BIOGEOGRAPHY AND POTENTIAL FACTORS REGULATING SHALLOW SUBTIDAL REEF COMMUNITIES IN THE WESTERN INDIAN OCEAN

by

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DECLARATION

This thesis documents original research, undertaken in the Zoology Department, University of Cape Town between 2004 and 2009. It has not been submitted in whole, or in part for a degree at any other university. Most of the data presented here are original and any sources are fully acknowledged. Any uncited interpretations are my own and any assistance I have received is also fully acknowledged.

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Date

This thesis is dedicated to my family and to those people who showed confidence and faith in my abilities during this period

To my brother David, for being a brother I am extremely proud of and admire

My mother Ingrid, who opened my eyes to the intrinsic natural beauty in nature without the need to measure everything

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TABLE OF CONTENTS

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ABSTRACT

The biogeography and ecology of benthic shallow subtidal reef communities in the western Indian Ocean is poorly known, particularly in north-eastern South Africa and southern Mozambique. This thesis uses quantitative information to resolve biogeographic patterns, define reef community types, elucidate potential abiotic determinants of community composition, and evaluate whether subsidies of riverine-derived particulate organic matter (POM) support filter-feeder biomass and drive biogeographic patterns.

A large-scale biogeographic analysis was conducted using quantitative biomass data derived from 55 shallow subtidal reefs spanning five countries in the western Indian Ocean. Two statistically distinct marine provinces, Tropical Indo-West Pacific and Subtropical Natal, were recognised by differences in community composition and separated by a biogeographic break in the vicinity of Cape Vidal, South Africa. The biogeographic break took the form of a transitional or overlap area corresponding in location to the Delagoa Bioregion, one of three bioregions also revealed by post-hoc analyses. Significant differences in total average biomass and trophic structure were evident among bioregions, with a number of inter-bioregional trends in trophic groups being apparent.

In total, 12 reef community types were recognised, based on similarity profile permutation tests. Most reefs in the Subtropical Natal Bioregion were dominated by a community type characterised by a high biomass of the filter-feeding ascidian *Pyura stolonifera* and various species of articulated coralline algae. In the Delagoa Overlap Bioregion, a comparatively high diversity of community types was defined, many dominated by algal turf, *P. stolonifera* and various Alcyonacea and Scleractinia. Further north, *P. stolonifera* diminished and the contributions of Scleractinia, especially *Porites* spp., *Pocillopora* spp. and *Galaxea* spp. increased. Many of these community types are not represented within protected area networks, particularly those in southern Mozambique.

When the biomass data were correlated with nine abiotic variables, likely determinants of community composition emerged at both inter- and intra-regional scales. Sea surface temperature, significant wave height, chlorophyll-*a* and suspended inorganic sediment were the variables highly correlated with community composition and therefore most likely to drive biogeographic differences. Within each bioregion, different sets of abiotic variables were found to be important in driving community differences among sites, including turbidity, chlorophyll-*a*, reef susceptibility to sand inundation, reef heterogeneity and sea surface temperature. Striking differences in the oceanographic conditions of bioregions were evident, especially between Subtropical Natal and Delagoa Overlap bioregions. In particular, the strong influence of wave height emerged as a novel and unexpected correlate at a biogeographic scale.

These differences initiated a trophic study conducted in the Subtropical Natal Bioregion, aimed at determining the importance of riverine-derived POM subsidies in supporting the high filter-feeder biomass in this bioregion. Using carbon, nitrogen and sulphur isotopes and a three-source Bayesian mixing model to calculate proportional contributions, I determined that marine-derived POM formed the bulk of the diets of four species of filter-feeders, but the assimilation of riverine-derived POM was nevertheless notable, ranging from 8 to 33 %. I concluded that riverine POM is likely to play an important but secondary role to factors such as increased levels of turbidity and productivity in explaining the high filter-feeder biomass in the Subtropical Natal Bioregion.

These findings provide the first evidence of riverine-inshore-pelagic coupling in filter-feeder communities in this bioregion, and throw light on the factors linked to large-scale biogeographic patterns.

CHAPTER 1

INTRODUCTION

This thesis focuses on three central issues: the identification of biogeographic patterns, the description of community composition at various scales, and the identification of factors that are likely to regulate community composition and influence biogeographic patterns.

Biological patterns can be quantified and analysed at a variety of spatial scales ranging from a few centimetres (Bourget *et al.* 1994; Archambault & Bourget 1996), to thousands of kilometres (Briggs 1974; van den Hoek 1984; Rex *et al.* 1993; Bolton 1994). Studying patterns is an imperative precursor providing the context and foundation for research on mechanisms and processes (Underwood *et al.* 2000), and the foundation of this thesis is the detection of both large-scale and small-scale patterns in shallow reef community composition on the east coast of Africa, and the advancement of explanations for those patterns.

Biogeography may be defined as the study of past and present organismal distribution patterns (Brown & Gibson 1983; Myers & Giller 1988). Distribution patterns and ranges of organisms are widely accepted as being non-random (Ball 1990). The processes that determine and influence distributions of biota have been recognized as being both historical and ecological (Ball 1990), and biogeography can be broadly divided into these two sub-disciplines.

My thesis deals with the east coast of Africa, part of which is an important constituent of the world's largest marine biogeographic province, the Tropical Indo-Pacific (Briggs 1974; Sheppard 1987; Adey & Steneck 2001). South of this province, on the east coast of South Africa, lies the Subtropical Natal Province (Emanuel *et al.* 1992; Bustamante & Branch 1996a; Sink *et al.* 2005), but the precise boundary is poorly resolved, and previous work to this end has concentrated on intertidal rocky shores, largely ignoring the shallow subtidal reefs that are central to my study.

Many western Indian Ocean biogeographic studies have focused on particular taxonomic groups, for example seaweeds (Farrell *et al.* 1993; Farrell *et al.* 1994; Leliaert *et al.* 2001; Bolton *et al.* 2004; Evans 2005), Porifera (Samaai 2006); Hydroida (Millard 1978), Scleractinia (Sheppard 1987, 1998; McClanahan *et al.* 2007), Octocorallia (Williams 1992; Benayahu *et al.* 2003), Actiniaria & Corallimorpharia (Acuna & Griffiths 2004), opisthobranch gastropods (Gosliner & Draheim 1996), Holothuroidea (Thander 1989; Samyn & Thander 2003; Thander & Samyn 2004; Samyn & Tallon 2005), Ascidiacea (Primo & Vázquez 2004) and Pisces (Turpie *et al.* 2000).

Other studies have adopted a more holistic approach encompassing a large variety of organisms across a number of Phyla (Stephenson 1947; Jackson 1976; Emanuel *et al.* 1992; Bustamante 1994; Bustamante & Branch 1996a; Bustamante *et al.* 1997; Richmond 1999a; Sink 2001; Sink *et al.* 2005; Lawrence 2005), with reviews by Stephenson & Stephenson (1972) and Brown & Jarman (1978). However, the majority of these studies have been confined to the intertidal zone in the southern part of the region with relatively few large-scale accounts of work being done north of the South African east coast (Field & Griffiths 1991), where the taxonomy of many invertebrate taxa remains a challenge (Richmond 1999b). In particular, knowledge regarding shallow subtidal reef systems is deficient, especially off the north-east coast of South Africa and southern Mozambique.

According to Bolton *et al.* (2004) biogeographic marine provinces have historically been defined by two main criteria:

1. the existence of a consistent biota that is separated by biotic discontinuities from other adjacent coastlines and regions with different biota and
2. the presence of a large proportion of endemic biota in a region.

Because most previous biogeographic studies in the region have used only discontinuity (criterion 1) to define the limits of biogeographic provinces, I employed the same approach given the uncertainty surrounding the status of endemic species associated with shallow subtidal reefs.

At a smaller spatial scale, within marine provinces, the concept of ‘bioregions’ has been introduced (Lombard *et al.* 2004; Spalding *et al.* 2007). Bioregions are defined as 'subdivisions' within marine provinces that are characterised by a relatively homogenous species composition, clearly distinct from adjacent systems (Spalding *et al.* 2007) but traversing different habitat types.

Myers & Giller (1988) have identified three levels of ecological biogeographic pattern that contextualize the work presented in this thesis. Primary biogeographic patterns are simply the non-random spatial distributions of biota as a result of the influence of large-scale environmental variables. Secondary patterns are those patterns deduced from a collection of characteristics pertaining to a suite of species or taxa, e.g., species richness, evenness, endemicity etc. Finally, tertiary patterns are those that explain the relationship between secondary patterns and abiotic variables, e.g., species richness/latitude relationships.

In my thesis, a hierarchical approach is employed to identify biogeographic patterns, community types, and key abiotic determinants that appear responsible for driving differences in community structure and composition in the western Indian Ocean. Using a standardised sampling protocol, based on the results of a pilot study, I examine the benthic biological composition on shallow subtidal reefs, and analyse a range of abiotic factors thought to be important in structuring subtidal communities. Four spatial scales are incorporated into the study in a hierarchical framework: (1) a biogeographic scale focusing over thousands of kilometres, (2) a regional scale extending over hundreds of kilometres, (3) inter-site comparisons conducted at a scale of tens of kilometres, and (4) intra-site comparisons at a scale of meters. Much of this work involves a comparative approach at the various spatial scales, whereas potential determinants of community composition were evaluated using a correlative approach. In addition, using stable isotopes as tracers, I focus on the trophic dynamics of filter-feeder communities and evaluate the relative role various sources of particulate organic matter play in supplying food for filter-feeder communities. In particular, I determine the importance of marine and riverine trophic subsidies in supporting filter-feeder communities, and to what extent this may explain why one of the bioregions I examined is dominated by filter-feeders.

Chapter 2 deals with primary and secondary biogeographic patterns within the western Indian Ocean region. Using quantitative biomass data collected from 55 shallow subtidal reefs in the western Indian Ocean, I delineate marine biogeographic provinces and compare community structure among the bioregions I distinguished, identifying characteristic and distinguishing taxa. I then focus on secondary biogeographic patterns comparing trophic group structure and biomass patterns among bioregions to gain an insight into community structure and the underlying mechanisms that may govern each bioregion, following the approach of Ricciardi & Bourget (1999).

In Chapter 3, I examine community composition at a finer scale. Among-site analyses of community composition were performed to define discrete reef community types at the scale of sites. This type of approach is fundamental for conservation planning. Using similarity profile permutation tests (Clarke & Gorley 2006) with a 95 % significance level cut-off, I could distinguish discrete community types. The distributions of these various types of communities were assessed relative to current marine protected area networks to evaluate their conservation status. In addition, I investigate community divergence between horizontal and vertical reefs at a subset of three sites to elucidate within-site variability in community composition.

In Chapter 4, I establish differences in the oceanographic conditions that exist among bioregions. I then focus on quantifying tertiary biogeographic patterns, and correlate community composition biomass data at 54 sites with nine abiotic variables that were remotely sensed or measured *in situ*. This revealed potential abiotic determinants driving biogeographic pattern and community composition at both the regional scale and among sites within particular bioregions. I also compare concentrations of nitrite, nitrate, phosphate and silicate between two of the bioregions I identified, to establish the extent to which nutrients may be driving community divergence via bottom-up mechanisms. As geology can operate at local-scales (Holmes *et al.* 1997), influencing community structure within bioregions, its affect on community composition was tested by comparing two different rock types at a subset of six sites within a single bioregion.

Building on the previous chapters, Chapter 5 evaluates the potential role that suspended riverine particulate organic matter (POM) plays in maintaining the dominance of filter-feeders I observed in the southernmost of the bioregions identified in Chapter 2. This involved the collection and isotopic analysis of riverine, seaweed and phytoplankton POM food sources and of four species of filter-feeders in four independent study areas, each of which encompassed a river and rocky reefs situated at varying distances from the river mouth. The resulting 520 samples were analysed for their carbon, nitrogen and sulphur isotope ratios, and the results were incorporated into three-source linear mixing models. I then calculated the relative proportions of riverine, seaweed and phytoplankton POM comprising the inshore POM pool and to what extent each was assimilated by filter-feeder communities, spatially and seasonally. On this basis, the relative importance of riverine POM inputs as a determinant of filter-feeder biomass was assessed.

Chapter 6 concludes the thesis with a synthesis of all findings covered in Chapters 2-5, reviewing key results and evaluating how my findings furthered understanding of patterns of community composition at various scales, and the likely factors underlying these patterns.

CHAPTER 2

BIOGEOGRAPHIC PATTERNS ON SHALLOW SUBTIDAL REEFS IN THE WESTERN INDIAN OCEAN

ABSTRACT

This chapter identifies large-scale biogeographic patterns in shallow subtidal reef community structure of the western Indian Ocean region. Quantitative biomass data for 247 taxa from 55 sites, spanning approximately 4800 km of coastline, were analysed using robust permutational multivariate statistics. Two distinct marine provinces, corresponding to the Tropical Indo-West Pacific and Subtropical Natal, were distinguished ($P_{(\text{perm})} = 0.0001$). The biogeographic boundary between these two provinces was similar in geographic location to that detected in earlier intertidal studies, but differed in that it took the form of a transitional region rather than an abrupt discontinuity comprising an overlap (of *ca.* 120 km), that is located between Leadsman's Shoal and Kosi Mouth on the northern-most section of South Africa. The region of overlap corresponds in locality to what has previously been called the Delagoa Bioregion, and was one of three bioregions revealed by post-hoc analyses in my study; but to acknowledge its transitional nature, I have named it the Delagoa Overlap Bioregion. Trophic structure differed significantly among bioregions ($P_{(\text{perm})} = 0.0001$), particularly between the Subtropical Natal and Tropical Indo-West Pacific bioregions. "Auto-heterotrophs" (species with autotrophic symbionts such as corals and clams), deposit-feeders and grazers contributed significantly more biomass to the Tropical Indo-West Pacific Bioregion, whereas filter-feeders contributed most towards biomass in the Subtropical Natal Bioregion. In the Delagoa Overlap Bioregion, filter-feeders were again the most abundant trophic group, but there was also a notable biomass of auto-heterotrophs. Total average subtidal biomass also differed significantly among the three bioregions and was considerably greater than that recorded by others for intertidal sites. The Tropical Indo-West Pacific Bioregion had the highest average biomass, which was unexpected, followed by the Subtropical Natal and Delagoa Overlap bioregions. Significant regional differences in community composition, trophic structure and biomass as well as high between-site variability were a characteristic of the shallow subtidal communities examined.

INTRODUCTION

Biogeography

Knowledge of large-scale patterns is an important aspect of ecology as it provides the basic framework to test underlying mechanisms that govern ecosystems (Ricciardi & Bourget 1999). In addition, biogeographic information is a necessary pre-cursor for the establishment of a representative network of marine protected areas (Hockey & Branch 1994, 1997; Roberts *et al.* 2003a).

The first biogeographic investigations in the western Indian Ocean region comprised qualitative works on intertidal rocky shores in South Africa (Stephenson 1939, 1944, 1947; Stephenson & Stephenson 1972). The north-east coast of South Africa was classified and named the Subtropical East Coast, with its southern border at Durban, South Africa and its northern border in the vicinity of Maputo Bay, southern Mozambique (Stephenson 1939, 1944, 1947; Stephenson & Stephenson 1972). Subsequently there have been a number of investigations substantiating and demarcating marine biogeographic provinces on the east coast of southern Africa, which are reviewed by Brown & Jarman (1978) and Spalding *et al.* (2007). These have focused mainly on the easily-accessible intertidal zone (Jackson 1976; Emanuel *et al.* 1992; Bustamante 1994; Bustamante & Branch 1996a; Bolton & Anderson 1997; Sink 2001; Bolton *et al.* 2004; Sink *et al.* 2005) and more recently the subtidal zone (Turpie *et al.* 2000; Evans 2005; Lawrence 2005).

Most of the KwaZulu-Natal political province on the north-east coast of South Africa is accepted as falling within the Subtropical East Coast Province, also known as the Subtropical Natal Province (Figure 2.1). However the geographic position of the northern limits of this province and the beginning of the Tropical Indo-West Pacific Province have been debated, particularly with respect to subtidal biota. Marine biogeographic divisions may depend greatly on the mode of life of organisms that are considered and on the depths at which they are sampled. Biota on subtidal reefs differs from that of the intertidal zone as most species are colonial, and many produce larvae with weak dispersal

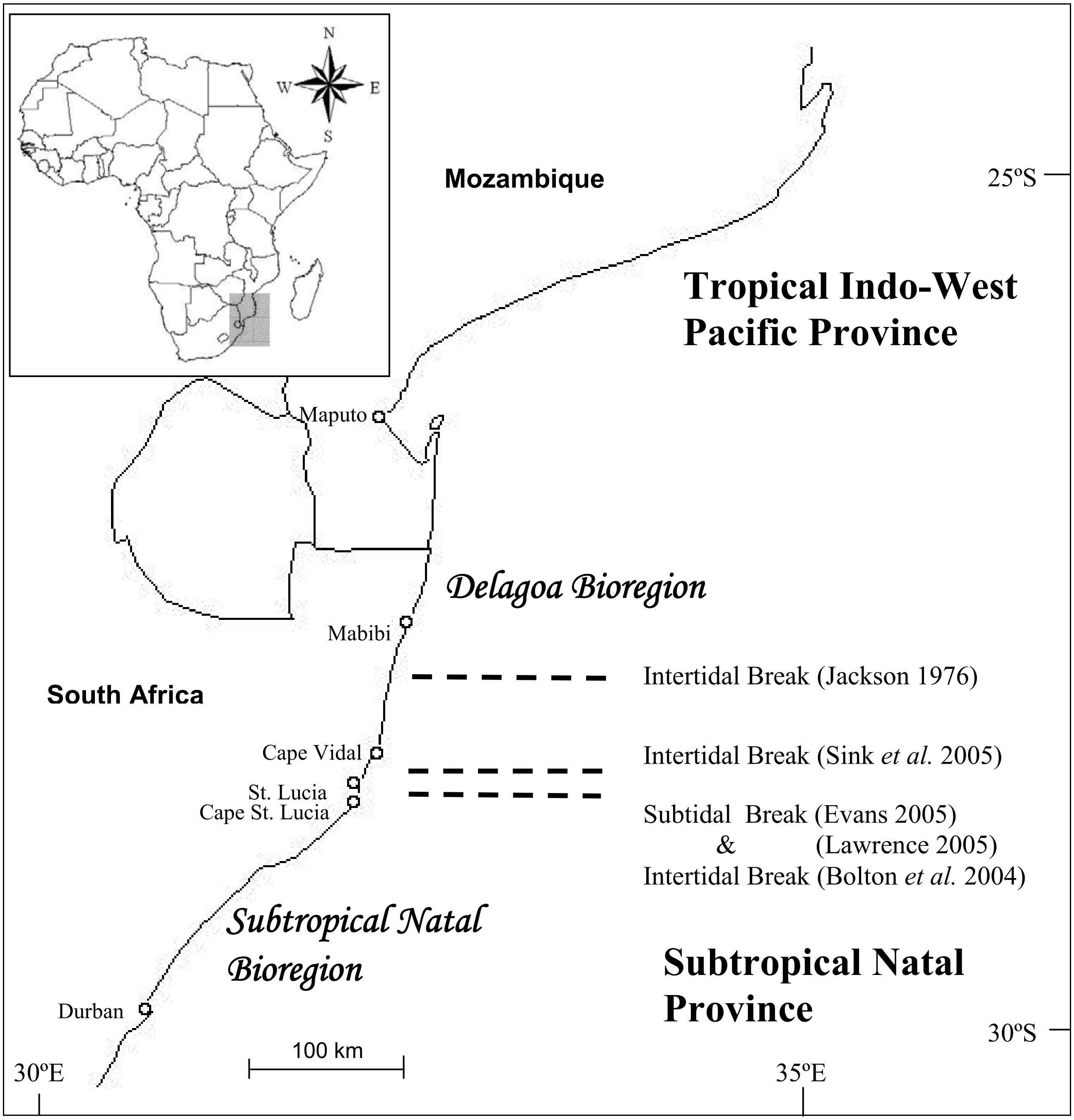


Figure 2.1. Positions of intertidal and subtidal biogeographic breaks previously proposed between the Subtropical Natal Bioregion and the Delagoa Bioregion at the southern limits of the Tropical Indo-West Pacific Province, according to studies specific to the east-coast region.

capabilities (Jackson 1986). In addition, very little subtidal work has been done north of Cape Vidal and into southern Mozambique (Sink 2001; Bolton *et al.* 2004) and therefore the precise location of the division between Subtropical Natal and Tropical Indo-West Pacific provinces remains uncertain.

At the commencement of this work no study had been done on the subtidal biogeography off the South African east coast and accounts further north on the east African coast were generally limited to small-scale investigations. Two unpublished subtidal benthic studies have recently examined reef biogeography and diversity on the east coast of South Africa. Evans (2005) focused specifically on seaweeds at depths of 2-29 m at 11 localities in the KwaZulu-Natal political province. Lawrence (2005) investigated both fauna and flora on reefs at depths of 10-30 m at nine sites in the same region. Both found indications of a subtidal biotic discontinuity between Subtropical Natal and Tropical Indo-West Pacific provinces in the vicinity of St. Lucia a few kilometres south of Cape Vidal (Figure 2.1). This is similar in location to where Bolton *et al.* (2004) and Sink *et al.* (2005) placed the biogeographic division between these two marine provinces based on intertidal analyses.

At a finer scale within biogeographic provinces, Lombard *et al.* (2004) classified South Africa into several 'bioregions', which they defined as “subdivisions based on large-scale biological variability and biogeography, plus large-scale habitat differences related to different current systems with different temperatures and productivity”. At this scale, the Natal Bioregion was identified as the northern component of the Subtropical Natal Province, while the Delagoa Bioregion was identified as the southern limit of the Tropical Indo-West Pacific Province on the east coast of Africa (Lombard *et al.* 2004) (Figure 2.1).

Trophic structure

Secondary biogeographic patterns and horizontal gradients of abundance in the marine environment are rarely described (Bustamante *et al.* 1995a). They are nevertheless essential precursors to studies that establish the mechanisms that govern ecosystems

(Ricciardi & Bourget 1999). The first trophic study of relevance to the southern part of my study region was conducted by Bustamante & Branch (1996a). Little of their work focused on the east coast, but they were able to establish definite regional trends based on comparisons of intertidal data between the South African west, south and east coasts (Bustamante *et al.* 1995a). They concluded that the intertidal trophic communities around southern Africa do not agree with the predictions and hypotheses proposed by Menge and Olson (1990) – which are outlined in the Discussion below – and that bottom-up effects such as nutrient availability had an important effect on community structure.

Biomass

Productivity in the oceans is largely limited by nutrient availability, light and temperature, and optimal conditions for all these factors do not often coincide (Polis 1999). Light hours and water temperatures are higher in tropical regions than in subtropical regions (Archibold 1995), but most tropical oceans have low annual net primary productivity relative to subtropical and temperate regions because nutrient concentrations are limiting (Polis 1999).

The majority of the western Indian Ocean is nutrient-limited and upwelling is weak or absent along most of the East African coast. The region is generally depleted in nutrients because downwelling prevails most of the year (Bell 1972) and benthic productivity is restricted in these low-nutrient warm waters (McClanahan 1988a). The dominant sources of nutrients are reportedly from water-column mixing, river discharge, and coastal runoff (McGill 1973).

Bustamante (1994) and Bustamante *et al.* (1995a) examined intertidal biomass patterns around the coast of South Africa, and found significantly higher biomass on the west coast than on the south and east coasts, but less clear-cut differences between south and east coasts (Bustamante 1994). He and his co-workers attributed the higher biomass on the west coast to elevated nutrient levels injected by upwelling, leading to increased primary productivity.

This chapter focuses on both primary and secondary biogeographic patterns of shallow subtidal reefs in the western Indian Ocean along the east coast of Africa and some of its inshore and offshore islands. The study spans five countries and ranges from Port Edward in South Africa to Mesali Island in northern Tanzania and east to the west coast of Madagascar including the Comoros Islands. The first part of the chapter deals with large-scale biogeographic patterns, establishing the existence of bioregions and location of boundaries between them in the Subtropical Natal and Tropical Indo-West Pacific provinces, and the identification of the species that account for differences among bioregions. The second part describes the trophic structuring of shallow subtidal reefs in each region and also deals with patterns of subtidal biomass.

Specifically this chapter addresses the following questions in relation to shallow subtidal reefs:

1) Where is the biogeographic boundary between the Subtropical Natal and Tropical Indo-West Pacific marine provinces situated, and how many bioregions can be recognised within these provinces?

2) What species characterise and distinguish the bioregions of the western Indian Ocean?

3) Does trophic structure differ among bioregions?

4) Does benthic biomass show bioregional patterns?

I test the following hypotheses:

- There are two distinct shallow subtidal marine provinces on the east coast of Africa separated by a discontinuity in the vicinity of St. Lucia on the north-east coast of South Africa.

- There will be differences in the trophic structure of shallow subtidal reefs among bioregions, and the proportion of 'auto-heterotrophs' (i.e., corals, clams and zoanthids with autotrophic symbionts) will be higher in the Tropical Indo-West Pacific Bioregion than in the Subtropical Natal Bioregion, whereas the proportion of filter-feeders will be lower in the Tropical Indo-West Pacific Bioregion than in the Subtropical Natal Bioregion.

- There will be differences in shallow subtidal benthic biomass among bioregions, and the Subtropical Natal Bioregion will have the highest average biomass.

METHODS

Pilot study

A pilot study was conducted between depths of 1-7 m at three sites along the north-east coast of South Africa in the KwaZulu-Natal political province: Vetch's Pier, Cape Vidal and Quarter Mile Reef (see Figure 2.3 for localities). The aims of this preliminary study were to determine (a) the appropriate number of replicate quadrats needed to adequately quantify within-site species variability relative to between-site differences, and (b) the feasibility of sampling at this intensity in the high-energy shallow subtidal zone, given that there was a limit on sampling time imposed by SCUBA air availability and diving limits.

Twenty five to thirty rectangular quadrats of 100 x 50 cm were used to quantify species composition at each site. The cumulative number of species for each of the three sites was plotted against the replicate number of quadrats (Figure 2.2). On this basis a replication level of 15 quadrats was selected for further studies, incorporating a minimum of 85 % of species at each site.

Biological sampling design

In total, 55 shallow subtidal reefs in the western Indian Ocean region were quantified (Figure 2.3, Table 2.1). 'Shallow subtidal reefs' were defined as those that lie at depths of 1-10 m during mean spring low tide. Study sites were distributed from Port Edward (31°S) on the east coast of South Africa, to Mesali Island (5°S) on the north coast of Tanzania, including various islands such as Madagascar and Comoros (Table 2.1). Sites were surveyed within a two-year period between 2004 and 2005, except for four sites in the extreme northern part of the study area at Tanga, Tanzania, which were opportunistically surveyed in September 2007. Study sites were concentrated in the northern South African and southern Mozambique region because this is where the biogeographic break was hypothesised to lie, and because reefs in this area were poorly known. Large gaps between sites, particularly in central Mozambique, correspond to extensive mangrove delta areas where reefs are reportedly absent and turbidity is high (Rodrigues *et al.* 2000).

Benthic sessile taxa were quantified visually in 15 replicate 100 x 50 cm gridded (10 x 10 cm) quadrats per site, surveyed using SCUBA (Dethier *et al.* 1993; English *et al.* 1994) (Figure 2.4). Quadrats of this size have been used for similar work in South Africa (Sink 2001; Lawrence 2005; Sink *et al.* 2005). Random sampling was conducted on horizontal reef and stratified by avoiding areas with slopes in excess of 25 ° and or with homogeneous sand cover. Percentage cover of all taxa was recorded in each quadrat. In addition, the numbers of mobile benthic taxa were quantified using 10 replicate 5 x 2 m belt transects. Mobile molluscan species were rare and therefore omitted. Destructive samples of 30 x 30 cm of each colonial and algal taxon, and at least three representative individuals of each dominant mobile species were collected to permit conversion of percent cover and density data into ash-free dry biomass. This was done to standardise and provide a common currency among different species of organisms, and to allow for comparison with other studies such as Bustamante and Branch (1996a). Organisms that could not be identified underwater were recorded as morpho-species and sampled for later identification by taxonomists.

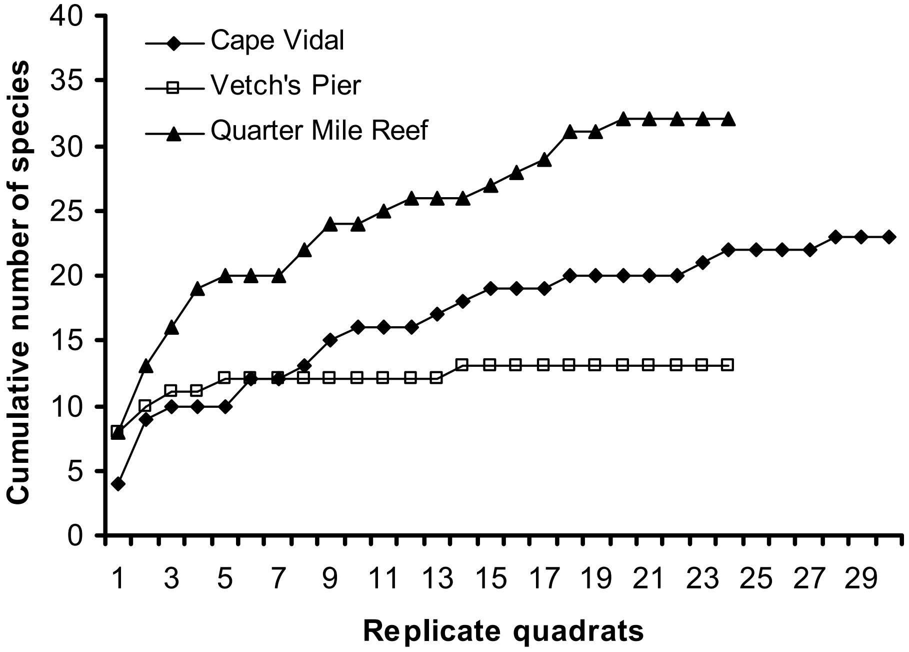


Figure 2.2. Pilot analyses of cumulative number of species versus sampling intensity for three shallow subtidal sites on the east coast of South Africa.

In the case of Porifera, spicules were prepared for microscope examination to allow identification. Most hydrozoans were identified to generic level only and crustose coralline algae were treated as a single functional group.

Data analysis

The data analysis is summarised in Figure 2.4.

Biogeography

Non-parametric multivariate statistics were used to analyse ash-free dry biomass data per taxon. The analytical approach followed that suggested by Anderson & Willis (2003) who stipulated an unconstrained non-metric multidimensional scaling (MDS) ordination and constrained MDS ordination, rigorous statistical tests of the hypotheses and an analysis that determines which species are responsible for any observed multivariate patterns. To test the *a-priori* null hypothesis that there is no difference between the region south (Subtropical Natal Province) and north (Tropical Indo-West Pacific Province) of the hypothesised biogeographic break at St Lucia, sites were assigned according to their latitude north or south of St. Lucia (see Figure 2.1).

Multivariate data were graphically represented by means of a constrained MDS ordination, unconstrained MDS ordination and a cluster analysis. A canonical analysis of principal components (CAP) was performed using the software program CAP (Anderson & Robinson 2003; Anderson & Willis 2003) on the two *a-priori* groups using sites as replicates to produce the constrained MDS ordination. The data were root-transformed, the Bray-Curtis dissimilarity distance measure used (Bray & Curtis 1957), and the number of eigenvectors (principal coordinate axes) selected by the program to maximise the number of correct classifications (Anderson & Robinson 2003). The constrained canonical axis scores (CAP values) for each sample for the two groups that were defined *a-priori* were then plotted on a single axis, resulting in a constrained MDS ordination. (As there were only two *a-priori* defined groups, only one canonical axis existed.) Plymouth Routines in Multivariate Ecological Research, version 6.0 (PRIMER 6; Clarke

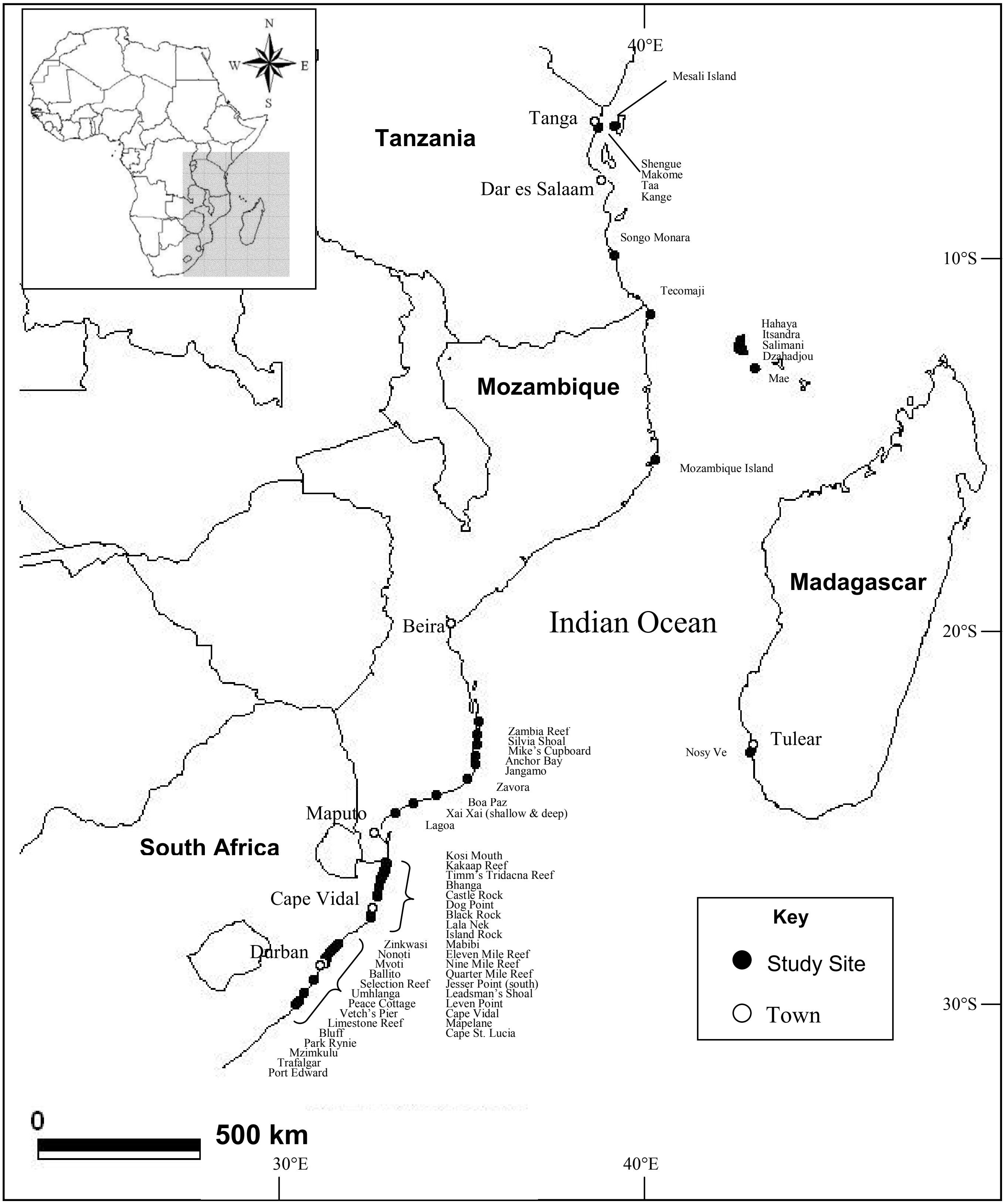


Figure 2.3. Shallow subtidal sites within the western Indian Ocean region surveyed during the biogeographic study.

Table 2.1. Geographical position (º) and sampling date of study sites arranged from north to south used in the biogeographical analysis and in Chapters 3 & 4. [1] = used only in pilot study & to test for differences in horizontal versus vertical community structure. [2] = used only in pilot study. [3] = used only in Chapter 2 biogeographical analysis.

Locality	Date sampled	Degrees South	Degrees East
Mesali Island, Tanzania	24 August 2004	-5.239	39.599
Shengue, Tanzania	2 October 2007	-5.242	39.105
Makome, Tanzania	22 September 2007	-5.282	39.114
Taa, Tanzania	22 September 2007	-5.300	39.103
Kange, Tanzania	23 September 2007	-5.309	39.117
Songo Monara, Tanzania	22 August 2004	-9.055	39.612
Tecomaji, Tanzania	18 August 2004	-10.755	40.640
Hahaya, Comoros	1 September 2004	-11.549	43.281
Itsandra, Comoros	31 August 2004	-11.667	43.263
Salimani, Comoros	3 September 2004	-11.784	43.241
Dzahadjou, Comoros	4 September 2004	-11.856	43.356
Mae, Comoros	5 September 2004	-12.376	43.737
Mozambique Island, Mozambique	6 September 2004	-15.059	40.778
Zambia Reef, Mozambique	11 April 2005	-22.760	35.582
Silvia Shoal, Mozambique	12 April 2005	-23.113	35.571
Mikes Cupboard, Mozambique	13 April 2005	-23.396	35.542
Nosy Ve, Madagascar	14 September 2004	-23.654	43.586
Anchor Bay, Mozambique	13 April 2005	-23.777	35.511
Jangamo, Mozambique	14 April 2005	-24.012	35.506
Zavora, Mozambique	16 April 2005	-24.441	35.268
Boa Paz, Mozambique	17 April 2005	-24.927	34.363
Xai Xai (deep), Mozambique	17 April 2005	-25.164	33.677
Xai Xai (shallow), Mozambique	17 April 2005	-25.165	33.679
Lagoa, Mozambique	20 April 2005	-25.436	33.173
Kosi Mouth, South Africa	22 November 2004	-26.894	32.884
Kakaap Reef, South Africa	22 November 2004	-26.958	32.878
Timm's Tridacna Reef, South Africa	22 November 2004	-26.928	32.885
Bhanga, South Africa	23 November 2004	-27.011	32.869
Castle Rock, South Africa	23 November 2004	-27.073	32.853
Dog Point, South Africa	23 November 2004	-27.099	32.843
Black Rock, South Africa	25 November 2004	-27.132	32.832
Lala Nek, South Africa	25 November 2004	-27.216	32.812
Island Rock, South Africa	25 November 2004	-27.276	32.778
Mabibi, South Africa	26 November 2004	-27.321	32.758
Eleven Mile Reef, South Africa	26 November 2004	-27.362	32.740
Nine Mile Reef, South Africa	26 November 2004	-27.416	32.725
Quarter Mile Reef, South Africa [1]	9 November 2006	-27.536	32.683
Jesser Point (south), South Africa	28 November 2004	-27.608	32.661
Leadsman's Shoal, South Africa	22 June 2005	-27.830	32.611
Leven Point, South Africa	22 June 2005	-27.877	32.603
Cape Vidal, South Africa [2]	21 June 2004	-28.124	32.560
Mapelane, South Africa	20 June 2005	-28.403	32.428
Cape St. Lucia, South Africa	20 June 2005	-28.498	32.415
Zinkwasi, South Africa	11 August 2005	-29.283	31.446
Nonoti, South Africa	20 November 2004	-29.312	31.421
Mvoti, South Africa	13 August 2005	-29.418	31.316
Ballito, South Africa	8 June 2005	-29.544	31.220
Selection Reef, South Africa	19 November 2004	-29.680	31.115
Umhlanga, South Africa	19 November 2004	-29.696	31.108
Peace Cottage, South Africa	19 November 2004	-29.696	31.106
Vetch's Pier, South Africa [3]	4 June 2004	-29.863	31.053
Limestone Reef, South Africa	26 May 2005	-29.872	31.061
Bluff, South Africa	19 November 2004	-29.878	31.053
Park Rynie, South Africa	17 November 2004	-30.334	30.739
Mzimkulu, South Africa	14 July 2005	-30.727	30.470
Trafalgar, South Africa	4 April 2005	-30.954	30.308
Port Edward, South Africa	8 December 2004	-31.048	30.231

& Gorley 2006) was then used to construct an unconstrained non-metric MDS ordination (Kruskal & Wish 1978) to provide an overall pattern of dispersion of points (Anderson & Willis 2003). A cluster analysis (Field *et al.* 1982), using root-transformed Bray-Curtis dissimilarity and group average linkages, was then plotted to further investigate the relationships among sites and determine the type of discontinuity (abrupt, or gradual overlap) between biogeographic provinces. Interpretation of the cluster diagram and the spatial identification of the biogeographic break were simplified by plotting sites according to which of the two primary clusters they belonged to, and in order of their ranked latitude.

Non-parametric one-way permutational multivariate analysis of variance (PERMANOVA), using a distance-based multivariate analysis for a linear model to test the *a-priori* hypothesis, was performed with the software program DISTLM v. 5 (Anderson 2001; McArdle & Anderson 2001). As the design was unbalanced (level 1 = 16 sites; level 2 = 39 sites) a design matrix for analysis of variance in linear models with orthogonal codes was calculated (Legendre & Anderson 1999) using the software program XMATRIX (Anderson 2003) and inputted into DISTLM and run for 9999 permutations (root-transformed, Bray-Curtis dissimilarity, residual mean square with no other terms in the model, unrestricted permutation of raw data or units). The CAP permutation test for significance using 9999 permutations was used to supplement this. Based on these results the data were further analysed post-hoc using permutational analysis of multivariate dispersions (PERMDISP2) (Anderson 2004) using 9999 permutations (root-transformed, Bray-Curtis dissimilarity), to determine if the two marine provinces differed according to community assemblage structure or on the basis of being more or less variable (in terms of multivariate dispersion), given that PERMANOVA is sensitive to differences in dispersion among groups. Finally, based on the interpretation and results of the MDS ordinations and cluster diagram from the biogeographic analyses, *a-posteriori* similarity percentage breakdown analysis (SIMPER) (Clark 1993) was performed to identify characteristic and distinguishing species within and between bioregions using the Bray-Curtis similarity value and root-transformed data.

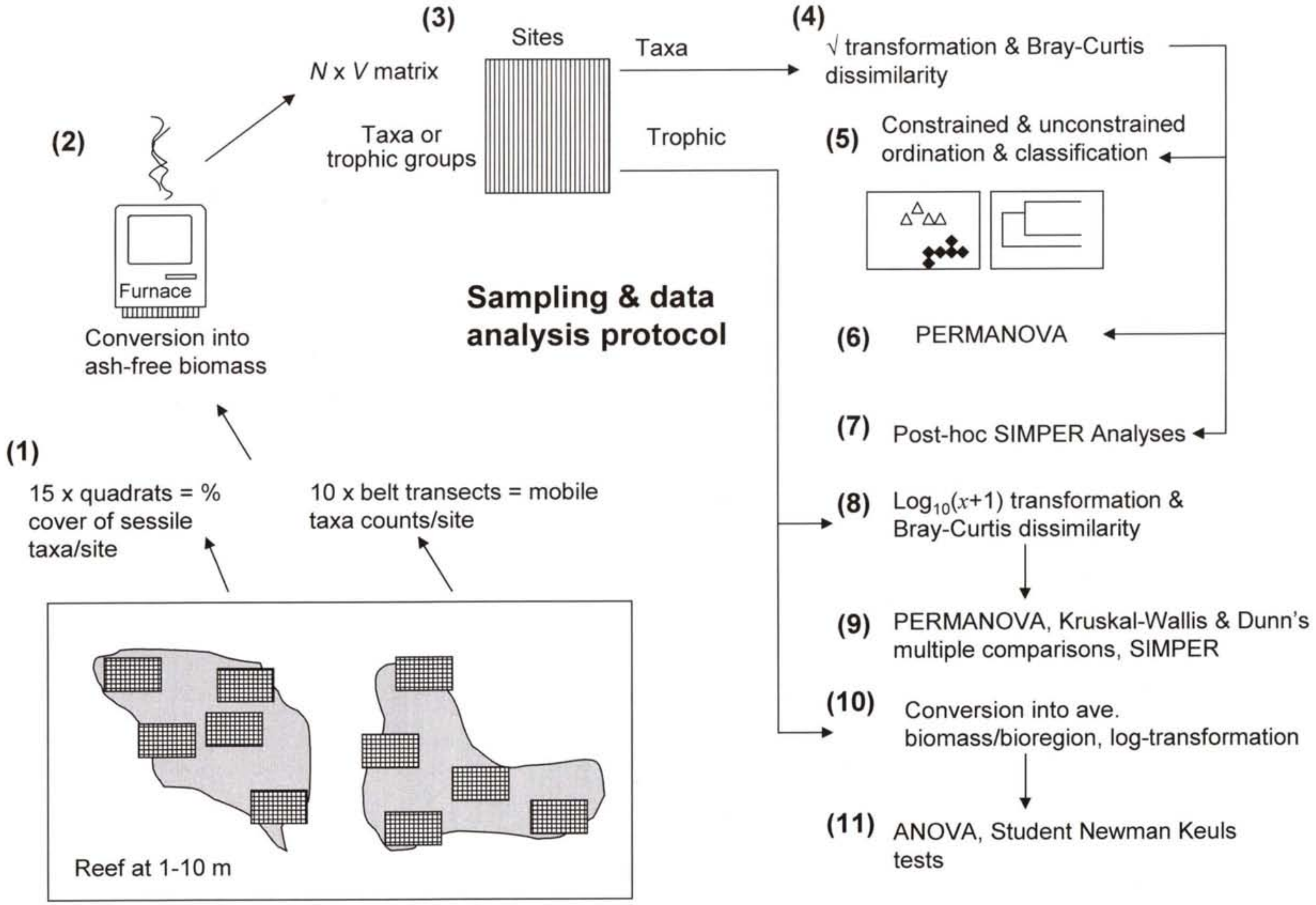


Figure 2.4. Schematic representation of the sampling and data analysis protocol for Chapter 2.

Trophic structure

Each taxon was assigned to one of six functional groups based on its mode of energy acquisition. Groupings were macrophytes (seaweeds & seagrasses), auto-heterotrophs (zooxanthellate filter-feeding corals, clams & zooanthids), deposit-feeders (e.g. sea cucumbers), filter-feeders (e.g. ascidians and sponges), grazers (e.g. urchins) and predators (e.g. rock lobsters). An $N \times V$ matrix where N equals sites (samples) and V equals trophic groups (cases) was created of biomass data, which were then transformed to $y' = \log_{10}(y+1)$ to remove large differences in scale between original variables (Anderson & Willis 2003). A PERMANOVA using DISTLM and XMATRIX to code for the analysis of variance (ANOVA) design was run using 9999 permutations ($\log_{10}(y+1)$ transformed, Bray-Curtis dissimilarity, residual mean square with no other terms in the model, unrestricted permutation of raw data or units). The same multivariate analysis was then run *a-posteriori* on pairs of bioregions derived from the initial biogeographic analysis to further investigate where differences lay, and a t-statistic calculated by means of square-rooting the value of the F-statistic (Anderson 2001).

Each trophic group was then tested independently for differences among bioregions using a non-parametric one-way Kruskal-Wallis ANOVA on ranks, as the $\log_{10}(y+1)$ transformed data were not normally distributed. *A-posteriori* Dunn's tests were then performed on each trophic group to further investigate where differences lay among bioregions. Data were analysed with SigmaStat 3.11 (Systat Software, Inc 2004).

Exploratory analysis of the average ± standard deviation values for trophic-group biomass within a particular region showed standard deviations were high, so using average trophic biomass values to define a community would have been of little value (Bustamante & Branch 1996a). Consequently, SIMPER (Clark 1993) analyses were performed using the Bray-Curtis distance measure on $\log_{10}(y+1)$ transformed trophic-group biomass data to determine the most consistent trophic groups characterising marine bioregions.

Biomass

To test for differences in ash-free dry biomass among bioregions identified in the biogeographic analyses, a one-way ANOVA was conducted on biomass per site using SigmaStat 3.11 (Systat Software, Inc 2004), after log-transformation to normalise the data (Kolmogorov-Smirnov test with Lilliefors correction, $P < 0.05$) and homogenise variances. *A-posteriori* Student Newman Keuls tests were performed on biomass data among bioregions to further investigate where differences lay within the factor levels. For each bioregion, untransformed mean biomass (± standard deviation) was plotted for graphical display, although the data were transformed for statistical analyses.

RESULTS

Biogeography

The constrained MDS ordination of sites defined *a-priori* showed clear separation between provinces (Figure 2.5). Multivariate dispersion of sites within the Subtropical Natal Province (CAP access score range = 0.25) was also higher than that for the Tropical Indo-West Pacific Province (CAP access score range = 0.16). Overall classification success of the canonical analysis of principal coordinates analysis was 98.18 % (Table 2.2). A single Subtropical Natal site (Vetch's Pier) was miss-classified as a Tropical Indo-West Pacific site. The two provinces that had been defined *a-priori* differed significantly (PERMANOVA, $F_{(1,53)} = 6.52$ $P_{(\text{perm})} < 0.0001$) (Table 2.3), confirmed by CAP permutation test with a canonical correlation of 0.8419 ($P_{(\text{perm})} < 0.0001$) (Table 2.2). No significant difference was found in either the deviations from group centroids (PERMDISP2, ANOVA $F_{(1,53)} =$ $P_{(\text{perm})} = 0.18130$) or deviations from spatial medians (PERMDISP2, ANOVA $F_{(1,53)} =$ $P_{(\text{perm})} = 0.20130$) between the two provinces (Table 2.4). This means that the two provinces did not differ because of differences in their variability associated with their inherent multivariate dispersion.

The unconstrained MDS ordination with a moderate 2-dimensional stress value of 0.16 did not show clear separation between provinces in the form of two distinct groups, as an area of interaction was evident (Figure 2.6). A number of sites classified as being Tropical Indo-West Pacific showed more similarity with Subtropical Natal sites. The cluster analysis divided sites into two primary clusters (labelled 1 & 2) of similar size (31 sites & 24 sites) at the 5 % Bray-Curtis similarity value (Figure 2.7). The first primary cluster consisted of almost all Tropical Indo-West Pacific sites with one outlier, i.e. Vetch's Pier. The second consisted of all Subtropical Natal sites (except for Vetch's Pier) and the nine remaining Tropical Indo-West Pacific sites. Amongst the latter, Leven Point, the first site north of the *a-priori* hypothesised biogeographic break, was in fact more similar to Subtropical Natal sites than Tropical Indo-West Pacific sites. Within both primary clusters a high degree of divergence between sites was found with Bray-Curtis

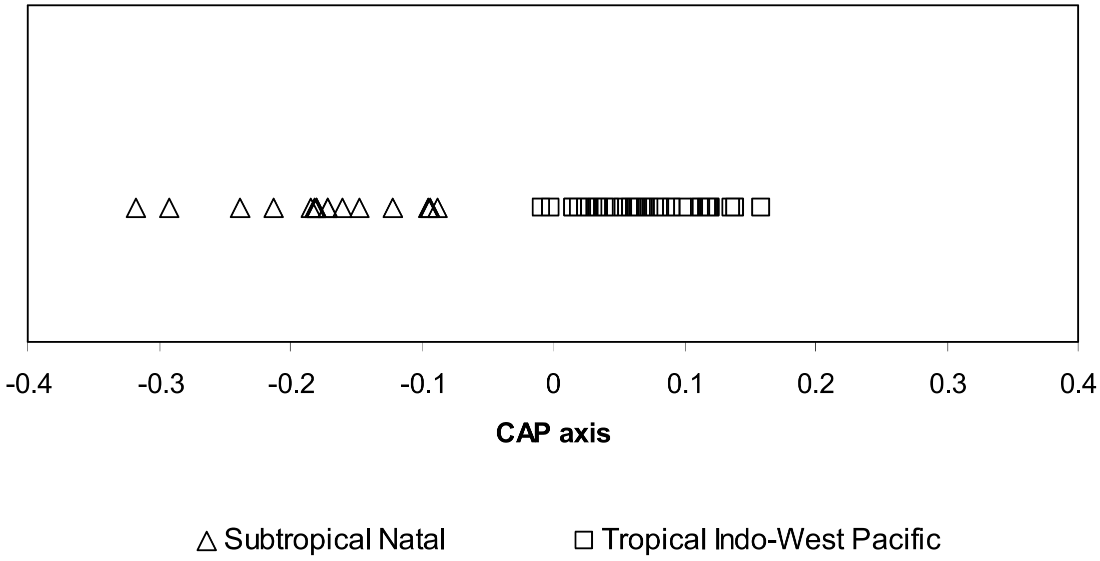


Figure 2.5. Constrained canonical analysis of principal coordinates (CAP) (constrained MDS) ordination plot of all 55 sites based on root-transformed biomass data using the Bray-Curtis similarity measure and sites grouped *a-priori* into Subtropical Natal (n = 16) or Tropical Indo-West Pacific (n = 39) provinces.

Table 2.2. Results of the canonical analysis of principal coordinates (CAP) on root-transformed biomass data using the Bray-Curtis similarity value, for all 55 sites grouped *a-priori* into either the Subtropical Natal Province or Tropical Indo-West Pacific Province. A significant difference ($P < 0.01$) in the benthic community structures of the Subtropical Natal and Tropical Indo-West Pacific provinces was found ($\delta^2 = 0.8419$, $P_{(perm)} < 0.0001$) according to the CAP permutation test. Overall classification success was 98.18 % according to the leave-one-out allocation success, a measure of how distinct groups are. δ^2 = squared canonical correlation. * indicates a significant difference.

Total classifications correct	98.18 %	δ^2	0.8419
Miss-classification error	1.82 %	P	0.0001*

Group (Province)	Allocation success			
	Subtropical	Tropical	Total	Correct (%)
Subtropical	15	1	16	93.75
Tropical	0	39	39	100.00

dissimilarity values spanning 32-90 % within the first primary cluster and 36-88 % within the second primary cluster.

The nine sites that had been defined *a-priori* as Tropical Indo-West Pacific sites, but grouped in the cluster analysis (and the unconstrained MDS ordination) with the Subtropical Natal sites, formed a discrete geographical region together with six Tropical Indo-West Pacific sites (Figure 2.8). Three bioregions were therefore recognisable within the geographical limits of this study: (1) the Subtropical Natal Bioregion (Port Edward, South Africa to Leven Point, South Africa); (2) an overlap region corresponding in location to the Delagoa Bioregion and hereon referred to as the Delagoa Overlap Bioregion (from Leadsman's Shoal to Kosi Mouth); (3) the Tropical Indo-West Pacific Bioregion (from the southern limit of the Tropical Indo-West Pacific Province at Lagoa, Mozambique, northwards to Mesali Island, Tanzania). The analysis also supported the idea that Vetch's Pier was an outlier.

Average Bray-Curtis dissimilarity between the Subtropical Natal Bioregion and Delagoa Overlap Bioregion was 86.13 % (Table 2.5A). The ascidian *Pyura stolonifera* was the top-ranking distinguishing species (Average Dissimilarity = 12.92 %) followed by algal turf (Av. Diss. = 5.01 %), the articulated coralline *Amphiroa ephedraea* (Av. Diss = 4.12 %) and the foliose Phaeophyte *Dictyopteris ligulata* (Av. Diss. = 3.69 %). These species collectively accounted for 29.89 % of the dissimilarity between bioregions. A total of 14 taxa were responsible for contributing more than 2 % each to dissimilarity and a total of 38 species to 80 % of the cumulative dissimilarity.

Average Bray-Curtis dissimilarity between the Delagoa Overlap Bioregion and Tropical Indo-West Pacific Bioregion was 87.49 % (Table 2.5B). The scleractinian genus *Galaxea* was the most distinguishing taxon (Av. Diss. = 6.64 %) followed by *Porites* (Av. Diss. = 6.12 %), *Pyura stolonifera* (Av. Diss. = 5.51 %) and algal turf (Av. Diss. = 4.44 %). These taxa collectively accounted for 25.95 % of the dissimilarity between regions. A total of 10 taxa contributed more than 2 % each to dissimilarity, and 41 taxa to 80 % of the cumulative dissimilarity.

Table 2.3. One-factor PERMANOVA using a distance-based multivariate analysis for a linear model based on Bray-Curtis dissimilarity values and root-transformed biomass data between the *a-priori* defined Subtropical Natal Province and Tropical Indo-West Pacific Province.

Source	*df*	MS	*F*	$p_{(perm)}$	MS_{denom}
Province	1	19492.41739	6.52	0.0001	Residual
Residual	53	2989.09798			
Total	54				

Table. 2.4. Results of the distance-based test for homogeneity of multivariate dispersion using permutational analysis of multivariate dispersions (PERMDISP2).

Test statistic	*P*- value method	*F*	$P_{(perm)}$
Deviations from centroids	ANOVA tables	2.46213	0.12257
	Perm LS residuals		0.18130
Deviations from spatial medians	ANOVA tables	1.8839	0.17567
	Perm LAD residuals		0.20130

Average Bray-Curtis dissimilarity between the Subtropical Natal and Tropical Indo-West Pacific bioregions was the highest out of the regional comparisons (Av. Diss. = 95.50 %) (Table 2.5C). *P. stolonifera* was the most distinguishing species between bioregions (Av. Diss. = 9.90 %) followed by the genera *Galaxea* (Av. Diss. = 6.83 %) and *Porites* (Av. Diss. = 6.66 %), and algal turf (Av. Diss. = 4.43 %). These taxa accounted for 29.13 % of the dissimilarity between regions; 10 taxa were responsible for contributing more than 2 % each to dissimilarity and 45 taxa to 80 % of the cumulative dissimilarity.

The reefs in the Subtropical Natal Bioregion were on average 20.55 % similar (Table 2.6A). *Pyura stolonifera* was the most characteristic species (Average Similarity = 8.12 %) followed by the chlorophyte *Halimeda* spp. (Av. Sim. = 2.66 %), algal turf (Av. Sim. = 2.25 %) and the articulated corallines *Amphiroa ephedraea* (Av. Sim. = 2.15 %) and *Amphiroa bowerbankii* (Av. Sim. = 1.39 %). *Halimeda* spp., *P. stolonifera, A. bowerbankii,* algal turf and *A. ephedraea*, in that order, were also the most consistently characteristic species as indicated by their high Sim/SD ratios.

The reefs of the Delagoa Overlap Bioregion were on average 23.66 % similar (Table 2.6B). *Pyura stolonifera* was again the most characteristic species (Av. Sim. = 5.79 %) followed by *Dictyopteris ligulata* (Av. Sim. = 2.58 %), algal turf (Av. Sim. = 2.46 %), the poriferan *Placospongia* sp. (Av. Sim. = 1.22 %) and the echinoderm *Echinometra mathaei* (Av. Sim. = 1.15 %). Twenty taxa contributed to 90 % of the similarity, compared with nine in the Subtropical Natal and fifteen in the Tropical Indo-West Pacific, because of a greater evenness of abundance and a fusion of taxa involved in these two bioregions.

The reefs of the Tropical Indo-West Pacific Bioregion were on average 22.89 % similar (Table 2.6C). Scleractinia such as *Porites* spp*., Pocillopora* spp. and *Galaxea* spp. were the most characteristic taxa (Av. Sims. = 4.58 %, 2.92 % & 2.17 %). *Echinophyllia aspera* (Av. Sim. = 1.74 %), algal turf (Av. Sim. = 1.69 %) and *Acropora* spp. (Av. Sim. = 1.31 %) were also important contributors.

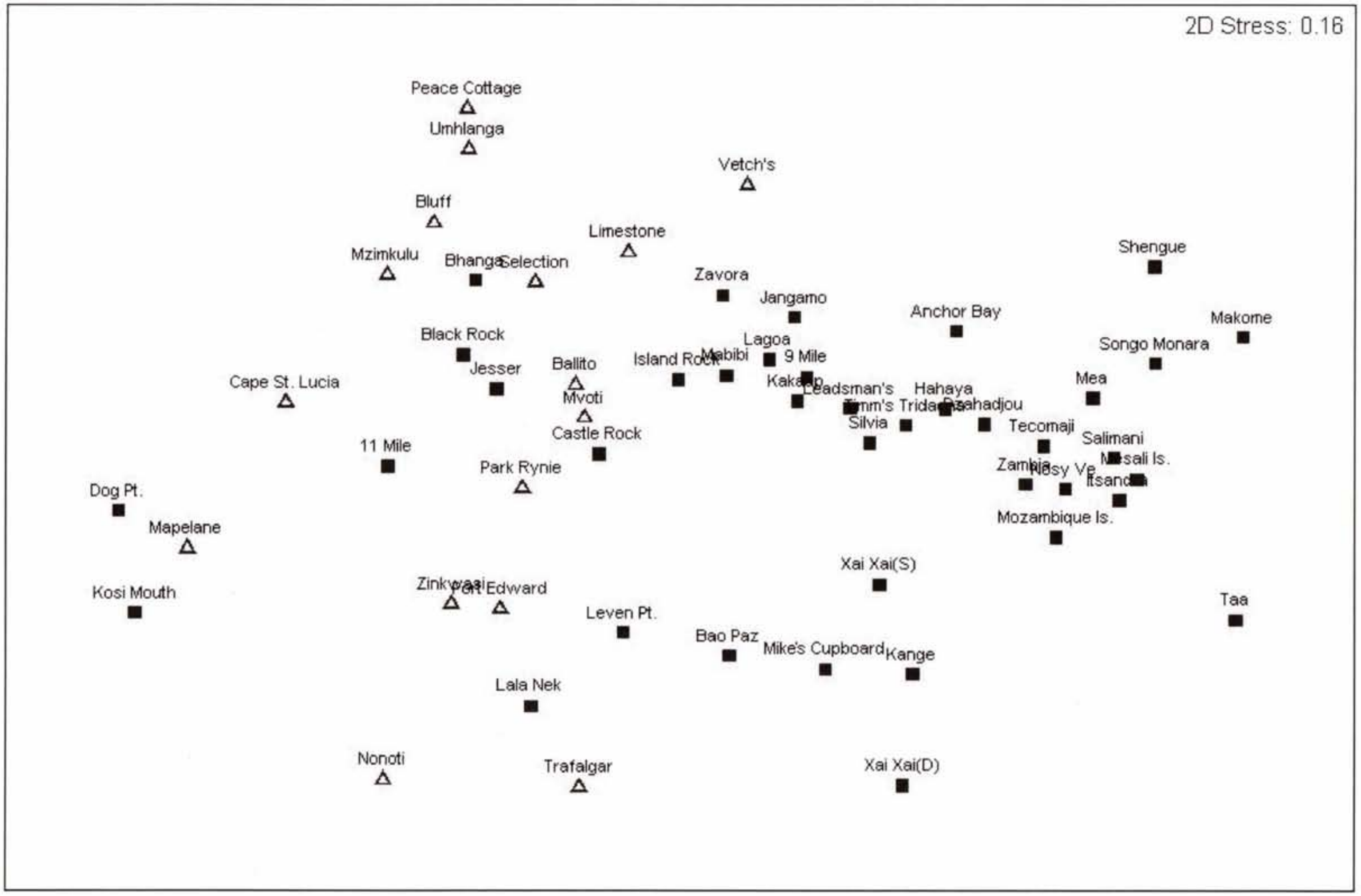


Figure 2.6. Non-metric multidimensional scaling (nMDS) ordination plot (unconstrained ordination) of all 55 sites based on root-transformed biomass data using the Bray-Curtis similarity value. Δ = sites from the Subtropical Natal Province. ■ = sites from the Tropical Indo-West Pacific Province.

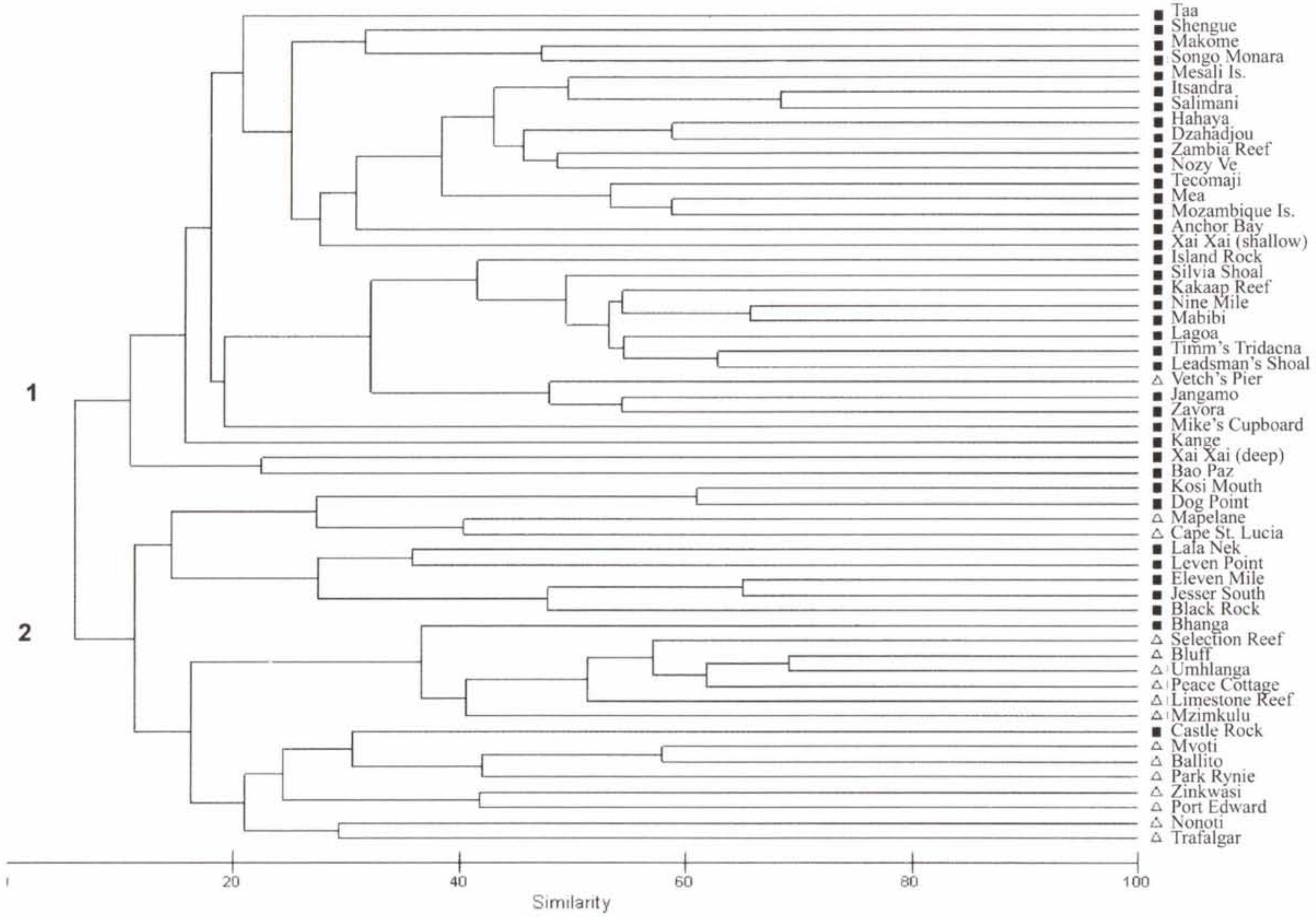


Figure 2.7. Cluster analysis of all 55 sites grouped according to marine province based on root-transformed biomass data using the Bray-Curtis similarity value (%) and group average linkages to define clusters. Δ = Subtropical Natal sites. ■ = Tropical Indo-West Pacific sites.

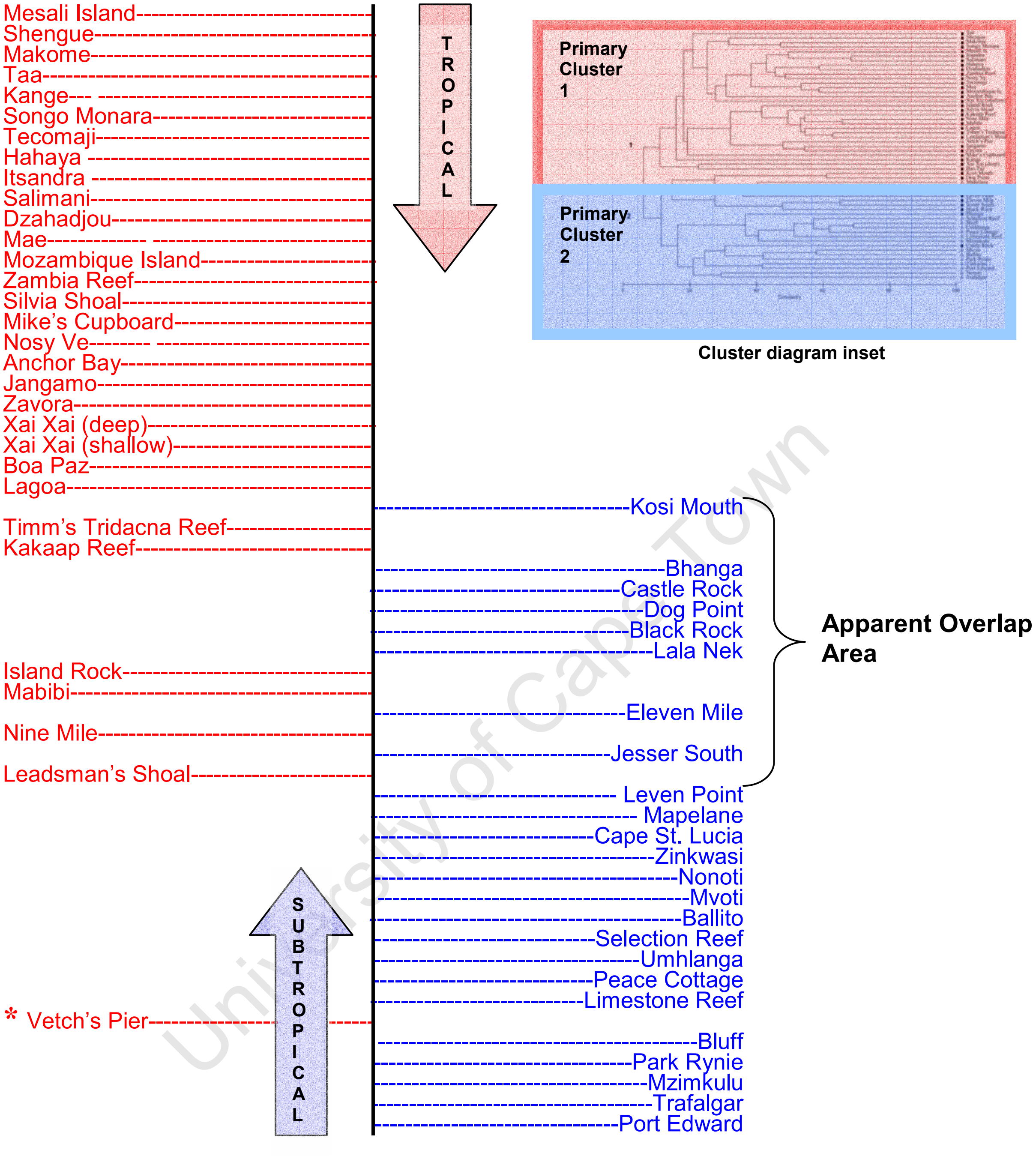


Figure 2.8. Schematic illustration to aid interpretation of cluster diagram. Sites are plotted in order of their rank latitude from north to south. Sites in red are those clustered within primary cluster 1, while those in blue are from primary cluster 2 (see Figure 2.7). The defined area of inconsistence can be interpreted as an area of transition or overlap between the Subtropical Natal and Tropical Indo-West pacific provinces, and geographically corresponds to Maputaland situated on the north-east coast of South Africa. * = the outlier Vetch's Pier.

Table 2.5A-C. Similarity percentage breakdown analyses (SIMPER) of bioregions based on root-transformed biomass data, showing the top 10 discriminating taxa between bioregions. Av. Abund. = average abundance of that taxon in g.m^{-2}. Av. Diss. = average contribution of that taxon to the overall dissimilarity between two bioregions. Diss./SD = average dissimilarity of that particular taxon divided by the standard deviation of its dissimilarity. Contrib. % contribution of that taxon to the overall dissimilarity between bioregions and Cum.% = cumulative contribution of taxa to the overall dissimilarity.

A) Subtropical Natal Bioregion vs. Delagoa Overlap Bioregion

Average Dissimilarity (%) 86.13

Distinguishing Species	**Subtropical Av.Abund. (g.m^{-2})**	**Delagoa Av.Abund. (g.m^{-2})**	**Av.Diss.**	**Diss./SD**	**Contrib.%**	**Cum.%**
Pyura stolonifera	436.25	143.18	12.92	1.11	15.00	15.00
Algal turf	31.21	51.96	5.01	1.11	5.82	20.82
Amphiroa ephedraea	42.06	0.00	4.12	0.68	4.78	25.61
Dictyopteris ligulata	0.40	18.60	3.69	0.67	4.28	29.89
Spirastrella spinispirulifer	10.28	4.88	2.93	0.65	3.40	33.29
Eutherdmania spp.	5.41	2.93	2.71	0.69	3.15	36.44
Halimeda spp.	10.49	0.07	2.26	1.09	2.62	39.07
Echinometra mathaei	0.00	15.49	2.15	0.83	2.50	41.57
Perna perna	7.44	1.31	2.12	0.46	2.46	44.03
Sargassum elegans	0.16	6.55	2.10	0.72	2.43	46.46

B) Delagoa Overlap Bioregion vs. Tropical Indo-West Pacific Bioregion

Average Dissimilarity (%) 87.49

Distinguishing taxa	**Delagoa Av.Abund. (g.m^{-2})**	**Tropical Av.Abund. (g.m^{-2})**	**Av.Diss.**	**Diss./SD**	**Contrib.%**	**Cum.%**
Galaxea spp.	0.00	289.79	6.64	0.52	7.59	7.59
Porites spp.	8.70	180.17	6.12	0.89	6.99	14.58
Pyura stolonifera	143.18	1.68	5.51	1.12	6.30	20.88
Algal turf	51.96	37.19	4.44	0.96	5.07	25.95
Echinophyllia aspera	0.00	66.66	3.41	0.79	3.90	29.85
Pocillopora spp.	4.69	48.79	3.25	1.08	3.72	33.57
Sinularia spp.	16.31	19.62	2.65	1.11	3.03	36.60
Dictyopteris ligulata	18.60	0.00	2.65	0.66	3.03	39.63
Acropora spp.	3.83	28.77	2.47	0.87	2.83	42.45
Diadema spp.	0.03	19.39	2.09	0.52	2.39	44.84

C) Subtropical Natal Bioregion vs. Tropical Indo-West Pacific Bioregion

Average Dissimilarity (%) 95.50

Distinguishing taxa	**Subtropical Av.Abund. (g.m^{-2})**	**Tropical Av.Abund. (g.m^{-2})**	**Av.Diss.**	**Diss./SD**	**Contrib.%**	**Cum.%**
Pyura stolonifera	436.25	1.68	9.90	0.90	10.37	10.37
Galaxea spp.	0.00	289.79	6.83	0.52	7.15	17.52
Porites spp.	0.00	180.17	6.66	0.92	6.97	24.49
Algal turf	31.21	37.19	4.43	0.95	4.64	29.13
Echinophyllia aspera	0.00	66.66	3.52	0.80	3.68	32.81
Pocillopora spp.	0.47	48.79	3.46	1.11	3.63	36.43
Amphiroa ephedraea	42.06	0.00	3.29	0.69	3.44	39.87
Acropora spp.	0.00	28.77	2.45	0.80	2.57	42.44
Sinularia spp.	0.00	19.62	2.22	0.89	2.32	44.76
Diadema spp.	0.00	19.39	2.12	0.51	2.22	46.99

Table 2.6A-C. Similarity percentage breakdown analyses (SIMPER) on bioregions based on root-transformed biomass data, showing the top ten characteristic taxa. n = number of sites. Av. Abund. = the average abundance of that taxon in g.m^{-2}. Av. Sim. = the average contribution of that taxon to the overall similarity in that bioregion. Sim/SD = the average similarity of that particular taxon divided by the standard deviation of its similarity. Contrib. % = the contribution of that taxon to the overall similarity and Cum.% = the cumulative contribution of taxa to the overall similarity.

A) Subtropical Natal Bioregion

n 17

Average similarity (%) 20.55

Characteristic taxa	Av. Abund. (g.m^{-2})	Av. Sim.	Sim/SD	Contrib.%	Cum.%
Pyura stolonifera	436.25	8.12	0.56	39.53	39.53
Halimeda spp.	10.49	2.66	0.77	12.96	52.49
Algal turf	31.21	2.25	0.47	10.96	63.46
Amphiroa ephedraea	42.06	2.15	0.40	10.45	73.91
Amphiroa bowerbankii	11.09	1.39	0.55	6.75	80.66
Eutherdmania spp.	5.41	0.93	0.36	4.51	85.18
Spirastrella spinispirulifer	10.28	0.57	0.22	2.77	87.94
Panulirus homarus	3.35	0.35	0.24	1.71	89.65
Placospongia spp.	0.85	0.18	0.27	0.88	90.53

B) Delagoa Overlap Bioregion

n 14

Average similarity (%) 23.66

Characteristic taxa	Av. Abund. (g.m^{-2})	Av. Sim.	Sim/SD	Contrib.%	Cum.%
Pyura stolonifera	143.18	5.79	0.78	24.49	24.49
Dictyopteris ligulata	18.60	2.58	0.42	10.90	35.39
Algal turf	51.96	2.46	0.52	10.39	45.78
Placospongia spp.	9.10	1.22	0.44	5.15	50.94
Echinometra mathaei	15.49	1.15	0.52	4.86	55.80
Sargassum elegans	6.55	1.09	0.38	4.61	60.40
Lobophytum spp.	11.11	0.98	0.48	4.14	64.55
Sinularia spp.	16.31	0.90	0.39	3.79	68.34
Favites spp.	6.23	0.57	0.42	2.41	70.75
Lobophora variegata	1.23	0.56	0.47	2.37	73.13

C) Tropical Indo-West Pacific Bioregion

n 24

Average similarity (%) 22.89

Characteristic taxa	Av. Abund. (g.m^{-2})	Av. Sim.	Sim/SD	Contrib.%	Cum.%
Porites spp.	180.17	4.58	0.86	20.02	20.02
Pocillopora spp.	48.79	2.92	0.88	12.74	32.76
Galaxea spp.	289.79	2.17	0.50	9.48	42.24
Echinophyllia aspera	66.66	1.74	0.57	7.59	49.83
Algal turf	37.19	1.69	0.35	7.40	57.23
Acropora spp.	28.77	1.31	0.70	5.74	62.97
Sinularia spp.	19.62	1.28	0.54	5.60	68.57
Montipora spp.	12.6	1.26	0.55	5.53	74.09
Favites spp.	11.24	0.95	0.61	4.15	78.25
Echinostrephus molaris	2.57	0.57	0.57	2.50	80.75

Trophic structure

Trophic structure differed significantly among bioregions (PERMANOVA, $F_{(2,52)}$ = 28.59, $P_{(\text{perm})} < 0.0001$) (Table 2.7). All combinations of paired comparisons between bioregions were found to be significantly different (PERMANOVA, t-statistic, $\alpha = 0.001$). Univariate statistics detected significant differences across all trophic groups except for macrophytes, which were marginally non-significant (Kruskal-Wallace ANOVA, $H = 6.16$, $P = 0.05$). Dunn's multiple comparisons ($\alpha = 0.05$) showed significant differences between the Subtropical Natal Bioregion and Tropical Indo-West Pacific Bioregion for most trophic groups, with the exception of macrophytes and predators. Significant differences in auto-heterotrophs, deposit-feeders and filter-feeders were found between the Delagoa Overlap Bioregion and the Tropical Indo-West Pacific Bioregion while only grazers were found to differ between the Subtropical Natal and Delagoa Overlap bioregions.

All trophic groups were represented in each of the bioregions except for predators, which were absent from samples taken in the Delagoa Overlap and Tropical Indo-West Pacific bioregions. An increasing northward trend in auto-heterotrophs, deposit-feeders and grazer biomass was noticeable, whereas there was an opposite trend for filter-feeders and macrophytes according to SIMPER percentage contribution values (Figure 2.9, Table 2.8A-C).

The Subtropical Natal Bioregion was dominated by filter-feeders (average ash-free biomass = 1270 $g.m^{-2}$), followed by macrophytes (300 $g.m^{-2}$) (Table 2.8A, Figure 2.9). The Delagoa Overlap Bioregion comprised mainly macrophytes (204 $g.m^{-2}$), filter-feeders (373 $g.m^{-2}$), grazers (42 $g.m^{-2}$) and auto-heterotrophs (232 $g.m^{-2}$) (Table 2.8B), whereas the Tropical Indo-West Pacific Bioregion was characterised by a high biomass of auto-heterotrophs (2540 $g.m^{-2}$) and nearly equal contributions from grazers (188 $g.m^{-2}$), filter-feeders (170 $g.m^{-2}$) and macrophytes (143 $g.m^{-2}$) (Table 2.8C).

Table 2.7. Trophic group data; one-factor PERMANOVA using a distance-based multivariate analysis for a linear model based on Bray-Curtis dissimilarity values and $\log_{10}(x+1)$ transformed biomass data between the Subtropical Natal Bioregion, Delagoa Overlap Bioregion and Tropical Indo-West Pacific Bioregion. * Indicates significant differences ($P < 0.05$). Pairwise *a-posteriori* multivariate comparisons between bioregions were further investigated with PERMANOVA before performing univariate non-parametric Kruskal-Wallace ANOVAs on each trophic group. Post-hoc Dunns' tests ($P < 0.05$) were used to further separate factors within each trophic group. S = Subtropical Natal Bioregion, D = Delagoa Overlap Bioregion, T = Tropical Indo-West Pacific Bioregion.

Source	*df*	MS	*F*	$P_{(perm)}$	MS_{denom}
Bioregion	2	24718.24	28.59	0.0001*	Residual
Residual	52	22479.99			
Total	54				

Multivariate Pairwise Comparisons	*t*	$p_{(perm)}$
Subtropical Natal vs. Delagoa	2.85	0.0002*
Delagoa vs. Tropical	4.24	0.0001*
Subtropical Natal vs. Tropical	5.57	0.0001*

Kruskal-Wallace ANOVAs

Trophic group	*df*	*H*	*p*
Macrophytes	2	6.16	0.050
Auto-heterotrophs	2	31.10	0.001*
Deposit-feeders	2	9.98	0.007*
Filter-feeders	2	16.26	0.001*
Grazers	2	24.64	0.001*
Predators	2	12.04	0.002*

Dunn's multiple comparisons between bioregions for:	
Macrophytes	S = D = T
Auto-heterotrophs	S = D < T
Deposit-feeders	S = D ≤ T
Filter-feeders	T < D = S
Grazers	S < D = T
Predators	S = D = T

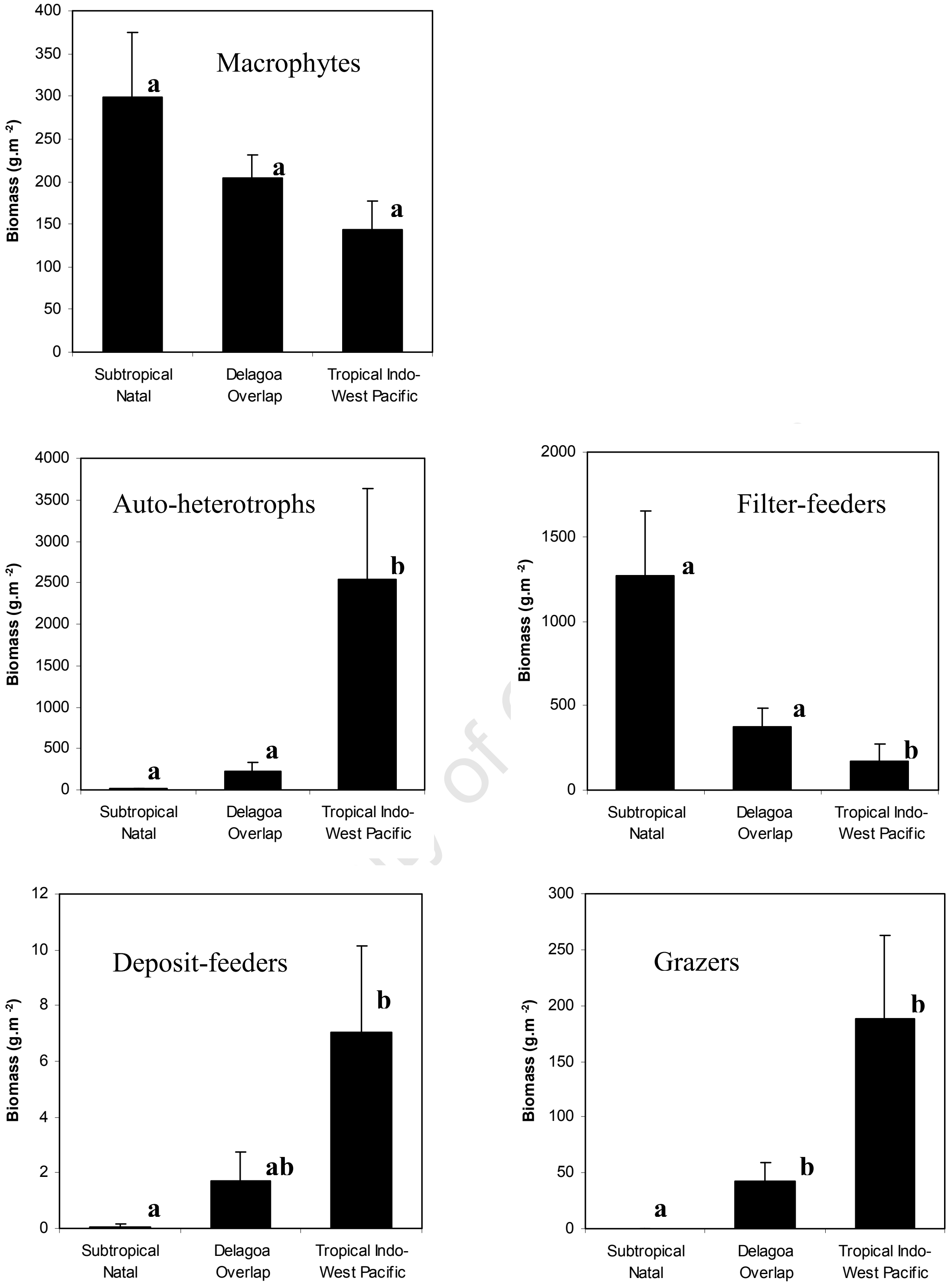


Figure 2.9. Average (+ SE) ash-free biomass of five trophic groups showing comparisons among bioregions. Letters above data differ in cases of significant differences among bioregions (PERANOVA and *a posteriori* Dunn's tests, $P < 0.05$). Predators were omitted as values were consistently low.

Table 2.8A-C. Trophic group data; similarity percentage breakdown analysis (SIMPER) for the three bioregions based on $\log_{10}(y+1)$ transformed trophic group biomass data using the Bray-Curtis similarity measure. Av. Abund. = the average abundance of that trophic group across *n* sites. Av. Sim. = the average contribution of that trophic group to the overall similarity in that region. Sim/SD = the average similarity of that particular trophic group divided by the standard deviation of its similarity. Contrib. % = the contribution of that trophic group to the overall similarity and Cum.% = the cumulative contribution of trophic groups to the overall similarity.

A) Subtropical Natal Bioregion

n 17

Average similarity (%) 74.76

Trophic Group	**Av. Abund. (g.m^{-2})**	**SD (g.m^{-2})**	**Av. Sim.**	**Sim/SD**	**Contrib.%**	**Cum.%**
Filter-feeders	1269.68	1561.37	37.46	3.72	50.10	50.10
Macrophytes	299.58	306.59	34.05	3.54	45.55	95.65
Auto-heterotrophs	10.84	24.10	1.77	0.34	2.37	98.02
Predators	16.11	41.26	1.45	0.27	1.94	99.97
Deposit-feeders	0.07	0.25	0.02	0.09	0.03	100.00
Grazers	0.02	0.08	0.00	NA	0.00	100.00

B) Delagoa Overlap Bioregion

n 14

Average similarity (%) 75.52

Trophic Group	**Av. Abund. (g.m^{-2})**	**SD (g.m^{-2})**	**Av. Sim.**	**Sim/SD**	**Contrib.%**	**Cum.%**
Macrophytes	204.36	102.94	31.69	4.15	43.70	43.70
Filter-feeders	373.21	431.01	26.63	2.67	36.72	80.42
Grazers	42.29	65.09	7.44	0.79	10.26	90.68
Auto-heterotrophs	232.11	341.55	5.12	0.52	7.06	97.74
Deposit-feeders	1.70	3.93	1.64	0.58	2.26	100.00

C) Tropical Indo-West Pacific Bioregion

n 24

Average similarity (%) 72.08

Trophic Group	**Av. Abund. (g.m^{-2})**	**SD (g.m^{-2})**	**Av. Sim.**	**Sim/SD**	**Contrib.%**	**Cum.%**
Auto-heterotrophs	2540.00	5365.42	31.29	3.70	43.41	43.41
Grazers	188.26	361.52	13.40	1.43	18.59	61.99
Filter-feeders	169.54	499.87	12.65	1.41	17.55	79.54
Macrophytes	142.65	173.45	12.20	1.27	16.93	96.47
Deposit-feeders	7.03	15.34	2.54	0.56	3.53	100.00

Biomass

A significant difference was found in average biomass among bioregions (ANOVA, $F_{(2,52)} = 3.80$, $P < 0.05$) (Table 2.9). The Delagoa Overlap Bioregion had the lowest average biomass of 853 $g.m^{-2}$. Subtropical Natal (1596 $g.m^{-2}$) had a value nearly double that and the biomass for Tropical Indo-West Pacific (3047 $g.m^{-2}$) was almost double again (Figure 2.10). Post-hoc Student Newman Keuls tests revealed that only the Delagoa Overlap Bioregion and the Tropical Indo-West Pacific Bioregion differed significantly ($P < 0.05$).

Table 2.9. Biomass data. One-way ANOVA to investigate differences in total biomass between bioregions. The data were log-transformed to meet the assumption of normality. Significant differences ($P < 0.05$) are indicated with a *. SNK tests were used to further separate significant levels within the factor.

Source	*df*	SS	MS	F	*P*
Bioregions	2	1.34	0.67	3.80	0.029*
Residual	52	9.16	0.18		
Total	54	10.5			

Comparison	Diff. of Means	q	*P*
Subtropical Natal vs. Delagoa	0.176	1.643	0.251
Delagoa vs. Tropical	0.382	3.826	0.025*
Subtropical Natal vs. Tropical	0.206	2.188	0.128

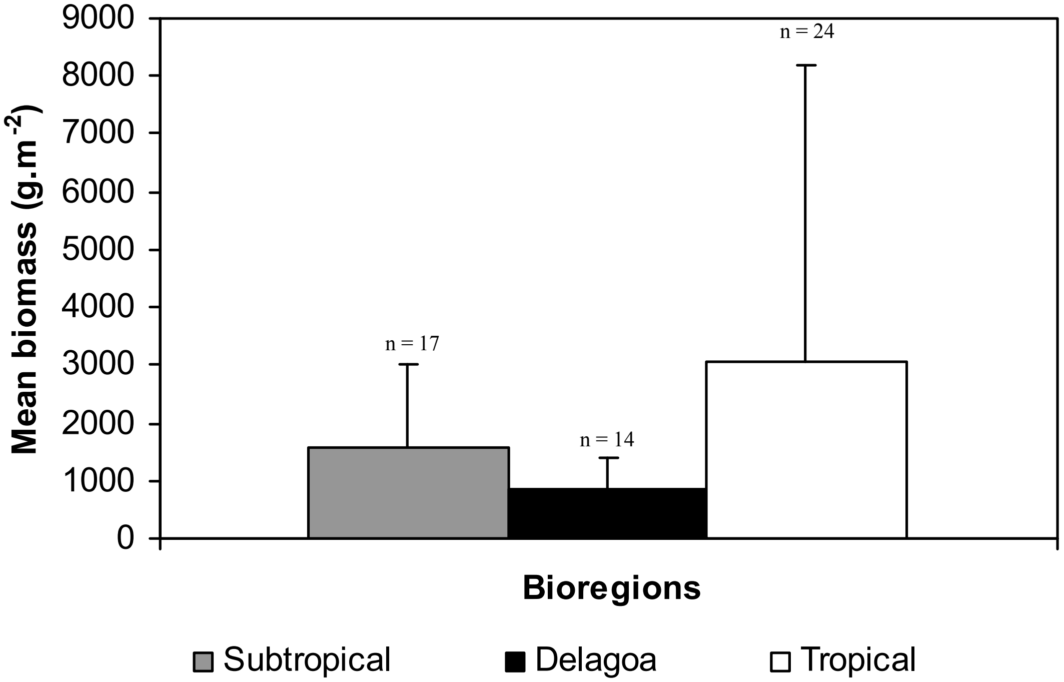


Figure 2.10. Mean (+ 1 SD) biomass (g.m^{-2}) of sites in the Subtropical Natal, Delagoa Overlap and Tropical Indo-West Pacific bioregions; n = number of sites.

DISCUSSION

Biogeography

Two distinct marine provinces (Subtropical Natal & Tropical Indo-West Pacific) were recognised from the biomass data collected from the 55 shallow subtidal reefs and tested with robust non-parametric multivariate statistical methods (Figures 2.5 to 2.7 & Tables 2.2, 2.3). Thus the null hypothesis could be rejected. Furthermore, the difference between the two marine provinces that were defined *a-priori* could be ascribed to differences in community composition rather than differences in variability between biogeographic regions, as reflected in the outcome of the distance-based test for homogeneity of multivariate dispersions (Table 2.4). The identification of two distinct marine provinces is in agreement with other quantitative studies conducted in the intertidal zone and in deeper subtidal areas that have dealt with the east coast of South Africa and further south (Jackson 1976; Emanuel *et al.* 1992; Bustamante 1994; Bustamante & Branch 1996a; Turpie *et al.* 2000; Sink 2001; Evans 2005; Lawrence 2005; Sink *et al.* 2005). However, my study differs from those that have used seaweed endemism as the main criterion for delineating biogeographic provinces (Bolton & Anderson 1997; Bolton *et al.* 2004). The two works concluded that the coast south of Cape St. Lucia represented a gradual transition zone between the Indo-West Pacific and Agulhas marine provinces and did not recognise a distinct Subtropical Natal Province (Bolton & Anderson 1997; Bolton *et al.* 2004). The lack of information on endemism for most species encountered in my study excluded its use, and conclusions may have differed had this approach been adopted.

These studies did not, however, generally extend into southern Mozambique, making the location of the boundary tenuous. According to the cluster and unconstrained MDS analyses, the biogeographic boundary between the Subtropical Natal and Tropical Indo-West Pacific provinces is not characterised by an abrupt discontinuity like that detected for intertidal organisms (Sink *et al.* 2005), but rather a finite region of transition or overlap in which six sites examined showed greater affinities with tropical communities and nine with subtropical communities (Figure 2.8). This overlap extends from Leven

Point to Kosi Mouth, a distance of approximately 120 km, and is 52 km north of St. Lucia where Evans (2005) & Lawrence (2005) established subtidal biogeographic breaks. It is also possible that the region of overlap is larger than this, in view of the absence of any sampling between Kosi Mouth and Lagoa, but from there northwards as far as Mesali Island (the northernmost site sampled) the community composition was distinctly different and comprised part of the Tropical Indo-West Pacific Province.

The concept of a region of overlap between two adjacent marine provinces rather than a distinct break is not new. Other overlap regions have been identified on the south-west (Stephenson & Stephenson 1949; Jackelman *et al.* 1991; Emmanuel *et al.* 1992; Stegenga & Bolton 1992) and south-east coasts of South Africa (Emmanuel *et al.* 1992; Bolton & Anderson 1997). The location of this overlap region corresponds with the Delagoa Bioregion (Lombard *et al.* 2004; Spalding *et al.* 2007). Bioregions are "subdivisions" within marine provinces that are characterised by a relatively homogeneous species composition, clearly distinct from adjacent systems (Spalding *et al.* 2007). In my study, three bioregions were recognisable; the Subtropical Natal Bioregion extending to the northern limits of the Subtropical Natal Province, the Delagoa Overlap Bioregion occupying an area of transition between the Subtropical Natal and Tropical Indo-West Pacific provinces and the Tropical Indo-West Pacific Bioregion, which incorporated the rest of my study region. Although the detection of the southern limit of the Subtropical Natal Bioregion was beyond the geographical scope of this work, its boundary reportedly lies near the Mbashe River mouth, in the Eastern Cape political province, where it meets the Warm Temperate Agulhas Bioregion (Lombard *et al.* 2004).

The dissimilarity between the Subtropical Natal Bioregion and the Tropical Indo-West Pacific Bioregion was high (95.5 %) (Table 2.5C), and comparable to values generated by other studies comparing bioregions in the area (Sink 2001; Lawrence 2005). Even comparisons of these two bioregions with the Delagoa Overlap Bioregion yielded relatively high dissimilarities of 86.1-87.5 % (Table 2.5A-B). Both invertebrate and algal taxa contributed to the dissimilarity between the Subtropical Natal Bioregion and the Delagoa Overlap Bioregion (Table 2.5A). The ascidian *Pyura stolonifera* was the most distinguishing species. Although present in both bioregions, it had a far lower abundance in the Delagoa Overlap Bioregion. The mussel *Perna perna* was the most distinguishing species identified by Sink (2001) in her analysis of intertidal rocky shores but *P. stolonifera* was the next most distinguishing species. However, *P. stolonifera* declines in abundance with depth, and Lawrence (2005) found that it made no contribution to distinguishing bioregions on reefs deeper than 10 m. *P. stolonifera* was also the most abundant species in both the Subtropical Natal and Delagoa Overlap bioregions and forms dense beds at some sites, similar to those recorded by Stephenson & Stephenson (1972). But in the Tropical Indo-West Pacific Bioregion, *P. stolonifera* declined radically, and was the third most important taxon distinguishing this bioregion from the Delagoa Overlap Bioregion.

Because of its abundance, algal turf ranked highly as a distinguishing group, but in reality its utility is reduced by the fact that it comprises an assortment of several algal species (Price & Scott 1992; Stuercke & McDermid 2004; Anderson *et al.* 2005) and because its abundance was persistently high, spanning values of 31.2-52.0 $g.m^{-2}$. Algal turf was followed by the articulated coralline *Amphiroa ephedraea* and the brown algae *Dictyopteris ligulata* as the most distinguishing algal species. With the exception of algal turf, these taxa were not found to be major discriminating species by Sink *et al.* (2005) or Lawrence (2005). The hard coral genera *Porites, Galaxea, Echinophyllia, Pocillopora, Acropora* and *Montipora* were more useful as an indicator of differences between bioregions, being absent or uncommon in the Subtropical Natal and Delagoa Overlap bioregions but abundant in the Tropical Indo-West Pacific Bioregion. Hard corals are not a dominant component in the intertidal zone (Sink *et al.* 2005) and on deeper reefs in the Delagoa Bioregion their high ranking as distinguishing species is replaced by alcyonaceans (Riegl *et al.* 1995; Lawrence 2005). It is widely accepted that Scleractinia are the dominant species characterising tropical reef communities (Veron 1995; Sheppard 2000).

Trophic structure

Striking differences were found in trophic structure among bioregions for many trophic groups (Figure 2.9). In particular, auto-heterotrophs such as corals contributed significantly more biomass in the Tropical Indo-West Pacific than in the Subtropical Natal Bioregion, whereas filter-feeders contributed significantly more in the Subtropical Natal Bioregion than in the Tropical Indo-West Pacific Bioregion, supporting my *a-priori* hypotheses. Corals, particularly the Scleractinia, are characteristic of warm waters low in nutrients (McClanahan 1988a) and filter-feeders have previously been found to dominate reefs in and south of the region of study in the Subtropical Natal Bioregion (Berry 1982; Celliers *et al.* 2007). Macrophytes displayed a pattern similar to filter-feeders, but deposit-feeders and grazers, both of which are mobile consumers, exhibited opposite trends.

While no standardized trophic studies have been done over regional scales in the western Indian Ocean, McClanahan (2008) has summarised a number of independent studies from the tropical east coast of Africa and provided estimated wet weights of various trophic levels per hectare. These estimates differ from my results as McClanahan (2008) found macrophytes to be the dominant trophic group whereas this study found auto-heterotrophs such as hard corals to be most dominant in the Tropical Indo-West Pacific Bioregion.

My results can also be compared with conceptual community-structure models. One of the predictions Menge and Olson (1990) have made is that under conditions of relatively high environmental stress, sessile species should dominate while mobile consumers should diminish, whereas with low environmental stress, the reverse will be true. Without an analysis of environmental variables it is difficult to determine which marine bioregion experiences more environmental stress. If, however, one assumes that stress generally increases with latitude, the prediction holds true for filter-feeders and to some extent macrophytes, which are sessile, and for deposit-feeders and grazers, which are both mobile.

However, the model fails when one considers auto-heterotrophs, which are far more abundant in the Tropical Indo-West Pacific Bioregion. Scale is an important consideration and different factors, both bottom-up and top-down, are likely to be operating to different degrees in different bioregions as well as among sites within any particular bioregion (Menge & Olson 1990; Menge 2000; Menge *et al.* 2002). High between-site variability is implied by the large standard deviations of trophic group biomasses within bioregions. In addition, another factor complicating interpretation is the treatment of the subtidal as a closed system independent of the intertidal and deeper subtidal systems. For example, predators such as fish from deeper reefs would not have been accounted for, but could have moved onto the shallow reefs and regulated urchin populations in a top-down manner (McClanahan 1988b, 1992, 1998, 1999; McClanahan & Shafir 1990).

Bottom-up and top-down effects have been found to operate synergistically in temperate marine systems on the South African west coast (Bosman *et al.* 1986; Bosman & Hockey 1986; Branch *et al.* 1987; Barkai & Branch 1988) and in New Zealand (Menge *et al.* 1999) as well as French Polynesia (Arias-González *et al.* 1997). Strong predominantly top-down effects have been demonstrated in Alaska (Estes & Palmisano 1974; Estes *et al.* 1978; Estes & Duggins 1995), and predominantly bottom-up effects in Oregon (Menge 1992; Menge *et al.* 1994; Menge *et al.* 1997; Sanford & Menge 2001). Furthermore, bottom-up oceanographic mechanisms that directly affect prey recruitment rates and indirectly affect rates of predation have been found to govern community structure in many marine systems (Menge *et al.* 2002). All these factors could be playing a role in determining trophic structure at a variety of spatial scales. Chapter 4 throws light on the potential role of a variety of factors at the scales of both the entire region and among reefs within bioregions.

Biomass

Average total biomass among bioregions differed to a lesser degree than within trophic groups, being higher in the Tropical Indo-West Pacific Bioregion, which had twice the biomass of the Subtropical Natal Bioregion and four times that of the Delagoa Overlap Bioregion (Figure 2.10). An intertidal biomass study around the whole coast of South Africa found significant differences in biomass among regions that were attributed to large-scale gradients of primary production (Bustamante 1994; Bustamante & Branch 1996a). Intertidal biomass on the South African east coast averaged approximately 465 g.m^{-2} with a maximum of 4461 g.m^{-2} (Bustamante 1994; Bustamante & Branch 1996a). The average subtidal ash-free biomass of all three bioregions in my study far exceeded that found by these authors for intertidal areas on the east coast and even on the highly productive west coast.

Two points of interest emerge. First, the shallow subtidal is clearly a high-biomass zone relative to intertidal rocky shores and, in all probability, is more productive although this cannot be taken for granted as their relative productivity:biomass ratios are unknown. A study by Berry (1982) at a single site on a shallow subtidal reef in the Subtropical Natal Bioregion independently supports the view that shallow reefs support high biomass, with an average dry biomass of 2259 g.m^{-2} being recorded for the ascidian *Pyura stolonifera*, the most dominant community component on shallow subtidal reefs in the Subtropical Natal Bioregion. Using a biomass conversion factor derived from my work, this equates to 1604 g.m^{-2} ash-free dry biomass, which closely approximates the average ash-free dry biomass of 1596 g.m^{-2} recorded for the Subtropical Natal Bioregion in this study.

Second, the high biomass in the Tropical Indo-West Pacific Bioregion was unexpected. A positive correlation between nutrient-induced primary productivity and overall biomass has been found around the South African coast (Bustamante *et al.* 1995a) and it is widely recognised that high nutrient concentrations enhance primary productivity (Dugdale 1967; Bosman & Hockey 1986). The west coast of South Africa, which experiences nutrient-rich water as a result of upwelling (Schumann *et al.* 1982), supports the highest biomass along the coast (Payne & Crawford 1989). The East African coast south of Somalia is, however, largely nutrient limited (Bell 1972; McClanahan 1988a) and one of the reasons is that a thermocline restricts the movement of nutrients to the surface (Dugdale 1967). The Tropical Indo-West Pacific Bioregion was therefore not expected to have a high average biomass relative to that of the other bioregions examined. I did predict differences in biomass among bioregions, but my hypothesis of higher biomass in the Subtropical Natal than in the Tropical Indo-West Pacific Bioregion was decisively rejected by the reverse trend that emerged.

Scleractinia contributed most to the Tropical Indo-West Pacific Bioregion biomass and are particularly well adapted to living in low-nutrient waters (Muscatine & Porter 1977). They are able to accumulate a high standing stock biomass as their growth is indeterminate and they may grow several meters in diameter and live for centuries (Jackson 1991). Biomass may thus accumulate over long periods even if productivity is low. The determination of relative productivities of bioregions lies outside the scope of my study, but does needs to be undertaken.

The Delagoa Overlap Bioregion had the lowest average biomass, possibly due to the fact that the area is exposed to warm tropical waters (Anderson *et al.* 2005; Lutjeharms 2006) low in nutrients yet not warm enough to allow for proliferation of Scleractinia in the form of biogenic accreting coral reefs (Riegl *et al.* 1995; Schleyer 1999), as occurs further north.

The average biomass of the Subtropical Natal Bioregion was greater than that of the Delagoa Overlap Bioregion, albeit non-significantly. This may be explained in part by prevailing oceanographic conditions. Topographic upwelling is a characteristic of a section of this coast (Lutjeharms *et al.* 2000) and may sustain a higher primary productivity with a net increase in benthic biomass. However, these waters are also cooler, and act as a barrier to many Tropical Indo-West Pacific species (Bolton *et al.* 2004) such as the Scleractinia that contribute so greatly to biomass in the Tropical Indo-West Pacific Bioregion. Additionally, light penetration is less in the Subtropical Natal Bioregion than further north in the Delagoa Overlap Bioregion, because of the greater river input of sediment in the south (Sink 2001). This is also likely to inhibit growth of Scleractinia (Fabricius 2005).

Another characteristic of the biomass values recorded in each bioregion, especially the Tropical Indo-West Pacific, was the large standard deviations. This reflects high variability among sites and implies that local-scale variables may be an important determinant of biomass (Fraschetti *et al.* 2005). Bustamante (1994) and Bustamante & Branch (1996a) have found that local scale variables, most importantly wave action, were central to explaining intertidal biomass patterns within biogeographic provinces.

Conclusions

Two distinct marine provinces are evident on the east coast of Africa: the Subtropical Natal Province and the Tropical Indo-West Pacific Province. These marine provinces are separated by a region of overlap on the north-east coast of South Africa, rather than by an abrupt biogeographic break. This area corresponds to localities where previous studies have identified biogeographic breaks on the South African east coast (Bolton *et al.* 2004; Evans 2005; Lawrence 2005; Sink *et al.* 2005). The hypothesis that there is a biogeographic discontinuity in the vicinity of St. Lucia is therefore supported.

Within the two marine provinces, three bioregions were identifiable, one of which forms an overlap area between Subtropical Natal and Tropical Indo-West Pacific provinces and corresponds in location to the Delagoa Bioregion. South of this bioregion lies the Subtropical Natal Bioregion, and north of it the Tropical Indo-West Pacific Bioregion.

Trophic structure among the three bioregions differed significantly for a number of trophic groups and also showed high variability among sites within bioregions. Filter-feeders and macrophytes decreased from south to north, while auto-heterotrophs, deposit-feeders and grazers displayed an opposite pattern. These findings support the hypothesis that the proportion of auto-heterotrophs is higher in the Tropical Indo-West Pacific Bioregion than in the Subtropical Natal Bioregion while the proportion of filter-feeders is lower in the Tropical Indo-West Pacific Bioregion than in the Subtropical Natal Bioregion.

Overall biomass also showed regional patterns with high between-site variability. The Tropical Indo-West Pacific Bioregion had the highest biomass and the Delagoa Overlap Bioregion the lowest. This was not expected, as I hypothesised that the Tropical Indo-West Pacific would have the lowest average biomass due to limited nutrient availability and low primary productivity. The hypothesis that the Subtropical Natal Bioregion has the highest average biomass was therefore not accepted.

The results of this Chapter also indicate considerable between-site variation. Chapter 3 therefore deals with the classification of shallow subtidal reef communities within the study region. A number of potential abiotic variables may underlie differences in regional and local community structure and in Chapter 4 I employ *in-situ* and remote sensing satellite data to analyze abiotic variables hypothesised to underpin variability at regional and local scales.

CHAPTER 3

COMMUNITY TYPES ON REEFS IN THE WESTERN INDIAN OCEAN

ABSTRACT

In this chapter I identify and define community types on horizontally orientated reef substrata in the three bioregions delineated in Chapter 2, i.e., the Subtropical Natal, Delagoa Overlap and Tropical Indo-West Pacific bioregions. Fifty-four sites were sampled, and biomass values used to quantitatively define discrete community types with similarity profile permutation tests. The most important characteristic and distinguishing taxa for each community type were then determined by similarity percentage breakdown analyses. In total, 12 statistically discrete horizontal community types were defined. One dominated most reefs in the Subtropical Natal Bioregion and was characterised by a high biomass of the solitary ascidian *Pyura stolonifera*, articulated coralline algae, particularly *Amphiroa ephedraea,* and algal turf. The Delagoa Overlap Bioregion however comprised a higher diversity of communities, which were often dominated by algal turf but also comprised noteworthy elements of *P. stolonifera,* and various Alcyonacea and Scleractinia. In the Tropical Indo-West Pacific Bioregion, eight communities were distinguished, although one was by far the most frequent, being found on 12 of the 24 reefs surveyed. Scleractinians, particularly *Porites* spp., *Pocillopora* spp. and *Galaxea* spp. dominated this community. Most other communities in this bioregion also included Scleractinia but were distinguishable by lower biomass values of *Galaxea* spp. and other taxa often unique to a particular community. In addition, I investigated community divergence between horizontal and vertically orientated reef substrata, at a subset of three sites in the Delagoa Overlap Bioregion. Using a two-way crossed permutational multivariate analysis of variance and a permutational analysis of multivariate dispersions, a significant difference was revealed between communities on horizontal and adjacent vertical reef surfaces ($P_{\text{(Monte-Carlo)}} = 0.0001$). Communities on vertical reef surfaces exhibited low variation within and between sites (13.1-18.6 %) and were dominated by *Pyura stolonifera* (72.4 %). Those on horizontal reef surfaces however had a more even abundance of species and comprised various species of large phaeophytes (7.4 %) and *P. stolonifera* (7.2 %), and exhibited high within- and between-site variation (72.7-100.0 %). The striking differences between communities on horizontal and vertical surfaces need to be considered when planning future studies in the region, and when prioritising regions for marine protected areas (MPAs). Many of the community types distinguished

(25 %) are not represented within MPA networks and, despite considerable progress in recent years, the region is still deficient in MPAs that will protect all community types.

INTRODUCTION

Reef community types

A community can be defined as a collection of species occurring in the same place at the same time (Fauth *et al.*1996). Others have proposed similar definitions, all governed by space and time and with "species" as their central operational unit, and most incorporate some degree of interaction among species (Krebs 1985; Freedman 1989; Ricklefs 1990; Tudge 1991; Begon *et al.* 1990; Smith 1992).

Communities have often been the focal unit of baseline studies in marine ecology (Dayton 1971; Underwood 1981; Lubchenco *et al.* 1984; McQuaid & Branch 1984; Leliaert *et al.* 2000), because they are statistically discrete, yet holistic entities that can be quantified. The study of ecological patterns, and thus communities, is therefore a necessary precursor for explanatory models about processes (Underwood *et al.* 2000).

In applied marine conservation, protection of communities is favoured rather than traditional single-species conservation (Norse 1993; Gray 1997; Emanuel *et al.* 1992). For this, biodiversity assessments need to be made at the community level (Ray 1991), and all communities (sometimes referred to as habitat types) need to be represented in marine protected areas (Attwood *et al.* 1997; Hockey & Branch 1997; Roberts *et al.* 2003a). This entails initially defining community types quantitatively in terms of species composition.

Such an approach has been adopted by many, including Hiscock (1995), Jones *et al* (2000), Tittley & Neto (2000), Sink (2001) and Wallenstein & Neto (2006). Of particular relevance to my study, Sink (2001) quantified and defined 69 intertidal community types in the political province of KwaZulu-Natal on the north-east coast of South Africa, and then assessed the conservation status of each type, revealing that only 28 % of the communities recognised occurred in fully protected areas.

The east coast of South Africa is subjected to warm water from the tropics which gradually cools as it moves southward (Brown & Jarman 1978) and begins to mix with the West Wind Drift and the waters of the Benguela Current. Larvae are transported southwards from tropical east Africa (Briggs 1974; Brown & Jarman 1978) and consequently the marine biota on the north-east coast of South Africa has a distinctly tropical component (Stephenson 1947; Ekman 1953; Hommersand 1986; Farrell *et al.* 1993).

North of South Africa, in Mozambique and Tanzania, the fauna and flora are dominated by an increasing number of tropical species and the appearance of true accretive coral reefs (Sheppard 2000). Approaching the equator, there is a general transition from reefs dominated by algal communities, through mixed algal-coral communities that do not form reefs, to domination by corals that form the accretive reefs defining tropical communities (Sheppard 2000).

Overview of previous surveys in the region

The Subtropical Natal Bioregion: Most subtidal research on the Natal Bioregion, which lies on the east coast of South Africa, has focused on reefs deeper than 10 m (see review by Schleyer 2000). Two unpublished studies report communities dominated by brown and red algae, most of which form algal turfs comprising multiple species (Evans 2005; Lawrence 2005), and a general decrease in algal biomass with depth (Evans 2005). A variety of poriferan and ascidian species contribute significantly to community structure but Scleractinia and Alcyonacea are almost absent from these reefs (Lawrence 2005). Brash (2006) and Schleyer et al. (2006) found a similar community composition on the offshore reef at Aliwal Shoal.

Reefs shallower than 10 m have received much less attention. Berry (1982) did investigate an artificial reef near Durban at approximately 2 m depth, and found it dominated by filter-feeders, particularly the bivalves *Perna perna* and *Striostrea margaritacea* and the ascidian *Pyura stolonifera*, but this is the only description of a shallow reef in this region. There is thus a considerable gap in knowledge about the community structure of shallow reefs in this area.

The Delagoa Overlap Bioregion: The northern region of South Africa and the southern limit of the Tropical Indo-West Pacific Province, identified in Chapter 2 as the Delagoa Overlap Bioregion, is characterised by communities that differ significantly from those further south. It contains some of the southern-most scleractinian species in the world (Schleyer 2000), but no true coral reefs that lead to biogenic accretion (Ramsey & Mason 1990; Riegl *et al.* 1995; Schleyer 1999).

Again, very little work has been done on subtidal reefs shallower than 10 m in this region, whereas considerable research has been focused on deeper reefs, including a detailed fine-scale community classification (Celliers *et al.* 2005; Schleyer & Celliers 2005). Alcyonacea and various species of Scleractinia dominate these deeper reef communities (Boshoff 1980; Riegl 1993; Riegl *et al.* 1995; Schleyer 1995, 1999, 2000; Schleyer & Celliers 2005; Lawrence 2005). Algal turf is also a major community component (Anderson *et al.* 2005; Evans 2005; Lawrence 2005). In contrast to reefs in the Subtropical Natal Bioregion, where poriferans and ascidians comprise a major proportion of the community (Lawrence 2005; Brash 2006; Celliers *et al.* 2007), they are less significant in the Delagoa Overlap Bioregion.

The first baseline studies at Inhaca Island on the Mozambique south coast were conducted in 1935 (Boshoff 1958, 1981). These revealed communities largely characterised by scleractinian hard corals at depths of 1 m, with diversity increasing in waters of 2-3 m. Few species of Alcyonacea were recorded.

More recently, a survey by Robertson *et al.* (1996) of ten reefs shallower than 30 m south of Inhaca Island recorded hard and soft coral cover of 33 to 93 %, dominated by Alcyonacea, similar to the reefs on the north-east coast of South Africa. Other studies have found community constituents comparable to those described by Boshoff (1958), but with varying degrees of algae, Scleractinia and Alcyonacea (Kalk 1959; Pereira & Gonçalves 2004). However, community structure can change significantly after floods, resulting in a community dominated by algal turf with low cover of Scleractinia and a near absence of Alcyonacea (Pereira & Gonçalves 2004).

The Tropical Indo-West Pacific Bioregion: Most of the coasts of Mozambique, Madagascar and East Africa fall in the enormous Tropical Indo-West Pacific Province although southern Mozambique most likely lies within part of the Delagoa Overlap Bioregion. A large proportion of the Mozambican coast is fringed with reefs that are interspersed with large deltas, mangrove swamps and seagrass beds (Sheppard 2000). However, very little is known about the subtidal reefs (Rodrigues *et al.* 2000).

Communities in the Bazaruto Archipelago in central Mozambique are dominated by coral cover of up to 90 % (Rodrigues *et al.* 2000), but with a high diversity of Alcyonacea (Benayahu & Schleyer 1996; Benayahu *et al.* 2003). No latitudinal trend seems to exist in alcyonacean diversity, with 38 species being recorded on the east coast of South Africa, dropping to 29 species in the Bazaruto Archipelago, rising to 46 species along the Mozambique north coast and 46 species along the Tanzanian coast (Benayahu *et al.* 2003).

Communities similar to those of the Bazaruto Archipelago and characterised by Scleractinia are also found further north at Mozambique Island (Kalk 1959), in the Segundas Archipelago (Frontier Mozambique 1997a), and in the Quirimbas Archipelago (Rodrigues *et al.* 2000), where a high diversity of algae has also been recorded (Carvalho & Bandeira 2001). In the Quirimbas Archipelago, shallow reef communities are dominated by *Acropora* and deeper reefs by *Montipora* and *Echinopora* (Frontier Mozambique 1997b; Frontier Mozambique 1998a, b, c).

The coast of Tanzania similarly comprises coral reefs, mangrove swamps, seagrass and algal beds (Darwall & Guard 2000). A relatively high diversity of scleractinian corals has been recorded in Tanzania (IUCN 1987; Darwall & Guard 2000; McClanahan *et al.* 2007) and these are the dominant community components on shallow reefs (Hamilton & Brakel 1984). Mafia Island reefs are dominated by as much as 50 % scleractinian cover in the shallows, but as depth increases there is a gradual decrease in scleractinian cover, associated with increasing alcyonacean cover (Gaudian & Richmond 1990; Horrill 1991; Horrill & Ngoile 1992; Darwall *et al.* 1995; Horrill & Church 2000; Horrill *et al.* 2000). The 1998 bleaching event has, however, drastically reduced coral cover (Garpe & Öman 2003).

Communities largely dominated by a diverse array of Scleractinia but with noteworthy elements of Alcyonacea and algae have also been recorded from the Songo Songo Archipelago in Tanzania and a number of baseline studies have described community structure on reefs there and at nearby Kilwa and Mtwara Districts (Darwall *et al.* 1994; Choiseul & Darwall 1996; Darwall 1996; Darwall & Choiseul 1996; Darwall *et al.* 1996a, b, c, d, 1997; Hanaphy & Muller 1996; Guard *et al.* 1998a, b, c).

The reef communities and biodiversity of the offshore oceanic islands of the Comoros are not well studied (Ahamada *et al.* 2002, 2004). Typical of most tropical reefs in the region, the major community component is scleractinian corals, spanning 42-70 % cover (Ahamada *et al.* 2004).

Madagascar is host to some of the largest expanses of reef in the western Indian Ocean: in the order of 2230 km^2 (Gabrié *et al.* 2000; Spalding *et al.* 2001). Very little is known about these reefs, particularly those on the north and east coasts (see McClanahan *et al.* 2007) but the south-west region of the island at Toliara (Tulear) has received some attention (Gabrié *et al.* 2000). Historical records document domination by Scleractinia in addition to encrusting coralline algae, Porifera and rhodophytes (Pichon 1978). *Acropora* was found to be a dominant community component of sunlit areas (Vasseur 1974; Pichon 1974a,b) while a high diversity of sponges, algae and other Scleractinia were prominent on deeper, more shaded areas (Jaubert & Vasseur 1974; Vasseur 1974, 1977; Vacelet & Vasseur 1977).

Recent accounts of Madagascar are rare. Higgs *et al.* (2007) agreed with historical reports in finding scleractinians as the dominant community component, and McClanahan *et al.* (2007) found coral communities there to be most similar in composition to those of southern Kenya, Mauritius and Seychelles, despite many reefs in Madagascar being subjected to high rates of sedimentation as a result of deforestation and poor farming practises (Cook *et al.* 2000).

The majority of works mentioned above have been broad taxonomic descriptions of reef community components, mostly for reefs deeper than 10 m. Only one account (Schleyer & Celliers 2005) has classified communities using repeatable quantitative statistical methods. There is thus also a considerable knowledge gap in terms of shallow reef community structure in the western Indian Ocean, particularly on the east coast of South Africa, southern Mozambique and Madagascar. Indeed, the western Indian Ocean as a whole is considered the least known of the tropical oceans (Sheppard 2000; Bergman & Öhman 2001).

Divergence between communities on horizontal and vertical reef surfaces

Several descriptive studies have detailed differences between the communities of horizontal and vertical reef surfaces (Knott *et al.* 2004; Perkol-Finkel *et al.* 2006). In addition, experimental studies have demonstrated differences (Glasby 2000; Glasby & Connell 2001; Fowler-Walker & Connell 2007) and have found that reef orientation may be a more important factor in determining community structure than whether the substratum is of natural or anthropogenic origin (Glasby & Connell 2001). Despite this, in most studies the community structure on vertically orientated reef surfaces has simply been ignored.

Scope of the study

This study focuses on the shallow subtidal community structure of horizontal reef surfaces at 54 sites located in the western Indian Ocean, in an area spanning 31°S to 10°S. It defines reef community types using multivariate statistical methodologies based on quantitative biomass data, and classifies and describes these community types according to their distinguishing and characteristic species. Divergence between communities on horizontal reef surfaces and those on adjacent vertical reef surfaces was also investigated for a subset of these sites, to quantify such heterogeneity and initiate discussion on why such differences exist and how they relate to ecosystem functioning.

Specifically, this chapter addresses the following questions:

1) How many statistically discrete horizontal community types can be recognised?
2) What species characterise and distinguish these communities?
3) Do communities on horizontally orientated reef surfaces differ from those on vertical reef surfaces?

METHODS

Biological sampling

Reef community types

Communities were sampled on the horizontal surfaces of 54 shallow subtidal reefs in the western Indian Ocean region (See Figure 2.3 and Table 2.1 on p 24 and 25 in Chapter 2 for positions and details). For detailed methodology, refer to Chapter 2 but, in brief, at each site 15 replicate quadrats were randomly placed on horizontal reef surfaces and percentage cover recorded for sessile and sedentary species, and mobile species counted in 10 replicate belt transects of 5 x 2 m. Percentage cover and species counts were then converted into ash-free dry biomass, and subjected to analyses summarised in Figure 3.1.

Divergence between communities on horizontal and vertical reef surfaces

Communities on horizontal reef surface (<20° from horizontal) and those on adjacent vertically orientated reef (80-100°) were quantified in November 2006 at a subset of three shallow subtidal sites in the Delagoa Overlap Bioregion: Quarter Mile Reef, Lala Nek and Bhanga (see Figure 2.3 & Table 2.1 in Chapter 2). Seven replicate quadrats of 100 x 50 cm were randomly placed on horizontal reef surface and seven on adjacent vertical reef surface at each of the three sites and percentage cover of all taxa recorded (Figure 3.1). Percentage cover data were then converted into ash-free dry biomass.

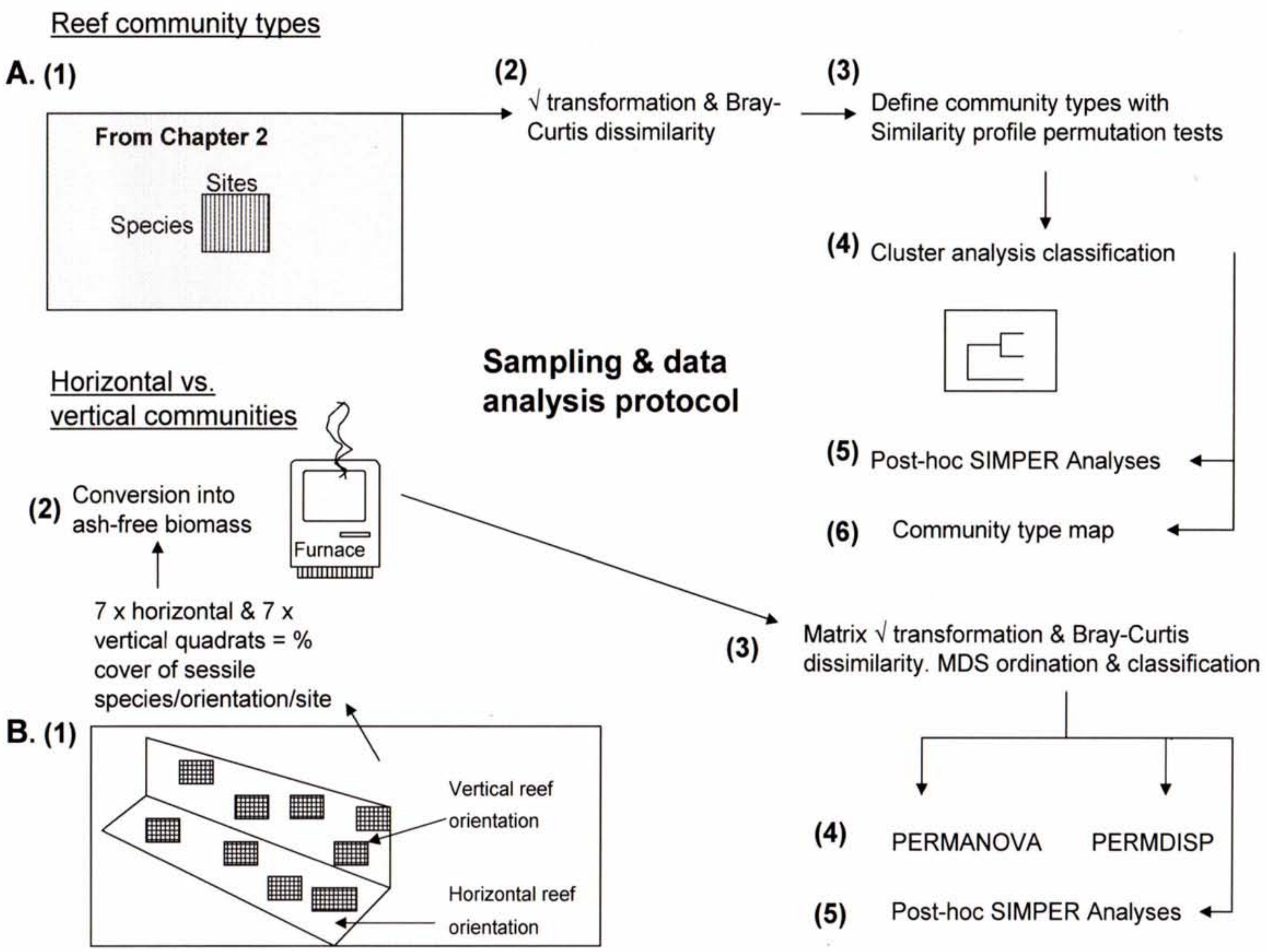


Figure 3.1. Sampling and data analysis protocol used in Chapter 3 for (A) definition of community types at 54 sites across the entire region, and (B) comparison of horizontal and vertical surface at a subset of three of the sites in the Delagoa Overlap Bioregion.

Data analysis

Reef community types

All sites analysed in Chapter 2 were considered in the analysis of reef community types, except for Vetch's Pier as it was shown to be an outlier and was the only site that was an artificial reef. Using root-transformed biomass data, community types were defined quantitatively with a multivariate similarity profile permutation test (SIMPROF) (Clarke & Gorley 2006) at a significance level of $P < 0.05$ using the Bray-Curtis similarity distance measure (Bray & Curtis 1957) and group average linkage with the Plymouth Routines In Multivariate Ecological Research version 6 (PRIMER 6.0) (Clarke & Warwick 2001). SIMPROF defines significantly different groups using permutation tests under the null hypothesis that samples (sites) within a cluster group do not differ in multivariate structure (Clarke & Warwick 2001). On this basis I was able to classify all sites into particular community types. The degree to which the actual similarity profile deviated outside of the 95 % simulated profile limits were captured formally in the π statistic.

Similarity percentage breakdown analysis (SIMPER) (Clarke 1993) was then used to determine characteristic and distinguishing species for each of the community types defined by SIMPROF and the Bray-Curtis similarity distance measure (Bray & Curtis 1957). Only the top five characteristic taxa of each community type and the top three taxa distinguishing between community types are reported.

Patterns in multivariate dispersion among sites were graphically represented with a cluster analysis dendrogram with group average linkage (Field *et al.* 1982), and community types defined by SIMPROF were superimposed. Finally, a map showing the spatial distribution of the various community types was generated for the entire region.

Divergence between communities on horizontal and vertical reef surfaces

The relationship between communities quantified on horizontal and vertical reef surfaces at the subset of three sites was represented graphically in the form of constrained and unconstrained non-metric MDS ordinations as well as a cluster analysis dendrogram. A canonical analysis of principal components (CAP) was performed using the software program CAP (Anderson & Robinson 2003; Anderson & Willis 2003) on the two communities defined *a-priori* (horizontal vs. vertical) to produce the constrained MDS ordination. Biomass data were root-transformed, the Bray-Curtis dissimilarity (Bray & Curtis 1957) distance measure used and the number of eigenvectors (principal coordinate axes) selected by the computer program to maximise the correct number of classifications (Anderson & Robinson 2003). The constrained canonical axis scores (CAP values) were then plotted for each sample (2 reef orientations x 3 sites x 7 replicates) on a single axis as only one canonical axis exists in the case of a comparison of only two groups (horizontal & vertical), yielding a constrained MDS ordination. An unconstrained non-metric MDS ordination (Kruskal & Wish 1978), using root-transformed biomass data and the Bray-Curtis dissimilarity distance measure, was created to provide an overall pattern of dispersion among points. The cluster analysis dendrogram was constructed using the Bray-Curtis dissimilarity distance measure and group average linkages. The unconstrained non-metric MDS ordination and cluster dendrogram were performed with PRIMER 6.0 (Clarke & Warwick 2001).

Two-factor non-parametric permutational multivariate analysis of variance (PERMANOVA) (Anderson 2001; McArdle & Anderson 2001) was used to test the differences in community composition between orientations and among sites, using the software program PERMANOVA 6 (Anderson 2005). The analysis followed that of a two-way crossed design, with “Orientation” as a fixed factor with two levels (horizontal and vertical) and “Site” as a fixed factor with three levels (Bhanga, Lala Nek and Quarter Mile Reef). The analysis was run with root-transformed biomass data, using the Bray-Curtis dissimilarity distance measure with 9999 unrestricted permutations of the raw data and type III sums of squares. Monte-Carlo simulations had to be used as the basis for rejecting the null hypothesis, as the required number of 9999 permutations could not be generated from the model.

The PERMANOVA analysis was supplemented with a permutational analysis of multivariate dispersions (PERMDISP) (Anderson 2004) to further investigate cases where the null hypothesis tested with PERMANOVA was rejected, as PERMANOVA is sensitive to dispersion among groups (Anderson 2004). PERMDISP helps determine whether the null hypothesis is rejected due to a difference in assemblage structure or because community types differ in terms of their variability (dispersion). The identical ANOVA design and methodology (root-transformation, Bray-Curtis dissimilarity, unrestricted permutation of raw data, 9999 permutations) used for the previous PERMANOVA were followed. The program does not however allow for the use of Monte-Carlo simulations in evaluating the null hypothesis.

Diversity measures such as total species, species richness, Pielou's evenness index (Pielou 1966) and Shannon-Weiner were calculated per quadrat. One-way permutational ANOVAs were performed on each diversity measure using quadrats as replicates to test for significant differences between orientations. *A-posteriori* SIMPER analyses (Clarke 1993) were used to determine characteristic and distinguishing species within and between vertical and horizontal communities. SIMPER and diversity analyses were performed with PRIMER 6.0 (Clarke & Warwick 2001).

RESULTS

Reef community types

In total, 12 horizontal community types were defined by SIMPROF and represented by a cluster diagram (Figure 3.2). The number of significantly different community types was indicated by the extent the actual similarity profile deviated outside of the 95 % confidence limits of the simulated profile at each rank value. This was quantified by the π statistic, which was significant (π = 4.43, *P* = 0.001). Average similarity among sites comprising a particular community type was generally low (Ave. = 37.97 %) and ranged from 18.23 % to 54.40 % (Table 3.1). Average dissimilarity between any two community types was high (Ave. = 90.74 %) and ranged from 64.22 % to 100.00 % (Table 3.1). In total, 22 taxa were recorded as top distinguishing variables between community types (Table 3.2).

Community A was found at 15 out of 54 sites, and was characterised by the solitary ascidian *Pyura stolonifera* (Table 3.2), which was also the most consistently characteristic species as reflected by its high similarity divided by the standard deviation of its similarity (Sim/SD) of 0.75. Other characteristic species were algal turf and the algae *Amphiroa ephedraea*, *Halimeda* spp. and *Amphiroa bowerbankii* (Table 3.2). This community type was almost exclusively confined to the Subtropical Natal Bioregion where it was uniformly the only community present in the south, but it also occurred at two sites in the Delagoa Overlap Bioregion (Figure 3.3). It was distinguishable from all other communities by its high biomass of *P. stolonifera*, or even the mere presence of *P. stolonifera* (Table 3.2).

Community B occurred at twelve sites, all in the Tropical Indo-West Pacific Bioregion (Figure 3.3). It was characterised by various species of Scleractinia, particularly *Porites* spp. (Table 3.2), *Pocillopora* spp., *Galaxea* spp., *Echinophyllia aspera* and *Montipora* spp. (Table 3.2). *Porites* spp. was the most consistently characteristic taxon (Sim/SD = 2.32). Community B in most cases was distinguishable based on its high biomass of *Porites* spp. and *Galaxea* spp. (Table 3.2).

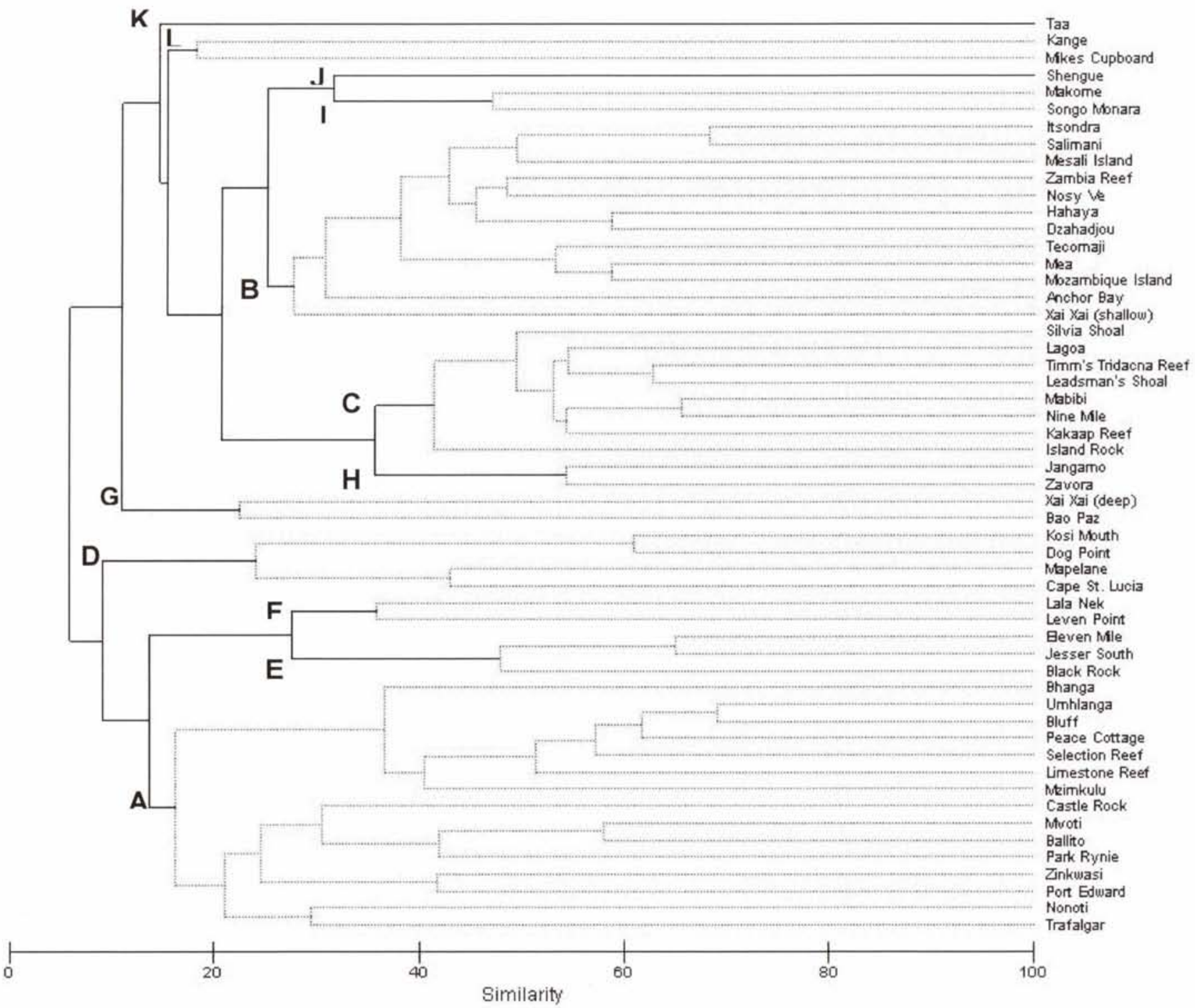


Figure 3.2. Cluster analysis dendrogram of the twelve community types (A to L) identified by terminating solid lines using similarity profile permutation tests (SIMPROF) with a 5 % significance level to define community types.

Table 3.1. Similarity percentage breakdown analyses (SIMPER) of all community types. Black cells indicate the average similarity (%) between sites for each community type while white cells indicate the average dissimilarity (%) between any two community types.

Community	A	B	C	D	E	F	G	H	I	J	K	L
A	25.35											
B	97.68	38.72										
C	84.09	74.41	50.46									
D	92.28	99.79	97.52	33.41								
E	82.86	98.17	82.83	82.82	53.59							
F	91.22	95.67	89.99	91.45	72.47	35.86						
G	94.22	89.49	83.17	99.48	93.84	92.66	22.57					
H	82.19	85.59	64.22	97.77	82.89	90.80	88.74	54.40				
I	99.76	74.09	89.51	100.00	99.70	98.59	98.25	93.87	47.11			
J	99.76	76.18	84.06	100.00	100.00	98.21	97.54	94.43	68.42	*NA*		
K	99.97	76.77	94.15	100.00	99.07	100.00	98.33	93.48	86.43	93.26	*NA*	
L	96.40	85.50	79.92	98.89	94.59	93.10	89.67	85.54	92.00	93.74	87.11	18.23

Community C was represented at eight sites, most located within the Delagoa Overlap Bioregion (Figure 3.3). Algal turf (Table 3.2), followed by *Pyura stolonifera*, the alcyonaceans *Sinularia* spp. and *Lobophytum* spp., and the scleractinian *Favites* spp. were the top five characteristic taxa (Table 3.2). Community C was largely distinguishable by its dominance of algal turf and to a lesser extent *P. stolonifera* (Table 3.2).

Community D was found at four sites in the northern parts of both the Subtropical Natal Bioregion and in the Delagoa Overlap Bioregion (Figure 3.3). This community was characterised by the large foliose phaeophyte *Dictyopteris ligulata*, the sand-incorporating colonial ascidian *Eutherdmania* spp. and the algae *Halimeda* spp., *Pachychaeta cryptoclada* and *Padina* spp. (Table 3.2). *Halimeda* spp. was the most consistently characteristic taxon (Sim/SD = 1.51 %). Community D was distinguishable from most others because of its high biomass of *D. ligulata* (Table 3.2).

Community E occurred at Eleven Mile, Jesser South and Black Rock in the Delagoa Overlap Bioregion (Figure 3.3). *Pyura stolonifera*, two species of brown algae (*Sargassum elegans* and *D. ligulata*), and a poriferan (*Placospongia* sp.) were characteristic of the community (Table 3.2). This community was consistently distinguishable from most others by its biomass of *P. stolonifera* and two species of large phaeophytes, *S. elegans* and *D. ligulata,* but also because it lacked scleractinians and alcyonaceans, and species specific to other communities such as *Hypnea pannosa* and *Spirastrella spinispirulifer* (Table 3.2).

Community F was found at Lala Nek and Leven Point in the Delagoa Overlap Bioregion (Figure 3.3). It was dominated by two poriferans, *Spirastrella spinispirulifer* and *Placospongia* sp., but also by phaeophytes such as *Zonaria tournefortii*, *Sargassum elegans* and *Lobophora variegata* (Table 3.2). It was distinguishable from almost all other communities because of its high biomass of *S. spinispirulifer* and by the absence of scleractinians.

Community G occurred at two sites, Bao Paz and Xai Xai (deep), both in southern Mozambique (Figure 3.3). It was characterised by the scleractinian genus *Montipora,* the urchin *Echinostrephus molaris* and various algae including *Metamastophora flabellata*, *Peyssonnelia capensis* and *Lobophora variegata* (Table 3.2). Community G was different from others because of the moderate biomass of *Stomopneustes variolaris* and, to an extent, the presence of *Cyphastrea crispa*. (Table 3.2).

Community H was also represented by two sites, Jangamo and Zavora, situated further north in Mozambique (Figure 3.3). This was mainly an algal turf community but had noteworthy contributions from *Perna perna*, *Pyura stolonifera*, *Pocillopora* spp. and *Echinothrix* spp. (Table 3.2). Community H differed from most others because of its high biomass of algal turf, moderate biomass of *P. stolonifera* and *Perna perna,* and the absence of many scleractinian species.

Community I was found at Songo Monara and Makome in Tanzania (Figure 3.3). It was dominated by a high biomass of scleractinians particularly *Galaxea* spp. which formed large monospecific stands at Makome. Other important taxa were *Porites* spp. and *Pocillopora* spp. (Table 3.2). The high biomass of *Galaxea* spp. distinguished this community from most other types.

Community J was unique, being found only at Shengue, Tanzania (Figure 3.3). It was characterised by a dominance of scleractinians particularly *Galaxea* spp., *Acropora* spp., *Echinophyllia aspera*, *Oulophyllia crispa* and the soft coral genus *Sinularia* (Table 3.2). In most cases it was its biomass of *Galaxea* spp. and *Acropora* spp. that distinguished this community type from others in the region.

Community K was found at Taa, Tanzania only, and comprised mainly *Porites* spp., algae including *Hypnea pannosa* and encrusting corallines, and mobile invertebrates such as *Diadema* spp. and *Protoreaster lincki*. Community K was distinguishable due to the dominance of *Porites* spp. and by the presence of *Hypnea pannosa* (Table 3.2).

Community L occurred at Mike's Cupboard and Kange (Figure 3.3). It was characterised by two genera of alcyonaceans, *Sinularia* spp. and *Sarcophyton* spp., two urchin taxa, *Echinothrix* spp. and *Echinostrephus molaris*, and the phaeophyte *Lobophora variegata*

Table 3.2. Similarity percentage breakdown analyses (SIMPER) of all community types. Black cells show the top five characteristic taxa of each community type along with the average abundance (g.m^{-2}) and (in brackets) average contribution (%) of that taxon to the overall similarity of that community type. White cells show the top three discriminating taxa between any two community types along with the average % contribution of that taxon to the overall dissimilarity. n = number of sites represented by that community type.

Community	A	B	C	D	E	F
A n = 15	*Pyura stolonifera*…….654(12.1) Algal turf…….......33(3.0) *Amphiroa ephedraea*……….54(2.8) *Halimeda* spp…...10(2.1) *Amphiroa bowerbankii*……..14(1.7)					
B n = 12	*Pyura stolonifera* 11.7 *Porites* spp. 8.4 *Galaxea* spp. 5.1	*Porites* spp……299(9.9) *Pocillopora* spp.101(5.5) *Galaxea* spp.....117(4.7) *Echinophyllia aspera*………...99(4.5) *Montipora* spp….29(2.8)				
C n = 8	*Pyura stolonifera* 11.2 Algal turf 5.6 *Sinularia* spp. 4.3	Algal turf 5.5 *Pyura stolonifera* 5.4 *Porites* spp. 5.3	Algal turf……….251(11.5) *Pyura stolonifera*……....169(5.6) *Sinularia* spp……..73(4.9) *Lobophytum* spp....47(4.9) *Favites* spp……...15(3.6)			
D n = 4	*Pyura stolonifera* 18.9 *Dictyopteris ligulata* 9.3 *Amphiroa ephedraea* 6.2	*Porites* spp. 10.8 *Dictyopteris ligulata* 6.9 *Pocillopora* spp. 6.5	Algal turf 10.5 *Pyura stolonifera* 8.2 *Dictyopteris ligulata* 6.9	*Dictyopteris ligulata*…………114(18.2) *Eutherdmania* spp...45(7.5) *Halimeda* spp……...7(2.6) *Pachychaeta cryptoclada*……….30(2.1) *Padina* spp……....…4(1.2)		
E n = 3	*Pyura stolonifera* 15.0 *Sargassum elegans* 6.5 *Amphiroa ephedraea* 5.4	*Porites* spp. 9.6 *Pyura stolonifera* 7.1 *Pocillopora* spp. 6.5	Algal turf 9.4 *Pyura stolonifera* 5.5 *Sargassum elegans* 5.3	*Pyura stolonifera* 12.0 *Dictyopteris ligulata* 9.2 *Sargassum elegans* 9.2	*Pyura stolonifera*………160(15.2) *Sargassum elegans*…………...80(14.2) *Placospongia* spp...41(8.4) *Dictyopteris ligulata*…………….10(4.5) *Dichotomaria diessingiana*……….6(3.2)	
F n = 2	*Pyura stolonifera* 16.6 *Spirastrella spinispirulifer* 8.4 *Amphiroa ephedraea* 5.3	*Porites* spp. 9.5 *Spirastrella spinispirulifer* 7.5 *Galaxea* spp. 5.7	Algal turf 9.2 *Spirastrella spinispirulifer* 7.7 *Pyura stolonifera* 7.5	*Spirastrella spinispirulifer* 14.3 *Dictyopteris ligulata* 10.6 *Eutherdmania* spp. 6.2	*Spirastrella spinispirulifer* 11.9 *Pyura stolonifera* 10.9 Ascidian sp.2 3.2	*Spirastrella spinispirulifer*...177(10.2) *Zonaria tournefortii*………16(6.7) *Sargassum elegans*…………28(6.4) *Lobophora Variegata*………..16(5.2)
G n = 2	*Pyura stolonifera* 13.7 *Stomopneustes variolaris* 9.4 *Cyphastrea* spp. 7.5	*Porites* spp. 8.0 *Stomopneustes variolaris* 7.7 *Cyphastrea* spp. 5.8	*Stomopneustes variolaris* 8.1 *Pyura stolonifera* 6.4 *Cyphastrea* spp. 6.1	*Stomopneustes variolaris* 12.0 *Cyphastrea* spp. 10.4 *Dictyopteris ligulata* 8.7	*Stomopneustes variolaris* 10.7 *Cyphastrea* spp. 8.9 *Pyura stolonifera* 8.6	*Stomopneustes variolaris* 10.5 *Spirastrella spinispirulifer* 9.2 *Cyphastrea* spp. 8.7
H n = 2	*Pyura stolonifera* 12.9 Algal turf 10.8 *Perna perna* 4.7	Algal turf 9.7 *Porites* spp. 7.7 *Galaxea* spp. 5.1	*Pyura stolonifera* 4.8 Algal turf 3.8 *Sinularia* spp. 3.6	Algal turf 19.7 *Dictyopteris ligulata* 9.5 *Pyura stolonifera* 6.6	Algal turf 17.0 *Sargassum elegans* 6.6 *Pyura stolonifera* 4.5	Algal turf 16.6 *Spirastrella spinispirulifer* 7.8 *Pyura stolonifera* 6.5
I n = 2	*Galaxea* spp. 42.96 *Pyura stolonifera* 8.9 *Echinophyllia aspera* 8.5	*Galaxea* spp. 33.9 *Echinophyllia aspera* 7.4 *Porites* spp. 2.4	*Galaxea* spp. 38.4 *Echinophyllia aspera* 7.6 Algal turf 5.2	*Galaxea* spp. 51.2 *Echinophyllia aspera* 10.0 *Porites* spp. 7.8	*Galaxea* spp. 47.4 *Echinophyllia aspera* 9.3 *Porites* spp. 7.2	*Galaxea* spp. 46.9 *Echinophyllia aspera* 9.2 *Porites* spp. 7.1
J n = 1	*Galaxea* spp. 11.44 *Pyura stolonifera* 6.2 *Acropora* spp. 5.8	*Galaxea* spp. 8.0 *Oulophyllia crispa* 5.0 *Acropora* spp. 3.7	*Galaxea* spp. 10.6 *Echinophyllia aspera* 5.3 *Oulophyllia crispa* 5.3	*Galaxea* spp. 12.9 *Acropora* spp. 6.5 *Echinophyllia aspera* 6.4	*Galaxea* spp. 12.2 *Acropora* spp. 6.2 *Echinophyllia aspera* 6.1	*Galaxea* spp. 12.2 *Acropora* spp. 6.1 *Echinophyllia aspera* 6.1
K n = 1	*Porites* spp. 29.8 *Pyura stolonifera* 7.4 *Hypnea pannosa* 5.5	*Porites* spp. 18.2 *Hypnea pannosa* 4.6 *Diadema* spp. 4.3	*Porites* spp. 23.7 Algal turf 6.4 *Pyura stolonifera* 5.3	*Porites* spp. 37.3 *Hypnea pannosa* 6.9 *Dictyopteris ligulata* 6.4	*Porites* spp. 33.7 *Pyura stolonifera* 6.7 *Hypnea pannosa* 6.2	*Porites* spp. 33.2 *Spirastrella spinispirulifer* 7.1 *Hypnea pannosa* 6.1
L n = 2	*Pyura stolonifera* 15.3 *Echinothrix* spp. 5.5 *Sinularia* spp. 5.2	*Porites* spp. 7.3 *Pocillopora* spp. 5.4 *Galaxea* spp. 5.3	Algal turf 7.1 *Pyura stolonifera* 7.0 *Echinothrix* spp. 4.5	*Dictyopteris ligulata* 10.3 *Echinothrix* spp. 7.6 *Sinularia* spp. 7.2	*Pyura stolonifera* 9.9 *Sargassum elegans* 7.1 *Sinularia* spp. 6.2	*Spirastrella spinispirulifer* 10.5 *Echinothrix* spp. 6.4 *Sinularia* spp. 6.0

G	H	I	J	K	L
Montipora spp......29(5.6) *Echinostrephus molaris*…………....15(3.9) *Metamastophora flabellate*………...22(2.9) *Peyssonnelia capensis*………….7(2.6) *Lobophora variegata*…………*9(2.5)*					
Algal turf 9.8 *Stomopneustes variolaris* 9.4 *Cyphastrea* spp. 7.5	Algal turf………522(27.9) *Perna perna*…...…58(9.5) *Pyura stolonifera*……….77(8.2) *Pocillopora* spp….32(6.3) *Echinothrix* spp….15(2.0)				
Galaxea spp. 41.5 *Echinophyllia aspera* 8.2 *Porites* spp. 6.3	*Galaxea* spp. 43.2 *Echinophyllia aspera* 8.5 Algal turf 8.4	*Galaxea* spp……13584(38.3) *Porites* spp…………314(6.9) *Pocillopora* spp……..39(1.9)			
Galaxea spp. 11.2 *Acropora* spp. 5.6 *Echinophyllia aspera* 5.6	*Galaxea* spp. 11.5 *Echinophyllia aspera* 5.8 *Oulophyllia crispa* 5.8	*Galaxea* spp. 13.9 *Echinophyllia aspera* 4.6 *Oulophyllia crispa* 4.5	*Galaxea* spp………2103 *Acropora* spp………534 *Echinophyllia aspera*…………..….526 *Oulophyllia crispa*………………524 *Sinularia* spp……….350		
Porites spp. 28.4 *Stomopneustes variolaris* 7.4 *Cyphastrea* spp. 5.5	*Porites* spp. 29.1 Algal turf 10.8 *Hypnea pannosa* 5.5	*Galaxea* spp. 36.1 *Porites* spp. 14.0 *Echinophyllia aspera* 7.2	*Porites* spp. 13.3 *Galaxea* spp. 10.2 *Acropora* spp. 5.1	*Porites* spp…...….4006 *Hypnea pannosa*…………....137 *Diadema* spp……....107 Encrusting coralline...86 *Protoreaster lincki*.....52	
Stomopneustes variolaris 9.9 *Cyphastrea* spp. 7.9 *Echinothrix* spp. 5.2	Algal turf 13.4 *Pyura stolonifera* 6.0 *Perna perna* 5.1	*Galaxea* spp. 44.6 *Echinophyllia aspera* 8.8 *Porites* spp. 5.6	*Galaxea* spp. 11.8 *Echinophyllia aspera* 5.9 *Oulophyllia crispa* 5.9	*Porites* spp. 29.6 *Hypnea pannosa* 5.8 Encrusting coralline 4.4	*Sinularia* spp……58(8.5) *Echinothrix* spp…74(3.8) *Echinostrephus molaris*…………..6(3.5) *Sarcophyton* spp…1(1.5) *Lobophora variegata*……….13(0.9)

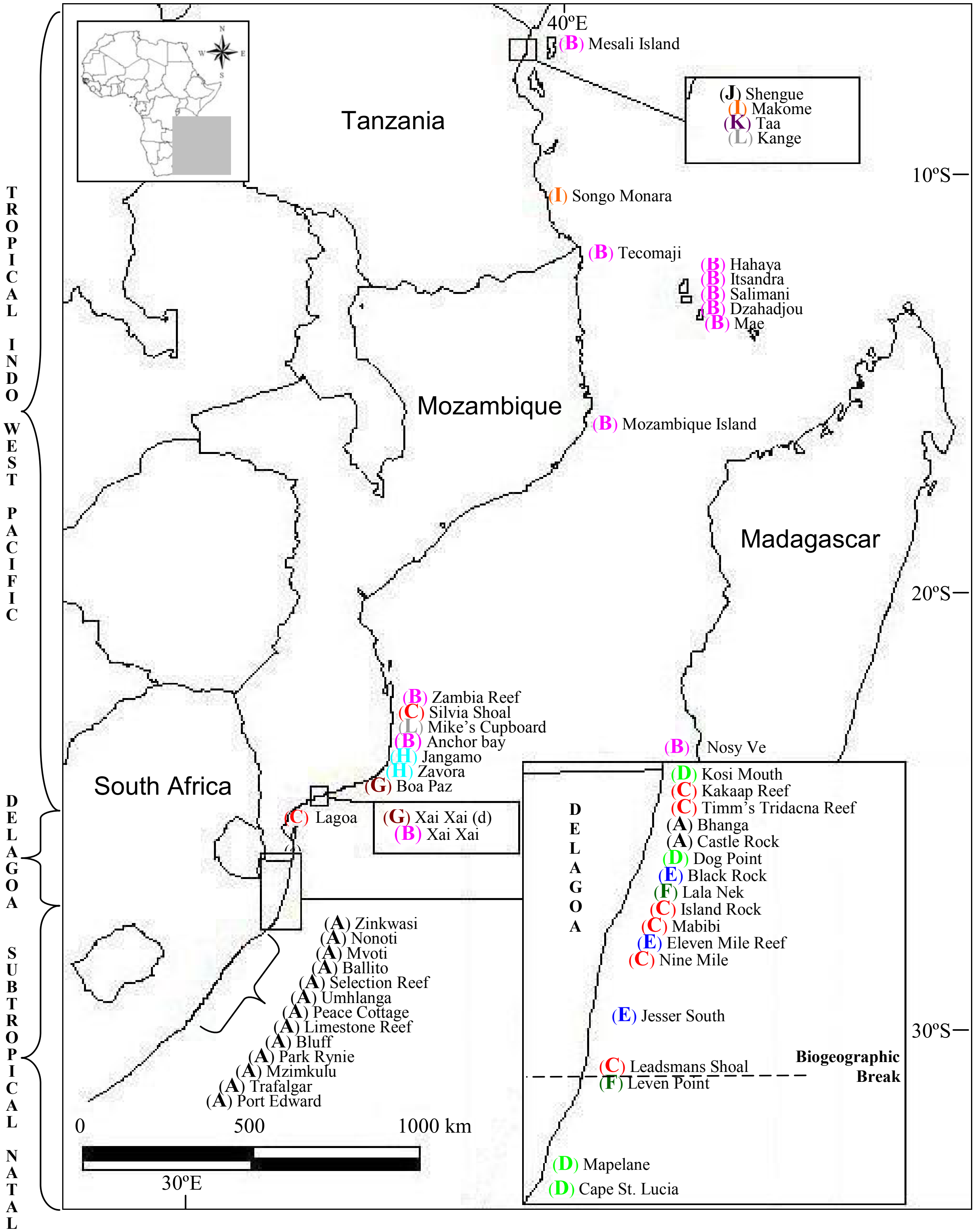


Figure 3.3. Distributions of 12 community types (A to L) defined by similarity profile permutation tests (SIMPROF) using a 5 % significance level to differentiate between community types.

(Table 3.2). It could be differentiated from most other communities by the abundance of the urchin genus *Echinothrix* spp. and in some cases *Sinularia* spp. (Table 3.2).

Divergence between communities on horizontal and vertical reef surfaces

A clear difference in community assemblage structure was found between horizontal and vertical reef surfaces (as defined *a-priori*), according to the constrained MDS ordination (Figure 3.4). There was also less variation (dispersion) in communities on vertical than on horizontal reef surfaces. The unconstrained non-metric MDS ordination showed a similar clear difference between communities on horizontal and vertical surfaces (Figure 3.5).

The associated cluster analysis dendrogram showed a low degree of similarity between them, ranging from 5 to 70 %, except for a single horizontal quadrat that was grouped within the vertical quadrats and shared 90 % similarity with them (Figure 3.6). The relationships between individual horizontal quadrats were also far more dissimilar than those between vertical quadrats, which characteristically had high levels of similarity.

PERMANOVA revealed a significant difference in community composition between communities of horizontal and vertical reef surfaces, between sites and a significant interaction between reef orientation and site ($P_{\text{(Monte-Carlo)}} \leq 0.0002$ in all cases) (Table 3.3). *A-posteriori* multivariate comparisons of the factor "Orientation" found significant differences between horizontal and vertical communities at all three sites ($P_{\text{(Monte-Carlo)}} < 0.005$). Pairwise *a-posteriori* multivariate comparisons of the factor "Site" found all sites to differ from one another in the case of horizontal communities ($P_{\text{(Monte-Carlo)}} < 0.005$), but not in the case of vertical communities ($P_{\text{(Monte-Carlo)}} > 0.05$), hence the significant interaction effect between site and orientation (Table 3.3). Bray-Curtis dissimilarity values between sites within a particular orientation were consistently lower for vertical communities (13.1-18.6 %) than for horizontal communities (72.7-100.0 %) at all three sites (Table 3.4). The same was true within sites, with values for vertical communities (4.2 – 19.0 %) being less than those for horizontal ones (20.1 – 77.4 %) (Table 3.4).

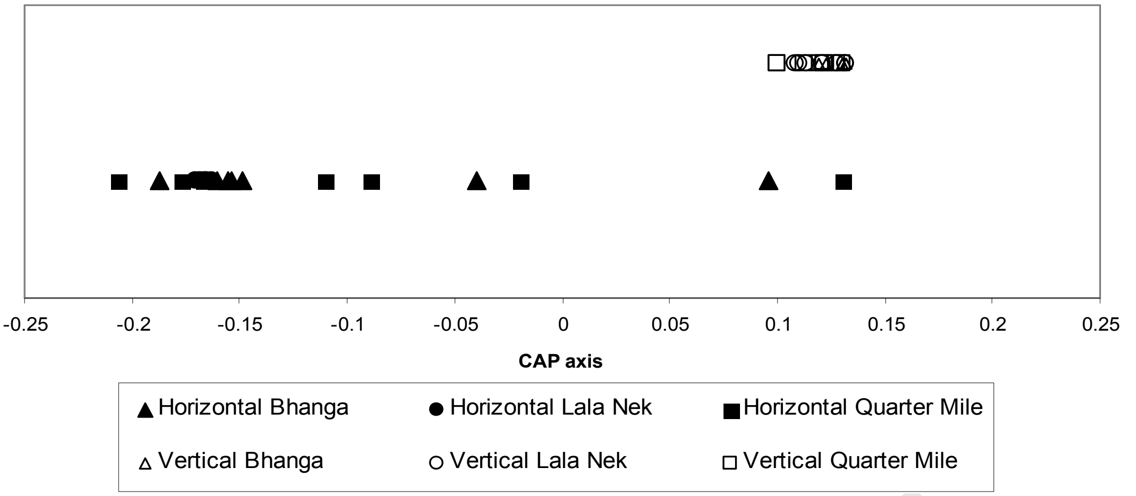


Figure 3.4. Constrained canonical analysis of principal coordinates (CAP) (constrained MDS) ordination plot of assemblages grouped *a-priori* according to whether they were sampled on horizontally or vertically orientated reef surfaces at Bhanga, Lala Nek and Quarter Mile Reef in the Delagoa Overlap Bioregion based on root-transformed biomass data using the Bray-Curtis similarity distance measure.

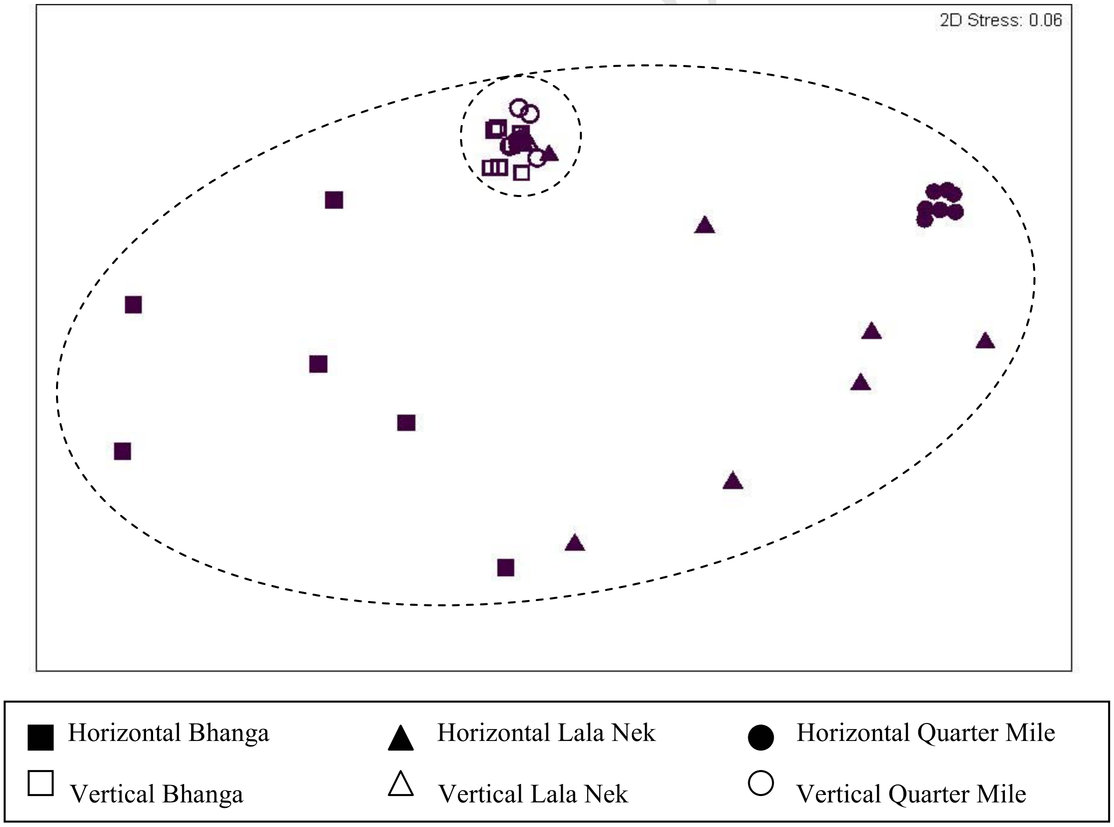


Figure 3.5. Unconstrained non-metric MDS ordination of assemblages quantified on two different reef orientations at three sites in the Delagoa Overlap Bioregion. n = 7 per orientation per site.

PERMDISP showed that the multivariate dispersion between communities of horizontal and vertical reef was significantly different ($P_{(perm)}$ = 0.0001), but that among sites was not $P_{(perm)}$ = 0.69) (Table 3.5). Pairwise *a-posteriori* tests found significant differences between horizontal and vertical communities at Bhanga ($P_{(perm)}$ = 0.0005) and at Quarter Mile ($P_{(perm)}$ = 0. 0006) but not at Lala Nek ($P_{(perm)}$ = 0.9232). Differences between sites within each orientation were always significant except for horizontal Bhanga *vs.* Quarter Mile, and vertical Lala Nek *vs.* Quarter Mile – hence the significant interaction term.

All diversity measures differed significantly ($P_{(perm)}$ = 0.0001) and horizontal communities were consistently more diverse than communities found on vertical reef surfaces (Table 3.6). There was almost double the number of species comprising communities of horizontal reef surfaces compared to communities on vertical surfaces. Communities on vertical surfaces also had a significantly lower Pielou's evenness index than those from horizontal reef surfaces.

SIMPER analyses showed that communities on horizontal reef surfaces (Table 3.7A) were dominated by *Pyura stolonifera* (Av. Sim. = 7.23 %) followed by two species of Phaeophyta, *Dictyopteris ligulata* (Av. Sim. = 3.77 %) and *Sargassum elegans* (Av. Sim. = 3.63 %), and algal turf (Av. Sim. = 3.11 %). Communities on vertical reef surfaces (Table 3.7B) were dominated almost exclusively by *P. stolonifera* (Av. Sim. = 72.36 %), which accounted for 93.06 % of the biomass. The most distinguishing taxa between horizontal and vertical communities (Table 3.7C) were *P. stolonifera* (Av. Diss. = 33.90 %), *S. elegans* (Av. Diss. = 4.63 %) and the sponge *Psammoclema* sp. (Av. Diss. = 4.58 %). *P. stolonifera* (Diss/SD = 1.87), algal turf (Diss/SD = 1.31) and *D. ligulata* (Diss/SD = 1.30) contributed most consistently to divergence between horizontal and vertical communities. In addition, the percentage cover of sand per quadrat differed significantly ($F_{1,41)}$ = 30.7, $P_{(perm)}$ = 0.0001) between orientations with an average ± SD of 29.9 ± 24.1 % on horizontal reef surfaces and a total absence on vertical reef surfaces.

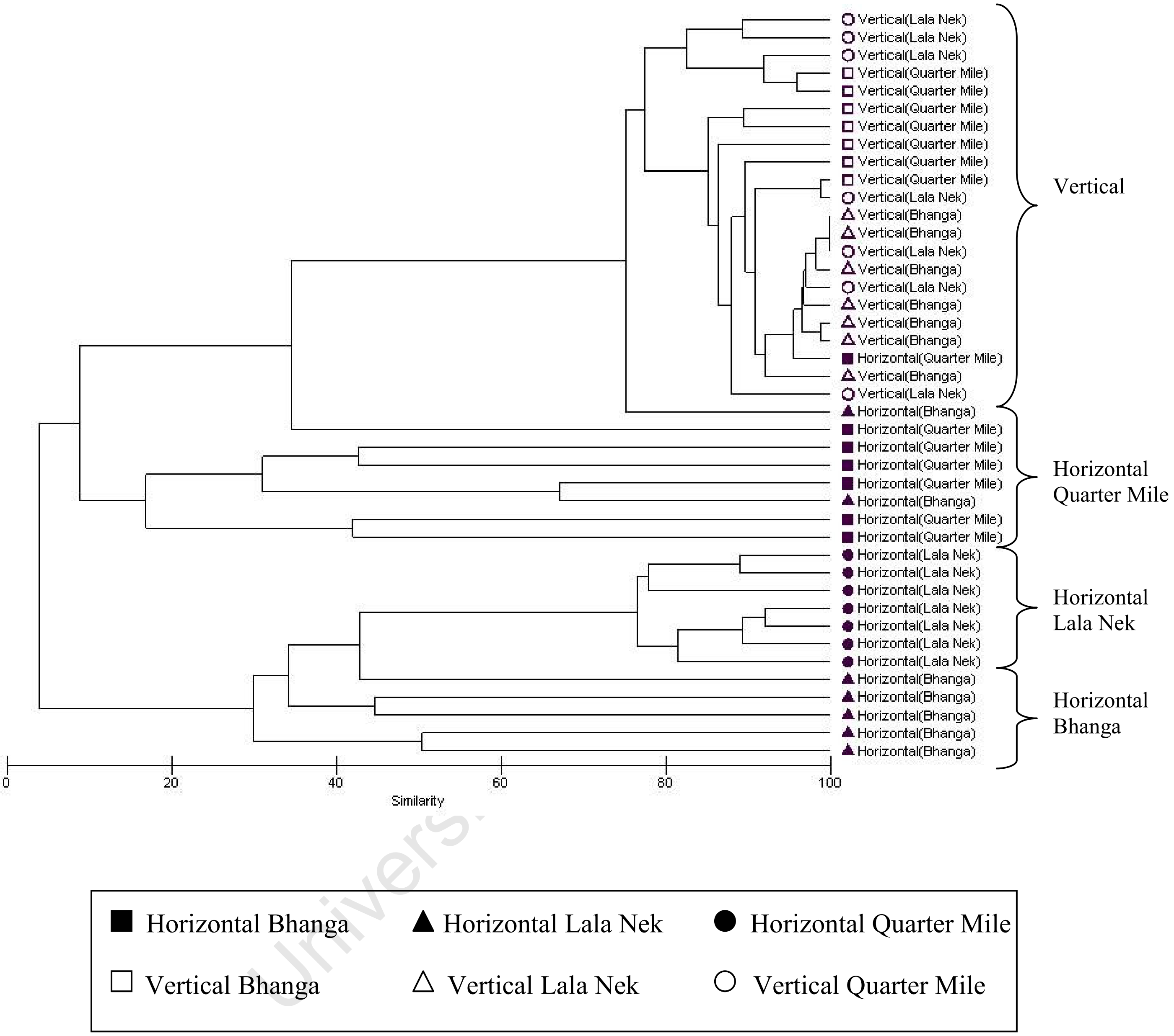


Figure 3.6. Cluster analysis dendrogram of assemblages quantified on two different reef orientations (horizontal & vertical) at three sites in the Delagoa Overlap Bioregion. n = 7 per orientation per site

Table 3.3. Results of the two-way crossed permutational multivariate analysis of variance (PERMANOVA) for differences in reef community structure on different reef orientations (horizontal versus vertical) at three sites. Pair-wise *a-posteriori* multivariate comparisons were further conducted to determine where significant differences lay for both factors with PERMANOVA. * = Significant differences α = 0.05.

Source of variation	df	SS	MS	F	$P_{\text{(Monte-Carlo)}}$
Orientation	1	47987	47987	42.54	0.0001*
Site	2	16952	8476	7.51	0.0001*
Orientation x Site	2	14502	7251	6.43	0.0002*
Residual	36	40609	1128		
Total	41	120050			

A-posteriori pair-wise comparisons (Orientation)	t	$P_{\text{(Monte-Carlo)}}$
Bhanga	3.32	0.0006*
Lala Nek	12.32	0.0001*
Quarter Mile	2.75	0.0021*

A-posteriori pair-wise comparisons (Site)	t	$P_{\text{(Monte-Carlo)}}$
Bhanga vs. Lala Nek	2.18	0.0161*
Bhanga vs. Quarter Mile	2.14	0.0046*
Lala Nek vs. Quarter Mile	3.92	0.0001*

A-posteriori pair-wise comparisons (Horizontal)	t	$P_{\text{(Monte-Carlo)}}$
Bhanga vs. Lala Nek	2.35	0.0019*
Bhanga vs. Quarter Mile	1.96	0.0047*
Lala Nek vs. Quarter Mile	3.95	0.0001*

A-posteriori pair-wise comparisons (Vertical)	t	$P_{\text{(Monte-Carlo)}}$
Bhanga vs. Lala Nek	1.94	0.0502
Bhanga vs. Quarter Mile	1.02	0.3823
Lala Nek vs. Quarter Mile	1.24	0.2088

Table. 3.4. Average Bray-Curtis dissimilarities (%) within and between orientations at particular sites, within and between sites and within and between sites within a particular orientation.

	Bhanga		Lala Nek		Quarter Mile	
Orientation	Horizontal	Vertical	Horizontal	Vertical	Horizontal	Vertical
Horizontal	77.4		20.1		76.4	
Vertical	82.8	4.2	99.1	19.0	73.5	17.8

Site	Bhanga	Lala Nek	Quarter Mile
Bhanga	63.4		
Lala Nek	67.0	62.4	
Quarter Mile	66.3	73.7	61.3

	Horizontal			Vertical		
	Bhanga	Lala Nek	Quarter Mile	Bhanga	Lala Nek	Quarter Mile
Bhanga	77.4			4.2		
Lala Nek	72.7	20.1		14.4	19.0	
Quarter Mile	91.5	100.0	76.4	13.1	18.6	17.8

Table 3.5. Results of the permutational test of multivariate dispersions (PERMDISP) based on the dispersions from group centroids. Pairwise *a-posteriori* multivariate comparisons were further conducted to determine where significant differences lay within the interaction between "Orientation" and "Site". * = Significant differences at $\alpha = 0.05$.

Source of variation	df	F	$P_{(\text{perm})}$
Orientation	1	297.27	0.0001*
Site	2	0.6393	0.6901
Orientation x Site	5	88.614	0.0001*
Residual	33		
Total	41		

A-posteriori pair-wise comparisons	t	$P_{(\text{perm})}$
Horizontal Bhanga vs. horizontal Lala Nek	9.8349	0.0011*
Horizontal Bhanga vs. horizontal Quarter Mile	0.19125	0.8529
Horizontal Bhanga vs. vertical Bhanga	13.495	0.0005*
Horizontal Bhanga vs. vertical Lala Nek	9.9601	0.0003*
Horizontal Bhanga vs. vertical Quarter Mile	10.98	0.0008*
Horizontal Lala Nek vs. horizontal Quarter Mile	9.5163	0.0005*
Horizontal Lala Nek vs. vertical Bhanga	6.1563	0.0013*
Horizontal Lala Nek vs. vertical Lala Nek	0.11188	0.9232
Horizontal Lala Nek vs. vertical Quarter Mile	0.79164	0.5042
Horizontal Quarter Mile vs. vertical Bhanga	13.117	0.0005*
Horizontal Quarter Mile vs. vertical Lala Nek	9.6382	0.0006*
Horizontal Quarter Mile vs. vertical Quarter Mile	10.621	0.0006*
Vertical Bhanga vs. vertical Lala Nek	6.2128	0.0007*
Vertical Bhanga vs. vertical Quarter Mile	9.9509	0.0007*
Vertical Lala Nek vs. vertical Quarter Mile	0.66918	0.5621

Table 3.6. Diversity measures: Total species and average ± standard deviation values of species richness, Pielou's evenness and Shannon-Weiner for quadrats placed on horizontal and vertical reef orientations at three reefs. Differences were tested using univariate permutational ANOVAs.

Diversity measure	**Horizontal**	**Vertical**	$P_{(\text{Monte-Carlo})}$
Total species	28	17	0.0001
Species richness	0.59 ± 0.17	0.19 ± 0.15	0.0001
Pielou's evenness	0.58 ± 0.23	0.15 ± 0.13	0.0001
Shannon-Weiner	0.84 ± 0.37	0.14 ± 0.17	0.0001

Table 3.7A-C. Similarity percentage breakdown analysis (SIMPER) for communities quantified on horizontal and vertical reef surfaces at three sites in the Delagoa Overlap Bioregion, showing characteristic and distinguishing taxa that accounted for 90 % of the cumulative similarity or 70 % of the cumulative dissimilarity. Av. Abund. = the average biomass of that species. Av. Sim. % = the average contribution of that species to the overall similarity. Av. Diss. % = the average contribution of that species to the overall dissimilarity. Sim/SD = the average similarity of that particular species divided by the standard deviation of its similarity. Diss/SD = the average dissimilarity of that particular species divided by the standard deviation of its dissimilarity. Contrib. % = the contribution of that species to the overall similarity or dissimilarity and Cum.% = the cumulative contribution of species to the overall similarity or dissimilarity.

A) Horizontal community

Characteristic species	**Av. Abund. (g.m^{-2})**	**Av. Sim.**	**Sim/SD**	**Contrib.%**	**Cum.%**
Pyura stolonifera	123	7.23	0.58	30.69	30.69
Dictyopteris ligulata	9	3.77	0.58	16.00	46.69
Sargassum elegans	19	3.63	0.58	15.39	62.09
Algal turf	26	3.11	0.58	13.18	75.26
Spirastrella spinispirulifer	20	2.73	0.58	11.57	86.83
Callophycus condominius	2	1.60	0.58	6.78	93.61

B) Vertical community

Characteristics species	**Av. Abund. (g.m^{-2})**	**Av. Sim.**	**Sim/SD**	**Contrib.%**	**Cum.%**
Pyura stolonifera	2017	72.36	12.87	93.06	93.06

C) Horizontal communities vs. Vertical communities

Distinguishing Species	**Horizontal Av. Abund. (g.m^{-2})**	**Vertical Av. Abund. (g.m^{-2})**	**Av. Diss.**	**Diss/SD**	**Contrib.%**	**Cum.%**
Pyura stolonifera	123	2017	33.90	1.87	44.45	44.45
Sargassum elegans	19	0.4	4.63	1.01	6.07	50.52
Psammoclema sp.	2	30	4.58	1.20	6.00	56.52
Algal turf	26	0	3.95	1.31	5.18	61.70
Spirastrella spinispirulifer	20	2	3.40	1.29	4.46	66.16
Dictyopteris ligulata	9	0	3.21	1.30	4.20	70.36

DISCUSSION

Overall patterns

Synthesis of my own data and those of previous surveys yields the patterns of relative abundance evident in Figure 3.7. Several major trends emerge. First, scleractinians are dominant throughout the Tropical Indo-West Pacific, but decline and form non-accretive reefs in the Delagoa Overlap, and are abruptly diminished to the point of virtual absence in the Subtropical Natal Bioregion. The same is true of the Alcyonacea, although they also appear to diminish near the equator. The range of cover of scleractinians is considerable even in the Indo-West Pacific, and several authors have documented substantial declines in coral cover following the 1998 bleaching event (Muhando & Mohammed 2002; Ahamada *et al.* 2002, 2004; Gorpe & Öman 2003), attacks by *Acanthaster planci* (Celliers 2001; Webster *et al.* 2003), or destructive fishing practices (IUCN 1987; Hempson 2008). Second, although algae are a significant component throughout, they become more important in the Delagoa Overlap Bioregion, never covering <15 % on average, and strikingly more dominant in the Subtropical Natal Bioregion where they attain 30-55 % cover. Finally, filter-feeders such as Porifera and Ascidiacea are a much more important component in the Subtropical Natal Bioregion than elsewhere.

It is against this backdrop of broad patterns in major functional groups that the community types were distinguished and defined.

Reef community types

Of the 12 statistically discrete community types defined on horizontal reef surfaces two were dominated by ascidians (A & E), one by sponges (F), two by algal turfs (C & H), one by a brown algae (D), one by alcyonarian soft corals (L) and five by scleractinian hard corals (B, G, I, J, K). The Subtropical Natal Bioregion supported only three community types (A, D & F), all of which also occurred in the Delagoa Overlap Bioregion. A total of eight community types (B, C, G, H, I, J, K, L) were recognised in the Tropical Indo-West Pacific Bioregion, only one of which (C) also occurred in the Delagoa Overlap Bioregion.

A further one community type (E) was unique to the Delagoa Overlap Bioregion and there were no community types that occurred in both the Subtropical Natal and Tropical Indo-West Pacific bioregions.

These community types were differentially distributed. The entire southern part of the Subtropical Natal Bioregion comprised a single community type, Community A, which was dominated by large beds of *Pyura stolonifera* similar to the single shallow subtidal community documented in that region by Berry (1982). On deeper reefs in the region, however, neither Lawrence (2005) nor Brash (2006) recorded communities characterised by a dominance of *P. stolonifera*. Although Sink (2001) did define a biotope dominated by *P. stolonifera* in the intertidal, this was recorded at a single site only in this bioregion. The scarcity of this community type in other zones suggests that it is essentially confined to the shallow subtidal. Its rarity in the intertidal zone may, however, reflect the fact that *P. stolonifera* is intensively harvested by subsistence fishers, particularly in northern KwaZulu-Natal (Kyle *et al.* 1997; Sink 2001). Other characteristic taxa comprising this community type in the depth range that I investigated were algal turf, *Amphiroa ephedraea* and *A. bowerbankii,* which are important characteristic species on deeper subtidal reefs as well (Lawrence 2005) but not on intertidal reefs where *Perna perna,* various foliose algae and other articulated corallines are the major contributors to communities (Sink 2001). Also characteristic was the scarcity of Scleractinia and Alcyonacea, as noted in previous surveys in this region (Lawrence 2005; Brash 2006; Schleyer *et al*. 2006; Celliers *et al.* 2007).

Further north, in the Delagoa Overlap and southern parts of the Tropical Indo-West Pacific bioregions, a high diversity of community types was present. The Delagoa Overlap Bioregion is a transitional area between the Subtropical Natal and the Tropical Indo-West Pacific marine provinces with the occurrence of community types from both of these provinces constituting evidence for the overlap nature of this area. Transitional or ecotonal areas have frequently been found to have relatively high diversity in both terrestrial (Risser 1995) and marine environments (Stephens & Zerba 1981). In this case it is likely that the co-occurrence of both tropical and subtropical species at the limits of their geographical

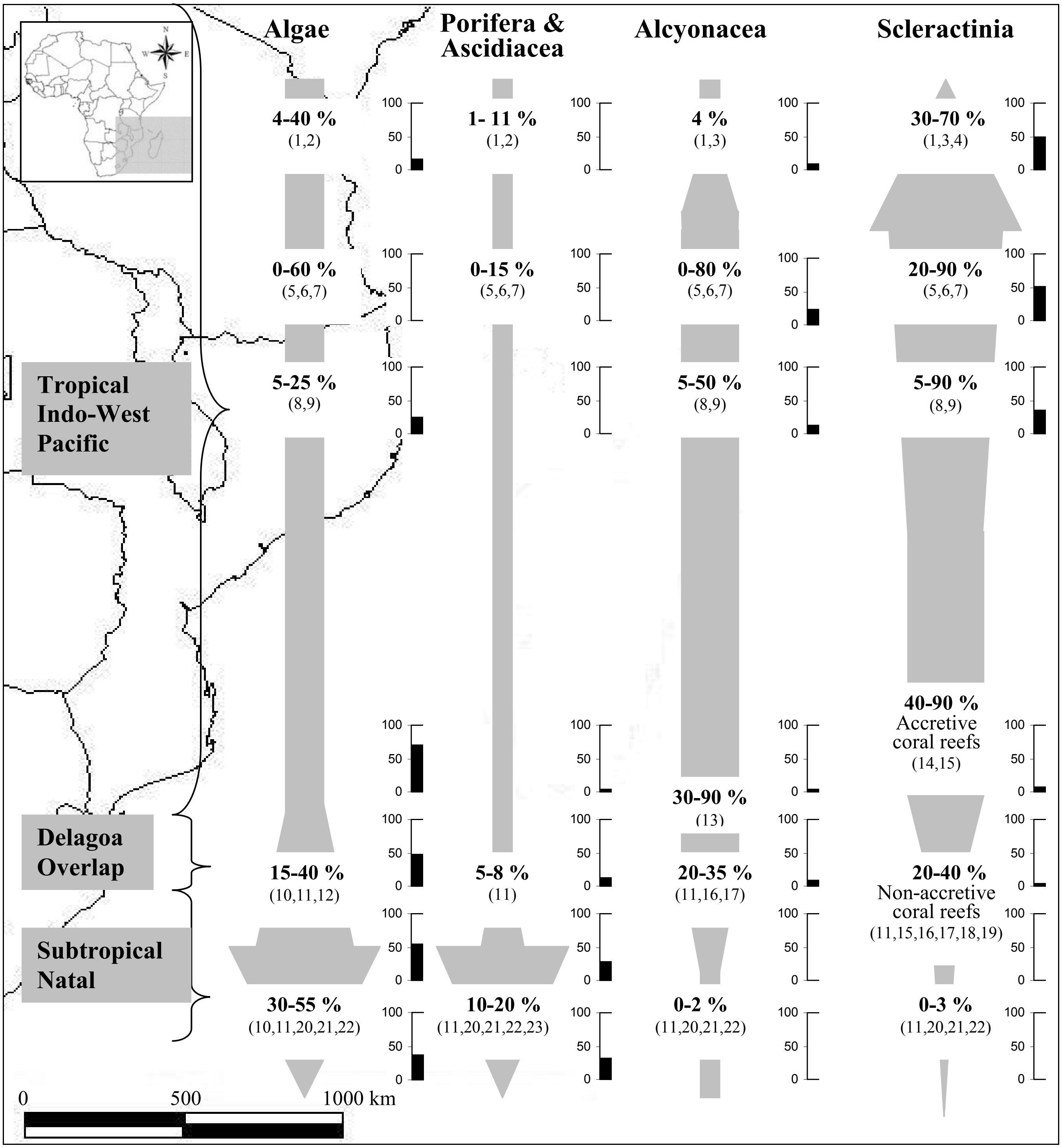


Figure 3.7. Generalized latitudinal trends of abundance (% cover) in five taxonomic groups across the three bioregions delineated in Chapter 2, according to literature, and according to this study (bar graphs). Numbers in brackets correspond to the following references: 1=McClanahan *et al.* (1999); 2=Horrill & Church (2000); 3=Daniels (2004); 4=Muhandon & Mohammed (2002); 5=Choiseul & Darwall (1996); 6 & 7=Darwall *et al.* (1996a,b,c,d,1997); 8 & 9=Frontier Mozambique (1997b, 1998b); 10=Evans (2005); 11=Lawrence (2005); 12=Anderson *et al.* (2005); 13=Robertson *et al.* (1996); 14=Rodrigues *et al.* (2000); 15=Sheppard (2000); 16=Riegl *et al.* (1995); 17=Schleyer & Celliers (2005); 18 & 19=Schleyer (1999, 2000); 20=Brash (2006); 21=Schleyer *et al.* 2006; 22=Celliers *et al.* (2007); 23=Berry (1982).

ranges in the Delagoa Overlap Bioregion promotes the diversification of community types (Gosz 1993).

A total of five community types was present in the Delagoa Overlap Bioregion with one (E) confined there. The most common community in the Delagoa Overlap Bioregion, Community C, was also found at Silvia Shoal and Lagoa in the southern portion of the Tropical Indo-West Pacific Bioregion (Figure 3.3). It was dominated by algal turf, the ascidian *P. stolonifera* and various species of Alcyonacea and Scleractinia (Table 3.2). Anderson *et al.* (2005) found the major taxa at depths of 0.5-27 m in the vicinity of Jesser Point (near Quarter Mile, Sodwana) were algal turf and various coral species, and also documented the presence of *P. stolonifera* on the pinnacles of one of the reefs investigated. Evans (2005) concurred with this, finding that shallow communities (< 15 m) were dominated by turf-forming algae. Two studies of deeper subtidal reefs by Lawrence (2005) and Schleyer & Celliers (2005) in the same area noted communities that were also dominated by algal turf, Alcyonacea and Scleractinia but no *P. stolonifera*.

Algal turfs are common components of both intertidal and subtidal reefs throughout the world (Stuercke & McDermid 2004) and on coral-dominated reefs they provide up to 80 % of the total primary productivity (Hackney *et al.* 1989). Algal turfs form characteristic morphologically-similar mats, generally less than 10 mm thick and often rich in diversity (Anderson *et al.* 2005). Evans (2005) recorded 294 species in only 4.5 m^2, and Anderson *et al.* (2005) recorded a similarly high species richness of 104 taxa in 1.56 m^2.

Only the intertidal work by Sink (2001) has recorded communities dominated by *P. stolonifera* in the Delagoa Overlap Bioregion, and then at only two sites. Again, this suggests that communities dominated by *P. stolonifera* are largely confined to the shallow subtidal, where it is a significant component in many of the community types of the region. Again, harvesting in the intertidal zone may diminish its abundance there (Kyle *et al.* 1997; Sink 2001).

The noteworthy presence of both alcyonacean and scleractinian corals in a number of the communities was a characteristic of the reefs in the Delagoa Overlap Bioregion and has received much attention in studies of deeper subtidal reefs (Riegl *et al.* 1995; Schleyer &

Celliers 2003a; Schleyer & Celliers 2003b; Schleyer & Celliers 2005). These reefs are known to support some of the southern-most coral communities on the African coast and are characterised largely by Alcyonacea that form a thin veneer on the aeolianite reefs (Ramsey 1994; Riegl *et al.* 1995). Although Alcyonacea dominate deeper reefs in terms of cover (Riegl *et al.* 1995), their diversity is low relative to the Scleractinia, which contribute less to community biomass but more to diversity (Schleyer & Celliers 2005). Indeed, scleractinian diversity in this region is higher than that recorded for a number of areas in the tropical Indian Ocean (Riegl 1996).

Many shallow reefs in the Delagoa Overlap supported three communities (D, E & F) with substantial contributions of relatively large phaeophytes (*Dictyopteris*, *Sargassum*, *Zonaria* and *Lobophora* spp.), particularly those reefs covered in places by sand. This concurs with surveys by Evans (2005), who reported an increase in the proportion of Phaeophyta relative to other algae in the Delagoa Overlap Bioregion on both shallow subtidal and deeper reefs.

The most abundant community type in the Tropical Indo-West Pacific Bioregion, Community B, was dominated by a variety of scleractinian genera, particularly *Porites* spp. followed by *Pocillopora* spp. and *Galaxea* spp. Other community types there were also largely dominated by various Scleractinia, but many had important algal and alcyonacean components too. There was thus a shift from communities dominated by *Pyura stolonifera* and algae in the Subtropical Natal Bioregion, to those dominated by algal turf, *P. stolonifera*, Alcyonacea and Phaeophyta in the Delagoa Overlap Bioregion, and a second shift to communities dominated by Scleractinia with only a few algae and Alcyonacea in the Tropical Indo-West Pacific.

Reef communities dominated by Scleractinia are typical of the tropical-western Indian Ocean where substantial fringing reefs are found discontinuously between 5°N and 20°S along the east African coast. Large monospecific stands of *Galaxea astreata,* like those I found at Makome, have been recorded before (Schleyer 2002). The fact that *Galaxea* spp. were a characteristic in three community types (B, I & J) at 15 sites is noteworthy, as *Galaxea fascicularis* in particular is an early-successional species (McClanahan *et al.*

1999) and may be an indicator of reef health and stage of succession. The scleractinian taxa that were characteristic components of many of the community types I recorded have frequently been noted as dominant elements in other studies in the region. However, perhaps because I used biomass rather than percentage cover as the unit of measure, *Porites* spp. assumed greater importance in my studies than other surveys (Boshoff 1958; Darwall *et al.* 1994; Choiseul & Darwall 1996; Darwall 1996; Frontier Mozambique 1997a; Frontier Mozambique 1998a; Frontier Mozambique 1998b; Frontier Mozambique 1998c; McClanahan *et al* 1999; Rodrigues *et al.* 2000; Sheppard 2000; Daniels 2004; McClanahan *et al.* 2007).

A characteristic of four of the community types (G, H, K & L) found in the Tropical Indo-West Pacific Bioregion was the high abundance of sea urchins. Some reefs surveyed in southern Mozambique and in Tanga, Tanzania were characterised by high urchin biomasses, and correspond in location to coastal towns that rely heavily on fish as a food source (Horrill 1997; See McClanahan *et al.* 1999; See Afonso 2006). Over-fishing may result in communities dominated by urchins as their natural predators become fished-out (McClanahan *et al*. 1994, 1996; McClanahan & Arthur 2001), and high urchin densities can in turn impact on reef formation (McClanahan & Shafir 1990; Eakin 1996) resulting in ‘artificial’ communities shaped by anthropogenic influences. This situation, induced by anthropogenic over-fishing, is comparable to that of Alaskan waters where high levels of fish predation by sea otters have exerted top-down effects resulting in communities with similarly high densities of urchins (Estes & Palmisano 1974; Estes *et al.* 1978).

Divergence between communities on horizontal and vertical reef surfaces

Significant differences were found between horizontal and vertical communities in PERMANOVA analyses across all 3 sites examined, allowing rejection of the null hypothesis that there is no difference between communities on horizontal and vertical reef surfaces (Table 3.3). Multivariate dispersion analyses (PERMDISP) also found significant differences between the two community types (horizontal and vertical) at all three sites (Table 3.5).

When both PERMANOVA and PERMDISP find significant differences between communities, one can conclude that divergence is due to both differences in assemblage composition, as indicated by the separation between the two community types in multidimensional space, and multivariate dispersion because of differences in variability within each community type. The latter was clearly demonstrated and supported by the differences found when comparing the within-community Bray-Curtis dissimilarity values of communities on horizontal surfaces (which were high) with those of the within-community Bray-Curtis dissimilarity values from vertical surfaces (which were very low) (Table 3.4). This was also responsible for the significant Site x Orientation interaction effect (Table 3.3).

Others have also found strong differences between communities from horizontal and vertical reef surfaces (Todd & Turner 1986; Hurlbut 1991a; Riegl *et al.* 1995; Glasby & Connell 2001; Goldberg & Foster 2002). Reasons for such differences are not fully understood, but they have variously been attributed to both abiotic variables such as light (Glasby 1999; Goldberg & Foster 2002), sedimentation (Riegl *et al.* 1996) and current flow at small spatial scales (Guichard & Bourget 1998), and to biotic variables such as larval behaviour (Hurlbut 1991b; Goldberg & Foster 2002) and grazing (Breitburg 1985). In my case, communities on vertical surfaces were almost exclusively dominated by filter-feeders and lacked any sand, while horizontal communities comprised more-or-less equal contributions of seaweeds and filter-feeders with an average of 30 % sand cover per quadrat. Communities on vertical surfaces also had lower values of Pielou's evenness due to the filter-feeding ascidian *Pyura stolonifera* comprising 93 % of the community biomass (Tables 3.6 & 3.7).

Sand could play an integral role in structuring shallow subtidal communities as it has been found to influence the diversity and composition of both intertidal (McQuaid & Dower 1990) and subtidal communities (Riegl *et al.* 1996). In the shallow subtidal, sand movements are highly dynamic, particularly on the high-energy coast of north-east South Africa (Berry 1982). On horizontal substrata where sediment is more likely to settle than on vertical substrata, this may cause intermediate levels of disturbance with an associated increase in diversity (Lubchenco & Menge 1978; McQuaid & Dower 1990), as predicted by the intermediate disturbance hypothesis (Connell 1978). Sporadic episodes of sand deposition and inundation on horizontal substrata could reduce the competitive advantage of *Pyura stolonifera*, as it cannot withstand long periods of sand burial (Berry 1982), similar to the case for other reef filter-feeders such as mussels (Littler *et al.* 1983) and photosynthetic soft corals (Riegl *et al.* 1995).

Seaweeds will benefit from greater access to light on horizontal as opposed to vertical surface. In addition, they may opportunistically colonise bare areas of horizontal reef surfaces between bouts of sand inundation, and then survive for extended periods even if they are later covered by sand (Anderson *et al.* 2008a), either because they grow tall enough to exist above the sand, or because they are sufficiently resilient to withstand inundation. Many seagrass angiosperms such as *Phyllospadix scouleri* tolerate sand specifically because they attain large sizes (Littler *et al.* 1983). The two phaeophyte species commonly recorded from the horizontal reef communities, *Dictyopteris ligulata* and *Sargassum elegans* have erect thalli and attain lengths of 37 cm and 50 cm respectively (De Clerk *et al.* 2005). In habitats that experience periodic sand inundation events, this would provide an advantage over other species that cannot grow tall. Sand-adapted seaweeds have been recorded as dominant community constituents in habitats periodically inundated by sand (Daly & Mathieson 1977; Anderson *et al.* 2008a). Crustose rhodophytes, many of which are found in algal turfs, are particularly resilient to sand inundation (Anderson *et al.* 2008a).

On vertical reef surfaces, where sand inundation is unlikely, filter-feeders may thrive because they are not exposed to this type of disturbance. In addition, the upper regions of vertically orientated reef surfaces favour filter-feeders as they are exposed to greater flow rates and therefore more food, enhancing growth rates (Leichter & Witman 1997). These factors result in communities of relatively low diversity with most of the biomass often dominated by a few select species as observed in this study and substantiated by the low Pielou's evenness index compared to that of horizontally-orientated communities (Table 3.6).

Divergence in community structure between communities on horizontal and vertical reef surfaces has important implications for community functioning. Communities on horizontal surfaces are perhaps structured more by disturbance events, such as inundations by sand, than by interspecific competition (Dayton 1971), and may never reach a stable climax equilibrium (see Petraitis *et al.* 1989), although others have argued that sand could be a sufficiently predictable intrinsic disturbance that the communities exist in a disturbance-mediated equilibrium (Caswell 1978; Karlson & Bus 1984; Caswell & Cohen 1991). Periodic sand inundation events may be necessary and routine for the maintenance of such communities much like fire plays an integral role in many terrestrial plant communities (Hanes 1971; Bond & Van Wilgen 1996; Thonicke *et al.* 2001; Bond & Keely 2005).

On the other hand, communities on vertical surfaces are more likely to be structured by biotic interactions such as interspecific competition for space, because disturbance by sand-inundation is unlikely to interrupt competitive dominance (see Connell 1983). Assemblages on vertical reef surface are thus more likely to reach the stage of a climax community because they are not repeatedly disturbed and reorganised by sand, and may be expected to be fairly low in diversity (Dayton 1971; Petraitis *et al.* 1989). This was the case in my study where significantly lower diversity was observed on vertical reef surfaces (Table 3.6), as would be predicted by both the intermediate disturbance hypothesis (Connell 1978) and the gradual change hypothesis (Hutchinson 1961) under conditions where disturbances are rare.

Implications for conservation planning

Methodology for identifying and selecting areas for conservation use to be governed predominantly by the hotspot approach, which focuses on protecting areas that are rich in species and have a high proportion of endemics (Myers 1988, 1990; Myers *et al.* 2000). This approach originated from terrestrial conservation biology (Myers 1988, 1990, 2003; Mittermeier *et al.* 1998; Reid 1998; Médail & Quézel 1999; Myers *et al.* 2000), but it has also been advocated for the marine environment (Pimm & Raven 2000). It has, however, been criticised (See Beger *et al.* 2003 and Fox & Beckley 2005; Blamey & Branch 2008) because (1) 'hotspots' can also be 'coldspots' depending on the diversity methods used (Awad *et al.* 2002; Price 2003), (2) productive areas such as those that support large fisheries are often relatively low in diversity (McQuaid & Branch 1984; Bustamante & Branch 1996a; Turpie *et al.* 2000) and thus risk being overlooked by the hotspot approach, (3) species data are often localised to particular areas and therefore unsuitable for regional conservation planning over large geographical scales (Margules & Austin 1994; Pressey *et al.* 2000; Turpie *et al.* 2000) and (4) many important ecosystems depend on subsidies from adjacent ecosystems that may be low in diversity but provide unique and essential ecosystem services (Bustamante *et al.* 1995b; Bustamante & Branch 1996b; Krenz 2007), and these would not be adequately rated by the hotspot approach.

An alternative hierarchical approach to the spatial delineation, selection and prioritisation of locations for marine protected areas (MPAs) has therefore been recommended, whereby biogeographic regions should first be defined, and then representatives of all community types within each region incorporated into a network of protected areas (Emmanuel *et al.* 1992; Hockey & Branch 1994, 1997; Roberts *et al.* 2003a; Roberts *et al.* 2003b). This, of course, demands that both biogeographic regions and community types be defined in a defendable manner. In Chapter 2, I identified three large-scale bioregional units in the western Indian Ocean, which I investigated further in this chapter, quantitatively defining 12 different community types. In addition, within sites I compared horizontal and vertical communities at a subset of three sites in the Delagoa Overlap Bioregion, demonstrating decisive differences in community composition between the two. Although surveys were not exhaustive, they can nevertheless provide significant insight into conservation planning with important implications.

This hierarchical approach provides the necessary framework to make decisions about the selection of MPAs. At a biogeographic scale, the three bioregions I recognised – the Subtropical Natal, Delagoa Overlap and Tropical Indo-West Pacific (see Chapter 2) – all incorporate some form of MPAs, but not all community types are represented within them.

In South Africa, three inshore MPAs are situated in the Subtropical Natal Bioregion, the Aliwal Shoal, Trafalgar and Pondoland MPAs, which range in length from 2 to 90 km of coastline (Figure 3.8). These three MPAs are however situated in the central and southern parts of the bioregion, and no MPAs conserve any areas of the coast north of Durban (approximately a 250-km stretch) within this particular bioregion.

In terms of the hierarchical approach, representatives of all community types within a particular bioregion need to be included in MPAs. Three community types (A, D, F) were defined in the Subtropical Natal Bioregion, two (A & F) of which fall within MPAs. Community F is protected as it falls within MPAs of the Isimangaliso Wetland Park World Heritage Site (which comprises the adjacent St Lucia and Maputaland MPAs), in the Delagoa Overlap Bioregion. It is however vulnerable as it is only found at two sites in the entire study region, which are in close proximity to one another (Figure 3.3). The closer two communities are together the higher the probability they may be struck by the same catastrophic event such as an oil spill, thus reducing viability (Wagner *et al.* 2007). Although Community A is conserved in the southern part of the Subtropical Natal Bioregion it would be beneficial to also conserve it further north, where it occurs commonly in the Natal Bight, an area where there is as yet no MPA.

The most practical way to improve conservation of Community D, which is already protected in the Delagoa Overlap Bioregion, would be to extend the St. Lucia MPA in the Delagoa Overlap Bioregion further south by approximately 50 km to Cape St. Lucia. This would result in its incorporation into an existing protected area but because Community D is protected at two sites in the Maputaland MPA in the Delagoa Bioregion, its protection in the Subtropical Natal Bioregion is not of paramount priority (Figures 3.3 & 3.8). Sink (2001) also recommended extending the St. Lucia MPA further south in her analysis of intertidal biotope conservation. An investigation into exactly this possibility has already been done and there is a proposal to extend the St. Lucia MPA further south (J.M. Harris, Ezemvelo KwaZulu-Natal Wildlife, *pers. comm.* 2009).

At a regional scale, the Delagoa Overlap Bioregion is well conserved as approximately 60 % is incorporated within the Isimangaliso Wetland Park World Heritage Site, part of

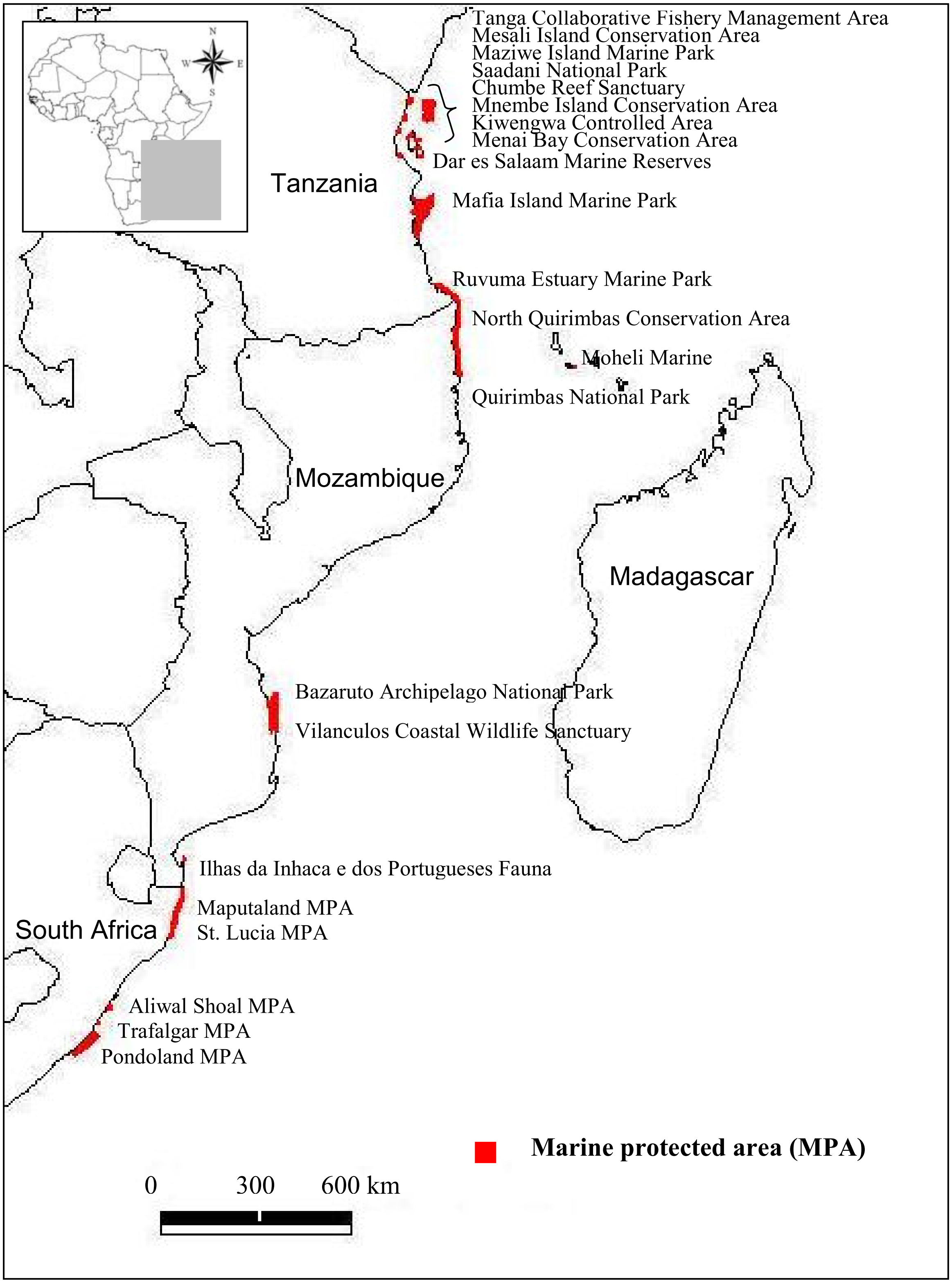


Figure 3.8. Current locations of marine protected areas (MPAs) in the study region of the western Indian Ocean.

which has been acknowledged as a globally important seascape (Eastern African Marine Ecoregion Programme 2004; WWF Eastern African Marine Ecoregion. 2004). All five communities identified in this bioregion, two of them unique to it, fall within these two MPAs.At the subset of sites within the Delagoa Overlap Bioregion at which comparisons were made between vertical and horizontal substrata, I showed that the two differed significantly (Table 3.3). While this was not examined in other bioregions, I did observe comparable differences there. For example, in the Subtropical Natal Bioregion many of the vertical reef surfaces were dominated by the oyster *Striostrea margaritacea*, an important commercial resource species (Clark *et al.* 2002; de Bruyn *et al.* 2009), while the horizontal surfaces comprised mixes of *Pyura stolonifera* and various coralline seaweeds. Surveys confined to horizontal reef surfaces may overlook communities associated with vertically orientated reef, and therefore fail to incorporate such communities into protected areas. This is an important issue that should be considered when prioritising areas for conservation, as the majority of assessments consider horizontal reef surfaces only and ignore vertical reef surfaces.

In the portion of the Tropical Indo-West Pacific Bioregion that I studied, 16 MPAs have been established in three countries – Mozambique, Tanzania & Comoros (see Richmond 2002; Wells *et al.* 2007) (Figure 3.8). Tanzania is particularly rich with 11 MPAs (Wells *et al.* 2007). The most recently-declared of these is the Mtwara-Quirimbas MPA, which straddles Tanzania and Mozambique and spans 9370 km^2, conserving extensive coral reefs and mangrove deltas (WWF Eastern African Marine Ecoregion 2004). This initiative forms part of the Eastern African Marine Ecoregion (EAME) Programme that has a 50-year vision plan to develop a biodiversity conservation strategy for southern Somalia, Kenya, Tanzania, Mozambique and northern South Africa (Eastern African Marine Ecoregion Programme 2004; WWF Eastern African Marine Ecoregion 2004).

A regional analysis of the EAME Programme has been conducted by Wells *et al.* (2007). The most important findings were that (1) existing MPAs still need to be expanded or new ones declared to reach the targeted 10 % area coverage, (2) the location of present MPAs does correspond with areas of coral reef and high diversity, (3) areas closed to fishing are still less than the recommended 20-30 % target, and (4) monitoring systems to measure progress towards goals, and the management of MPAs need urgent attention (Wells *et al.* 2007).

Important seascapes have been identified and defined by the EAME Programme (www.worldwildlife.org/ecoregions) and categorised as being either globally, eco-regionally or sub-regionally important. In southern Mozambique, the Inharrime Complex has been given 'sub-regionally important' status (Wells *et al.* 2007), and corresponds to the area encompassing my study sites between Lagoa and Zavora, where I identified four community types (B, C, G & H), two of which (G & H) are thus far been found only at one other site each (Figure 3.3). A few hundred kilometres north in Mozambique, Inhambane Bay has also been categorised as 'sub-regionally' important. This area corresponds to three of my sites (Mike's Cupboard, Anchor Bay & Jangamo) where I defined three community types (B, H & L), two of which (H & L) are represented at one other site only (Figure 3.3). Providing MPA status to both the Inharrime Complex and Inhambane Bay area would conserve five out of eight (63 %) of the community types defined in this bioregion, two of which are unique (G & H) to this area, and one of which (L) only occurs at two sites in the region.

Further north in the Tropical Indo-West Pacific Bioregion, priority areas for conservation have been classified as being of eco-regional or global importance (see Wells *et al.* 2007). Most of the communities in this area are of type B, but four other community types (I, J, K & L), were recorded in the Tanga area of northern Tanzania (Figure 3.3). Communities from the Tanga region are afforded varying degrees of protection by the Tanga Collaborative Fisheries Management Areas MPA (Figure 3.8). However, destructive fishing practices, particularly the use of dynamite, have obliterated many reefs in the area (S.N. Porter, *pers. obs*.). Community B was found in the Mesali Island Marine Park (Tanzania) and in Moheli Marine Park (Comoros), and is also likely to occur in the North Quirimbas Conservation Area and in the Quirimbas National Park (both in Mozambique) because of its widespread distribution within the region studied (see Figure 3.3).

Only 63 % of the community types I defined in the Tropical Indo-West Pacific are located within some form of MPA network. Establishing MPAs in the Inharrime Complex and in the Inhambane Bay area could increase this to 100 % depending on how large such MPAs become. However, some of the community types I defined could be products of anthropogenic factors, like over fishing, and therefore careful consideration should be given to their conservation value. Future research on anthropogenic influences and how they affect community structure and composition should be conducted. The Tropical Indo-West Pacific Bioregion is nevertheless still deficient in MPAs and communities C, G and H are not represented in MPAs. While significant progress has been made, no east African country protects more than 10 % of its continental shelf and less than 1 % of this is zoned as 'no-take' (Wells *et al.* 2007).

Conclusions

In total, 12 reef community types were defined at the scale of sites within the three bioregions I studied. The majority of the Subtropical Natal Bioregion was relatively depauperate in community types with most reefs surveyed representing a single community type, dominated by *Pyura stolonifera*, algal turf and coralline algae. The Delagoa Overlap Bioregion, despite consisting of only 120 km of coastline, incorporated a high diversity of five community types, with on average one out of every three reefs being classified as distinct. Three of these community types were, however, found in other bioregions. The inherent richness of community types in the Delagoa Overlap Bioregion is likely due to it being a transitional area between the subtropics and tropics, where species from the limits of both regions co-exist. Communities in the Delagoa Overlap Bioregion often comprised *Pyura stolonifera* and algal turf but were distinguishable based on the presence of various Alcyonacea, Scleractinia and Phaeophyta. The much larger Tropical Indo-West Pacific Bioregion was also diverse, with eight community types, seven found solely in this bioregion, and two that occurred at single sites only. Scleractinians dominated most communities, but there were also important algal turf, alcyonacean and phaeophyte components. The trends of increasing algal, poriferan and ascidian cover and decreasing alcyonacean and scleractinian abundance with latitude – as reported by Sheppard (2000) and summarised in Figure 3.7

– were also evident in my surveys. More specifically, many sites in the south were almost exclusively dominated by the ascidian *P. stolonifera.*

A significant divergence in community structure was found between assemblages on horizontal and vertical reef surfaces within the Delagoa Overlap Bioregion. Communities on horizontal surfaces were more diverse and comprised *Pyura stolonifera* and various phaeophytes, whereas communities on vertical reef surfaces were dominated almost completely by *P. stolonifera*. Such differences may be caused by periodic sand inundations, which are likely to affect horizontal reef surfaces most, and probably act as disturbance events that increase diversity by reducing the competitive domination by *P. stolonifera*. Such differences between horizontal and vertical communities need to be considered when planning future studies, as they are likely to significantly alter approaches to conservation.

Of the 12 community types defined in my study, only 75 % are represented within MPAs. The Delagoa Overlap Bioregion is particularly well conserved with all 5 community types there being located within MPAs. Although the Subtropical Natal Bioregion was not diverse in community types and is fairly well conserved in terms of protecting representative community types, establishment of an MPA in the Natal Bight area would enhance and secure a better protected area network. It would increase the percentage of shelf conserved, and increase the network's viability by reducing the chance of localised community extinction. In addition, it would also be beneficial to extend the St. Lucia Marine Reserve in the Delagoa Overlap Bioregion further south to Cape St. Lucia, as this would increase conservation of community type D. The Tropical Indo-West Pacific Bioregion is the most deficient in terms of conservation. Only half of the communities defined in this study are represented within MPAs. Many of these communities are located in southern Mozambique. By establishing MPAs in the Inharrime Complex and in the Inhambane Bay area, all community types could be represented within MPAs. The latest findings by Wells *et al.* (2007) show that significant progress has been made towards this, although the amount of shelf conserved is well below the targeted area of 10 % for each country, and less than 1 % of this is protected in 'no take' MPAs.

CHAPTER 4

CORRELATION OF ABIOTIC VARIABLES WITH SHALLOW SUBTIDAL REEF COMMUNITIES IN THE WESTERN INDIAN OCEAN

ABSTRACT

Determinants of shallow subtidal reef community structure in the western Indian Ocean are poorly known at broad geographic and local spatial scales. In this chapter I compare community structure with nine abiotic variables quantified at 54 sites using a correlative approach to elucidate potential abiotic determinants of community structure. In addition, I compare oceanographic characteristics of each of the three bioregions identified in Chapter 2, as well as nutrient concentrations between the Subtropical Natal and Delagoa Overlap bioregions, and the influence of geology at a subset of six sites within Subtropical Natal alone. Canonical correspondence analysis was used to correlate community structure with abiotic variables collected either *in situ* or with remotely sensed satellite imagery, at both geographic and bioregional scales. Using univariate and multivariate permutational analyses of variance, all six abiotic variables used to characterise the oceanographic conditions were shown to differ significantly among bioregions ($P_{(\text{perm})} \leq 0.005$). At the scale of the entire region, sea surface temperature (SST) and significant wave height, chlorophyll *a* and suspended inorganic sediment correlated most strongly with community structure and had intra-set correlations of -0.809, 0.779, 0.506 and -0.458 respectively in terms of the first three canonical axes. Within the Subtropical Natal Bioregion, turbidity and chlorophyll *a* (which were auto-correlated), followed by depth, had highest correlations with community structure. By contrast, in the Delagoa Overlap Bioregion, susceptibility to sand inundation and reef heterogeneity had the highest correlations with community composition, and in the Tropical Indo-West Pacific Bioregion, temperature and chlorophyll *a* were most highly correlated with community structure. Nitrate and phosphate concentrations were significantly greater in Subtropical Natal than in the Delagoa Overlap Bioregion ($P_{(\text{perm})} <$ 0.05), and phosphate also varied significantly seasonally, being greater in summer than winter ($P_{(\text{perm})} < 0.01$). Within Subtropical Natal, no significant difference was found between communities on Aeolianite versus Vryheid Formation sandstones ($P_{(\text{Monte-Carlo})} =$ 0.2399). Thus, at the largest scale, SST and wave height emerged as the dominant potential biogeographic determinants, whereas other, more locally-operating abiotic factors were the major correlates with different communities within bioregions.

INTRODUCTION

Distribution patterns, species abundances and community assemblages are determined by an intricate interaction between abiotic and biotic variables (Santos 1993). The abstraction that defines the ecological position of a species within a community and the array of physical conditions and resources it requires is termed its ecological niche (Grinnell 1904). The theoretical range of physical conditions a species can occupy defines its fundamental niche (Hutchinson 1957). However, few species have their distributions determined solely by tolerance to abiotic factors (Wolcott 1973), and biological interactions, particularly competition and predation, also play a role (Connell 1961a; Connell 1961b; Dayton 1971; McClanahan 1992, 1995; Connolly & Roughgarden 1999), confining each species to a portion of its fundamental niche, which is termed its realised niche. However, the precise processes that organize communities are often poorly understood (Santos 1993).

Abiotic factors are considered to underpin the biogeographic framework within which biotic interactions exert their influence at smaller spatial scales (McQuaid & Branch 1984). The causal processes that determine these patterns of species distribution are ideally identified using manipulative experimentation techniques (Underwood 1986). However, to develop hypotheses and design appropriate experiments, initial quantification of community structure and identification of associated abiotic variables are essential pre-cursors (James & McCulloch 1990; Underwood *et al.* 1991; Underwood *et al.* 2000).

A number of abiotic variables can influence benthic community composition and structure. These include sea temperature (Broekhuysen 1940; McQuaid & Branch 1984; Foster *et al.* 1988; Lüning 1990), depth (Barkai & Branch 1988; Underwood *et al.* 1991; Santos 1993; Schiel *et al.* 1995) and wave exposure (Jones & Demetropoulos 1968; Dayton 1971; Tsuchiya 1979; McQuaid & Branch 1985; Fuji & Nomura 1990; Bustamante 1994; Engledow & Bolton 1994; Bustamante *et al.* 1997; Alfaro & Carpenter 1999); substratum geology (Barnes & Powell 1950; McGuinness 1987; Holmes *et al.* 1997), topography (Fuji & Nomura 1990, Archambault & Bourget 1999) and colour (James & Underwood 1994); turbidity (Kleypas 1996; Fabricius & De'ath 2001) and sand inundation (Daly & Mathieson 1977; Littler *et al.* 1983; Foster *et al.* 1988; McQuaid & Dower 1990; Rogers 1990; Kendrick 1991; Airoldi & Cinelli 1997; Airoldi & Virgilio 1998).

Many of the studies cited above were based on small-scale investigations and there are few accounts of how abiotic factors correlate with community composition and structure over large biogeographic scales that span different regions. The east coast of Africa in the western Indian Ocean provides an opportunity for investigating such relationships. A strong gradient of decreasing water temperature with increasing latitude is found south of the equator as the Mozambique and Agulhas currents cool (Lutjeharms 1981; Ridderinkhof *et al.* 2001; Lutjeharms 2006). Turbidity (Jackson 1976; Sink 2001) and nutrient gradients, with associated differences in local primary production (McClanahan 1988a) are also evident as a result of river deposition. At more local scales, sand movements, largely associated with storms, have also been implicated as a major determinant of community composition on shallow subtidal reefs (Berry 1982).

Narrowing the focus, riverine input is 1000 times greater in the Subtropical Natal Bioregion than in the Delagoa Overlap Bioregion (Sink 2001). The multitude of rivers causes an increase in nearshore turbidity (Sink 2001). The resultant combination of differences in particulate materials and nutrients may be responsible for some of the divergence found between communities in the Subtropical Natal and Delagoa Overlap bioregions (see Chapter 2).

Such differences create a diverse combination of oceanographic conditions across the region. For example, sea temperature and turbidity change over large scales whereas depth and susceptibility to sand inundation vary over small scales specific to particular reefs. The study region is therefore ideal for investigating relationships between community patterns and abiotic correlations at both biogeographic and local scales.

This chapter focuses on possible abiotic determinants of community structure and quantifies the correlation between benthic shallow subtidal reef community structure and various abiotic variables at both biogeographic and intra-bioregional scales. It does not attempt to test causality but elucidates abiotic variables potentially responsible for differences in community structure variance, as a necessary pre-cursor to hypothesis testing. Data for temperature, wave height, turbidity, chlorophyll *a*, suspended sediments, depth, sand inundation, reef profile and reef heterogeneity were obtained for all sites and incorporated into a canonical correspondence analysis (CCA) to explore their relationships with community composition across the entire region. Data for nutrients could not be obtained for the Tropical Indo-West Pacific Bioregion, so this variable was omitted from the CCA analysis of abiotic determinants, but nutrient levels were compared at various sites between the Subtropical Natal and Delagoa Overlap bioregions. The effects of geology were considered in isolation for a subset of six sites limited to the Subtropical Natal Bioregion only.

Specifically, this chapter addresses the following questions:

1) Do abiotic variables differ among bioregions in a manner that correlates with benthic community structure and, if so, which variables correlate most strongly?

2) Do different sets of abiotic variables correlate with benthic community structure within each bioregion?

These questions could be fully explored for most abiotic variables, but in the case of nutrients (no data available for one biogeographic region) and rock type (sampled only in Natal and only for two rock types), two subordinate questions were addressed:

3) Do inshore nutrient concentrations differ between the Subtropical Natal Bioregion and Delagoa Overlap Bioregion?

4) Within the Subtropical Natal Bioregion, does rock type influence community composition?

Based on previous publications relating to southern African biogeography (McQuaid & Branch 1984, 1985; Bustamante & Branch 1996a; Bustamante *et al.* 1997; Sink 2001; Evans 2005; Blamey & Branch 2008) I test the following hypotheses:

a. Temperature will be the abiotic variable showing the highest correlation with community structure at a biogeographic scale.

b. Wave height will be strongly correlated with community composition at a local inter-site scale but not at a regional scale.

METHODS

Figure 4.1 summarises the data-collection and analyses followed in this chapter.

Data acquisition

Biological data

Community structure was sampled on the horizontal surfaces of 54 shallow subtidal reefs in the western Indian Ocean (for locations of sites, see Figure 2.3, p 24). For the analyses of the effects of geology on benthic community structure, I used a subset of 6 sites in Subtropical Natal, and for nutrients a subset of 19 sites in Subtropical Natal and the Delagoa Overlap bioregions was sampled. Analyses of other abiotic correlates drew on all 54 study sites quantified in Chapter 2, excluding Vetch's Pier, as it is an artificial reef with an outlying community composition. For detailed methodology relating to the biological surveys, see Chapter 2, but in short, at each site 15 replicate quadrats were randomly placed on horizontal reef and percentage cover recorded for sessile and sedentary species, whereas mobile species were counted using 10 replicate 5 x 2 m belt transects per site. The data were then converted into ash-free dry biomass.

Abiotic data

Abiotic data were collected either *in situ* or using remote-sensing satellite imagery. Remotely sensed data included 11-µm sea-surface temperature (SST), significant wave height, turbidity, chlorophyll *a*, and suspended inorganic sediments measured as normalized water-leaving radiances (nLw) at 551 nm and 667 nm. Level-2 Aqua Moderate Resolution Imaging Spectroradiometer data (Aqua-MODIS; Esaias *et. al.* 1998) for 11-µm SST (Brown & Minnett 1999), turbidity (diffuse attenuation coefficient, light attenuation at 490 nm or k490), chlorophyll *a* concentration (OC3M) (O'Reilly *et. al.* 1998) and nLw 551 nm and nLw 667 nm (O'Reilly *et. al.* 2000) were acquired for a 3-yr period from 2003 to 2005 from the NASA Goddard Distributed Active Archive Center. Data for nLW 551 nm and nLw 667 nm are widely considered good indicators of total suspended inorganic solids such as those from river plumes, and repeatedly used for this purpose (Gordon & Voss 1999; Li *et. al.* 2003; Yuan *et. al* 2008).

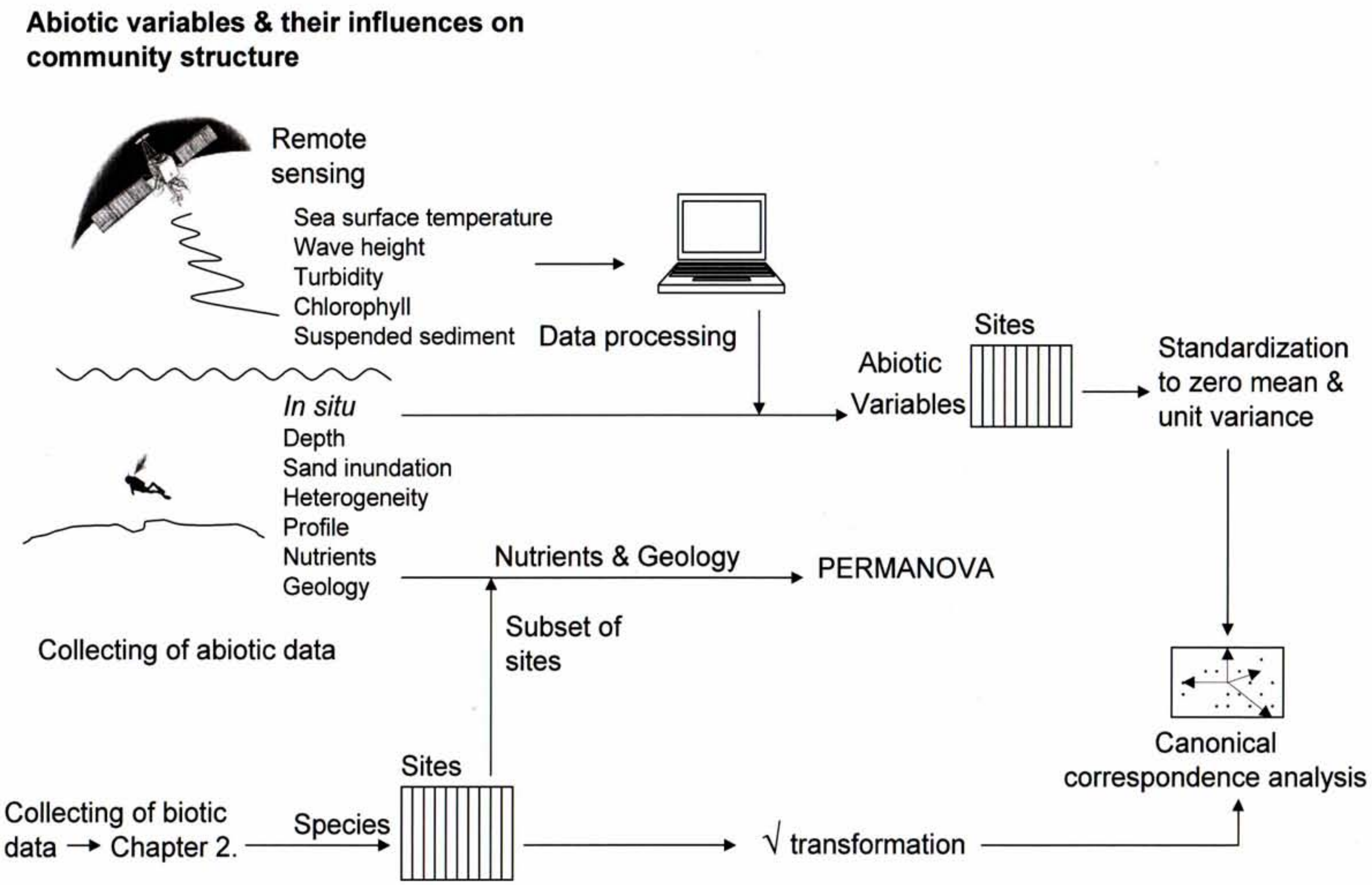


Figure 4.1. Schematic representation of the sampling and data analysis protocol for Chapter 4.

These remotely-sensed data were processed to Level-3 standard mapped time-composite images using default NASA coefficients and standard community algorithms as implemented by SeaWiFS Data Analysis System version 5.2 (SeaDAS ver. 5.2; Baith *et. al.* 2001) image processing software on a LINUX-based operating system. Unix shell scripts were used to batch-process the 16000 data files, which exceeded 300 gigabytes when unzipped. Unzipped ocean colour files (as opposed to the SST & significant wave height files) were spatially binned (l2bin) to a resolution of 1 km with standard NASA default flags (Patt *et. al.* 2003) using scripts from the Unix command line.

SST files were spatially binned to a 1-km resolution using additional flags to derive quality levels q0 and q1, which are the best and second-best-quality pixels suggested for coastal areas (Labiosa *et al.* 2003), and according to whether the files were daytime or night-time scenes. The accuracy of the inshore remotely-sensed SST satellite data was validated using *in situ* temperature-logger data in 15 m of water offshore of Ballito in the Subtropical Natal Bioregion, and offshore of Leadsman's Shoal and Quarter Mile Reef in the Delagoa Overlap Bioregion (see Figure 4.2 for site positions).

Using list files, spatially binned files were time-binned (l3bin) 64 files at a time due to the limits of the l3bin program, until a single three-year (2003-2005) time-composite L3b_GAC file was created for ocean colour products and for SST. In the case of the SST validation exercise, monthly time-composite L3b_GAC files were created.

Data for each product were derived directly from 1-km resolution three-year average time-composite L3b_GAC files using the SeaDAS read and profile graphical user interface. A 3x3 pixel-box was placed over each of the study sites where at least two pixel values were extracted and used in calculating the median value to increase data quality by reducing the affect of any outlying pixel values. If necessary, the pixel box was shifted offshore to secure two valued pixels, but data were always obtained within 4 km of each study site. SST validation data were extracted from monthly time-binned L3b_GAC files using the same 3x3 pixel-box approach around each *in situ* temperature logger. No other nearshore *in situ* data were available to ground-truth other remote-sensed products. Finally, the SeaDAS Smigen program was used to produce standard mapped colour-composite images (1-km resolution, 2003-2005) of the mean for each product.

Multi-mission, 1° x 1° gridded, Level-2 altimetry data of significant wave height (AVISO & PODAAC 2006) for a two-year period from 2004 to 2005 were acquired from Archiving, Validation and Interpretation of Satellite Oceanographic Data (AVISO) as part of the Segment Sol multimissions d'AL Timétrie, d'Orbitographie et de localisation précise (SSALTO) ground-processing unit. Significant wave height is the average of the highest ⅓ of wave heights recorded during a particular interval (Denny 1988, 1995). Four satellite sensors were used: TOPEX/Poseidon, Jason-1, Environmental Satellite (ENVISAT), and the GeoSat Follow-On (GFO). I processed these Level-2 data files to a Level-3 average time-composite image (plate career projection) by merging the data from the four satellites using the Basic Radar Altimetry Toolbox version 1.1.1. (BRAT ver. 1.1.1. 2007). Multi-mission merged altimetry data using optimal interpolation improves temporal and spatial coverage and thus accuracy (Le Traon *et. al.* 1998; Le Traon & Dibarboure 1999; Le Traon & Dibarboure 2004; Zhang & Chen 2006). A step value defining the spatial resolution at ⅓° and a Loess filter cut-off value of 29 were used to smooth and interpolate data values (BRAT 2006). The average significant wave height over the 2-year period was then extracted for each of the 54 sites. Wave height has been shown to be a good surrogate for wave force as the two are tightly correlated (Helmuth & Denny 2003).

Nutrient analyses were conducted at a subset of sites. Three replicate 10-ml inshore water samples were collected at 12 sites south of St. Lucia in the Subtropical Natal Bioregion and at 7 sites north of St. Lucia in the Delagoa Overlap Bioregion (Figure 4.2). This was done within 21-day periods in May 2005 (during the non-rainy season) and in January 2006 (during the rainy season). Samples were placed on ice in the field and stored frozen until analysed by the Autoanalyzer Laboratory at the department of Environmental Affairs and Tourism, Marine and Coastal Management, South Africa, for nitrite (NO_2), nitrate (NO_3), silicate (SiO_3) and phosphate (PO_4), using an Astoria Pacific series 300 autoanalyzer (Astoria-Pacific, Inc., Clackamas, Oregon). Duplicate check standards,

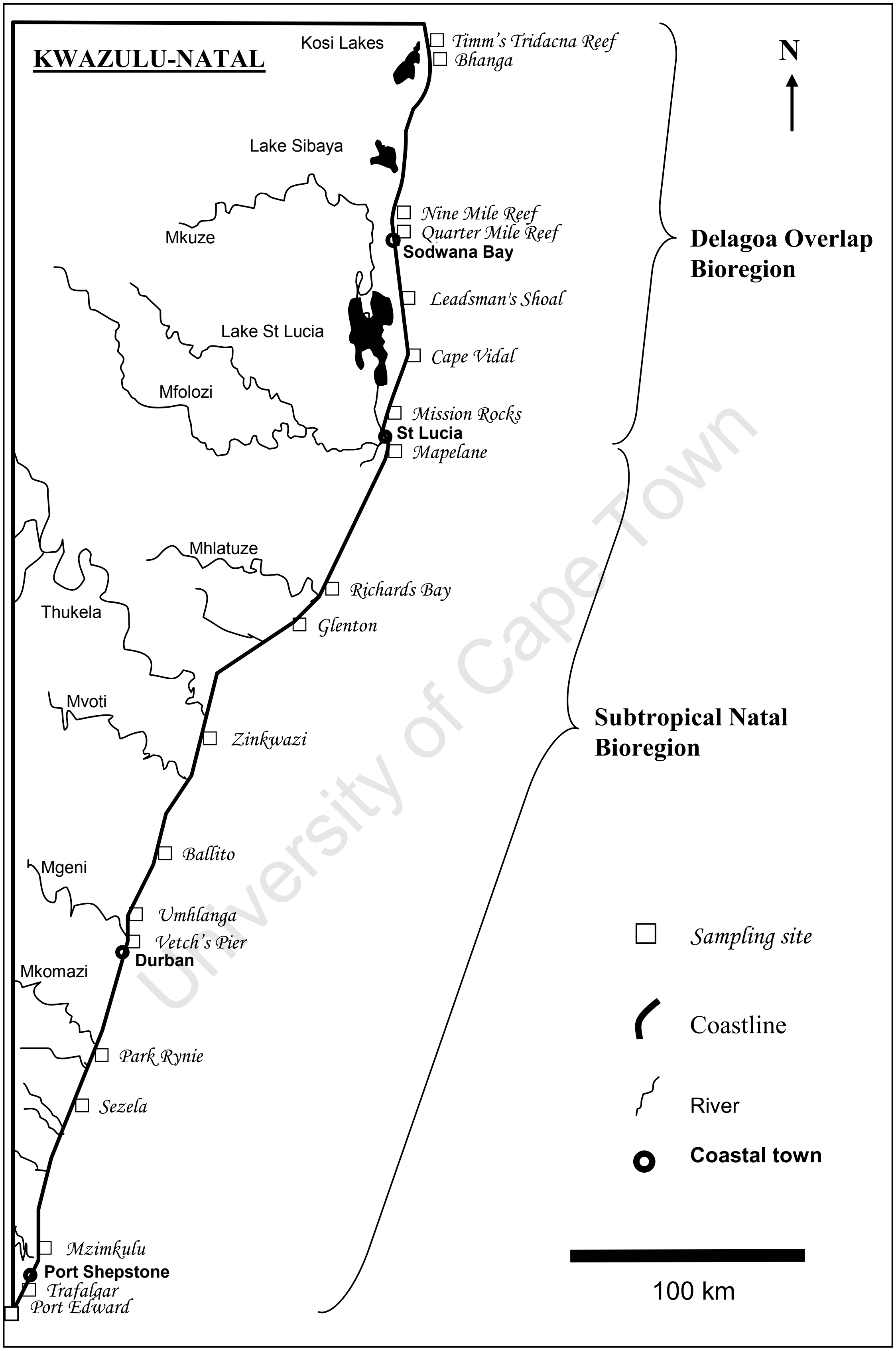


Figure 4.2. The KwaZulu-Natal political province in north eastern South Africa showing the 19 nutrient sampling sites, major rivers and coastal towns.

followed by duplicate blanks were interspersed at intervals of every nine samples. Nutrient concentrations were expressed in micromoles per litre (µmoles l^{-1}).

Four abiotic variables of reef characteristics were recorded *in situ* at each of the 54 study sites: depth, reef susceptibility to sand inundation, reef profile and reef heterogeneity. Depth was quantified with a Mares M1 dive computer while the other *in situ* variables were estimated semi-quantitatively as follows.

Sand inundation could not be measured directly as sand cover is notoriously fickle, fluctuating seasonally and even daily (Sink 2001), so single measurements would have been meaningless, and regular monitoring was logistically impractical. Instead, I developed an index of Sand Inundation Susceptibility, defined as the potential of a reef to be inundated by sand, based on: (1) Proximity to sand source (i.e. distance from quadrats to sand source); (2) Elevation of reef above surrounding sand; (3) Topographic potential of the reef to trap sand (i.e. broken substratum with intervening sandy gulleys or continuous substratum).

It was scored on a scale from 1 to 4, where:

1 = Low: Large reef (i.e. large distance from quadrats to sand source), highly elevated from surrounding sand, continuous substratum.
2 = Medium: Medium size reef, moderately elevated from surrounding sand, continuous substratum.
3 = High: Medium or small reef, moderately elevated from surrounding sand, broken substratum with sand patches; or large reef, level with surrounding sand, continuous substratum.
4 = Very high: Small reef, level with surrounding sand, broken substratum with patches of sand.

Reef profile was scored as the elevation of the reef relative to surrounding reef or sand, where:

1 = Low profile: < 1 m
2 = Medium: 1 – 3 m
3 = High: 3 – 5 m
4 = Very high: >5 m

Reef heterogeneity was defined as the range in height of the reef topography in the area where quadrats were placed, where:

1 = Low: < 1 m
2 = Medium: 1 < 3 m
3 = High: 3 >m

Geology was investigated at a subset of sites within the Subtropical Natal Bioregion. Three site pairs of two contrasting rock types, Aeolianite and Vryheid-Formation Sandstone, were selected to test for differences between benthic communities from dissimilar geologies. Aeolianite reefs were Bluff, Limestone Reef and Cape St. Lucia while Selection Reef, Ballito and Nonoti were composed of Vryheid-Formation Sandstone (see Figure 2.3 p 24).

Data analysis

The interpretation and importance of abiotic variables were evaluated univariately and multivariately. Univariate analyses involved characterising oceanographic conditions in each of the three bioregions using the remotely sensed and *in situ* data. This was done independently among the three bioregions delineated in Chapter 2 using sites as replicates except for the nutrient analyses, which were conducted only for the Subtropical Natal and Delagoa Overlap bioregions. Univariate one-way permutational analysis of variance (PERANOVA) (Anderson 2001) using DISTLM v. 5 (McArdle & Anderson 2001; Anderson 2001) and XMATRIX (Anderson 2003) to formulate orthogonal codes for the unbalanced designs, were performed on each remotely sensed abiotic variable independently (untransformed, Euclidean distance measure, 9999 unrestricted permutations of the raw data). Post hoc comparisons were carried out using the same model to investigate where significant differences ($\alpha = 0.05$) lay.

The validity of remotely-sensed SST was tested by calculating the Pearson product moment correlation coefficient between monthly mean temperature data acquired from each *in situ* temperature logger and the AquaMODIS sensor.

Nutrient data for the Subtropical Natal and Delagoa Overlap bioregions were similarly analysed. Independent univariate three-factor unbalanced PERANOVAs (Anderson 2001; McArdle & Anderson 2001) were performed on each nutrient type using log(x+1) transformed data and the Euclidian distance measure (9999 permutations of residuals under a reduced model, type III sums of squares) with the software PERMANOVA+ (Anderson *et al.* 2008b). Bioregion was orthogonal and fixed with 2 levels (Subtropical Natal and Delagoa Overlap), Season was orthogonal and fixed with 2 levels (high rainfall & low rainfall) and Site was a random factor nested within Bioregion with 19 levels (12 in Subtropical Natal and 7 in Delagoa Overlap).

Analyses of *in situ* semi-quantitative reef characteristics, i.e. depth, susceptibility to sand inundation, reef profile and heterogeneity, were examined per bioregion using frequency graphs with sites as replicates and descriptive statistics of the average and standard deviation. As the data were semi-quantitative and categorical, non parametric Kruskal-Wallace one-way ANOVAs on ranks were performed on each reef characteristic, and Dunn's post hoc multiple pairwise comparisons performed if the *a priori* analysis found significant differences.

To explore relationships between subtidal species assemblages and selected environmental variables, a unimodal model for non-linear multivariate direct gradient analysis was performed. Canonical correspondence analysis (CCA) was used to correlate benthic community structure with abiotic variables (Ter Braak 1986; Palmer 1993; Ter Braak & Verdonschot 1995) using ECOM version 1.37 (Henderson & Seaby 2000). Root-transformed ash-free biomass data were correlated with standardized (zero mean and unit variance) abiotic data (Ter Braak 1986) at two spatial scales: that of the entire region (all 54 sites), and independently for each of the three bioregions identified in Chapter 2. This determined if different abiotic variables correlated with benthic community structure at different spatial scales (entire region vs. within-bioregion) and if different sets of abiotic variables correlated with benthic community structure within different bioregions. Many authors have noted great variability in diversity, community structure (see Chapters 2 & 3) and abiotic variables among sites within any geographical region (Jackson 1976; Schiel & Foster 1986; Barkai & Branch 1988; McGuinness 1990;

Morrisey *et al.* 1992; Schiel *et al.* 1995; Archambault & Bourget 1996; Thompson *et al.* 1996), requiring analyses at finer spatial scales (within bioregions).

Nine abiotic variables were included in the CCA analysis. Nutrient and geological data were excluded as they were not collected from all 54 sites. The variables nLw 551 nm and nLw 667 nm were highly correlated (r = 0.82), and both measure suspended inorganic sediment, so they were added to make a composite variable “sediment”. Other abiotic variables were included in the analysis even if there was colinearity between some of them. The rationale for their inclusion was that (1) there was an absence of consistency between correlating pairs of variables among the different bioregions, and (2) their exclusion reduced the total canonical variance explained by the model. Including correlated variables in the CCA does not compromise the analysis as the intra-set correlations are not effected (Ter Braak 1986), but needs to be considered when interpreting the results (Palmer 1993). Intra-set correlation coefficients were used to examine the relative importance of abiotic variables: values of ≥ ± 0.4 were regarded conservatively as being most likely to be biologically important (Rakocinski *et al.* 1996). The results of the CCA were plotted in the form of a biplot comprised of sites and abiotic variables denoted by vectors. For interpretation of such ordination plots see Ter Braak (1986) and Ter Braak & Verdonschot (1995).

Finally, the influence of geology on community structure was tested using a two-factor permutational multivariate analysis of variance (PERMANOVA) (Anderson 2001; McArdle & Anderson 2001) on root-transformed biomass data using the Bray-Curtis distance measure and 9999 unrestricted permutations of the raw data. Rock type was orthogonal and fixed with two levels and Site was a random factor nested within Rock type.

RESULTS

Bioregional oceanographic conditions and reefs characteristics

Mean SST over the three-year period differed significantly among bioregions (PERANOVA $F_{(2,51)} = 41.41$, $P_{(\text{perm})} = 0.0001$). An overall trend of increasing temperature was observed with decreasing latitude (Figures 4.3 & 4.4), with the means for each region differing from each other ($P_{(\text{perm})} < 0.0001$).

The inshore remotely-sensed SST data were found to be reliable and validated by significant positively correlated linear relationships between mean monthly remotely sensed SST and *in situ* recorded sea temperature data for all three temperature loggers (Figure 4.5).

Mean significant wave height increased with increasing latitude (Figure 4.6), from a mean (±SD) of 1.6 ± 0.3 m in the Tropical Indo-West Pacific Bioregion to 2.3 ± 0.1 m in the Subtropical Natal Bioregion (Figure 4.7). Significant differences were found among all three bioregions (PERANOVA $F_{(2,51)} = 59.78$, $P_{(\text{perm})} = 0.0001$; *a-posteriori* pairwise comparisons significant at $P < 0.0001$ in all comparisons).

Mean turbidity (Figures 4.8 & 4.9) differed significantly among bioregions over the three-year period (PERANOVA $F_{(2,51)} = 19.57$, $P_{(\text{perm})} = 0.0001$). The Delagoa Overlap Bioregion had the lowest turbidity of 0.049 ± 0.002 m^{-1}, significantly less than both the Subtropical Natal Bioregion (0.110 ± 0.025 m^{-1}, PERANOVA $t_{(1,28)} = 8.55$, $P_{(\text{perm})} = 0.0001$) and Tropical Indo-West Bioregion (0.088 ± 0.033 m^{-1}, PERANOVA $t_{(1,36)} = 4.30$, $P_{(\text{perm})} = 0.0008$). A smaller, but also significant, difference existed between the Subtropical Natal and Tropical Indo-West Pacific bioregions (PERANOVA $t_{(1,38)} = 2.17$, $P_{(\text{perm})} = 0.0352$).

Mean chlorophyll *a* concentrations (Figures 4.10 & 4.11) exhibited patterns almost exactly parallel to those of turbidity, with significant differences among all bioregions (PERANOVA $F_{(2,51)} = 23.97$, $P_{(\text{perm})} = 0.0001$). The Subtropical Natal Bioregion had the highest concentration (1.188 ± 0.448 mg/m^3) followed by the Tropical Indo-West Pacific

Bioregion (0.683 ± 0.385 mg/m^3) and the Delagoa Overlap Bioregion (0.270 ± 0.030 mg/m^3).

Across all nutrient species, average concentrations (and their associated standard deviations) were greater in the Subtropical Natal Bioregion than in the Delagoa Overlap Bioregion (Figure 4.12). Nitrate and phosphate differed significantly between these bioregions (PERANOVA $P_{(perm)}$ = 0.0048 and 0.0239 respectively), whereas nitrite and silicate exhibited the same pattern but the differences were marginally non-significant (PERANOVA $P_{(perm)}$ = 0.07 and 0.05 respectively; Table 4.1). Only phosphate varied significantly between seasons, being greater in summer than winter (PERANOVA $P_{(perm)}$ = 0.0072). For all nutrient species, significant differences existed among sites within bioregions (PERANOVA $P_{(perm)}$ = 0.0001) and there was a strong interaction between seasons and sites within bioregions (PERANOVA $P_{(perm)}$ = 0.0001).

Mean suspended inorganic sediment (nLw) at 551 nm (Figure 4.13) and at 667 nm (data not shown, but similar in pattern and an order of magnitude less) showed patterns similar to those of turbidity and chlorophyll *a*, with the Delagoa Overlap Bioregion having the lowest radiance values, followed by the Subtropical Natal and Tropical Indo-West Pacific bioregions (Figures 4.14). Significant difference in nLw at 551 nm and at 667 nm were found among bioregions (PERANOVA $F_{(2,51)}$ = 16.09 and 5.67, $P_{(perm)}$ = 0.0002 and 0.0050 respectively) and between all *a-posteriori* pairwise comparisons at 551 nm (PERANOVA, α = 0.01), whereas *a-posteriori* pairwise comparisons at 667 nm revealed no significant difference between the Subtropical Natal and Tropical Indo-West Pacific Bioregions (PERANOVA $t_{(1,38)}$ = 0.94, $P_{(perm)}$ = 0.3507).

Reef characteristics (Figure 4.15) were similar among bioregions according to average ± standard deviations. The greatest difference was found in average depth between Subtropical Natal and Delagoa Overlap bioregions, but even that differed by only 1.1 m and was not significant (H = 4.2, P = 0.124). Although average ± SD values were similar, different frequency distributions were found among bioregions for all variables, particularly between the sand inundation potential for sites in the Tropical Indo-West

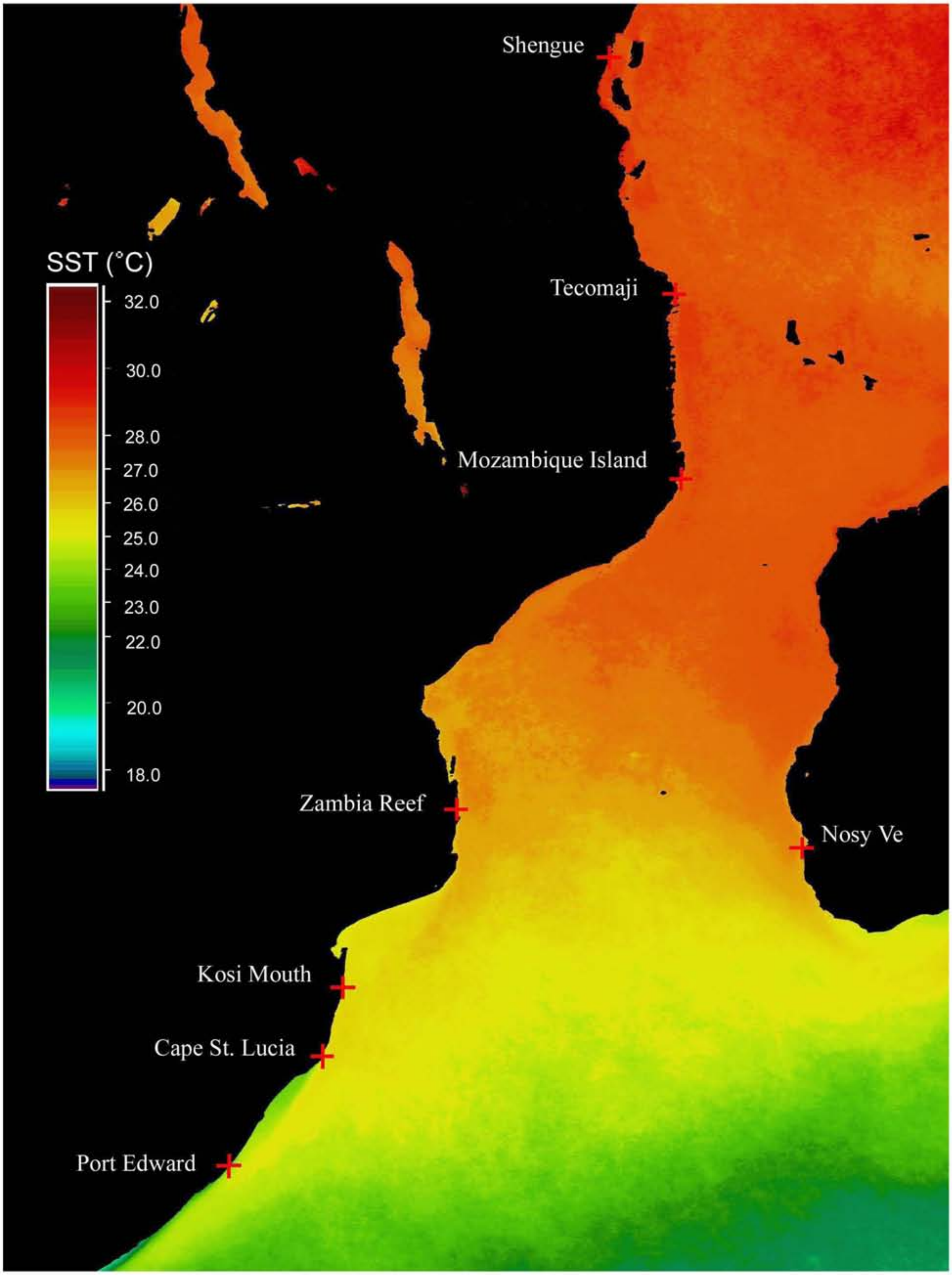


Figure 4.3. Mean sea surface temperature: AquaMODIS 1-km resolution 3-yr time-composite image (2003-2005) for the western Indian Ocean.

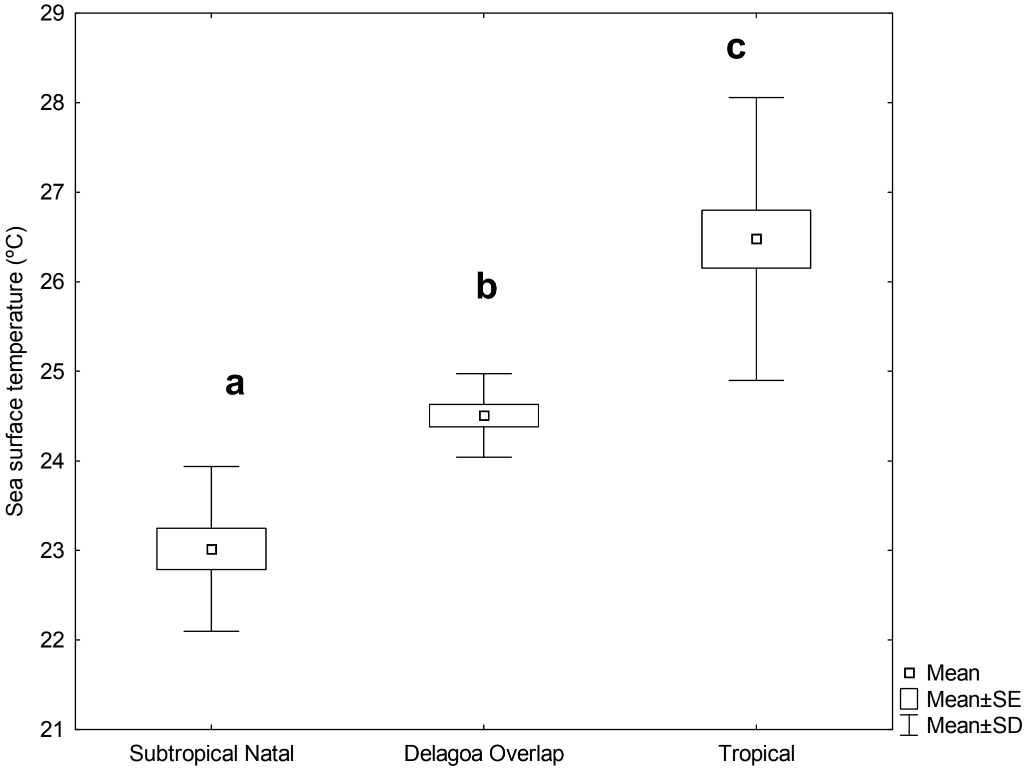


Figure 4.4. Sea surface temperature: means ± standard error and standard deviation for the Subtropical Natal, Delagoa Overlap and Tropical Indo-West Pacific bioregions. Letters above data differ in cases of significant differences among bioregions (PERANOVA and *a- posteriori* comparisons, c > b > a, $P < 0.0001$).

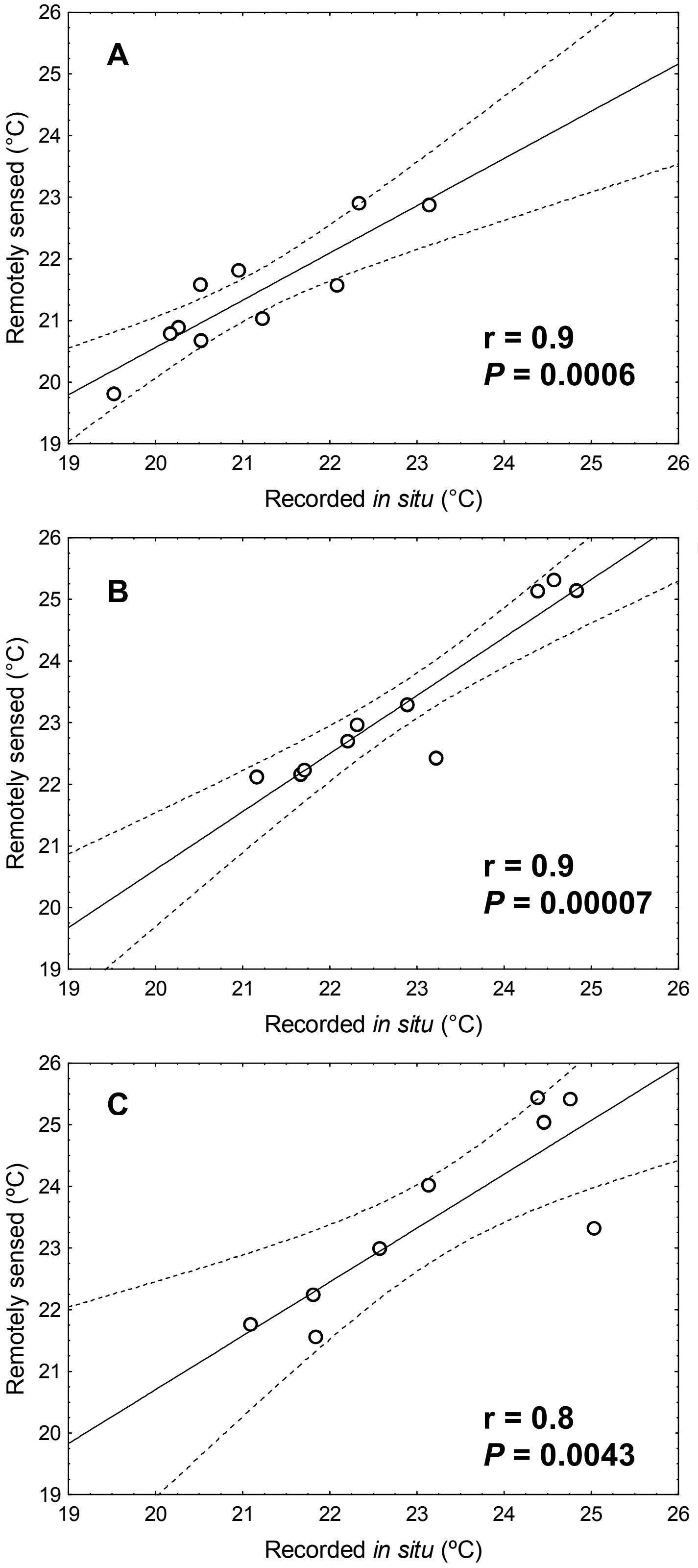


Figure 4.5. Relationships between remotely sensed SST and *in situ* recorded sea temperature for (A) Ballito, (B) Leadsman's Shoal and (C) offshore of Quarter Mile Reef, Sodwana Bay. Dotted lines indicate 95 % confidence limits; r = Pearson product moment correlation coefficient.

Pacific and Subtropical Natal bioregions. Sand inundation potential showed a general decreasing trend among bioregions from south to north from an average ± SD of 3.1 ± 0.7 m (high potential to inundate) in the Subtropical Natal Bioregion to 2.2 ± 0.7 m (medium potential to inundate) in the Tropical Indo-West Pacific Bioregion. Sand inundation potential between reefs from the Subtropical Natal and Tropical Indo-West Pacific was the only reef characteristic to differ significantly ($Q = 2.9$, $P < 0.05$). All other *a-priori* analyses of reef characteristics found no significant differences ($P \geq 0.124$).

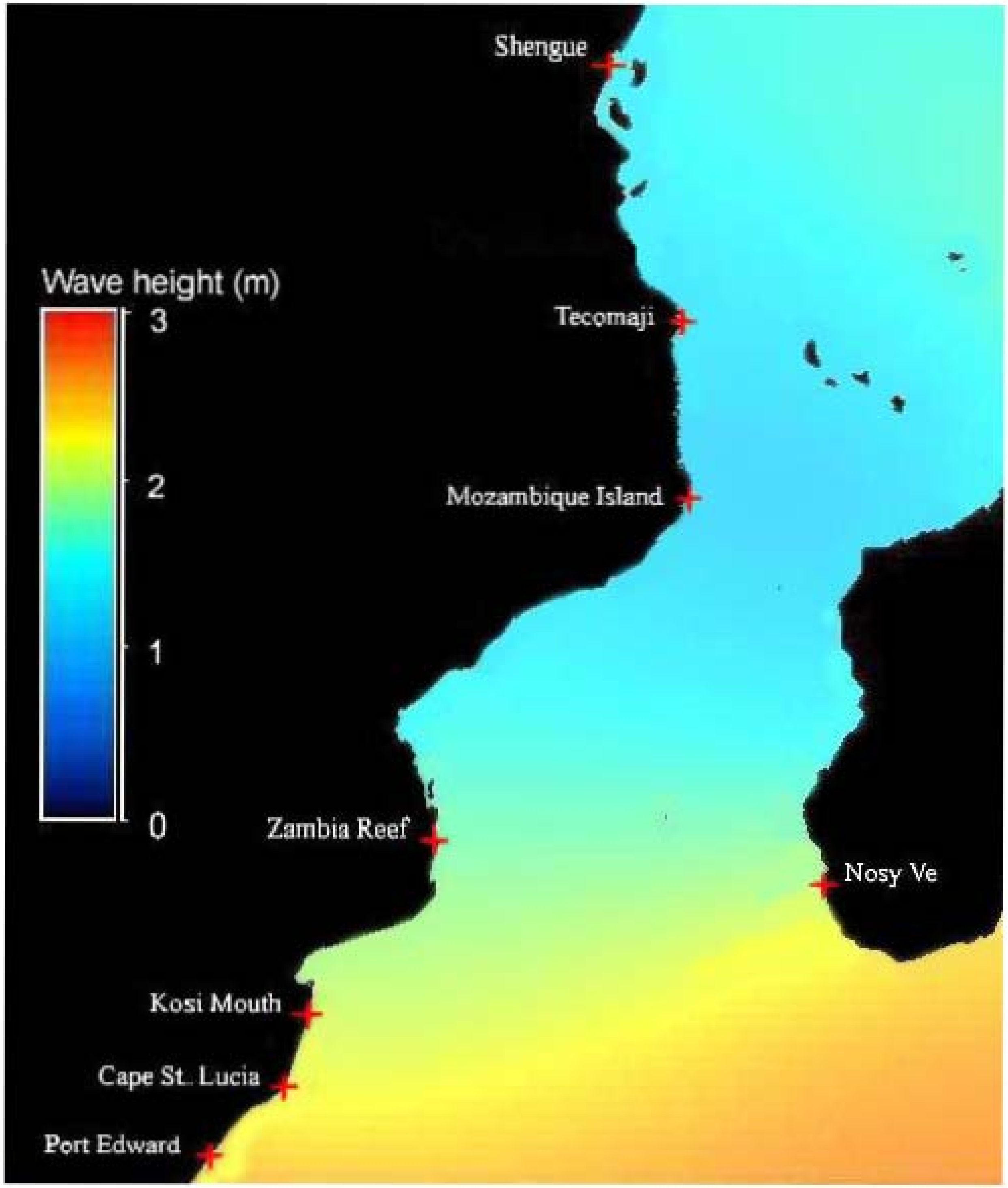


Figure 4.6. Mean significant wave height: multi-mission 0.33° resolution 2-yr time-composite image (2004-2005).

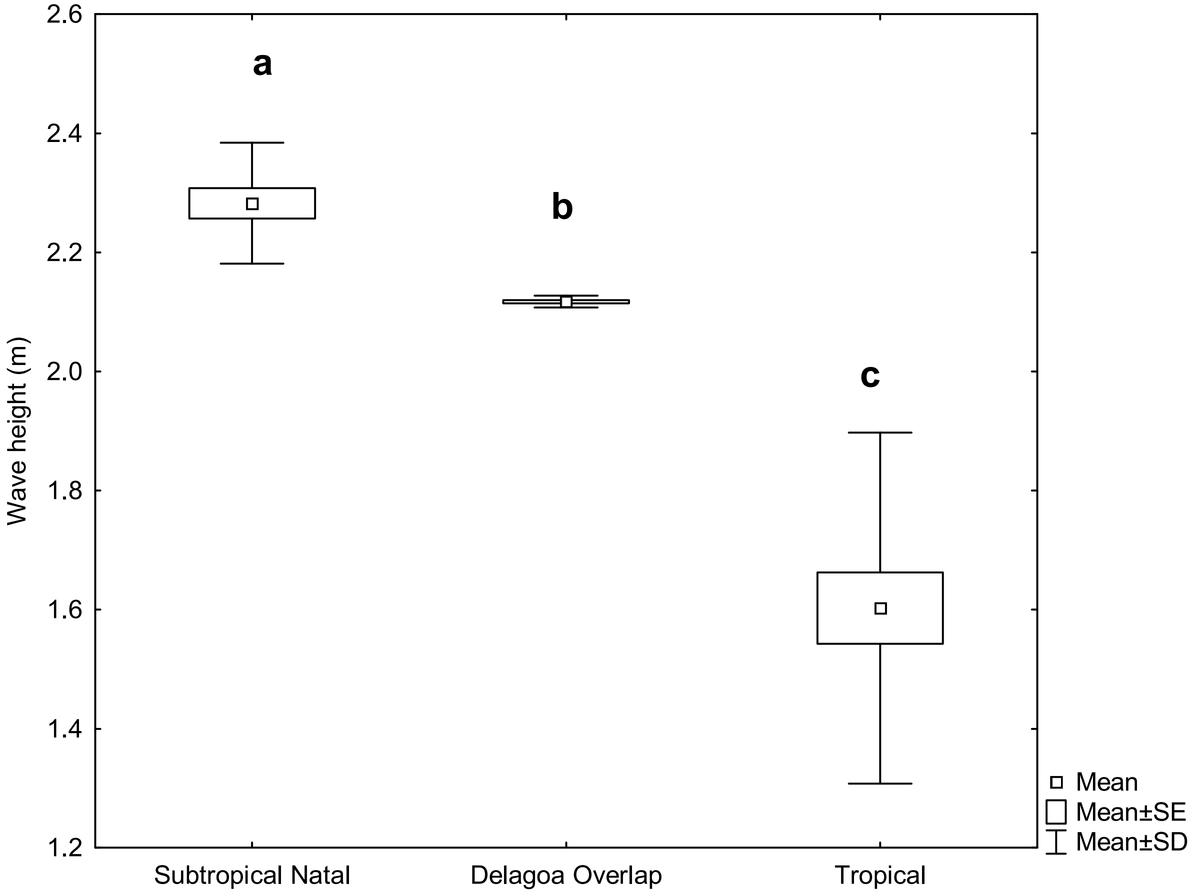


Figure 4.7. Significant wave height: mean ± SE and SD for the Subtropical Natal, Delagoa Overlap and Tropical Indo-West Pacific bioregions. Letters above data differ in cases of significant differences among bioregions (PERANOVA and *a-posteriori* comparisons, a > b > c; $P < 0.0001$).

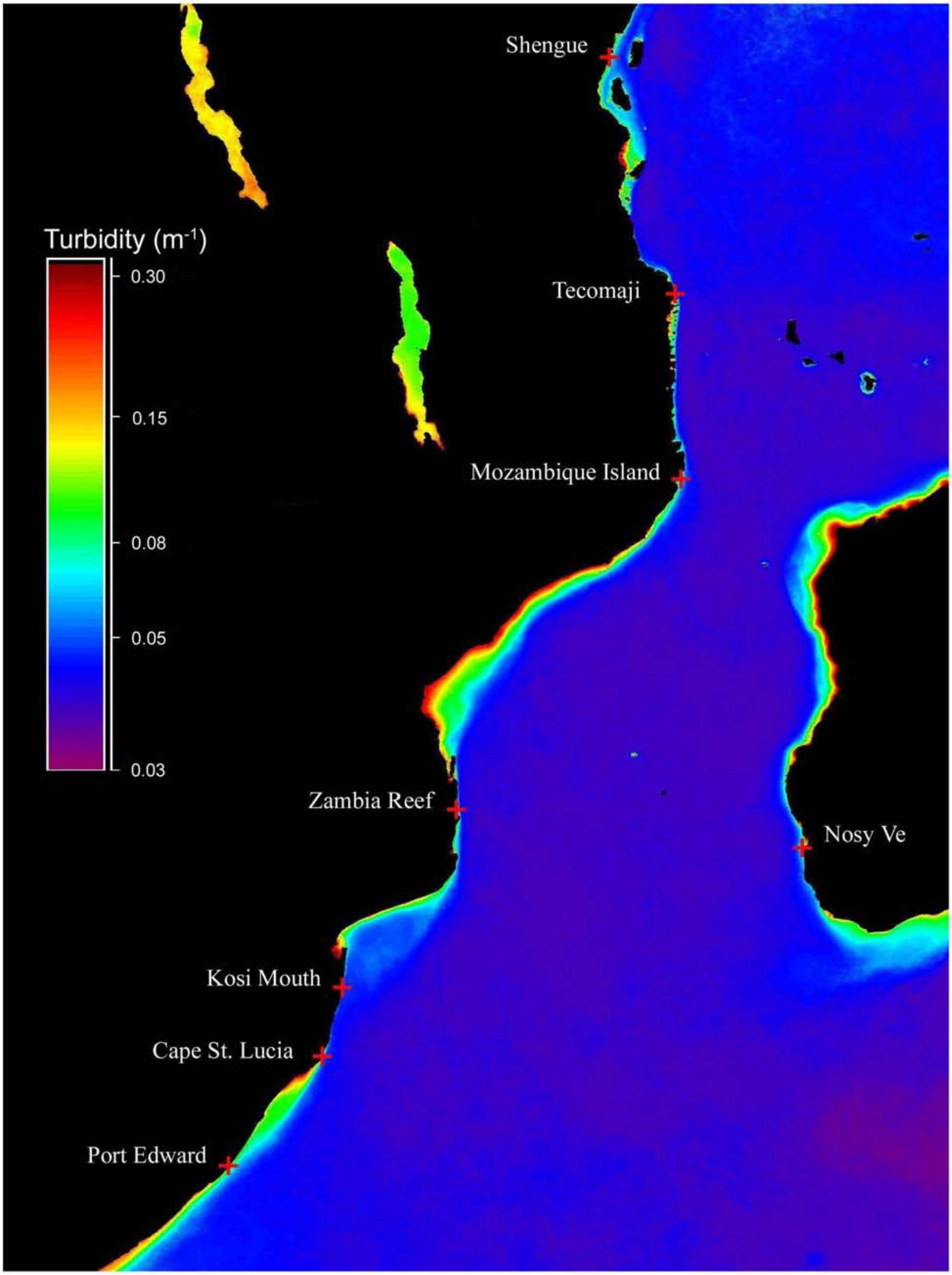


Figure 4.8. Mean turbidity: AquaMODIS 1-km resolution 3-yr time-composite image (2003-2005).

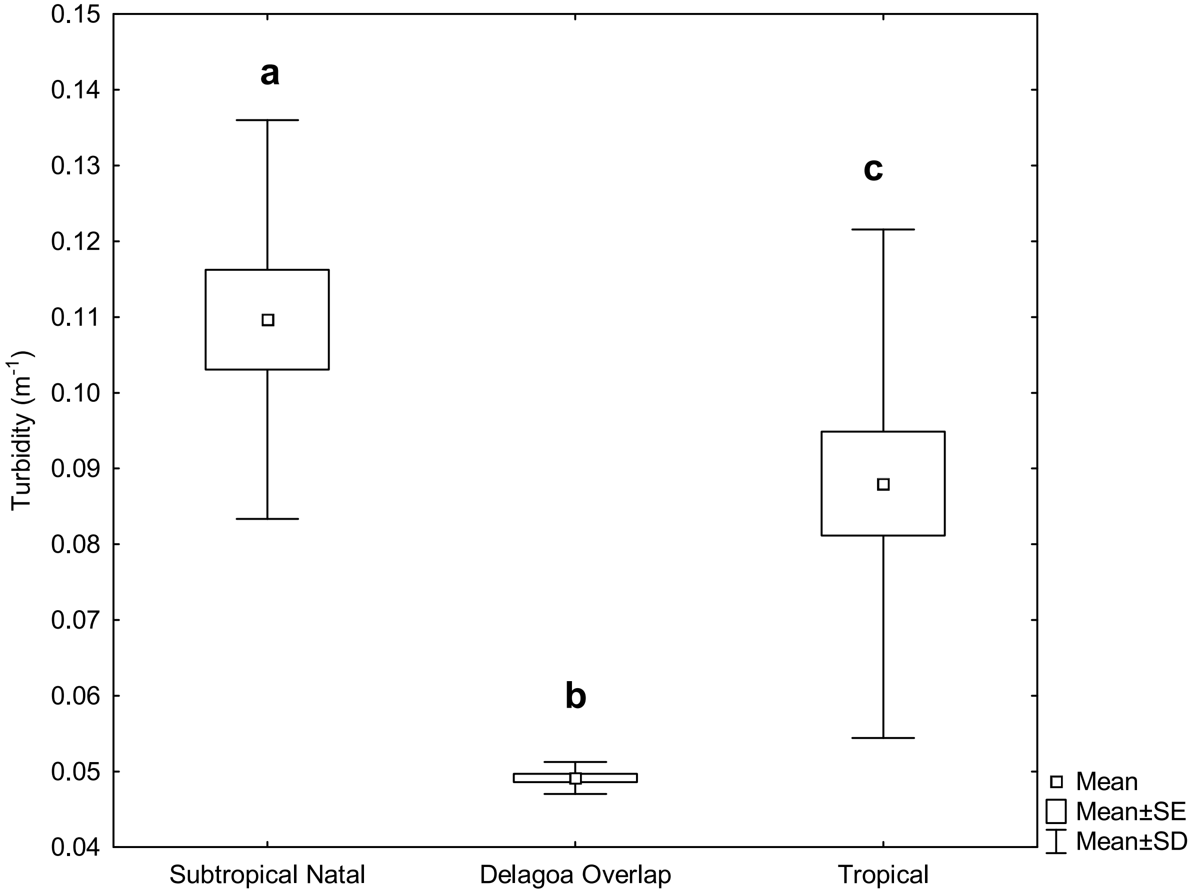


Figure 4.9. Means, ± SE and ± SD for turbidity for the Subtropical Natal, Delagoa Overlap and Tropical Indo-West Pacific bioregions. Letters above data differ in cases where significant differences existed among bioregions according to PERANOVA (a > c > b; $P < 0.05$ and < 0.001 respectively).

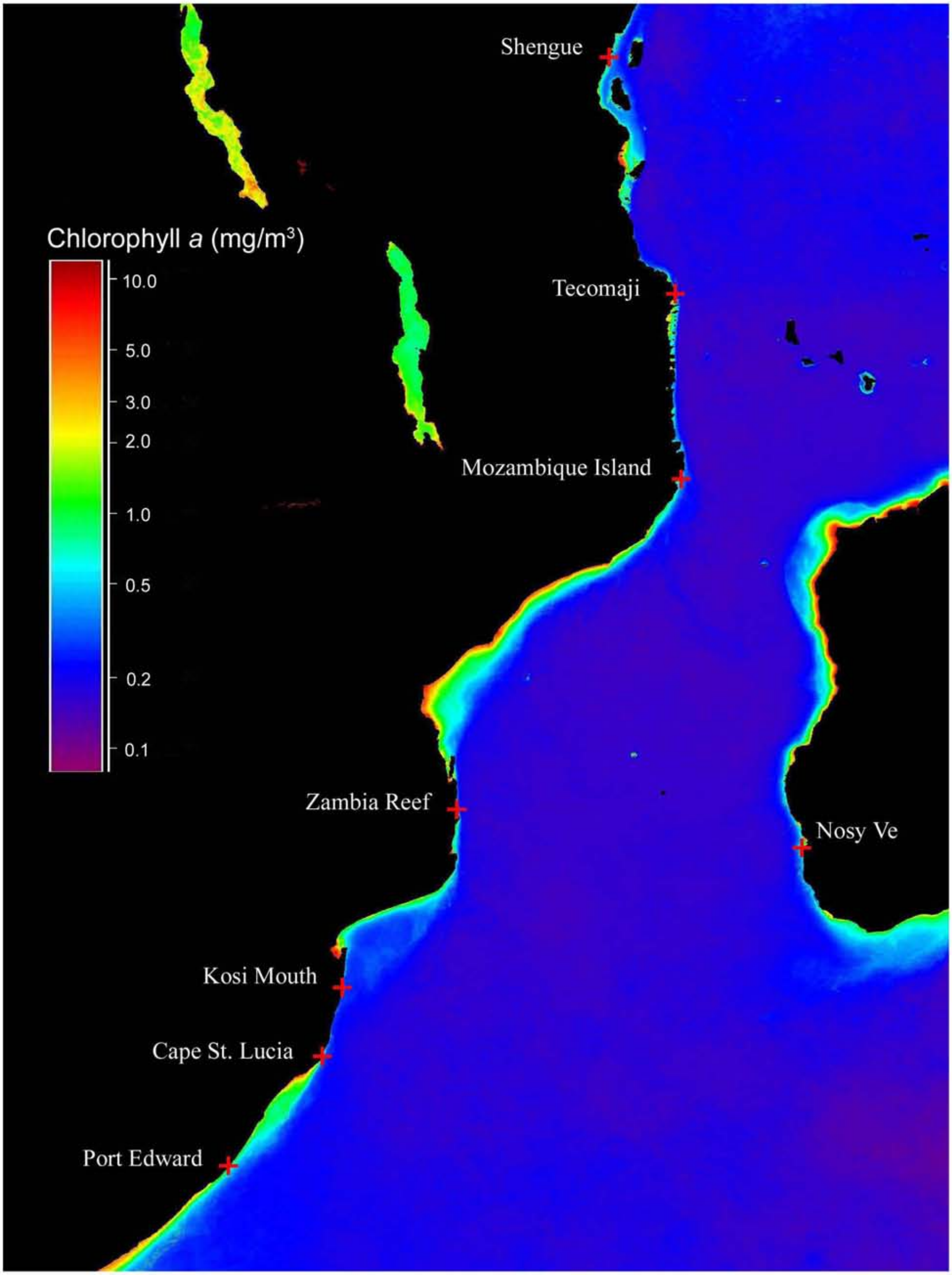


Figure 4.10. Mean chlorophyll *a* concentration: AquaMODIS 1-km resolution 3-yr time-composite image (2003-2005).

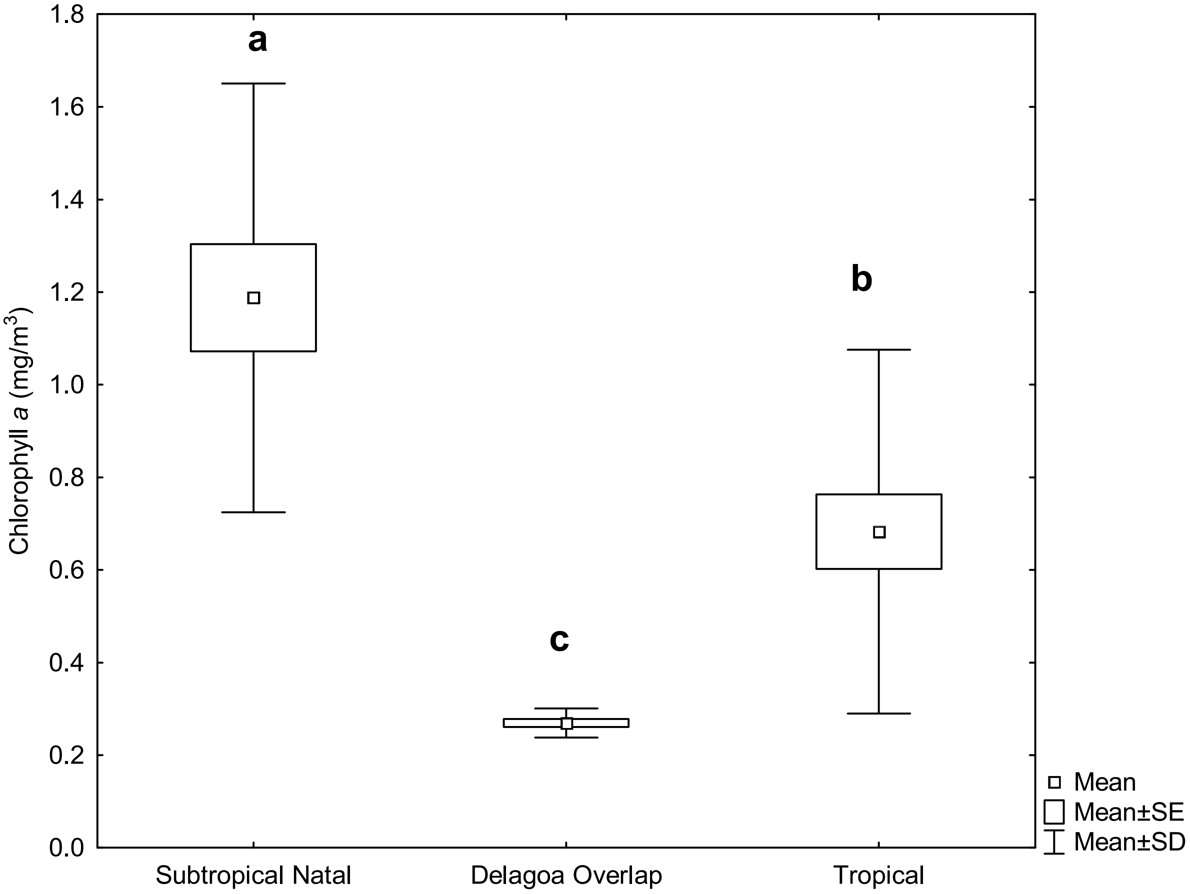


Figure 4.11. Means ± SE and ± SD for chlorophyll *a* concentrations for the Subtropical Natal, Delagoa Overlap and Tropical Indo-West Pacific bioregions. Letters above data differ where significant differences existed among bioregions (PERANOVA and *a-posteriori* comparisons a > b > c; $P < 0.001$).

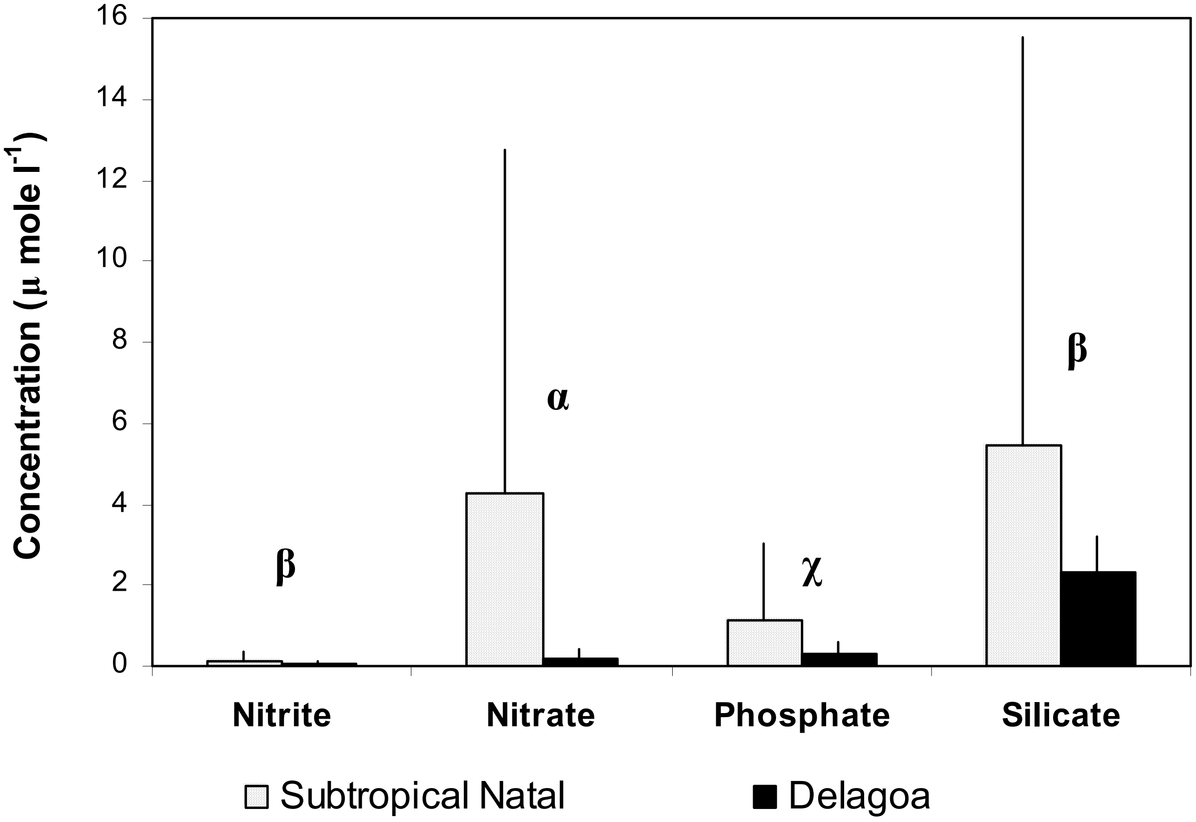


Figure 4.12. Average (± SD) nutrient concentrations of nitrite, nitrate, phosphate and silicate for the Subtropical Natal Bioregion and the Delagoa Overlap Bioregion. Probabilities of differences between bioregions according to PERANOVAs are indicated by symbols: $\alpha = P < 0.01$; $\chi = P < 0.05$; $\beta = P < 0.1$.

Table 4.1. Univariate PERANOVA for each dissolved nutrient from sites in the Subtropical Natal Bioregion and Delagoa Overlap Bioregion using log(x + 1) transformed nutrient concentrations and Euclidian distance. * = Significant difference (α = 0.05).

		Nitrite			**Nitrate**		
Source	df	MS	*F*	$P_{(perm)}$	MS	*F*	$P_{(perm)}$
Bioregion	1	0.158	3.355	0.0775	21.582	11.105	0.0048*
Season	1	0.054	1.462	0.2403	4.107	2.619	0.1213
Site (Bioregion)	17	0.047	335.600	0.0001*	1.943	6484.100	0.0001*
Bioregion x Season	1	0.038	1.027	0.3298	0.487	0.311	0.5932
Season x Site (Bioregion)	17	0.037	261.090	0.0001*	1.5678	5231	0.0001*
Residual	76	0.000			0.000		
Total	113						

		Phosphate			**Silicate**		
Source	df	MS	*F*	$P_{(perm)}$	MS	*F*	$P_{(perm)}$
Bioregion	1	2.597	4.751	0.0239*	3.685	3.708	0.0521
Season	1	3.023	8.826	0.0072*	1.286	2.188	0.1567
Site (Bioregion)	17	0.547	2555.200	0.0001*	0.994	3005.300	0.0001*
Bioregion x Season	1	0.414	1.208	0.2868	1.125	1.914	0.194
Season x Site (Bioregion)	17	0.342	1600.900	0.0001*	0.588	1777.500	0.0001*
Residual	76	0.000			0.000		
Total	113						

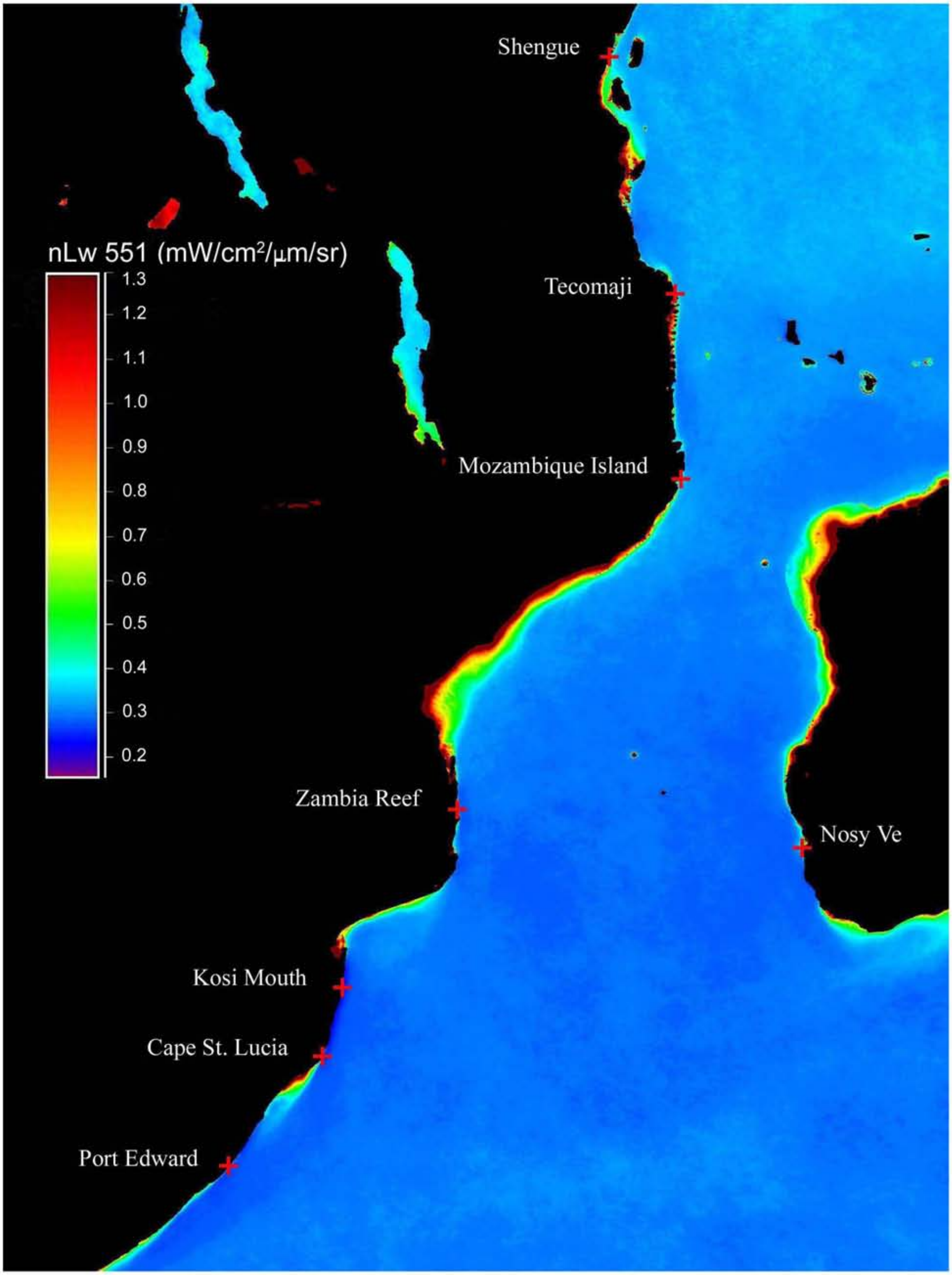


Figure 4.13. Mean suspended inorganic sediment measured according to normalized water-leaving radiances at 551 nm. AquaMODIS 1-km resolution 3-yr time-composite image (2003-2005).

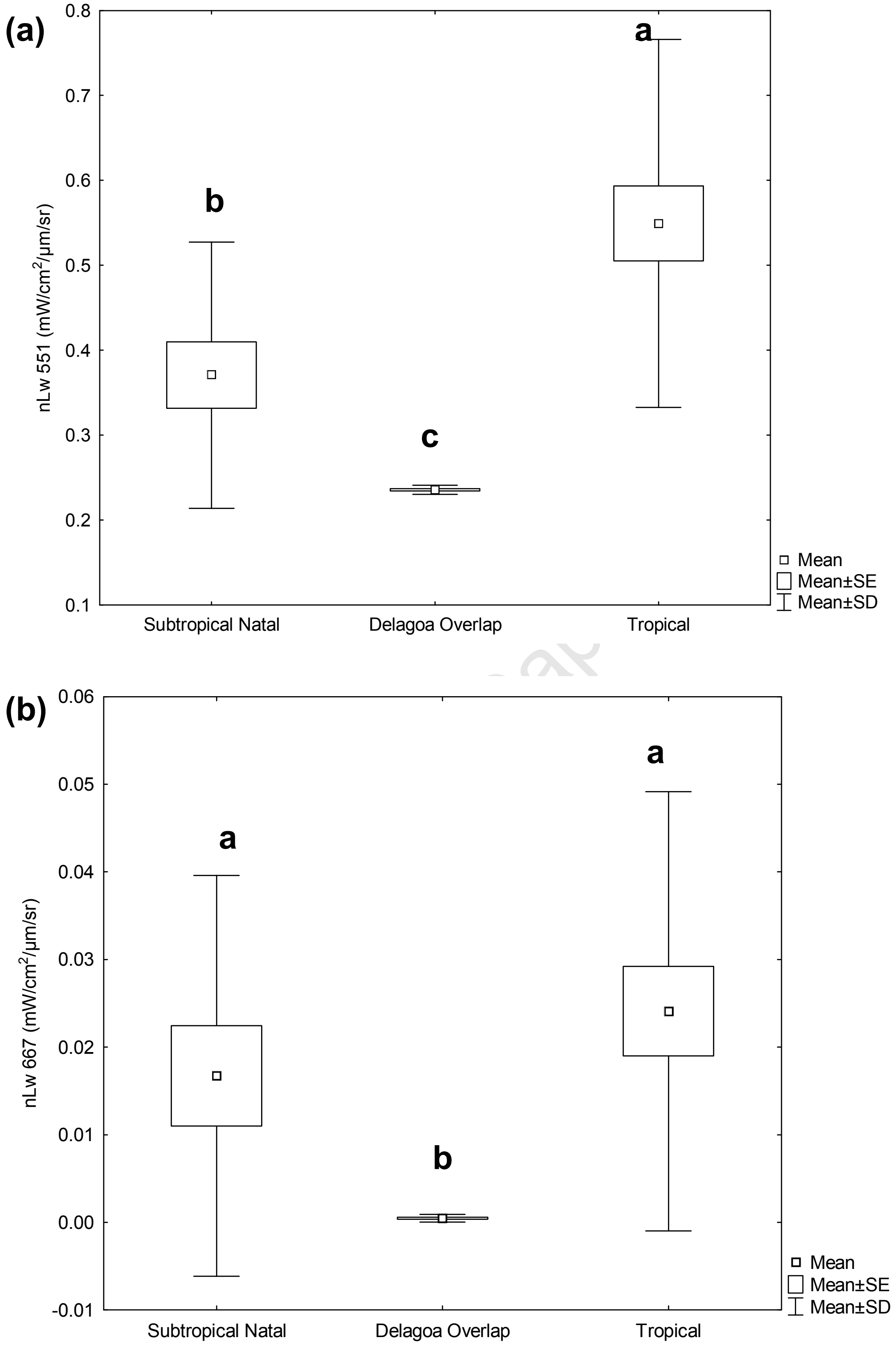


Figure 4.14. Means, ± SE and ± SD for suspended inorganic sediment measured according to normalized water leaving radiances at (a) 551 nm and (b) 667 nm for the Subtropical Natal, Delagoa Overlap and Tropical Indo-West Pacific bioregions. Letters above data differ if significant differences existed (PERANOVA and *a-posteriori* comparisons a>b>c; $P < 0.01$ in all cases).

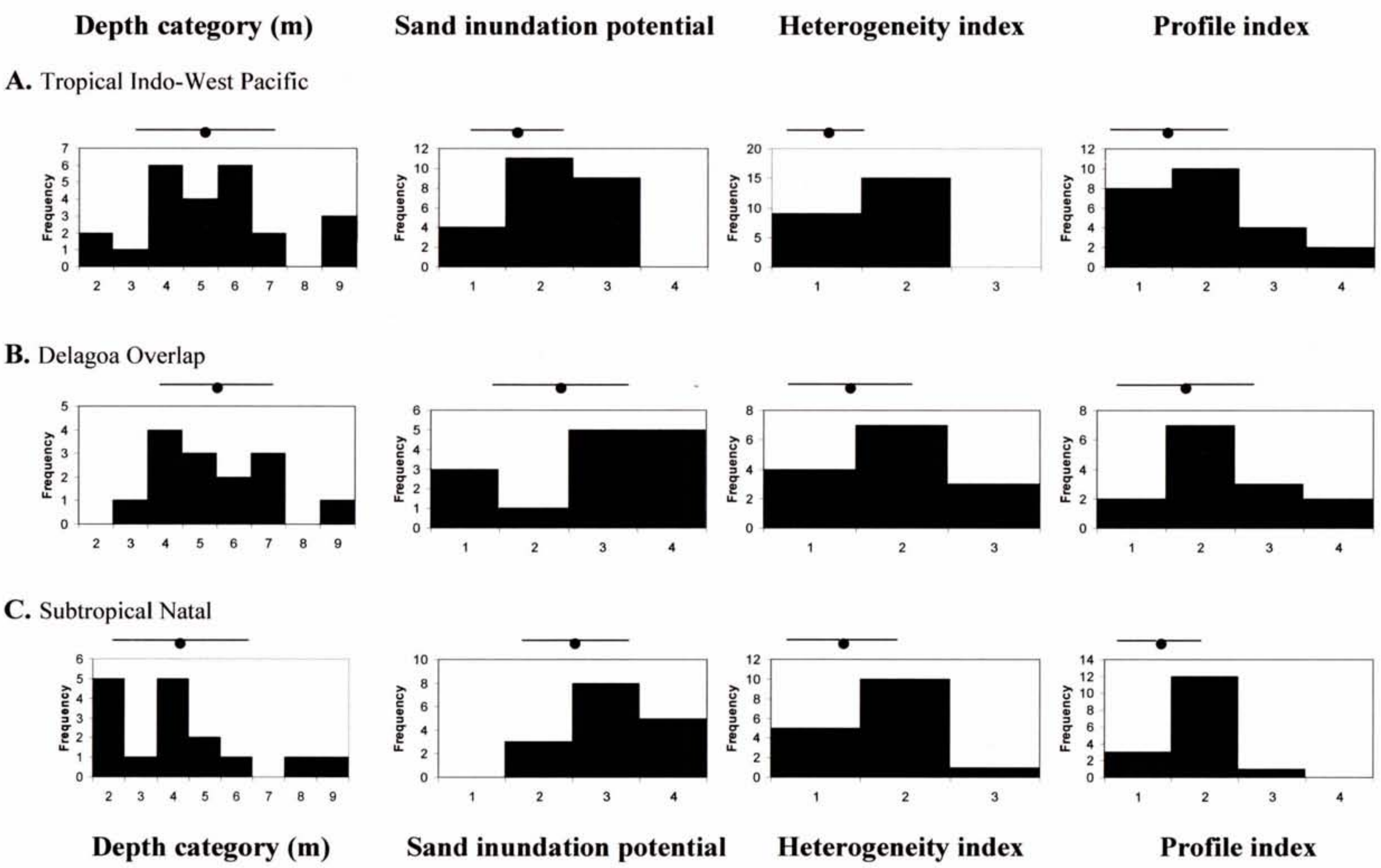


Figure 4.15. Frequency graphs of reef characteristics; depth, sand inundation potential, heterogeneity index and profile index (columns) for each of the three bioregions; (A) Tropical Indo-West Pacific, (B) Delagoa Overlap and (C) Subtropical Natal (rows). Dots and whiskers indicate the average ± SD. Sand inundation potential between the Subtropical Natal and Tropical Indo-West Pacific bioregions were the only pairwise comparisons to differ (Dunn's post hoc comparisons: $Q = 2.9$, $P < 0.05$).

Influence of abiotic variables on community structure

Correlations between abiotic variables and benthic community structure were analysed using canonical correspondence analysis (CCA). The first three eigenvalues for the regional analysis were 0.755 for CCA axis 1, 0.436 for axis 2 and 0.378 for axis 3, which accounted for 6.60 %, 3.82 % and 3.31 % of the total canonical variance (23.79 %) respectively (Table 4.2). The combined sums of the canonical and non-canonical eigenvalues (total inertia – canonical eigenvalues) were 2.718 and 8.709 respectively. Total inertia of the model was 11.43 and the first three eigenvalues were found to be significant ($P < 0.005$) (Table 4.2). Temperature, turbidity, wave height, chlorophyll *a*, suspended inorganic sediment (hereon referred to as 'suspended sediment'), depth and sand inundation all had intraset correlation coefficients greater than 0.4 (Table 4.3) and are considered as being biologically important.

The biplot produced by CCA site scores (Figure 4.16) illustrates their dispersion, along with abiotic variables as vectors that indicate the directions and strengths of the environmental relationships within the first two dimensions of the ordination biplot. Generally, sites clustered according to whether they were in the Natal, Overlap or Tropical bioregions, and separated out over temperature and wave-height gradients, as both temperature and wave height (which were strongly negatively correlated; Table 4.4), correlated particularly well with CCA axis 1. There was also strong separation due to sand inundation potential on CCA axis 1 and to a lesser extent chlorophyll *a* and turbidity on axis 2. Reef heterogeneity, depth and profile contributed to minor or negligible degrees.

In the Subtropical Natal Bioregion, the first three eigenvalues were 0.603 for CCA axis 1, 0.534 for axis 2 and 0.373 for axis 3 (Table 4.2). This accounted for 13.46 % (axis 1), 11.92 % (axis 2) and 8.32 % (axis 3) of the total canonical variance of 63.92 %. The combined sums of the canonical and non-canonical eigenvalues were 2.865 and 1.618 respectively. Total inertia of the model was 4.48 and only the second eigenvalue was found to be significant ($P < 0.05$). Temperature, turbidity, chlorophyll *a*, depth, profile and heterogeneity all had intraset correlation coefficients greater than 0.4 (Table 4.3). The biplot showed sites separating out according to depth and profile on CCA axis 1, and mainly turbidity, chlorophyll and temperature on CCA axis 2 (Figure 4.17).

In the Delagoa Overlap Bioregion, the first three eigenvalues were 0.645 for CCA axis 1, 0.459 for axis 2 and 0.374 for axis 3 (Table 4.2). These eigenvalues accounted for 20.52 %, 14.62 % and 11.90 % consecutively of the total canonical variance of 76.44 %. The combined sums of the canonical and non-canonical eigenvalues were 2.401 and 0.740 respectively. Total inertia of the model was 3.14 and only the second eigenvalue was found to be significant ($P < 0.05$). Sand, heterogeneity, profile and depth had intraset correlation coefficients greater than 0.4 (Table 4.3). The biplot of the Delagoa Overlap Bioregion (Figure 4.18) showed sites separating out according to sand, heterogeneity and profile on axis 1. On axis 2, sites separated out largely due to depth.

In the Tropical Indo-West Pacific Bioregion, the first three eigenvalues were 0.611 for CCA axis 1, 0.530 for axis 2 and 0.364 for axis 3 (Table 4.2), and accounted for 9.75 %, 8.45 % and 5.81 % of the total canonical variance of 43.08 % consecutively. The combined sums of the canonical and non-canonical eigenvalues were 2.699 and 3.567 respectively. Total inertia of the model was 6.27 and only the second eigenvalue was found to be significant ($P < 0.01$). Temperature, chlorophyll *a* and turbidity had intraset correlation coefficients greater than 0.4 (Table 4.3). The biplot of the Tropical Indo-West Pacific Bioregion showed sites predominantly separating according to chlorophyll and turbidity on CCA axis 1 and temperature on axis 2 (Figure 4.19).

Table 4.2. Eigenvalues and percentage of variance accounted for by the nine axes of the canonical correspondence analysis ordination of samples and abiotic variables for the entire study region and for each of the three bioregions. Values in brackets indicate the total inertia (weighted variance). Probability values indicate the likelihood that the observed magnitude of eigenvalue could have occurred by random chance.

	Entire region (11.43)			Subtropical Natal (4.48)			Delagoa Overlap (3.14)			Tropical Indo-West Pacific (6.27)		
Axis	Eigenvalue	% Variance	$P_{(perm)}$	Eigenvalue	% Variance	$P_{(perm)}$	Eigenvalue	% Variance	$P_{(perm)}$	Eigenvalue	% Variance	$P_{(perm)}$
1	0.755	6.60	0.001	0.603	13.46	0.140	0.645	20.52	0.113	0.611	9.75	0.133
2	0.436	3.82	0.003	0.534	11.92	0.035	0.459	14.62	0.028	0.530	8.45	0.006
3	0.378	3.31	0.001	0.373	8.32	0.576	0.374	11.90	0.053	0.364	5.81	0.201
4	0.275	2.41		0.355	7.92		0.278	8.85		0.302	4.82	
5	0.249	2.18		0.280	6.25		0.212	6.74		0.278	4.43	
6	0.220	1.92		0.232	5.16		0.137	4.36		0.178	2.84	
7	0.146	1.28		0.185	4.13		0.123	3.91		0.165	2.63	
8	0.136	1.19		0.172	3.84		0.104	3.31		0.145	2.32	
9	0.123	1.08		0.131	2.93		0.070	2.23		0.127	2.02	
Total	2.718	23.785		2.865	63.922		2.401	76.436		2.699	43.075	

Table 4.3. Intraset correlations for the nine environmental variables with the first three canonical correspondence analysis (CCA) axes of the entire region and for each of the three bioregions. Bold values denote those variables regarded as being biologically important for the CCA axis.

Entire region

Variable	CCA axis 1	CCA axis 2	CCA axis 3
Temperature	**-0.809**	-0.145	-0.089
Turbidity	0.109	**0.455**	-0.111
Chlorophyll	0.303	**0.506**	-0.116
Wave height	**0.779**	0.098	0.039
Suspended sediment	**-0.458**	0.251	0.027
Depth	0.028	0.175	**0.442**
Sand inundation	**0.458**	-0.164	-0.010
Profile	-0.054	-0.010	0.012
Heterogeneity	0.035	0.190	0.051

Subtropical Natal

Variable	CCA axis 1	CCA axis 2	CCA axis 3
Temperature	0.338	**0.497**	-0.214
Turbidity	-0.237	**-0.608**	0.081
Chlorophyll	-0.147	**-0.584**	-0.118
Wave height	-0.150	-0.336	-0.057
Suspended sediment	0.043	-0.304	0.283
Depth	**0.553**	-0.397	0.121
Sand inundation	0.107	0.374	0.088
Profile	**-0.406**	-0.160	-0.114
Heterogeneity	-0.058	**-0.427**	0.370

Delagoa Overlap

Variable	CCA axis 1	CCA axis 2	CCA axis 3
Temperature	0.149	0.036	-0.007
Turbidity	-0.141	-0.071	0.103
Chlorophyll	0.015	-0.276	0.168
Wave height	0.196	-0.004	0.079
Suspended sediment	-0.185	-0.020	0.014
Depth	0.058	**0.414**	0.061
Sand inundation	**-0.725**	0.116	0.071
Profile	**0.672**	-0.177	0.018
Heterogeneity	**0.685**	-0.081	0.100

Tropical Indo-West Pacific

Variable	CCA axis 1	CCA axis 2	CCA axis 3
Temperature	0.368	**0.584**	0.051
Turbidity	**-0.459**	0.120	0.013
Chlorophyll	**-0.581**	0.048	0.003
Wave height	-0.374	-0.359	-0.042
Suspended sediment	-0.301	0.274	0.168
Depth	-0.228	-0.359	0.049
Sand inundation	-0.040	-0.175	-0.113
Profile	-0.001	0.049	0.138
Heterogeneity	-0.134	0.119	-0.065

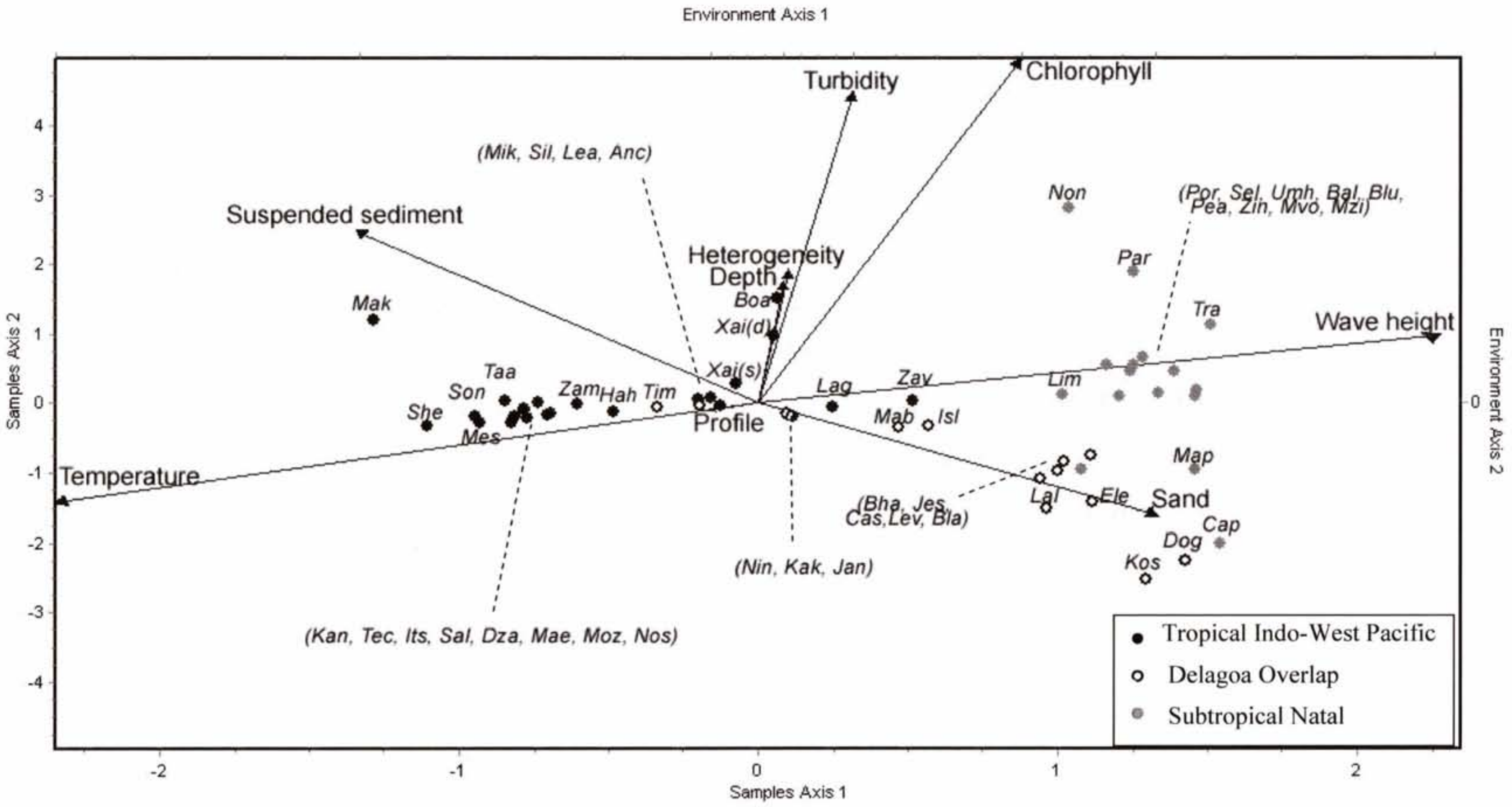
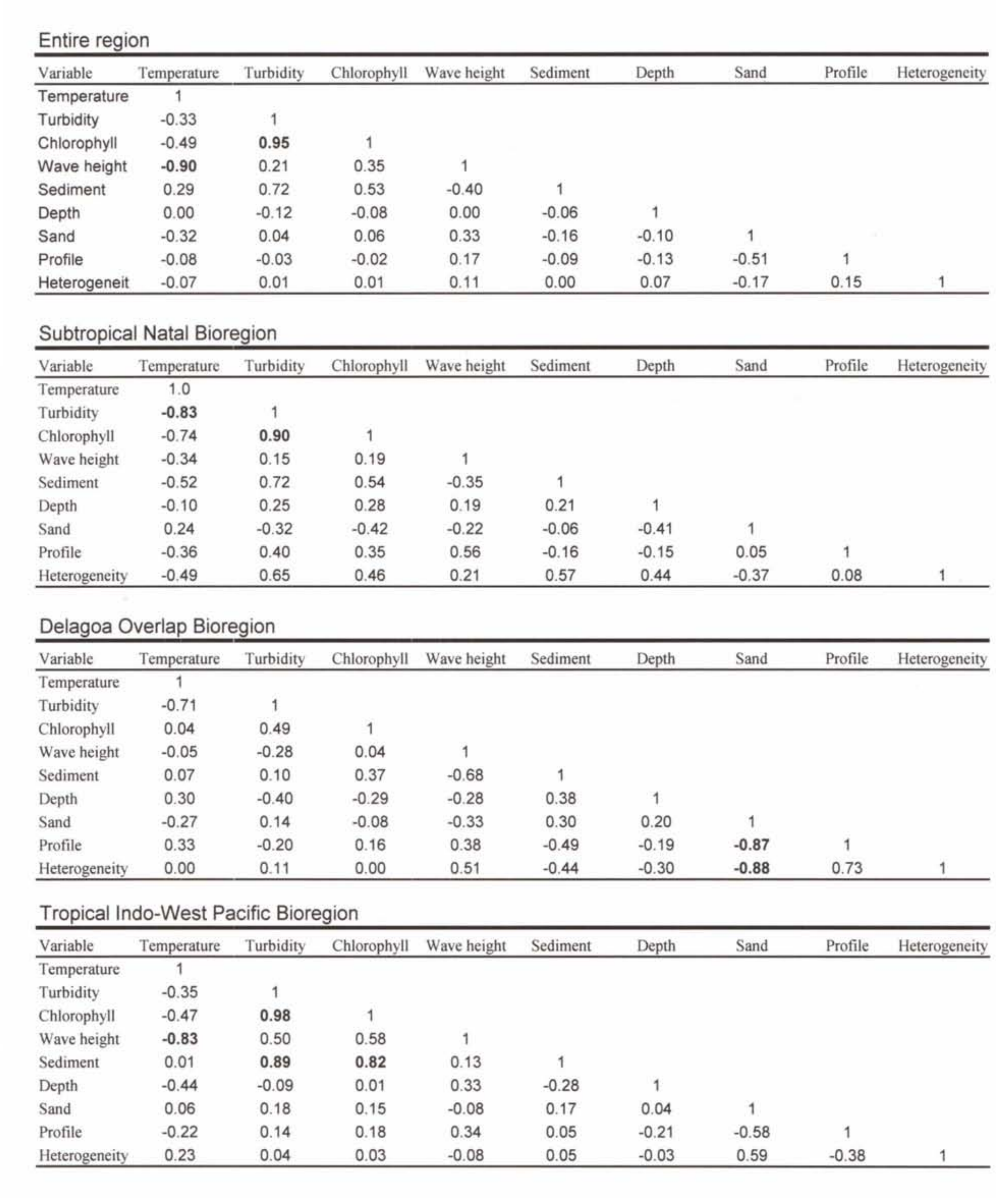


Figure 4.16. Ordination biplot based on a canonical correspondence analysis of the entire study region showing biotic similarity between 54 sites based on the ash-free biomass of species and the constrained effects of nine abiotic variables indicated by vectors. The eigenvalues of axis 1 (horizontal) and axis 2 (vertical) are 0.755 and 0.436 respectively. The biplot displays 10.42 % of the inertia (weighted variance) and 43.82 % of the variance in weighted averages and relative class totals. Site names are italicised and abbreviated to the first three letters (See Figure 2.3, page 24 for positions and full names of sites).

Table 4.4. Pearson product moment correlations between paired combinations of abiotic variables for the entire study region, Subtropical Natal, Delagoa Overlap and Tropical Indo-West Pacific bioregions. Bold values are considered as being noteworthy due to high correlation.



Entire region

Variable	Temperature	Turbidity	Chlorophyll	Wave height	Sediment	Depth	Sand	Profile	Heterogeneity
Temperature	1								
Turbidity	-0.33	1							
Chlorophyll	-0.49	**0.95**	1						
Wave height	**-0.90**	0.21	0.35	1					
Sediment	0.29	0.72	0.53	-0.40	1				
Depth	0.00	-0.12	-0.08	0.00	-0.06	1			
Sand	-0.32	0.04	0.06	0.33	-0.16	-0.10	1		
Profile	-0.08	-0.03	-0.02	0.17	-0.09	-0.13	-0.51	1	
Heterogeneit	-0.07	0.01	0.01	0.11	0.00	0.07	-0.17	0.15	1

Subtropical Natal Bioregion

Variable	Temperature	Turbidity	Chlorophyll	Wave height	Sediment	Depth	Sand	Profile	Heterogeneity
Temperature	1.0								
Turbidity	**-0.83**	1							
Chlorophyll	-0.74	**0.90**	1						
Wave height	-0.34	0.15	0.19	1					
Sediment	-0.52	0.72	0.54	-0.35	1				
Depth	-0.10	0.25	0.28	0.19	0.21	1			
Sand	0.24	-0.32	-0.42	-0.22	-0.06	-0.41	1		
Profile	-0.36	0.40	0.35	0.56	-0.16	-0.15	0.05	1	
Heterogeneity	-0.49	0.65	0.46	0.21	0.57	0.44	-0.37	0.08	1

Delagoa Overlap Bioregion

Variable	Temperature	Turbidity	Chlorophyll	Wave height	Sediment	Depth	Sand	Profile	Heterogeneity
Temperature	1								
Turbidity	-0.71	1							
Chlorophyll	0.04	0.49	1						
Wave height	-0.05	-0.28	0.04	1					
Sediment	0.07	0.10	0.37	-0.68	1				
Depth	0.30	-0.40	-0.29	-0.28	0.38	1			
Sand	-0.27	0.14	-0.08	-0.33	0.30	0.20	1		
Profile	0.33	-0.20	0.16	0.38	-0.49	-0.19	**-0.87**	1	
Heterogeneity	0.00	0.11	0.00	0.51	-0.44	-0.30	**-0.88**	0.73	1

Tropical Indo-West Pacific Bioregion

Variable	Temperature	Turbidity	Chlorophyll	Wave height	Sediment	Depth	Sand	Profile	Heterogeneity
Temperature	1								
Turbidity	-0.35	1							
Chlorophyll	-0.47	**0.98**	1						
Wave height	**-0.83**	0.50	0.58	1					
Sediment	0.01	**0.89**	**0.82**	0.13	1				
Depth	-0.44	-0.09	0.01	0.33	-0.28	1			
Sand	0.06	0.18	0.15	-0.08	0.17	0.04	1		
Profile	-0.22	0.14	0.18	0.34	0.05	-0.21	-0.58	1	
Heterogeneity	0.23	0.04	0.03	-0.08	0.05	-0.03	0.59	-0.38	1

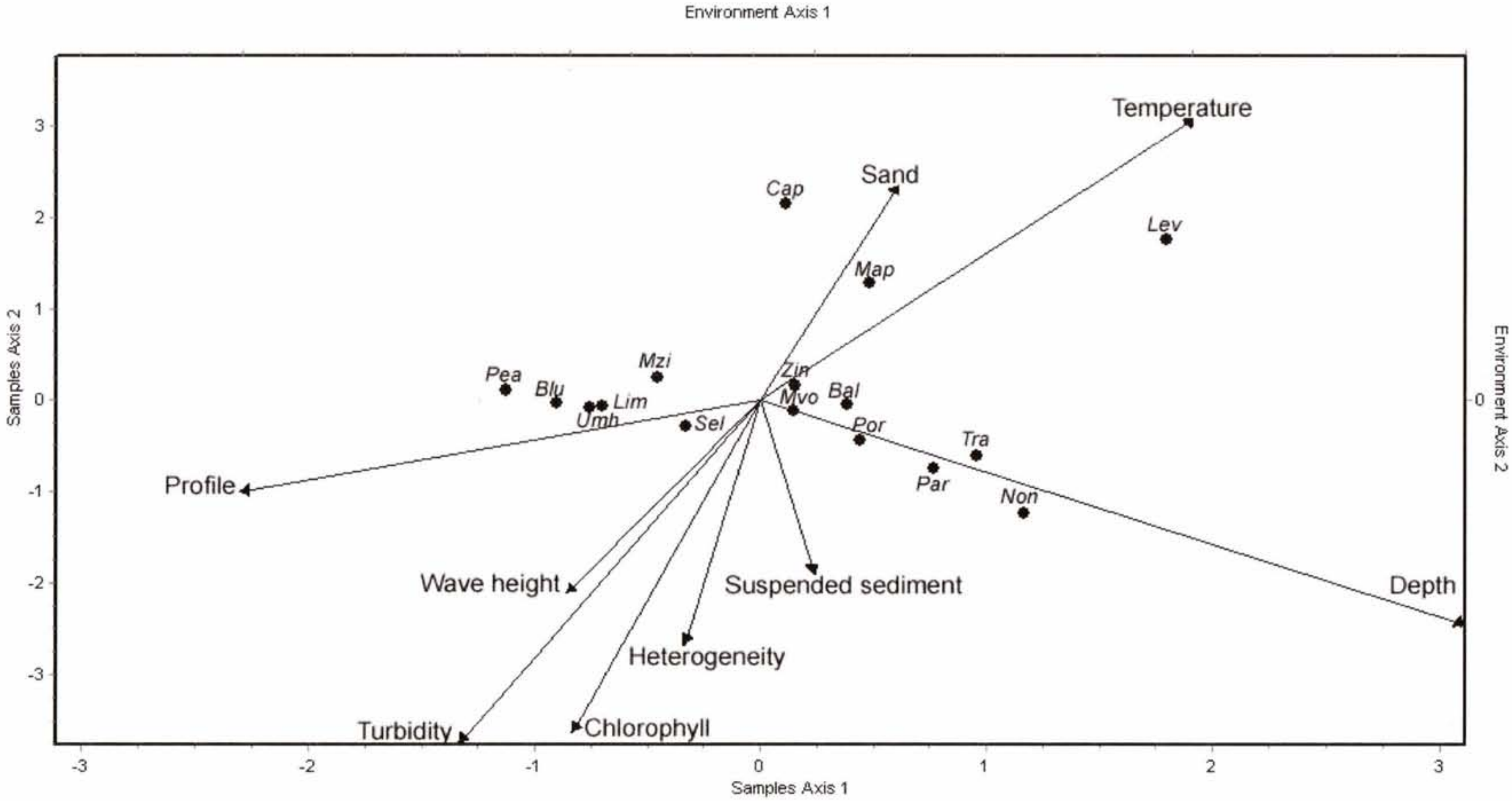


Figure 4.17. Ordination biplot based on a canonical correspondence analysis of the Subtropical Natal Bioregion showing biotic similarity between sites based on ash-free biomass and the constrained effects of nine abiotic variables indicated by vectors. The eigenvalues of axis 1 (horizontal) and axis 2 (vertical) are 0.603 and 0.534 respectively. The biplot displays 25.38 % of the inertia (weighted variance) and 39.69 % of the variance in weighted averages and relative class totals. Site names are italicised and abbreviated to the first three letters.

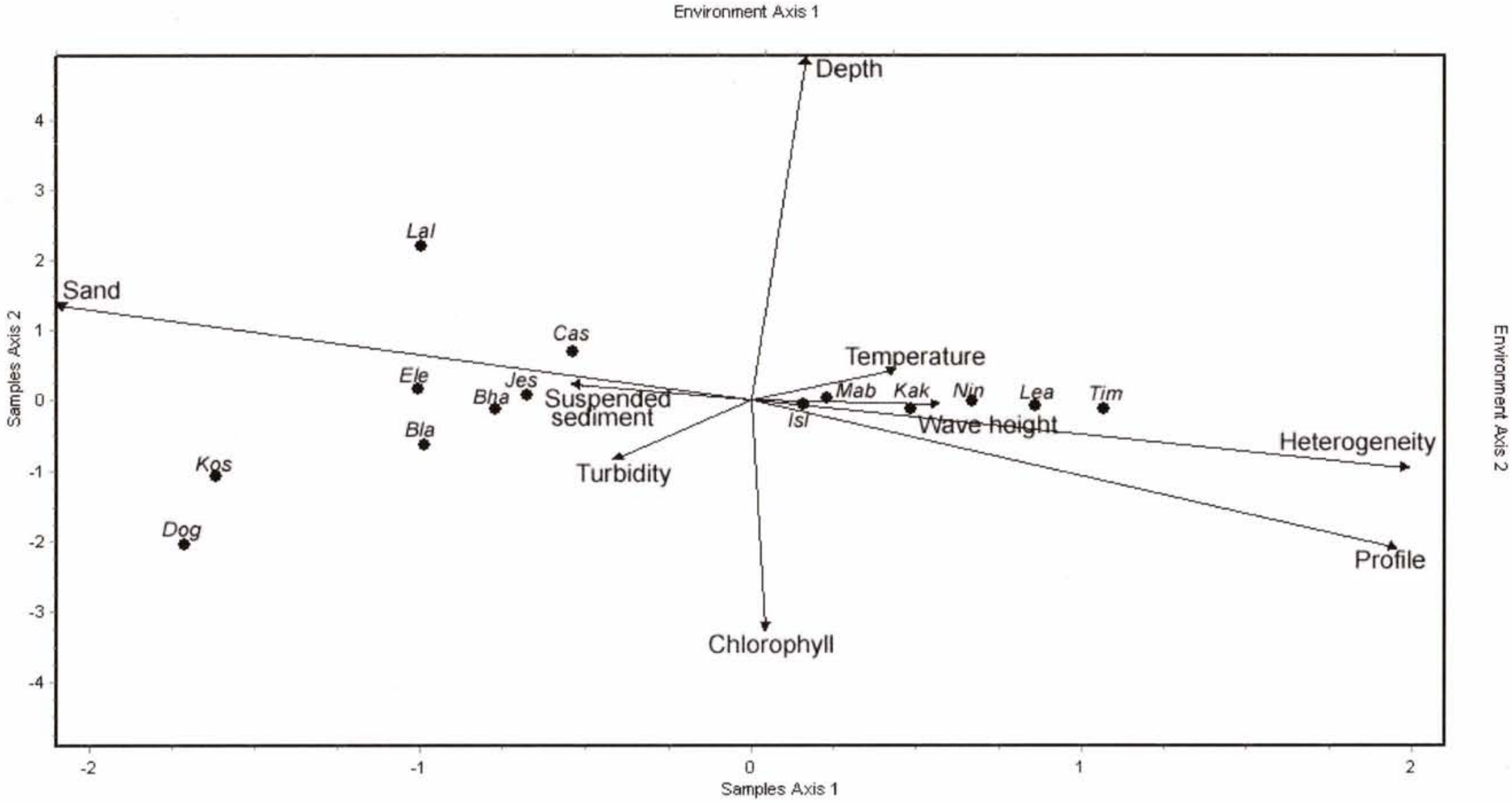


Figure 4.18. Ordination biplot based on a canonical correspondence analysis of the Delagoa Overlap Bioregion showing biotic similarity between sites based on ash-free biomass and the constrained effects of nine abiotic variables indicated by vectors. The eigenvalues of axis 1 (horizontal) and axis 2 (vertical) are 0.645 and 0.459 respectively. The biplot displays 35.16 % of the inertia (weighted variance) and 45.98 % of the variance in weighted averages and relative class totals. Site names are italicised and abbreviated to the first three letters.

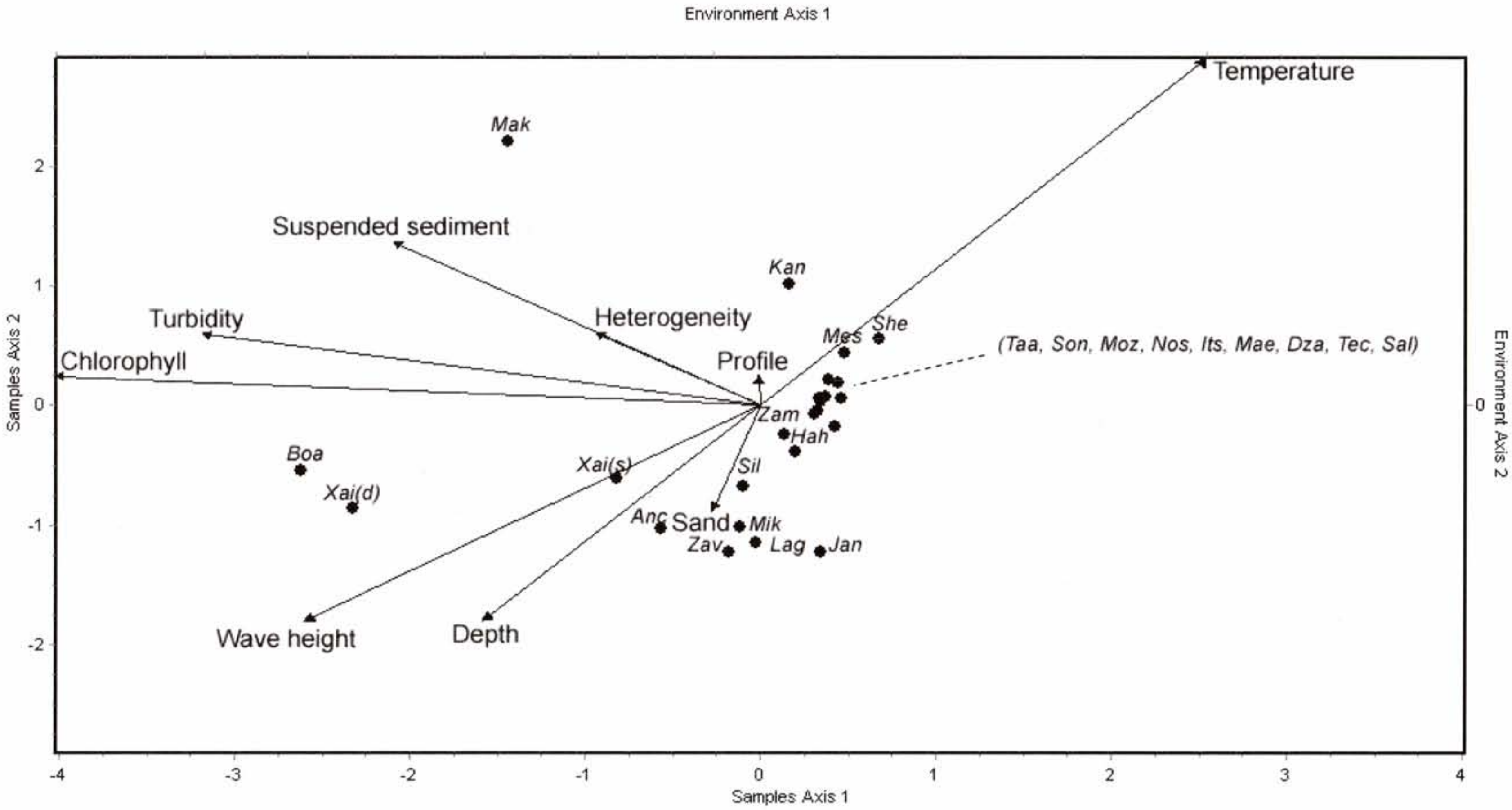


Figure 4.19. Ordination biplot based on a canonical correspondence analysis of the Tropical Indo-West Pacific Bioregion showing biotic similarity between sites based on ash-free biomass and the constrained effects of nine abiotic variables indicated by vectors. The eigenvalues of axis 1 (horizontal) and axis 2 (vertical) are 0.611 and 0.530 respectively. The biplot displays 18.20 % of the inertia (weighted variance) and 42.27 % of the variance in weighted averages and relative class totals. Site names are italicised and abbreviated to the first three letters.

Geology

No significant difference was found between communities on Aeolianite and Vryheid Formation Sandstone ($P_{(\text{Perm})} = 0.2011$) in the Subtropical Natal Bioregion (Table 4.5). However, a significant difference was found between sites nested within a particular rock type ($P_{(\text{Perm})} = 0.0001$).

Table 4.5. Two-factor PERMANOVA to investigate variation in community structure between reefs composed of Aeolianite and Vryheid Formation Sandstone geology.

Source of variation	df	SS	MS	F	$P_{(\text{perm})}$
Rock type	1	47334.28	47334.28	1.45	0.2011
Site (Rock type)	4	130241.73	32560.43	27.98	0.0001
Residual	84	97758.89	1163.8		
Total	89	275334.9			

DISCUSSION

Bioregional oceanographic conditions and reef characteristics

The two central goals of this chapter were to explore whether significant differences existed in abiotic factors (1) among bioregions, and (2) among sites within regions, and whether these differences were correlated with differences in community composition. Figure 4.20 provides a synopsis of the relative importance of the various abiotic factors examined and their trends among regions.

Among bioregions, temperature, as expected, was highest in the Tropical Indo-West Pacific Bioregion and lowest in the Subtropical Natal Bioregion (Figures 4.3 & 4.4). Temperatures recorded remotely within each of the three bioregions corresponded to those recorded by previous regional studies in Tanzania (McClanahan 1988a) and on the east coast of South Africa (Schumann 1989). The accuracy of inshore remotely-sensed sea surface temperatures was confirmed by significant relationships between them and *in situ* temperature-logger data at three independent sites (Figure 4.5). On the whole, remotely-sensed temperatures were consistently warmer than temperatures recorded *in situ* (by about 0.5°C), probably because the former are measured at the sea surface, which is more prone to solar heating than deeper water measured by temperature loggers. Temperature change was fairly constant along the coast except in the vicinity of Cape St. Lucia, where it dropped at a faster rate in a southerly direction, in the Natal Bight. This corresponds with the biogeographic break between the Natal and the Delagoa Overlap bioregions (Sink *et al.* 2005; Chapter 2).

Wave height showed a generally consistent increase in height with increased latitude and significant differences between each bioregion (Figures 4.6 & 4.7). The same trend has been recorded by Chen *et al.* (2002). In the Tropical Indo-West Pacific the average significant wave height recorded remotely fell within the range of 0.9 m to 1.9 m previously documented by McClanahan (1988a) further north at Mombassa, Kenya. Moving south, significant wave height increases to approximately 2.5 m off the east coast of South Africa (Chen *et al.* 2002). This corroborates the wave-height magnitudes I found in the Delagoa Overlap and Subtropical Natal bioregions.

Temperature and wave height clearly emerged as the two factors most related to inter-regional differences among the three bioregions. While I had hypothesised that temperature would be an important explanatory factor for differences among bioregions, I forecast that significant wave height would be important at a local scale only, based on previous findings to this effect (McQuaid and Branch 1984, 1985, Sink 2001, Sink *et al.* 2005). Turbidity, chlorophyll *a*, suspended sediments and sand inundation also emerged as significant contributors to differences among regions, but were about half as important as temperature and wave height.

Turbidity was consistently low in the Delagoa Overlap Bioregion (Figures 4.8 & 4.9), and appeared to be responsible for causing much of the divergence in community structure between that region and the adjacent two bioregions (see Chapter 2). When the units of turbidity (m^{-1}) are converted to meters (m), Z_{90} – the depth at which ninety percent of the downwelling irradiance is attenuated – can be derived (Gordon & McCluney 1975). Mean Z_{90} was reached at a depth of approximately 9 m in the Subtropical Natal Bioregion, 20 m in the Delagoa Overlap Bioregion and 12 m in the Tropical Indo-West Pacific Bioregion. The relative magnitudes of these measurements correspond with the visibility measurements often observed while on SCUBA in these regions (Porter, S. N., *unpubl. data*). Light intensity was measured *in situ* on a single day by Anderson *et al.* (2005) in the Delagoa Overlap Bioregion. They found that Z_{90} was reached at a depth of 22.5 m. This closely approximates the 20 m average I derived from the remotely-sensed data over a 3-year period for all sites in the Delagoa Overlap Bioregion.

Greater penetration of light in the Delagoa Overlap Bioregion has the potential to enhance phytoplankton production there relative to the Subtropical Natal Bioregion, but in reality chlorophyll *a* values there were low (Figures 4.10 & 4.11), implying that the low levels of nutrients in the Delagoa Overlap Bioregion (Figure 4.12) are limiting. Chlorophyll *a* concentrations were highest in the Subtropical Natal Bioregion and closely approximated average values documented there by Carter & Schleyer (1989) and Meyer *et al.* (2002). Concentrations I obtained for the Tropical Indo-West Pacific Bioregion were lower and fell within the range of those recorded by Mordasova (1980) and Kyewalyanda *et al.* (2007) in the Delagoa Bight, southern Mozambique and in nearshore waters off Tanzania (Bryceson 1982). Chlorophyll *a* in the Delagoa Overlap Bioregion was the lowest of the three bioregions and corresponded with the low concentrations of approximately 0.1-0.2 mg/m^3 recorded by Kyewalyanda *et al.* (2007), and the low nutrient concentrations in this area noted above. At a sub-continental scale, my measurements support the presence of an inshore productivity gradient around the tip of Africa. The west coast of southern Africa is highly productive while productivity decreases north eastwards around the tip of Africa (Brown 1992; Bustamante *et al*. 1995a).

A significant contrast, particularly in nitrate and phosphate concentrations, was evident between the Subtropical Natal and Delagoa Overlap bioregions, with values being lower in the Delagoa Bioregion (Figure 4.12), coincident with lower chlorophyll *a* values there. Average nutrient levels for all nutrient types corresponded well with those found by Bustamante *et al.* (1995a) for intertidal sites in the Subtropical Natal Bioregion. Nutrient concentrations of nitrate and phosphate were also similar to those found in continental shelf surface waters off the Subtropical Natal Bioregion and were only slightly higher than those found further offshore in the Agulhas current (Carter & d'Aubrey 1989; Meyer *et al.* 2002). However, the average silicate concentration in the Subtropical Natal Bioregion did not correspond well with the above literature due to anomalously high concentrations recorded at one site (Mapelane); but silica concentrations were considerably lower at all other sites in this bioregion and approximated those recorded by Bustamante *et al.* (1995a).

The area between Bluff and Cape St. Lucia (see Figure 2.3 p 24), known as the Durban or Natal Bight, is characterised by cold, relatively nutrient-rich waters that are produced by topographic upwelling (Lutjeharms *et al.* 1989; Meyer *et al.* 2002). Three out of the seven sampling sites in the Subtropical Natal Bioregion were located in the Natal Bight, but they did not have nutrient concentrations any higher than at other sites in the

Subtropical Natal Bioregion situated outside the Natal Bight. Other sources of nutrients in the Subtropical Natal Bioregion, particularly in the nearshore zone, could come from rivers, and their input may mask any effects of upwelling.

The amount of riverine input in the Subtropical Natal Bioregion is 1000 times greater than in the adjacent Delagoa Overlap Bioregion to the north (Sink 2001). Rivers have been identified as injecting important sources of nutrients into coastal waters further north in east Africa, particularly as a result of poor inland soil conservation practices (McClanahan 1988a). Rivers in the Subtropical Natal Bioregion also carry large amounts of sediments (Anon 1986): nutrient levels of major rivers are above recommended water quality guidelines for plant life and phosphate levels exceed recommended levels for aquatic animal life (De Villiers & Thiart 2007). Nitrate concentrations above 12 μmol. l^{-1} and 20 μmol. l^{-1} have frequently been recorded in the Mvoti and Mgeni rivers respectively (Ramm *et al.* 1990). These are higher concentrations than are found in deep shelf water between 100-150 m, which is brought to the surface during upwelling events in the Natal Bight. Nitrate levels at such depths in this region are generally less than 10 μmol. l^{-1} (Carter & d'Aubrey 1989).

The Delagoa Overlap Bioregion receives very little riverine input (Sink 2001) and does not experience upwelling like that occurring in portions of the Subtropical Natal Bioregion (Meyer *et al.* 2002). Nutrient inputs are therefore likely to come predominantly from the Mozambique and East Madagascar currents, which merge to form the Agulhas Current in this region (Ramsey 1994; Lutjeharms 2006). The Mozambique and East Madagascar currents are however intermittent and comprise eddies rather than constituting strong unidirectional flows (Lutjeharms & Jorge da Silva 1988; Gründlingh 1992; de Ruijter *et al.* 2001; Lutjeharms 2006), so their input of nutrients will be limited. The relatively narrow shelf along this part of the coast allows these currents to move close inshore (Ramsey 1994; Lutjeharms 2006) and bathe the Delagoa Overlap Bioregion with primarily pelagic oligotrophic water. Nutrient concentrations in these waters are therefore low. Nitrate, silicate and phosphate concentrations of approximately 0.1, 1.4, and 0.5 μmol. l^{-1} respectively, have been recorded in this region (Kyewalyanda *et al.* 2007). These measurements deviate – although only moderately so – from the concentrations recorded in my study, possibly because my measurements were taken inshore, whereas those of Kyewalyanda *et al.* (2007) were taken several kilometres offshore. Further north in the Tropical Indo-West Pacific, nutrient levels are expected to be higher than in the Delagoa Overlap Bioregion because of inputs from rivers (McClanahan 1988a).

Suspended inorganic sediment, measured by normalized water-leaving radiances (nLw) at 551 nm and 667 nm, differed significantly among bioregions (Figure 4.14) in a manner that supports the above arguments that riverine inputs have important influences on oceanographic conditions. Overall, nLw at 551 nm was more effective than nLw at 667 nm in detecting suspended sediments, as indicated by their order-of-magnitude higher water-leaving radiance values. The Delagoa Overlap Bioregion had significantly lower values than the adjacent bioregions on either side of it, most likely because of the absence of any significant riverine input (Sink 2001), but perhaps also because primarily pelagic water moves close inshore (Ramsey 1994; Lutjeharms 2006). Further north in the Tropical Indo-West Pacific Bioregion a multitude of large rivers also drains the African continent (McClanahan 1988a; Global River Discharge database 2008), and can be anticipated to have similar effects.

Although mean values of reef characteristics for particular abiotic variables were similar among bioregions, actual frequency distributions were very different, indicating that it is inappropriate to make generalisations about the characteristics of individual reefs based on bioregion (Figure 4.15). For example, in the Subtropical Natal Bioregion most reefs had medium reef profiles whereas in the Tropical Indo-West Pacific Bioregion a high proportion of reefs that I sampled had low profiles and a few very high profiles, yet average values between these two bioregions differed by only 0.1. Sand inundation potential decreased towards the equator, despite reef profile and heterogeneity peaking for my sites in the Delagoa Overlap, and this was the only reef characteristic to differ significantly, and then only between the Subtropical Natal and Tropical Indo-West Pacific bioregions.

In summary (Figure 4.20), temperature declined and wave height increased with latitude, whereas turbidity, suspended inorganic sediments, chlorophyll *a* and (probably) nutrient levels all dipped in the Delagoa Overlap Bioregion relative to the values further south in the Subtropical Natal Bioregion and further north in the Tropical Indo-West Pacific Bioregion. Reef characteristics, although generally not significantly different in terms of mean values among bioregions, differed in terms of their frequency distributions. This, plus the fact that they were quantified more subjectively than other variables, made it difficult to generalize reef characteristics for a particular bioregion.

Influences of abiotic variables on community structure

The relative importance of different abiotic variables in determining community structure varies with spatial scale (McQuaid & Branch 1984; McGuinness 1990; Bustamante & Branch 1996a). Therefore, direct gradient analyses of correlations between abiotic variables and community structure (CCA) were conducted first for the entire region and then separately for each bioregion, to elucidate the relative roles of abiotic variables at both scales.

At a regional scale CCA could account for only 23.8 % of the total canonical variance (Table 4.2), indicating that other variables that were not considered are also likely to be important. However, bioregional analyses accounted for much more of the canonical variance (43.1-76.4 %), so abiotic variables in these models explained the majority of among-site community variability within bioregions.

Biotic variables were not considered, but including them in future analyses is likely to explain more of the variance. For instance, many reef communities were characterised and distinguished by urchins, particularly in the Tropical Indo-West Pacific Bioregion (see Chapter 3). Elevated urchin densities are often symptomatic of high fishing pressure: as predatory fish are reduced there is a concomitant increase in urchin numbers (McClanahan & Shafir 1990; McClanahan 1994, 1995; McClanahan *et al.* 1994; McClanahan & Arthur 2001). Fishing pressure can therefore indirectly influence benthic reef community structure and composition (McClanahan 1990, 1992, 1994; Roberts 1995; McClanahan & Arthur 2001).

As hypothesised in the Introduction, at the regional scale, sea surface temperature correlated more strongly with benthic community structure than any other factor (Table 4.3). In addition it was the most important correlate within the Tropical Indo-West Pacific Bioregion and was important in the Subtropical Natal Bioregion. Temperature is likely to have a dominant influence, particularly at a regional scale (Isaac 1938; Stephenson 1947; Moore 1958; Murray & Littler 1981; van den Hoek 1982; McQuaid & Branch 1984, 1985; Breeman 1988; Lüning 1990), as it governs a number of important physiological processes influencing growth rate, photosynthetic rate and reproductive output (Purves *et al.* 1995).

Correlations between temperature and benthic intertidal community structure and species composition have frequently been found off southern Africa (McQuaid & Branch 1984, 1985; Bolton & Anderson 1987, 1990) and on the west coast of North America (Blanchette *et al*. 2008) where the role of thermal stress has received much attention (Helmuth 1999; Helmuth & Hofmann 2001; Helmuth 2002). Bolton & Anderson (1990) have also established that in the intertidal zone of South Africa, temperature is correlated with the absolute ranges of individual species of seaweeds in addition to community structure and composition. Others have found clear temperature optima for individual species (Branch 1974; Bolton & Anderson 1987; Anderson & Bolton 1989).

In my study, two key taxa are likely to have been responsible for the high correlation between temperature and community structure. *Pyura stolonifera* was one of the key characteristic species of both the Subtropical Natal and Delagoa Overlap bioregions as well as being a top distinguishing species between all three bioregions (see Chapter 2), consistently increasing in abundance with latitude (Chapter 2). *P. stolonifera* is, however, considered a temperate species, extending from Namibia to southern Mozambique (Day 1974; Berry 1982). A number of scleractinians that were important characteristic and distinguishing taxa between bioregions (Chapter 2) showed the opposite trend to *P. stolonifera*. These taxa are tropical (Brown & Jarman 1978; Veron 1995; Sheppard 2000) and temperature greatly affects their competitive ability because it is highly correlated with aragonite saturation state (Guinotte *et al.* 2003) and a principle cause of coral bleaching (Gates *et al.* 1992; Brown 1997; Lesser 1997; McClanahan *et al.* 2007; Ruiz Sebastián *et al.* 2009). Both these taxa have distributions that appear strongly related to temperature, and both play a key role in characterising and distinguishing bioregions, so they are likely to be strongly responsible for the high intraset correlation found for temperature.

Significant wave height was the second most important abiotic correlate at a regional scale (Table 4.3). This directly contradicted my hypothesis regarding the role of wave action, which I expected to act at a local scale of meters to kilometres (Bustamante & Branch 1996a; Sink 2001) rather than at a regional scale over 1000s of km. In the majority of other studies, wave force has been considered as operating at local scales, strongly influencing community structure and biomass between sites within bioregions (McQuaid & Branch 1984; Bustamante & Branch 1996a; Blamey & Branch 2008) and being an important source of mortality (Denny 1995). Over a geographic scale of ~500 km covering much of the Subtropical Natal and Delagoa Overlap bioregions, Sink (2001) found no evidence that *in situ* wave force measurements contributed to regional differences in community structure, but at local scales it exerted a strong influence. In strong contrast, my data revealed strong inter-bioregional differences in wave height, and wave action correlated with community composition at this scale, but not at the scale of sites within regions. The spatial resolution of the wave height data (0.33º) may, however, have down-played its significance at a more local scale. The striking differences between the effects of wave action in the intertidal zone, where most previous studies have been done, and on subtidal reefs are also likely related to the influence of depth on water movements. In the intertidal, waves break as they shallow, and small-scale topographic features profoundly alter wave impact. Such small-scale topographic differences may mask or over-ride any regional trends in wave height under these circumstances. At the subtidal reefs I examined, waves do break over them, but the effects of depth will damp wave force, reducing local topographic effects, so that regional trends may become more apparent as a result. Subtidal reefs are also intrinsically different from intertidal rocky shores because water can flow over and around them, whereas this is not possible on rocky shores which therefore experience maximal wave force.

At the regional scale, wave height may determine where particular taxa can occur. For instance, reduced wave height in the tropics may allow branched species of scleractinians such as *Acropora* to exist at greater abundances at shallower depths in the Tropical Indo-West Pacific Bioregion where wave height is 25 % less than in the Delagoa Overlap Bioregion. In the Delagoa Overlap Bioregion, coral breakages due to episodic storms have previously been linked to differences in community structure (Riegl & Riegl 1996), and annual high-energy wave-events stunt coral to such small sizes that no reef framework can be built (Riegl 2001), a disturbance considered in their conservation management (Celliers & Schleyer 2007). By extension, at a biogeographic scale wave height may similarly influence which species can occur in different bioregions. Filter-feeder abundance is known to be promoted by water movement (Bustamante & Branch 1996b; Leichter & Witman 1997; Steffani & Branch 2003) and their notably higher biomass in the Subtropical Natal Bioregion correlates with the greater wave action there.

Turbidity was of subordinate importance as a correlate at a regional scale but of primary importance within the Tropical Indo-West Pacific and Subtropical Natal bioregions (Table 4.3). Turbidity reduces the amount of light reaching the benthos and thus diminishes photosynthetic efficiency (Rogers 1990; Anthony & Fabricius 2000; Anthony *et al.* 2004). There are, however, few publications regarding the affect of turbidity on community structure at large geographic scales.

Sink (2001) implicated riverine runoff, which results in high levels of turbidity and suspended inorganic sediment, as one of the key abiotic factors responsible for her proposed intertidal biogeographic break at Cape Vidal between the Delagoa and Natal bioregions. My own data showed the Delagoa Overlap Bioregion had very low levels of turbidity, dissolved nutrients, chlorophyll *a* and suspended sediment compared to adjacent bioregions. The synergistic effects of increased light penetration, relatively high temperature and low nutrients would favour the development of coral-reef organisms (Fabricius 2005) in the Delagoa Overlap Bioregion where riverine input is minimal, and are a likely cause of community divergence between this bioregion and the Subtropical Natal Bioregion.

North of the Delagoa Overlap Bioregion high temperatures favour coral reefs and associated organisms except in areas of relatively high turbidity and suspended sediment (Rogers 1990), where heterotrophic filter-feeders proliferate (Fabricius 2005). Not all species of coral can shift between autotrophy and heterotrophy to maintain a positive energy balance (Anthony & Fabricius 2000) and in those that cannot switch, turbidity-related light reduction reduces calcification, tissue thickness, photosynthesis and colony survival (Fabricius 2005). Areas of high turbidity are therefore likely to favour heterotrophic organism rather than seaweeds and corals (Fabricius 2005). High chlorophyll *a* concentrations, while enhancing feeding rates and growth in some corals, will benefit heterotrophic filter-feeders even more, so that shifts in competitive advantage are likely to alter community structure (Fabricius 2005).

Chlorophyll *a* is a proxy for microalgal biomass, which has been found to influence intertidal filter-feeder and grazer biomass around the coast of southern Africa (Bustamante *et al*. 1995a) and can provide an important source of food for filter-feeders (Wieters *et al*. 2003). Low chlorophyll *a* concentrations in the Tropical Indo-West Pacific Bioregion and even more so in the Delagoa Overlap Bioregion, are associated with zooxanthellate coral communities, and low benthic productivity linked with low-nutrient warm waters (Muscatine & Porter 1977; McClanahan 1988a). Low nutrient levels were recorded in the Delagoa Overlap Bioregion relative to the Subtropical Natal Bioregion, and are likely to be the primary reason for the low chlorophyll concentrations in this bioregion. In the Subtropical Natal Bioregion, the multitude of rivers and the topographic upwelling in the Natal Bight result in local areas of high or low turbidity that differ in temperature, nutrient and chlorophyll *a* concentrations, and community structure appears to respond by the proliferation of filter-feeders such as *P. stolonifera* (see Chapter 2). Similarly, in the Tropical Indo-West Pacific Bioregion, areas of low and relatively high nutrient levels are also expected to occur because of the many large rivers, and these may influence chlorophyll concentrations and between site community composition unlike in the Delagoa Overlap Bioregion.

Important depth-related correlations with communities were found within the Subtropical Natal and Delagoa Overlap bioregions (Table 4.3) even though I operated over a limited depth range because I was focusing on shallow reefs. Depth can influence community structure and temporal dynamics (Garrabou *et al.* 2002), and Evans (2005) found depth to be an important correlate of subtidal algal assemblages in the political province of KwaZulu-Natal, South Africa. In subtidal algal communities off Australia, depth particularly influences the more dominant species (Goldberg & Kendrik 2004) and in New Zealand, a shallow subtidal study at depths of 1-12 m found community structure, algal species composition and mobile macroinvertebrate assemblages to vary with depth (Shears 2007).

Depth did not differ significantly among regions (Figure 4.15) but was a particularly important correlate with community composition in the Subtropical Natal Bioregion, possibly because light penetration there decreases at a faster rate with depth than in bioregions with relatively less turbidity and suspended sediment. Alternatively – or additionally – because this bioregion experiences greater wave heights than either of the other bioregions, depth may exert its influence by alleviating this force.

Reef susceptibility to sand inundation was important at a regional scale and within the Delagoa Overlap Bioregion (Table 4.3). Sand movements can affect benthic organisms directly by smothering or scouring, or indirectly by altering biological interactions (Littler *et al.* 1983; Riegl 1995). Sand movements therefore play an important role in structuring communities and can increase diversity by increasing habitat heterogeneity if their effects are patchy (McQuaid & Dower 1990). Different community types occur under different regimes of sand inundation (Daly & Mathieson 1977; Littler *et al.* 1983; Riegl *et al.* 1995; Airoldi & Cinelli 1997; Sink 2001). Sand inundation susceptibilities of reefs in the Subtropical Natal Bioregion were never recorded as 'low', whereas this was not the case in the other bioregions (Figure 4.15). An important characteristic of the Subtropical Natal Bioregion is the movement of large amounts of sand (Jackson 1976; Berry 1982).

Reef profile and heterogeneity were important abiotic correlates in the Subtropical Natal and Delagoa Overlap bioregions (Table 4.3). Both may influence small-scale current dynamics (Abelson *et al.* 1993) and a reef's susceptibility to sedimentation, thereby indirectly influencing the performance of resident biota (Lenihan 1999). The effects of small-scale, abrupt, topographic features on local current conditions can lead to physical gradients across rock walls and divergence in community structure between passive and facultatively-active filter-feeders (Leichter & Witman 1997). In a controlled experiment, Lenihan (1999) found that shallow subtidal reefs of different profiles had a profound influence on ambient current speed and sedimentation rates, which ultimately had a significant influence on oyster performance. This may be particularly important in the Subtropical Natal Bioregion as filter-feeders were found to be the dominant trophic group there, and in the Delagoa Overlap Bioregion where *Pyura stolonifera* was a bioregional dominant (see Chapter 2).

Specifically in the Delagoa Overlap Bioregion, sites with low profiles and/or low heterogeneity usually exhibited high sand inundation susceptibilities and were dominated by various species of large foliar phaeophytes. Those reefs of relatively high profile and heterogeneity usually had low sand inundation and were dominated by various species of turf-forming algae, alcyonaceans and scleractinians. Different species of alcyonaceans and scleractinians occurring in this bioregion are known to differ in their abilities to deal with sedimentation (Riegl 1995; Riegl & Branch 1995).

The effect of rock type was examined only within the Subtropical Natal Bioregion, where it had no significant influence on subtidal community structure (Table 4.5). Significant differences were however identified among sites with the same rock type indicating that any effect of rock type is overridden by other factors. Although the two kinds of rock examined could be argued as being similar, as they are both sandstones (Aeolianite & Vryheid-Formation Sandstone) and therefore unlikely to induce differences in community structure, the results are nevertheless consistent with other studies in the region. Both Sink (2001) and Jackson (1976) found relatively little difference between intertidal communities with different geologies. In their analyses of community composition in the Cape Peninsula, McQuaid and Branch (1984, 1985) considered that temperature dictated biogeographic differences, wave action was the dominant factor influencing local differences, and rock type had only minor effects. Similarly, no effects of rock types on intertidal seaweed community structure were detected by Bolton & Anderson (1990) on the south-western coast of South Africa.

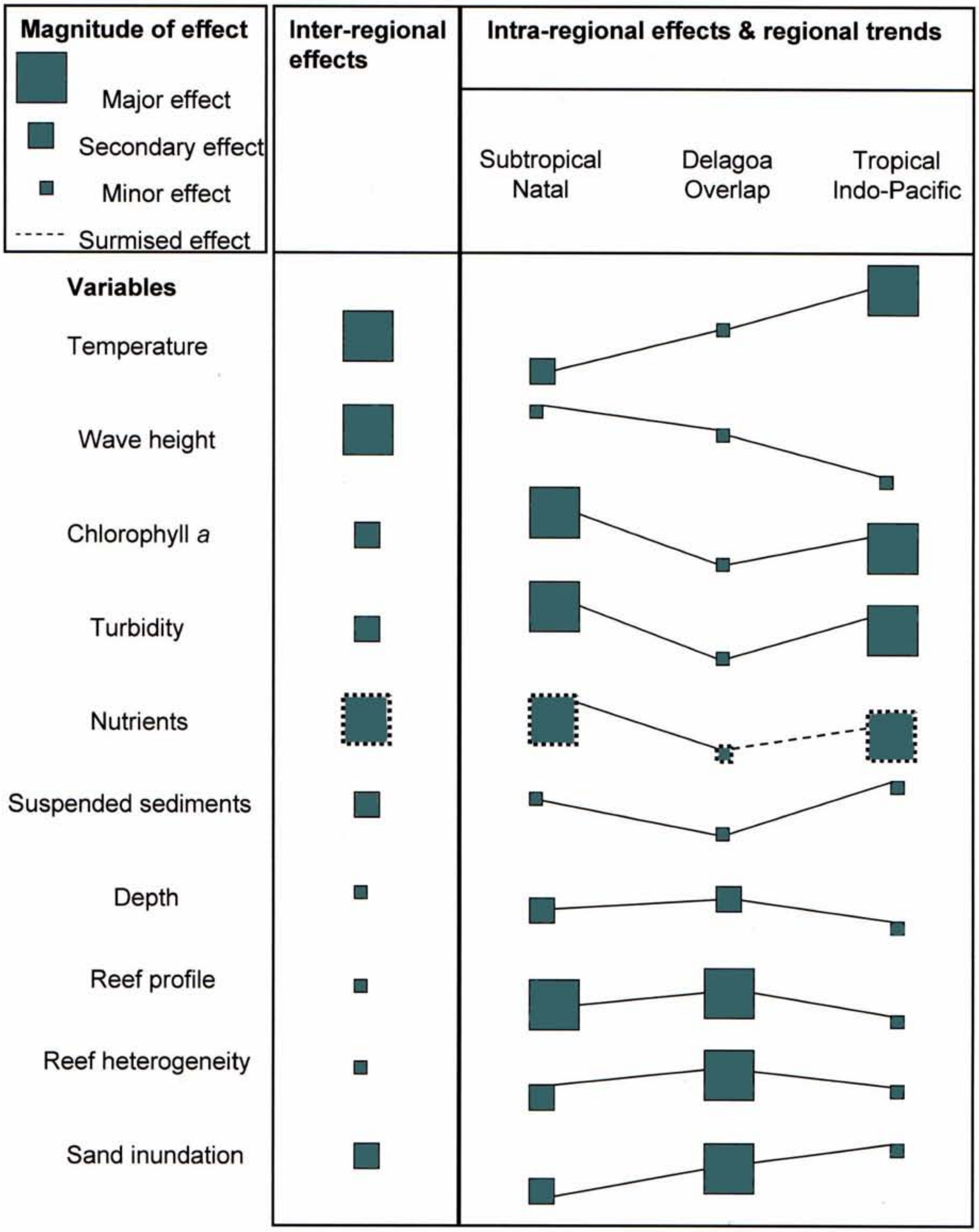
Conclusions

Striking differences were found in oceanographic characteristics among the three bioregions in all six remotely-sensed variables and in nutrient levels between Subtropical Natal and Delagoa Overlap bioregions. With the exception of geology, reef characteristics were also important, but at an intra-regional scale, not among regions. The different oceanographic characteristics of each bioregion and the local characteristics of each reef within a particular bioregion are likely to account for a large proportion of the differences in benthic community structure within and among bioregions that are detailed in Chapters 2 and 3, and displayed high intraset correlations with community composition.

Direct gradient analyses (CCA) revealed that different groups of abiotic variables correlated with community structure at different spatial scales. The two variables that yielded the highest correlations at the regional scale were temperature and wave height (Figure 4.20). I had anticipated and hypothesised that temperature would be a significant and major correlate at this scale because multiple previous studies have linked biogeographic differences to temperature (see above for references) but the region-wide affects of wave height were unexpected and contradicted my hypothesis that wave height would be important at a local (site-specific) scale within regions, but not among regions.

In contrast, within particular bioregions, variables that operate at local between-site scales often gave higher correlations than variables that operate over large scales. When each bioregion was considered independently, different dominant abiotic factors emerged. Chlorophyll, turbidity, depth and reef profile were of primary importance in Subtropical Natal; sand inundation, reef profile and heterogeneity in the Delagoa Overlap; and temperature, chlorophyll and turbidity in the Tropical Indo-West Pacific Bioregion. In

Figure 4.20. Synopsis of abiotic variables showing their relative effects on inter and intra-regional community composition and their regional trends in magnitude among bioregions. Dashed lines and squares indicate surmised magnitude of effects. Rock type has been omitted as it was examined only in the Subtropical Natal, where it had no effect.



general, large-scale gradients of temperature, wave height and (probably) nutrients were most important at the scale of the entire region and in defining bioregional differences,whereas more local-scale abiotic factors such as turbidity, and reef characteristics like depth, sand inundation, profile and heterogeneity, predominated within bioregions. At this more local scale, the factors of greatest importance distilled to (a) those influencing food/energy supply (chlorophyll, turbidity, depth and nutrients, which were of particular importance in the Natal and Tropical bioregions), and (b) those altering sand inundation and small-scale current dynamics of reefs (depth, sand inundation potential, profile and heterogeneity), which emerged as leading factors in the Delagoa Overlap Bioregion.

While correlations between benthic community structure and abiotic variables give valuable insight into ecosystem functioning, it is important to remember that the nature of this work and the types of analyses performed do not provide direct evidence of causative relationships. The following chapter therefore focuses on food sources to explore why there are a greater proportion of heterotrophic filter-feeders in the Subtropical Natal Bioregion relative to that in the Delagoa Overlap Bioregion. The approach I adopted was to elucidate the role that riverine particulate organic matter input plays as an energy source in the diets of inshore filter-feeders, as opposed to the role rivers may play in increasing turbidity and decreasing light penetration, which could alternatively or synergistically favour the development of heterotrophic communities in the Subtropical Natal Bioregion.

Chapter 5

RELATIVE TROPHIC IMPORTANCE OF RIVERINE PARTICULATE ORGANIC MATTER FOR INSHORE FILTER-FEEDER COMMUNITIES IN THE SUBTROPICAL NATAL BIOREGION

ABSTRACT

In the Subtropical Natal Bioregion, biomass of shallow subtidal filter-feeders is particularly high relative to bioregions to the north, and makes a central contribution to distinguishing these bioregions. This study focuses on the trophic role of riverine suspended particulate organic matter (POM) and the extent to which subsidies from rivers may explain the high filter-feeder biomass in the Natal Bioregion. The isotopic composition of inshore POM available to filter-feeders was determined, and stable isotope analyses conducted for four filter-feeder species, three possible end-member food sources and inshore POM (of mixed-source origin) for sites lying various distances from four river mouths. Using carbon, nitrogen and sulphur isotopes, and a 3-end-member Bayesian-mixing model, I determined the proportions of various primary producers comprising the inshore POM pool and the relative amounts of seaweed, pelagic POM and river POM assimilated by filter-feeder communities at various distances from four river mouths during two different periods – the rainy summer and dry winter seasons. Depending on season and study area, riverine-derived POM contributed 17-62 % of the inshore POM pool, 18-77 % was derived from pelagic POM and 6-53 % from seaweed. Analysis of covariance showed that the contribution of river POM to inshore POM was significantly related to distance from river mouth, but was not related to river size. Most material assimilated by the filter-feeders was of marine origin, especially seaweed detritus (39-62 %); but a noteworthy amount of riverine-derived POM ranging from 9 to 33 % was also assimilated, demonstrating riverine-inshore-pelagic coupling in the region. Minimal seasonal differences (<10 %) and biologically insignificant spatial trends in the proportions of the three food sources assimilated by filter-feeders were detected, possibly due to slow tissue equilibrium rates and constraints on digestive physiology. I concluded that although important, river POM is likely to play a subordinate role to other factors such as turbidity and productivity in explaining the high biomass of filter-feeders in the Subtropical Natal Bioregion.

INTRODUCTION

Stable isotopes are widely used in marine ecology, particularly to identify sources of carbon, nitrogen and sulphur entering ecosystems, to track their assimilation by photoautotrophs and their subsequent incorporation into higher trophic levels (Peterson 1999; Smit 2001). This study focuses on determining the relative contributions of various pools of suspended particulate organic matter (POM) to the diets of inshore filter-feeders.

Several sources of organic matter are potentially important in the assimilated diets of marine consumers. In intertidal and shallow subtidal systems, POM derived from macroalgae has been identified as a significant source of carbon and nitrogen for consumers (Seiderer & Newell 1985; Mann 1988; Bustamante & Branch 1996b; Kaehler *et al.* 2000; Dunton 2001; Norderhaug *et al.* 2003; Corbisier *et al.* 2004; Behringer & Butler IV 2006; Bode *et al.* 2006; Hill *et al.* 2008) as has POM from phytoplankton (Seiderer & Newell 1985; Stephenson *et al.* 1986; Newell *et al.* 1995; Kaehler *et al.* 2000; Kang *et al.* 2003; Darnaude *et al.* 2004a; Yokoyama *et al.* 2005; Bode *et al.* 2006) and, to a lesser degree, POM from terrestrial macrophytes (Salen-Picard & Arlhac 2002; Salen-Picard *et al.* 2002; Yamanaka *et al.* 2003; Darnaude *et al.* 2004a; Darnaude *et al.* 2004b; Wai *et al.* 2008; Schlacher & Connolly 2009; Tallis 2009). In addition, interspecific (Darnaude *et al.* 2004b; Yokoyama *et al.* 2005) and intraspecific (Riera & Richard 1996) selective dietary preferences for particulate organic material of marine versus terrestrial origin have been recorded, particularly in estuaries (Haines & Montague 1979; Peterson & Howarth 1987; Deegan & Garritt 1997; Hsieh *et al.* 2002; Perissinotto *et al.* 2003).

By virtue of their position, inshore reefs are exposed to both autochthonous sources of primary production and allochthonous sources from the marine and terrestrial environments. Autochthonous sources constitute primarily macroalgae (Schleyer 1984; Dunton & Schell 1987; Behringer & Butler 2006; Hill *et al.* 2008; Branch 2008; Kang *et al.* 2008) while allochthonous sources include pelagic phytoplankton (Dunton & Schell 1987; Gili & Coma 1998; Branch 2008) and terrestrial and aquatic POM introduced by rivers (Berry *et al.* 1979; Schleyer 1981; Schleyer 1984; Fabricius & Dommisse 2000; Rolff & Elmgren 2000; Wai *et al.* 2008). In the Subtropical Natal Bioregion, the two dominant sources of detritus are thought to be seaweed-derived POM and terrestrial plant material introduced into the sea by rivers (Berry *et al.* 1979; Schleyer 1981), and the most abundant intertidal filter-feeder in the region, the brown mussel *Perna perna*, relies mainly on inshore carbon and nitrogen in its assimilated diet (Hill *et al.* 2006). However, the seaweed flora of the Subtropical Natal Bioregion is dominated by unpalatable coralline species and there are no kelp beds (Sink 2001, Evans 2005; Lawrence 2005; Sink *et al.* 2005).

In Chapter 2, I showed that the average ash-free dry biomass of filter-feeders in the Subtropical Natal Bioregion was 1270 $g.m^{-2}$ whereas in the adjacent Delagoa Overlap Bioregion, where there is no significant river input, it was only 373 $g.m^{-2}$. On intertidal rocky shores in the region, Sink *et al.* (2005) have shown a comparable decline of filter-feeders, with the brown mussel *Perna perna* being chiefly responsible for the divergence between these two bioregions. They suggested that the greater cover of *P. perna* in the Subtropical Natal Bioregion might be attributable to a greater input of terrestrial detritus via rivers in that bioregion.

Alternatively, the significantly higher levels of turbidity and suspended inorganic sediment from rivers found in the Natal Bioregion (see Chapter 4) may reduce light penetration to such an extent that this influences subtidal trophic structure, which may be reflected in the high biomass of filter-feeders recorded in that region (see Chapter 2). This does not, of course, preclude the possibility that additional non-trophic factors such as larval retention and delivery by particular oceanographic conditions (Chiswell & Roemmich 1998; Roughan *et al.* 2005) may influence filter-feeder biomass in the region, but that has been the subject of separate research (Reaugh 2006) and was not the focus of my study.

For stable isotope investigations, the identification and quantification of assimilated dietary contributions require that available food sources are isotopically distinguishable (Peterson & Fry 1987; Smit 2001). This is not always the case. For instance, in East Africa, material from terrestrial primary producers in the savanna biome is isotopically indistinguishable from marine sources in terms of both carbon and nitrogen isotopes

(Muzuka 1999). To avoid this potential problem, some estuarine trophic studies have made use of stable sulphur isotopes in addition to carbon and nitrogen isotopes, to reduce ambiguity between terrestrial and marine sources of organic matter (Peterson *et al.* 1985; Sullivan & Morncreiff 1990; Currin *et al.* 1995; Deegan & Garritt 1997; Wissel & Fry 2005). Despite the presence of 71 significant rivers and estuaries that collectively introduce approximately 1 x 10^{10} m^3 of water into the inshore zone of the Subtropical Natal Bioregion annually (Begg 1978; Sink 2001), no previous attempts have been made to use sulphur isotopes to trace energy flows there.

In this chapter, I explore the possibility that inputs from rivers provide supplementary support for the high biomass of filter-feeder communities in the Subtropical Natal Bioregion. Specifically, I focus on the role river input plays in providing potential energy subsidies to inshore filter-feeders in the form of riverine POM, as distinct from its potential influence on turbidity and light penetration. To achieve this, I quantified the relative importance of riverine POM over small spatial scales at various distances from river mouths and during different seasons spanning times of high and low river flow.

This chapter investigates the following hypotheses:

(1) Inshore POM composition will be influenced by riverine inputs, and the extent of this influence will be dependent on distance from river mouth, season, mean annual runoff and the amount of river runoff experienced in preceding months, with the influences of riverine input being greater during the summer rainy season and close to river mouths.

(2) Inshore filter-feeders will assimilate suspended river-derived POM in addition to pelagic POM and seaweed detritus, and the proportion of river POM assimilated will be higher during the rainy season and at sites close to river mouths.

METHODS

Study areas

Four independent study areas (A, B, C & D), each incorporating a river mouth, were chosen along the coast of the Subtropical Natal Bioregion (Figure 5.1). The river mouths encompassed in each of the four study areas were relatively isolated from other rivers and covered a range of simulated mean annual runoffs (MARs): ~ 400 x 10^6 m^3 for the Mvoti, ~ 1000 x 10^6 m^3 for the Mfolozi, ~ 1100 x 10^6 m^3 for the Mkomasi, ~ 4 000 x 10^6 m^3 for the Thukela (Sink 2001; see Table 5.1). Within each of the four study areas, multiple intertidal rocky reefs, situated at various distances from each river mouth, were employed to sample filter-feeders. The four study areas were chosen to meet four criteria: (1) they each contained a river mouth (2) they spanned a range of river sizes (MARs), (3) they were relatively isolated from the influence of other large rivers and their river plumes were never observed to merge with other adjacent plumes; (4) they had multiple intertidal rocky reefs within 15 km of the river mouths.

Collection of potential food sources

Three potential POM food sources were subjected to stable isotope analysis: suspended river POM, seaweed detritus, and suspended pelagic POM (assumed to be essentially phytoplankton). Five-litre water samples (n=3 replicates) containing suspended river POM were collected 2-5 km upstream of each river mouth during low or outgoing tide to reduce the possibility of marine contamination – an assumption supported by refractometer readings of zero salinity on all sampling occasions. Particulate seaweed detritus samples (n=3) were acquired immediately adjacent to the rocky intertidal site closest to each of the four river mouths by dragging a 200-µm mesh plankton net through the water before picking out identifiable fragments from bulk samples in the laboratory. Twenty-litre pelagic POM samples (n=3) of Agulhas Current surface water containing phytoplankton were collected at a depth of < 50 cm, 40-km offshore to ensure there was no terrestrial contamination by the large eddy system that operates in the Natal Bight and has the potential to circulate inshore water relatively far offshore (see Gründlingh & Pearce 1990; Lutjeharms *et al.* 2000; Lutjeharms 2006). Due to logistic constraints, pelagic POM samples were collected at two sites only, one offshore of the Mkomasi

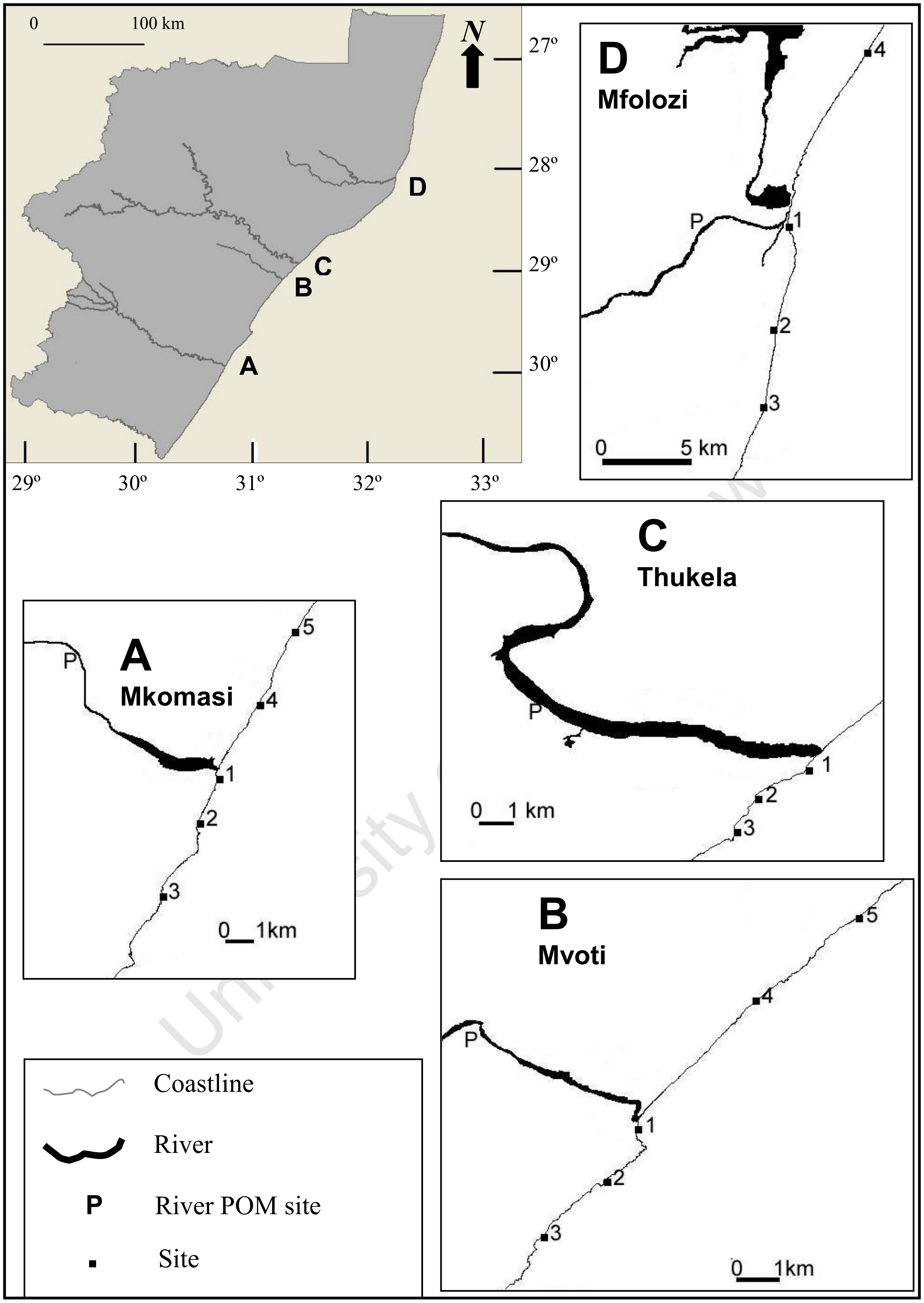


Figure 5.1. Study areas A-D, showing numbered sites at which filter-feeders (1-5) and inshore POM samples (1) were collected, and river POM sampling sites (P). Pelagic POM sites (not shown) were located 40 km offshore and due east of the Mkomasi and Mvoti river mouths.

Table 5.1. Values of the three covariates used in the permutational multivariate analysis of covariance (PERMANCOVA) of inshore POM for each study area (A-D) per sampling period (1 = early summer, 2 = late summer, 3 = early winter, 4 = late winter). Distance = distance between river mouth and inshore POM sampling site. MAR = mean annual runoff (taken from Sink 2001). 3-monthly runoff = the total runoff during the month sampled plus two months previous according to *in situ* Department of Water Affairs (DWAF 2009) gauges and modelled data (Lawrie, R. unpublished data 2009. University of KwaZulu-Natal). [1] = historical records. [2] = modelled estimates. [3] = data from DWAF.

Study area	**Sampling period**	**Covariates**		
		Distance (m)	**MAR (x 10^6 m^3)**	**3-monthly runoff (x 10^6 m^3)**
A (Mkomasi)	1	400	1100	291[3]
	2	400	1100	255[3]
	3	400	1100	136[3]
	4	400	1100	58[3]
B (Mvoti)	1	280	400	129[1]
	2	280	400	198[1]
	3	280	400	112[1]
	4	280	400	41[1]
C (Thukela)	1	1370	4000	818[3]
	2	1370	4000	810[3]
	3	1370	4000	363[3]
	4	1370	4000	79[3]
D (Mfolozi)	1	1390	1000	250[2]
	2	1390	1000	115[2]
	3	1390	1000	46[2]
	4	1390	1000	31[2]

River mouth and the other offshore of the Mvoti River mouth. In addition to the three end-member food sources, 20-litre inshore water samples (n=3) of POM, assumed to contain a mixture of these three food sources were collected at the intertidal site closest to each river mouth in all four study areas within 3 hours of low tide. This entire sampling protocol was conducted within three-week periods, on two separate occasions in the austral summer rainy season (December 2006 – March 2007) when riverine input was expected to be high, and on two separate occasions in the austral winter dry season (May – August 2007) when riverine input was expected to be relatively low (Schulze 1997). All water samples were collected in plastic containers pre-rinsed in deionised water and then by sample water, stored in a dark refrigerator and processed within 5 days.

Collection of filter-feeders

Three replicate samples per site of each of four filter-feeders – the solitary ascidian *Pyura stolonifera* and the bivalves *Perna perna*, *Striostrea margaritacea* and *Saccostrea cuccullata* – were randomly collected for stable isotope analysis from 3-5 intertidal and infratidal rocky reefs north and/or south of each river mouth (Figure 5.1). Individuals of similar size were chosen to avoid possible ontogenetic variability that influences isotope results in some species (Bouillon *et al.* 2002; Ruiz-Cooley *et al*. 2004; Jennings *et al.* 2008). Samples were immediately placed on ice in the field and stored frozen (-15ºC) until processed.

Preparation of potential food sources and filter-feeders for isotopic analysis

Water samples containing suspended POM were filtered through pre-combusted (500°C, 8 h), 47-mm diameter, 0.7-µm pore size Whatman® GF/F glass microfibre filter papers under moderate vacuum (≤ 4 cm Hg) until clogged. Thereafter, filter papers were thoroughly rinsed in deionised water. Large particles (>1 mm) and zooplankton were removed manually under a dissecting microscope (Hill *et al.* 2006; Søreide *et al.* 2006). From each POM water sample, two filter papers were obtained. The filter intended for carbon and nitrogen isotope analysis was treated with dilute HCl (1 %) solution to remove any inorganic carbonates, then thoroughly rinsed with deionised water (Darnaude *et al.* 2004b). The other, intended for sulphur isotope analysis, was left untouched. Finally, all filter papers were oven-dried at 60°C for 24 h. Seaweed particulate material was acquired by picking out discernable pieces of macroalgae from the plankton net hauls. Samples were rinsed in distilled water and visible epibionts removed. To standardize the pre-processing of food sources, one half of each seaweed sample was used for carbon and nitrogen isotope analysis, and the other for sulphur isotope analysis, employing the same procedures as for POM, and both halves finally oven-dried (60°C for 48 h).

Adductor muscles of the bivalves *P. perna*, *S. cuccullata* and *S. margaritacea* (following Hill *et al.* 2006), and muscular atrial siphons of *P. stolonifera* were extracted from each sample and thoroughly rinsed with deionised water. Samples were then dried at 60°C for 48 h. As muscle tissue has a slow turnover rate, it provides a time-integrated signature of assimilated diet over a period of months (Gearing 1991; Gorokhova & Hansson 1999).

Isotopic analysis

δ^{13}C (of the isotopes ^{12}C & ^{13}C) and δ^{15}N (of the isotopes ^{14}N & ^{15}N) signatures of all samples were simultaneously determined using a Delta Plus XP isotope ratio mass spectrometer (Thermo Electron, Germany) after sample combustion in a Flash EA 1112 series elemental analyzer (Thermo Finnigan, Italy) yielded CO_2 and N_2 which was passed via a Conflo III gas control unit (Thermo Finnigan, Germany). δ^{34}S (of the isotopes ^{32}S & ^{34}S) was determined on a ThermoFinnigan MAT Delta Plus Advantage isotope ratio mass spectrometer in continuous flow mode after the addition of 5 mg vanadium pentoxide to each sample before combustion. Choc, lentil, Merck gelatine, seal, sucrose, valine, nasturtiums and ammonium chloride were used as internal reference standards for carbon and nitrogen, while cystine, elemental sulphur and silver sulphide were used as internal reference standards for sulphur. These were compared against International Atomic Energy Agency reference materials based on the original Vienna Pee Dee Belemnite, atmospheric N_2 and triolite (FeS) from the Vienna Canyon Diablo meteorite for carbon, nitrogen and sulphur respectively. Results are expressed in standard delta notation (Peterson & Fry 1987):

$$\delta X = [(R_{sample}/R_{standard})-1] \times 1000$$

where *X* is the element in question and R is the ratio of heavy to light isotope. Precision of replicate determinations based on their standard deviations was ± 0.1 ‰ for both carbon and nitrogen and ± 0.4 ‰ for sulphur.

Data analysis

Defining of end-member food source signatures

Before input to the mixing models, isotope signatures of the three primary-producer end-member food sources (river POM, inshore seaweed detritus and pelagic POM) were subjected to a canonical analysis of principle coordinates (CAP) with PERMANOVA+ for PRIMER (Anderson *et al.* 2008b) to determine if the *a-priori* end-member food sources were isotopically distinguishable, and a separate CAP analysis of inshore POM was afterwards undertaken to test if it showed any resemblances to these end-members. This was done for each of the four study areas and during both summer and winter. As pelagic POM was not collected offshore of the Thukela and Mfolozi rivers, the mean of pelagic POM sampled offshore of the Mvoti and Mkomasi rivers was used for these two study areas in all analyses requiring pelagic POM end-member signatures.

Composition of inshore POM

Stable Isotope Analysis in R (SIAR) (Jackson *et al.* 2008) was used within the environment for statistical computing R v. 2.7.2 (R Development Core Team 2009) to determine the proportions of various primary producer end-member sources (river POM, seaweed detritus and pelagic POM) contributing to the inshore POM mixture, using all three isotope ratios simultaneously (i.e. C, N and S). SIAR uses a Bayesian-model based upon a Gaussian likelihood function to calculate source contributions and has advantages over IsoError (Phillips & Gregg 2001) and IsoSource (Phillips & Gregg 2003) because it accounts for uncertainty associated with multiple food sources, fractionation and isotope signatures (Jackson *et al.* 2008), and has advantages over MixSIR (Moore & Semmens 2008) which fails to identify the correct dietary proportions more than 50 % of the time because additional unquantified error is added (see Jackson *et al.* 2008). End-member food sources typically have high standard deviations (Phillips & Gregg 2001), and as the SIAR mixing model can incorporate such error, it is preferred.

The SIAR mixing model was applied to each replicate inshore POM signature, using average ± SD values from each of the three primary producer end-member sources collected during the same sampling period and study area (Table 5.2). Fractionation values were not incorporated and each time the model was run for 200000 iterations. The median value from each of the three end-member feasible contribution outputs from SIAR was then extracted and used in the following ANOVA models and in bar graphs.

To investigate differences in seaweed detritus and pelagic POM contributions to inshore POM, a two-factor crossed permutational multivariate ANOVA (PERMANOVA) (unbalanced, untransformed data, Euclidian distance measure, 9999 permutations of residuals under a reduced model, type III partial sums of squares) was run with PERMANOVA+ for PRIMER (Anderson *et al.* 2008b). Study area was fixed with four levels and Season was fixed with two levels. Variation in river POM contribution to inshore POM was investigated using a permutational multivariate analysis of covariance (PERMANCOVA) so that the variability in river POM contribution could be partitioned among the covariates: (1) distance from river mouth to inshore POM collection site, (2) mean annual river runoff and (3) three-monthly runoff for the two months preceding POM collection and the month during POM collection (Table 5.1). The same model outlined previously for seaweed and pelagic POM was run on river POM, although type I sequential sums of squares had to be used because the sums of squares for individual terms in a PERMANCOVA model cannot be considered as being independent from one another (see Anderson *et al.* 2008b). In addition, because type I sums of squares had to be used in this multi-factorial design, the analysis was run twice, with a different order of the two factors Study area and Season as type I sums of squares can influence conclusions in multi-factorial designs depending on the order these factors are run during analysis (Anderson *et al.* 2008b). Only the most conservative results are shown and re-ordering of factors did not alter conclusions.

For graphical representation, seasonal average ± SD $\delta^{13}C$, $\delta^{15}N$ and $\delta^{34}S$ values of end-members, inshore POM mixture and filter-feeders for each study area were plotted independently.

Table 5.2. Average ± standard deviation $\delta^{13}C$, $\delta^{15}N$ and $\delta^{34}S$ isotope values of end-member food sources and inshore POM for each of the four study areas (A-D) per sampling period (1-2 in summer, 3-4 in winter), that were used in mixing models where appropriate. n = the number of replicate samples.

Study area	**Sampling period**		**River POM**				**Seaweed**				**Pelagic POM**				**Inshore POM**		
		n	**$\delta^{13}C$**	**$\delta^{15}N$**	**$\delta^{34}S$**	**n**	**$\delta^{13}C$**	**$\delta^{15}N$**	**$\delta^{34}S$**	**n**	**$\delta^{13}C$**	**$\delta^{15}N$**	**$\delta^{34}S$**	**n**	**$\delta^{13}C$**	**$\delta^{15}N$**	**$\delta^{34}S$**
A Mkomasi	**1**	3	-21.87±0.43	4.65±0.68	1.66±0.36	3	-21.68±0.94	6.26±0.59	21.14±0.06	3	-21.34±0.49	5.73±0.71	16.11±4.28	3	-21.80±0.48	4.21±0.35	12.81±6.63
	2	1	-20.94	1.24	1.29	3	-21.71±2.44	5.14±0.60	21.34±0.29	3	-20.60±0.17	5.62±0.93	14.14±1.37	2	-21.63±0.04	2.86±0.43	9.42±0.16
	Summer	4	-21.64±0.58	3.80±1.79	1.57±0.35	6	-21.69±1.65	5.70±0.81	21.24±0.22	6	-20.97±0.52	5.67±0.74	15.12±3.04	5	-21.73±0.35	3.67±0.81	11.45±5.04
	3	3	-23.56±2.05	2.32±1.45	1.92±4.67	3	-18.33±1.23	5.63±0.31	20.80±0.22	3	-22.50±0.08	6.81±0.85	14.22±3.89	3	-19.25±1.54	5.95±1.50	9.84±1.86
	4	3	-21.76±0.51	4.17±0.80	8.31±1.07	3	-19.72±2.86	5.25±0.52	20.56±0.28	3	-20.27±0.17	5.78±0.02	16.66±1.58	3	-20.94±0.55	5.92±0.86	6.27±1.11
	Winter	6	-22.66±1.66	3.24±1.46	5.11±4.63	6	-19.02±2.11	5.44±0.44	20.68±0.26	6	-21.39±1.23	6.30±0.77	15.44±2.97	6	-20.10±1.39	5.93±1.09	8.06±2.39
B Mvoti	**1**	3	-21.49±1.68	6.88±0.71	4.17±0.86	3	-20.21±2.14	6.29±0.57	20.35±0.36	3	-19.53±0.30	5.43±0.46	16.66±1.35	3	-19.12±1.05	3.11±0.99	9.86±6.08
	2	3	-18.56±1.94	2.34±0.49	4.48±14.39	3	-19.03±1.96	6.06±0.41	20.92±0.51	3	-22.71±0.74	4.62±0.54	14.61±2.16	3	-19.36±0.50	4.69±0.19	12.13±1.16
	Summer	6	-20.02±2.28	4.61±2.55	4.32±9.12	6	-19.62±1.95	6.17±0.46	20.64±0.50	6	-21.12±1.82	5.03±0.63	15.78±1.92	6	-19.24±0.74	3.90±1.08	11.00±4.12
	3	3	-16.57±0.37	3.06±1.04	-1.86±0.59	3	-17.43±1.81	4.75±0.19	20.75±0.50	3	-20.51±0.10	7.48±0.80	13.87±0.73	3	-20.34±0.53	6.16±0.74	13.06±0.30
	4	3	-15.48±0.52	4.84±0.18	4.99±1.08	3	-20.45±0.68	5.27±0.69	20.57±0.24	3	-21.20±0.11	6.24±0.22	13.66±0.69	3	-20.52±0.44	5.15±1.42	8.91±4.34
	Winter	6	-16.02±0.72	3.95±1.18	1.57±3.84	6	-18.94±2.05	5.01±0.54	20.66±0.36	6	-20.86±0.39	6.86±0.89	13.77±0.65	6	-20.43±0.45	5.65±1.16	10.98±3.57
C Thukela	**1**	3	-22.14±0.75	3.96±0.50	-3.16±2.06	3	-18.70±0.23	5.92±0.16	20.62±0.08	6	-20.43±1.05	5.58±0.56	16.42±2.67	0			
	2	3	-23.93±0.48	1.22±0.89	-2.95±16.84	3	-20.78±4.59	5.56±0.32	21.58±0.18	6	-21.65±1.26	5.12±0.87	14.37±1.64	3	-21.07±1.19	4.79±0.23	8.64±0.84
	Summer	6	-23.03±1.13	2.59±1.63	-3.06±10.73	6	-19.74±3.12	5.74±0.30	21.10±0.54	12	-21.04±1.28	5.35±0.74	15.48±2.41	3	-21.07±1.19	4.79±0.23	8.64±0.84
	3	3	-25.76±0.14	3.42±1.07	5.48±1.09	3	-17.13±0.28	5.04±0.09	20.49±0.13	6	-21.51±1.09	7.15±0.82	14.05±2.15	3	-21.40±0.23	5.82±0.27	8.75±0.60
	4	3	-25.17±0.20	2.29±0.41	4.74±1.87	3	-27.61±1.60	6.42±0.31	19.52±0.20	6	-20.74±0.52	6.01±0.29	15.16±1.97	2	-19.51±0.29	7.26±0.05	10.26±1.92
	Winter	6	-25.46±0.36	2.86±0.96	5.11±1.43	6	-22.37±5.83	5.73±0.78	20.01±0.55	12	-21.12±0.91	6.58±0.83	14.60±2.23	5	-20.64±1.06	6.39±0.81	9.36±1.34
D Mfolozi	1	3	-19.80±1.23	2.66±0.42	0.13±0.98	3	-19.63±0.63	5.23±0.62	20.71±0.31	6	-20.43±1.05	5.58±0.56	16.42±2.67	3	-20.51±0.50	4.20±0.89	18.02±1.74
	2	3	-25.83±0.42	5.37±1.50	5.25±11.36	3	-19.02±2.28	4.91±0.64	20.56±0.10	6	-21.65±1.26	5.12±0.87	14.37±1.64	3	-21.07±1.19	4.79±0.23	8.64±0.84
	Summer	6	-22.81±3.40	4.02±1.78	2.69±7.74	6	-19.33±1.53	5.07±0.59	20.64±0.22	12	-21.04±1.28	5.35±0.74	15.48±2.41	6	-20.80±0.76	3.81±0.80	15.27±5.76
	3	3	-23.97±0.34	6.01±0.18	7.74±2.11	3	-17.42±0.79	5.29±0.35	20.36±0.31	6	-21.51±1.09	7.15±0.82	14.05±2.15	3	-20.19±0.27	5.66±0.31	13.46±2.35
	4	3	-23.23±0.34	6.44±0.23	16.30±1.70	3	-27.61±1.60	6.42±0.31	19.52±0.20	6	-20.74±0.52	6.01±0.29	15.16±1.97	3	-20.50±0.51	7.66±0.52	6.26±0.41
	Winter	6	-23.60±0.51	6.22±0.31	12.02±4.99	6	-22.37±5.83	5.73±0.78	20.01±0.55	12	-21.12±0.91	6.58±0.83	14.60±2.23	6	-20.71±0.43	6.66±1.16	9.86±4.22

Proportions of food sources assimilated by filter-feeders

SIAR (Jackson *et al.* 2008) was used to model the contributions of the three end-member food sources to the assimilated diets of filter-feeders. Study-area and season-specific average ± SD isotope values of river POM, seaweed and pelagic POM (Table 5.2) were used for each individual filter-feeder. Trophic fractionation was assumed to be constant among species and average ± SD values of 0.47 ± 1.23 ‰ for carbon (Vander Zanden & Rasmussen 2001), 2.52 ± 2.5 ‰ for nitrogen (Vander Zanden & Rasmussen 2001) and 0.5 ± 1.9 ‰ for sulphur (McCutchan *et al.* 2003) were used. Concentration dependence was also incorporated into the model because the proportional contribution of the three elements (C, N & S) among the end-member food sources was not equal (see Phillips & Koch 2002). Average ± SD percentage values of carbon, nitrogen and sulphur concentration in seaweed were obtained from seaweed-sample isotopic analyses while those for river POM were obtained from the isotopic analyses of small (<10 mm) decaying identifiable terrestrial plant pieces collected from the shore near river mouths. Values for pelagic POM, assumed to be largely phytoplankton, were obtained from phytoplankton analyses by Hedges *et al.* (2002). Average ± SD values for carbon [C], nitrogen [N] and sulphur [S] of 32.61 ± 5.88 %, 3.03 ± 0.70 % and 2.43 ± 0.99 % respectively were used for seaweed; 41.87 ± 3.50 % [C], 0.86 ± 0.36 % [N] and 0.62 ± 0.31 % [S] were used for river POM, and 16.20 ± 3.02 % [C], 3.16 ± 0.62 % [N] and 0.86 ± 0.42 % [S] were used for pelagic POM. Median values were then extracted from the feasible contribution outputs produced by SIAR for each end-member food source, graphed and used in subsequent univariate permutational ANOVA (PERANOVA) models. When appropriate, post-hoc tests were run only for Site and the interaction term Site x Season as the other factors were not relevant to the primary hypothesis.

RESULTS

Defining of end-member food source isotope signatures

The canonical analysis of principal coordinates analyses confirmed that the *a-priori* end-member food sources for all study areas and for each season were statistically distinguishable ($P_{(\mathrm{perm})} \leq 0.0026$) and thus suitable for input into subsequent mixing models (Table 5.3). Leave-one-out allocation successes for end-member food sources (i.e. excluding inshore POM mixture) were generally high, ranging from 77.8 to 100.0 %, with an average ± SD classification success of 86.1 ± 10.6 %. End-member food sources were generally not misclassified with other end-member sources but when this did occur, it was most often pelagic POM and seaweed that were confused. When inshore POM was included with the end-members it had a lower average ± SD classification success (70.4 ± 24.6 %) than end-member sources, which is to be expected, as it comprised a mixture of the other sources. Inshore POM was misclassified 14 times; 57 % of the time as pelagic POM, 29 % as river POM and 14 % as seaweed.

For river POM, average ± SD carbon isotopic signatures ranged from -15.5 ± 0.5 to -25.8 ± 0.14 ‰; nitrogen signatures from +1.2 ± 0.9 to +6.4 ± 0.2 ‰ (Table 5.2). Sulphur signatures had a greater range from -3.2 ± 2.1 to +16.3 ± 1.7 ‰, but most $\delta^{34}S$ values were < +5 ‰.

Seaweed detritus had similar carbon signatures to river POM ranging from -17.4 ± 0.8 ‰ to -27.6 ± 1.6 ‰; nitrogen signatures were generally enriched relative to river POM and ranged from +4.8 ± 0.2 ‰ to +6.4 ± 0.3 (Table 5.2). Sulphur signatures were more enriched than river POM and ranged from +19.5 ± 0.2 ‰ to +21.6 ± 0.6 ‰.

Pelagic POM had similar carbon isotope signatures to both seaweed and river POM ranging from -19.5 ± 0.3 to -22.7 ± 0.7; nitrogen signatures were similar to seaweed ranging from +4.6 ± 0.5 ‰ to +7.5 ± 0.8 ‰ (Table 5.2). Sulphur signatures were different from both river POM and seaweed, and ranged from +13.7 ± 0.7 ‰ to +16.7 ± 1.6 and +16.7 ± 1.4 ‰.

Table 5.3. Canonical analysis of principle coordinates (CAP) on raw isotope signatures using Euclidian distance, for the three end-member food sources and inshore POM (mixture) for each of the four study areas (A-D) according to summer and winter periods.

Area & (Season)	**Classified as**							
A (Summer)	**River POM**	**Seaweed**	**Pelagic POM**	**Inshore POM mix**	**Total**	**% Correct**	**Trace Statistic**	***P***
River POM	4	0	0	–	4	100.0	1.110	0.0001
Seaweed	0	6	0	–	6	100.0		
Pelagic POM	0	1	5	–	6	83.3		
Inshore POM mix	0	1	0	4	5	80.0	1.185	0.0001
A (Winter)								
River POM	5	0	1	–	6	83.3	0.993	0.0002
Seaweed	0	5	1	–	6	83.3		
Pelagic POM	0	1	5	–	6	83.3		
Inshore POM mix	1	0	0	5	6	83.3	1.659	0.0001
B (Summer)								
River POM	5	1	0	–	6	83.3	0.720	0.0026
Seaweed	0	5	1	–	6	83.3		
Pelagic POM	0	1	5	–	6	83.3		
Inshore POM mix	2	0	2	2	6	33.3	0.625	0.0002
B (Winter)								
River POM	6	0	0	–	6	100.0	1.616	0.0001
Seaweed	0	6	0	–	6	100.0		
Pelagic POM	0	0	6	–	6	100.0		
Inshore POM mix	0	0	3	3	6	50.0	1.613	0.0001
C (Summer)								
River POM	5	0	1	–	6	83.3	0.787	0.0001
Seaweed	0	4	2	–	6	66.7		
Pelagic POM	0	2	10	–	12	83.3		
Inshore POM mix	0	0	0	3	3	100.0	0.765	0.0001
C (Winter)								
River POM	6	0	0	–	6	100.0	1.073	0.0002
Seaweed	0	4	2	–	6	66.7		
Pelagic POM	0	2	10	–	12	83.3		
Inshore POM mix	0	0	0	5	5	100.0	1.646	0.0001
D (Summer)								
River POM	5	0	1	–	6	83.3	0.778	0.0001
Seaweed	0	6	0	–	6	100.0		
Pelagic POM	0	2	10	–	12	83.3		
Inshore POM mix	1	1	1	3	6	50.0	0.738	0.0005
D (Winter)								
River POM	4	0	2	–	6	66.7	0.835	0.0002
Seaweed	0	5	1	–	6	83.3		
Pelagic POM	2	0	10	–	12	83.3		
Inshore POM mix	0	0	2	4	6	66.7	1.148	0.0001

Inshore POM had similar carbon signatures to all three end-members ranging from -19.1 ± 1.1 ‰ to -21.8 ± 0.5 ‰; nitrogen signatures were similar to seaweed and pelagic POM but were enriched relative to river POM, and ranged from +2.9 ± 0.4 ‰ to +7.7 ± 0.5 ‰ (Table 5.2). Sulphur signatures were, however, generally more enriched than river POM but more depleted than both seaweed and pelagic POM, ranging from +6.3 ± 1.1 and +6.3 ± 0.4 ‰ to +18.0 ± 1.7 ‰.

Composition of inshore POM

Considering the signatures from C, N and S together, the inshore POM at study areas A and B (Figure 5.2a) was most similar to the isotope signatures of pelagic POM and river POM, whereas the inshore POM at study areas C and D (Figure 5.2b) most closely resembled that of pelagic POM. At all study areas, inshore POM isotope signatures least resembled those of seaweed which is not surprising as inshore POM was collected close to river mouths that inject POM into the nearshore. Mixing models indicated that inshore POM comprises a mixture of all three end-members to varying degrees (Figure 5.3a-d). Average ± SD river POM contribution to inshore POM per study area per season ranged from 17.1 ± 15.9 to 61.9 ± 38.1 %. Seaweed material contributed 6.0 ± 4.5 to 52.8 ± 20.4 %, while pelagic POM added 17.9 ± 22.7 to 76.6 ± 19.4 %.

Significant seasonal differences ($P_{(perm)} < 0.05$) existed in the contributions to inshore POM by seaweed material (higher in summer) and pelagic POM (higher in winter) (Table 5.4), but no significant seasonal differences in riverine POM contributions ($F_{(1,28)} = 1.768$, $P_{(perm)} > 0.2$). Although inshore POM at two of the study areas (B & C) comprised respectively 23.1 % and 8.4 % more river POM in summer than in winter, the reverse was true at Study Area A where river POM contributed 16 % more in winter than in summer, and at Study Area D river POM contribution was approximately equal in summer and winter (Figure 5.3a-d).

An inshore-offshore gradient of enrichment in $\delta^{34}S$ of POM existed from river to pelagic systems (Figure 5.4), best described by a non-linear regression between $\delta^{34}S$ and distance from coast (d) in km:

$\delta^{34}S_{POM} = 10.41 + 4.58(1 - 0.83^{d})$, $r^2 = 1$.

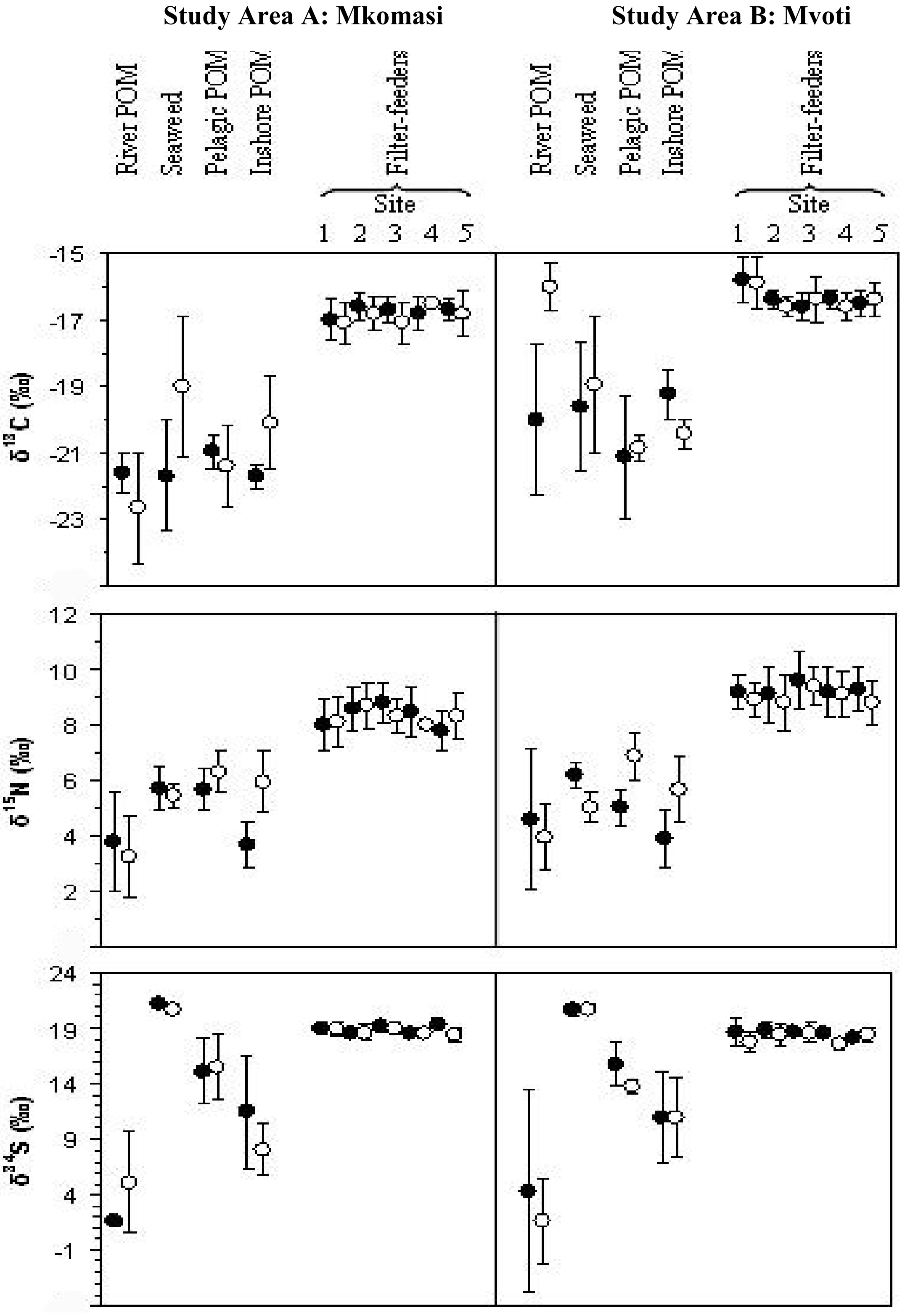


Figure 5.2a. Average ± standard deviation $\delta^{13}C$, $\delta^{34}S$ and $\delta^{15}N$ isotope values (‰) for the three end-member food sources, inshore POM mixture and filter-feeders averaged across each site in summer ● (n = 2) and in winter ○ (n = 2) for Study Area A (Mkomasi River) and Study Area B (Mvoti River).

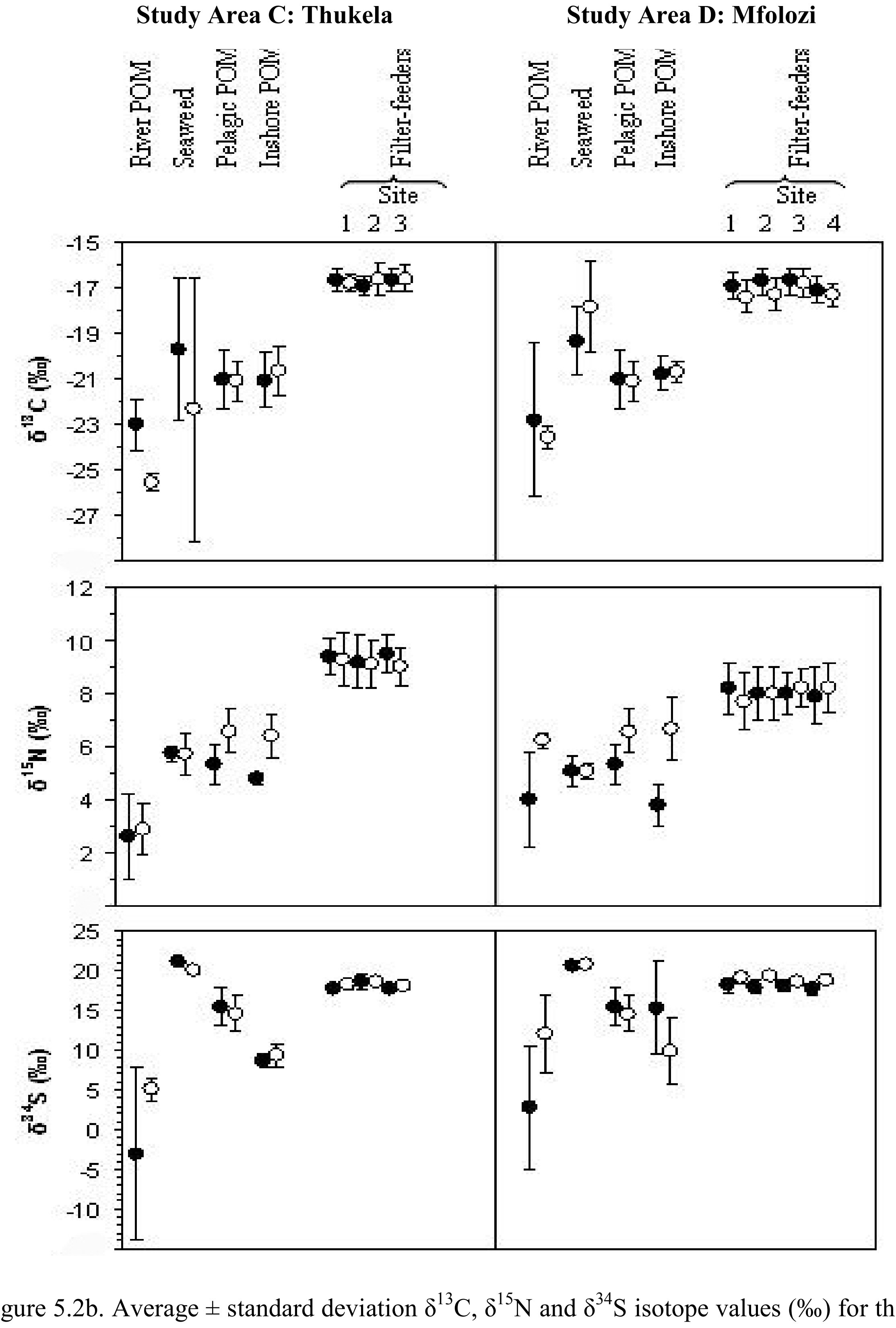


Figure 5.2b. Average ± standard deviation δ^{13}C, δ^{15}N and δ^{34}S isotope values (‰) for the three end-member food sources, inshore POM mixture and filter-feeders averaged across each site in summer ● and in winter ○ for Study Area C (Thukela River) and Study Area D (Mfolozi River).

Analysis of covariance (PERMANCOVA) on river POM contribution did reveal significant differences among samples taken at different distances along the shore from river mouths (covariate) ($F_{(1,28)} = 31.616$, $P_{(perm)} = 0.0001$), for study area ($F_{(1,28)} = 4.128$, $P_{(perm)} < 0.05$) and for all interaction terms involving alongshore distance from river mouth ($P_{(perm)} < 0.05$) (Table 5.4). River POM contributions to inshore POM versus alongshore distance (km) from river mouths showed a significant decreasing linear trend (river POM % contribution = -0.0265[distance] + 57.548; $r^2 = 0.23$, $P = 0.001$). Other covariates (mean annual runoff, and 3-monthly runoff) did not explain any significant amounts of variation in river POM contribution.

δ^{13}C, δ^{15}N and δ^{34}S of filter-feeders

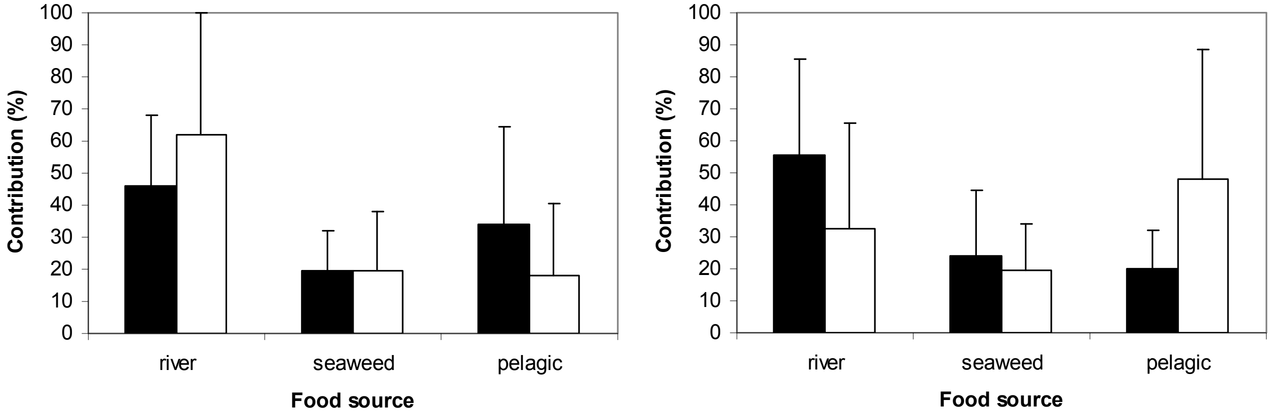
The isotope signatures of the four species of filter-feeders more closely resembled those of seaweed than any of the other end-member food sources or the inshore POM mixture (Figure 5.2a-b). All four species had tightly clustered similar isotopic signatures, although statistically significant differences were found due to the small variances of each species. Differences among study areas, sites, and seasons were slight and ranged from -18.1 to -15.1 ‰ for carbon, +6.2 to +10.6 ‰ for nitrogen, and +17.0 to +19.9 ‰ for sulphur isotope signatures (Table 5.5a-b).

Spatial and seasonal patterns in food source assimilation

Spatial and seasonal patterns were assessed by pooling across species because of their close isotopic similarity, and because the mixing models predicted maximum interspecific assimilation differences of only 6.08 % for river POM assimilation, 5.94 % for seaweed detritus and 2.97 % for pelagic POM.

Mixing models indicated that seaweed detritus was the dominant food source for all filter-feeders at all four study areas, with an average ± SD ranging from 38.7 ± 1.7 to 62.1 ± 3.0 % (Figure 5.5a-d).

A. Mkomasi River **B. Mvoti River**



C. Thukela River **D. Mfolozi River**

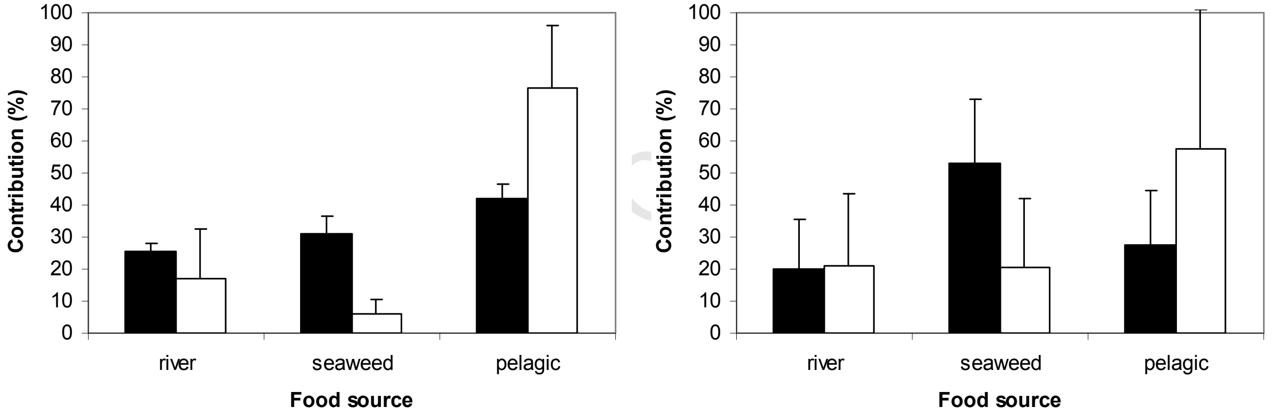


Figure 5.3a-d. Average ± standard deviation percentage contributions of the three end-member food sources to the inshore POM mixture adjacent to (**A.**) Mkomasi River in Study Area A, (**B.**) Mvoti River in Study B, (**C.**) Thukela River in Study Area C) and (**D.**) Mfolozi River in Study Area D), for summer ■ and winter □ periods.

Table 5.4. Two-factor PERMANOVAs and a permutational multivariate analysis of covariance to investigate variation in the contributions of the three end-member food sources to the inshore POM mixture, between study areas and seasons, based on SIAR mixing models. Long shore distance from river mouth to where the inshore POM sample was collected, mean annual runoff (MAR) and 3-monthly runoff were added as covariates in the analysis of river POM contributions. Significant differences ($P < 0.05$) are indicated by a *.

	Pelagic POM				**Seaweed**		
Source	df	MS	F	$P_{(perm)}$	MS	F	$P_{(perm)}$
Study area	3	0.179	2.268	0.0972	0.079	2.746	0.0588
Season	1	0.371	4.702	0.0381*	0.247	8.541	0.0041*
Study area x Season	3	0.149	1.886	0.1520	0.069	2.378	0.0883
Residual	35	0.079			0.029		
Total	42						

River POM

Source	df	MS	F	$P_{(perm)}$
Long shore distance	1	0.828	31.616	0.0001*
MAR	1	0.002	0.0836	0.7749
3-monthly runoff	1	0.004	0.1523	0.6887
Study area	1	0.108	4.128	0.0471*
Season	1	0.046	1.768	0.1986
Long shore distance x 3-monthly runoff	1	0.607	23.184	0.0001*
Long shore distance x Season	1	0.741	28.279	0.0001*
MAR x 3-monthly runoff	1	0.041	1.549	0.2185
MAR x Season	1	0.038	1.438	0.2317
3-monthly runoff x Study area	1	0.024	0.906	0.3414
3-monthly runoff x Season	1	0.058	2.197	0.1458
Study area x Season	1	0.071	2.708	0.1064
Long shore distance x 3-monthly runoff x Season	1	0.086	6.929	0.0148*
MAR x 3-monthly runoff x Season	1	0.086	3.283	0.0774
Residual	28	0.026		
Total	42			

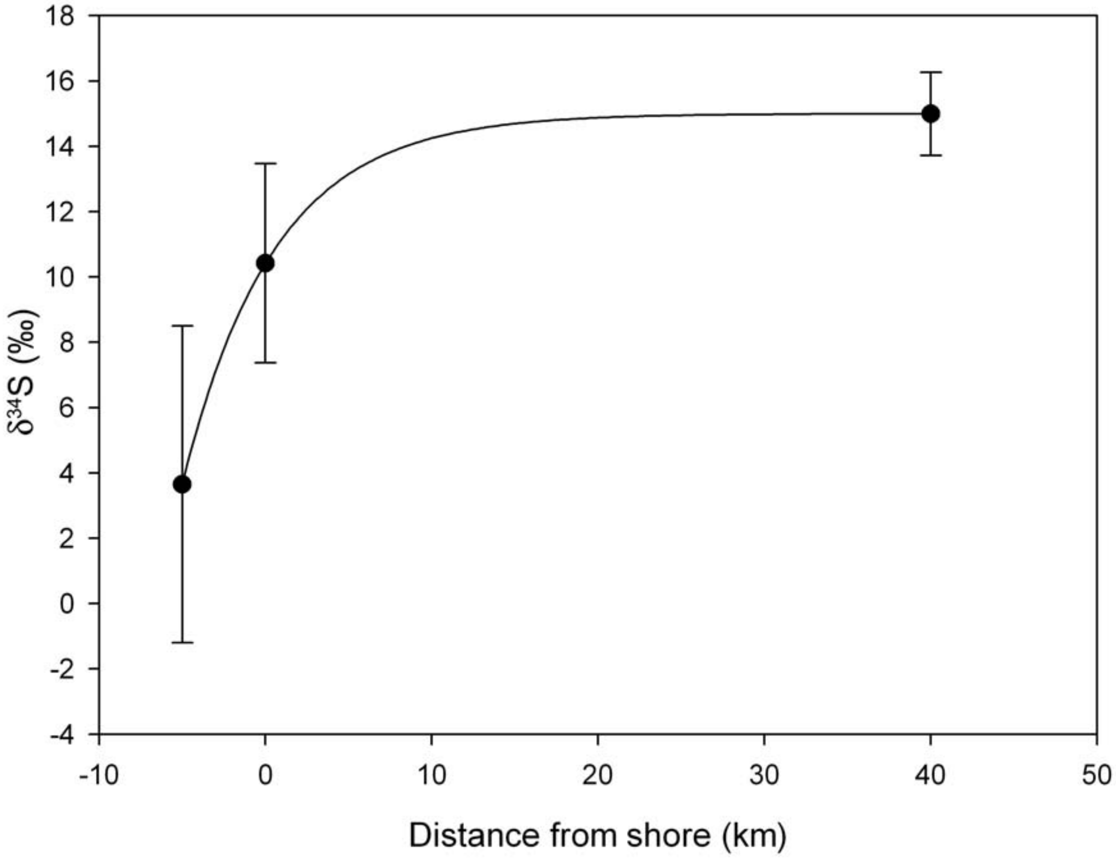


Figure 5.4. Average ± SD $\delta^{34}S$ isotope signatures of particulate organic matter versus distance from shore (d, in km). Negative distance equals distance inland up river. Regression: $\delta^{34}S_{POM} = 10.41 + 4.58(1\text{-}0.83^{d})$, $r^2 = 1$.

The proportion of seaweed detritus assimilated varied little among sites lying at different distance from river mouths (1.5 – 5.0 %). Nevertheless, significant differences among sites were found within all four study areas ($P_{(perm)} < 0.01$), although this was not usually the case in the interaction term between Sites and Seasons (Tables 5.6a & b). Only during summer at Study Area A and winter at Study Area B, were slight but consistent trends of increasing seaweed assimilation found with increasing distance from river mouth. Generally, about 2 – 10 % more seaweed was assimilated in summer than in winter, with the differences being significant ($P_{(perm)} \leq 0.0002$) in all areas except Study Area B ($F_{(1,76)} = 3.876$, $P_{(perm)} = 0.0521$); and Study Area D reversed the trend as 7 % more seaweed was assimilated in winter than in summer ($F_{(1,54)} = 562.520$, $P_{(perm)} = 0.0001$).

Pelagic POM, assumed to be largely phytoplankton, was the next-most assimilated food source after seaweed at three of the four study areas, with average ± SD dietary contributions ranging from 23.7 ± 5.6 to 36.2 ± 1.4 % (Figure 5.5a-d). Spatial variation among sites was small (0.4 - 4.1 %) although significant differences ($P_{(perm)} < 0.01$) were found at all study areas bar one: Area A, which was also the only place where no significant interaction was found between Sites crossed with Seasons ($F_{(4,61)} = 1.635$, $P_{(perm)} = 0.1770$) (Tables 5.6a & b). Very gradual decreasing trends in pelagic POM assimilation with respect to distance from river mouth were evident at study areas A and C during winter, and evidence of minor increasing trends were observed at Study Area B during both summer and winter. Significant seasonal differences were found within all study areas ($P_{(perm)} = 0.0001$) except at Study Area D ($F_{(1,54)} = 0.006$, $P_{(perm)} = 0.9439$), with marginally more pelagic POM (10.4 %) on average being assimilated in winter than in summer.

River POM was assimilated at all study areas and sites in proportions spanning 8.6 ± 1.3 to 33.3 ± 6.2 % (Figure 5.5a-d). Little spatial variation in assimilation (0.9 – 4.5 %) was evident among sites but these small differences were statistically significant ($P_{(perm)} < 0.005$) (Tables 5.6a & b). The interaction term between Sites and Seasons was significant at study areas B and D ($P_{(perm)} < 0.005$). Small spatial trends of decreasing river POM assimilation with distance from river mouth were evident at Study Area A in summer but not in winter, during both seasons at Study Area B and in winter only at Study Area D.

As was the case with seaweed and pelagic POM, there was a small seasonal shift in the amount of river POM assimilated, which was significant at study areas A, C and D ($P_{\text{(perm)}} = 0.0001$) but was inconsistent across study areas, with 0-3 % more being assimilated during winter in study areas A and B, and 1-8 % more in summer in areas C and D.

When post-hoc tests were run, they revealed two trends. Firstly, in terms of river POM assimilation, sites were most often significantly different ($P < 0.05$) if comparisons were being made between sites situated at the mouth versus those at some distance from the mouth, or between sites that lay far apart. Secondly, when Site x Season interactions were compared for pelagic POM assimilation, significant differences were always more frequent in winter, when pelagic POM levels were highest, than in summer.

Table 5.5a. Summer average ± SD δ^{13}C, δ^{15}N and δ^{34}S isotope values (‰) of various filter-feeders per site in each study area. *Asterisks indicate n = 2 replicates per species; in all other cases n = 3 per species.

Site	Species	A (Mkomasi)			B (Mvoti)			C (Thukela)			D (Mfolozi)		
		δ^{13}C	δ^{15}N	δ^{34}S	δ^{13}C	δ^{15}N	δ^{34}S	δ^{13}C	δ^{15}N	δ^{34}S	δ^{13}C	δ^{15}N	δ^{34}S
1	*Perna perna*	-16.8±0.0	7.0±0.2	18.3±0.3	-15.9±0.1	8.6±0.1	19.0±0.2	-16.7±0.1	8.5±0.2	17.3±0.3	-17.1±0.2	7.0±0.5	17.4±0.4
	Striostrea margaritacea	-17.6±1.3*	7.3±0.0*	19.5±0.2*	-15.1±0.3	8.9±0.3	17.0±0.9	-16.2±0.2	9.2±0.0	18.0±0.2	-16.2±0.0	8.3±0.2	17.8±0.2
	Saccostrea cucullata	-16.4±0.3	8.6±0.2	19.1±0.2	-15.6±0.4	9.4±0.2	19.1±0.3	-16.6±0.1	9.5±0.1	17.6±0.2			
	Pyura stolonifera	-17.4±0.2	9.0±0.1	19.6±0.3	-16.7±0.0	10.0±0.1	19.9±0.1	-17.5±0.2	10.4±0.1	18.3±0.1	-17.5±0.2	9.2±0.2	19.4±0.1
	Average ± SD	-17.0±0.6	8.0±0.9	19.0±0.6	-15.8±0.7	9.2±0.6	18.7±1.2	-16.7±0.5	9.4±0.7	17.8±0.4	-16.9±0.6	8.2±1.0	18.2±1.0
2	*Perna perna*	-16.3±0.2	7.7±0.2	18.3±0.2	-16.6±0.1	8.0±0.3	18.7±0.3	-17.2±0.1	7.8±0.2	17.6±0.2	-16.5±0.1	6.9±0.5	16.9±0.2
	Striostrea margaritacea				-16.1±0.1	8.8±0.2	19.2±0.2	-16.6±0.1	9.0±0.1	18.8±0.2	-16.2±0.1	8.1±0.4	18.3±0.3
	Saccostrea cucullata	-16.4±0.2	8.8±0.2	18.5±0.2	-16.1±0.2	9.3±0.2	18.1±0.3	-16.5±0.2	9.4±0.1	18.4±0.2			
	Pyura stolonifera	-17.2±0.3	9.4±0.1	19.1±0.3	-16.6±0.4	10.5±0.1	19.2±0.5	-17.2±0.2	10.4±0.1	19.7±0.3	-17.5±0.1	9.1±0.2	18.6±0.3
	Average ± SD	-16.6±0.4	8.6±0.8	18.6±0.5	-16.4±0.3	9.1±1.0	18.8±0.6	-16.9±0.4	9.2±1.0	18.6±0.8	-16.7±0.6	8.0±1.0	17.9±0.8
3	*Perna perna*	-16.4±0.1	7.9±0.2	19.4±0.5	-16.5±0.2	8.4±0.3	18.4±0.0	-17.0±0.1	8.7±0.3	17.8±0.1	-16.5±0.0	7.1±0.0	17.3±0.2
	Striostrea margaritacea							-16.0±0.2	9.2±0.1	17.2±0.2	-16.2±0.1	8.0±0.0	17.7±0.2
	Saccostrea cucullata	-16.5±0.2	9.0±0.4	18.8±0.6	-16.1±0.1	9.8±0.3	18.6±0.3	-16.5±0.2	9.7±0.2	17.4±0.2			
	Pyura stolonifera	-17.2±0.1	9.5±0.2	19.6±0.3	-17.0±0.2	10.6±0.1	19.2±0.3	-17.3±0.2	10.5±0.0	18.7±0.2	-17.5±0.1	9.0±0.1	18.8±0.3
	Average ± SD	-16.7±0.4	8.8±0.7	19.2±0.5	-16.6±0.4	9.6±1.0	18.7±0.4	-16.7±0.5	9.5±0.7	17.7±0.6	-16.7±0.6	8.0±0.8	18.0±0.7
4	*Perna perna*	-16.5±0.1	7.7±0.1	19.0±0.3	-16.4±0.1	8.3±0.3	18.2±0.3				-17.2±0.2	6.6±0.2	17.0±0.4
	Striostrea margaritacea	-16.4±0.0	8.2±0.1	18.4±0.3	-16.5±0.2	8.8±0.2	19.1±0.4				-16.4±0.2	8.0±0.1	17.5±0.1
	Saccostrea cucullata				-16.0±0.2	9.4±0.3	18.8±0.4						
	Pyura stolonifera	-17.5±0.0	9.6±0.0	18.5±0.5	-16.8±0.1	10.5±0.1	18.4±0.2				-17.6±0.0	9.2±0.1	18.6±0.1
	Average ± SD	-16.8±0.5	8.5±0.9	18.6±0.4	-16.4±0.3	9.2±0.9	18.6±0.4				-17.1±0.6	7.9±1.1	17.7±0.7
5	*Perna perna*	-16.9±0.2	7.1±0.2	19.0±0.3	-16.4±0.1	8.5±0.0	17.8±0.2						
	Striostrea margaritacea	-16.6±0.2	7.7±0.2	19.5±0.1	-16.1±0.1	9.1±0.2	18.8±0.2						
	Saccostrea cucullata	-16.4±0.1	8.7±0.3	19.6±0.2	-16.4±0.2	9.3±0.5	17.8±0.5						
	Pyura stolonifera				-17.1±0.3	10.4±0.2	18.2±0.2						
	Average ± SD	-16.7±0.3	7.8±0.7	19.4±0.3	-16.5±0.4	9.3±0.8	18.2±0.5						

Table 5.5b. Winter average ± SD δ^{13}C, δ^{15}N and δ^{34}S isotope values (‰) of various primary consumers per site for each study area during winter. Values are based on 3 replicate samples.

Site	**Species**	**A (Mkomasi)**			**B (Mvoti)**			**C (Thukela)**			**D (Mfolozi)**		
		δ^{13}C	**δ^{15}N**	**δ^{34}S**	**δ^{13}C**	**δ^{15}N**	**δ^{34}S**	**δ^{13}C**	**δ^{15}N**	**δ^{34}S**	**δ^{13}C**	**δ^{15}N**	**δ^{34}S**
1	*Perna perna*	-16.8±0.3	6.9±0.0	18.4±0.2	-15.4±0.1	8.3±0.1	16.6±0.3	-16.8±0.2	8.1±0.3	17.6±0.4	-17.8±0.2	6.2±0.3	18.3±0.2
	Striostrea margaritacea	-16.7±0.2	7.9±0.4	19.2±0.0	-15.3±0.1	8.6±0.1	17.5±0.2	-16.5±0.1	9.0±0.2	18.8±0.7	-16.8±0.3	7.5±0.1	19.7±0.2
	Saccostrea cucullata	-16.9±0.2	8.6±0.0	18.3±0.3	-15.9±0.1	9.5±0.5	18.5±0.1	-16.5±0.1	9.9±0.5	18.3±0.3	-16.8±0.0	8.4±0.3	18.7±0.3
	Pyura stolonifera	-17.9±0.4	9.2±0.4	19.5±0.2	-17.2±0.0	9.3±0.2	18.8±0.1	-17.5±0.2	10.4±0.0	18.1±0.4	-18.1±0.3	8.9±0.3	19.9±0.4
	Average ± SD	-17.1±0.6	8.1±0.9	18.9±0.6	-15.9±0.8	8.9±0.6	17.8±0.9	-16.8±0.4	9.3±1.0	18.2±0.6	-17.4±0.7	7.7±1.1	19.1±0.7
2	*Perna perna*	-16.6±0.3	7.7±0.2	17.8±0.1	-16.7±0.2	7.3±0.3	17.1±0.2	-16.9±0.2	7.7±0.2	18.3±0.5	-17.3±0.1	6.7±0.1	18.7±0.5
	Striostrea margaritacea				-16.2±0.1	8.9±0.1	18.7±0.3	-15.7±0.3	9.2±0.3	18.9±0.3	-16.5±0.1	8.3±0.1	19.4±0.1
	Saccostrea cucullata	-16.9±0.0	9.0±0.1	18.8±0.0	-16.4±0.1	9.1±0.2	18.5±0.2	-16.4±0.0	9.4±0.4	18.3±0.3			
	Pyura stolonifera	-17.1±0.7	9.5±0.1	19.3±0.2	-16.9±0.2	10.0±0.1	19.3±0.6	-17.4±0.1	10.0±0.4	18.8±0.4	-18.1±0.3	9.0±0.1	19.7±0.4
	Average ± SD	-16.8±0.5	8.7±0.8	18.6±0.7	-16.6±0.3	8.8±1.0	18.4±0.9	-16.6±0.7	9.1±0.9	18.6±0.4	-17.3±0.7	8.0±1.0	19.3±0.6
3	*Perna perna*	-16.6±0.1	7.8±0.2	18.5±0.2	-16.1±0.0	8.4±0.1	18.1±0.3	-16.5±0.1	8.1± 0.4	17.9±0.2	-16.7±0.2	7.3±0.3	18.0±0.2
	Striostrea margaritacea				-15.9±0.4	9.4±0.6	18.9±0.4	-16.0±0.1	9.0±0.1	18.6±0.2	-16.3±0.2	8.0±0.2	19.1±0.0
	Saccostrea cucullata	-16.8±0.1	8.0±0.1	19.0±0.1	-16.1±0.4	9.6±0.2	17.5±0.6	-16.6±0.1	9.1±0.1	17.9±0.3	-16.5±0.1	8.5±0.3	18.1±0.3
	Pyura stolonifera	-17.8±0.2	9.0±0.2	19.6±0.4	-17.4±0.3	9.9±0.3	19.7±0.2	-17.4±0.3	9.7±0.3	18.3±0.4	-17.7±0.4	8.9±0.2	19.2±0.0
	Average ± SD	-17.1±0.6	8.3±0.6	19.0±0.6	-16.4±0.7	9.4±0.7	18.6±0.9	-16.6±0.6	9.0±0.7	18.1±0.4	-16.8±0.6	8.2±0.7	18.6±0.6
4	*Perna perna*				-16.4±0.1	8.2±0.0	17.4±0.1				-17.5±0.2	7.1±0.4	18.2±0.3
	Striostrea margaritacea	-16.5±0.1	8.0±0.1	18.5±0.2							-16.9±0.4	8.3±0.3	19.1±0.2
	Saccostrea cucullata				-16.3±0.3	9.2±0.4	17.5±0.1				-16.9±0.2	8.2±0.2	18.4±0.2
	Pyura stolonifera				-17.1±0.1	9.9±0.4	17.9±0.8				-18.0±0.2	9.3±0.1	19.5±0.3
	Average ± SD	-16.5±0.1	8.0±0.1	18.5±0.2	-16.6±0.4	9.1±0.8	17.6±0.5				-17.3±0.5	8.2±0.9	18.8±0.6
5	*Perna perna*	-16.8±0.1	7.4±0.4	17.9±0.3	-16.4±0.2	7.8±0.3	17.7±0.3						
	Striostrea margaritacea	-16.6±0.2	7.9±0.4	18.9±0.5	-16.2±0.0	8.6±0.2	19.1±0.1						
	Saccostrea cucullata	-16.2±0.5	8.9±0.4	18.0±0.2	-16.1±0.6	8.9±0.5	18.2±0.2						
	Pyura stolonifera	-17.8±0.2	9.2±0.3	19.0±0.4	-17.0±0.4	9.8±0.3	18.7±0.7						
	Average ± SD	-16.8±0.7	8.3±0.8	18.4±0.6	-16.4±0.5	8.8±0.8	18.4±0.6						

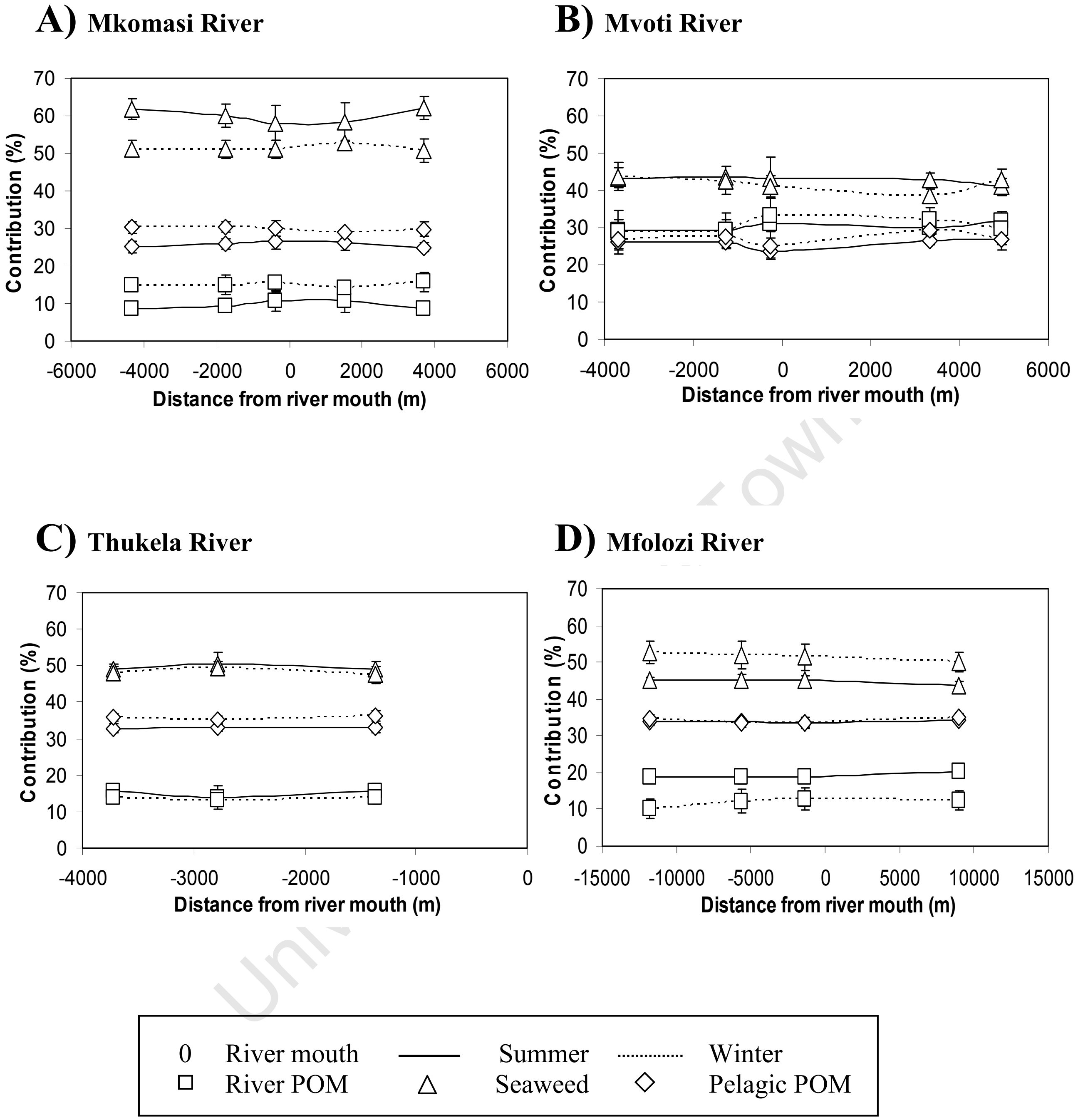


Figure 5.5a-d. Average ± SD percentage contributions of river POM, seaweed and pelagic POM assimilated by filter-feeders according to the median value derived from mixing model outputs per season, expressed relative to distances South (-ve) and North of the river mouths (+ve), for **(A)** Mkomasi River in Study Area A, **(B)** Mvoti River in Study Area B, **(C)** Thukela River in Study Area C and **(D)** the Mfolozi River in Study Area D.

Table 5.6a. Univariate PERANOVAs conducted on each food source independently to investigate variation in their assimilation within Study Area A adjacent to the Mkomasi River mouth and Study Area B adjacent to the Mvoti River mouth. Significant differences (α = 0,05) are indicated by a *. ^{1} = Term has one or more empty cells.

Study Area A: Mkomasi		**River POM**			**Seaweed**			**Pelagic POM**		
Variation	df	MS	*F*	$P_{(perm)}$	MS	*F*	$P_{(perm)}$	MS	*F*	$P_{(perm)}$
Site	4	0.0010	4.251	0.0044*	0.0020	3.7149	0.0095*	0.0002	2.051	0.0996
Season	1	0.0531	228.230	0.0001*	0.1327	250.65	0.0001*	0.0274	232.360	0.0001*
Species	3	0.0031	13.171	0.0001*	0.0093	17.582	0.0001*	0.0047	40.152	0.0001*
Site x Season	4	0.0003	1.368	0.2550	0.0009	1.7351	0.1552	0.0002	1.635	0.1770
Site x Species^1	9	0.0008	3.608	0.0014*	0.0019	3.5471	0.0016*	0.0003	2.352	0.0259*
Season x Species	3	0.0012	5.301	0.0020*	0.0021	4.0315	0.0120*	0.0006	5.375	0.0016*
Site x Season x Species^1	6	0.0006	2.598	0.0253*	0.0015	2.7619	0.0195*	0.0003	2.339	0.0419*
Residual	61	0.0002			0.0005			0.0001		
Total	91									

Study Area B: Mvoti		**River POM**			**Seaweed**			**Pelagic POM**		
Variation	df	MS	*F*	$P_{(perm)}$	MS	*F*	$P_{(perm)}$	MS	*F*	$P_{(perm)}$
Site	4	0.0032	12.400	0.0001*	0.0014	4.327	0.0032*	0.0034	20.890	0.0001*
Season	1	0.0000	0.054	0.8201	0.0012	3.876	0.0521	0.0040	24.933	0.0001*
Species	3	0.0332	128.590	0.0001*	0.0113	35.962	0.0001*	0.0059	36.463	0.0001*
Site x Season	4	0.0017	6.453	0.0001*	0.0022	6.866	0.0003*	0.0004	2.756	0.0331*
Site x Species	12	0.0044	17.129	0.0001*	0.0029	9.112	0.0001*	0.0005	2.836	0.0030*
Season x Species	3	0.0052	20.028	0.0001*	0.0015	4.843	0.0044*	0.0054	33.546	0.0001*
Site x Season x Species^1	10	0.0019	7.261	0.0001*	0.0017	5.335	0.0001*	0.0002	1.023	0.4352
Residual	76	0.0003			0.0003			0.0002		
Total	113									

Table 5.6b. Univariate PERANOVAs conducted on each food source independently to investigate variation in their assimilation within Study Area C adjacent to the Thukela River mouth and Study Area D adjacent to the Mfolozi River mouth. Significant differences (α = 0,05) are indicated by a *.

Study Area C: Thukela		**River POM**			**Seaweed**			**Pelagic POM**		
Variation	df	MS	F	$P_{(perm)}$	MS	F	$P_{(perm)}$	MS	F	$P_{(perm)}$
Site	2	0.0014	20.879	0.0001*	0.0019	16.653	0.0001*	0.0002	5.376	0.0082*
Season	1	0.0035	51.346	0.0001*	0.0031	26.506	0.0002*	0.0127	365.450	0.0001*
Species	3	0.0047	68.331	0.0001*	0.0049	42.073	0.0001*	0.0010	29.811	0.0001*
Site x Season	2	0.0002	2.900	0.0680	0.0000	0.038	0.9624	0.0002	5.882	0.0043*
Site x Species	6	0.0006	8.344	0.0001*	0.0005	4.575	0.0011*	0.0002	5.742	0.0003*
Season x Species	3	0.0008	11.401	0.0001*	0.0016	13.724	0.0001*	0.0004	12.825	0.0001*
Site x Season x Species	6	0.0003	5.084	0.0007*	0.0003	2.858	0.0201*	0.0001	2.249	0.0537
Residual	48	0.0001			0.0001			0.0000		
Total	71									

Study Area D: Mfolozi		**River POM**			**Seaweed**			**Pelagic POM**		
Variation	df	MS	*F*	$P_{(perm)}$	MS	*F*	$P_{(perm)}$	MS	*F*	$P_{(perm)}$
Site	3	0.0010	9.159	0.0001*	0.0013	9.713	0.0002*	0.0004	10.794	0.0001*
Season	1	0.0841	799.150	0.0001*	0.0780	562.520	0.0001*	0.0000	0.006	0.9439
Species	3	0.0093	88.780	0.0001*	0.0089	64.417	0.0001*	0.0009	24.865	0.0001*
Site x Season	3	0.0006	5.653	0.0024*	0.0003	1.916	0.1344	0.0002	4.213	0.0092*
Site x Species[1]	8	0.0004	3.429	0.0022*	0.0004	2.763	0.0101*	0.0001	1.436	0.2026
Season x Species[1]	2	0.0015	14.324	0.0001*	0.0047	34.100	0.0001*	0.0008	21.333	0.0001*
Site x Season x Species[1]	6	0.0001	0.531	0.7825	0.0001	0.923	0.4896	0.0001	2.104	0.0671
Residual	54	0.0001			0.0001			0.0000		
Total	80									

DISCUSSION

End-member sources and their contribution to the inshore POM pool

End-member primary producers were sufficiently isotopically distinct to discriminate their proportional contributions to the inshore POM mixture and to the assimilated diets of the filter-feeders examined (Table 5.3).

Carbon, nitrogen and sulphur isotope signatures of seaweeds lay within the ranges found by other studies (Stephenson *et al.* 1984; Peterson & Fry 1987; Pinnegar & Polunin 2000; Smit 2001; Yamanaka *et al.* 2003) and carbon and nitrogen values were similar to those reported specifically for the South African east coast (Hill *et al.* 2006).

River POM carbon isotopic signatures ranged from -15.5 to -25.8 ‰ with most values approximating -20 ‰, implying more or less equal proportions of C_3 and C_4 plants (Sternberg *et al.* 1984; Pate 2001), which reflects the mix of savanna and grassland biomes in the region (Acocks 1975; Cole 1986; Scholes & Archer 1997; Mucina *et al.* 2006; Rutherford *et al.* 2006a, b). Carbon and nitrogen isotopic values of seaweed closely corresponded with those of river POM (Table 5.2). Sulphur isotope signatures were therefore important in distinguishing between river POM and seaweed: river POM was far more depleted than seaweed, which derives its sulphur from oceanic sulphate with a $\delta^{34}S$ of +20 to +21 ‰ (Reece *et al.* 1978; Longinelli 1989). Terrestrial and aquatic plants, thought to comprise the bulk of river POM in this case, derive most of their sulphur from precipitation with a $\delta^{34}S$ of +2 to +6 ‰ (Michener & Schell 1994). The assimilation of different pools of inorganic sulphur (terrestrial versus marine) into organic matter and the mixing of these in the inshore zone was illustrated by the inshore-offshore trend in $\delta^{34}S$, which rose exponentially with distance offshore (Figure 5.4), reflecting differential inputs of riverine, inshore and pelagic sources. Sulphur isotope signatures were therefore the primary discriminant separating terrestrial from marine organic matter sources.

Carbon and nitrogen isotope signatures of pelagic POM, assumed to be largely phytoplankton, closely approximated those found on the east coast of South Africa (Hill *et al.*

2006, 2008). Sulphur, on the other hand, was ca. 3 ‰ more depleted than the lower range limit (+17 to +21 ‰) found in those few studies that have previously measured plankton $\delta^{34}S$ (Peterson & Fry 1987). This cannot easily be explained but may be due to a number of reduced sulphur sources include biogenic sulphides ($\delta^{34}S$ = 0 to -40 ‰) in marine sediments (Passier *et al.* 1999) and those derived from rainfall over the oceans ($\delta^{34}S$ = +13 ‰) (Chukhrov *et al.* 1980). However, these reduced sources are likely to be negligible when one considers the high concentrations of sulphate sulphur (2.6 mg/l) in oceanic surface waters ($\delta^{34}S$ = +21 ‰) that are available to phytoplankton (Barnes 1954).

Although standard isotope pre-processing methods were used, filtration followed by rinsing of filter papers with deionised water to remove inorganic sulphate and oven-drying could have resulted in the selective loss of some fraction of the cellular sulphur, such as the dimethylsulfoniopropionate (DMSP) component, due to the rupturing of cytoplasm and even due to its degradation into dimethylsulphide (Kiene & Slezak 2006). Fractionation could have been a consequence of this. However, DMSP can be lost naturally by phytoplankton communities when under stress (Kiene *et al.* 2000) or can be directly assimilated by bacterioplankton (Cosquer *et al.* 1999; Kiene *et al.* 2000). There is also evidence suggesting that some types of phytoplankton replace their phospholipids with sulfolipids when phosphate is limited, which may also cause fractionation (R.P. Kiene, University of South Alabama, *pers. comm.* 2009). One or a combination of these factors could explain the slightly depleted $\delta^{34}S$ signatures obtained from pelagic POM, when compared to those in the literature (Peterson & Fry 1987). To test whether any artefactual depletion of sulphur could have biased my results, I re-ran mixing models using a value of +21 ± 0.5 ‰, which is regarded as the accepted norm for organisms deriving their sulphur exclusively from marine sulphate (Michener & Schell 1994). The proportions of various types of POM assimilated by inshore filter-feeders were consistently little influenced by these re-runs. River POM could have been underestimated by 5.6 ± 4.2 %, whereas seaweed and pelagic POM appeared to be overestimated by 2.1 ± 4.3 % and 3.0 ± 4.5 % respectively. Thus, my results would not have been materially affected even if there was an artefactual effect, and my conclusions remain robust.

The inshore POM mix was isotopically different from all of the end-member sources contributing to it, demonstrating that no single end-member dominated its composition. Relative to other end-member sources, river POM contributed most to the inshore POM pool when samples were taken within hundreds of meters of a river mouth but contributed less to inshore POM at distances exceeding 1000 m (Figure 5.5).

Hill *et al.* (2008) found macroalgae usually contributed more than 50 % of the material to the inshore POM pool when they sampled on the Eastern Cape Coast, approximately 700 km south of where I worked. The area they studied is, however, much less influenced by riverine input, as the two main rivers within 25 km – the Kariega and Kowie – are heavily impounded and exude a combined mean annual runoff of only 38 x 10^6 m^3, and the closest large river, the Fish River 55 km away, releases approximately 479 x 10^6 m^3 (Noble & Hemens 1978). My study, on the other hand, is more likely to show a proportionally higher input of riverine POM because it specifically focused on sampling rocky shores within kilometres of relatively larger rivers (with runoffs of 400 – 4000 x 10^6 m^3) and was in a coastal area that experiences high river input.

Unexpectedly, riverine contribution to inshore POM was not consistently greater in summer (the rainy season) than in winter, pattern being evident only in study areas (B & C); nor was it significantly related to river size in terms of mean annual runoff (Figure 5.3a-d, Table 5.4). This indicates that although river runoff is greater in summer than in winter (Midgley *et al.* 1994), and rivers of different sizes were investigated, the amount of river POM injected into the inshore zone is not necessarily a function of seasonal or annual runoff. In the Danube River, which flows into the Black Sea, the amount of river POM has similarly been shown to be unrelated to runoff (Bănaru *et al.* 2007), nor was any relationship found between river discharge and river POM concentration at the point where the Mattaponi River in Virginia USA flows into the sea, which Hoffman & Bronk (2006) concluded was due to the multiple fates and sources of POM.

Factors that could explain the absence of river-size and seasonal effects include the nature and quantity of terrestrial vegetation, the time between plant growth and litter-fall, the intensity of agricultural abstraction, local rainfall patterns and relative rainfall runoff.

River POM contributions to inshore POM did, however, decline linearly with distance from river mouth (Table 5.4). River plume processes are influenced by a range of complex factors that are not fully understood (Dagg *et al.* 2004), but river POM can be expected to be diluted by marine POM sources with distance from river mouth. In the case of the Changjiang River, which drains into the East China Sea, river POM contribution decreases non-linearly with distance (Wu *et al.* 2003) whereas POM from the Vistula River, which drains into the Baltic Sea, decreases linearly along a salinity gradient and with distance from river mouth (Vos *et al.* 2005) in a pattern similar to the one that I recorded. Coastal wind direction and ambient coastal flow are likely to be the dominant agents determining plume direction (Walker 1996; Hickey *et al.* 1998; Berdeal *et al.* 2002). Prevailing wind velocity and its temporal variability, inshore vertical stratification and the degree of mixing due to turbulence (Gibbs 1983; Gibbs & Konwar 1986; Alldredge & Gotschalk 1990), are likely to influence the concentration of riverine derived POM in the inshore POM pool (Naudin *et al.* 1997) and whether or not its dilution precedes linearly with distance from source.

In summary, river POM did contribute notably to inshore POM and its concentration was related to distance from source river supporting the first part of hypothesis (1), but it did not contribute consistently more in summer than winter, nor did larger rivers contribute more than smaller rivers, thus not supporting the second part of this hypothesis.

Relative trophic contributions of seaweed detritus, pelagic POM & river POM to inshore filter-feeder communities

Many studies have found pelagic phytoplankton to be of major trophic importance to filter-feeders (Asmus & Asmus 1981; Dame & Prins 1998; Sanford & Menge 2001; Leslie *et al.* 2005). However, on the South African west coast, filter-feeders rely mostly on nearshore production in the form of seaweed (Stuart *et al.* 1982; Klumpp 1984; Stuart & Klumpp 1984; Fielding & Davis 1989; Bustamante & Branch 1996b) as does *Perna perna* on the south east coast, where it has a more than 50 % reliance on nearshore production (Hill & McQuaid 2008; Hill *et al.* 2008).

My study showed a similarly high reliance on nearshore production, with seaweed contributing between 40 and 60 % of inshore filter-feeder diets according to mixing model results (Figure 5.5a-d). In addition to inshore seaweed production, pelagic POM, assumed to be largely phytoplankton, comprised 25 to 35 % of their diets. The high amount of seaweed detritus assimilated by filter-feeders may be inflated, as it may include some inshore-derived phytoplankton, which cannot be distinguished from seaweed because they both assimilate similar sources of carbon, nitrogen and sulphur. Nevertheless, trophic subsidies from river POM contributed between 8.8 and 33.3 % to the assimilated energy of filter-feeders examined. This provides the first evidence of noteworthy riverine–inshore–pelagic coupling in inshore filter-feeder communities of the Subtropical Natal Bioregion.

In general, the assimilated dietary contributions of river POM and seaweed to filter-feeder communities did not correspond with their proportions in the inshore POM pool. Considerably less river POM was assimilated than its proportional contribution to the inshore POM pool, while the opposite was true for seaweed. Pelagic POM was assimilated in proportions approximately equal to availability. This suggests preferential ingestion of certain components of the inshore organic matter pool (see also Kiørboe & Møhlenberg 1981; Birkbeck & McHenery 1982) or the unequal digestion or assimilation of various types of organic matter (Hylleberg Kristensen 1972; Foale & Day 1992; Boenigk *et al.* 2001; Zimmer *et al.* 2002; Ren *et al.* 2006). Seaweed and phytoplankton tend to be more easily assimilated in particulate form than terrestrial plant material because they lack complex polysaccharides (Mann 1988). This could explain why a greater proportion of marine POM is assimilated relative to riverine POM, despite the latter often having a higher concentration in the inshore POM pool. The high amount of riverine POM in the inshore POM pool is, however most likely characteristic of inshore waters close to river mouths such as those I measured, and it is unlikely to comprise a significant amount of the inshore POM far away from river mouths. In addition, the composition of the inshore POM pool is likely to be highly dynamic temporally and spatially, whereas the consumers offer an isotopic signature that integrates over months what has been assimilated from the organic-matter pool (Gearing 1991), further complicating quantification of uptake versus availability (see Hill *et al.* 2008).

Consumption of POM by filter-feeders can proceed in two ways. A portion of the POM and attached micro-organisms may be digested and assimilated (Adams & Angelovic 1970; Bowen 1979). Alternatively, only the micro-organisms attached to the POM may be digested and assimilated while the remaining indigestible POM is expelled as faeces (Sorokin 1972; Newell 1965; Darnell 1967; Schleyer 1981; Newell *et al.* 1982). There is some evidence that in the case of the mussel *Perna perna*, the former takes place (Berry & Schleyer 1983). In addition, a major source of organic material may be dissolved organic matter leached from seaweed and terrestrial plant pieces when broken up by wave action and attrition by sand particles, which enters the microbial loop (Wotton 2004) because it is readily available to micro-organisms, and they in turn can be efficiently assimilated by filter-feeders (Schleyer 1981; Mann 1988).

While there is much evidence that POM is assimilated by filter-feeders via the microbial loop (Schleyer 1981; Mann 1988; Wotton, 2004; Meranger *et al*. 2005; Wai *et al*. 2008), the role of enzymes that can digest POM directly cannot be underestimated. Digestive enzymes found in bivalves include carbohydrases such as α-amylase, cellulase and α-glucosidase (Hylleberg Kristensen 1972; Seiderer *et al.* 1982; Teo & Sabapathy 1990; Simon & McQuaid 1999) as well as peptidases, lipases (Bayne *et al.* 1976; Seiderer *et al.* 1982) and lysozymes (McHenery *et al.* 1978; Seiderer *et al.* 1982; Simon & McQuaid 1999). There is also evidence suggesting that the mussel *Mytilus chilensis* can alter its response to ambient trophic conditions and past feeding history by varying its carbohydrase and protease activities during periods of acclimation to optimise energy gains depending on available food quality (Bayne *et al.* 1993; Fernández-Reiriz *et al.* 2001). The same could be true for filter-feeders I examined; such an ability would allow them to take advantage of a variety of POM inputs that can be temporally variable and demanding to digest.

Enzymatic digestion in ascidians is less studied but there is evidence of certain carbohydrases including α-amylase (Berrill 1929; Seiderer & Newell 1988; Cima *et al.* 2002). In *Pyura stolonifera* from kelp forests on the west coast of South Africa, α-amylase has been detected but very little cellulase activity or bacterial involvement was recorded. This suggested that phytoplankton was the dominant food source (Seiderer & Newell 1988), contradicting earlier work by Newell *et al.* (1982) who emphasised the importance of bacteria in the kelp forest ecosystem. My study suggests that *P. stolonifera* relies to a greater extent than other filter-feeders on acquiring indigestible POM indirectly by assimilating bacteria. This would concur with its consistently enriched δ^{15}N values (Tables 5.5a & b), indicative of a higher trophic level (Post 2002).

The assimilation of terrestrially-derived organic matter introduced by rivers, either particulate or dissolved, is more likely to occur in the Subtropical Natal Bioregion than on other parts of the coast such as the west coast where large, highly productive, subtidal kelp beds form the basis of the intertidal (Stuart *et al.* 1982; Stuart & Klumpp 1984; Bustamante & Branch 1996b) and shallow subtidal food webs (Velimirov *et al.* 1977; Newell *et al.* 1982; Fielding & Davis 1989), or in the Delagoa Overlap Bioregion where there is virtually no river input (Sink 2001). A marked productivity gradient has been found around the South African coast, decreasing from west to east (Bustamante *et al.* 1995a) and it is possible, based on the results of my study, that trophic subsidies from the multitude of rivers on the east coast play a more notable role in supporting filter-feeder biomass there than elsewhere. In the Subtropical Natal Bioregion, the absence of subtidal kelp communities (Evans 2005; see Chapter 2), the relatively low average ± SD chlorophyll *a* levels (1.18 mg.m^{-3}; see Chapter 4), and the dominance of refractive (unpalatable) articulated coralline seaweeds (Sink 2001; Evans 2005; and see Chapter 2) that probably release little suspended material all reinforce the argument for trophic involvement of riverine introduced organic matter.

In terms of summer versus winter proportions of all three food-sources assimilated by filter-feeders, differences were small (<10 %) and inconsistent among study areas (Figures 5.6). It was expected that a greater amount of riverine POM would be assimilated during the summer rainy season but this was only the case at two of the study areas. However, during summer, seaweed production and formation of seaweed POM may have increased due to the warmer water temperature and longer daylight hours, thereby diluting the contribution of riverine-derived POM. This view is supported by the fact that seaweed contribution to inshore POM was significantly greater in summer than in winter.

The dominant factor reducing the ability to detect seasonal changes may be tissue equilibrium rates. Equilibrium rates in the adductor muscle of *Perna perna* fed on a diet of seaweed predict 100 % turnover in 2.5 years (Hill 2007), which means that in the 5-6 month seasonal periods used in my study, there would have been only 20 % tissue turnover. Such a turnover rate would inhibit the detection of short- to medium-term changes in isotope signatures. Other types of tissue such as gill and mantle have turnover rates approximately twice as fast as muscle (Hill 2007) and may be more useful in any future studies examining seasonal variability.

Although statistically significant spatial differences in the proportions of various food sources assimilated by filter-feeders were detected among sites (and in many cases the interaction term Site x Season), they have little biological importance as the differences were small, typically less than 5 % for all food sources, and in no cases were there prominent decreasing trends in the amount of riverine POM assimilated relative to distance from river mouths (Figure 5.5a-d). In addition, those study areas that had sites north and south of river mouths (A & B & D) showed little differences in the amount of river POM assimilated by filter-feeders regardless of whether they lay north or south of the river mouth. This suggests that river plumes move north and south with similar frequency, which is supported by the fact that coastal winds in general move with similar frequencies north and south parallel to the coast, which lies in a roughly northeast/southwest direction (Hunter 1989).

Several scenarios could explain the lack of long-shore gradients. First, inshore POM could be well mixed over the range of distance sampled, such that any variations in the proportions of various types of POM comprising the inshore POM pool were imperceptible at the scales I studied. This seems unlikely, however, considering that there was a decreasing trend in the amount of riverine-derived POM with distance from river mouths. Published evidence certainly suggests that POM derived from rivers does decrease in concentration with distance from river mouth (Wu *et al.* 2003; Vos *et al.* 2005). However, the rivers in the Subtropical Natal Bioregion are so numerous that they may nullify such long-shore gradients, particularly given that both nearshore currents and winds run parallel to the coast (Schumann 1981; Hunter 1989). The clear change in the δ^{34}S isotope signal in an offshore direction (Figure 5.4) argues strongly for a diminishing input of riverine POM, albeit in that direction.

Alternatively, river POM concentration may reach a point in the inshore POM pool beyond which assimilation does not increase. In many bivalve species, material is filtered from suspension but rejected as pseudofaeces before ingestion and assimilation (Bayne *et al.* 1993). Assimilation is not only a function of ingestion rate (i.e. the Holling functional feeding responses – see Holling 1959, 1965, 1966) but is also related to digestibility, digestive enzyme activity, nutrient content of food, gut fullness and availability of organic compounds (Mayzaud *et al.* 1998). It is likely that filter-feeders have species-specific physiological limits in their abilities to digest various types of materials, regardless of the concentrations of ingested materials. Percentage assimilation appears unrelated to the quantity of food available to zooplankton communities (Conover 1966), and studies on hummingbirds have shown that rates of sucrose hydrolysis can reach near maximum levels (McWhorter & Martínez del Rio 2000), with an upper limit of sugar assimilation being imposed regardless of ingestion and availability (Karasov *et al.* 1986). Filter-feeders could have similar physiological constraints that restrict the digestion and assimilation of riverine POM beyond a certain threshold. The absence of any spatial trends in assimilated riverine POM, despite a demonstrable gradient in availability, does suggest that filter-feeders are at their upper limits regarding their ability to assimilate river POM.

In short, filter-feeders did assimilate notable amounts of riverine-derived POM, but no spatial or seasonal trends could be detected. Therefore hypothesis (2) that inshore filter-feeders will assimilate river-derived POM in addition to pelagic POM and seaweed detritus was upheld, but the proportion of river POM assimilated was not higher during the rainy season and at sites close to river mouths, therefore not supporting the second part of the hypothesis.

Conclusions

Sink (2001) hypothesised that inputs from rivers may be a major factor governing the abundance of the mussel *Perna perna* and a key driver of the biogeographic break in the vicinity of St. Lucia between the Subtropical Natal and Delagoa Overlap bioregions. Previous chapters have shown the asymmetry in filter-feeder biomass between the two bioregions and significant differences in oceanographic conditions between them, many of which could be attributed to the significantly greater riverine input in the Subtropical Natal

Bioregion. This Chapter provides three lines of evidence supporting the notion that POM introduced by rivers is important to filter-feeder communities. First, the analyses of inshore POM composition showed that a high proportion of it (17 – 62 %) comprised particulate organic material derived from rivers. Second, the mixing model results obtained using three isotope ratios (of carbon, nitrogen & sulphur) revealed that riverine POM contributed significantly (9 – 33 %) to the assimilated diets of inshore filter-feeders. Finally, in the context of the Subtropical Natal Bioregion, where there are no subtidal kelp forests, relatively low chlorophyll levels and a seaweed biomass dominated by unpalatable coralline species, the likelihood of riverine POM being an important dietary component is heightened.

However, it should not be forgotten that rivers alter the inshore environment in other ways, including inputs of nutrients and alterations of turbidity, which may affect productivity and favour filter-feeders over other trophic levels in indirect ways that complement dietary supplementation. Lamberth *et al.* (2009) have shown that catches of important commercial predatory linefish on the Thukela Banks, which lie approximately 40 km off the mouth of the Thukela River (Flemming & Hay 1988), are correlated with riverine runoff, with lags in time corresponding to the time it takes different species to recruit into a catchable size range. Based on my results it is plausible that higher levels of productivity and riverine-induced turbidity play an important role in promoting filter-feeder biomass in the Subtropical Natal Bioregion, complementing the influence of trophic subsidies from rivers.

The primary goal of this work was to determine if riverine-derived POM is being assimilated by filter-feeders in the Subtropical Natal Bioregion, and to what extent this could enhance filter-feeder biomass in this region where riverine inputs are characteristic. In all four study areas riverine POM was assimilated in similar amounts by all four species of filter-feeders examined. Relative uptake of riverine derived POM, however, was secondary to that of marine origin. It is therefore unlikely that the dietary subsidies of POM from rivers can alone account for the high biomass of filter-feeders in this region. In order to investigate the importance of riverine subsidies further, large-scale studies across bioregions on POM biomass and limitation as well as ingestion, palatability and assimilation rates would be required.

Chapter 6

SYNTHESIS

Introduction

This thesis was undertaken to improve knowledge and understanding about the biogeography, community composition and ecological functioning of shallow subtidal reefs in the western Indian Ocean. It includes quantitative descriptions of biogeographic patterns and community types, demonstrates their implications for conservation planning, and provides a better understanding of factors that regulate subtidal communities. This was achieved by sampling shallow subtidal reef communities at 55 sites spanning five countries in the western Indian Ocean, and obtaining measurements of physical factors to test the extent to which they correlate with community composition at different scales. In addition, the relative extent to which different sources of organic matter contribute to the assimilated diets of inshore filter-feeders was quantified using stable isotopes in one of the bioregions that was characterised by a high biomass of this trophic group. My research merged the disciplines of classical comparative marine ecology with satellite remote sensing and coastal biogeochemistry to enhance our understanding of shallow subtidal reef systems on the east African coast. The underlying framework structuring the thesis was that of a hierarchical approach governed by various scales of biogeography, whereby general patterns were first determined over thousands of kilometres before subsequently focusing on relatively smaller scales.

Biogeographic patterns

In Chapter 2, I addressed patterns of community composition and structure at a biogeographic scale spanning the east coasts of South Africa, Mozambique, Tanzania, and the west coast of Madagascar and the Comoros islands. Biogeographic analyses of this nature are important as they enhance our understanding of species distribution patterns and what governs them, and can be directly applied to conservation planning. Prior to the commencement of this work very little standardised shallow-subtidal sampling had been conducted in the region, particularly in north-east South Africa, southern Mozambique and Madagascar.

A previously proposed intertidal biogeographic break between Subtropical and Tropical marine provinces in this region has been contentious as sampling in southern

Mozambique, directly to the north of the proposed break, was limited, potentially introducing sampling bias that could artificially have influenced the positioning of the break. This limitation was directly addressed by my research. Two significantly different marine provinces were identified within the region, the Subtropical Natal and Tropical Indo-West Pacific provinces, with a biogeographic discontinuity separating the two between Leadsman's Shoal and Kosi Mouth on the north-east coast of South Africa, approximately 50 km north of where the previously identified intertidal break lies. This discontinuity was however not abrupt but constituted a region of transition or overlap, and because of its transitional nature I termed it the Delagoa Overlap Bioregion. To the south and north lie the two other bioregions identified by post-hoc analyses: the Subtropical Natal and Tropical Indo-West Pacific bioregions respectively.

The three bioregions were characterised by different suites of species. The Subtropical Natal Bioregion was dominated by the solitary ascidian *Pyura stolonifera,* various species of articulated calcified algae such as *Halimeda* spp. and *Amphiroa ephedraea*, and algal turf. *P. stolonifera* also comprised most of the biomass in the Delagoa Overlap Bioregion, but was considerably less abundant than in the Subtropical Natal Bioregion, and was the chief distinguishing species between these two regions. In addition, species of brown algae, algal turf and soft coral were noteworthy contributors in the Delagoa Overlap Bioregion. Further north in the Tropical Indo-West Pacific Bioregion, *Pyura stolonifera* diminished further, and most biomass comprised hard corals, particularly *Porites* spp. and *Galaxea* spp., interspersed with algal turf. My study is one of the first to quantify shallow subtidal community composition over such large scales in this region. It highlighted the importance of the ascidian *Pyura stolonifera* as a major distinguishing species among all bioregions. With increasing latitude, there was a general decreasing trend in hard corals and algal turf, giving way in the Delagoa Overlap to reefs comprising soft corals, algal turf and *P. stolonifera,* and to reefs dominated by filter-feeders such as *P. stolonifera* and articulated calcified algae in the Subtropical Natal Bioregion.

Trophic group structure differed considerably among bioregions. Macrophyte and filter-feeder biomasses decreased to the north, while the opposite trend was true for auto-heterotrophs such as zooxanthellate corals, and for deposit-feeders and grazers. In terms of total biomass, the Tropical Indo-West Pacific unexpectedly had nearly double the value of the Subtropical Natal Bioregion, and approximately four times that of the Delagoa Overlap Bioregion.

My study is the first to quantitatively compare subtidal trophic structure and total biomass patterns among bioregions in east Africa and highlights two important points. Firstly, even in waters of low productivity, like those of the Tropical Indo-West Pacific, biomass can still be relatively high as it can accumulate, especially when it comprises hard corals that can live for centuries and grow metres in diameter (Jackson 1991). Secondly, total shallow-subtidal biomass on reefs greatly exceeded that of intertidal biomass, even when comparisons were made with intertidal rocky shores on the highly productive west coast of South Africa.

Community types and implications for conservation planning

In Chapter 3, my focus moves to finer scales in terms of the hierarchical framework on which the descriptive component of my thesis was built. I define discrete community types at the scale of sites throughout the study region, highlighting their characteristic and distinguishing species, and investigate differences between communities on horizontal and vertical reef surfaces at a subset of three sites situated in the Delagoa Overlap Bioregion. This culminates in a discussion of the implications for conservation planning.

Twelve distinct reef community types were distinguished. The Subtropical Natal Bioregion was fairly depauperate relative to other bioregions with only three types of communities, and most sites were dominated by a single community that was characterised by high biomasses of *Pyura stolonifera*, various calcified algae and algal turf. The Delagoa Overlap Bioregion was richer in community types, with a total of five despite its small size. Many of these communities comprised brown algal assemblages, while others were a mixture of soft and hard corals interspersed with algal turf and varying amounts of *Pyura stolonifera*. Eight community types were found in the Tropical Indo-West Pacific Bioregion, one of which was also common in the Delagoa Overlap Bioregion. A particularly high abundance of community types occurred in southern

Mozambique whereas the rest of the region was largely dominated by a single community in which hard corals were prevalent. No community types spanned more than two adjacent bioregions.

Several implications for regional conservation planning emerged from this work when the distributions of community types were compared with the positions of current marine protected area (MPA) networks. In terms of the hierarchical approach used in conservation planning, which focuses initially on large scales, all three bioregions do incorporate some form of MPA. However, at smaller spatial scales, not all community types are represented within them. In the Subtropical Natal Bioregion, two of the three community types are found within MPAs. The Delagoa Overlap Bioregion is well conserved as at least 60 % of it falls within MPAs and all five community types there are protected. The Tropical Indo-West Pacific, however, is the least well conserved as only 63 % of the community types I defined are located within some form of MPA. Southern Mozambique is particularly rich in different community types and establishing MPAs in the Inharrime Complex and in the Inhambane Bay area could allow for 100 % of community types to be conserved in this bioregion.

My analyses of community composition, variability and diversity between areas of horizontal and vertical reef surfaces at three sites in the Delagoa Overlap Bioregion found significant differences: communities on horizontal reef surfaces were more diverse and variable, and comprised species of brown algae with patches of sand. Those found on vertical surfaces were less diverse and extremely homogeneous, and largely dominated by the filter-feeding ascidian *Pyura stolonifera.*

Most surveys of subtidal reefs consider only horizontal reef surfaces in assessments. Future surveys should also quantify vertical surfaces as they are distinct and an important component of biodiversity that should not be neglected.

Factors regulating community composition

In Chapter 4, abiotic variables considered most likely to regulate shallow subtidal reef communities are examined. The approach followed was to first characterise each bioregion in terms of its physical characteristics using *in situ* and remotely-sensed satellite image data for nine variables. Then the abiotic data were correlated with the biological data, and environmental variables with high correlations were interpreted as those most likely to regulate shallow subtidal communities. As in previous chapters, a similar spatial-scale hierarchical protocol was followed whereby the analysis was conducted first for the entire region and then for each of the three bioregions independently. Identification of biological patterns in community composition and their potential abiotic determinants at various scales is important for the development and evaluation of models of community regulation, and can ultimately contribute to the management of shallow subtidal reefs.

All five remotely-sensed variables, i.e., sea surface temperature, chlorophyll *a*, turbidity, suspended inorganic sediment and significant wave height, were found to differ significantly among the three bioregions. One of the most noteworthy differences among regions was a substantial increase in turbidity levels from the Delagoa Overlap to the Subtropical Natal Bioregion, which corresponds with high riverine input experienced in Subtropical Natal. Other notable differences between bioregions were those of reef susceptibility to sand inundation, which was significantly higher in Subtropical Natal compared to the Tropical Indo-West Pacific Bioregion, and levels of nutrients, which were higher in Subtropical Natal than in the Delagoa Overlap Bioregion.

I was able to separate out key environmental variables most likely influencing subtidal reef community structure, and my study is the first of its nature to directly correlate satellite image data with subtidal community composition at a biogeographic scale. I confirmed that at a large inter-regional biogeographic scale, water temperature was the most important environmental variable linked with species distributions – a phenomenon that is widely accepted but has never been tested in the western Indian Ocean at the scale at which I worked.

Wave height, which decreased equator-wards, was used as a proxy for wave force, and was the next-most important factor. I had not expected wave height to show such a pronounced correlation with community composition at this scale. Indeed, I began with a hypothesis that its effects would be evident only at a local, between-site-scale within bioregions. Its emergence as a determinant of shallow reef community composition at a biogeographic scale was thus novel.

The third-most important factor to emerge as a correlate at the biogeographic scale was chlorophyll *a*, which reached a minimum in the Delagoa Overlap. Nutrient levels could not be measured throughout the region, but were lower in the Delagoa Overlap than in the Subtropical Natal Bioregion, and are likely to be lower in the Western Indo-Pacific as well.

Within each bioregion different variables governing community composition emerged. Temperature, turbidity, chlorophyll *a* and depth were the most likely factors determining among-site community composition in the Subtropical Natal Bioregion. Among-site variability in the Delagoa Overlap Bioregion was attributed to locally-operating site-specific factors including reef susceptibility to sand inundation, reef heterogeneity, profile and depth. In the Tropical Indo-West Pacific, however, it was variables operating over large scales such as water temperature, chlorophyll *a* and turbidity that were the most likely factors regulating community composition among reefs.

Riverine trophic inputs

In Chapter 5, my study focuses on the trophic dynamics of filter-feeder communities in the Subtropical Natal Bioregion. Previous chapters highlighted the differences in community structure (Chapters 2 & 3) and oceanography (Chapter 4) between bioregions, and the fact that the Subtropical Natal Bioregion is dominated by filter-feeders (Chapter 2). This bioregion also has extensive rivers that exude 1×10^{10} m^3 of water into the inshore zone annually (Sink 2001). In contrast, the Delagoa Overlap has virtually no riverine input. Sink (2001) has previously noted that the high abundance of the brown mussel *Perna perna* in the Natal Bioregion is chiefly responsible for intertidal divergence between this bioregion and the Delagoa Overlap. She argued that this difference could be the result of additional energy inputs from rivers in the Natal Bioregion. It was against this backdrop that I initiated a study quantifying the extent to which rivers may be supporting the high filter-feeder biomass in the Natal Bioregion. Using carbon, nitrogen and sulphur isotopes I characterised the isotopic signals of riverine-, seaweed- and phytoplankton-derived suspended particulate organic matter (POM) and then quantified the relative contributions of these sources to the uptake of POM by a suite of filter-feeders. My research was the first to use sulphur isotopes for this purpose in the Subtropical Natal Bioregion. Previous work employed only carbon and nitrogen isotopes, which may have restricted the ability to detect riverine inputs. In addition, trophic isotope studies in general are characterised by having a significant amount of variability, and my work is novel in that it is some of the first to model assimilation using Bayesian theory that can incorporate the variability in food source signatures, concentrations of carbon, nitrogen and sulphur in particulate sources, and trophic fractionation factors of different isotopes.

Inshore waters within kilometres of river mouths were found to contain notable amounts of riverine POM in addition to seaweed detritus and phytoplankton. Most material assimilated by filter-feeder communities was of marine origin, but an important component did come from rivers. Rivers in the Subtropical Natal Bioregion therefore not only influence light penetration by increasing turbidity and suspended inorganic sediment, but also play an important role in the trophic dynamics of this bioregion and provide conditions that synergistically favour and enhance the proliferation of filter-feeders via bottom-up mechanisms. This work provides some of the first evidence of riverine-inshore-pelagic coupling by inshore filter-feeder communities in the world.

Together with the findings of Lamberth *et al.* (2009) showing that stocks of marine linefish are dependent on the amounts of river flow, my research highlights the influence of riverine inputs on marine communities. National Legislation (Republic of South Africa 1998; Thompson 2006; van Wyk *et al.* 2006) requires that 'ecological reserves' be determined and met to ensure adequate freshwater supplies to maintain the ecological integrity of ecosystems. With water supplies for human needs at a premium, and many rivers already impounded for this purpose, establishing ecological reserves is a pressing task.

Conclusions

This thesis presents some of the first standardised cross-border work on shallow subtidal reef ecology in east Africa and the western Indian Ocean. It has resolved the biogeographic patterns of shallow subtidal reefs, quantified their community composition and trophic structure (Chapters 2 & 3), and revealed processes involved in determining the structure and functioning of shallow reefs at regional and between-site-scales (Chapters 4 & 5). The results contribute to general community ecology theory by highlighting trophic links between adjacent riverine, inshore and pelagic ecosystems, and strengthen knowledge about subtidal reef ecology.

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