - 15 m	20 - 25 m	0.278	0.1
10 - 15 m	25 - 30 m	0.173	0.2
15 - 20 m	20 - 25 m	0.119	1.2
15 - 20 m	25 - 30 m	0.099	1.8
20 - 25 m	25 - 30 m	0.122	1.1
b). Regions		R	Significance (%)
North	Central	0.792	0.1
North	South	0.792	0.1
Central	South	0.264	0.1

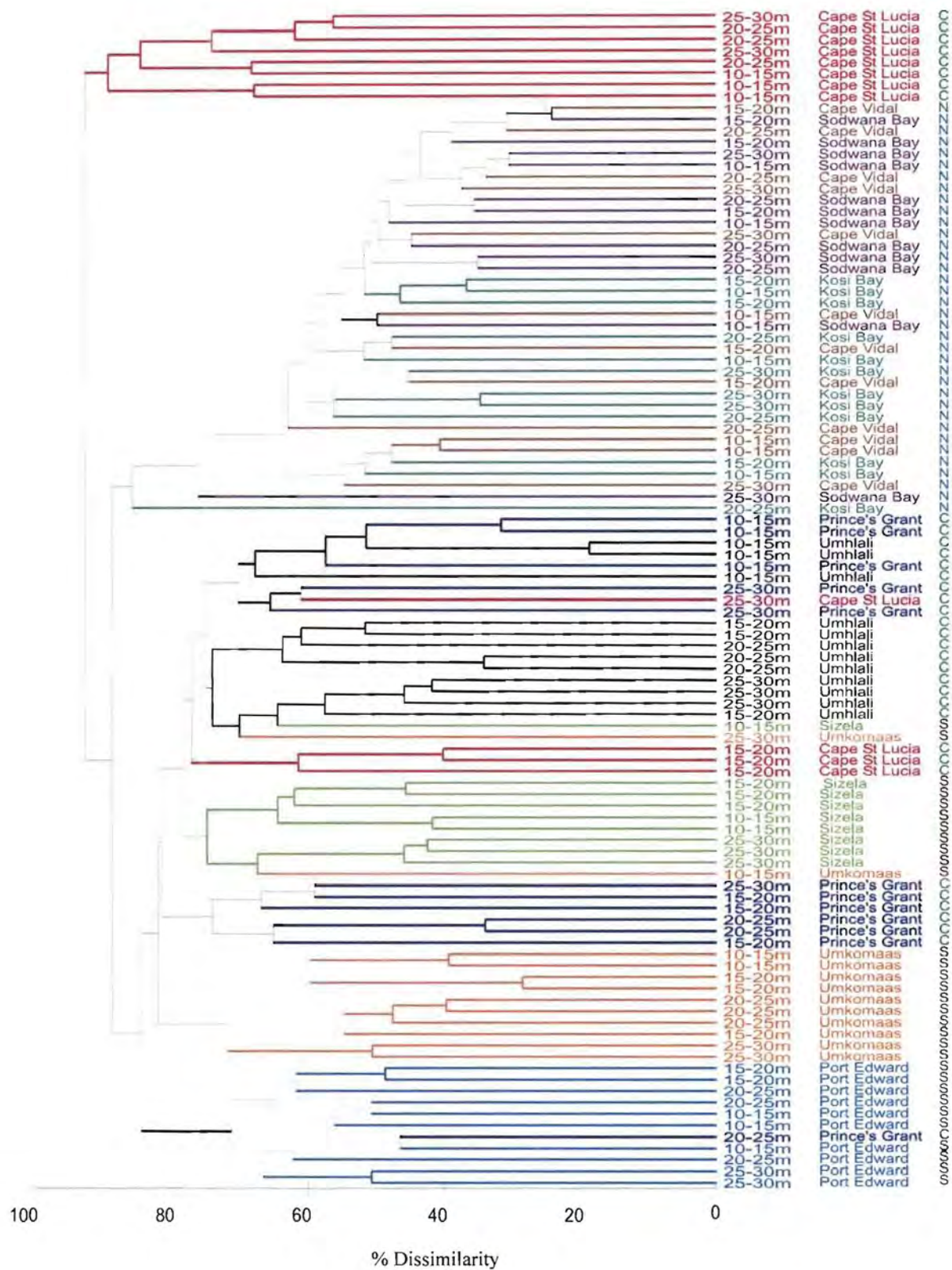


Figure 5: Cluster analysis based on Bray-Curtis dissimilarity (data group-averaged and standardised) with localities and depth categories colour coded. Regions are also depicted in unique colours (N=North, C=Central and S=South)

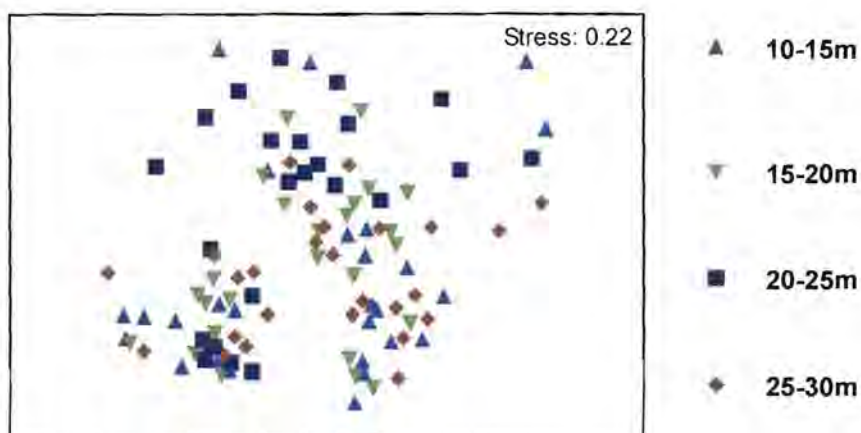


Figure 6: MDS plot of each depth category depicted in a unique colour to detect patterns of similarity in community structure.

In the north, hard and soft corals peaked at 15 - 20 m and diminished deeper than 20 m (Fig. 4), being replaced by a greater algal cover. Low mix turf cover increased with depth to a maximum of 39.5% at 25 – 30 m. The proportion of sand increased as depth increased.

In the central region low mix turf dominated all depth categories except 20 – 25 m where the highest coverage was attributed to sand. Encrusting and foliose algae were most abundant at 10 – 15 m, but declined till 25 m and were virtually absent at 25 – 30 m. Percentage cover of worms, bryozoans and ascidians increased on deeper reefs in this region (Fig. 4).

In the southern region low mix turf and foliose algae remained very abundant across all depths with an exception of 20 – 25 m where they were replaced mostly by sand. Foliose algae were most abundant in this region and declined marginally on deeper reefs but did extend to 25 – 30 m in fair abundance (18.6%). Sponge cover remained fairly constant across all depth categories (Fig. 4).

Percentage cover of low mix turf was high throughout all depths at all regions but declined at 20 to 25 m in the central and southern regions. Sponge cover remained constant across all depth categories. The deepest depth was dominated by sponges, low mix turf and foliose algae.

3.1.4. Replicate Transects

Transects or replicates in similar depth categories were less than 60% dissimilar at eight of the nine localities (Fig 7). Transects in the shallow and mid depth zones clustered together in the north with the exception of Cape St Lucia, while in the southern and central localities, depth categories were more distinct (Fig. 7).

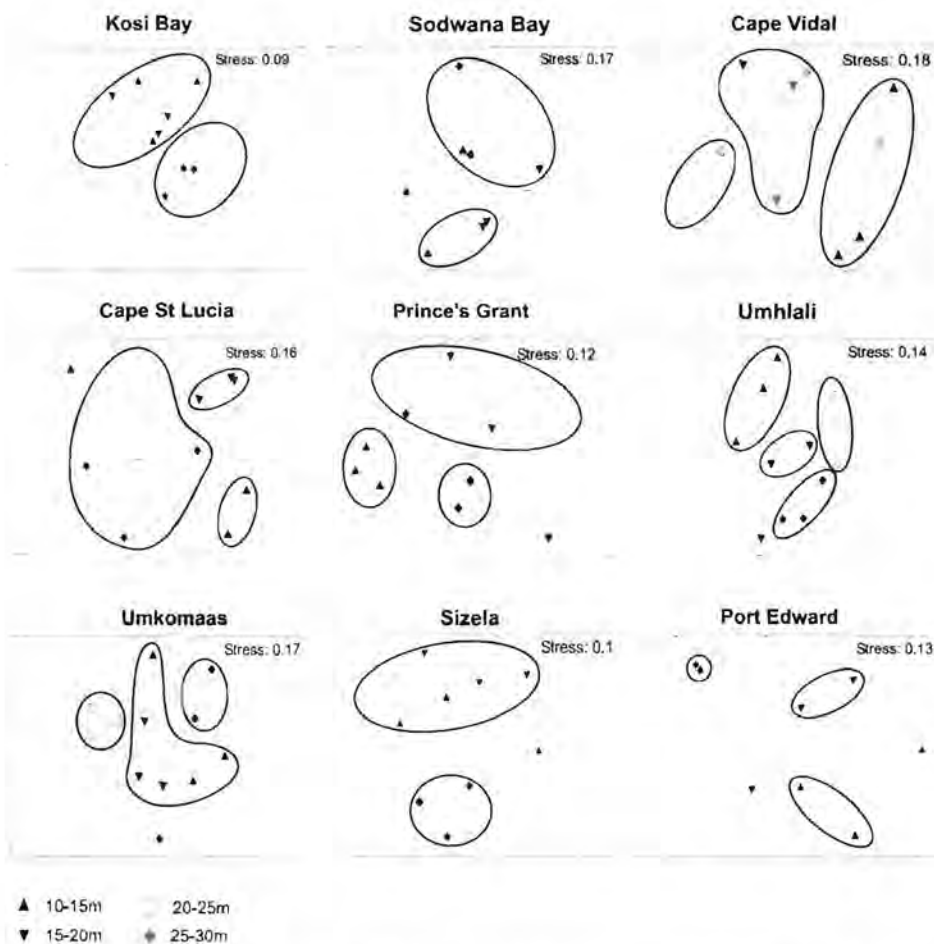


Figure 7: Multidimensional scale plots of all data at each depth at each locality ($n=12$). Shallow (10 – 20 m) and deep (20 – 30 m) are grouped at 60% dissimilarity cut-off as identified in the corresponding Bray-Curtis cluster dendrogram. There are only three depth categories represented at Sizela since no reef was found at 20 – 25 m.

3.1.5. Fauna versus Algae and Sand

A broad categorical plot of fauna, algae and sand cover at each depth and at each locality (Fig. 8) revealed a higher percentage cover of animals than plants at the shallow depths in the north and a greater algal dominance in localities further south. However, algal cover increased with an increase in depth in the northern sites eventually becoming dominant deeper than 25 m (Fig. 8). At Cape St Lucia, fauna was dominant at all depth categories except 15 – 20 m. In the remaining two localities in the central region, algae dominated the shallowest and deepest depths and provided less overall

cover in the intermediate depth ranges. Algae had the highest cover at all depth categories in the southern three localities (Fig. 8).

As a general trend, sand cover was greatest at 15 – 20 m and 20 – 25 m, with the highest overall cover recorded in the southern region. Sand cover was low at 10 – 15 m in all the localities except Port Edward (18.4%) and generally increased at 15 – 25 m at all sites, but declined beyond 25 m. Port Edward had consistent sand cover at all depths although peaking at 20 – 25 m, and showed the highest average percentage cover overall (37.2%). Prince's Grant also contained a relatively high cover of sand reaching a maximum of 52.3% at 20 – 25 m. Biotic cover tended to be low where sand cover was high (Fig. 8).

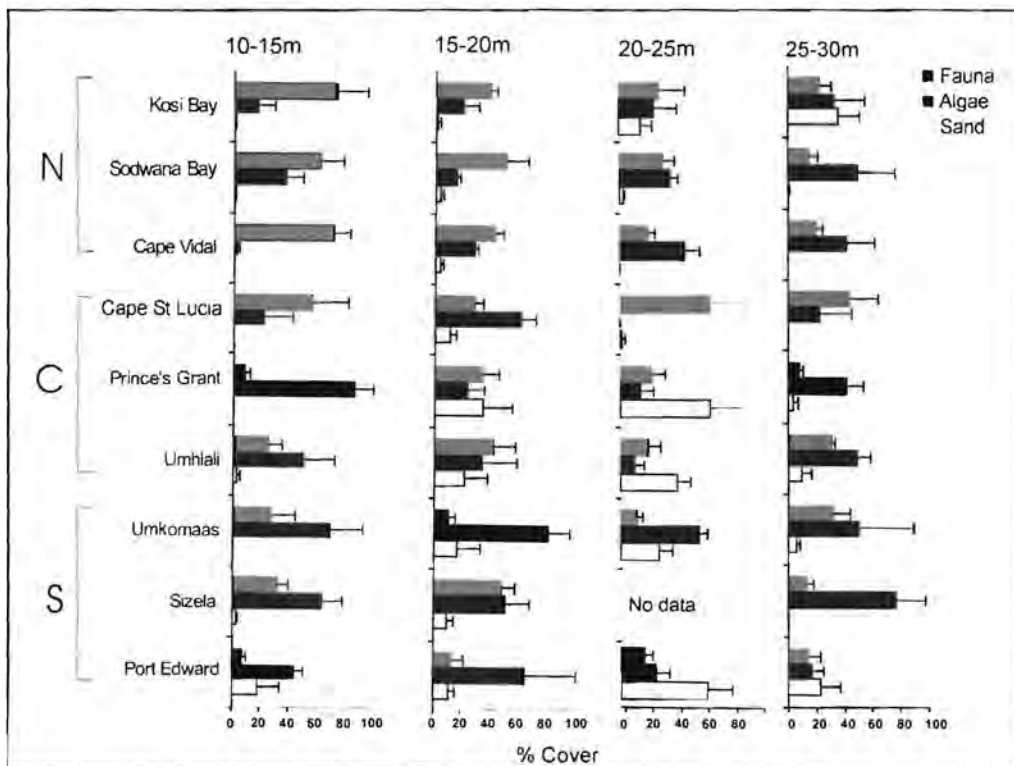


Figure 8: Mean percent cover of benthic fauna, algae and sand at each locality. N = North, C = Central and S = South regions.

3.2. SPECIES DIVERSITY

At 10 – 15 m species diversity (H') was highest in the north but declined in the central part of the province with the lowest diversity recorded at Prince's Grant (Fig. 9). Diversity increased at this depth on reefs in the south except Umkomaas. A similar pattern was observed for cumulative species richness (S) and evenness (J') at this depth (Fig. 9).

In the 15 – 20 m depth zone, species diversity peaked at Kosi Bay and gradually decreased on reefs further south reaching the lowest value at Umkomaas. Diversity was higher on the southernmost two localities. No clear overall trend in cumulative species richness was observed, but the highest value (22.00) was recorded for Cape St Lucia. Evenness was lowest (0.66) at this locality but remained fairly constant across all three regions (Fig. 9).

A similar pattern was observed at 20 – 25 m as diversity decreased from north to south. Species richness was highest at Sodwana Bay and Cape St Lucia and lowest at Prince's Grant while the other localities were not markedly different. Species evenness remained fairly consistent across all localities (Fig. 9).

The pattern observed at 25 – 30 m was different to those of the other three depth categories. Species diversity increased from north to south with the lowest value recorded at Kosi Bay (1.35) and the highest at Port Edward (2.15). Species richness was high at Sodwana Bay and Cape Vidal but decreased on reefs in the central region.

The gradual increase in richness in the southern region culminated in a peak and overall recorded high at Port Edward (21.50) for this depth category (Fig. 9).

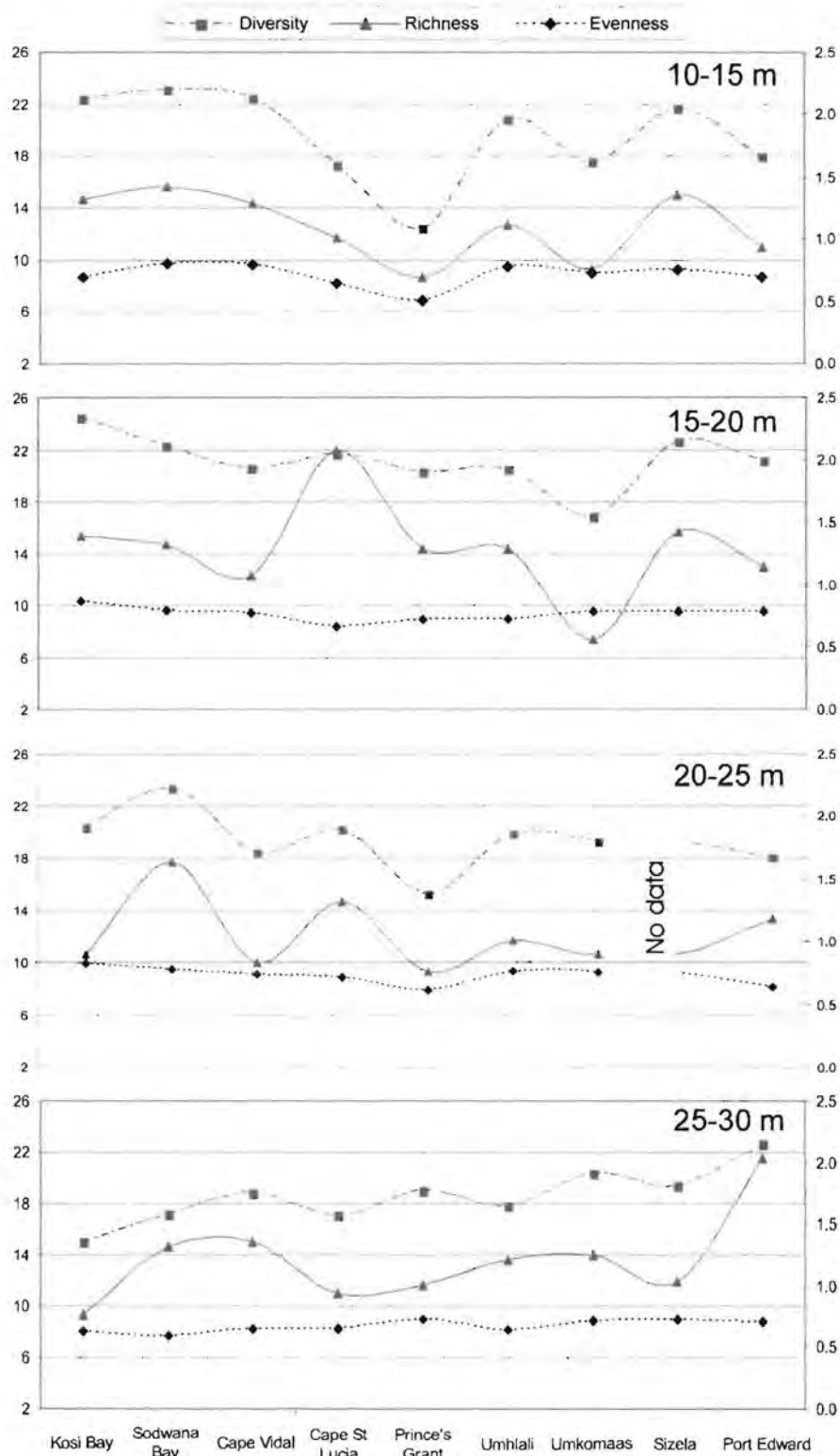


Figure 9: Average cumulative species richness, Shannon diversity and Pielou's evenness across all depth categories in each locality.

Four out of the nine localities sampled comprised the highest species diversity (Shannon index, H') at the 15 – 20 m depth category and these localities were spread across all regions. This depth zone also had the highest species richness and evenness values at five localities. Species diversity, richness and evenness was highest at 15 – 20 m at Kosi Bay, Prince’s Grant and Sizela and this depth emerged as the most diverse depth zone overall (Fig. 10).

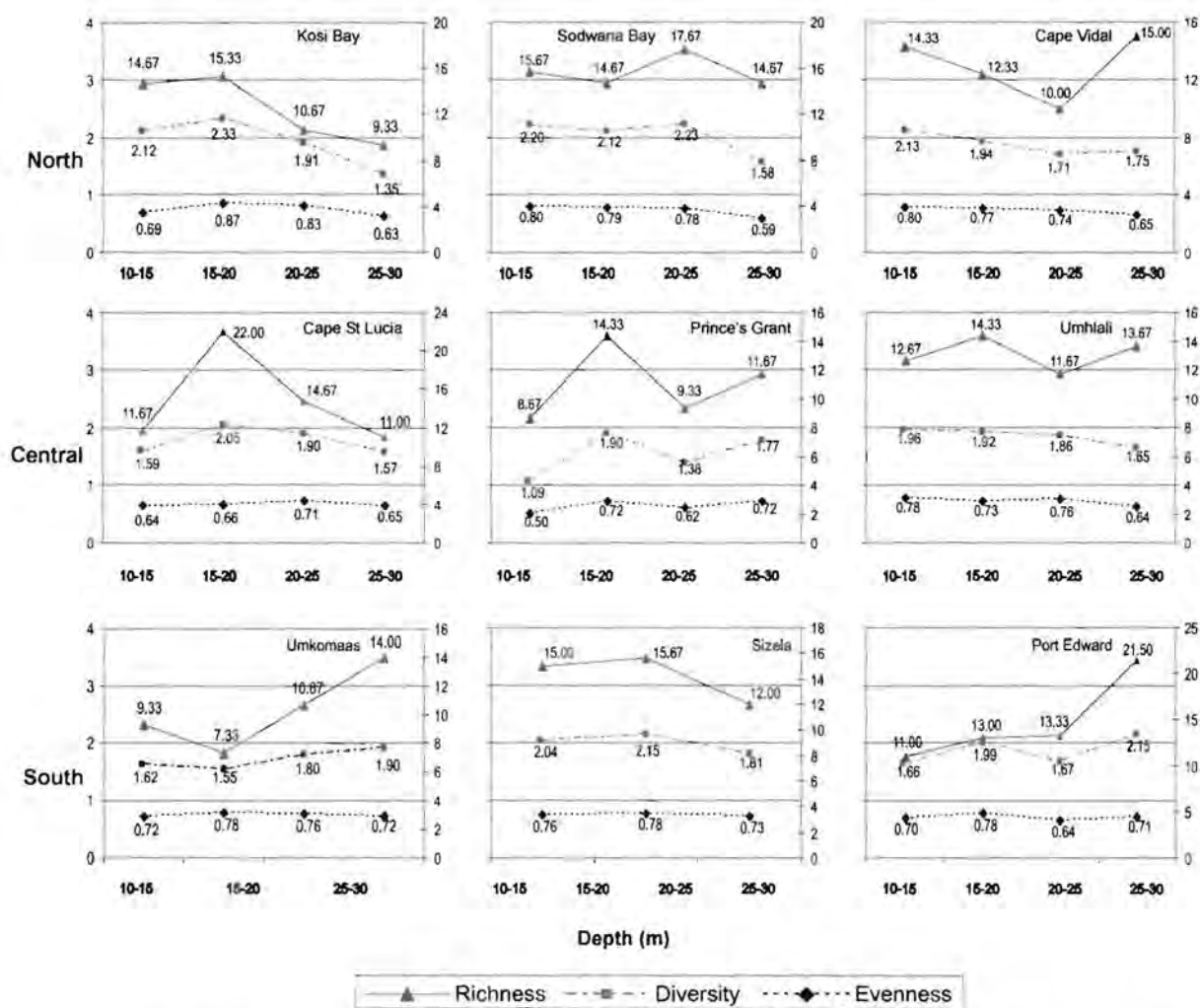


Figure 10: Species richness, Shannon diversity and Pielou’s evenness indices calculated for nine localities at each of the four depth category.

4. DISCUSSION

4.1. COMMUNITY STRUCTURE

Quantitative samples analysed by multivariate and univariate analyses revealed patterns across longitudinal (depth) and latitudinal (geographical) gradients. Distinct differences in community structure were found at a regional level (between north and south/central regions), as well as at a local level (between localities). Localities were less dissimilar to other localities within their region than to those in other regions. While no marked difference in community structure was found across the depth gradient, the composition and relative proportion of taxa did differ, as did the distributional patterns of functional groups.

4.1.1. Regions

Regional differences in community structure were clearly evident. There were four localities that overlapped in composition in the southern and central regions, defining this area as a unit and not two separate regions. The northern region emerged as clearly separate from both the central and south regions. The clearest pattern emerging from these results was a distinct biogeographic break between the north and south/central communities. This concurs with a biogeographic division at Cape Vidal identified by Sink et al. on the basis of analyses of rocky-shore intertidal communities (2005). To some extent, this break may be explained by the biogeographical influences of oceanographic and climatic phenomena, as outlined below.

Tropical coral reef communities occur only in the north-eastern part of South Africa and constitute three major complexes (Riegl et al., 1995, Schleyer, 1999). The subtropical

warm and clear waters in the north provide a suitable habitat for scleractinian and alcyonacean fauna (Ramsay and Mason, 1990) and these reefs are largely dominated by soft coral in the shallow waters (10-20 m), with a higher proportion of hard coral on deeper reefs (20 - 25 m; Fig. 5). The absence of rivers and the consequent limited sediment influx in the north are partly responsible for the low turbidity and nutrient concentrations there (Schleyer, 1999). In nutrient-poor waters the intensity of sunlight at shallower depths encourages coral growth since it favours photosynthetic food production by symbiotic zooxanthellae (Schlöder and D'Croza, 2004). High hard and soft coral cover was a defining feature of the northern region, but diminished with depth and was replaced by low mixed turf (Fig. 5).

The distinction between the northern and south/central regions could also be a result of changes in the influences of the rapid southward-flowing Agulhas Current. Off northern KZN this warm western-boundary current flows close inshore as a result of the narrow continental shelf and also flows at reduced velocities compared to those experienced further south (Schumann, 1988). It then veers offshore with the widening of the shelf at Cape St Lucia where a relatively shallow eddy, the Natal Bight, is formed off central KZN (Lutjeharms pers. comm.; Schumann, 1988). This induces upwelling close inshore, resulting in a greater introduction of nutrients and cooler waters to the southern part of the province (Schumann, 1988; Lutjeharms et al., 2000) yielding a more temperate reef environment evident in the central/south regions (Bolton et al., 2004).

4.1.2. Localities

Whereas the three northern localities (Kosi Bay, Sodwana Bay and Cape Vidal) clustered tightly at a relatively high level of similarity, in the south/central regions localities were observably more different from one another (Figs 3 and 5; Table 6). There was some hint of a sub-clustering of Prince's Grant, Umhlali and (some) Cape St Lucia samples in the cluster analysis, albeit at a lower level of similarity (Fig. 5). This sub-cluster may possibly be related to shallow inshore upwelling and the relatively cooler sea surface temperatures there as compared to the north (Lutjeharms et al., 2000; Schumann, 1988). This upwelling feature of the Natal Bight runs from Cape St Lucia to Durban (Schumann, 1988), thus encompassing these central localities.

With the exception of samples at 15 – 20 m, species composition at Cape St Lucia was notably different from all the other localities (Fig. 5, Table 6). The high turbidity on this reef at all depths (personal observation) and associated particulate incursion may have favoured the proliferation of filter feeders, and this was evident in the high occurrence of hydroids, ascidians and sponges observed there. A striking biological feature on this reef was the abundance of organisms growing over hydroid stalks. Hydroids provided a holdfast for animals such as encrusting bryozoa, ascidians and sponges, thereby increasing overall species cover. Bradshaw et al. (2003) demonstrated the effect of upright sessile epifauna such as hydroids on benthic biodiversity in the Irish Sea. Encrusting organisms are favoured by a degree of elevation off the sediment substrate into the water column to facilitate exploitation of pelagic food supplies (Bradshaw et al., 2003), and gain this elevation by growing epizootically on erect species.

Another biological attribute of this reef was the occurrence of a unique substrate (a fine mix of organic granules) that formed a thin blanket over the reef. This may have been the residue from an oil spillage that had occurred a year before the reef was surveyed and may have influenced its community structure. However, further biochemical analyses of the substrate will be required to determine if this is the case. The reef at Cape St Lucia is located approximately 50 km north of a pipeline that extends out of the Richards Bay harbour. As a result it is subjected to toxic effluent that is discharged through the pipeline (Connell and Pillay, 2004), which may also explain the distinctive composition of the community observed there.

The Agulhas current produces a well-mixed coastline with some areas of relatively high biological productivity (Zacharias et al., 1998; Lutjeharms et al., 2000). Major sediment deposits and higher turbidity levels as a result of riverine outflow punctuate the southern coastline. The shelf waters of the southern localities are characterised by cooler sea temperatures, and the rapid flowing current carries a richer supply of nutrients to benthic organisms (Ramsay, 1994) than in the northern localities. The provenance of this primary pelagic food source is reflected in the high abundance of suspension and deposit feeding infauna such as sponges, bryozoa and hydroids in the south/central region (Fig. 4).

Foliose (mainly red and brown) algae were a dominant feature within the southern localities. This may be as a consequence of an amplification of nutrients to the south coast of KZN through industrial and sewage effluent discharge (Schleyer, 2001) exacerbating turbid conditions (personal observation). The key functional group at Umkomaas, Sizela and Port Edward was coralline algae, mainly *Amphiroa bowerbankii*

(average 54.6%), *A. ephedraea* (average 26.2%) and an unidentified coralline species (average 45.2%). These algae contain hard 'skeletons' and are structurally important reef builders providing fine calcareous sand from dead material (Björk et al., 1995) which could explain the high concentration of sand at Port Edward. The calcareous sand from coralline algae skeletons fills up crevices and contributes to overall expansion of reef (Björk et al., 1995).

4.1.3. Depth Categories

At the three northern localities, samples failed to cluster in any manner reflecting depth categories. Here the continental shelf is narrow (~10 km wide), whereas it expands at Cape St Lucia to reach a maximum of 45 km in the central area and then narrows again to roughly 12 km in southern KZN (Garratt, 1984; Ramsay, 1994). As a result, the geographical distance between depth categories within a locality was smaller at Kosi Bay, Cape Vidal and Sodwana Bay than elsewhere. Sites that were sampled within these localities were within tens of meters apart indicating a substantial change in depth over a narrow spatial scale.

Some depth patterns were observed within localities south of Cape St Lucia, but even there they were not striking (Fig. 5). In most cases, samples from different depths clustered together within their particular locality rather than with similar depth categories from other localities. Reefs within the south/central localities were spread over distances of hundreds of meters as a consequence of a wider continental shelf (Garratt, 1984; Ramsay, 1994). This could account for the contrast between depth categories within a locality (Fig. 6) although ANOSIM test results revealed limited or no significant differences in community structure across all depths (Table 7). The range

of depths surveys (10 – 30 m) may simply be too narrow to exhibit any spatial effects. Lombard et al. (2004) classified this depth range as a single zone in the South African National Spatial Biodiversity Assessment thereby regarding it as a uniform depth component.

When assessing between-transect (replicate) variability, i.e. variability within a depth category, most replicates were relatively similar (<60% dissimilarity), with the exception of those at Port Edward (Fig 7). Transects were placed at least 5 m apart and differences among them reflect patchiness of the reefs and the disjunctive distribution of species.

4.1.4. Fauna versus Algae and Sand

Three main features emerged from a comparison of faunal, floral and sand cover. First in the north, fauna dominated over algae whereas the reverse was true in the south/central region (Fig. 8). Second, in the north, fauna were dominant in the shallows but were superseded by algae in deeper waters. Third, wherever sand cover was high, biotic cover was low. These patterns probably reflect interplays between light availability, nutrient supply and sand inundation, and both geography and depth will alter all three of these elements.

The high abundance of algae, particularly foliose algae (Fig. 4), at all depth categories in the south was an unpredicted and unexpected result given the limiting light availability on these reefs (personal observation). One of the main attributes of this region is the outflow from rivers, which limits light penetration but does, however,

introduce nutrients, thereby favouring algal growth. I had expected algae to be more prevalent in the north than in the south/central region because of the greater light penetration in the north, and to be more abundant in shallow than deeper waters. Neither expectation was realised.

In the northern region, higher coverage of fauna (mainly corals) was found at shallower depths (10 – 20 m), with algae dominating as depth increased. Depth has been identified as important in structuring communities and acts as an environmental stress gradient restricting certain abiotic factors such as light, water movement, wave action, nutrient availability, sedimentation and temperature (Garrabou et al., 2002). Post-settlement mortality also limits the distribution of benthic organisms and is a function of physical tolerance along environmental stress gradients (Garrabou et al., 2002). The reduction in coral cover on deeper reefs in the north may have been a response to these limiting factors and a consequence of the stress gradient.

Inshore-offshore differences in community composition along gradients of light, temperature, nutrients and organic matter have been described by McClanahan et al. (2002) in East Africa. They observed a decline in plant-animal symbiosis and an increase in abundance of algae and heterotrophic suspension feeders along a depth gradient and from oligotrophic to eutrophic (McClanahan et al., 2002). A similar trend and abundance in algal cover was observed on reefs in the northern region where the reduction of coral cover at deeper depths could have provided a greater area for algae to thrive.

Sedimentation is a key factor determining the distribution of benthic organisms and the general development of reef ecosystems (Hubbard, 1986; Rogers, 1990). The higher coral cover and generally well-developed reefs found in the northern region can be attributed to the distance from sources of river runoff and lower concentrations of water-borne debris and sand in overlying waters (Rogers, 1990; Riegl, 1995). The preference of soft coral for shallower depths (between 10 – 25 m, Fig. 6) (Riegl, 1995; Schleyer, 1999) subjects them to water movement and surge impacts from wave action, which may reduce settlement of sand.

Reefs in the central region displayed varying degrees of abundance of algae and fauna at different depths or along the environmental stress gradient. Faunal groups that occupied the central/southern regions were mainly suspension and demersal filter feeders rather than corals, since the high turbidity, reduction of light, reduced water temperature and nutrient influx all limit coral distribution (Yentsch et al., 2002). Light transparency is consistently lower in areas with high fluvial inflow as a result of higher concentrations of organic and inorganic particles in addition to a higher abundance of plankton in the water column (Cleary et al., 2005) and reefs in the central region are subjected to these conditions as a result of riverine and effluent influx.

Wherever sand cover was high, biotic cover was low. This was particularly evident at depths of 20 – 25 m (Fig. 8). The highest concentration of sand was found in the southern region, especially at Port Edward, a region of the coast characterised by numerous estuaries (~30 between Durban and Transkei, Begg, 1978) that churn out vast amounts of mud and silt. This intensifies turbidity levels, which in turn reduce the light available for photosynthesis by algae and symbiotic zooxanthellae found within the

tissues of corals, anemones and other benthic organisms. The consequence of this is the reduction of general reef metabolic activity (Barnes and Hughes, 1982). Rogers (1990) found that extreme levels of sediment can alter complex food webs by smothering and killing sponges and other reef organisms. These organisms serve as a food source for commercially vital fish and shellfish and the interaction between organisms and their habitat is affected (Rogers, 1990).

4.2. SPECIES DIVERSITY

Regional differences in species diversity (H'), evenness (J') and cumulative species richness (S) did exist, although they yielded no obvious patterns. Each locality displayed unique community structure. Overall, species diversity and evenness was highest in the shallowest depth zone (10 m) at two of the three northern localities, a pattern that is typical of light-dependant communities (Jackson, 1991; Mundy and Babcock, 1998; Yentsch et al., 2002). Cleary et al. (2005) also found species evenness in a coral community to be highest in the shallower depth zone i.e. down to 20 m, with a peak in species richness (H') between 10 and 20 m. Patterns in species diversity of coral reefs along a depth gradient have been observed by other studies although there have been exceptions. These patterns may be explained by the effects of both physical factors (light, temperature, nutrient and sediment transport) as well as biological factors (competition, predation, mutualism and bioturbation) (Glynn, 1976).

The coral reefs in the northern KZN region are at their southern-most distributional range and also occur in fairly deep water compared to other more typical tropical reef systems such as those in the Red Sea (Riegl, 1995). Huston (1985) observed an increase in species diversity with depth on tropical reefs near Eilat in the Red Sea (40 – 50 m)

and Discovery Bay, Jamaica (60 – 70 m). Several diversity indices (H' , J' , Simpson's D) displayed the same pattern of increase from the surface to a depth of 8 – 12 m and thereafter a relatively constant level down to 30 m (Huston, 1985). Corals in South Africa may have reached a limit with regards to temperature and light gradients (Jackson, 1991; Mundy and Babcock, 1998) and therefore do not occur in large abundances on deeper reefs (Fig. 8).

In the central/southern regions diversity, evenness and richness was highest between 15 – 25 m with the exception of Umhlali where diversity and evenness peaked around 10 m. Once again, variability in depth has been identified as a significant parameter in the distribution and diversity of various taxa, not just coral. The main contributing factors to the high diversity in these regions could be terrestrial runoff and high nutrient concentrations from riverine influx as well as the influences of a strong current despite reduced light transparency (Fabricius, 2005). The high species richness and array of species observed in these regions may be as a consequence of the adaptation of reef organisms to high turbidity levels and to the prevalent strong current flow in the south which may reduce sedimentation constraints.

5. CONCLUSIONS

Regional and local differences in community structure highlight the need for a more refined approach to conservation and management of reef ecosystems in KZN. The distinct biogeographic divide south of Cape Vidal, as identified for the intertidal ecosystem by Sink et al. (2005), has now also been established for subtidal reefs in the province. The distinction between reef communities in the northern versus south/central regions has emphasized the need for separate conservation management plans for these areas. Knowledge of the biogeographic distribution and boundaries of communities is crucial if representative habitats within each biogeographic zone are to be adequately conserved.

The fluctuating abundances and diversity of fauna and algae at different depth categories differed also between regions. Although the shallower depth groups appeared more diverse in some regions, there were no significant differences among depth zones and they should not be considered separately for conservation. Linkages and oceanic processes between depth categories still remain unexplored and therefore can not be ignored. It is also impractical to manage depth zones independently since it is easier to protect entire stretches of coastline that incorporate all depth zones than to afford separate conservation measures to different depth zones.

Currently protection of subtidal habitats in KZN is restricted to the northern ~150 km of the coast, which incorporates the northern coral reef region. Subtidal habitats are not protected at all in the central region. In the south, a 20-km stretch of coastline protects the Aliwal Shoal reef, and the tiny Trafalgar Marine Reserve is encompassed in a 2 km strip of coastline stretching 500 m out to sea. Varying degrees of extractive and non-

extractive uses such as pelagic fishing, snorkelling and scuba diving are allowed in certain areas within these MPAs. The remaining reef ecosystems in the province remain subjected to immense pressure. Protection in the form of a marine reserve would be particularly beneficial in the central region where extensive commercial and recreational fishing and trawling is carried out. This would allow comparisons between exploited and unexploited reefs to be made in order to determine the ecological state of the reef environment and to also provide a benchmark for rehabilitation requirements.

The findings of this survey will be used as part of the systematic conservation planning programme for the marine environment in KZN. This initiative undertakes to spatially map marine biodiversity features and to set targets for their conservation. The process identifies gaps in biodiversity conservation and focuses attention on those areas that require urgent management action if their target is to be reached.

This initial study has provided a snapshot description of benthic community structure of reef in the province and stresses the need for further studies to better understand this dynamic ecosystem. Many reef ecosystems are currently under threat and experience no protection from extractive use and anthropogenic pressures. Protection can be afforded in the form of marine protected area status, a means of marine ecosystem management already used extensively in the country. Monitoring of physical and environmental elements needs to be put in place to establish spatial and temporal trends in sea-surface temperature changes, turbidity and nutrient levels, current velocity and light intensity. These data coupled with more detailed biological surveys of species cover and ecological interactions would provide a cohesive understanding of the subtidal ecosystem and allow for better management and conservation.

6. REFERENCES

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APPENDIX 2

Results of simpler analysis of dissimilarities between localities.

Group		Kosi Bay	Sodwana Bay	Average Diss. = 62.9%
Species	Functional Group	Av.Abund	Av.Abund	Av.Diss
Sand	Sand	12.78	1.39	2.8
Low mix turf	Algae	19.13	28.76	2.51
<i>Diplosoma sp</i>	Ascidian	5.87	0.24	2.43
<i>Platygyra sp</i>	Hard Coral	1.08	2.37	2.43
<i>Policarpa sp</i>	Ascidian	0	1.88	2.21
<i>Echinopora hirsutissima</i>	Hard Coral	0.36	3.22	2.14
<i>Montipora sp</i>	Hard Coral	3.93	10.43	2.12
<i>Sarcophyton sp</i>	Soft Coral	4.23	2.83	2.09
<i>Favites sp</i>	Hard Coral	3.76	1.1	2
Group		Kosi Bay	Cape St Lucia	Average Diss. = 93.5%
Species	Functional Group	Av.Abund	Av.Abund	Av.Diss
<i>Simularia sp</i>	Soft Coral	10.17	0	4.25
<i>Lobophytum sp</i>	Soft Coral	9.43	0	4.2
Low mix turf	Algae	19.13	22.12	3.57
Sand	Sand	12.78	2.53	3.06
<i>Diplosoma sp</i>	Ascidian	5.87	0	2.81
<i>Montipora sp</i>	Hard Coral	3.93	0.08	2.78
Hydroid unid.	Hydroid	0.25	3.62	2.71
<i>Favites sp</i>	Hard Coral	3.76	0	2.29
Worm unid.	Worm	0	13.63	2.22
<i>Psammoclema sp</i>	Sponge	0	3.76	2.04
Group		Kosi Bay	Cape Vidal	Average Diss. = 63.2%
Species	Functional Group	Av.Abund	Av.Abund	Av.Diss
Sand	Sand	12.78	0.64	3.25
Low mix turf	Algae	19.13	25.77	3.05
<i>Echinopora hirsutissima</i>	Hard Coral	0.36	7.42	2.75
<i>Diplosoma sp</i>	Ascidian	5.87	0.15	2.74
Rock	Abiotic substrate	6.78	6.49	2.54
<i>Sarcophyton sp</i>	Soft Coral	4.23	3.53	2.44
<i>Montipora sp</i>	Hard Coral	3.93	9.12	2.29
Group		Kosi Bay	Prince's Grant	Average Diss. = 88.2%
Species	Functional Group	Av.Abund	Av.Abund	Av.Diss
<i>Simularia sp</i>	Soft Coral	10.17	0	4.71
<i>Lobophytum sp</i>	Soft Coral	9.43	0	4.67
Sand	Sand	12.78	20.65	3.88
Low mix turf	Algae	19.13	33.16	3.38
<i>Montipora sp</i>	Hard Coral	3.93	0	3.2
<i>Diplosoma sp</i>	Ascidian	5.87	0	3.1
<i>Favites sp</i>	Hard Coral	3.76	0	2.53
<i>Sarcophyton sp</i>	Soft Coral	4.23	0	2.12
Group		Kosi Bay	Umlhali	Average Diss. = 85.7%
Species	Functional Group	Av.Abund	Av.Abund	Av.Diss
<i>Lobophytum sp</i>	Soft Coral	9.43	0	4.28
<i>Simularia sp</i>	Soft Coral	10.17	0.5	4.1
Sand	Sand	12.78	15.66	3.18
<i>Montipora sp</i>	Hard Coral	3.93	0	2.94
Rock	Abiotic substrate	6.78	9.67	2.92
<i>Acabaria rubra</i>	Gorgonian	0	4.87	2.87
<i>Diplosoma sp</i>	Ascidian	5.87	0	2.86
Low mix turf	Algae	19.13	25.3	2.74
Group		Kosi Bay	Umkomaas	Average Diss. = 87.8%
Species	Functional Group	Av.Abund	Av.Abund	Av.Diss
<i>Simularia sp</i>	Soft Coral	10.17	0	4.69
<i>Lobophytum sp</i>	Soft Coral	9.43	0	4.64
<i>Dictyota sp</i>	Algae	0	13.37	4.35
Sand	Sand	12.78	10.23	3.47
Low mix turf	Algae	19.13	24	3.27
<i>Montipora sp</i>	Hard Coral	3.93	0	3.19
<i>Diplosoma sp</i>	Ascidian	5.87	0	3.09
Group		Kosi Bay	Sizela	Average Diss. = 89.3%
Species	Functional Group	Av.Abund	Av.Abund	Av.Diss
<i>Simularia sp</i>	Soft Coral	10.17	0	4.14

<i>Lobophytum sp</i>	Soft Coral	9.43	0	4.09
Sand	Sand	12.78	3.22	3.02
<i>Montipora sp</i>	Hard Coral	3.93	0	2.81
<i>Diplosoma sp</i>	Ascidian	5.87	0	2.74
Coralline algae unid.	Algae	0	9.76	2.74
Low mix turf	Algae	19.13	29.19	2.37
<i>Favites sp</i>	Hard Coral	3.76	0	2.24
<i>Placospongia sp</i>	Sponge	0	3.6	2.18
<i>Suberites sp</i>	Sponge	0	3.2	2.12
Group		Kosi Bay	Port Edward	Average Diss. = 89.1%
Species	Functional Group	Av.Abund	Av.Abund	Av.Diss
<i>Simularia sp</i>	Soft Coral	10.17	0	4.28
<i>Lobophytum sp</i>	Soft Coral	9.43	0	4.23
Sand	Sand	12.78	29.6	3.47
Low mix turf + Sand	Mixed substrate	0	13.25	3.3
<i>Amphiroa bowerbankii</i>	Algae	0	7.16	3.12
Red foliose algae unid.	Algae	0	10.49	2.98
<i>Montipora sp</i>	Hard Coral	3.93	0	2.9
Low mix turf	Algae	19.13	6.81	2.9
Group		Sodwana Bay	Cape Vidal	Average Diss. = 55.4%
Species	Functional Group	Av.Abund	Av.Abund	Av.Diss
Low mix turf	Algae	28.76	25.77	2.4
<i>Echinopora hirsutissima</i>	Hard Coral	3.22	7.42	2.38
<i>Sarcophyton sp</i>	Soft Coral	2.83	3.53	2.19
<i>Montipora sp</i>	Hard Coral	10.43	9.12	2.17
<i>Platygyra sp</i>	Hard Coral	2.37	1.38	1.81
<i>Policarpa sp</i>	Ascidian	1.88	2.39	1.79
<i>Galaxea sp</i>	Hard Coral	1.75	0.53	1.78
<i>Favites sp</i>	Hard Coral	1.1	2.63	1.77
<i>Dendronephthya sp</i>	Soft Coral	1.74	0.55	1.75
Group		Sodwana Bay	Cape St Lucia	Average Diss. = 91.9%
Species	Functional Group	Av.Abund	Av.Abund	Av.Diss
<i>Lobophytum sp</i>	Soft Coral	9.97	0	4.23
<i>Simularia sp</i>	Soft Coral	9.71	0	4.18
Low mix turf	Algae	28.76	22.12	3.38
<i>Montipora sp</i>	Hard Coral	10.43	0.08	3.3
<i>Platygyra sp</i>	Hard Coral	2.37	0	2.55
<i>Favia sp</i>	Hard Coral	1.76	0	2.38
Hydroid unid.	Hydroid	0.33	3.62	2.36
<i>Policarpa sp</i>	Ascidian	1.88	0	2.15
<i>Echinopora hirsutissima</i>	Hard Coral	3.22	0	2.11
Worm unid.	Worm	0	13.63	2.04
Group		Sodwana Bay	Prince's Grant	Average Diss. = 86.9%
Species	Functional Group	Av.Abund	Av.Abund	Av.Diss
<i>Lobophytum sp</i>	Soft Coral	9.97	0	4.64
<i>Simularia sp</i>	Soft Coral	9.71	0	4.59
<i>Montipora sp</i>	Hard Coral	10.43	0	3.76
Sand	Sand	1.39	20.65	3.25
<i>Platygyra sp</i>	Hard Coral	2.37	0	2.8
<i>Favia sp</i>	Hard Coral	1.76	0	2.61
Low mix turf	Algae	28.76	33.16	2.41
<i>Echinopora hirsutissima</i>	Hard Coral	3.22	0	2.32
Group		Sodwana Bay	Umhlali	Average Diss. = 86.1%
Species	Functional Group	Av.Abund	Av.Abund	Av.Diss
<i>Lobophytum sp</i>	Soft Coral	9.97	0	4.31
<i>Simularia sp</i>	Soft Coral	9.71	0.5	3.99
<i>Montipora sp</i>	Hard Coral	10.43	0	3.49
Sand	Sand	1.39	15.66	3.14
<i>Acabaria rubra</i>	Gorgonian	0	4.87	2.63
<i>Platygyra sp</i>	Hard Coral	2.37	0	2.6
<i>Favia sp</i>	Hard Coral	1.76	0	2.43
Rock	Abiotic substrate	0	9.67	2.35
Hydroid unid.	Hydroid	0.33	4.23	2.18
Group		Sodwana Bay	Umkomaas	Average Diss. = 89.4%
Species	Functional Group	Av.Abund	Av.Abund	Av.Diss

<i>Lobophytum sp</i>	Soft Coral	9.97	0	4.63
<i>Simularia sp</i>	Soft Coral	9.71	0	4.57
<i>Dictyota sp</i>	Algae	0	13.37	3.95
<i>Montipora sp</i>	Hard Coral	10.43	0	3.75
Wall sponge unid.	Sponge	0	3.37	2.82
<i>Platygyra sp</i>	Hard Coral	2.37	0	2.79
Sand	Sand	1.39	10.23	2.74
<i>Favia sp</i>	Hard Coral	1.76	0	2.6
Group		Sodwana Bay	Sizela	Average Diss. = 86.9%
Species	Functional Group	Av.Abund	Av.Abund	Av.Diss
<i>Lobophytum sp</i>	Soft Coral	9.97	0	4.13
<i>Simularia sp</i>	Soft Coral	9.71	0	4.09
<i>Montipora sp</i>	Hard Coral	10.43	0	3.35
Coralline algae unid.	Algae	0	9.76	2.52
<i>Platygyra sp</i>	Hard Coral	2.37	0	2.49
<i>Favia sp</i>	Hard Coral	1.76	0	2.33
<i>Echinopora hirsutissima</i>	Hard Coral	3.22	0	2.06
<i>Placospongia sp</i>	Sponge	0	3.6	2.01
<i>Ircinia sp</i>	Sponge	0	1.66	1.94
<i>Suberites sp</i>	Sponge	0.13	3.2	1.92
Group		Sodwana Bay	Port Edward	Average Diss. = 90.1%
Species	Functional Group	Av.Abund	Av.Abund	Av.Diss
<i>Lobophytum sp</i>	Soft Coral	9.97	0	4.25
<i>Simularia sp</i>	Soft Coral	9.71	0	4.2
Sand	Sand	1.39	29.6	3.99
<i>Montipora sp</i>	Hard Coral	10.43	0	3.44
Low mix turf + Sand	Mixed substrate	3.43	13.25	3.04
<i>Amphiroa bowerbankii</i>	Algae	0	7.16	2.84
Low mix turf	Algae	28.76	6.81	2.8
<i>Halimeda sp</i>	Algae	0	3.38	2.74
Group		Cape Vidal	Cape St Lucia	Average Diss. = 93.7%
Species	Functional Group	Av.Abund	Av.Abund	Av.Diss
<i>Lobophytum sp</i>	Soft Coral	12.79	0	4.72
<i>Simularia sp</i>	Soft Coral	9.23	0	4.15
Low mix turf	Algae	25.77	22.12	3.64
<i>Montipora sp</i>	Hard Coral	9.12	0.08	3.54
Hydroid unid.	Hydroïd	0	3.62	2.77
<i>Echinopora hirsutissima</i>	Hard Coral	7.42	0	2.71
<i>Favites sp</i>	Hard Coral	2.63	0	2.67
<i>Sarcophyton sp</i>	Soft Coral	3.53	0	2.2
Worm unid.	Worm	0	13.63	2.2
Group		Cape Vidal	Prince's Grant	Average Diss. = 90.0%
Species	Functional Group	Av.Abund	Av.Abund	Av.Diss
<i>Lobophytum sp</i>	Soft Coral	12.79	0	5.23
<i>Simularia sp</i>	Soft Coral	9.23	0	4.6
<i>Montipora sp</i>	Hard Coral	9.12	0	4.06
Sand	Sand	0.64	20.65	3.48
Low mix turf	Algae	25.77	33.16	3.17
<i>Echinopora hirsutissima</i>	Hard Coral	7.42	0	2.99
<i>Favites sp</i>	Hard Coral	2.63	0	2.96
<i>Sarcophyton sp</i>	Soft Coral	3.53	0	2.43
Group		Cape Vidal	Umhlali	Average Diss. = 88.8%
Species	Functional Group	Av.Abund	Av.Abund	Av.Diss
<i>Lobophytum sp</i>	Soft Coral	12.79	0	4.82
Sand	Sand	0.64	15.66	4.09
<i>Simularia sp</i>	Soft Coral	9.23	0.5	4
<i>Montipora sp</i>	Hard Coral	9.12	0	3.74
Rock	Abiotic substrate	6.49	9.67	2.89
<i>Acabaria rubra</i>	Gorgonian	0	4.87	2.84
<i>Echinopora hirsutissima</i>	Hard Coral	7.42	0	2.76
<i>Favites sp</i>	Hard Coral	2.63	0	2.73
Group		Cape Vidal	Umkomaas	Average Diss. = 91.2%
Species	Functional Group	Av.Abund	Av.Abund	Av.Diss
<i>Lobophytum sp</i>	Soft Coral	12.79	0	5.21
<i>Simularia sp</i>	Soft Coral	9.23	0	4.57

<i>Dictyota sp</i>	Algae	0	13.37	4.3
<i>Montipora sp</i>	Hard Coral	9.12	0	4.04
Low mix turf	Algae	25.77	24	3.21
Sand	Sand	0.64	10.23	3.1
Wall sponge unid.	Sponge	0	3.37	3.07
Group		Cape Vidal	Sizela	Average Diss. = 89.4%
Species	Functional Group	Av.Abund	Av.Abund	Av.Diss
<i>Lobophytum sp</i>	Soft Coral	12.79	0	4.61
<i>Simularia sp</i>	Soft Coral	9.23	0	4.04
<i>Montipora sp</i>	Hard Coral	9.12	0	3.58
Coralline algae unid.	Algae	0	9.76	2.71
<i>Echinopora hirsutissima</i>	Hard Coral	7.42	0	2.64
<i>Favites sp</i>	Hard Coral	2.63	0	2.6
<i>Placospongia sp</i>	Sponge	0	3.6	2.16
Low mix turf	Algae	25.77	29.19	2.16
<i>Sarcophyton sp</i>	Soft Coral	3.53	0.56	2.15
<i>Favia sp</i>	Hard Coral	2.49	0	2.14
Group		Cape Vidal	Port Edward	Average Diss. = 93.3%
Species	Functional Group	Av.Abund	Av.Abund	Av.Diss
Sand	Sand	0.64	29.6	5.19
<i>Lobophytum sp</i>	Soft Coral	12.79	0	4.75
<i>Simularia sp</i>	Soft Coral	9.23	0	4.17
<i>Montipora sp</i>	Hard Coral	9.12	0	3.69
Low mix turf + Sand	Mixed substrate	0	13.25	3.26
Low mix turf	Algae	25.77	6.81	3.21
<i>Amphiroa bowerbankii</i>	Algae	0	7.16	3.08
<i>Halimeda sp</i>	Algae	0	3.38	2.97
Group		Cape St Lucia	Prince's Grant	Average Diss. = 87.1%
Species	Functional Group	Av.Abund	Av.Abund	Av.Diss
Low mix turf	Algae	22.12	33.16	4.09
Sand	Sand	2.53	20.65	3.48
Hydroid unid.	Hydroid	3.62	1.27	2.52
Worm unid.	Worm	13.63	0	2.39
<i>Psammoclema sp</i>	Sponge	3.76	0	2.2
Hydroid complex	Hydroid	1.72	0	1.93
Gorgonian red unid.	Gorgonian	0.17	1.93	1.9
<i>Hymeniacidon perlevis</i>	Sponge	2.45	0	1.86
<i>Axinella sp</i>	Sponge	0.51	2.05	1.81
Gorgonian orange unid.	Gorgonian	0.65	1.35	1.81
<i>Ircinia arenosa</i>	Sponge	0.33	1.62	1.69
Encr. coralline unid.	Algae	0.13	3.48	1.64
Group		Cape St Lucia	Umhlati	Average Diss. = 84.2%
Species	Functional Group	Av.Abund	Av.Abund	Av.Diss
Low mix turf	Algae	22.12	25.3	3.6
Sand	Sand	2.53	15.66	3.47
<i>Acabaria rubra</i>	Gorgonian	0.65	4.87	2.57
Rock	Abiotic substrate	0	9.67	2.51
Hydroid unid.	Hydroid	3.62	4.23	2.22
Worm unid.	Worm	13.63	0	2.21
<i>Psammoclema sp</i>	Sponge	3.76	0	2.02
<i>Schizoretepora tessellata</i>	Bryozoa	3.78	1.48	1.98
<i>Mycale (Carmia) toxifera</i>	Sponge	0	3.91	1.93
Hydroid complex	Hydroid	1.72	0	1.78
<i>Hymeniacidon perlevis</i>	Sponge	2.45	0	1.73
Group		Cape St Lucia	Umkomaas	Average Diss. = 90.9%
Species	Functional Group	Av.Abund	Av.Abund	Av.Diss
<i>Dictyota sp</i>	Algae	0	13.37	4.22
Low mix turf	Algae	22.12	24	3.89
Wall sponge unid.	Sponge	0	3.37	3.02
Sand	Sand	2.53	10.23	2.99
Hydroid unid.	Hydroid	3.62	1.25	2.85
Worm unid.	Worm	13.63	0.33	2.55
Coralline algae unid.	Algae	0	3.73	2.51
<i>Vidalia serrata</i>	Algae	0	3.83	2.46
<i>Psammoclema sp</i>	Sponge	3.76	0	2.19

Brown foliose algae unid.	Algae	0	4.18	2.04
Group		Cape St Lucia	Sizela	Average Diss. = 86.8%
Species	Functional Group	Av.Abund	Av.Abund	Av.Diss
Low mix turf	Algae	22.12	29.19	3.49
Coralline algae unid.	Algae	0	9.76	2.67
<i>Placospongia sp</i>	Sponge	0	3.6	2.13
Worm unid.	Worm	13.63	0	2.11
<i>Suberites sp</i>	Sponge	0	3.2	2.06
<i>Ircinia sp</i>	Sponge	0.33	1.66	1.97
<i>Psammoclema sp</i>	Sponge	3.76	0	1.93
Sand	Sand	2.53	3.22	1.9
Hydroid unid.	Hydroid	3.62	1.91	1.86
<i>Hymeniacedon perlevis</i>	Sponge	2.45	1.33	1.83
<i>Styopodium zonale</i>	Algae	0	5.49	1.79
<i>Isodictia sp</i>	Sponge	0	1.8	1.75
Hydroid complex	Hydroid	1.72	0	1.71
Group		Cape St Lucia	Port Edward	Average Diss. = 89.7%
Species	Functional Group	Av.Abund	Av.Abund	Av.Diss
Sand	Sand	2.53	29.6	4.33
Low mix turf	Algae	22.12	6.81	3.34
Low mix turf + Sand	Mixed substrate	0	13.25	3.21
<i>Amphiroa bowerbankii</i>	Algae	0	7.16	3.03
<i>Halimeda sp</i>	Algae	0	3.38	2.92
Red foliose algae unid.	Algae	0	10.49	2.9
Hydroid unid.	Hydroid	3.62	0.05	2.64
Worm unid.	Worm	13.63	0	2.18
Hydroid complex	Hydroid	0.17	2.3	2.14
<i>Psammoclema sp</i>	Sponge	3.76	0.66	1.98
Group		Prince's Grant	Umhlali	Average Diss. = 74.7%
Species	Functional Group	Av.Abund	Av.Abund	Av.Diss
Sand	Sand	20.65	15.66	3.91
Low mix turf	Algae	33.16	25.3	2.81
Rock	Abiotic substrate	0	9.67	2.8
<i>Acabaria rubra</i>	Gorgonian	1.33	4.87	2.76
Hydroid unid.	Hydroid	1.27	4.23	2.52
<i>Mycale (Carmia) toxifera</i>	Sponge	2.08	3.91	2.32
Encr. coralline unid.	Algae	3.48	3.78	2.25
<i>Ircinia arenosa</i>	Sponge	1.62	1.04	1.98
Gorgonian red unid.	Gorgonian	1.93	0	1.95
Group		Prince's Grant	Umkomaas	Average Diss.= 83.6%
Species	Functional Group	Av.Abund	Av.Abund	Av.Diss
<i>Dictyota sp</i>	Algae	0	13.37	4.72
Sand	Sand	20.65	10.23	4.08
Low mix turf	Algae	33.16	24	3.43
Wall sponge unid.	Sponge	0.13	3.37	3.24
Coralline algae unid.	Algae	0	3.73	2.8
<i>Vidalia serrata</i>	Algae	0	3.83	2.75
Brown foliose algae unid.	Algae	0	4.18	2.3
<i>Mycale (Carmia) toxifera</i>	Sponge	2.08	3.23	2.24
Group		Prince's Grant	Sizela	Average Diss. = 81.0%
Species	Functional Group	Av.Abund	Av.Abund	Av.Diss
Sand	Sand	20.65	3.22	3.38
Coralline algae unid.	Algae	0	9.76	2.93
<i>Placospongia sp</i>	Sponge	0	3.6	2.34
<i>Suberites sp</i>	Sponge	0	3.2	2.27
Hydroid unid.	Hydroid	1.27	1.91	2.09
<i>Ircinia sp</i>	Sponge	0.53	1.66	2.09
Low mix turf	Algae	33.16	29.19	2.08
Encr. coralline unid.	Algae	3.48	3	2.08
<i>Styopodium zonale</i>	Algae	0	5.49	1.99
<i>Amphiroa bowerbankii</i>	Algae	1.67	5.39	1.96
<i>Isodictia sp</i>	Sponge	0	1.8	1.92
Group		Prince's Grant	Port Edward	Average Diss. = 84.04%
Species	Functional Group	Av.Abund	Av.Abund	Av.Diss
Sand	Sand	20.65	29.6	4.15

Low mix turf	Algae	33.16	6.81	3.72
Low mix turf + Sand	Mixed substrate	1.83	13.25	3.53
<i>Amphiroa bowerbankii</i>	Algae	1.67	7.16	3.32
<i>Halimeda sp</i>	Algae	0	3.38	3.25
Red foliose algae unid.	Algae	0	10.49	3.21
Hydroid complex	Hydroid	0	2.3	2.42
Gorgonian red unid.	Gorgonian	1.93	0	1.93
Group		Umhlali	Umkomaas	Average Diss. = 81.6%
Species	Functional Group	Av.Abund	Av.Abund	Av.Diss
<i>Dictyota sp</i>	Algae	0	13.37	4.31
Sand	Sand	15.66	10.23	3.4
<i>Acabaria rubra</i>	Gorgonian	4.87	0	3.08
Wall sponge unid.	Sponge	0	3.37	3.08
Rock	Abiotic substrate	9.67	4.53	3.02
Low mix turf	Algae	25.3	24	2.86
Hydroid unid.	Hydroid	4.23	1.25	2.61
Coralline algae unid.	Algae	0	3.73	2.56
Group		Umhlali	Sizela	Average Diss. = 78.2 %
Species	Functional Group	Av.Abund	Av.Abund	Av.Diss
Sand	Sand	15.66	3.22	3.44
Coralline algae unid.	Algae	0	9.76	2.72
<i>Acabaria rubra</i>	Gorgonian	4.87	0.33	2.62
Rock	Abiotic substrate	9.67	0	2.44
<i>Ircinia sp</i>	Sponge	2.46	1.66	2.17
<i>Placospongia sp</i>	Sponge	0	3.6	2.17
<i>Suberites sp</i>	Sponge	0	3.2	2.1
Hydroid unid.	Hydroid	4.23	1.91	2.09
<i>Mycale (Carmia) toxifera</i>	Sponge	3.91	0.94	1.99
<i>Amphiroa bowerbankii</i>	Algae	1.62	5.39	1.86
Group		Umhlali	Port Edward	Average Diss. = 81.7%
Species	Functional Group	Av.Abund	Av.Abund	Av.Diss
Low mix turf + Sand	Mixed substrate	0	13.25	3.27
<i>Halimeda sp</i>	Algae	0	3.38	2.98
<i>Amphiroa bowerbankii</i>	Algae	1.62	7.16	2.97
Red foliose algae unid.	Algae	0	10.49	2.96
Low mix turf	Algae	25.3	6.81	2.85
Sand	Sand	15.66	29.6	2.71
<i>Acabaria rubra</i>	Gorgonian	4.87	0.6	2.64
Rock	Abiotic substrate	9.67	0.49	2.58
Hydroid unid.	Hydroid	4.23	0.05	2.37
Group		Umkomaas	Sizela	Average Diss. = 79.3%
Species	Functional Group	Av.Abund	Av.Abund	Av.Diss
<i>Dictyota sp</i>	Algae	13.37	0.04	3.98
Sand	Sand	10.23	3.22	2.95
Wall sponge unid.	Sponge	3.37	0	2.94
Coralline algae unid.	Algae	3.73	9.76	2.83
<i>Vidalia serrata</i>	Algae	3.83	0	2.39
<i>Placospongia sp</i>	Sponge	0.67	3.6	2.31
Low mix turf	Algae	24	29.19	2.3
Hydroid unid.	Hydroid	1.25	1.91	2.3
<i>Suberites sp</i>	Sponge	0.17	3.2	2.25
Group		Umkomaas	Port Edward	Average Diss. = 87.2 %
Species	Functional Group	Av.Abund	Av.Abund	Av.Diss
<i>Dictyota sp</i>	Algae	13.37	0	4.25
Sand	Sand	10.23	29.6	3.86
Low mix turf + Sand	Mixed substrate	0.9	13.25	3.49
Low mix turf	Algae	24	6.81	3.39
<i>Amphiroa bowerbankii</i>	Algae	0	7.16	3.35
<i>Halimeda sp</i>	Algae	0	3.38	3.23
Red foliose algae unid.	Algae	0	10.49	3.2
Wall sponge unid.	Sponge	3.37	0	3.04
Group		Sizela	Port Edward	Average Diss. = 85.8%
Species	Functional Group	Av.Abund	Av.Abund	Av.Diss
Sand	Sand	3.22	29.6	4.21
Low mix turf + Sand	Mixed substrate	0	13.25	3.13
Low mix turf	Algae	29.19	6.81	2.88

<i>Halimeda sp</i>	Algae	0	3.38	2.85
Red foliose algae unid.	Algae	0	10.49	2.83
<i>Amphiroa bowerbankii</i>	Algae	5.39	7.16	2.79
Coralline algae unid.	Algae	9.76	0	2.68
<i>Placospongia sp</i>	Sponge	3.6	0	2.14
Hydroid complex	Hydroid	0	2.3	2.13
<i>Suberites sp</i>	Sponge	3.2	0	2.07